Status and development of old-growth elements and biodiversity during secondary succession of unmanaged temperate forests

Kris Vandekerkhove

RESEARCH INSTITUTE
NATURE AND FOREST

GHENT
UNIVERSITY
FACULTY OF
BIOSCIENCE ENGINEERING

Auteurs:
Vandekerkhove Kris

Promotor:
Prof. dr. ir. Kris Verheyen, Universiteit Gent, Faculteit Bio-ingenieurswetenschappen, Vakgroep Omgeving, Labo voor Bos en Natuur (ForNaLab)

Uitgever:
Instituut voor Natuur- en Bosonderzoek
Herman Teirlinckgebouw
Havenlaan 88 bus 73
1000 Brussel

Het INBO is het onafhankelijk onderzoeksinstituut van de Vlaamse overheid dat via toegepast wetenschappelijk onderzoek, data- en kennisontsluiting het biodiversiteits-beleid en -beheer onderbouwt en evalueert.

e-mail:
Kris.vandekerkhove@inbo.be

Wijze van citeren:
Vandekerkhove, K. (2019). Status and development of old-growth elements and biodiversity during secondary succession of unmanaged temperate forests.
Doctoraatsscriptie 2019(1). Instituut voor Natuur- en Bosonderzoek, Brussel.

D/2019/3241/257
Doctoraatsscriptie 2019(1).
ISBN: 978-90-403-0407-1
DOI: doi.org/10.21436/inbot.16854921

Verantwoordelijke uitgever:
Maurice Hoffmann

Foto cover:
Grote hoeveelheden zwaar dood hout en monumentale bomen in het bosreservaat Joseph Zwaenepoel (Zoniënwoud, Hoeilaart): een zeer goed ontwikkeld voorbeeld van 'secondary old-growth forest'.

Deze doctoraatsscriptie van het INBO is een overdruk van het gelijknamige doctoraat, ingediend en verdedigd aan de faculteit Bio-ingenieurswetenschappen van de Universiteit Gent.

GHENT
UNIVERSITY

FACULTY OF
BIOSCIENCE ENGINEERING

© 2019, Instituut voor Natuur- en Bosonderzoek

STATUS AND DEVELOPMENT OF OLD-GROWTH ELEMENTS AND BIODIVERSITY DURING SECONDARY SUCCESSION OF UNMANAGED TEMPERATE FORESTS

Kris VANDEKERKHOVE

Thesis submitted in fulfillment of the requirements
for the degree of Doctor (PhD) in Applied Biological Sciences:
Forest and Nature Management

Promotor: Prof. dr. ir. K. Verheyen
Ghent University
Faculty of Bioscience Engineering
Department of Environment

Decaan: Prof. dr. ir. M. Van Meirvenne

Rector: Prof. dr. ir. R. Van de Walle

Vertaling van de titel:
Status en ontwikkeling van structuurelementen en biodiversiteit tijdens secundaire successie van onbeheerde gematigde bossen.

The author and the promotor give the authorisation to consult and to copy parts of this work for personal use only. Every other use is subject to the copyright laws. Permission to reproduce any material contained in this work should be obtained from the author.

Woord Vooraf

‘Allez, het is er dan toch nog van gekomen!’ hoor ik sommigen zeggen. Inderdaad, dit proefschrift was een werk van (zeer) lange adem, 10 jaar om precies te zijn. Met horten en stoten ging het dan weer even vooruit, om daarna voor een half jaar of langer stil te liggen. Mijn ambitie was om het vóór mijn 50ste verjaardag af te werken, maar dat is net niet gelukt. Ik wil dan ook beginnen met mijn promotor Professor Kris Verheyen te bedanken, niet alleen voor zijn deskundige en motiverende coaching, maar in de eerste plaats voor zijn engelengeduld, zeker wanneer ik weer eens een deadline die ik mezelf had opgelegd, schromelijk had overschreden. Omgekeerd moest ik echter nooit lang wachten op feedback: binnen de kortste keren was het manuscript nagelezen, en voorzien van motiverende suggesties, correcties en commentaren die er altijd ‘boenk’ op waren. Een betere promotor had ik me dus niet kunnen inbeelden. Merci, Kris!

Vervolgens wens ik ook het management van het INBO te bedanken, in het bijzonder onze administrateur-generaal Prof. Maurice Hoffmann, die mij de mogelijkheid heeft geboden om een deel van mijn werktijd aan dit doctoraat te spenderen. Vooral de zes maanden ‘sabbatical’ waar ik kon van gebruik maken om het proefschrift af te werken waren welgekomen en eigenlijk onontbeerlijk. Tegelijk ook dank aan mijn huidige en vroegere teamleiders Gerald Louette en Geert Deblust, voor hun steun en aanmoedigingen.

Geen doctoraat zonder data, geen data zonder veldwerk, geen veldwerk zonder veldwerkteam. Dank aan Peter Van de Kerckhove, Marc Esprit, Stefaan Goessens en Bart Christiaens; altijd secuur en volledig, zelfkritisch en gedreven. Dank voor de vele uren in de lentezon, maar ook in de ijzige vrieskou, of bakkend in de auto in de file. Jullie werk wordt ongelooflijk geapprecieerd. Ook het team dat de eerste opmetingen deed in Zoniën: Koen, Peter, Paul, Bart, Danny, Seppe, dank dat we jullie dataset mochten adopteren en valoriseren. Merci ook aan het INBO-labo voor de uitgevoerde bodemanalyses.

Dank ook aan allen die hun steentje –sommigen een volledige gemetselde muur- hebben bijgedragen aan de dataverwerking: de meesters van de statistiek, genieën van Inventory Analyst, tovenaars met R-figuren en modellen, … Dankjewel Anja Leyman, Margot Vanhellemont, Arno Thomaes, Pieter Verschelde, Hans Van Calster en Thierry Onkelinx. Dank ook aan Luc De Keersmaeker om mee te brainstormen over de proefopzet en aanpak van de dataverwerking. Merci ook aan de andere leden van ons onderzoeksteam, voor jullie steun en enthousiasme, en jullie begrip toen ik weer eens een taak of vraag naar jullie moest doorschuiven. Dank u Beatrijs, Kristine, Stefaan en de rest (zie hierboven). Jullie hebben nog wat te goed.

Geen onderzoek in de bosreservaten zonder… bosreservaten. Mijn dank en appreciatie aan al wie vanuit de academische wereld en de administratie ervoor zorgden dat we ook in Vlaanderen beschikken over een netwerk van onbeheerde bossen, en een monitoringprogramma dat de vergelijking met het buitenland kan doorstaan: Prof. Noël Lust, Vera Dua, Roel Vanhaeren, Danny Maddelein, Martine Waterinckx, Johnny Cornelis en Bernard Van Elegem, evenals de leden van de vroegere adviescommissies voor de bosreservaten, en andere bosreservaten-enthousiastelingen zoals Paul Stryckers. Seppe Zwaenepoel verdient hier een bijzondere vermelding omdat hij in 1983 al inging tegen de toenmalige stroming (en zijn bazen), en een stuk officieus bosreservaat afbakende in het Zoniënwoud. Het blijft nog altijd onze belangrijkste onderzoekssite en de kern van waaruit de Unesco Werelderfgoedsite is ontstaan. Visionair en tegendraads, zo hebben we ze graag, merci Seppe! Ook Prof. Lust verdient hierbij nog een extra bloemetje: hij was de mentor die mij op weg hielp bij mijn eerste stappen in het bosonderzoek, en mij ook motiveerde om voor de job van bosecoloog bij het toenmalige IBW te postuleren.

De beheerders, huidige en vroegere houtvesters, regiobeheerders en boswachters van de respectievelijke reservaten waar we ons onderzoek mochten uitvoeren wil ik nog eens bedanken voor het verlenen van de nodige machtigingen om ons onderzoek uit te voeren. Dank ook voor jullie hartverwarmende enthousiasme en interesse voor onze resultaten en de flexibiliteit als er weer eens een thesisstudent zonder machtiging door het bos laveerde. Merci Patrick, Bart, Theo, Klaar, Wim, Koen, Chris, Erik en Dirk, en al wie ik hier eventueel vergeten ben.

Thank you to all the co-authors of the original publications who so kindly trusted me with the datasets that made this manuscript possible: Peter Meyer, Tomas Vrška, Norbert Menke, Vath Tabaku, Leen Govaere, Luc Crevecoeur and Frank Köhler. Dank ook aan Emile Vandeven, FUNBEL-databankbeheerder, om de paddenstoelgegevens beschikbaar te stellen.
My sincere gratitude also goes to the members of my jury: Prof. Lander Baeten, Prof. Bart Muys, Prof. Tibor Standovár, Prof. Hans Verbeeck, and the chairman Prof. Filip Tack. Your valuable comments, suggestions and corrections have strongly improved this dissertation.

Een aantal mensen wil ik postuum bedanken voor wat zij betekenden. Zij waren heel belangrijk in mijn leven maar hebben ons veel te vroeg verlaten. Eerst en vooral mijn vader Cyriel. Hij bood mij niet alleen de mogelijkheid om te studeren, maar bracht mij ook de liefde voor de natuur bij, leerde mij het verschil tussen een Frioentje en een Êrelke, en toonde mij de ‘Hemelwerke’ hoog in de lucht. Hij zou met trots dit heuglijke moment hebben meegemaakt. Dat geldt ook voor mijn professionele ‘vader’, Jos van Slycken. Hij gaf mij alle vertrouwen, maar ook ruggensteun en advies bij het uitstippelen van mijn weg binnen het IBW en het latere INBO, en zorgde er samen met Roel voor dat het onderzoeksprogramma voor de bosreservaten er kon komen. Hij zou nu ongetwijfeld ergens achteraan staan glunderen, onopvallend, met een glas in de hand. En naast hem misschien wel Ruben Walleyn, collega maar vooral ook vriend, die mij introduceerde in de wondere en zo essentiële wereld van de zwammen. Dankzij hem hebben we met zijn allen onze blik verruimd en geleerd dat een bos zoveel meer is dan wat je met het blote oog te zien krijgt.

Tenslotte wil ik uiteraard ook mijn familie bedanken, mijn moeder, broers en schoonfamilie en in het bijzonder Annelise, Milan en Lukas. Dank voor jullie begrip en geduld, wanneer ik weer geen tijd voor jullie had, of met mijn hoofd elders zat (en ondertussen maar ‘jaja’ zeggen op een vraag die ik eigenlijk niet gehoord had…). Of die keren dat ik door de stress nogal kort van stof kon zijn. Dat is nu eindelijk achter de rug, en ja, ik weet het, die badkamer is nog altijd niet af en die garage moet dringend geschilderd. Ik begin er sebiet aan… Mañana…

La nature d'elle-même, quand nous la laissons faire, se tire doucement du désordre où elle est tombée. C'est notre inquiétude, c'est notre impatience qui gâte tout.

Molière (1622- 1673)
Le Malade imaginaire, III, 3 (1673)

"It is not so much for its beauty that the forest makes a claim upon men's hearts, as for that subtle something, that quality of air that emanation from old trees, that so wonderfully changes and renews a weary spirit."

Robert Louis Stevenson (1850 – 1894)

Die Natur hat sich so viel Freiheit vorbehalten, dass wir mit Wissen und Wissenschaft ihr nicht durchgängig beikommen oder sie in die Enge treiben können.
Sie shafft ewig neue Gestalten; was da ist, war noch nie, was war, kommt nicht wieder – alles is neu und doch immer das Alte. Sie hat sich einem eigenen allumfassenden Sinn vorbehalten, den ihr niemand abmerken kann. Alles ist immer da in ihr. Vergangenheit und Zukunft kennt sie nicht. Gegenwart ist ihr Ewigkeit. Sie is ganz, und doch immer unvollendet.

Johan Wolfgang Goethe (1749-1832).

Contents

Summary

Our forests in Western Europe have been managed and altered by humans for many centuries. This management has distinctly changed the characteristics of these forests. Typical elements of the senescent state of primary old-growth forests, such as large amounts of dead wood and large, overmature trees are often missing in managed forests, together with the species related to them.

This study analyses the development of previously managed forest towards so-called secondary old-growth forests. How fast do typical characteristics of old-growth forest develop when we decide to introduce a non-intervention management, by means of ‘strict forest reserves’? Spontaneous developments in these formerly managed forests are clearly different from primary old-growth sites. Whereas the latter are considered to be in a dynamic equilibrium, the newly established reserves are still developing in a more unidirectional way towards this equilibrium. Their development thus may be considered as a successional pathway rather than the typical disturbance dynamics of a climax vegetation. We focused our study on the development of the two predominant structural features that distinguish old-growth forests from close-to-nature managed forests: the amounts of dead wood and the presence of large, overmature trees.

The study of the development of dead wood focused on a large set of oak- and beechdominated reserves in Flanders and elsewhere in Europe, with different periods of non-intervention. Based on these data, we could derive that net accumulation of dead wood takes place at an average pace of 1 to 1.5 $m^3.ha^{-1}.year^{-1}$. We could also conclude that the average decay-time for larger logs can vary greatly, from 10-20 years for full decay of large poplar logs and 30-40 years for beech and maple, up to over 100 years for oaks. Knowing that the average amounts of dead wood in natural forests fluctuates between 50 and 300 $m^3.ha^{-1}$, we can conclude that it may take 50-100 years to reach natural amounts of dead wood, in all its stages of decay.

For the study of large, overmature trees, we made a case-study of the large trees in the oldest part of the forest reserve in the Sonian Forest. We discovered that the large beech trees here apparently combine very high growth rates with high longevity, resulting in exceptional sizes and densities of large trees, surpassing all expectations, based on literature. We came to the conclusion that they are amongst the biggest beech trees in the world, and reach very high densities. This can be explained by the favorable climate and site conditions that promote high increments, in combination with the former management interventions of tending and thinning that resulted in continuous non-suppressed growth. These results tend to reset certain baseline assumptions for tree size and longevity potential of beech in Northwestern Europe.

In the following chapters, we analysed the effects of non-intervention on the development of biodiversity. The results for the herbal layer showed that the total species richness decreased in sites with non-intervention. Especially light-demanding and disturbance-related species declined. This is not unexpected, as the cessation of active human intervention leads to lower frequency of canopy and soil disturbance. However, the characteristic species of closed-canopy forests -often vernal geophytes- clearly benefit from the absence of disturbance and expand their cover. For fungi and beetles we found that the late-successional communities are indeed impoverished, as compared to primary old-growth forests, but still appear to be quite diverse, comparable to sites in neighbouring regions. The results also illustrated that the process of recovery and recolonization is still ongoing.

Based on these results, we formulated recommendations for forest management, focusing on functional networks of old-growth elements and strategic zoning in larger forest complexes with closed-canopy core zones essential to microclimate-requiring late-successional species, combined with sun-exposed forest structures and gradients, catering for light-demanding and thermophilous species concentrated in the periphery of the forest. We conclude with an appeal for a regained ambition on establishment and continued monitoring of strict forest reserves, and an outlook for innovative and cooperative research in these intriguing ecosystems.

Samenvatting

Onze bossen in West-Europa worden al eeuwenlang intensief beheerd door de mens. Hierdoor verschillen deze bossen sterk van natuurlijke bossen. Typische elementen uit de verouderingsfase van natuurlijke bossen, zoals grote hoeveelheden dood hout of oude, monumentale bomen zijn er verdwenen, samen met de soorten die eraan gebonden zijn. In dit onderzoek analyseerden we voormalig beheerde bossen in hun ontwikkeling terug naar een natuurlijke toestand. De natuurlijke dynamiek in deze voorheen beheerde bossen is anders dan in natuurlijke bossen. Deze bossen vertonen nog niet de typische cyclische verstoringsdynamiek van een natuurlijk climaxbos maar volgen een uni-directionele successie in de richting van dit evenwicht. Wij concentreerden ons bij deze studie op de ontwikkeling van twee prominente en typische structuurelementen die natuurlijke bossen onderscheiden van half-natuurlijke beheerde bossen, met name de hoeveelheid dood hout en de aanwezigheid van oude monumentale bomen.

Het onderzoek naar de opbouw van dood hout in onbeheerde bossen was toegespitst op eik- en beukgedomineerde reservaten met uiteenlopende periodes van spontane ontwikkeling. Hieruit konden we opmaken dat de netto accumulatie van dood hout verloopt aan een tempo van 1-1.5 m³ per ha per jaar. De afbraaksnelheid van grote stammen kan heel variabel zijn: van 10-20 jaar voor de volledige vertering van populierenstammen en 30-40 jaar voor beuk en esdoorn, tot meer dan 100 jaar voor eiken. Wetende dat de hoeveelheid dood hout in natuurlijke bossen fluctueert tussen 50 en 300 m³ per ha, kunnen we besluiten dat het 50-100 jaar zal duren vooraleer een voormalig beheerd bos de hoeveelheden dood hout van een natuurlijk bos (in de verschillende afbraakstadia), zal bereiken.

Voor het onderzoek naar oude monumentale bomen voerden we een case-studie uit in het oudste gedeelte van het bosreservaat van het Zoniënwoud. We stelden vast dat de grote beuken hier alle verwachtingen, gebaseerd op literatuur, overtreffen. Blijkbaar combineren deze bomen een uitzonderlijk goede groei met hoge leeftijd, wat ervoor zorgt dat ze vermoedelijk behoren tot de grootste beuken ter wereld. Ook hun aantallen per ha zijn uitzonderlijk hoog. De verklaring ligt in een combinatie

van zeer gunstige groei-omstandigheden, maar ook het vroegere beheer dat ervoor zorgde dat de bomen ook in hun jeugdfase voldoende ruimte hadden om ongehinderd te groeien. Deze resultaten dwingen ons om een aantal basis-aannames over dimensies en maximale leeftijd van beuken in Noordwest Europa bij te stellen.

In de volgende hoofdstukken analyseerden we de gevolgen van niets-doen op de ontwikkeling van de biodiversiteit. Als we naar de kruidlaag kijken zien we een afname van de soortenrijkdom als we nulbeheer introduceren. Vooral lichtminnende soorten en soorten die gebonden zijn aan verstoring gaan achteruit. De karakteristieke soorten van loofbossen, zoals de typerende voorjaarsflora (met bosanemoon), reageert echter zeer gunstig, en neemt significant toe. De soortgemeenschappen van houtbewonende zwammen en kevers in onze bosreservaten is duidelijk verarmd in vergelijking tot natuurlijke bossen, maar is toch nog soortenrijk en kan de vergelijking met reservaten in onze buurlanden goed doorstaan. De resultaten tonen aan dat ook deze soorten gunstig reageren op de toename van het aandeel dood hout en oude bomen. De mate waarin ze deze nieuwe habitat kunnen koloniseren hangt sterk af van de dispersiecapaciteit en habitateisen van de individuele soorten.

Op basis van al deze resultaten formuleerden we een aantal aanbevelingen voor het bosbeheer in functie van de typische soorten van de verouderingsfase in bossen, zowel voor schaduw- als lichtminnende soorten. Dit omvat functionele netwerken van oud-bos-elementen, waarbij centraal in het bos bewust wordt gewerkt naar een gesloten boskern die essentieel is voor de schaduwsoorten die een bosmicroklimaat vereisen. In de periferie van het boscomplex wordt ruimte voorzien voor lichtminnende soorten met lichtrijke bosbeheertypes en permanente en tijdelijke open plekken. We eindigen met een aantal aanbevelingen voor het beleid, met een pleidooi voor hernieuwde aandacht voor onbeheerde bossen en hun langlopende wetenschappelijke opvolging en een verkenning van veelbelovende pistes voor toekomstig onderzoek.

List of abbreviations and symbols

Abbreviations

Aa = *Abies alba* – silver fir

AD = *Anno Domini* = years and centuries after year 0 of Common Era

AIV = Average Indicator Value (according to Ellenberg, 2001)

AIV-N = AIV for nitrogen

AIV-L = AIV for light

AIV-R = AIV for soil reaction

AIV-F = AIV for soil moisture

BA = Basal area: area (per ha) occupied by the combined cross-section of tree trunks in a forest stand, measured at 1.3 meter above ground level.

BAI = Basal area increment: measure for tree increment, expressed in square cm per year; if applied to forest stands (expressed in square meter per ha) it is a measure for increment of growing stock

BC = *Before Christ*, indication of years and centuries before year 0 of Common Era.

CC = Characteristic cover = average cover of a species considering all occupied plots

CCC = Cumulative canopy cover: combined cover of canopy of tree and shrub layer

CEC=Cation Exchange Capacity

DBH = Diameter at Breast Height – diameter of a tree trunk or coppice branch, measured at 1.30 m from ground level

Fs = *Fagus sylvatica* – European beech

GLM = generalised linear model

GLS = generalised least square model

IEC = Index of Ecological Continuity (Alexander 2004)

MCPFE = Ministerial Conference on the Protection of Forests in Europe (Helsinki Process)

Natura 2000 = network of protected areas in execution of the European Birds Directive (1979) and Habitat Directive (1992). Term often also used for all policy and measures related to these directives

NMDS = non-metric multidimensional scaling analysis
Q = *Quercus* species: *Quercus robur + petraea* – pedunculate and sessile oak
R-index = aggregation index R of Clark and Evans (1954)
SFR = Strict Forest Reserve
SD = Standard Deviation = measure that is used to quantify the amount of variation of a set of data values; square root of the variance
SQI = Saproxylic Quality Index (Fowles et al. 1999)
TAB = Total Aboveground Biomass
VLT = very large tree = tree with diameter at breast height of 80 cm and more

Symbols and measures

Δ DBH = difference in diameter at breast height
βsör = Sörensen dissimilarity index
βsim = Simpson index of dissimilarity (Turnover)
βnest = index for nestedness (=βsör – βsim)
µm = micrometer = 0.001 millimeter
ha = hectare (= 10.000 square meters)
m^2 = square meter
$m^2.ha^{-1}$ = square meter per ha
m^3 = cubic meter
$m^3.ha^{-1}$ = cubic meter per ha
$m^3.ha^{-1}.year^{-1}$ = cubic meter per ha per year (measure for biomass increment)
H’ = Shannon index for species richness (also known as Shannon-Wiener and Shannon-Weaver-index)
L function= a transformation of Ripley’s K function, measure for spatial aggregation
Mg = Mega-gram = 1000 kg
$N.ha^{-1}$ = number per ha

‘Du point de vue scientifique le but primordial des réserves est de permettre l'étude de l'évolution des associations, cette grandiose evolution de nos forêts, quelles qu'en soient les modalités, constituerait une donnée fondamentale pour le biologiste comme pour le forestier.

(...) Il serait grand temps d'entreprendre chez nous les études de biosociologie, études très longues qui exigent la coordination et la continuation des travaux de plusieurs générations de chercheurs. Or, seules les réserves intangibles peuvent assurer la realization d’un tel oeuvre. Dans ces sortes de parcelles d'expérience, des diverses disciplines biologiques pourraient collaborer à une mission de fierté et d'intérêt national.(...) Tôt ou tard, de telles études s'imposeront chez nous avec le progrès des scéances.

Raoul Mosseray (1908-1940) - Bulletin de la Société Royale de Botanique de Belgique, 1938

Chapter 1

“No one has yet described for me the difference between the wild forest which once occupied the oldest townships, and the tame one which I find there to-day. The civilized man not only clears the land permanently to a great extent, and cultivates open fields, but he tames and cultivates to a certain extent the forest itself. By his mere presence, almost, he changes the nature of the trees as no other creature does. (...) It has lost its wild, damp and shaggy look, the countless fallen and decaying trees are gone, and consequently that thick coat of moss which lived on them is gone too’

Henry David Thoreau (1817 – 1862) – The Maine Woods (published 1864)

nihil ita ut immobile esset natura concepit

Nature framed nothing to be immovable

Lucius Annaeus Seneca (4 BC -, 65 AD) Quaestiones Naturales, Liber VII, par. 1

Chapter 1: Introduction. Old-growth and secondary old-growth: concept, characteristics and historic development

1.1 Definition of old-growth forests and stands

The term ‘Old-growth forests’ is a quite recent concept, and was originally mainly used in Northern American literature (e.g. Frelich and Reich, 2003; Wirth et al., 2009). It refers to forest sites and stands that have developed a high degree of naturalness, and were not, or not for a longer time altered or disturbed by human activities such as timber extraction. In Central European literature, terms like ‘primeval forest’, ‘virgin forest’ or ‘natural woodland’ (Peterken, 1996) were often used, but in recent European literature (e.g. Bauhus et al., 2009; Burrascano et al., 2013; Di Filippo et al., 2017; Gilg, 2005; Lingua et al., 2011; Ziaco et al., 2012), the term old-growth is also more and more established.

The definition and delineation of old-growth forest is enigmatic and not straightforward. These forests are not defined or identified by a single attribute, but a combination of several factors may serve as important indicators. There is a wide variability and combination of features exhibited in old-growth forests, and the features do not simply ‘add-up’ as the sum of a series of rigid criteria (Greenberg et al., 1997). Instead of applying strict dichotomous decisions on determining old-growth, there is a strong tendency to apply a gradual scale (index of old-growthness or OGI) to indicate the extent to which a forest or stand meets specific criteria thresholds or approximates certain reference values (Kimmins, 2003). Buchwald (2015) developed a 14-level-scale system to define the level of naturalness of forests, based on origin, composition, continuity and processes and structures of the site, with the levels n6 to n10 referring to ‘old-growth forest’ up to ‘primeval’ forest.

Based on literature, the most often used indicators and descriptors of old-growth are given below (Barton and Keeton, 2018; Bauhus et al., 2009; Buchwald, 2015; Burrascano et al., 2013; Frelich and Reich, 2003; Gilg, 2005;Greenberg et al., 1997; Hayward, 1991; Hilbert and Wiensczyk, 2007; Hunter, 1989; Kaufmann et al., 1992;

Kimmins, 2003; Uhlig et al., 2001; USDA Forest service, 1992.; Wells et al., 1998; Wirth et al., 2009; Ziaco et al., 2012).

- Structural complexity of the canopy: the tree layer is characterized by a natural tree species composition and typically exhibits an irregular multi-layered canopy, including canopy gaps and understory patchiness. This is the result of the interaction of small-scaled and larger-scaled natural disturbance events. In temperate regions, the small-scaled disturbances prevail over larger scale, stand-replacing disturbances. This leads to fine-grained irregular patterns of canopy structure, both horizontal and vertical.

- Old-growth stands contain a wide range of different age and size classes of trees, both living and dead (which can be quantified by the standard deviation or quadratic mean of diameter). Most conspicuous in this context is the presence of large and old, overmature trees. Large trees (over 50 cm or even 80 cm DBH) make up an important share of the tree population (indicators: number per ha; share of total biomass).

- Overall, the stands often have a high basal area and aboveground biomass. Also, the large amounts and wide variety in size and decay stage of dead trees, both lying and standing, are characteristic

- Pit-and-mound micro-topography is widespread over the area, as a result of the uprooting of large trees.

- Trees are not regularly dispersed and distributed, but occur in random pattern (Wolf, 2005; Vandekerkhove et al., 2018;)

- Trees often contain a high density and variety of microhabitats such as cavities, cracks and fungal fruit bodies resulting in high conservation value (Larrieu et al., 2018).

- The presence of indicator species of old-growth forests (cfr. Christensen et al., 2004; Müller et al., 2005; …) may also help to identify these sites that are less obvious based on the current stand characteristics (Greenberg et al., 1997). Indeed, an important share of forest biodiversity is strictly or primarily dependent on old-growth related microhabitats and dead wood amounts for their survival (e.g. Esseen et al., 1997; Harmon et al., 1986; Heilmann-Clausen and Christensen, 2003; Kirby and Drake, 1993; Økland et al., 1996 , Stokland et al., 2012; Siitonen, 2001). They require a long continuity of these characteristics in order to subsist. There mere presence is a good indicator of this continuity.

- Conversely, they can also be negatively characterized by the absence of direct evidence of human activities (such as roads and tracks, stumps,…).

1.1.1 Primary vs. secondary old-growth

According to Frelich and Reich (2003), old-growth forests can be subdivided in 'primary old-growth', being old-growth forests whose dynamics are driven exclusively by natural processes while human impacts are absent, and 'secondary old-growth', being previously managed forests that have developed old-growth features after decades of (intentional or non-intentional) non-intervention (Piovesan et al., 2008; Ziaco et al., 2012). Also the FAO definition of old-growth includes the subdivision in primary and secondary old-growth. It rather vaguely describes old-growth as 'primary or a secondary forest which has achieved an age at which structures and species normally associated with old primary forests of that type have sufficiently accumulated to act as a forest ecosystem distinct from any younger age class (UNEP/CBD/SBSTTA, 2001). In this context 'primary forests' is defined as naturally regenerated forests of native species where there are no clearly visible indications of human activities and the ecological processes are not significantly disturbed (FAO, 2015). Also Buchwald explicitly states that old-growth is not necessarily "virgin" or "primeval.", but can develop following human disturbance (secondary old-growth).

Contrary to the primary old-growth forests, secondary old-growth forests have not yet reached, but are still in a transition towards the so-called shifting mosaic steady state, typical for primary old-growth forests (Bormann and Likens, 1979). In this study, we will focus on secondary old-growth forests in Flanders, and compare them to other sites in North-Western Europe, and study the successional pathways towards old-growth status.

1.2 Old-growth and wilderness conservation and study: a historic background

1.2.1 The demise of old-growth in the Northwest-European lowlands: deforestation and cultivation of remaining forest

1.2.1.1 Forest and wilderness converted to farmland

Forests in Europe, especially in the Northwest-European lowland plain, have already for a large extent been cleared and replaced by agriculture for many centuries. As early as the first century BC, forest cover in the North-West European lowlands had gradually decreased to about 50% of the total land cover, followed by a slight recovery during the Dark Ages (4th-8th century AD) (Verhulst, 1995). In the lowlands of the current area of Flanders, a steep decline of forest cover took place especially during the Full Middle Ages (12th-13th century AD). At that time, financial means, organisation and manpower were available for large-scale clearing of ‘wilderness’. High population density indeed created demographic pressure to convert woodland and wasteland to farmland and provided the required manpower to perform it. Means were available, as the region was at that time one of the most wealthy regions of the world, with powerful and rich landlords and cities. Organisation and facilities were provided by monasteries. Deforestation was so efficient that the count of Flanders (Philip of Alsace – 1142-1191) already in the second half of the 12th century stated that ‘at this pace of clearings, there will soon be no forests left for hunting, heating and construction’. Around 1250, indeed less than 10% of forest cover in the ancient County of Flanders (the Western part of the current region of Flanders) was left (Verhulst, 1995; Tack and Hermy, 1998). In the Duchy of Brabant, the large-scale deforestation also took place, be it about 100 years later.

Since that time, total forest cover has remained at a similar level, with a slight increase in the 18th century to about 12%, and a minimum of about 9% halfway through the 19th century. This stable overall figure, however, conceals large deforestations (30-50% decrease on fertile silt loam deposits), mainly for agriculture and infrastructure, that were outbalanced by new afforestations, primarily on former heathlands and alluvial meadows, targeted at the delivery of industrial wood products (De Keersmaeker et al., 2015; Hermy et al., 2008; Vandekerkhove et al., 2016a).

As a result the actual forest is severely fragmented both in space and time. Only a small fraction (15 %) of the current forest cover is considered to be ancient woodland, meaning it remained continuously forested between the end of the 18th century and now (De Keersmaeker et al., 2015; Hermy and Verheyen 2007; Hermy et al., 2008). This history of low forest cover is comparable with other regions in the Northwest-European lowlands (Netherlands, NW-Germany, Southern England) (Buis, 1985; Rackham, 1986; Peterken, 1993; Watts, 2006; Schmidt et al., 2014).

1.2.1.2 Forest management: no place for old-growth elements

Besides centuries of very low forest cover, the remaining forests in Flanders and other parts of the North-West European lowland were also used very intensively in order to maximise the production of resources like firewood, utensils and construction wood (Tack et al., 1993; Tallier, 2004). Already as early as the 14th century, strict regulations and control on the harvest of wood and grazing of domestic cattle were imposed in order to prevent the depletion of the essential wood resource (Goblet d'Alviella, 1930; Tack et al., 1993; Vandekerkhove et al., 2016a; 2018). Most forests were managed as coppice systems, and coppice with standards in the larger estates of nobility and monasteries. High forest was exceptional (Tack et al., 1993; Tack and Hermy, 1998; Tallier, 2004). The study of archives and historic descriptions of specific woodlands makes clear that forest management in the 15th to 18th century involved much more craftsmanship and knowledge and was more sustainable than was often assumed. (for Flanders see: Tack et al., 1993; Adriaenssens and Verheyen 2013; Vandekerkhove et al., 2016a).

However, in these management systems, primarily focused on the production of firewood and charcoal, there was no place for late successional development stages and conservation of dead wood, large and old trees (except in the royal hunting reserves – see below, paragraph 1.2.4). The harvest included the removal of all dead wood. Century-old user rights also gave local people the privilege to collect all dead and dying trees both in private and public forests (Tack et al., 1993; Tallier, 2004;

Baeté et al., 2007). Senescent and dead trees and even dead branches on trees were promptly removed. Even the smallest branches were sought after. Dead and older coppice stools that became less productive were entirely taken out, including the root bole. The same was done with the standard trees: they were not cut down, leaving dead stumps, but felled by digging and cutting over of the roots. The root bole was a too precious resource to be left in the forest (Tack et al., 1993; Vandekerkhove et al., 2009b). Large and old standard trees were also absent. No standard trees were left to reach sizes over 60-80 cm DBH, as they were too heavy to manipulate and had higher risks of defects. They were also of limited use: most construction wood such as beams was gained from single stems of mid-sized trees, by removing the rounded sides. Only few large constructions (such as shipbuilding and standards of windmills) required exceptionally large sized trees.

In the 19th and 20th century, traditional management systems were replaced by high forest management and plantation forestry. These management systems also excluded dead wood and large trees (Branquart et al., 2004). Large tree dimensions were economically not desired (no specific market, difficult to transport, risk of hidden defects like discoloration and rotten core) and forest management was tailored to this. The retention of dead wood was considered as a form of negligence, income loss or even bad management, as dead wood was - and sometimes still is - considered a source of diseases. (De la Blanchère and Robert, 1889; Korpel', 1997; Nageleisen, 2005).

This history of continuous intensive use was comparable to other regions in the Northwest-European lowlands, (the Netherlands, northwest Germany, southern England) (Buis, 1985; Peterken, 1993; Rackham, 1986; Watts 2006). We can conclude that for many centuries, dead wood and overmature trees, the prominent features of old-growth forests were absent from the remaining forests of North-Western Europe. In some of these regions though, the use of wood pastures was widespread, e.g. in Northwest Germany (Hutewald), Southern England and South Sweden (e.g. Hartel and Plieninger, 2014; Rackham, 1986). In these wood pastures, large and old trees (often pollarded) were still present. In Flanders however, there was no tradition of such wood pastures: common lands had been transformed to grasslands and heathlands long before (cfr. Read et al., 2012; Vandekerkhove et al., 2011).

Only over the last decades, the ecological value of dead wood and veteran trees has been highlighted (Harmon et al., 1986; Kirby and Drake, 1993; Read et al., 2012) and progressively been recognized and integrated in principles and practices of everyday sustainable forest management (Bauhus et al., 2009; Kraus and Krumm, 2013). Until then, they were confined to strict forest reserves and other protected forest areas with intentional non-intervention policies (see below).

1.2.2 From foe to fairy - attitude towards wilderness and old-growth forests in Western Europe and North America over the last centuries

1.2.2.1 Wilderness to be feared and to be tamed

For many centuries, Western attitude towards wilderness and old-growth forests has been dominated by a primitive fear of uncontrolled nature. Unmanaged forests were considered as areas of darkness, threatening sources of unlawfulness and disorientation, hosting fierce creatures and diseases (Manning, 1989; Peterken, 1996). It was opposed to the cultivated world where nature was subjugated and shaped by humans to an Arcadian landscape that allowed harmonious co-existance and provision of goods and services for humans.

Wilderness was also considered as an area to be conquered and used. In the tradition of Judaeo-Christian tradition and philosophy, God has given people dominion over nature. Wilderness was regarded as the world of the Devil, the antithesis of the Garden of Eden (Manning, 1989). This lead to a mainstream imperialist advocacy in the Western world that man has the authority and moral mission to conquer and control wild nature and make nature serve the needs of humans. This was also the philosophy behind the manifest destiny, a widely held belief in the United States that its settlers were destined to expand to the wild and untamed land beyond the frontier of Western civilization in order to remake the west in the image of the cultivated America.

1.2.2.2 Rehabilitation of Wild nature

Appreciation for wild nature mainly surged under the influence of Romanticism in the 19th century, although also baroque painters of the low countries, such as Peter Paul Rubens, Alexander Keirincx, Jan Brueghel and Gillis van Conincxloo showed fascination for crooked and torn old and dead trees giving them a prominent place in their landscape paintings (Fig. 1.1).

Fig. 1.1 Fascination for crooked and torn old and dead trees by Flemish painters in the 16th century. Left: forest landscape by Gillis van Conincxloo (1588-KHM-Vienna); right: forest view by Jan Brueghel (Albertina – Vienna)

Romanticism was a cultural and intellectual movement, originating in Europe at the end of the 18th century. Confronted with the consequences of rationalization and rapid societal, landscape and environmental changes due to the economic growth model of the Industrial Revolution, a countermovement originated, with emphasis on emotion and individualism. Nature plays an important role in Romantisism, as a source of physical and mental health and aesthetic experience. Woodlands came to be regarded as suitable places for meditation and solitude (Peterken, 1996). There was a specific fascination for wild, undisturbed nature, as Romanticism shows a strong distrust for the human world, and an explicit nostalgia and appreciation towards the unspoiled (the Noble Savage). Large old trees were venerated as symbols of eternity, continuity and stability. English landscape parks and gardens were embellished with ‘wildernesses’ (Peterken, 1996). At the same time, the last remaining areas of old-growth forest, both in the mountain areas of Central Europe and North-West America, were rapidly disappearing, to be replaced by agriculture and plantations for industrial roundwood production.

Initiatives for conservation of the last relics of ‘virgin forest’ and ‘wilderness’ started simultaneously at both sides of the Atlantic, initiated by philosophical contributions and pamphlets by John Muir and Henry David Thoreau, or William Wordsworth. In the USA, this resulted in the protection of wilderness areas such as Hot Springs Reservation (as early as 1832), followed by Yosemite Valley (1864) and Yellowstone National Park (1872). In Europe, the first initiatives for conservation of the last remnants of old-growth forests that had survived in remote mountainous and border areas in the Alps, Carpathians and Šumava mountains, were taken by aristocratic landowners such as Augustin Langeval-Buquoy or Albert de Rothschild, who set aside parts of their estates that had not been exploited. Their motivation was primarily aesthetic and ethical (Welzholz and Johann, 2007; Bücking, 2007). The first reserve was established already in 1827 (Ziesbuch forest – now called ‘Cisy Staropolskie Reserwat’ – PL) (Zielony, 1999), soon followed by other sites such as Žofinsky Prales (CZ – 1838), Boubínský Prales (CZ - 1858) and Poľana Prales (1861) (Peterken, 1996). In 1875, Albert de Rothshild bought a large forest estate in the Austrian alps, containing two areas of old-growth, together covering about 500 ha, and promptly decided to protect them from harvest (Kleines and Grosses Urwald Rothwald) (Mayer et al., 1979). In Slovenia, the forest manager of Kočevje mountains, decided in 1892 to protect ca. 50 ha of old-growth from felling, the current reserve Rajhenavski Rog (Hartman, 1999). Other sites like Peška, Rožok, Dobročský prales,… soon followed. In Switzerland a first old-growth remnant, Urwald Scatlè, was purchased by a local conservation NGO and protected in 1907. In Germany, sites such as Wilder See - Ruhestein (1911 - Baden-Württemberg) and Höllbachgspreng and Mittelsteighütte in Bayerische Wald (1914 - Bayern) were the first sites to be protected as strict forest reserves.

In lowland and submontane areas of Europe, no such untouched forest remnants remained. Concentrations of old trees were only present in ancient royal hunting reserves and wood pastures. The most famous ‘primeval forest’ of lowland Europe is Białowieża forest. It still contained vast areas that were never commercially harvested at the beginning of the 19th century (Von Bricken, 1828). Still, there are clear indications and evidence that the Białowieża forest, even the National Park area before the installation of a strict non-intervention protection in 1923, was significantly altered by human activities like frequent burning, cattle grazing and litter raking, potash and charcoal production,… (Bobiec, 2012; Daszkiewicz et al., 2008; Mitchell and Cole 1998; Niklassen et al., 2010; Samojlik, 2010). This vast forest was the royal hunting ground of Lithuanian and Polish kings (14th-18th century) and later of the Russian Tsars, so game numbers were kept at an artificially high level and active measures (such as burning) were performed to create and conserve a more open forest that provided good feeding conditions for bison and other big game (Bobiec, 2012; Daszkiewicz et al., 2008; Samojlik, 2010). Commercial wood harvest only started in 1915, but local communities were allowed to harvest and collect wood (Kartsov, 1903). After the collapse of the Russian Empire, the forest became state owned and in 1923 a first area of barely 50 ha was protected as 'Reserwat'. Later it was further extended to its current area of 5700 ha with non-intervention management (Zielony, 1999). At that time, traditional user rights were abolished and large parts of the remaining forest (especially on the Polish side) were transformed to commercial forests.

As grazing rights were abolished all over Europe, many wood pastures also lost their use, and were transformed to conifer production forest (Fig. 1.2). As early as 1809, August Christian Heinrich Niemann (1761 – 1832), a professor at the Royal Danish forest school in Kiel, already opposed to the admixture of conifers in these areas and urged for the protection of veteran trees,'whose value is more than the planks they contain' (Mölder et al., 2014). Only at the beginning of the 20th century, a few relics of wood pastures with ancient trees, erroneously called 'Urwald', were protected from further fellings, and often a non-intervention management was installed. Exemples are Neuenburger Urwald (1870) Hasbrucher Urwald (1889) and Urwald Sababurg (1907).

Fig. 1.2 Felling of old wood pastures: Hermann Kauffmann (1808 - 1889): Tree fellers in the Sachsenwald. Painted around 1850. Stiftung Historische Museen Hamburg – Altonaer Museum – cited in Mölder et al., (2014)

In France, under the impulse of the Romantic painters of the School of Barbizon, a number of ‘réserves artistiques’ were installed in the forest of Fontainebleau in 1861. They were former hunting reserves and wood pasture stands, open forests that contained many crooked ancient trees that provided an interesting scenery for landscape paintings. No more forestry operations were allowed, and halfway the 20th century, these sites (such as La Tillaie, Le Gros Fouteau and Chêne Brulée) received the official protection statute of Réserve Biologique Intégrale.

In the USA, the protection of vast non-intervention areas was already regulated in the Wilderness Act of 1964. It organized the protection of large areas (at least 5000 acres = over 2000 ha) of ‘pristine’ landscapes, showing, ‘no human impact and habitation’. In Europe, similar initiatives for large unmanaged wilderness areas only recently developed, but are becoming more important (see chapter 1.2.2.4).

1.2.2.3 Towards a scientific network of strict reserves

The arguments for installation of non-intervention forests gradually evolved from aesthetic-ethical towards scientific reference and nature conservation (Bücking, 2007; Parviainen et al., 1999). At the beginning of the 20th century, some conservationists and academics started arguing for the installation of a network of forest areas to be left for free development. C.A. Weber (1901) pleaded from a conservation approach for the 'restoration of natural woodlands' in Germany. Forest academics discovered the importance of strict forest reserves as reference sites of close-to-nature forestry. As a reaction to the 'rational forestry', focusing on mass production of standardised roundwood in even-aged monocultures, Gayer (1868) introduced the principals of silviculture of mixed forest, inspired and to the image of natural forests. These were further developed in the close-to-nature forestry of the so-called 'Central-European Forestry School', further developed by Mayr (1909), Dengler (1935), Schädelin and Leibundgut (1966). Already in 1910, Čermak indicated the importance of 'virgin forest' as reference and inspiration for close-to-nature forestry, and urged for their protection and study, later repeated by a.o. Podhorsky (1929), Buchwald (1958) and Leibundgut (1959). Herbert Hesmer (1934) advocated to install a set of areas, 5 to 20 ha large, where the forest could develop freely, without human intervention, covering all major forest communities of Germany, as areas of study and demonstration. Still, it took several more decades before this network was realized. The year 1970, European Year for Nature Conservation, was the impulse for many German Länder to activate the ideas on the installation of such a network, urged by researchers like Trautmann (1969) and notorious scientists like Tüxen (1970) and Leibundgut (1957; 1966). By the end of the 1970's, networks were already deployed in Baden-Württemberg (38 sites in 1970; 129 at present), Niedersachsen (63 sites by 1974; 201 at present) and Bayern (135 sites in 1978; 164 at present), followed shortly by the other Länder (Bücking and Schmidt, 1999; Meyer et al., 2007). Based on this example, also other European countries such as Austria, the Netherlands and Denmark developed a representative network of strict reserves during the 1980's and 1990's (Koop and Molenaar, 1981; Parviainen et al., 1999; Van der Jagt, 1980; Zukrigl, 1978).

As the main aims for forest reserves evolved over time, so did the selection criteria. Halfway the 20th century, scientific criteria like representativity and natural species composition became primary selection topics: the aim was to develop a network of unmanaged forests that represented all forest types and site conditions present in a certain area or country (Leibundgut, 1959; Mlinšek, 1976; Meyer et al., 2007; Parviainen et al., 1999; 2000). As a consequence, new reserves had to be selected in managed forests, as no unmanaged 'primary' forests remained for many of the targeted forest types. Focus thus developed more towards 'future natural woodlands' (*sensu* Peterken, 1996) where succession from man-made or altered towards natural forests takes place ('Naturwaldreservate: Urwald von Morgen'). In Flanders and Belgium, it was only in the late 1990's that a network of unmanaged forest reserves was developed (see chapter 1.2.3).

1.2.2.4 Strict forest reserves as scientific reference for close-to-nature forestry

Already during the first half of the 19th century, forest scientists were aware of the importance of virgin forest relics as reference sites for forest management (Von Brincken, 1828; Seidel, 1848). Detailed descriptions and interpretations are published by Von Brincken (1828 - Białowieża), Fuchs (1861 - Hungary) and Göppert (1868 - Bohemia). Also specific measurements already started at that time. The first permanent plot of 1 ha was installed and recorded in Boubín in 1847 (Šebková et al., 2011). The paper of Seidel (1848) contains full dendrometric data for six sample plots of ¼ ha each, and Von Brincken included several tables with diameter, height and increment measurements. This tradition is followed amongst others by Čermak (1910), Gehrhardt (1923), Schenck (1924), Tkatschenko (1929), Müller (1929), Hesmer (1930; 1934), Markgraf and Dengler (1931), Mauve (1931), Zednik (1938), … Jones (1945) first published an overview paper on dynamics and disturbance ecology of natural forests, based on numerous literature sources from both Europe and America.

But it was mainly under the impulse of Leibundgut (1959; 1966), Mayer (1969; 1978) and other central European academics that the study of strict reserves, especially virgin forest relics, received major attention, and generated several reference works on forest structure (Korpel', 1995; Průša, 1982; Leibundgut, 1982; 1993). These studies were mainly focused on descriptive research on stand developmental phases, species composition, regeneration and gap formation, using full surveys and strip transects. In the 1970’s and 1980’s, improving the representativeness of forest reserves based on plant associations or on forest site type classifications was an important topic in many long-running reserve programmes in Central Europe (Diaci, 1999; Mlinšek, 1976; Parviainen et al., 1999; 2000). Monitoring techniques evolved from descriptive strip transects and mapping of gaps and developmental phases towards more standardised systematic surveys using fixed core areas, networks of circular sample plots or combinations of both (Projektgruppe Naturwaldreservate, 1993; Schuck et al., 1994; Vandekerkhove, 2000), also taking into account the dead wood component, ground vegetation and standardized faunistic surveys (e.g. Köhler, 2000; 2010). Recommendations were formulated to standardize methodologies with permanent plots (COST-action E4) allowing for international comparison, and initiatives were taken to develop a Europe-wide scientific network of monitored strict reserves (Hochbichler et al., 2000; Parviainen et al., 2000).

1.2.2.5 21st century: renewed interest for ‘wilderness’ and strict forest reserves in Western Europe

By the end of 20th century, however, attention of policy makers and forest conservationists shifted more to integrative conservation concepts in forest management (Kraus and Krumm, 2013) and to Natura 2000-networks, focusing on specific vegetation types and target species, and less on natural processes. The standardised surveys and resurveys of strict reserves were still ongoing, but were not designed for short-term delivery of conclusions. This lead to a loss of interest from policy makers (see chapter 6) and a sense of saturation on knowledge to be acquired from strict forest reserves, leading to diminishing interest and resources for monitoring and designation of new reserves.

Since the last decade, however, a renewed attention for unmanaged forests and areas arose in Europe, as illustrated by the following examples. Next to conservation of species and ecosystems, also the protection of natural processes is considered to be an essential aspect of biological diversity, that needs conservation: in German-speaking areas this is known as the so-called *Prozeßschutz* (Sturm, 1993). In 2007 the German Biodiversity Strategy was voted stating that 2% of the total surface area of Germany should be under non-intervention (‘*Wildnis*’), comprising of large areas such as coastal strips, alpine areas, abandoned military training areas and core areas of national parks. Furthermore, the strategy specifies that 5% of the total forest area of Germany and 10% of all public forest (Federal and Länder) should be in non-intervention protection by the year 2020. At this moment, over 200.000 ha, or 1.9% of the forest area in Germany, is included in official statutes of non-intervention; a further 250.000 ha is also unmanaged (e.g. because it is not accessible for harvest), but not officially protected. If this surface is also included the goal of 5% is practically reached. Initiatives are taken to further develop and officialise areas of non-intervention (Engel et al., 2016).

Also in France, the network of Réserves Biologiques Intégrales has been drastically expanded over the last years, from 15.500 ha in 2007 to 22.000 ha in 2016. Also, a new national park, focused at lowland broadleaved forest, is being created, including a 3000 ha strict forest reserve core area in the Domanial Forest of Arc-Châteauvillain (Bourgogne). In Denmark, the long-term objective, set in the Danish Strategy for Natural Forests from 1992, for designation of 40,000 ha of natural forest, untouched forest and old forest management systems by 2040, was recently reconfirmed and reinforced by a government decision in January 2018 to appoint 10.000 ha of new strict reserves in Denmark in the coming years, resulting in 20% of all state forests to be left unmanaged.

At European level, protection of undisturbed old-growth forests and non-intervention forests became increasingly important on the policy agenda. Already in 1995, the Pan-European Biological and Landscape Diversity Strategy (PEBLDS) submitted by the Council of Europe and approved by the Ministers of the Environment at the Ministerial Conference "Environment for Europe" (Sofia, Bulgaria, 23-25 October 1995) explicitly mentioned among its Pan-European objectives:

Objective 9.1: Conserve adequate areas to secure the conservation of all types of forests in Europe, and specifically prioritize conservation efforts towards protection of 100 per cent of the remaining alluvial and virgin forests, the majority of the remaining ancient secondary woodland
Objective 9.2: Conserve forest habitats of species requiring large undisturbed forest ecosystems (…)

The goal to preserve large forest wilderness areas was also repeated in the European Biodiversity Strategy 2020 (Target 3b Increase contribution of forestry to maintaining and enhancing biodiversity–Action 12: ensure the preservation of wilderness). (European Commission, 2011). On February 3rd 2009, the European Parliament voted a resolution on Wilderness and Wild areas in Europe. It calls on the Commission and the Member States to develop a wilderness strategy, to protect remaining wilderness areas and develop new wilderness and wild areas through the process of rewilding (= non-intervention). A technical report (EU-DG Environment, 2013) clarifies that wilderness and rewilding goals are considered compatible with the provisions of the Habitat and Birds Directives for selected species and habitats that support non-intervention (such as forests). Due to enhanced legal and illegal logging of old-growth forests outside strictly protected areas in central Europe (Romania, Slovakia, Ukraine and Poland) the protection of old-growth forest remnants in Europe is also back on the political agenda (old-growth protection conference by the Committee of the Regions, 2017; EU Court of Justice rule against harvests in Białowieża in 2018). Finally, also in 2017, a network of 78 old-growth non-intervention beech forest reserves (including the strict forest reserves of Sonian Forest), covering an area of over 92.000 ha in 12 countries received the status of Unesco Natural World Heritage site, underlining the international importance given to non-intervention areas and recognizing the outstanding natural value of unmanaged beech forests in Europe.

1.2.3 Old-growth forests in Europe: where are they located ?

As stated before, primary old-growth forests have disappeared in most parts of Europe. According to Forest Europe (2015), about 4% of all forests in the EU (3.1 million ha) are reported to be ‘undisturbed’. However, there is a wide range of interpretation to this term. Some countries like Denmark report all their currently unmanaged forests (=5.4%), although these are definitely all previously managed sites. Some of these sites are unmanaged for longer time (secondary old-growth), some of them for only a few years. Other countries like the Ukraine, did not report any undisturbed forest, although primary old-growth sites are indeed present in this country and probably cover 40-55.000 ha (University of Padova, 2008; Volosyanchuk et al., 2017). Many of these ‘undisturbed’ forests are located in the Boreal and Hemiboreal regions of Europe, with vast areas of primary old-growth forest still existing in the Russian Federation, but also in Sweden, Finland and Norway, important areas of old-growth remain (MCPFE, 2015). Sabatini et al. (2018) estimates the area of ‘primary forest’ (= undisturbed and long time unmanaged) at 1.4 million ha, or 0.7% of Europe’s forests. Most of them are located in the Boreal region (1 million ha), and Alpine regions, especially the Carpathians, but also the Alps, Apennines, Dynaric mountains and Pyrenees.

Sabatini et al. (2018) includes a map of so-called ‘primary’ forests. The definition of ‘primary’ in this paper follows the definition by Buchwald (2015) (classes n6 to n10), and therefore also incorporates secondary old-growth forests that are left unmanaged for at least ca. 50 years (Fig. 1.3 - left). This map however is incomplete and based on input from various country correspondents. Sabatini et al. (2018) also contains a map of areas with high likelihood of presence of primary forests, based on the analysis of (topographic, demographic, climatic…) characteristics of reported primary forests. Areas with the highest likelihood of occurrence of primary forest in Europe are given at a 1 × 1 km resolution. The top-ranking 5% pixels were highlighted in purple and the 90–95th percentile in blue (Fig. 1.3 - right).

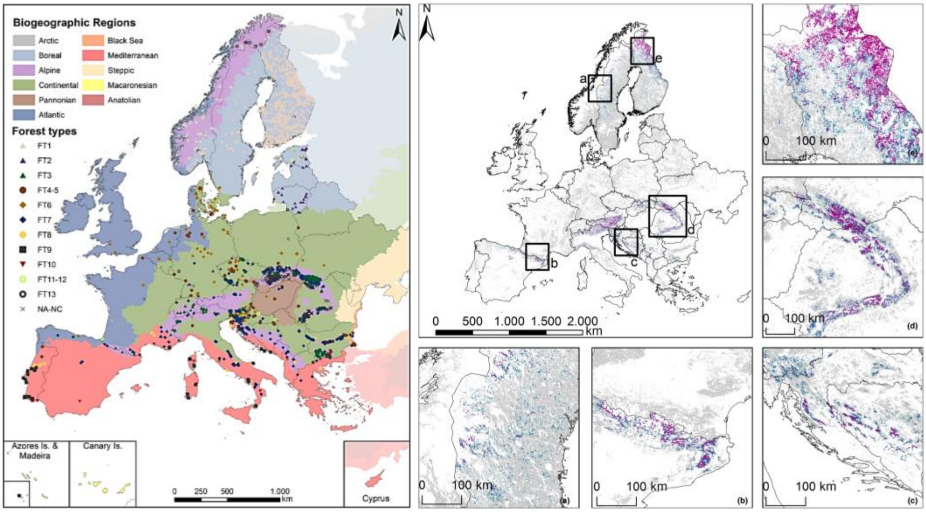


Fig 1.3 Location of old-growth forests in Europe. Left: Map of so-called ‘primary’ forests in Europe (class n6 to n10 according to Buchwald, 2015). Right: areas with high probability of presence of ‘primary’ forest. Both graphs were originally published in Sabatini et al. (2018)

In temperate Europe, the largest areas of primary old-growth are predominantly located in the Carpathian mountain range in Slovakia, Poland, Romania and the Ukraine (Sabatini et al., 2018). The total area of primary old-growth forest in the Carpathians was estimated at 322.000 ha (University of Padova, 2008), with the largest extent in Romania (207.000 ha), Poland (55.000 ha) and the Ukraine (40.000 ha). Biris and Veen (2005) estimated the area in Romania at 218.000 ha of primary old-growth and another 200.000 ha of ‘quasi-virgin’ forest (secondary old-growth). Old-growth forests are thus most abundant, but also most at risk in Romania. Borlea (1999) already indicated that only ¼ of the primary forests are strictly protected, and almost none of the important secondary old-growth forests. According to Knorn et al. (2013) and Luick (2017), vast areas of primary and secondary old-growth have been harvested since. They state that the area of primary old-growth was reduced by almost half (120.000 ha remaining) and the area of secondary old-growth to ¼ of the area ten years before (50.000 ha). In Poland, vast areas of old-growth in the Carpathians are included in strictly protected parts of the Bieszczady National Park (18.500 ha), and Tatra NP (11.500 ha). Other large strictly protected areas (not in the Carpathians) involve Kampinos NP (4800 ha) and Białowieża (4750 ha) (Zielony, 1999). In Ukraine, the largest patches of primary old-growth are found in the UNESCO WH-sites of Uholka-Shyrikyi Luh (11.800 ha), Svydovets (3000 ha), Maramarosh (2250 ha) and Stuzhytsia – Uzhok (2500 ha). Although some areas of old-growth were and still are threatened by legal and illegal logging, the situation appears to have improved over the last years (Volosyanchuk et al., 2018). In Slovakia, the largest contiguous areas of old-growth are Stužnica – Bukovské Vrchy (3000 ha) and Vihorlat (2600 ha). Although the majority of primary old-growth are strictly protected in Slovakia, salvation harvests of spruce in the surroundings (and according to some sources even inside the sites) have an important impact on the protected sites. Outside of the Carpathians, Bulgaria has the largest remaining area of old-growth in temperate Europe: 35.000 ha are considered 'virgin forest' (primary old-growth), while another 55.000 ha is classified as 'semi-virgin' (Raev and Veen, 2005). Most of the primary old-growth forests are located in the Central Balkan area and are strictly protected in forest reserves and core zones of national parks. Larger remnants of old-growth are also found in the Dinaric mountains (Čorkova Uvala, Croatia – 600 ha; Sutjeska NP including Perućica –Bosnia ca. 2000 ha) and in Albania, where 11.000 ha of old-growth beech forests occur (Diku and Shuka, 2018). Finally, small patches of primary old-growth remain in the Alps, such as the spruce reserves of Scatlè and Derborence in Switzerland, or the beech forest of Rothwald in Austria.

In other countries, where no primary old-growth remains, efforts have been made to develop scientific networks of strict forest reserves, that already can be characterized as, or develop towards secondary old-growth (Parviainen et al., 2000). In total, an area of 3.6 million ha of forest in Europe is reported under category 1.1. 'no active intervention', and another 7.7 million ha under category 1.2. 'minimum intervention' (MCPFE, 2015). This last category may involve interventions to prevent forest fires or the spread of invasive exotic species, but no commercial wood harvest (Vandekerkhove et al., 2007). As stated before, countries like Germany, Denmark and France have recently expanded their networks of non-intervention forests. At this moment, over 200.000 ha, or 1.9% of the forest area in Germany, is included in official statutes of non-intervention, developing towards secondary old-growth. Large sites are the National Parks of Bayerischer Wald (13.000 ha), Hainich (4000 ha) and Kellerwald (4000 ha). A further 250.000 ha is also unmanaged (e.g. because it is not accessible for harvest), but not officially protected. (Engel et al., 2016). In France, the area of secondary old-growth forests is estimated at 30.000 ha (Mansourian et al., 2013). The network of strict forest reserves covers 22.000 ha and is expanding (Barthod and Trouvilliez, 2002). The largest strict reserves (RBI) are for now Sylve d'Argençon (2500 ha – since 2006), RBI des Maures (2500 ha), RBI du Vercors (2160 ha), RBI d'Assan (1000 ha), RBI Saint-Pé-de-Bigorre (1000 ha) and over 1000 ha of RBI in Forêt de Fontainebleau. The nature reserve of Massane (ca. 350 ha) in the Pyrenees, is often described as one of the few examples of primary old-growth forest in France (Mansourian et al., 2013). A total of 31 secondary old-growth sites that are unmanaged for at least 50 years are listed at www.foretsanciennes.fr. Also in Italy and Spain, patches of secondary old-growth remain in the Alps, the Apennines and the Pyrenees. They also receive increased attention and protection (including UNESCO-WH-recognition) and networks of strict reserves are further expanded for their development (Marchetti and Blasi, 2010; Piovesan et al., 2005; Schwendner in Kirchmeir and Kovarovics, 2016).

1.2.4 Strict forest reserves in Belgium: a strenuous course

Unmanaged forest reserves in Flanders and Belgium are a recent phenomenon. Still initiatives for old-growth conservation and non-intervention go back to the 15th century, and the first official plea to install unmanaged reserves dates from the beginning of the 20th century.

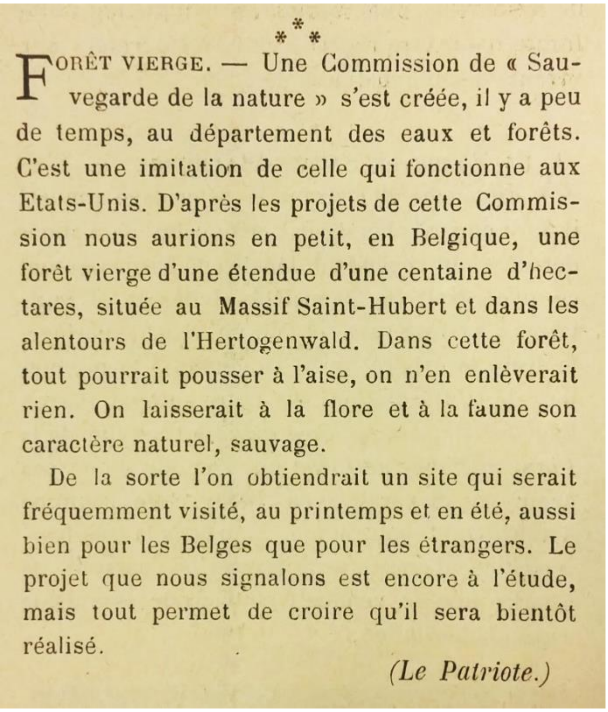
In the early 15th century, the Sonian forest, close to Brussels, came in possession of the house of Burgundy as dukes of Brabant. They decided to select areas in the forest (hunting reserves) that were to be used exclusively for hunting purposes. They comprised approximately 250 ha, and no trees were to be felled or harvested. At the time of emperor Charles V, the hunting reserves must have consisted of high forest of very old scattered trees (Fig. 1.4). In an Ordnance, dated 1516, the emperor mentions that it has been brought to his attention that the trees at one of the hunting reserves were dying in large number because of old age. He therefore decided that the reserve could be abandoned and remaining trees be harvested, but that this had to be compensated by new reserves, where, from that moment onward, no trees were to be harvested, in order for them to reach large size and old age. He even suggested specific areas where mature trees already occurred (Pierron, 1935). These hunting reserves were probably abolished at the end of the 17th century, and subsequently integrated in the regular forest management.

Fig. 1.4 The Wild Boar Hunt by P.P. Rubens (ca. 1620)– Staatliche Kunstsammlungen Dresden. The landscape may have been inspired by the royal hunting reserves of Sonian Forest.

In 1902, Charles Bommer, head of department of the Botanical Garden, published a brief report on the creation of nature reserves in Belgium for the newly installed Commission for Conservation of Nature at the forest administration. In this document, he pleaded for the installation of strictly unmanaged reserves in several moorland and forest areas. The idea was picked up by the journal 'Vieux Liège', that published a short communication stating that very soon, a 'Forêt Vierge' of about

100 ha would be installed in both the forest massive of Saint-Hubert and in the surroundings of Hertogenwald (Fig. 1.5).

For whatever reason, the idea was not further developed and ten years later, Massart (1912), in his standard work on nature conservation in Belgium, repeated the need for a set of unmanaged nature reserves, suggesting specific sites like Sonian Forest and Muziekberg (Ronse). He also described a discussion in the Belgian Parliament on forest management in the Sonian Forest, that took place in 1909, illustrating the explicit positive attitude of parliament at that time for non-intervention. The minister of Agriculture (Schollaert), interpellated on the tree fellings in Sonian forest, stated that he would do all in his possibilities to prevent any further tree felling in the forest by stating: *“Laissons la forêt s'embellir elle-*



⁂

FORÊT VIERGE. — Une Commission de « Sauvegarde de la nature » s'est créée, il y a peu de temps, au département des eaux et forêts. C'est une imitation de celle qui fonctionne aux Etats-Unis. D'après les projets de cette Commission nous aurions en petit, en Belgique, une forêt vierge d'une étendue d'une centaine d'hectares, située au Massif Saint-Hubert et dans les alentours de l'Hertogenwald. Dans cette forêt, tout pourrait pousser à l'aise, on n'en enlèverait rien. On laisserait à la flore et à la faune son caractère naturel, sauvage.

De la sorte l'on obtiendrait un site qui serait fréquemment visité, au printemps et en été, aussi bien pour les Belges que pour les étrangers. Le projet que nous signalons est encore à l'étude, mais tout permet de croire qu'il sera bientôt réalisé.

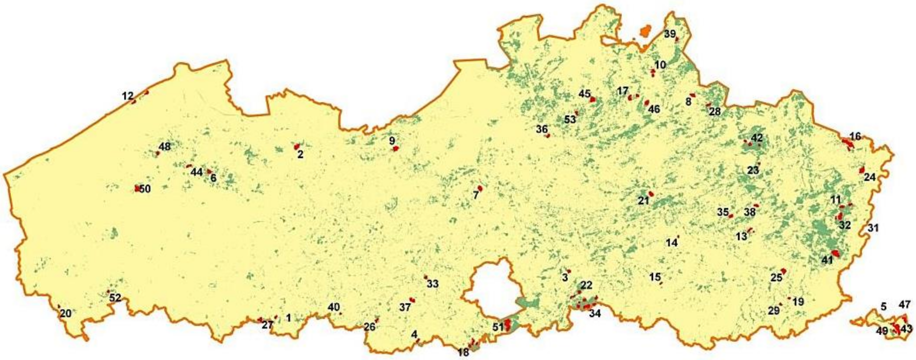
(Le Patriote.)

Fig. 1.5 Short communication announcing the establishment of ‘virgin forest’ of some 100 ha, to be installed shortly in the forest of Saint-Hubert and in the surroundings of Hertogenwald. (published in ‘Le Vieux Liège’ – 4th year, no.7; September 20th, 1902) *même. Mieux vaut ne pas intervenir et laisser faire la nature..... Il faut laisser aux forêts leur caractère sauvage"* ('Let us allow the forest to adorn itself. It is better not to intervene and let nature do… One should leave to the forests their wild character'). He was unanimously supported and applauded by the members of parliament. However, his words were not applied in the field, and shortly after, World War I halted the animosity towards nature conservation and non-intervention reserves, not to be resumed after the war (Hoste et al., 2016).

It was only twenty years later that Mosseray (1938) published an opinion paper in the Belgian Journal of Botany, pleading again to set up a network of nature reserves, and to exclude them from the 'devastating disturbance of man'. He was the first in our country to stress the scientific importance of these sites: he wanted to preserve them, not only as living museums but also as important sites for biological research. He appealed also to include unmanaged forest reserves, even if the forests were altered by humans. He stated that, at first sight, it may be strange to suggest the inclusion of man-made forest stands, even degraded or clear-cut areas, but that these sites would learn us more about dynamics and succession, the 'readjustment' of the 'liberated nature' from the human undertaking. According to him, this type of research was to be essential to observational sciences, both for biologists and foresters. He further clarified that according to some, these man-made forests may go to ruin if left abandoned, and only could prosper thanks to the continued prudent intervention of the forester, but that he was convinced that after a temporary state of senescence and decay, a new sub-spontaneous natural forest would develop and progressively replace the original cultivated forest, by way of very diverse developmental stages. He therefore appealed for the installation of a network of strict reserves, covering at least the most typical forest types of each district, and for the urgent set up of long term interdisciplinary studies, continuing over generations of researchers. He concluded that 'sooner or later, such studies will be demanded, as science will progress'. His prophetic and visionary plea, however, was not endorsed, and smothered by the dawn of World War II. Mosseray did not get the chance to resume his plea after the war: he died in combat in 1940.

After World War II, first initiatives for nature protection in Belgium were focused on the conservation of moorlands (Hautes Fagnes, 1957), coastal dunes and estuaries (Westhoek and Zwin – 1957 and 1951), or heathlands (Mechelse and Kalmthoutse Heide – 1967; 1968), lakes and swamps (De Zegge and Snepkensvijver -1953). It was only in the Law on Nature Protection (1973) that the possibility of strict forest reserves was legally inscribed, but never implemented. Already during the discussion in parliament on the adoption of this new law, explicit concern and mistrust to these non-intervention reserves is expressed by the agricultural sector, and the law was only adopted after the minister assured that strict reserves would always be enclosed by a large, managed buffer zone and in case of disaster or damage to crops, interventions would still be possible. (Notules of the Chambre of Parliament, june 21, 1973). Also after implementation of the law, no initiatives were taken by the forest administration to establish forest reserves and an administrative circular (1979) regulating criteria for selection of strict reserves (mixed stands, originating from natural regeneration, balanced age structure,…) further made this impossible as no sites in Belgium whatsoever could meet all these requirements. Only informal initiatives were taken by local foresters (Zwaenepoel: 1983: Sonian Forest; Vandenbroucke early 1980’s: Withoefse heide-Kalmthout) to set aside some forest stands as unofficial strict reserves. Forestry academics (Dua, 1975; Van Miegroet, 1977; Lust 1982) repeated the necessity to develop a representative network of strict forest reserves, as reference sites for silviculture, to the example of and in line with other European countries, but with no result.

The Flemish Forest Decree of 1990 and Executive Order on Forest Reserves (1993) eventually provided an adequate legal framework for the development of a network of strict forest reserves. At that time, the overall mindset among policy makers, managers and academics was positive towards strict reserves. In the original words of the decree, forest reserves had to fulfil a primarily scientific function for forestry, in 1999 reformulated to an (equally important) ‘ecological and scientific’ function. Criteria for selection and size of sites were formulated (Vandekerkhove, 1998). The scientific network of strict reserves should contain at least one site for every major forest vegetation type (some 20 types) that is of sufficient size to cover and study the spatial dynamics of unmanaged forest stands (20-50 ha, depending on the forest vegetation type). By 2010 the network covered a total area of about 3000 ha (of which 2500 ha of strict reserve), distributed over more than 50 sites (Fig. 1.6). The target was a network covering approximately 4000 ha (Van Elegem, 2006). A monitoring strategy and programme was developed and operational by the year 2000 (De Keersmaeker et al., 2005).



1	Beiaardbos	18	Hallerbos	35	Melisbroek-Vieversel
2	Bellebargiebos	19	Hasselbos	36	Muizenbos
3	Bertembos	20	Hellegatbos	37	Neigembos
4	Bos Ter Rijst	21	Helschot	38	Op den Aenhof
5	Broekbos	22	Heverleebos	39	Overheide
6	Bulskampveld	23	In de Brand	40	Parikebos
7	Coolhembos	24	Jagersborg	41	Pietersembos
8	De Goorbossen	25	Jongenbos	42	Pijnven
9	De Heirnisse	26	Karkoolbos	43	Roodbos-Veursbos-Vossenaerde
10	Doolhof	27	Kluisbos	44	Rooiveld
11	Dilserbos-Platte Lendenberg	28	Koeimook	45	s'Herenbos
12	Duinbos Jan De Schuyter	29	Kolmontbos	46	Sevendonck
13	Galgenberg	30	Konenbos	47	Teuvenerberg
14	Gasthuisbos	31	Kraaienbos	48	Vloetemveld
15	Groot Gasthuisbos	32	Lanklaarderbos-Saenhoeve	49	Vrouwenbos
16	Grootbroek	33	Liedekerkebos	50	Wijnendalebos
17	Grotenhout	34	Meerdaalwoud	51	Zoniënwoud: Joseph Zwaenepoel reservaat

Fig 1.6 Location and listing in alphabetic order of all forest reserves (now incorporated as nature reserves) in Flanders, representing a total surface are of 3000 ha. About 2400 ha of these are strict reserves (non-intervention).

In Wallonia, the new Code Forestier (2008) provided a legal framework for the development of a network of strict forest reserves. It states that in all public broadleaved forests of over 100 ha, an area of at least 3% should be classified as strict reserve. This law, however, does not provide specific criteria on representativity and size of these reserves. Although these strict reserves now cover a total area of over 5000 ha (Carbonnelle and Lezaca-Rojas, 2016), very few larger areas are selected, and most sites are strips of unmanaged forest, located on slopes and other areas with limited accessibility for commercial harvest. From a conservation perspective, these sites may be very interesting, as they were often already extensively managed or unmanaged before, thus may have a higher level of continuity for late-successional species, but from a scientific perspective, this setup is less favorable, as it lacks a comprehensive and representative network (including the common productive forest types) of sufficiently large sites to study spontaneous dynamics (Heyninck, 2009). Moreover, this network of strict reserves is only inscribed in local management plans, there is no overarching database or register, which further complicates the development of a functional network.

Finally, in Flanders, it was decided in 2014 (Decree on the Amendment of Legislation on Nature and Forests) to withdraw the articles on forest reserves from the Forest Decree, and incorporate the forest reserves in the legal framework of nature reserves (in accordance with the Flemish Nature Decree of 1997). Although the objective of non-intervention forests is still distinctively specified (nature target ‘unmanaged climax vegetation’), the outspoken scientific goal, as mentioned in the Forest Decree, is no longer explicit. Also, a certain disinterest for strict reserves has re-entered policy: like in other countries, the focus turned towards species and habitat conservation of the European Habitat and Birds directive (see also paragraph 1.2.2.5 and chapter 6). In order to further develop and strengthen the network and the research programme in strict reserves, there is a need for renewed recognition of the scientific potential and ecological value of non-intervention, as is the case in countries like Germany, Denmark and France (see 1.2.2.5).

1.3 Focus of this study: the status and development of key structural elements and biodiversity during secondary old-growth succession

1.3.1 The forest cycle concept: shifting patch-mosaic (or not…)

The dynamics of primary old-growth forests are often described and depicted in the form of a life cycle (e.g. Emborg et al., 2000): trees regenerate, grow and compete among each other for light and space, mature, grow old and eventually decline, die and decompose (Fig. 1.7). These life cycle phases can occur on different spatial scales, depending on the disturbance events that take place. They can occur at individual tree level scale, resulting in uneven aged forests (sometimes called 'plenter phase') or on larger scale. If several trees simultaneously die or are blown over during windstorm events, patchy patterns may develop, that evolve over time and space, described as the 'dynamic steady state' or 'mosaic cycle' (e.g. Emborg et al., 2000; Bormann and Likens, 1979; Leibundgut, 1978; Korpel', 1995; Saniga and Schütz, 2001a).

In the event of a stand-replacing disturbance, for instance due to fire, bark beetle outbreak or large windthrow, the life cycle stages of trees may even occur on large scale, resulting in more or less even-aged large patches and stands, that follow a more unidirectional pathway towards maturity before re-entering the mosaic cycle (e.g. Bormann & Likens, 1979). Depending on the forest type, these large-scaled disturbance events are virtually absent (e.g. in temperate broadleaved forests) up to relatively frequent (boreal pine and spruce forests), shaping the age patterns in the forest (Angelstam, 1998) (Fig. 1.8 and Fig. 1.9).

This conceptual model of the shifting mosaic cycle, and its spatial and temporal sequence of phases, has been debated by recent research. It has been criticized as being too simplistic and has been questioned several times using quantitative spatial analyses, fruitlessly looking for non-random 'patchy' arrangements of growth and mortality processes (e.g. Szwagrzyk & Szewczyk, 2001).

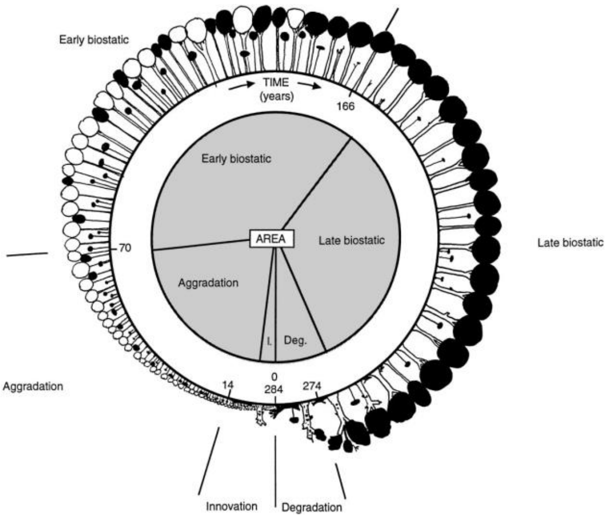


Fig 1.7 The so-called mosaic cycle in time and space, as depicted for Suserup Skov (DK) by Emborg et al. (2000). , 1992. The pie in the middle shows the accumulated area of each phase of the shifting mosaic. The outer circle indicates the calculated duration of each phase of the forest cycle

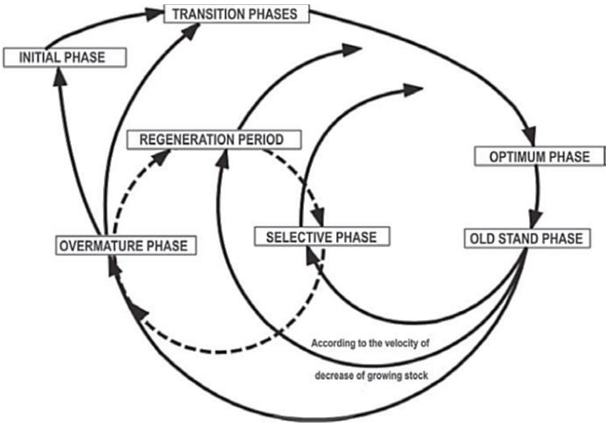


Fig 1.8 Schematic visualisation of the shifting mosaic cycle for natural beech-fir-spruce forests in Central Europe (source: Rüther and Walentowski, 2008, based on Zukrigl et al., 1963) showing the different disturbance scales: stand-replacing disturbance pathway is shown in the upper-left cycle and individual tree-dieback scale in the smallest cycle; patchy disturbances in the middle cycle.

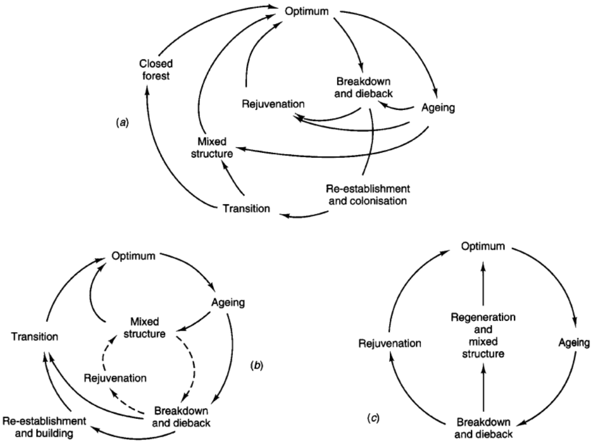


Fig. 1.9 Alternative portrayals of the shifting mosaic cycle: altered representation of the model by Zukrigl (b) confronted to alternative versions of the mosaic cycle by Leibundgut (a) and Mueller-Dombois (c) (figure source: Peterken, 1996)

However, Král et al. (2014) did find a patch pattern of basic stand characteristics in natural beech-dominated forests through multi-scale spatial analyses: what appeared to be random at the fine scale of individual trees was revealed as a periodic patchy pattern at larger scales (patches usually 400–1100 m^2 in size).

Still, Král et al. (2017) found that the consecutive sequence of developmental stages (from regeneration and growth, through maturity and senescence, to breakdown and back to regeneration) is oversimplifying the development. When analysing shifts over time, less than 40% of all observed transitions could be classified as cyclic (following the model cycle), and thus more than 60% of the transitions were acyclic (moving across or backward in the model cycle). The overall pattern of all observed transitions resembled a complex web rather than a simple repeating cycle. We can conclude that the life-cycle of forests, like many processes in nature, is much more complex than can be depicted in conceptual models.

1.3.2 Beyond the harvest shortcut

In managed forests, the full life cycle of trees and shifting mosaic cycle of stands is no longer present. First of all, the life cycle of the trees is aborted by the final harvest of trees. Trees are removed at their harvestable age, around the economic optimum of tree value, which is located at about one third or half of their natural life span (e.g. Christensen & Emborg, 1996; Scherzinger, 1996). Moreover, the stands are more even-aged than natural forests, ranging from moderately less uneven-aged, lacking the older age classes (as in 'Plenterwald'), up to fully even-aged. In this case, their development resembles the successional pathway of natural forests after stand-replacing disturbances. The stands indeed follow the sequential shift from innovation (rejuvenation) and aggradation (transition) to the 'early biostatic' (or optimal) stage, although their development is still altered and influenced by sylvicultural tending and thinning operations. The late-successional phases of senescence ('late biostatic') and breakdown ('degradation') of both trees and stands are missing. The tree and forest life-cycle is, so to say, short-cut by final fellings. This also has a devastating effect on the whole community of species, that rely on the features and structures of the late-succesional stages of tree and forest development, such as rotting tree cavities, large amounts of dead wood, etc… (Siitonen, 2001; Stokland et al., 2012).

As described before, several countries and regions (including Flanders) have decided over the last decades to select formerly managed forests, and deliberately leave them unmanaged to develop freely. Their establishment was motivated both for science and conservation: to be able to study the dynamics after cessation of human interventions, and develop habitat for these late-successional species. Our study analyses these successional pathways 'when nature takes over from humans': how newly established strict forest reserves in previously managed and altered forests develop towards a new dynamic steady-state of secondary old-growth, focusing on specific structural features (dead wood and overmature trees), and the response of the associated biodiversity to this new development.

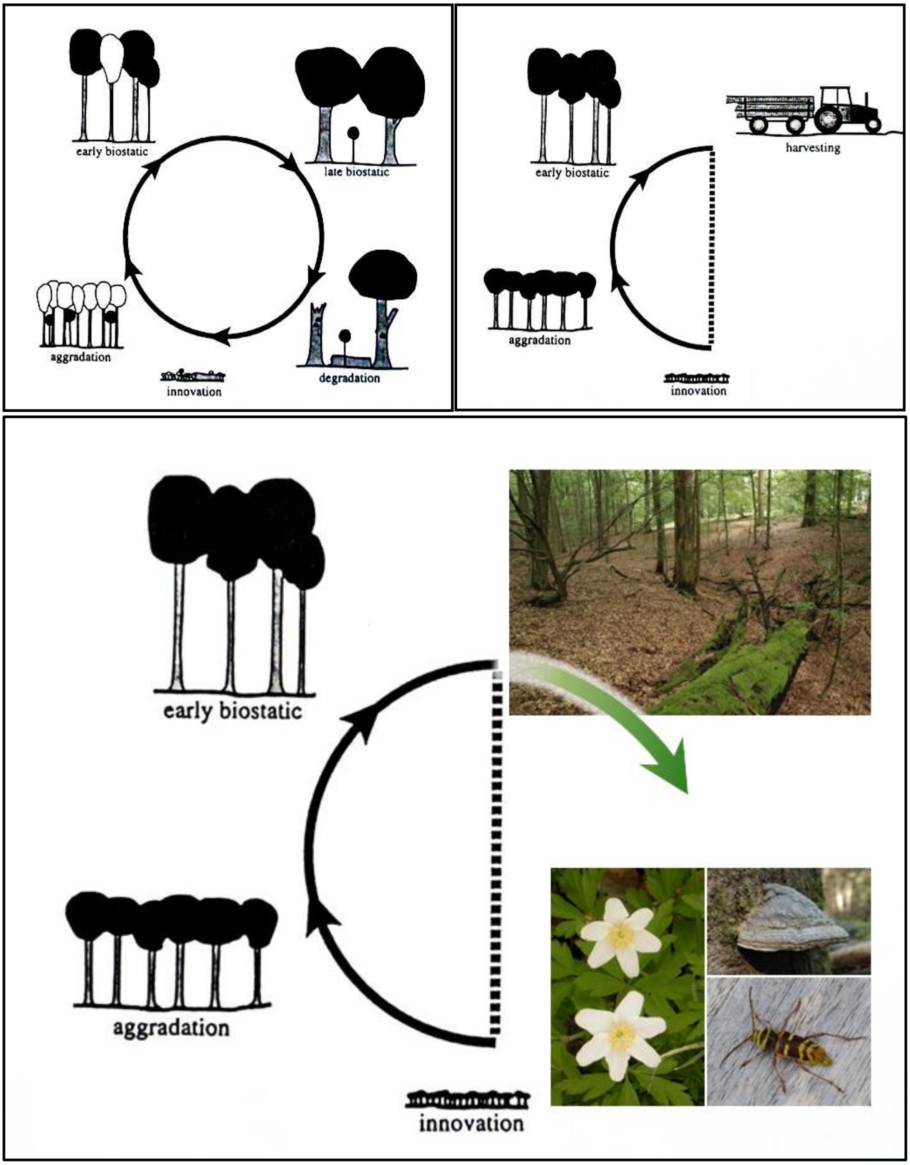


Fig. 1.10 Visualisation of the concept of our study. The life-cycle of natural forests (above left) is aborted by the harvest short-cut in managed forests, skipping the late-successional phases of the life cycle (above right). Our study focuses on the restoration of structural features of the late-successional phases in previously managed and altered forests, and how the associated biodiversity responds to this new development (below). Figure based on Christensen and Emborg, 1996)

1.3.3 Development towards secondary old-growth forests

Many studies have been published on dynamics and developments, and associated species richness in old-growth forests. Most of these studies focus on primary old-growth forests, sometimes compared to managed stands (e.g. Moning and Müller, 2009; Müller et al., 2010; Müller and Bütler, 2010).

Our study, however, specifically focuses on the successional pathways ‘when nature takes over from humans’: how newly established strict forest reserves in previously managed and altered forests develop towards a new dynamic steady-state of secondary old-growth, and how biodiversity responds to this development. Such studies are less common (e.g. Christensen et al., 2005a; Müller et al., 2010; Bílek et al., 2011; Meyer and Schmidt, 2011; Burrascano et al., 2017).

Spontaneous developments in these formerly managed forests are clearly different from the dynamics in primary old-growth sites. Whereas the latter are considered to be in a dynamic equilibrium where the different developmental phases are interchanging in a dynamic steady-state (e.g. Bormann and Likens, 1979; Leibundgut, 1978; Korpel', 1995; Saniga and Schütz, 2001a), the newly established reserves are still developing in a more unidirectional way towards this equilibrium.

Indeed, they all start from a man-made structure, that is more or less divergent from this equilibrium. The stands take off less stocked, more uniform and with lower dead wood amounts than primary forests, and sometimes also with a species composition altered by humans. Most of the strict forest reserves in Europe, originating from previously managed forests are on this successional pathway. This is evident for recently established reserves, but this is also the case for sites that are left unmanaged for more than a century. In the famous ‘virgin forest’ of Białowieża, important species compositional shifts have been registered over the last 50 years (Brzeziecki et al., 2016), indicating that the forest is still on a successional pathway towards a dynamic steady-state after –often underestimated- human alterations in the past.

Moreover, it is unclear how these developments will evolve towards a new level of dynamic steady-state: will the unidirectional succession gradually slow down and fade out to reach a steady-state, or will structural characteristics of the past continue to influence the forest structure over several tree generations ? Bormann and Likens (1979) already describe the possible occurrence of an ‘overshoot peak’ at the end of the aggradation phase for forest stands in succession after large-scale disturbance. A similar stand structure and development have been described for other secondary old-growth beech stands as well (Von Oheimb et al., 2005; Ziaco et al., 2012). This overshoot peak may continue to influence the structure and age distribution in the forest, due to larger-scale synchronous maturation, and result in undulating patters that persist over several tree generations. Koop and Hilgen (1987) studied a secondary old-growth beech stand in La Tillaie, Fontainebleau (France) and related peaks in the age distribution to several generations of trees reverberating a large-scale regeneration of the stand after extensive clearcuts dating back 600 years. However, this age structure could also reflect the massive regeneration of trees at the site after abolishment of forest grazing, as was the case also in Suserup Skov (Emborg, 2000) and Hasbrucher Urwald (Koop, 1981).

1.3.4 Two prominent structural features of old-growth forests

Two elements of difference are most striking when comparing managed forests with ‘old-growth’ sites:

- the share of ancient trees
- the amount of CWD (Coarse Woody Debris), both standing and lying.

They are often referred to as ‘typical’ elements or ‘primary structural indicators’ for old-growth forests, that are absent or rare, even in forests under close-to-nature commercial management (e.g. Bobiec, 2002; Christensen and Emborg, 1996; Korpel', 1997). They are more exclusive to old-growth forests than most of the other characteristics (like structural complexity and species composition; see chapter 1.1), that can also occur in managed forests where close-to-nature silviculture with continuous cover forestry and selection fellings is applied. As they are prominent and measurable features, these two characteristics are most frequently used as basic descriptors of old-growth forests (Bobiec, 2002; Burrascano et al., 2013; Greenberg et al., 1997; Nilsson et al., 2002; Von Oheimb et al., 2005; Wirth et al., 2009; Ziaco et al., 2012).

These two features are also very relevant to forest and conservation policy. Over the last decades, dead wood and overmature trees are increasingly recognised as important components in the functioning of the forest ecosystems, such as biogeochemical cycles, trophic chains, natural regeneration, carbon storage, … (Brown et al., 1997; Harmon et al., 1986; Knohl et al., 2003; Lindenmayer et al., 2012; Luyssaert et al., 2008). Reintroduction of late-successional structures such as large overmature trees and dead wood are thus increasingly part of a modern, multifunctional forestry and forest conservation biology. Whereas these structures before were regarded as sanitary risks and loss of income, they are now more and more considered as essential elements in a healthy and bio-diverse forest ecosystem, not only by conservationists, but also by foresters. As they are relatively easy to measure, and a significant share of forest biodiversity is linked to them, overmature trees and the amount of dead wood are often used as important structural indicators in the framework of Biodiversity Evaluation Tools (Corona et al., 2003; Larsson, 2001; Marchetti, 2004; Van Loy et al., 2003) and as a basic descriptor of old-growth characteristics and naturalness in forests (Bobiec, 2002; Peterken, 1996). They are primary indicators of sustainable forest management, as required by forest certification programmes like FSC, and are important structural criteria in the evaluation of ‘favourable conservation status’ of forest habitats according to the EU Habitat directive. In Europe, the volume of standing and fallen dead wood is also one of nine pan-European indicators for Sustainable Forest Management for the criterion on biodiversity conservation (criterion 4: maintenance conservation and appropriate enhancement of biological diversity in forest ecosystems) (MCPFE, 2002; 2015). Periodical reporting on these indicators is mandatory to all signatory states.

A better knowledge of the characteristics and development of these old-growth elements in reference sites with no management intervention is very relevant in this context, as it provides reference and benchmark values and new insights on the consequences of policy choices and their implementation in management concerning non-intervention and the incorporation of dead wood and overmature trees in regular forest management.

The first two chapters of our study, concerning structural dynamics and developments, accordingly focus on the characteristics of large overmature trees and the net accumulation of large dead wood in the unidirectional succession from managed to secondary old-growth forests in newly installed non-intervention forests.

1.3.5 Consequences for associated biodiversity

In the following two chapters, we analyse the development of forest-related species when non-intervention and late-successional elements are re-introduced to the forest after centuries of intensive management. We focused on specific groups that can be indicative for overall forest biodiversity: vascular plants on the one hand, and a selection of taxa related to dead wood and overmature trees on the other.

Vascular plants were chosen as they are well known and well studied, and often used as indicator taxa for abiotic conditions and overall species richness of forests (REF). They are relatively easy to sample in a standardised way, and a long tradition of such vegetation relevees exist They are prime species to describe forest communities, and play an important role in the evaluation of the natural value and condition of ecosystems, as they can be reliable indicators of disturbance (acidification, nitrification, drainage…), former land use (e.g. Ancient Woodland indicators),… They are prominent in several ecosystem evaluation tools, such as the criteria for the evaluation of 'favourable conservation status' of habitats according to the EU Habitat directive.

Moreover, for vascular plants it is often debated whether non-intervention is detrimental to species diversity when previously managed forests are deliberately left for free development (e.g. Plue et al., 2013; Kopecký et al., 2013; Müllerová et al., 2015). Many vascular plants occurring in forests are presumed to be associated with continued human interventions, as they may require the higher share of sun-exposed conditions and soil disturbance related to wood harvest (Brunet et al., 1996;

Von Oheimb & Brunet, 2007; Heinrichs & Schmidt, 2017). Species richness of vascular plants is therefore expected to decline when non-intervention is introduced. It is however debated how large this species loss is expected to be, and what species will be lost or decline. Several studies indeed show a loss of species richness of ground vegetation with the introduction of non-intervention (e.g. Boch et al., 2013; Mölder et al., 2014); other studies (Burrascano et al., 2017; Kaufmann et al., 2017) do not detect a lower species richness in unmanaged forests, but significant differences between both plant communities. Some authors assert that even characteristic shade-tolerant plant species may eventually disappear from these forests, as they undergo an unnatural, prolonged period of deep shade, due to the man-made, uniform age structure of the original forest stands (Plue et al., 2013) or a pulse succession of shade-casting climax tree species such as beech, that were for centuries suppressed by human interventions (Mölder et al., 2008; 2014).

In our study, we focused on ground vegetation development in four formerly managed, recently established strict reserves on fertile loamy soils and assessed if indeed species richness declined, and especially, how species composition changed over time, and if indeed also shade-tolerant species were negatively influenced by prolonged canopy closure. We specifically focused on forest reserves on fertile loess-soils, as these sites often contain a high number of vascular plant species that may be influenced by long periods of canopy closure, associated with the introduction of non-intervention.

As stated before, the development of large amounts of dead wood and overmature trees are the two most characteristic structural features of secondary old-growth succession. These structural features are essential for forest biodiversity conservation, as up to 1/3 of all forest biodiversity is apparently associated to them (Harmon et al., 1986; Larrieu et al., 2014; 2018; Moning and Müller, 2009; Nilsson et al., 2002; Økland et al., 1996; Ódor et al., 2006; Paillet et al., 2017 Stokland et al., 2013 Vallauri et al, 2003). Their ecological importance, as habitat for this wide range of species is therefore increasingly recognized and stressed by conservation ecologists (e.g. Stokland et al., 2013).

Due to deforestation and intensive use of the remaining forests, these old-growth elements became virtually absent. Only over the last decades, they progressively reappeared in our forests, and have now reached their highest level over the last 500-1000 years, offering important possibilities for recolonization by old-growth associated species. The ability of species to recolonize the newly available habitat is strongly determined by their dispersal abilities and habitat requirements for establishment. In order to evaluate whether this recolonization has been successful, we analysed the status and development of two specific species groups, focusing on wood decaying fungi and saproxylic beetles. These two groups were selected as they show a strong link to old-growth elements and cover a wide range of dispersal abilities and habitat requirements (Kallio, 1970; Solbreck, 1980; Nilsson, 1984; Ranius and Hedin, 2001; Edman et al., 2004a, 2004b). Moreover, these are two groups for which sufficient and reliable data were available, both on past and present occurrence.

1.3.6 Approach of the research

For the study of the two main characteristics (dead wood and overmature trees) of old-growth forests in the Flemish strict forest reserves, two important challenges are encountered: the lack of real reference sites and the absence of long time series in order to analyse developments over time. As the Flemish forest reserve programme is only two decades old, long time-series are simply inexistent.

For the study on the dead wood accumulation process (**chapter 2**), we used a ‘space for time’ chronosequence in order to overcome the absence of long time series. For this purpose, we could use a large set of data on dead wood amounts in sites with similar species composition and site conditions, but with a wide range of time intervals of non-intervention. Chronosequences should always be treated with the necessary caution, as site conditions, initial situation, etc… are not entirely comparable, but are quite reliable to discern global trends.

In **chapter 3**, status and development of overmature trees in secondary old-growth forests is studied. For this analysis, we focused on one specific case concentrating on very large beech trees (DBH>80cm) in the strict forest reserve of Sonian forest, and compared the results again to a large compiled set of reference sites (descriptive and comparative case study).

For both these chapters, we could incorporate a wide set of data, both published and unpublished, provided by co-authors and colleagues through an active network of researchers involved in strict forest reserves studies.

As stated above, the analysis of status and development of biodiversity during secondary old-growth succession focuses on vascular plants, and saproxylic beetles and fungi.

For the study of the development of vascular plants (**Chapter 4**), we selected four recently erected strict forest reserves, where repeated measurements of vegetation relevés were performed in a systematic grid of permanent plots. As stated, we specifically selected forest reserves on fertile loess-soils, as these sites often contain a high number of vascular plant species that may be influenced by the introduction of non-intervention. Our results are confronted to a large set of similar studies, focusing on vegetation development after abandonement or extensivation of management.

In **chapter 5**, we analysed the response of two specific groups of saproxylic organisms (saproxylic fungi and beetles) on the reappearance of dead wood and overmature trees. Their response was analysed both using nationwide historic and recent distribution data (if available) and active inventories of specific sites with high potential for recolonization: secondary old-growth sites with large amounts of dead wood and very large trees.

In the final **chapter 6**, further conclusions are drawn, combining the results of previous chapters and additional information. Here, we provide a global synthesis on the dynamics of newly installed strict forest reserves and their development towards old-growth status, and the expected consequences for biodiversity. From this synthesis, we derive important benchmarks for policy makers and management guidelines for conservation of late-successional forest biodiversity.

The overall structure and concept of the study connection between the different chapters is illustrated in the conceptual overview figure below (Fig. 1.10).

1.3.7 Hypotheses

The presented study, like many studies on forest dynamics, is mainly an observational study. In such observational studies, a wide set of response variables and potential explanatory variables is periodically measured on a representative set of sampling areas in order to record, in a standardized way, developments and changes of the response variables, and relate them to the explanatory variables. Unlike in an experimental field set-up, the research questions in these type of studies are less hypothesis-driven. Still, it is possible to formulate hypotheses on the expected developments, based on general ecological principles and knowledge on forest dynamics from other publications.

For our study, some of the hypotheses that can be formulated are given below. In chapter 6, these hypotheses are confronted to our results and answered.

<u>On dead wood accumulation:</u>

- In secondary old-growth forests, the average amount of dead wood is lower than in primary old-growth forests
- During secondary succession to old-growth, the input of dead wood is higher than the decay rate, resulting in gradual net accumulation of dead wood.
- Dead wood accumulation rates differ between beech and oak dominated forests
- Dead wood accumulation rates depend on the average age of the dominant trees at the onset of non-intervention
- Dead wood accumulation rates depend on site fertility (rich vs. poor sites)
- Dead wood accumulation rates depends on geographical location.

- On the ratio of lying to total dead wood, it is expected that this ratio is higher for beech dominated forests than for oak dominated forests, as beech trees are more prone to windthrow compared to oak trees.

On Very Large Trees (Case study of a secondary old-growth lowland beech forest)

- The diameter distribution of the secondary old-growth sites differs from the typical inverse J-curve (or rotated sigmoid curve) of primary old-growth forests
- The density of VLT is higher in the previously managed stand in the SFR Joseph Zwaenepoel as compared to primary old-growth forests, due to the 'overshoot'-effect (more even-aged stand reaching over-mature state).
- Higher growth rates lead to shorter life expectancy, thus higher mortality.
- Due to the combined effect of high growth rates and short life expectancy, the size range of VLT is similar in lowland conditions compared to montane and high elevation sites.
- Spatial distribution of VLT gradually evolve towards random pattern during secondary succession.

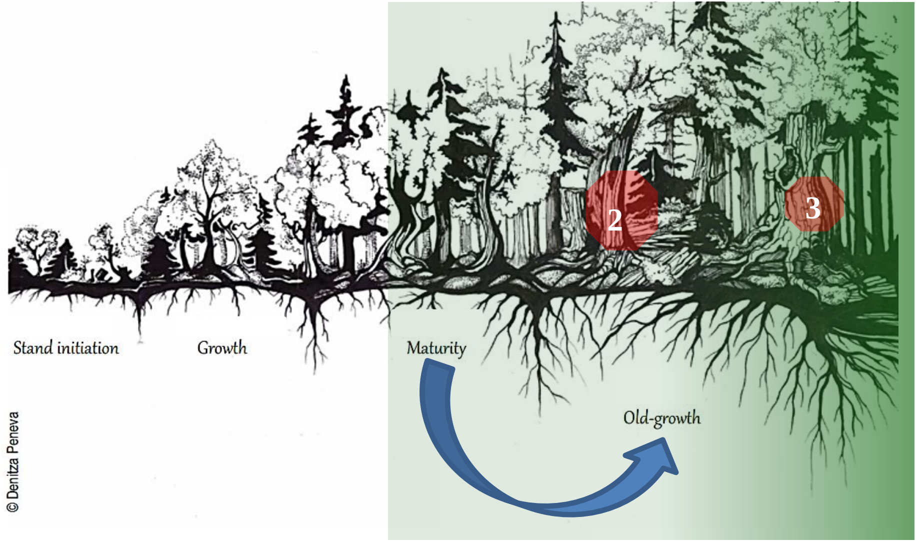
On status and development of the herbal layer after introduction of non-intervention

- Based on the Intermediate Disturbance Hypothesis, the species richness of vascular plants will decrease if formerly managed forest stands are left unmanaged.
- Species loss is not random: especially light-demanding and disturbance-related species will be lost.
- This process of non-random species loss leads to homogenization of the vegetation.
- Even typical shade-tolerant and –evading species may be jeopardized due to prolonged deep shade, leading to species loss and lower cover rates.

On status and development of biodiversity associated to the late-successional stage of old-growth forests (case study for Flanders)

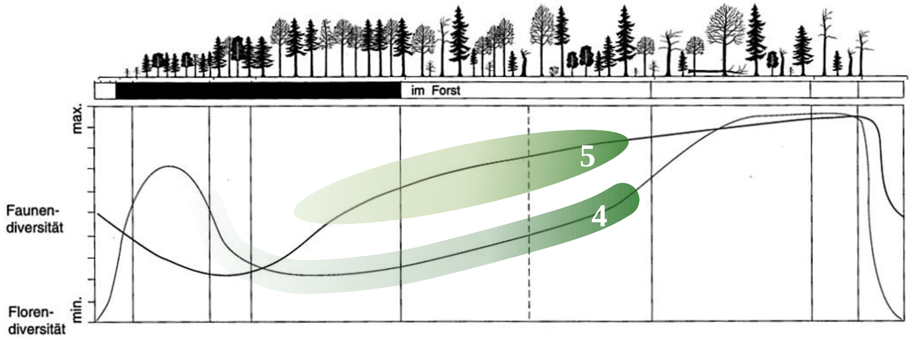
- Species richness of saproxylic fungi and beetles is low in secondary old-growth forests: due to centuries of absence of suitable substrate, the associated species disappeared and are not able to recolonise.
- Species composition of saproxylic fungi and beetles is different in secondary old-growth forests, lacking highly demanding species with low dispersal abilities.

Development of old-growth characteristics in formerly managed forests



Chapter 1: Introduction: history and concepts of old-growth, definition and application

Status and development of stand characteristics of old-growth forests during secondary succession:	**Chapter 2**: **Dead wood** accumulation
	Chapter 3: Characteristics of **Very Large Trees**



Status and development of Biodiversity during secondary succession:	**Chapter 4**: Development of the **herbal layer** in previously managed forests, left for free development – case study for 4 reserves
	Chapter 5: Reappearance of old-growth elements: do the associated species follow ? **Saproxylic fungi and beetles**

Chapter 6: Conclusions and application: benchmarks and guidelines for forest management.

Fig 1.5. Schematic overview of the structure of this study. Numbers in the drawings refer to the respective chapters in the study (*Drawings: upper figure by Denitza Peneva in 'Old-growth forests: the unknown treasures of Bulgaria' (WWF, 2013). – Lower figure adapted from Scherzinger (1996), page 64).*

Chapter 2

Quae bene cognita si teneas, natura videtur
libera continuo, dominis privata superbis,
ipsa sua per se sponte omnia dis agere expers.

What a good thought to know that nature,
fully free of any master, appears to be governing itself,
without interference of a higher god’

Titus Lucretius Carus (99 – 55 AD)
de Rerum Natura, II, v. 1090-1092

Le forestier y voit avec intérêt, comment sans le secours de l'homme la nature aménage les forêts, comment elle sème, élève, détruit, et comment les débris des bois morts servent de berceau aux nouvelles générations. (...)
enfin les plus jeunes arbrisseaux jonchent le sol qui est couvert souvent de troncs renversés et pourris, d'un aspect désagréable, mais dont la décomposition offre une nourriture abondante à la jeunesse qui les entoure.

Baron Julius Carl Holte von Brincken (1790-1846)
Mémoire descriptif sur la forêt impériale de Bialowieza en Lithuanie (1828).

Chapter 2: dead wood buildup in previously managed forests, left for free development

---

After: Vandekerkhove, K., De Keersmaeker, L., Menke, N., Meyer, P. & Verschelde P. 2009. When nature takes over from man: dead wood accumulation in previously managed oak and beech woodlands in North-West- and Central Europe. Forest Ecology and Management 258, 425–435.

2.1 Abstract

The net accumulation of dead wood and its characteristics are analysed in forests that have been withdrawn from regular silvicultural management and left unmanaged between 10 and 150 years ago (average: 35 years; median 24 years). These forests are dominated by beech (*Fagus sylvatica)* and oak (*Quercus robur* and *Quercus petraea*) and located in the lowlands of North-western and Central Europe.

The total volumes of dead wood ranged from 6 to nearly 500 $m^3.ha^{-1}$, with a median value of 53 $m^3.ha^{-1}$. The average accumulation rate ranged from <0.1 to 19 $m^3.ha^{-1}$ $year^{-1}$. Variation was significantly higher in beech- than in oak-dominated forests. The variables and factors influencing dead wood volumes and net accumulation rates were tree genus, stand age at the time of the onset of non-intervention, and the interaction between geographical location and tree genus. The ratio of dead wood to the total aboveground biomass averaged 12.8 % (median value: 8.9%; range: 1.4 to 90 %). This figure was reached after on average two to three decades of spontaneous development (time of non intervention: average 32 years, median: 24 years)

In beech-dominated stands, the ratio of lying to total dead wood was more or less constant at 75%; in oak-dominated stands, this ratio was related to the length of time non-intervention had occurred, rising from <50% in recently assigned areas to 75% in the long-established sites. It is concluded that in the absence of major disturbances, dead wood accumulation in man-made forests left to develop freely is

a slow process. It may take a very long time to achieve the average amount and dynamic steady state of dead wood as described for virgin forests in Central Europe.

2.2 Introduction

Publications on base-line or reference values for dead wood in primary forests which have never been subjected to silvicultural management (subsequently referred to as primary old-growth forests in this study) are numerous for Europe (a.o. Leibundgut, 1993; Korpel', 1995; Saniga and Schutz, 2001a; 2001b). However, very little is published on the processes of dead wood accumulation in forests that have been withdrawn from regular silvicultural management and deliberately assigned to a non-intervention regime (subsequently referred to as 'secondary old-growth'). This study comprises a meta-analysis of data (published and original) on dead wood volume (standing and lying) in these forests, focusing on oak and beech forests in the lowlands of Central and North-western Europe. Over the last three decades, dead wood is increasingly recognised as an important component in the functioning of forest ecosystems. It plays an important role in biogeochemical cycles, trophic chains, natural regeneration, and is an important element in carbon storage as well as providing key niches for many species (Dajoz, 1974; Maser and Trappe, 1984; Harmon et al., 1986; Ferris-Kaan et al., 1993; Kirby and Drake, 1993; Rauh, 1993; Samuelsson et al., 1994; Falinski and Mortier, 1996; Økland et al., 1996; Esseen et al., 1997; Bücking, 1998; Denis, 1998; Köhler, 2000; Heilmann-Clausen, 2001; Siitonen, 2001; Grove, 2002; Vallauri et al., 2003; Vandekerkhove et al., 2003; Brustel, 2004; Brustel and Dodelin, 2005; Ódor et al., 2006). A combination of forest fragmentation and forest management (including the removal of dead wood) has led to a substantial decline in species that are dependent on dead wood. Many species are threatened or have become extinct locally and regionally (Siitonen, 2001). This is especially true for highly fragmented and intensively treated forests in North-western Europe (Ódor et al, 2006).

The amount of dead wood is often used as an important structural indicator in the context of Biodiversity Evaluation Tools (Larsson, 2001; Van Loy et al., 2003; Corona et al., 2003; Marchetti, 2004) and as a basic indicator of old-growth characteristics and naturalness in forests (Peterken, 1996; Bobiec, 2002). It has become one of the primary indicators of sustainable forest management in Europe (MCPFE, 2002) and periodic reporting on this indicator is mandatory for all signatory states. (MCPFE, 2003; 2007).

Although its importance in practice and in policy has dramatically increased, amounts of dead wood in European forests, especially in the lowlands, are still extremely low. Average figures per country in Europe vary from less than 1 to 25 $m^3.ha^{-1}$ (MCPFE, 2007; 2015). This is far below the amounts typically found in primary old-growth forests (Green and Peterken, 1997; Kirby et al., 1998; Ódor and Standovár, 2001; Winter and Nowak, 2001), and below the amount that may be required to safeguard the complete spectrum of species that rely on dead wood, which is widely agreed to be at least 20-30 $m^3.ha^{-1}$ (Stokland, 2001; Siitonen, 2001; Angelstam et al., 2003; Humphrey et al., 2004).

Regional forest policies have an explicit goal to significantly increase both the quantity and quality of dead wood (Ammer, 1991; ONF, 1993; Hodge and Peterken, 1998). In order to achieve this objective a two-way policy has been developed incorporating an integrative and a segregative approach. An integrative approach aims to retain a certain quantity and quality of dead wood in regular multifunctional forest management. A segregative approach concentrates conservation efforts in protected forest areas. Both are necessary and complementary to generally attain the biodiversity conservation objective in forests (Frank et al., 2007).

In both primary and secondary old-growth forests, the conservation policy objective on dead wood is realised through processes of spontaneous development. These reserves cover less than 5% of the total forest area in Europe (Parviainen et al., 2000; MCPFE, 2007; Bücking, 2007). In the 19th century, the main objective for the assignation of reserves was aesthetic and ethical, namely to conserve the last remains of primary old-growth forest in Central Europe (Welzholz and Johann, 2007; Bücking, 2007). Over time, the value of these ‘virgin forest’ reserves for nature conservation and scientific research became increasingly important (Parviainen et al., 1999; Bücking, 2007). They proved to be essential to the development of nature-based silviculture, as they provide reference base-line values and ranges for forest structural parameters such as the amounts of living and dead wood, species composition and gap dynamics (Leibundgut, 1959; 1978; Korpel', 1992). Hence, scientific criteria such as representativeness became a focus in the selection of new sites. The aim was to develop a network of unmanaged reference sites that represent all forest types and site conditions present in a certain area or country (Leibundgut, 1959; Mlinšek, 1976; Parviainen et al., 1999; 2000; Meyer et al., 2007). As a consequence, new reserves are and have been selected in managed forests, as there are no primary old-growth forests remaining for many of the target forest types. Spontaneous developments in these, previously managed forests are clearly different from primary old-growth forests. Whereas the latter are considered to be in a dynamic equilibrium with respect to the different developmental phases that are interchanging (e.g. Leibundgut, 1978; Korpel', 1995; Saniga and Schütz, 2001a), the newly established secondary old-growth forests are still developing in a more unidirectional way towards equilibrium. Indeed, they all start from a man-made structure that is more or less divergent from this equilibrium. They generally have a lower growing stock than primary old-growth forests and species composition and dominance has been influenced and altered by human intervention. Most of the semi-natural forests in the European lowlands are dominated by beech or oak. This dominance, especially where oak is concerned, is often the result of centuries-old management regimes. The structural difference however, is most striking in the typical old-growth elements, particularly ancient trees and dead wood volume (Bobiec, 2002; Korpel', 1997). This chapter analyses the process of dead wood net accumulation in secondary old-growth forests in the lowlands of Northwest and Central Europe.

2.3 Materials and methods

2.3.1 Selection criteria for study sites

This study comprised a meta-analysis of data (published and original) on dead wood volume (standing and lying) in secondary old-growth forests. From a large dataset, sites were selected that met the following criteria:

1. Before the adoption of a non-intervention management regime the forest was subject to regular forest management typical of current forest practice in the region, i.e. regular thinning, felling, planting, and removal of dead wood. As a consequence sites that are considered as ‘primary old-growth forest’ in Europe were not included in this study.
2. The sites chosen were subject to non-intervention for at least 10 years.
3. Locations were within the natural range and typical site conditions of Beech woods, Birch-oak woods and Hornbeam-oak woods (*Fagion, Quercion robori-petraea* and *Carpinion* resp. *sensu* Jahn, 1991).
4. The study was confined to the lowlands of North-western and Central Europe. The study included sites from the following countries: Belgium, Czech Republic, Denmark, France Germany, Hungary, the Netherlands, Poland and the United Kingdom. The altitudinal range only included lowlands and submontane ranges (up to 700 m).
5. The sites were dominated by oak (*Quercus robur* and *Quercus petraea*) and beech (*Fagus sylvatica*). Oak or beech was considered as ‘dominant’ if they comprised the largest proportion of all tree species with respect to the living volume.
6. Information on selected sites had to be sufficient to be included. This meant data were available on all response variables and the essential explanatory variables. Also, mensuration methodology had to be clearly described and had to comply with clear standards of quality and comparability (see below).

2.3.2 Assessment of response and explanatory variables

The response variables that were selected for this study were

(a) the total volume of dead wood ($m^3.ha^{-1}$)
(b) the net accumulation rate of dead wood (m^3 $ha^{-1}.year^{-1}$)
(c) the ratio of dead wood volume to Total Aboveground Biomass (TAB) (%)
(d) the ratio of the lying dead wood volume to the total volume of dead wood (%).

Potential explanatory variables were the length of time of non-intervention, stand age at the time non-intervention management commenced, site fertility (poor versus rich), dominant tree genus (oak versus beech) and geographical location of the sites (North-western Europe versus Central Europe).

Total volume of lying and standing dead wood were sampled in a number of unmanaged forest reserves in Belgium and Germany. Sampling consisted of grid points covering at least 10% of the area (systematic grid with complete inventories in circles of 500 or 1000 m² at grid intersections), or complete surveys of larger 'core area' plots of 1 ha. Threshold diameter for living and dead wood was 5 cm for Belgian sites and 7 cm for German sites (except for lying dead wood in circular plots where it was 20 cm). Volume calculations were made for living and fresh dead trees using regional tariffs based on DBH and height measurements (Dagnélie et al., 1985). Volumes of wood fragments were calculated using formulas of truncated cones. The resulting volumes were converted and expressed in $m^3.ha^{-1}$ (De Keersmaeker et al., 2005; Meyer et al., 2006). The dataset was further completed with published data that met the above criteria.

The dead wood ratio expresses the share of dead wood volume to the TAB, being the sum of total living and dead wood volumes. It is expressed as a percentage. The ratio of lying to total dead wood volume was also expressed as a percentage. The dead wood accumulation rate is the net increase of dead volume over the recorded interval, divided by the number of years in this interval. The net increase of dead wood captures the balance between inputs and outputs (decay) of dead wood, and was calculated by subtracting the volume of dead wood at the moment the reserve was initiated from the recorded volume of dead wood at the time of measurement. For sites where this starting amount was unknown it was set at 2 $m^3.ha^{-1}$. This is an average value for traditionally managed forests (Kappes and Topp, 2004). Sites where the volume was known to be much higher but not quantified, were omitted from the dataset.

In order to evaluate the impact of the differences in diameter threshold applied in the different studies, we calculated the dead wood volumes in 5 cm classes for 10 Belgian sites (threshold diameter 5 cm; total dead wood volume ranging from 4 to 113 $m^3.ha^{-1}$, average 42.2 $m^3.ha^{-1}$), generating a correction factor for the 'missed fraction' in case of higher thresholds. We adjusted the dead wood volumes, accumulation rates and lying to total dead wood ratios, to a standard minimum threshold diameter of 5 cm, using this correction factor. This resulted in very marginal changes in recorded values as compared to the original dataset (e.g. mean total dead wood volume: 75.71 versus 75.26 $m^3.ha^{-1}$; median value remained unaltered). The modified dataset was also tested using an identical statistical procedure as for the original dataset (see below), resulting in models which included the same explanatory variables and interactions, with minor changes for coefficients and significance levels as compared to the models on the original data. We concluded that the impact of the harmonisation process on the results and the statistics was marginal, and therefore preferred to maintain the original data for further analysis and discussion.

The length of time of non-intervention was assigned using reports or information derived from managers and/or researchers. Unlike Christensen et al. (2005) we did not derive the number of years of non-intervention from the official date of reserve establishment as these do not necessarily coincide. Some sites were, in practice, left unmanaged for many years before non-intervention was officially designated by means of a reserve statute. In other cases, reserve status still allowed or could not prevent human intervention such as the removal of dead wood, especially during World Wars I and II. Sites where this information was missing or unreliable, were omitted. Stand age at the time of assigning the reserve was determined as the average age of the dominant tree layer at the time of measurement subtracted by the length of time of non-intervention. The 'fertility' factor was derived from the phytosociological description of the sites; *Quercion*, *Luzulo-Fagetum* and *Milio-Fagetum* sites were classified as 'poor', and *Carpinion*, *Endymio-Fagetum* and *Asperulo-Fagetum* were classified as 'rich'. The dominant tree species was determined based on the proportion of a particular tree species to the total living volume. Only sites where beech or oak had the highest proportion of all tree species present were selected and were allocated to the genus classes ‘beech’ and ‘oak’ respectively. The geographical subdivision (North-western versus Central) was primarily based on the Atlantic and Continental regions as defined in Roekaerts (2002). These biogeographical regions are based on the natural vegetation map of Europe, and are discerned by means of indicator plant species for local climatic conditions such as temperature and annual rainfall. As this study was primarily concerned with the effects of windstorm conditions, we added information on windstorm regimes, derived from the Europe Windstorm Model for Extra-Tropical Cyclones (ETC) risk assessments (www.rms.com). As a consequence, a few sites were moved into new categories with respect to the biogeographical subdivision.

2.3.3 Data analyses

Linear models were developed in S-PLUS 8.0 to determine the variables that were significant in explaining the total volume of dead wood, the net accumulation rate of dead wood and the ratio of lying to total dead wood volume. Exploratory data analyses revealed that data transformation was necessary for normalisation. A log transformation was applied to the total volume of dead wood and the accumulation rate. The ratio of lying to total dead wood was normalised by means of a quadratic function. The stepwise model building started with an upper model, which included all the above mentioned potential explanatory variables and their interactions. The least significant term was removed and this procedure was repeated until all remaining terms were significant. The ratio of lying to total dead wood was modelled by means of a generalised linear model (GLM). The exploratory data analysis indicated that variance of dead wood volume and accumulation rate were related to tree genus and therefore a generalised least square model (GLS) was applied. The akaike information criterion (AIC) was used to select the most appropriate variance structure model. Significance of variables and interactions were tested by means of restricted maximum likelihood (REML), which can produce unbiased estimates of variance and covariance structures (Fitzmaurice et al., 2004).

2.4 Results

A total of 109 sites in North-western and Central European lowlands were represented in the dataset. Summary details and references of all sites are given in Annex 1. In total, 74 sites were dominated by beech and 35 by oak. The sites were well distributed with respect to the variables ‘Geographic region’ and ‘site fertility’. The average age of the dominant trees at the onset of non-intervention varied between 3 and 178 years for the oak stands and 33 and 280 years for the beech stands. However most were between 100 and 150 years old. Very few stands were less than 50 years or over 200 years of age.

Most sites in the dataset had only recently been withdrawn from ongoing regular management; the mean time of non-intervention was 35 years. More than half of the sites were left unmanaged for 25 years or less. Only 22 sites had a history of non-intervention for more than 50 years and only 3 for more than a century.

2.4.1 Total dead wood volume

Summary data on total dead wood volume are shown in Table 2.1 and illustrated in the boxplots (Fig. 2.1, 2.2 and 2.3).

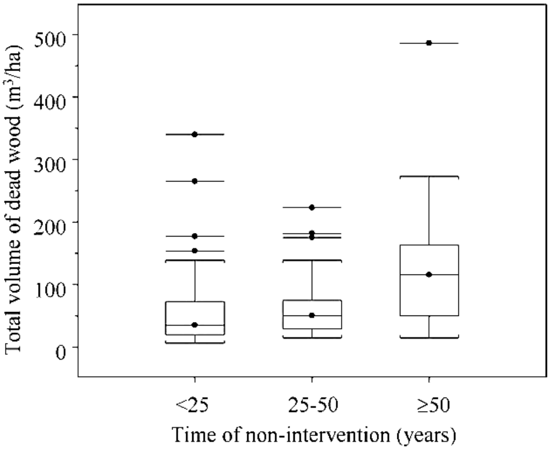


Fig. 2.1 Boxplots representing the total dead wood volume in forest reserves, subdivided in three classes, defined by the length of time of non-intervention.

Table 2.1 Summary statistics on total dead wood volume, net accumulation rate and ratio of lying to total dead wood volume for the complete dataset, and specific subsets (oak and beech in Northwest and Central Europe).

	Beech			**Oak**			**Total**
	NW	C	**All**	NW	C	**All**	
N	24	50	**74**	12	23	**35**	**109**
Total volume ($m^3.ha^{-1}$)							
Mean:	130.4	64.9	**86.1**	24.8	66.8	**52.4**	**75.3**
Standard error of mean	23.2	8.2	**9.9**	4.3	9.8	**7.4**	**7.3**
Median	96.0	39.0	**59.0**	23.4	57.0	**39.2**	**53.0**
Lower quartile	53.2	20.8	**26.9**	15.9	38.6	**25.2**	**26.4**
Upper quartile	145.0	92.4	**120.5**	28.4	69.6	**62.4**	**95.0**
Accumulation rate ($m^3.ha^{-1}.yr^{-1}$)							
Mean:	5.13	2.13	**3.10**	1.04	1.75	**1.51**	**2.59**
Standard error of mean	0.98	0.29	**0.40**	0.21	0.20	**0.16**	**0.29**
Median:	3.44	1.26	**1.89**	1.00	1.72	**1.24**	**1.64**
Lower quartile	1.94	0.63	**1.00**	0.46	1.18	**0.83**	**0.96**
Upper quartile	6.62	2.87	**4.03**	1.25	2.31	**2.07**	**3.00**
Lying dead wood (%)							
Mean:	75.6	70.1	**71.7**	42.3	54.9	**50.9**	**65.2**
Standard error of mean	3.6	2.5	**2.03**	5.9	5.5	**4.3**	**2.1**
Median:	74.7	75.8	**75.0**	44.1	65.0	**50.7**	**70.4**
Lower quartile	70.0	63.2	**65.5**	31.3	31.3	**31.2**	**53.4**
Upper quartile	87.7	79.9	**82.2**	54.7	77.4	**68.8**	**79.2**
Missing values	4	1	**5**	2	2	**4**	**9**

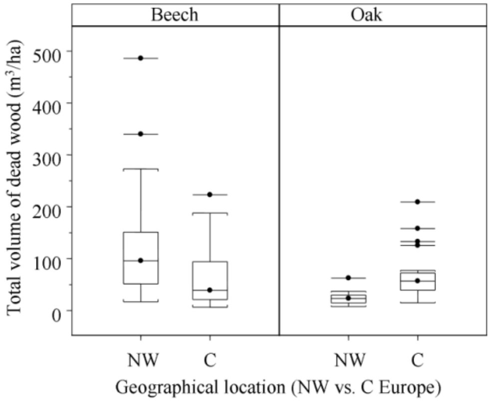


Fig. 2. 2 Boxplots representing the total dead wood volume in forest reserves, subdivided by tree genus (beech versus oak) and geographical location (Northwest versus Central Europe).

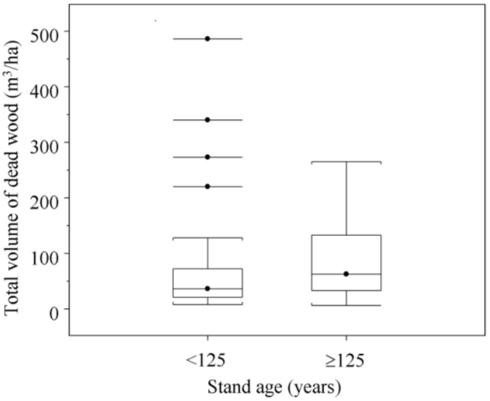


Fig. 2.3 Boxplots representing the total dead wood volume, subdivided in two classes of average stand age at the onset of non-intervention.

The recorded total amount of dead wood ranged from 6 to nearly 500 m³.ha^{-1}, with a mean value of 75 m³.ha^{-1}. The results were not evenly distributed; 3 out of 4 sites contained less then 100 m³.ha^{-1}. Mean and standard deviations are therefore not very indicative for the recorded range of values. Median and quartiles are better measures in this case. Median, upper and lower quartile values were 53, 95 and 26 m³.ha^{-1} respectively. As shown in Fig. 2.1, there was an evident gradual increase in the amount of dead wood as the non-intervention time interval increased. The range of values was particularly high and unevenly distributed in the first 25 years of non intervention. After 50 years and beyond, the distribution was more balanced and there were fewer outliers.

Both oak and beech showed strong differences between mean and median values illustrating a left-skewed distribution. The median value for oak was lower than for beech but was in the same order of magnitude. However, the interquartile range was much higher in beech and was unequally distributed. The upper quartile and maximum values were quite different; 120.5 and 486.0 m³.ha^{-1} for beech and 62.4 and 209.0 m³.ha^{-1} for oak. Lower quartiles and minima on the other hand were comparable. The increase of the total dead wood volume appeared to be a more steady and balanced process for the oak-dominated sites compared to the beech-dominated sites.

The GLS model (Table 2.2) confirmed that the variance of the total amount of dead wood was significantly larger in beech forests than in oak forests (beech=1; oak=0.663 respectively). As data was incomplete for some of the tested variables, only 87 of the 109 sites could be used in this analysis. Tree genus and stand age at the time of assignation of non-intervention, the length of time of non-intervention, and the interaction between tree genus and geographical location (North-western versus Central Europe) were significant variables which explain the total amount of dead wood. All other interactions and the site fertility factor did not appear to have a significant impact on the amount of dead wood recorded. The corresponding linear model (with a fixed variance structure) resulted in a multiple R-Squared value of 0.51.

Tree genus and the interaction between tree genus with geographical location were significant factors with respect to the total amount of dead wood . In beech stands, total dead wood amount was significantly higher than in the oak stands, and this was particularly true for the beech sites in North-western Europe. The effect of geographical location is apparent from Fig. 2.2: under North-western European conditions, median values for beech were markedly higher than in Central Europe. Also the spread of values (quartiles and min/max) was clearly different. In contrast, median values and variance for oak were similar in the two geographical regions, and equivalent to Central European beech forests.

The model further indicated that the total amount of dead wood was significantly influenced by the length of time of non-intervention and by the average age of the stand at the time when regular silvicultural management ceased, i.e. the older the stand at that time, the higher the amount of dead wood that accumulated. Fig 2.3 illustrates that in stands that were younger than 125 yr when non-intervention was initiated, smaller amounts of dead wood were likely to occur than in older stands. However a wide variation in values occurred and some middle-age-range sites showed extremely high values when the stands were severely damaged by catastrophic storm events.

Table 2.2 GLS models for total dead wood amount and accumulation rate and GLM model for lying to total dead wood ratio.

GLS-model: LogDEADT ~ AGE + TIME + TREE + LOCATION + TREE:LOCATION

Parameter estimates:	*Fagus*	*Quercus*		
	1.000000	0.663320		
Coefficients:	Value	Std.Error	t-value	p-value
Intercept	2.292000	0.269539	8.503422	<.0001
AGE	0.007396	0.001612	4.587713	<.0001
TIME	0.017120	0.002871	5.963933	<.0001
TREE	-0.206533	0.075403	-2.739072	0.0076
LOCATION	-0.071844	0.073190	-0.981614	0.3292
TREE:LOCATION	0.351292	0.073519	4.778236	<.0001

GLS-model: LogACCU ~ AGE + TREE + LOCATION + TREE:LOCATION

Parameter estimates:	*Fagus*	*Quercus*		
	1.000000	0.5952156		
Coefficients:	Value	Std.Error	t-value	p-value
Intercept	-0.768236	0.202834	-3.787505	0.0003
AGE	0.009498	0.001512	6.282741	<.0001
TREE	-0.203331	0.076483	-2.658501	0.0094
LOCATION	-0.207103	0.074234	-2.789847	0.0066
TREE:LOCATION	0.366134	0.073957	4.950652	<.0001

GLM-model: LYING^2 ~ TIME + TREE + TIME:TREE

Coefficients:	Value	Std. Error	t value	p-value
Intercept	3534.0183	448.5739	7.8783	0.0000
TIME	23.6266	9.5450	2.4753	0.0156
TREE	-2324.9926	448.5739	-5.1831	0.0000
TIME:TREE	27.4825	9.5450	2.8792	0.0052

2.4.2 Average net accumulation rate

The average net accumulation rate indicated many similarities with respect to the total amount of dead wood: the distribution was also clearly skewed, with many low values, and a limited number of extremely high values. The recorded average accumulation rate ranged between <0.1 to 19 $m^3.ha^{-1}.year^{-1}$. The median value over all study sites was 1.64 $m^3.ha^{-1}.year^{-1}$. 75 % of the sites had accumulation rates of 3 $m^3.ha^{-1}.year^{-1}$ and less, and one out of four sites had <1. Similar to the total amount of dead wood, an analysis was made of the variables and factors influencing the accumulation rate using a GLS fit by REML (after correction for differences in variance between the tree genus; beech=1; oak=0.59). The same 87 sites were used in this analyses and the same variables tested, except for ‘length of time of non intervention’, as it is directly related to accumulation rate. Tree genus, geographic location, and their interaction, and age of the stand at the time of non-intervention significantly affected the accumulation rate. The corresponding linear model (with a fixed variance structure) resulted in a multiple R-Squared value of 0.48.

Dead wood accumulation was significantly faster in beech than in oak forests. There was also a strong interaction between geographic location and tree genus: in North-western Europe, the median accumulation rate for beech was markedly higher than in Central Europe. This difference in beech between North-western and Central Europe was even more pronounced for the higher accumulation rates, with upper quartile values of 6.62 and 2.87 $m^3.ha^{-1}.year^{-1}$ respectively. Also all outlying high values were situated in North-western Europe. For oak, the accumulation rate (median and variance values) was similar in Central and North-western Europe and comparable to accumulation rates for beech at Central European sites. The average age of the oak and beech stands at the onset of non-intervention was positively related to the expected accumulation rate of dead wood. This pattern is somewhat distorted in the beech stands, as the dataset contains some middle-age beech stands in the UK that were severely damaged by an exceptional storm event in 1987. The ratio of dead wood to the total aboveground biomass (=sum of living and dead volume) averaged 12.8 %. The range on this figure was very wide (1.4 to 90 %), as values tend to increase to very high figures after stand replacing disturbances. The median value after on average two to three decades of non-intervention was 8.9%.

2.4.3 Ratio of lying dead wood volume to the total dead wood volume

There was a difference in the ratio of lying to total dead wood volume between oak and beech stands. In beech stands, this ratio was constant at about 75 % regardless of the length of time of non-intervention and geographical location. In oak stands, this ratio increased from <50 % in recently assigned reserves to 75% in the long-established sites (Fig. 2.4).

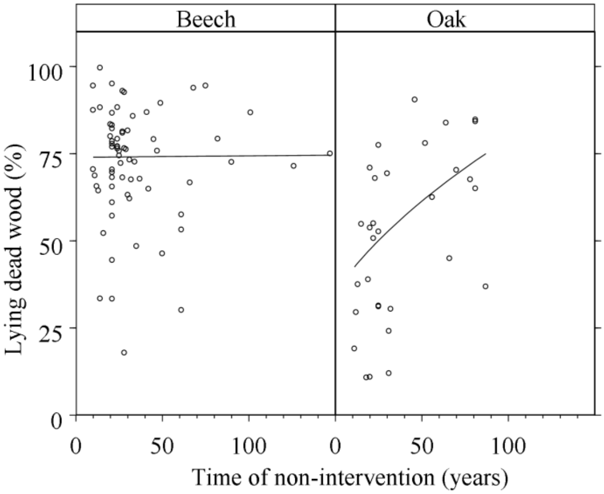


Fig. 2.4 Scatterplot of the ratio of lying to total dead wood subdivided for beech and oak dominated forest reserves. The line represents the fitted linear model.

The GLM confirmed that tree genus, length of time of non-intervention and the interaction between these two variables were the significant factors affecting this ratio; geographic location was not significant in this case. The linear model gave a multiple R-Squared value of 0.32.

2.5 Discussion

Primary old-growth forests no longer exist in the North-western and Central European lowlands. Forests in these regions have been altered and intensively managed since prehistoric times. Their dynamics, when left unmanaged, are influenced by natural processes (e.g. ageing, mortality, decay; catastrophic events) but also by their current structure as a result of management history. Most sites studied have only recently been withdrawn from regular management (mean value 35 years). Their dynamics appear to be more unidirectional and successional, rather than cyclical as in primary old-growth forests.

2.5.1 Limitations and imperfections of this study.

The dataset, used for the meta-analysis, was compiled from different sources, using different methodologies. This is often the case in such analyses, and should not be problematic, provided all data sources produce reliable and comparable figures (cfr. also Christensen et al., 2005). A clear description of the methodology which conforms with European standards on sample size and diameter thresholds (Hochbichler et al., 2000) was required for the selected data in this study. However an important but unavoidable inconsistency was the difference in threshold diameter for dead wood inventory ranging from 5 to 20 cm. Dead wood volume is considered to be a robust descriptor for stand comparison as it is less affected by size thresholds compared to variables such as stand density (Peterken, 1996; Nilsson et al., 2003; Piovesan et al., 2005). We perceived that the differences in diameter threshold that were applied in the different countries did not affect the results and statistics of this study (outlined in the Methods section).

This study focused only on the quantitative aspects of dead wood and did not consider qualitative aspects such as size distribution and decomposition classes. Dead wood of larger dimensions and advanced decomposition status has a higher capacity to support species and this wood contains the majority of threatened species (Speight, 1989; Hekhuis et al., 1994; Rauh, 1993; Siitonen and Martikainen 1994;

Høiland and Bendiksen, 1997; Grove, 2002; Heilman-Clausen and Christensen, 2003; Christensen et al., 2005; Ódor et al., 2006). In many of the more recently assigned strict forest reserves, dead wood at more advanced stages of decay is absent or underrepresented (Vandekerkhove et al., 2005; Ódor et al., 2006).

Another limitation is the timeframe involved when considering deadwood accumulation. Most sites had a short non-intervention period (<30 years). This is well below the general lifespan of beech and oak trees. For Central European montane forests, these are estimated at 200-250 years for beech and 300-350 years for oak respectively (Korpel', 1995). In the more temperate Central and North-western European lowlands the life cycle for beech may be extended to 300 years, but older stands are likely to collapse (Von Oheimb et al., 2007; Rademacher et al., 2001; Rademacher and Winter, 2003). In extreme montane conditions, beech may even live for up to 500 years and more (Biondi, 1993; Bourquin-Mignot and Girardclos, 2001; Piovesan et al., 2003; 2005). Since all age classes were not well represented in this study, the predictive value of the models was limited, especially in the higher age and time period classes. Due to the lack of real reference sites and scarcity of long-time records, conclusions regarding long term dynamics should be considered speculative to a certain degree (see also Pontailler et al., 1997). As limited information was available on age structure, only data on the average age of the dominant tree layer could be used in this analysis. However as discussed later, age- and/or diameter distribution may play an important role in the development of the dynamics.

2.5.2 Dead wood volume and net accumulation

Compared to primary old-growth beech and oak forests in Europe and elsewhere, recorded dead wood volumes were lower as the accumulation process is still ongoing. Christensen et al. (2005) report an average value of 132 $m^3.ha^{-1}$ for primary old-growth and long-established lowland and montane beech forest reserves; other studies indicate a natural range of 50 to 200 $m^3.ha^{-1}$ (Koop, 1989; Leibundgut, 1993; Korpel', 1995; Saniga and Schutz, 2001a; Meyer et al., 2003). European primary old-growth oak sites in Poland and Slovakia show values between 70 and 160 $m^3.ha^{-1}$ (Bobiec, 2002; Korpel', 1997), and for the USA, Harmon et al.

(1986) measured 82-132 m³ for Tennessee oak-beech forests. In this study, sites left unmanaged for <50 years had 10 to 75 m³ of dead wood, well below the values of primary old-growth forests. Only after approximately 60-80 years will secondary old-growth sites accumulate volumes of dead wood comparable to primary old-growth forests. This is in line with the observations of Peterken (1996), who postulates that accumulation of 'near natural' volumes of dead wood can occur within a century. In many sites however, the accumulation rate appeared to be much slower with <50 $m^3.ha^{-1}$ of dead wood after several decades of non-intervention.

The age of the stand at the onset of non-intervention, tree genus, geographic location and the interaction between these latter two factors were significant in explaining the amount of dead wood and the net accumulation rate. Mortality rate (and dead wood recruitment) increases as mature trees grow older and become more vulnerable to disease and physical instability (Harmon et al., 1986; Harcombe, 1987 in Peterken, 1996). The lowest mortality rates correspond with mature vigorous trees of around 40-70 cm DBH (Parker et al., 1985). Most sites in our study were dominated by mature trees aged 100-150 years, within the 40-70 cm DBH-range at the time of reserve assignation, which explains the low net accumulation rate of dead wood in most stands. Sites in older age classes had higher accumulation rates. In some cases where stands reach their natural age limit, the dead wood amounts of primary old-growth forests are achieved relatively quickly, i.e. within one or two decades (Vandekerkhove et al., 2005; Von Oheimb et al., 2005; 2007). This pattern is somewhat distorted as the dataset also contained some extremely high values for mature-aged stands on steep chalk slopes in the UK that were severely damaged by an exceptional storm event in 1987, almost levelling the study sites under investigation (Mountford and Ball, 2004; Mountford and Groome, 2004).

The process of dead wood accumulation was clearly different between beech and oak forests especially in North-western Europe. In oak forests, dead wood accumulation appeared to be a steady process, similar in forests in North-western and Central Europe with few exceptions. For beech forests, the process was much more irregular with higher overall values, especially under North-western European climatic conditions.

Interaction between both factors appears evident: windstorm patterns are considered to be different between both regions, with greater frequency of storms in North-western Europe and shallow rooted trees such as beech are much more vulnerable to uprooting. Oak and other deep-rooted trees generally remain standing, and usually only shed crown branches during storm events (Peterken, 1996). Their stand dynamics are less influenced by different storm regimes. These assumptions are also in line with those from other studies of beech: storms and windthrow are considered to be more important factors in the North-western European lowlands compared to Continental beech forests, triggering the stand dynamics in these forests (Koop and Hilgen, 1987; Pontailler et al., 1997; Parviainen et al., 2000; Christensen et al., 2005; Vandekerkhove et al., 2005). This conclusion may however need some further perspective (see below). For the ratio of dead wood to the total aboveground biomass, the range on this figure was very wide (1.4 to 90 %). This is explained by the fact that in the event of larger disturbances, and especially in stand-replacing disturbances, strong increases in dead wood biomass are combined with corresponding losses of living biomass. The median value relates to overall average figures in stands without large disturbances and reflects the slow and steady increase of dead wood amounts after introduction of non-intervention. After two to three decades of non-intervention, the average figure reaches 8.9% of TAB. This is already quite high, knowing that most sites took of at levels under 2%, but still lower than the 15-30% of dead wood characteristic for primary old-growth forests (Korpel', 1997; Saniga and Schütz, 2001a, Christensen et al., 2005). This is fully in line with the conclusion for net accumulation of dead wood. The reserves in this study are only halfway on their succession towards natural levels of both absolute and relative dead wood amounts.

2.5.3 Ratio of lying dead wood volume to the total dead wood volume: just a matter of time

The ratio of lying dead wood volume to the total dead wood volume was specific to tree genus only and was not significantly influenced by geographic location and storm incidence. These findings are contrary to the conclusions of Christensen et al. (2005). In the beech forests this ratio was quite constant at about 75 % irrespective of the period of time of non-intervention and geographical location. Typical values from similar studies in primary old-growth beech forests also show a ratio of between 75 and 85% (Korpel', 1995; 1997; Meyer, 1999; Bobiec, 2002; Meyer et al., 2003). In Central European sites, the majority of the beech trees die standing (especially due to fungal attacks), but fall quite soon after and subsequently decay on the forest floor (Korpel', 1992; Borrmann, 1993; Peterken, 1996; Schmaltz and Lange, 1999; Saniga and Schutz, 2001a; von Oheimb et al., 2007). In North-western Europe, it is reported that most beech are windthrown while still alive (and vigorous) (Mountford, 2004; Vandekerkhove et al., 2005). However, this difference is not reflected in the ratio of lying dead wood volume in North-western Europe when compared to Central Europe. The fact that trees die standing and topple over afterwards, or are blown down while still alive does not significantly influence this ratio. It is primarily determined by the total time of decay and the proportion of this time that is related to standing trees before they fall over. Trees that died standing, most often fall over within one decade (Korpel', 1992; Schmalz and Lange, 1999; Von Oheimb et al., 2007) and the total decay time for beech is estimated at 25 to 50 years depending on site conditions (Koop, 1981; Korpel', 1995; Saniga and Schutz, 2001a; Müller-Using and Bartsch, 2003; Christensen et al., 2005). In beech, the lying status in this total decay process thus takes on average four times longer than the standing status, resulting in this long term average ratio of 75-80%. A severe storm event may in one day topple the equivalent of what would normally fall over a 5 year period, resulting in erratic pulses of lying deadwood (Peterken, 1996). This may lead to a temporary distortion of the ratio of lying to total wood volume in the short to medium term, but will not alter this ratio in the long run. Christensen et al. (2005) however obtained different lying to total dead wood ratios for montane versus lowland beech forests. This difference may not be related to the beech trees per se, but may be explained by the presence of an important proportion of large dead (standing) fir trees (*Abies alba*) in the montane beech forests. Indeed Saniga and Schutz (2001b) reveal that 75 to 95% of standing dead wood in the primary old-growth forests of Badínsky and Dobročský prales consists of fir. If we disregard the fir trees and only consider the beech, the recorded ratios are indeed comparable in both regions and in line with our results.

In primary old-growth oak sites (Korpel', 1995; 1997; Bobiec, 2002) the ratio of lying to total dead wood volume is also comparable to that of beech forests (75-80%), and higher compared to values in this study where a steady increase of this ratio occurred, rising from less than 50 % in recently assigned strict forest reserves to 75% in long-established sites. The effect of geographic location was not significant with respect to lying versus standing deadwood volume. In oak stands the large majority of the trees die standing (Peterken, 1996). Root anchorage and the slow, gradual decay process mean that standing trees take several decades to fall over. Trees of middle to large diameters, with a high amount of heartwood may take >150 years before decay is complete (Schowalter et al., 1998). Hence, also the oak trees that died standing will have undergone at least 80% of their decay process in the lying status, resulting, in the longer term, in a similar ratio as obtained for beech stands. In the more recently assigned unmanaged oak forest reserves, the majority of the dead wood consists of standing trees. After several decades these trees start to fall over, initially the smaller trees and latterly the mature trees. Although the recruitment ratio of standing versus lying dead wood remains constant, the proportion of lying dead wood will increase, as the standing dead trees accumulate on the forest floor. This is in line with the results of our model that shows a steady increase of the ratio of lying to total dead wood volume for oak as a function of the length of time of non-intervention.

2.5.4 Large scale dynamics; a regional effect or otherwise ?

The disturbance regime in temperate deciduous forests is characterised by a combination of frequent small-scale disturbance events caused by natural senescence, competition, disease, fungal attacks, drought, and occasional stand replacing disturbances predominantly caused by storms (Leibundgut, 1978; 1982; Průša, 1985; Koop and Hilgen, 1987; Korpel', 1995; 1997; Mountford et al., 1999; Tabaku and Meyer, 1999; Emborg et al., 2000; Bobiec, 2002; Meyer et al., 2003; Christensen et al., 2005). In the absence of large disturbances the death of individual trees or small groups of trees is the principle form of natural disturbance providing a continuous and constant but limited supply of dead wood of different size and decay categories (Korpel', 1995; Peterken, 1996; Saniga and Schutz, 2001a; Standovár and Kenderes, 2003; Hahn and Christensen, 2004).

Fluctuations and variability in dead wood recruitment appears to be significantly higher for lowland and submontane secondary old-growth forests in North-western Europe when compared to montane sites in Central Europe. This is often related to the more frequent storm events and windthrows in Western European lowlands resulting in pulses of dead wood accumulation (Koop and Hilgen, 1987; Pontailler et al., 1997; Parviainen et al., 2000; Mountford, 2001; Christensen et al., 2005; Vandekerkhove et al., 2005). This study suggests to support this observation: in lowland and submontane regions there is a gradient in dead wood fluctuation and accumulation rate in beech sites coinciding with a gradient in frequency of severe storm events. However, recent analyses of gap size in unmanaged beech forest reserves throughout Europe, show little differences in dynamics between regions; in both montane and lowland beech forests small gaps are the rule with gaps of over 1000 m² being the exception (Mountford, 2001). Over the past few years Central European lowland and montane sites were also subjected to large storm events (i.e. 1999 and 2007). These are not reflected in the dataset as most measurements were taken before these storms. The incidence of severe storm events and larger windthrows have increased not only in North-western but also in Central Europe (Steinfath, 2007; Diaci and Zeibig 2001; Roženbergar et al., 2003; Vrška, pers. comm.). If we disregard the exceptional windthrow records from the UK and include new windthrow records from Central Europe, regional differences become less obvious. Stochasticity and stand age structure related to stand management history are probably more likely to explain the occurrence of large disturbances than regional differences in windstorm events (Vandekerkhove et al., 2005; Von Oheimb et al., 2007).

Primary old-growth montane forests of Central Europe are characterised by a relatively stable age and size distribution (inverse J-distribution or rotated sigmoid curve) and a balanced, long term constant proportion of the different developmental phases (Korpel', 1995; Peterken, 1996; Saniga and Schutz, 2001a; Standovár and Kenderes, 2003; Hahn and Christensen, 2004; Westphal et al., 2006). Most of the strict forest reserves in the North-western and Central European lowlands originate from relatively even-aged stands, resulting from regeneration cohorts and abandoned old wood pastures (Koop, 1981; Koop and Hilgen, 1987; Koop, 1989; Peterken, 1996; Mountford et al., 1999; Schmalz and Lange, 1999; Emborg et al., 2000; Vandekerkhove et al., 2005; Meyer et al., 2006; von Oheimb et al., 2007). They have a more bell-shaped or two-peaked age and size class distribution of the dominant tree layer, with disproportional fractions of the developmental stages (Smaltz and Lange, 1999; Emborg et al., 2000; Vandekerkhove et al., 2005; Meyer et al., 2006; von Oheimb et al., 2005; 2007). When they have average ages of 100-150 years, mortality and dead wood input is often low. When average age reaches 200 to 300 years unnaturally high proportions of senescent trees may be present and stands could begin to collapse with mortality and dead wood accumulation rates becoming much higher than average (Van den Berge et al., 1990a; Vandekerkhove et al., 2005; Von Oheimb et al., 2005; 2007; but see chapter 3). At this stage, these even-aged stands may attain even higher amounts of dead wood than primary old-growth forests (Mountford, 2002; Von Oheimb et al., 2005). This is subsequently characterised by a larger scale rejuvenation stage , where dead wood accumulation is minimal and the total amount of dead wood declines again. In secondary old-growth forests, age structure rather than geographical location will almost certainly determine future small or large gap dynamics. Effects of past management are likely to survive for 200 years or more in the size- and age-distribution of the trees (Peterken, 1996). This undulating process may even continue for several generations and still be detected after 500 years or more (Von Oheimb et al., 2007). Koop (1989) linked rejuvenation waves in the reserve of La Tillaie in Fontainebleau to the last clearcut that occurred in this area, dated in the 14th century. The theoretical model of dynamic steady-state over larger areas might not be realised in most of the secondary old-growth forests even after many centuries of non-intervention. Instead, an undulating sequence of rejuvenation cycles and dead wood pulses could occur.

Sehet die Halle, wie stolz sie sich hebt,
Stolz zu der Bläue des Himmels aufstrebt;
Riesige Buchen, mit Tannen gepaart,
Stehen als Säulen der edelsten Art,

Und als ein Kuppeldach, luftig und weit,
Wölbt sich der Wipfel laubgrünendes Kleid.
Wandelt zur Lichtung der Höhe empor!
Das ist der Waldesbasilika Chor:
(...)
Stimmet die Lauten und Zimbeln nun rein,
Vögel im Laubversteck, fallet mit ein,
Schalle ernstkräftig, du Waldespsalm, auf,
Wirble mit Weihrauch zum Himmel hinauf:
Ehre und Preis sei dem Bauherrn der Welt,
Der sich als Tempel den Wald hat bestellt!

Victor von Scheffel (1826-1886),
Frau Aventiure – Kapitel 10: „Waldpsalm“ (1863).

„Es sind die uralten Baumriesen, wie sie hie und da vereinzelt stehen in Wald und Feld, die ob sie nun in vollem frischen Wuchse oder nur mehr als morsche Ruinen die alten Glieder im Lichte der Sonne wiegen, mit Bewunderung von dem betrachtet werden, der nicht nur die ältesten Lebewesen der Natur, der auch lebende Zeugen einer großen Vergangenheit in ihnen erblickt.

Friedrich Stützer,
Die größten, ältesten oder sonst merkwürdigen Bäume Bayerns in Wort und Bild, München (1900)

Chapter 3: Characteristics of Very Large Trees in secondary old-growth forests: a case study from the SFR 'Joseph Zwaenepoel', Sonian Forest

---

After: Vandekerkhove, K., Vanhellemont, M., Vrška, T., Meyer, P., Tabaku, V., Thomaes, A., Leyman, A., De Keersmaeker, L. & Verheyen, K., 2018. Very large trees in a lowland old-growth beech (Fagus sylvatica L.) forest: Density, size, growth and spatial patterns in comparison to reference sites in Europe . Forest Ecology and Management 417: 1-17.

3.1 Abstract

The frequent occurrence of very large trees (diameter at breast height DBH ≥ 80 cm) is a typical element of both primary and secondary old-growth forests. We analyzed the characteristics of very large trees in one of the few stands of lowland old-growth beech forest in Northwestern Europe, regenerated around 1775 and left unmanaged since 1986. We examined their density, diameter range, increment, mortality rate and spatial distribution, based on repeated full dendrometric surveys. In order to evaluate the results, we compared them to original datasets from primary and secondary old-growth beech forests in Europe, and an extensive reference table, compiled from inventories and literature.

In our study site, the density of very large trees increased from 31.5 to 34.3 trees ha^{-1} over the last 25 years, reaching a median DBH of 97 cm (mean 98.9), with the largest tree attaining a DBH of 159 cm. Although the trees were over 240 years old, they still showed an average DBH increment of 4.75 mm. year^{-1} and a low mortality rate (0.89%. year^{-1}), indicating that they were still vital. These figures are remarkably high compared to other old-growth beech forest reference sites, where the density of very large trees generally varies between 5 and 20 trees ha^{-1} (median value 13.1), with a median diameter of 85 to 90 cm and maximum DBH for beech trees rarely exceeding 100 to 130 cm.

The regular spatial distribution pattern of the very large trees in the studied stand clearly differed from a typical old-growth stand, in which very large trees are

randomly distributed. Over the last 25 years though, because of random mortality and ingrowth, the spatial distribution gradually became more random.

The extraordinary densities and sizes of the very large trees in our study site can be explained by the favorable climate and site conditions that promote high increments, in combination with the former management interventions of tending and thinning that resulted in continuous non-suppressed growth. Although derived from a very specific case with particular conditions, our observations may be relevant to other beech forests, as they tend to reset certain baseline assumptions for tree size and longevity potential of beech in Northwestern Europe.

3.2 Introduction

Old-growth forests are defined as forest sites and stands that have developed a high degree of naturalness. According to Frelich and Reich (2003), old-growth forests can be subdivided in ‘primary old-growth’, being old-growth forests whose dynamics are driven exclusively by natural processes while human impacts are absent, and ‘secondary old-growth’, being previously managed forests that have developed old-growth features after decades of (intentional or non-intentional) non-intervention (Piovesan et al., 2008; Ziaco et al., 2012). Next to large quantities of dead wood, the frequent occurrence of large old trees is a prominent structural characteristic of old-growth forests (Bobiec, 2002; Burrascano et al., 2013; Greenberg et al., 1997; Ziaco et al., 2012). Very large trees are therefore among the features most frequently used as basic descriptors of natural or old-growth forests (Nilsson et al., 2002; Von Oheimb et al., 2005; Wirth et al., 2009; Ziaco et al., 2012).

Several definitions and size thresholds are used to define very large trees. In this study, we applied the frequently used threshold of 80 cm DBH for very large trees (further shortened to ‘VLT’), also called ‘giant trees’ or ‘oversized trees’ (Bílek et al., 2011; Burrascano et al., 2008; Heiri et al., 2011; 2012; Hobi et al., 2014; Kucbel et al., 2012; Meyer et al., 2003; Petriţan et al., 2015; Von Oheimb et al., 2005; Zenner et al., 2015). In forestry, 70-80 cm often is the maximum target diameter (e.g. Schütz, 2006), so that larger trees are rarely occurring in commercially managed forest stands.

Already in ancient times, VLT were missing in lowland European forests managed for wood production (e.g. Vandekerkhove et al., 2009; 2011). They only occurred in hunting reserves, deer parks and wood pastures. In many regions their numbers are still declining (Lindenmayer et al., 2012) although in other areas, they are more and more protected and integrated in forest management as their recreational and ecological value is better known and appreciated (e.g. Fedrowitz et al., 2014; Gustafsson et al., 2012). Still, the numbers of VLT are low. In Germany, the density of VLT in forests was 66 per 100 ha in 2012 (Thünen-Institut, 2017), an increase of 50 % compared to 2002 (Kroiher and Bolte, 2015). In northern Belgium, a similar density of 65 VLT per 100 ha was registered (Vandekerkhove et al., 2011). In Switzerland, VLT density is somewhat higher, with 120 VLT per 100 ha in the beech-dominated colline and submontane height range, twice as high as during the previous survey ten years before (Brändli et al., 2010).

VLT fulfill a wide range of ecosystem services. They occupy a revered position in the human psyche (Lindenmayer, 2016), and specific aesthetic, social and cultural values are assigned to them (Blicharska and Mikusiński, 2014). Several studies indicated that the general public has a clear preference for forest landscapes and stands containing large trees and this preference increases with increasing tree size and advancing stage of stand development, thus representing a higher recreational value (e.g. Edwards et al., 2012; Gundersen and Frivold, 2008; Ribe, 1989). VLT have also been identified as essential elements for biodiversity conservation (e.g. Lindenmayer et al., 2012; Moning and Müller, 2009; Nilsson et al., 2002). They show a higher incidence and diversity of tree-related microhabitats than smaller trees (Larrieu and Cabanettes, 2012; Larrieu et al., 2014; 2018; Paillet et al., 2017; Regnery et al., 2013; Vuidot et al., 2011; Winter and Möller, 2008), and these microhabitats provide specific microclimatic conditions and substrates to a wide range of specialized species or species assemblages (Larrieu et al., 2014; 2018; Paillet et al., 2017). Large old trees also show a higher incidence of rare epiphytic bryophytes and lichens (Brunet et al., 2010; Fritz et al., 2009; Moning and Müller, 2009). Finally, VLT also have a major influence on hydrological regimes, nutrient cycles (Lindenmayer, 2016) and carbon sequestration. For instance, old-growth forests are important carbon sinks (Knohl et al., 2003; Luyssaert et al., 2008), and a large proportion of the above-ground biomass in old-growth forests is concentrated in VLT (Brown et al., 1997).

Several studies have been published on old-growth beech forests in the submontane regions of Central and Southern Europe, including information on the size range, density and longevity of beech trees in these old-growth stands (e.g. Di Filippo et al., 2015; Hobi et al., 2014; Meyer et al., 2003; Piovesan et al., 2005a). However, little is known about the performance of VLT in lowland beech forests. We analyzed the presence and characteristics (density, diameter range and increment, mortality rate and spatial distribution) of VLT in one of the rare old-growth beech forest stands in the lowlands of Northwestern Europe, over a time period of 25 years. As reference values for lowland beech forests are scarce (e.g. Von Oheimb et al., 2005), we compared our data to a set of primary and secondary, lowland and submontane old-growth stands in Central and Southeastern Europe for which equivalent datasets were available. Finally, we supplemented the study and comparison sites with literature data in a comprehensive reference table on VLT in old-growth beech forests in Europe.

3.3 Material and methods

3.3.1 Study site

The study site is located in the center of the Sonian forest (50°75’ N, 4°39’ E) (site 51 on the map in Fig. 1.6). This forest complex covers an area of 4400 ha and is located 10 km south of Brussels, Belgium. It contains over 400 ha of old beech stands (>200 years old) and more than 25,000 VLT, mainly beech (Vandekerkhove et al., 2011). It can therefore be considered one of the most important hotspots for VLT in Northwestern Europe. Many of the VLT are located in patchy remnants of old stands or in avenues. The study site contains one of the largest remaining old stands (17 ha), known as ‘Kersselaerspleyn’. It originates from a beech stand that was regenerated around 1775 and then regularly thinned with final fellings only performed in two small patches in the east and upper northwest corner of the stand (replanted with beech in 1921 and 1967). The 10.06 ha study area was selected in the central area of Kersselaerspleyn, excluding a 50 m buffer zone near the stand borders and the two artificially regenerated patches. The stand has been left unmanaged since 1983 and became an official strict forest reserve in 1995, enlarged to its current size of 230 ha in 2010 (‘Forest Reserve Joseph Zwaenepoel’). In July 2017, this forest reserve was included in the UNESCO World Heritage site ‘Primeval Beech Forests of the Carpathians and Other Regions of Europe’. The study site is located on a slightly undulating flat area, with an altitude ranging from 100 to 120 m asl. The substrate consists of tertiary calcium-rich sandstone and flint stone, covered with a 3-4 m thick layer of quarternary niveo-aeolic loess deposits of the Weichselian glaciation. The upper layer of the loess deposit is lessivated and moderately acidic (pH H2O 4.0 - 4.5); deeper layers are more saturated with base cations. This results in productive forest soils (FAO: Luvisols and Podzoluvisols), which is reflected in the canopy height of the tree layer: old beech stands reach canopy heights of 45 m and more. The climate is characterized by a mean annual temperature of 10.5°C and an annual precipitation of 852 mm. Mean temperatures in January and July are 3.3°C and 18.4°C. The vegetation consists of Atlantic acidophilous beech forest (Milio-Fagetum sensu Noirfalise, 1984; European habitat type 9120, EUNIS-code G1.62). The ground vegetation is scarce and dominated by *Pteridium aquilinum* and *Milium effusum*. *Oxalis acetosella, Convallaria majalis* and *Anemone nemorosa* scarcely occur.

3.3.2 Data collection and processing

Full dendrometric surveys of all trees in the study area were made in 1986, 2001 and 2011 (Van den Berge et al., 1990a; 1990b; Vandekerkhove et al., 2005). The positions of all trees relative to reference points were registered using a total station in 1986 and 2001 and a Laser Rangefinder and Mapstar Digital Compass incorporated in the Fieldmap hardware configuration (http://www.fieldmap.cz) in the 2011 survey. For every tree, tree status (alive/dead), species and diameter at breast height (DBH) were recorded. In 1986, all trees with a DBH ≥ 30 cm were included in the inventory, in 2001 and 2011 the minimum DBH was 10 cm, but for comparative reasons the diameter threshold of 30 cm was also implemented to the other surveys in the data analysis. During the first interval, two heavy windstorms occurred in February 1990, with an important impact on mortality at the site.

Therefore the trees that died during and within 6 months after the heavy windstorms were additionally registered in 1991. First, for the VLT (DBH ≥ 80 cm), we calculated the density, diameter distribution and share in the total basal area for each of the three surveys. The basal area share of VLT is often applied as an important indicator of old-growth (e.g. Brown et al., 1997). As all trees have been positioned and can be identified over time, we could also asses the diameter increment and mortality of the individual trees over the subsequent surveys, and calculate the basal area increment (BAI) and decadal mortality and relate them to original tree size at the first survey. Second, we tested whether the trees in the study site were randomly distributed or tended towards a more regular or more clustered spatial distribution by analyzing the distribution patterns of the trees for the different surveys. Fig. 3.1 gives a theoretical visualisation of random (Poisson) vs. regular (uniform) and clustered (clumped) spatial distribution patterns.

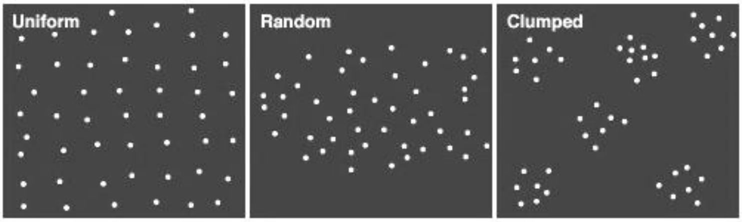


Fig. 3.1 theoretical representation of spatial distribution patterns (figure source: Encyclopaedia Britannica, 2006).

According to Wolf (2005), the change in spatial distribution patterns is a powerful indicator for the development of a forest stand towards a more natural stand structure. We calculated the aggregation index R of Clark and Evans (1954) with ‘cdf’ edge correction and an estimate of the L function, a transformation of Ripley’s K function (Besag, 1977; Ripley, 1976), with isotropic edge correction (Ohser, 1983; Ripley 1988) in R (version 4.3.4, R Development Core Team, 2019) using the spatstat library (Baddeley et al., 2015). In order to test the spatial patterns of the trees at the study sites against a hypothetical pattern of complete spatial randomness, we produced p-values for the Clark-Evans test of aggregation based on 99 Monte Carlo simulations and calculated pointwise simulation envelopes for the L function (based on 99 simulations, significance level 5 %). The spatial analysis was performed separately for all trees with DBH ≥ 30 cm and for the VLT (DBH ≥ 80 cm). The aggregation index R was also calculated for the trees that died during the two intervals to check for spatial patterns in mortality.

3.3.3 Comparison sites

The additional datasets we used as a comparison for the forest stand at our study site concerned similar full surveys in large sampling plots in beech-dominated strict forest reserves in Germany, Albania and the Czech Republic (Table 3.1) . These comparison sites covered a wide range of old-growth beech forest types including both lowland and submontane sites and the complete old-growth spectrum, from primary to secondary old-growth, including one site (Limker Strang) originating from a regularly managed beech stand, which has been left unmanaged only for a few decades, and can still be considered a mature stand rather than old-growth. The German and Albanian reserves are strongly dominated by beech (> 90 % of the basal area); the Czech reserves involve mixed beech-fir and beech-spruce-fir forest (with beech > 50 % of the basal area). For detailed site and stand descriptions of the comparison sites, we refer to Janík et al. (2014, 2016), Král et al. (2014), Meyer et al. (2003) and Šamonil et al. (2013).

Table 3.1. Description of the forest stand at the study site (bold) and the eight comparison sites that were used to pair with the studied stand

Site	**Country**	**Description**	**Survey**	**Plot size (ha)**	**Reference**
Kersselaerspleyn	BE	Secondary old-growth beech forest	1986 2001 2011	10.06	Van den Berge et al. 1990 Vandekerkhove et al. 2005
Limker Strang	DE	Mature to secondary old-growth beech forest	1999	9.81	Tabaku, 2000
Heilige Hallen	DE	Secondary old-growth beech forest	1999	13.57	Tabaku, 2000
Mirdita	AL	Primary old-growth beech forest	1999	5.00	Tabaku, 2000
Puka	AL	Primary old-growth beech forest	1999	3.64	Tabaku, 2000
Rajka	AL	Primary old-growth beech forest	1999	6.00	Tabaku, 2000
Razula	CZ	Primary old-growth beech-fir forest	1972 1995 2009	10.00	Průša, 1985 Vrška et al. 2001 Janík et al. 2014
Salajka	CZ	Primary old-growth beech-fir forest	1974 1994 2007	10.00	Průša, 1985 Vrška 1998 Janík et al. 2014
Žofín	CZ	Primary old-growth beech-fir-spruce forest	1975 1997 2008	10.00	Průša, 1985 Král et al., 2014 Janík et al. 2016

A detailed overview of basic dendrometric data for the stands of the study and comparison sites, including stem density, basal area, living stock and dead wood amounts for the different tree species is presented in Annex 2.

Full surveys of all trees were made once (Germany, Albania) or three times (Czech Republic). The species, DBH and status (alive/dead) were measured. Tree position coordinates (x, y) were recorded using a 50 m x 50 m grid as a reference (Germany and Albania; Meyer et al., 2003), tripod-based theodolites (Czech Republic in the 1970s and 1990s) or Field-Map (Czech Republic in the years 2000). We applied the 30 cm DBH threshold from our studied stand to the trees at the comparison sites and included the full plot of the German and Albanian sites and a randomly selected 10 ha plot for each of the Czech sites (from an original survey of 25-70 ha), to be in line with the plot sizes of the other sites. We performed similar data analyses for the VLT (density, size range and share of basal area) and the spatial patterns of VLT and all trees over 30 cm DBH. All comparative statistics were done in R3.4.2.

3.3.4 Compiled reference table

Finally, we compiled a comprehensive table with reference data on density and maximum recorded sizes of VLT in beech-dominated old-growth forests from our study site, the comparison sites and an extensive set of reference sites from literature. We searched the literature using a Web-of-Science search combining ‘old-growth’, ‘natural’ ‘virgin’ ‘old’ and ‘pristine’ with ‘beech’ and ‘*Fagus sylvatica’*. Additional references were derived from reference lists in the retrieved papers and standard works on European strict forest reserves (Brang et al., 2011; Korpel', 1995; Leibundgut, 1993; Průša, 1985). We involved both primary and secondary old-growth beech-dominated forests all over Europe. Only stands in which beech covered over 50 % of the basal area or growing stock were admitted, including both pure beech forests and mixed forests of beech-silver fir (*Abies alba* Mill.) and beech-oak (*Quercus robur* L. and *Quercus petraea* Liebl.). Basic information on climatic conditions (mean average temperature and precipitation, elevation) was added when available in the original reference. VLT density figures and maximum diameters were copied directly from the reference papers when available, or were approximated from stand diameter distribution tables and figures.

3.4 Results

3.4.1 Density, diameter distribution and diameter range

At the study site, the density of VLT (DBH ≥ 80 cm) in the forest stand amounted to 31.3 trees ha^{-1} in 1986, and further increased to 33.5 in 2001 and 34.3 trees ha^{-1} in 2011. The range of diameters of the VLT was wide and the mean DBH increased from 92.7 cm over 96.1 to 98.9 cm. The median DBH also increased from 90 over 94 to 97 cm. Several trees reached a DBH over 140 cm, with the largest living tree attaining a DBH of 159 cm in 2011.

The diameter distribution of the stand in 1986 showed a bell-shaped distribution. Over the 25 year period, the bell shape shifted towards higher diameters and became wider and lower. A strong increase in the lower diameter classes over the last decade, due to ingrowth of young trees up to the threshold diameter, caused an overall shift to a bimodal distribution pattern (Fig. 3.2).

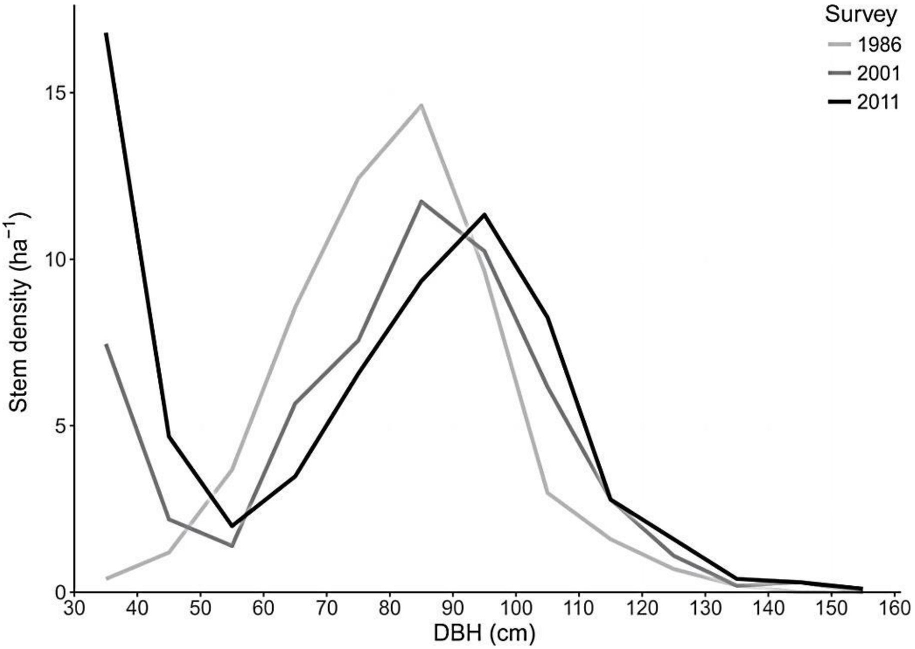


Fig. 3.2 Diameter distribution of the trees with a diameter at breast height (DBH) of 30 cm and more (expressed in stem density per ha) at the study site (Kersselaerspleyn, BE) for the three surveys

When confronting the most recent diameter distribution at the studied stand with the stands at the comparison sites, clear differences can be observed (Fig. 3.3). In the lowest diameter class (10-20cm DBH), two of the Czech primary old-growth sites show high figures around 300 trees ha^{-1}, while the other primary sites, together with Kersselaerspleyn show comparable densities around 100 trees ha^{-1}. The secondary old-growth stand of Limker Strang shows very low figures for the lowest diameter classes. (For Heilige Hallen, a threshold diameter of 35 cm was applied, so no data are available for the lower diameter classes.) In the larger diameter classes, all Albanian stands show steadily decreasing densities, while the Czech stands and Heilige Hallen show a sigmoidal pattern with lower figures at mid-size diameters (40-60 cm) and a second culmination between 60 and 80 cm DBH. All comparison stands show low and steadily declining figures above 80 cm DBH, while Kersselaerspleyn shows an apparent second peak around 100 cm DBH. Several stands have already reached their maximum tree size at this diameter. Limker Strang clearly bears the legacy of its former intensive management, showing a totally divergent bell-shaped pattern with its culmination around 60 cm DBH, and a maximum tree size below 90 cm DBH.

For VLT, the diameter range of the stand at the study site was significantly higher than for the comparison sites (Wilcoxon rank sum test with continuity correction in R; $p<0.01$) and also median and quartile diameter values were higher (Fig. 3.4).

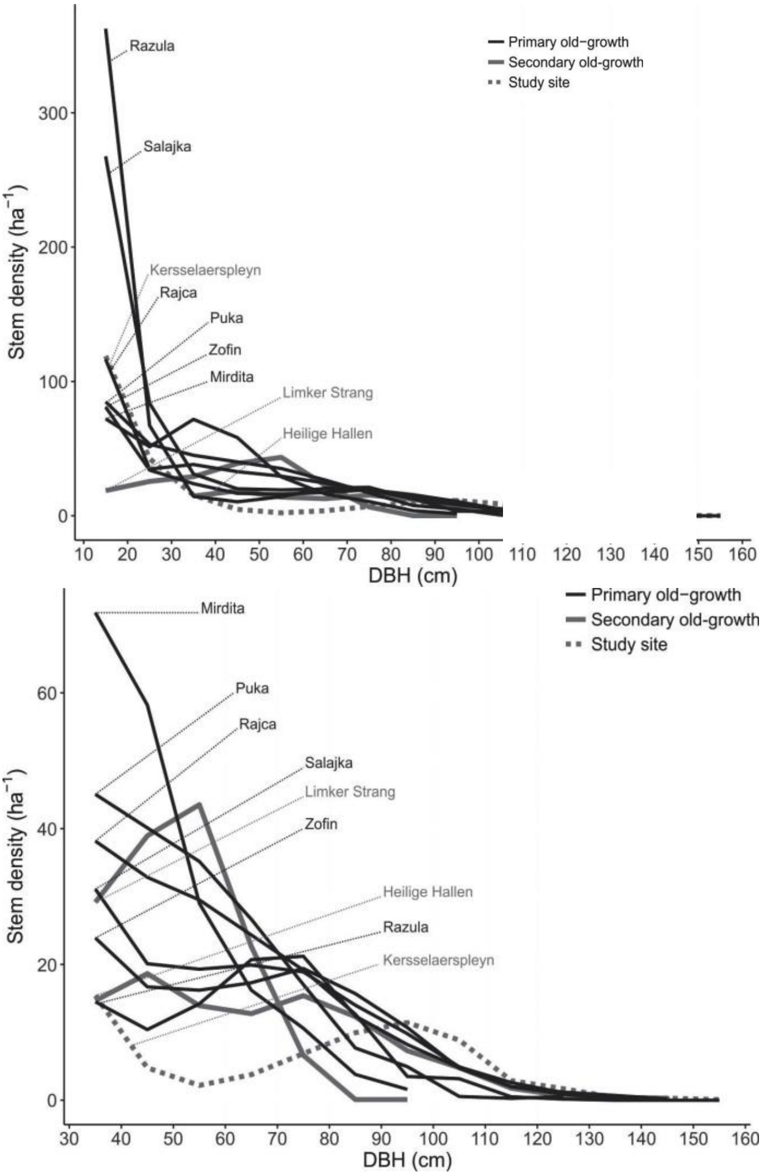


Fig. 3.3 Diameter distribution (expressed in stem density per ha) at the studied stand and the comparison stands applying DBH thresholds of 10 cm (above) and 30 cm (below). For stands with repeated survey data, only the most recent survey is shown.

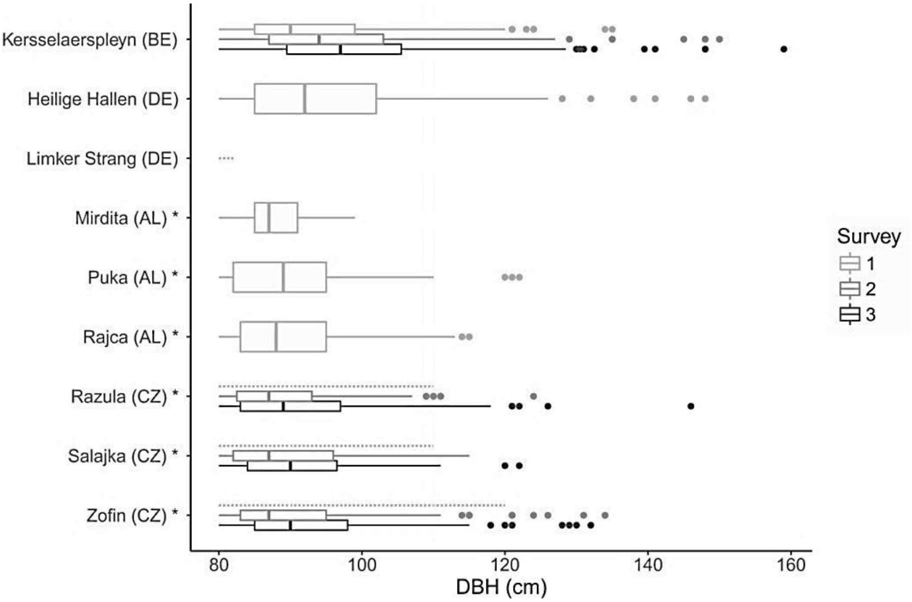


Fig. 3.4 Boxplots representing the diameter range of very large beech trees (DBH ≥ 80 cm) at the study site (Kersselaerspleyn, BE) and the eight comparison sites (* indicates the primary old-growth forests). For Limker Strang and the first surveys in the Czech sites, only a range of DBH is indicated (dotted lines) as there were too few VLT for meaningful boxplots.

Almost half of the VLT in the studied stand were over 100 cm DBH at the time of the 2011 survey, whereas the median diameter in the comparison stands varied between 85 and 90 cm. The upper quartile value and the outliers, indicating the largest trees in the surveys, were also notably higher in the study stand than in the comparison stands. The share of VLT in the stand basal area was much higher in the study stand (70-80 %) than in the comparison stands (Table 3.2). In the primary old-growth forests, 24-52 % of the basal area were VLT, except for Mirdita (9.5 %). The secondary old-growth stand of Heilige Hallen showed an intermediate value (56.3 %). In the forest reserve of Limker Strang, the share of VLT in the basal area was less than 2 %.

Across primary and secondary lowland to high-elevation old-growth beech forests in Europe, the density of VLT ranged from 0 to 36 trees ha^{-1} (Table 3.3). The mean density was 13.9 trees ha^{-1} (standard deviation (SD) 9.1), the median 13.1 trees ha^{-1}, and the lower and upper quartiles 5 and 20 trees ha^{-1}. The mean density of very large beech trees (excluding large fir, spruce and oak in the mixed stands) was 12.0 trees ha^{-1} (SD 8.7), with median value of 11.1 trees ha^{-1} and quartile values of 5 and 16 trees ha^{-1}.

Table 3.2 Total basal area (BAtot) based on all trees in the plot (threshold DBH = 30 cm) and share of the basal area covered by very large trees (BA_{VLT}); stands marked with * are primary old-growth stands; the stand in bold is at the study site.

Site	Survey	BA_{tot} (m².ha^{-1})	BA_{VLT} (%)
Kersselaerspleyn	**1986**	**28.4**	**70.7**
	2001	**30.6**	**80.0**
	2011	**31.3**	**79.9**
Heilige Hallen	2000	24.4	56.3
Limker Strang	2000	30.2	1.4
Mirdita*	2000	37.2	9.5
Puka*	2000	45.4	24.1
Rajka*	2000	43.4	31.5
Razula*	1972	25.7	30.1
	1995	26.8	44.3
	2009	27.0	52.0
Salajka*	1974	26.2	47.1
	1994	24.3	39.6
	2007	27.0	37.8
Žofín *	1975	35.1	46.8
	1997	34.3	46.7
	2008	30.4	48.7

Excluding the three records for Kersselaerspleyn, the average value decreases to 13.0 (11.1 trees ha^{-1} when selecting only beeches). In the high elevation stands (average altitude over 1000 m asl) densities were surprisingly higher than at lower elevation: mean densities of 15.2 trees ha^{-1} were recorded (14.2 including only beech trees - SD 9.4 and 8.7 respectively). The figures for lower elevation stands (up to 500 m asl) were fully in line with the overall figure, attaining 13.7 trees ha^{-1} (SD 11.6) for all tree species and 11.7 trees ha^{-1} including only beech trees (SD 11.7).

Table 3.3. Reference values for the density and size of very large trees (VLT, DBH ≥ 80 cm) in primary and secondary old-growth pure beech and beech-dominated sites in Europe. Sites with * are primary old-growth; the study and comparison stands are indicated in bold. Forest type: Fs = pure beech forests (>90% of basal area) - Fs-Q: mixed stands of beech and oak (*Quercus robur/petraea*) – Fs-Aa: mixed stands of beech and silver fir (*Abies alba*) both with beech>50% of basal area – Elevation range in m above sea level (m asl) - MAT = Mean Annual Temperature – MAP: Mean Annual Precipitation - Density: number of trees ≥80 cm DBH ha^{-1}; for mixed stands separate figures for beech trees only and including other tree species (between brackets). Density figures with + are approximated from stand diameter distribution tables and figures - Dmax=maximum reported DBH for beech (and other tree species between brackets); Hmax.= maximum reported height for beech.

Site	**Coun-try**	**Forest type**	**Elevation (m asl)**	**MAT (°C)**	**MAP (mm)**	**Density VLT ha^{-1}**	**D_{max} (cm)**	**H_{max} (m)**	**Reference**
Kersselaerspleyn (1986)	BE	Fs	100-120	10.5	860	31.3	135	49	this study
Kersselaerspleyn (2001)	BE	Fs	100-120	10.5	860	33.5	150	49	this study
Kersselaerspleyn (2011)	BE	Fs	100-120	10.5	860	34.3	158	47	this study
Heilige Hallen	DE	Fs	120-140	7.9	590	19	148	49	this study; Knapp and Jeschke, 1991
Limker Strang	DE	Fs	380-420	7.3	1030	0.7	93	-	this study
Mirdita *	AL	Fs	1370-1430	6	2200	5.4	99	32	this study; Meyer et al., 2003
Puka *	AL	Fs	1370-1430	6	2200	15.4	122	37	this study; Meyer et al., 2003
Rajka *	AL	Fs	1300-1500	6	2200	19.3	115	38.5	this study; Meyer et al., 2003
Žofín (1975) *	CZ	Fs-Aa	735-829	6.2	866	15.4 (26.0)	120 (140)	41 (47)	this study; Průša, 1985
Žofín (1997) *	CZ	Fs-Aa	735-829	6.2	866	16.5 (23.0)	134 (145)	46 (49)	this study; Král et al., 2014
Žofín (2008) *	CZ	Fs-Aa	735-829	6.2	866	17.8 (21.2)	132 (146)	45 (53)	this study; Janík et al., 2016
Salajka (1974) *	CZ	Fs-Aa	711-820	6.2	1140	4.1 (19.3)	120 (190)	42 (51)	this study; Průša, 1985
Salajka (1994) *	CZ	Fs-Aa	711-820	6.2	1140	6.7 (14.2)	115 (142)	38 (52)	this study; Vrška, 1998
Salajka (2007) *	CZ	Fs-Aa	711-820	6.2	1140	7.5 (14.3)	122 (135)	42 (55)	this study; Janík et al., 2014
Razula (1972) *	CZ	Fs-Aa	660-810	6.5	1120	4.5 (13.6)	110 (125)	45 (53)	this study; Průša, 1985
Razula (1995) *	CZ	Fs-Aa	660-810	6.5	1120	10.3 (17.8)	124 (129)	48 (56)	this study; Vrška et al., 2001
Razula (2009) *	CZ	Fs-Aa	660-810	6.5	1120	12.4 (19.4)	146 (146)	45 (54)	this study; Janík et al., 2014
Urwald Dobra *	AT	Fs	390-550	7	650	-	150	45	Mayer, 1987

Site	Coun-try	Forest type	Elevation (m asl)	MAT (°C)	MAP (mm)	Density VLT ha^{-1}	D$_{max}$ (cm)	H$_{max}$ (m)	Reference
Polom (1973) *	CZ	Fs-Aa	541-625	7.4	775	9.9 (12.7)	145 (120)	39 (46)	Průša, 1985
Polom (1995) *	CZ	Fs-Aa	541-625	7.4	774	4.9 (8.1)	145 (130)	40 (45)	Vrška et al., 2002
Žákova hora (1974) *	CZ	Fs-Aa	727-806	6.1	780	9.3 (15.2)	140 (120)	35 (47)	Průša, 1985; Vrška et al., 2002
Žákova hora (1995) *	CZ	Fs-Aa	727-806	6.1	780	7.3 (10.4)	110 (130)	37 (49)	Vrška et al., 2002
Stožec-Medvědice (1974) *	CZ	Fs-Aa	845-995	5.6	939	15.9 (23.4)	104 (130)	40 (52)	Průša, 1985; Vrška et al. 2012
Stožec-Medvědice (1998) *	CZ	Fs-Aa	845-995	5.6	939	13.9 (21.8)	125 (130)	42 (55)	Vrška et al., 2012
Mionší (1995) *	CZ	Fs-Aa	823-892	5.2	1207	6.1 (11.1)	110 (130)	37 (56)	Vrška et al., 2000
Öserdö *	HU	Fs	830-900	6.1	896	-	100	47	Kenderes et al., 2008
Valle Cervara (Low) *	IT	Fs	1200-1500	-	1500	10-15	102	-	Di Filippo et al., 2017
Valle Cervara (High) *	IT	Fs	1600-1850	-	1500	10-15	100	30	Piovesan et al., 2005b, 2008
Vallone Cervara *	IT	Fs	1600-1850	10.6	1035	0.4^{+}	105	-	Burrascano et al., 2008
Sasso Fratino *	IT	Fs	1100-1500	9	1750	28^{+}	115	44	Bianchi et al., 2011
Łabowiec reserve *	PL	Fs-Aa	840-960	4.5	1050	10^{+}	107	-	Paluch, 2007
Runcu-Grosi (pure beech) *	RO	Fs	350-600	8.5	850	5^{+}	98	44	Petriţan et al., 2012
Runcu-Grosi (mixed Fs-Q) *	RO	Fs-Q	350-600	8.5	850	4 (7)$^{+}$	102	51	Petriţan et al., 2012
Sinka *	RO	Fs-Aa	850-1350	4.5	1000	15 (27)$^{+}$	113 (124)	45	Petriţan et al., 2015
Kukavica *	RS	Fs	1000-1100	-	-	-	110	-	Westphal et al., 2006
Kopa forest *	SI	Fs	980-1080	9.9	1240	-	110	41	Rugani et al., 2013
Gorjanci forest (1974) *	SI	Fs	990-1150	9.5	1290	13^{+}	115	45	Rugani et al., 2013
Gorjanci forest (2009) *	SI	Fs	990-1150	9.5	1290	23^{+}	115	45	Rugani et al., 2013
Bukov *	SI	Fs	1200-1300				90		Westphal et al., 2006
Hrončokovský grúň *	SK	Fs-Aa	730-1000	5	825	6	92 (141)	47	Holeksa et al., 2009
Kyjov *	SK	Fs	750-780	5.5	975	9	121	35	Kucbel et al., 2012
Havešová *	SK	Fs	575-600	6.5	825	14	117	49	Kucbel et al., 2012
Badín *	SK	Fs	700-850	5.5	900	15	121	45	Kucbel et al., 2012
Badín * (5ha plot) *	SK	Fs	700-850	5.5	900	23	121		Kucbel et al., 2010

Site	Country	Forest type	Elevation (m asl)	MAT (°C)	MAP (mm)	Density VLT ha^{-1}	D$_{max}$ (cm)	H$_{max}$ (m)	Reference
Stužica *	SK	Fs	650-900	4.5	1100	12	110	36	Kucbel et al., 2012
Rožok *	SK	Fs	650-700	6.5	850	18	115.5	45	Kucbel et al., 2012
Raštún *	SK	Fs	650-720	7.5	725	2	92.2	27	Kucbel et al., 2012
Vtáčnik *	SK	Fs	1150-1180	4.5	1000	1^{+}	81.5	30	Kucbel et al., 2012
Dobročský prales *	SK	Fs-Aa	800	4.5	900	16	118 (190)		Nilsson et al. 2003
Borzhava *	UA	Fs	560-740				90		Westphal et al., 2006
Majdan - pure beech plot *	UA	Fs	795	6.1	935	5	100	40	Mauve, 1931
Uholka (core area) 2010 *	UA	Fs	700-800	7.7	1100	23.3	129.9		Zenner et al., 2015
Uholka (core area) 2000 *	UA	Fs	700-800	7	1100	21	132.6		Commarmot et al., 2005
Uholka -sampling plots *	UA	Fs	450-900	7	1100	12	140	53	Hobi et al., 2014
Shyrokyi Luh (sample plots) *	UA	Fs	700-1300	6	1100	8	115		Commarmot et al., 2013
Adenberg	CH	Fs	500			1.96			Heiri et al., 2009; 2011; 2012
Bannhalde	CH	Fs	420			9.82			Heiri et al., 2009; 2011; 2012
Fürstenhalde	CH	Fs				1.75			Heiri et al., 2009; 2011; 2012
Langgraben	CH	Fs	420			0.23			Heiri et al., 2009; 2011; 2012
Strassberg	CH	Fs	480	8.8	1070	0.32			Heiri et al., 2009; 2011; 2012
Tariche Haute Côte	CH	Fs	750	7.8	1228	1.17			Heiri et al., 2012
Voděradské bučiny - plot6	CZ	Fs	345	7.8	623	36	110		Bílek et al., 2011
Voděradské bučiny -plot7	CZ	Fs	345	7.8	623	10	108		Bílek et al., 2011
Serrahn	DE	Fs	100	7.8	593	12.5 (13.3)	120		Von Oheimb et al., 2005
Vilm	DE	Fs-Q	0-50	8.2	570	18 (21)	145	43	Schmalz and Lange, 1999
NWR Gitschger	DE	Fs	600-685	6.5	850		172	38.8	Straussberger, 2003
Suserup Skov	DK	Fs-Q	10-30	8	644	10-15(20)*	126 (190)	41	Emborg et al., 2000
32 mature stands in NW Spain	ES	Fs	160-1400	6-13.5	1200-2000	14	130		Merino et al., 2007
Caviedes	ES	Fs-Q	40-240	14	1200		80 (130)	30	Rozas, 2006
La Tillaie-Fontainebleau-plot1	FR	Fs	140	11	650	14*	110		Koop and Hilgen, 1987

Site	**Coun-try**	**Forest type**	**Elevation (m asl)**	**MAT (°C)**	**MAP (mm)**	**Density VLT ha^{-1}**	**D$_{max}$ (cm)**	**H$_{max}$ (m)**	**Reference**
La Tillaie-Fontainebleau-plot2	FR	Fs	140	11	650	7(11) $^{+}$	110 (160)		Koop and Hilgen, 1987
La Tillaie-Fontainebleau	FR	Fs	140	11	650	9 $^{+}$	165		Bédéneau, 2003
Le gros fouteau-Fontainebleau	FR	Fs	140	11	650	19			Pontailler et al., 1997
Le gros fouteau-Fontainebleau	FR	Fs	140	11	650	7.5 $^{+}$	120 (140)		Bédéneau, 2005
Frankenthal-Missheimle	FR	Fs-Aa	690-1363	4	1600		83 (111)		Closset-Kopp et al., 2006
Grand Ventron	FR	Fs-Aa	720-1200	4	1600		64 (70)	30+	Closset-Kopp et al., 2006
Coppo del Principe	IT	Fs	1500		1500	10-15	95		Alessandrini et al., 2011
Monte Cimino	IT	Fs	950-1050	10.8	1300	25-30 $^{+}$	140	48	Piovesan et al. 2008; Ziaco et al. 2012
Biskopstorp	SE	Fs	50-150	7	1000	0.75 $^{+}$	91		Chursky, 2006
Bjurkärr	SE	Fs	140	7	600	5			Nilsson et al., 2003
Siggaboda	SE	Fs	140-165	6	600-700	1			Nilsson et al., 2003

The largest diameters (up to 190 cm DBH) were all from fir and oak trees intermixed in the mixed beech-dominated stands. For beech, the largest recorded trees at most sites were in the range of 100-130 cm DBH, both at lower and higher elevation. Diameters over 150 cm were exceptional, and only recorded at lower elevations at Dobra (AT), La Tillaie (Fontainebleau, FR) and Gitschger (DE).

3.4.2 Mortality rates and diameter increments

The annual mortality rate of all trees (threshold 30 cm DBH) in the studied stand over the whole survey period (1986-2011) averaged 0.88 %. During the first interval (1986-2001), the annual mortality was 1.27 %, with a higher mortality (3.40 %) for the period 1986-1991 (covering the storm of 1990) and lower mortality (0.47 %) for 1991-2001 (after the storm). For the second interval (2001-2011), the annual mortality was even lower at 0.39 %. The mortality rate of the VLT was not significantly different from the other trees (Chi² test, $p < 0.01$) for the full survey period (0.91 %) and the two intervals (1.29 % for 1986-2001, with 2.23% before the storm and 0.82% after, and 0.46 % for 2001-2011).

Annual diameter and basal area increments are presented in Table 3.4. Significantly higher diameter increments were registered for the VLT compared to the mid-sized trees with DBH 30-80 cm (one-tailed T-test; $p < 0.01$). Both for mid-sized trees (30-80 cm DBH) and for VLT, the increments were significantly lower (one-tailed T-test for paired observations, $p < 0.01$) in the second interval compared to the first interval.

For basal area increment (BAI), this result is even more pronounced.. For the VLT, the basal area increment for the 25 year survey period amounted to 74 cm² year^{-1}, which was significantly higher ($p < 0.01$) than for the 30-80 cm DBH trees (48 cm² year^{-1}). Also for BAI, the increment was significantly lower in the second compared to the first interval.

Table 3.4 Average yearly diameter increment (Δ DBH) (mm year^{-1}) and basal area increment (BAI) (cm² year^{-1}) for trees in different size classes at the study site (Kersselaerspleyn, BE) for the first interval (1986-2001) and second interval (2001-2011) and for the full survey period (1986-2011). The standard deviation is shown between brackets.

DBH	**Δ DBH**			**BAI**		
	1986-2001	**2001-2011**	**1986-2011**	**1986-2001**	**2001-2011**	**1986-2011**
≥ 30 cm	4.77 (2.51)	4.01 (2.47)	4.46 (2.05)	64.8 (40.6)	58.0 (41.7)	62.1 (35.1)
30-80 cm	4.34 (2.58)	3.80 (2.07)	4.13 (2.10)	49.0 (34.1)	46.4 (28.4)	48.0 (28.7)
≥ 80 cm	5.12 (2.39)	4.18 (2.77)	4.75 (1.97)	78.3 (41.0)	67.9 (48.1)	74.1 (35.5)

3.4.3 Spatial patterns

Results for the Aggregation index R are shown in Fig. 3.5. The trees in the study stand showed an explicit regular spatial distribution at all three surveys, both for all trees (DBH ≥30 cm) and for the VLT (DBH ≥ 80 cm). For the trees with diameter larger than 30 cm, regular-dominated patterns were also observed in the German sites (very explicit in Limker Strang) but also in the primary old-growth sites of the Czech Republic (Salajka, Razula and Žofín). The Albanian primary old-growth forests showed a random pattern for trees ≥ 30 cm DBH. The VLT in the comparison sites, were distributed randomly in all primary old-growth sites in Albania and 4 out of 9 surveys in the Czech reserves and also in the long-time unmanaged site in Germany (Heilige Hallen).

Comparing the different surveys over time, the VLT in the stand at the study site showed a tendency from regular towards more random distributions in 2001 and 2011 compared to 1986. The stands at the comparison sites with multiple surveys (Czech sites Salajka, Razula and Žofín) did not show any consistent trend over time, the spatial distribution of the trees (both all trees and VLT) shifting from random to more regular or vice-versa.

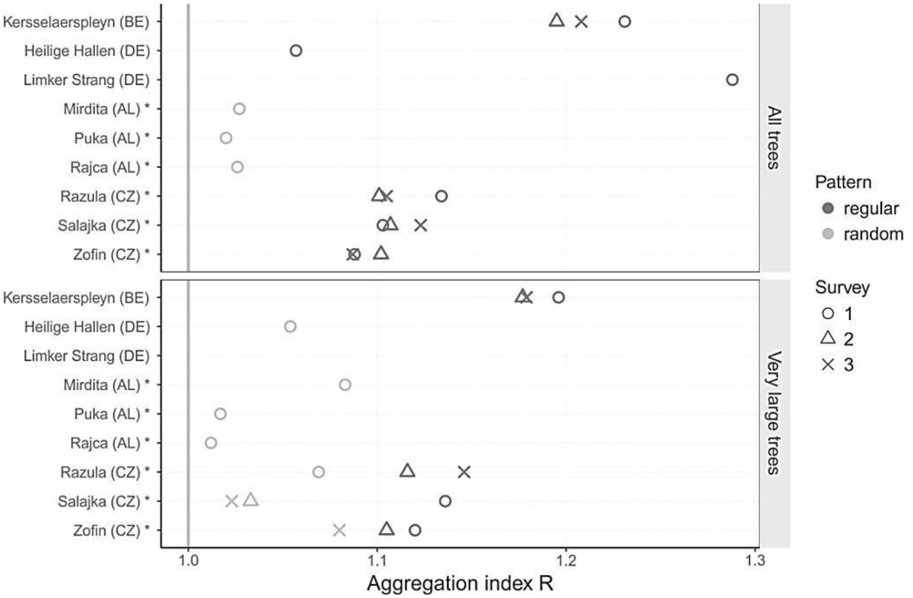


Fig.3.5 The aggregation index R for all trees (diameter at breast height ≥ 30 cm - above) and the very large trees (DBH ≥ 80 cm - below) at the study site and the comparison sites (* indicates the primary old-growth forests). Left of the grey line = clustered pattern (not present); on the grey line = perfect random pattern, right of the grey line = more regular pattern

The results of the Ripleys L-functions for the stand at the study site are shown in Fig. 3.6. For the 1986 dataset we see a significant negative divergence from a random distribution up to distances of 20-25 meters, both for all trees and VLT, indicating that trees are wider spaced (thus more regularly distributed) than random. From 25 m distance onwards, the pattern is less pronounced but still with tendency to regular, especially for the VLT. In the two consecutive surveys, the indications for regular distribution for trees over 30cm DBH are less pronounced: they are only significant for distances up to 12-15 meters, and from 25 meters onwards tend towards random distributions. For the VLT, the indication for more regular pattern remains significant up to 25 meters. At longer distances the trend towards regular distribution that was still visible in 1986 is fading and distribution becomes random. These results are in line with the Clark and Evans aggregation figures: both show a dominance of regular patterns in 1986, that is shifting towards randomness.

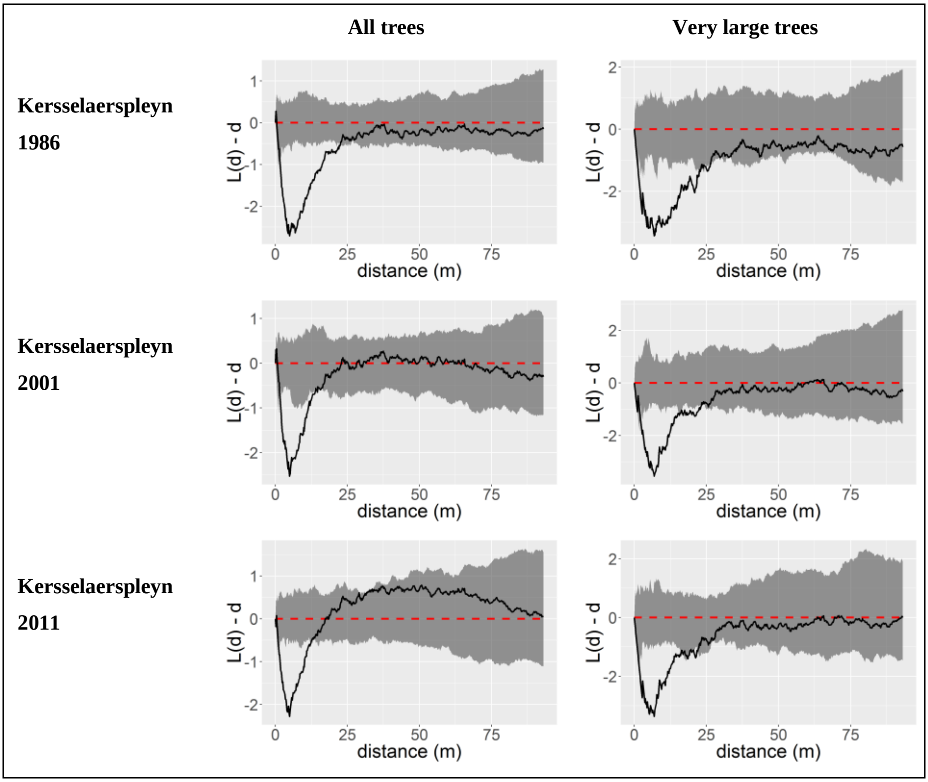


Fig. 3.6 Ripley's L for all trees (DBH ≥ 30 cm) and the very large trees (DBH ≥ 80 cm) at the study site (Kersselaerspleyn, BE) for the three surveys. The grey zone is the $p = 0.05$ confidence interval around the red dotted 0 line (random pattern). Values < 0 indicate a regular pattern; values > 0 a clustered pattern. Where the line exceeds the grey zone, the pattern is significantly different from random.

The Ripleys L-functions for the stands at the comparison sites are given in Annex 3. The trend for trees with DBH ≥30cm in the recently unmanaged site of Limker Strang in Germany is clearly similar to the study stand, and also shows a significant indication for wider spacing up to 15-25 meters. Also the primary forests Salajka, Razula and Žofín show this tendency towards regular spacing for trees ≥30 cm DBH, be it less pronounced. For the Albanian stands and Heilige Hallen however, the spacing of the trees is random even at short distances, and tends towards clustering at longer distance. For VLT, all primary old-growth forests in Albania and Czech republic, and the long-time unmanaged German site of Heilige Hallen indicate random patterns at all distances.

For the stands with repeated measurements, no trends towards more or less regularity or clumping over time can be discerned neither for all trees over 30 cm DBH, nor for the VLT separately.

Finally, the dead trees at our study site showed a clustered distribution pattern (all trees, i.e. with DBH ≥ 30 cm, and the VLT over the entire study period) or a random pattern (VLT for the separate inventories) (Table 3.5).

Table 3.5. The aggregation index R for the beech trees that died in between surveys and during the 1990 wind storms at the study site (Kersselaerspleyn, BE). The index has been calculated for all trees (diameter at breast height ≥ 30 cm) and for the very large trees (DBH ≥ 80 cm) separately. The p values indicate whether the spatial distribution pattern of the trees differed significantly from a random pattern (pp) and whether R was significantly larger than 1, indicating a regular pattern (pr), or smaller than 1, indicating a clustered pattern (pc).

	All trees					**Very large trees**				
Died	**R**	**p_p**	**p_c**	**p_r**	**Pattern**	**R**	**p_p**	**p_c**	**p_r**	**Pattern**
between 1986-1990	0.557	0.02	0.01	-	clustered	-	-	-	-	-
during storm 1990	0.859	0.08	0.08	-	clustered	0.967	1	-	-	random
between 1991-2000	0.821	0.14	0.07	-	clustered	0.912	0.70	-	-	random
between 2001-2011	0.467	0.02	0.01	-	clustered	0.864	0.74	-	-	random
between 1986-2011 (total)	0.707	0.02	0.01	-	clustered	0.736	0.02	0.01	-	clustered

3.5 Discussion

3.5.1 Density, size and share of basal area of VLT

The forest stand at our study site was quite exceptional when compared to other old-growth beech forests in Europe. First, the density of VLT was unusually high (over 30 trees ha^{-1}), and increasing. This was more than double the average value (13.0 trees ha^{-1}) for the wide range of primary and secondary old-growth beech forests in Europe that were included in the reference table (Table 3.3). Only one site in the table showed higher VLT densities: a small 1 ha plot in the Czech Republic (Voděradské bučiny, plot 6, Bílek et al., 2011). Merino et al. (2007) found even higher densities of 57 trees per ha in a set of three abandoned pollard tree stands in NW Spain, but these stands are strongly influenced and altered in the past by human activities. Holeksa et al. (2009) stated that sites with high VLT densities are often small (1 ha) and subjectively selected in larger unmanaged reserves, because these areas are perceived to be typical for old-growth forests. According to Holeksa et al. (2009), observer dependent selection of such small sites often leads to a positive bias in estimates of stand characteristics compared to large-scale, systematic surveys. At our study site, however, the survey involved a full inventory of the stand on an area of over 10 ha and was therefore far less influenced by this selection bias. Yet, Peck et al. (2015) still found significant selection biases for basal area and tree diameters when comparing a 10 ha sampling plot to a systematic sampling survey in the 10.000 ha old-growth forest of Uholka (Ukraine).

Second, the diameter range of the VLT in the studied stand was remarkable. The maximum tree diameter for mesic broadleaved forests is commonly set at 100 cm (Greenberg et al., 1997; Peterken, 1996), and the largest beech trees in most of the European old-growth beech forests seldom reach diameters over 120 cm (Table 3.3). In the surveyed stand, 24 trees had reached a diameter of 120 cm and more in 2011, and the largest tree had a diameter of 159 cm. Diameters over 150 cm are exceptional for beech in closed forest stands and have only been recorded in beech forests at lower altitudes (Table 3.3: Dobra (AT), La Tillaie (FR) and Gitschger (DE)). Even compared to old-growth beech forests on other continents, the diameters in the studied stand were exceptional. In North-American old-growth forests of *Fagus grandifolia*, the largest recorded trees had a diameter of 108 and 110 cm (Greenberg et al., 1997; Lorimer, 1980), and in Japanese old-growth forests of *Fagus crenata*, the maximum diameter was 99 cm (Ariya et al., 2015). Only in the Iranian *Fagus orientalis* old-growth forests, similar diameters up to 130 and 150 cm were recorded (Amanzadeh et al., 2013; Sefidi et al., 2016). When looking at the height of trees, the reference table only provides fragmentary information, but still it is obvious that the trees at the study area were not only amongst the biggest, but also amongst the tallest beech trees of Europe, reaching heights of up to 49 m.

Third, the proportion of the basal area covered by VLT in the stand was extraordinarily high. The share of the VLT in the overall basal area of the stand varied between 70 and 80 % over the different survey periods, while in the comparison sites, it varied between 25 and 50 %. The high threshold DBH of 30 cm we applied contributed only marginally to these high values: if recalculating this share for the whole population (threshold 10 cm DBH) for the surveys of 2001 and 2011, the basal area share of the VLT was only 1-5 % lower. The high figure at the studied stand indeed reflects a remarkable dominance of VLT. Share of basal area can be considered as a proxy for share of biomass, a variable often used in literature as indicator for old- growth status. Brown et al. (1997) state that in old-growth deciduous broadleaved forest, at least 20-30 % of the aboveground biomass is found in trees over 70 cm DBH.

3.5.2 Causes for the exceptional density and size of the trees in the studied stand

Several elements related to site conditions and management history may help to explain the exceptional density and size of the VLT in our studied stand. The Sonian forest is a very productive forest with maximum mean annual increments of 12 $m^3.ha^{-1}.year^{-1}$ and a dominant height at the age of 100 years of over 40 m (Aertsen et al., 2014). At our study area, similar increments and tree heights of up to 50 m have been recorded (Vandekerkhove et al., 2005).

Site conditions are indeed favorable for good tree growth. The soil at the study site developed in a 2-5 m thick quarternary eolian loess deposit that covers marine sandy sediments of the Eocene. The silt layer is lessivated and acid (median pH KCl value of 3.2; pH H2O 4.0 - 4.5) in the upper first meter, and rests on a textural B-horizon. However, the C horizon of the silt layer and the tertiairy sand below are not acidified and relatively rich in base cations. The tertiary layers originate from marine deposits and consist of fine and coarse sand layers with high calcium content. Deeper tree roots penetrate into these layers through cracks in the B-horizon. The loess layer also has a high capillary water storage capacity (gravitary water content 15-30%), without impairing water drainage (Brahy et al., 2000). These properties (deep and well drained upper layer, but with good water storage properties and sublayer with a high base saturation) constitute excellent site conditions for a productive forest soil and good growth conditions for beech (Langohr and Sanders, 1985).

The climatic conditions at the site also support tree growth. The Oceanic climate of the Northwest-European lowland (Cfb-climate according to Köppen, cfr. Peel et al., 2007) is characterized by a long growing season, mild winters and warm summers with low frequency of pronounced water deficits. These conditions are particularly favorable for tree growth in beech (Alessandrini et al., 2010; Dittmar et al., 2003; Schmitt et al., 2000) and thus for the development of VLT. Also Di Filippo et al. (2012, 2015) clearly showed higher growth rates for lowland areas than for cooler higher elevation sites. Other lowland old-growth beech stands in the Oceanic climate zone, located in France, Denmark and Germany, also contain very large beech trees (Table 3.3, e.g., Fontainebleau, Suserup, Vilm and Heilige Hallen), clearly contradicting the assumption by Holeksa et al. (2009) that VLT are naturally confined to small, wind-protected coves in mountain areas.

Nevertheless, the origin and management history of the stand are probably the most important factors in explaining the extraordinarily high densities of VLT. The stand originates from a large-scale man-made regeneration during the last quarter of the 18th century, which has resulted in a rather even-aged stand and a higher-than-natural share of late-successional stages at the time of the surveys. Hence, the observed overrepresentation of VLT can be considered an overshoot peak at the end of the aggradation phase for forest stands in succession after large-scale disturbance as described by Bormann and Likens (1979). A similar stand structure and development have been described for other secondary old-growth beech stands as well (Von Oheimb et al., 2005; Ziaco et al., 2012). The observed high density of VLT may fade out during a subsequent transition phase towards the shifting mosaic steady state, in which densities can be expected in line with the range of 10-20 VLT ha^{-1} in old-growth beech forests in Europe (Table 3.3). A similar overshoot peak was also suggested for the secondary old-growth beech forest of Serrahn (Von Oheimb et al., 2005). Yet, the age structure of the stand at the study site, characterized by a high share of even-aged trees, may also persist for at least two or three generations, due to larger-scale synchronous maturation. Koop and Hilgen (1987) studied a secondary old-growth beech stand in La Tillaie, Fontainebleau (France) and could relate peaks in the age distribution to several generations of trees reverberating a large-scale regeneration of the stand after extensive clearcuts dating back 600 years. Next to the large-scale regeneration, also the past management probably played an important role in the development of the VLT in the studied stand. Over a period of 200 years, the stand was subjected to regular moderate thinning. The diameter increment of beech is distinctly related to suppression and release of the trees; tree-ring analyses in primary old-growth beech forests typically show a pattern of multiple suppression-and-release episodes in the period before the beeches reach the upper canopy (Di Filippo et al., 2012; 2015; Hobi et al., 2014). During the suppression stages, tree ring widths of beech trees are typically less than 0.5 mm (Emborg, 2007; Manso et al., 2015; Piovesan et al., 2005b) while in periods of released growth, ring widths of 1.5-2 mm and more are common (Emborg, 2007; Manso et al., 2015; Remeš et al., 2015). In this context, the competitive strategy of beech is described as a ‘stop and go’ strategy (Emborg, 2007): beech trees step by step slowly approach a dominant position in the upper canopy, where a continued released growth can be realized. Young understorey beech trees can survive suppression periods of up to 150 years before they reach the upper canopy (Hobi et al., 2014), which can result in very old but mid-sized trees (Di Filippo et al., 2015; Trotsiuk et al., 2012). In managed stands, however, regular thinnings exclude or reduce the suppression stages. In beech, especially in the younger stages, such regular thinnings result in higher diameter increments (e.g., Remeš et al., 2015; Štefančík, 2013). The trees at our study area have been released regularly and thus did not encounter longer periods of suppression, continuously growing in released conditions. Hence the large size of the VLT in our site (mean diameters of 90 and 97 cm at age 200-240 years), corresponding to a mean tree ring width of more than 2 mm over the whole lifespan of the trees. Emborg et al. (2000) and Von Oheimb et al. (2005) found similar growth patterns, with beech reaching diameters of 80 cm at age 160-170 years in secondary old-growth forests originating from colonization of a former wood pasture, where the youth growth of the trees occurred in continuously released open-growth conditions.

3.5.3 Combining productivity and longevity

Notwithstanding their age and size, the VLT in our study area were still vital and vigorous, with a mean annual diameter increment of 4.75 mm over the last 25 years, a relatively high increment compared to other beech forests. Aertsen et al. (2014) found average tree ring widths between 2 and 3 mm per year for beech trees in normally stocked, regularly thinned, stands aged 15-160 years in the Sonian forest. The average ring width of the VLT at our study site (2.38 mm) was thus completely in line with the recorded increments for productive continuously released middle-aged trees in similar site conditions.

Compared to other stands in Europe, the tree ring widths of the trees in our studied stand were higher than the average figures of 1-2 mm for released trees in managed (regularly thinned) forests (e.g. Lebourgeois et al., 2005; Manso et al., 2015; Remeš et al., 2015; Utschig and Küsters, 2003). They are also in line with the average figures for released trees in old-growth beech forests in Italy (Di Filippo et al., 2012; 2015; Piovesan et al., 2005b). For 24 sites, Piovesan et al. (2005b) found average tree ring widths ranging from 1.08 to 4.58 mm with an average of 2.13 mm.
As a consequence of high diameter increments for trees with high original diameter, the mean Basal Area Increment (BAI) of 74 cm². year^{-1} is remarkably high. Boncina et al. (2007) and Pretsch et al. (2016) mention BAI of 15-28 and 20-28 cm². year^{-1} resp. for codominant mid-sized trees in diameter ranges of 30-40 cm. Piovesan et al. (2008) found mean BAI of 15-40 cm².year for dominant trees in old-growth sites in Italy, with only one lowland site (Oriolo Romano) reaching comparable figures of 50-60 cm². year^{-1}. For 12 old-growth stands, Di Filippo et al. (2012) found maximum BAI rates (99th percentile) of 30-145 cm². year^{-1}. A similar 99th percentile figure for the study stand would correspond with a BAI of 166.5 cm². year^{-1}.

These very high growth rates for the VLT at the study site can also be related to the management history with regular thinnings as they allowed the trees to develop large tree crowns. The fact that the highest BAI are found in the largest trees is not exceptional: also Di Filippo et al. (2012) found higher BAI in the largest trees. BAI-curves normally peak at great age, as they are positively influenced by tree size: the larger the original tree basal area, the higher its BAI (Diaconu et al., 2015; Di Filippo et al., 2012; Piovesan et al., 2005b). Still the highest values that were recorded by these authors at large DBH, were generally only half as much as the increments we recorded.

Dendroecological research has shown that the age/size trend in BAI of dominant, healthy trees should be positive or at least approaching an asymptotic level for many decades (Piovesan et al., 2008). Over the last decade, the diameter increment and BAI of the trees at the study site significantly decreased as compared to the previous interval. Decreasing growth rates can indicate decreased vitality and an increased risk of mortality (Gillner et al., 2013) and are considered evidence that a tree may have entered a declining senescent phase (Piovesan et al., 2008). Yet, reduced growth has been observed in beech trees all through lowland Europe (e.g. Dittmar et al., 2003) and may be related to nitrogen deposition stress and increased drought stress due to climate change (Aertsen et al., 2014; Kint et al., 2012; Latte et al., 2016). Similar growth decrease in beech was also observed in the central Apennines, where BAI started to decline in the 1970s (Di Filippo et al., 2012; Piovesan et al., 2008). This drought stress may be more important for older trees as aged trees are more likely to suffer from water stress due to a larger ratio between the transpiring surfaces and root absorption capacity (Penninckx et al., 1999). However, in our study area, we did not see a more explicit growth reduction in the VLT compared to the smaller trees. Climate effects may not only result in lower average growth rates, but may also lead to much larger and frequent growth fluctuations (Penninckx et al., 1999). Our dataset did not allow to discern whether the lower growth during the last decade reflects a reduced growth trend or mere growth fluctuations. The lower growth rate during the last decade at our study stand may also be caused by increased competition between the canopy trees, as the overall growing stock and basal area has increased. The higher growth rates during the first 15 years of the study period may still reflect lagging effects of former thinnings and natural spacing after the storm events of 1990. As stands close, the intraspecific competition increases, which leads to lower increments in individual trees (e.g., Remeš et al., 2015; Štefančík, 2013). The growth rates may be decreasing over the last decade, yet continue to be high indicating that these VLT are still vital and vigorous.

Also, the low mortality rate indicates the vigor and vitality of the VLT at our study site. We recorded an average annual mortality rate of 0.89 % for the VLT, which is fully in line with typical mortality rates of 0.7-1.3 % per year for mesic deciduous forests (Harmon et al., 1986; Peterken, 1996; Runkle, 1985). Other studies for beech forest have reported mortality rates ranging from 0.5 up to 3.3 % per year (Peterken and Mountford, 1996). Wolf et al. (2004) distinguished between low background mortality and pulses of mortality related to heavy disturbance events such as exceptional windstorms. In our stand, the mortality rate of 2.23 % for the period 1986-1991 can be fully related to the exceptional disturbance of the Vivian and Wiebke windstorms (February 1990) while over the last 20 years a mortality of 0.64 % is registered, which is completely in line with the background mortality reported for old-growth beech forests by Janík et al (2016) and lower than the average figures of Szwagrzyk and Czerwczak (1993) and Rohner et al. (2012).

Moreover, the recorded mortality rate of the VLT is fully in line with the overall mortality of the stand at our study site (0.88 %). For tree mortality, a U-shaped function is often assumed indicating higher mortality for both young and old trees, and lower risks for mid-sized, mid-aged trees (Holzwarth et al., 2012; Hülsmann et al., 2016; Lorimer et al., 2001; Westphal et al., 2006). In our case, no elevated mortality was recorded for the VLT, which indicated that their susceptibility to disturbance-driven mortality was not higher than for younger trees. The average age of the VLT at the studied stand (240 years) was indeed well below the average longevity figures for beech, presented by Di Filippo et al. (2015), with median values of 320 years. Still, the low mortality of the VLT is quite surprising, as longevity in beech trees is highly dependent of growth rate and site conditions. In beech, old age is indeed strongly related to slow growth, in sites characterized by a colder climate, lower soil fertility and a development in old-growth forest conditions with several long phases of suppression (Di Filippo et al., 2012; 2015; Piovesan et al., 2005a). Fast-growing trees are considered to be subject to trade-offs, such as reduced investment in defenses and a lower mechanical wood strength, which can reduce their life expectancy and makes them more likely to reach the high-risk diameter, associated with the U-shaped mortality curve, at younger age. Therefore, much lower longevity figures, as low as 100-150 years, are related to low-elevation beech trees growing in warm temperate forests on fertile soils (Di Filippo et al., 2015). In the comprehensive study of Di Filippo et al. (2015), average ring widths of 1.5-2 mm, as found in our study site, corresponded to a maximum life expectancy well under 200 years. Yet, the large beech trees of our study area appeared to combine longevity with high tree growth rates, resulting in exceptional tree sizes.

3.5.4 Spatial patterns of VLT: from regular to random

The spatial distribution patterns of the trees at our study area clearly differed from the old-growth comparison stands and from other literature references. We found distinctly regular patterns for all trees (DBH ≥ 30 cm) and for the VLT. The comparison stands showed mainly random patterns for VLT and a tendency towards more regular distributions when all trees (DBH ≥ 30 cm) where considered, which can be related to intraspecific competition. The spatial patterns of VLT in primary old-growth beech forests have been described most often as random (e.g. Commarmot et al., 2005; Janík et al., 2014; Petriţan et al., 2014; Rozas, 2006; Zenner et al., 2015), although some studies found tendencies towards clustering (Meyer et al., 2003; Szwagrzyk and Czerwczak, 1993) or a more regular pattern (Rugani et al., 2013). Because of the past management interventions, the tree spacing in the study stand was more regular than in natural beech forests. The other secondary old-growth stands we considered (Table 3.1) also still bore the legacy of their previous management, presenting more regular tree patterns than natural forests. The stand of Heilige Hallen, which was managed in the past but has been left unmanaged for over 100 years already reached a comparable spatial pattern as for the primary old-growth stands. Previously managed sites may gradually develop from regular to random spacing of the trees, as both natural regeneration and mortality appear randomly or clustered (see Table 3.5). At our study stand, we did see a tendency from a more regular distribution in the direction of random patterns over time. Wolf (2005) also saw a shift from regular to random tree distribution over a period of 50 years in the secondary old-growth beech of Draved Skog (Denmark), with the regular pattern related to former management and recruitment and mortality changing the pattern towards more randomness when management ceased. According to Wolf (2005), monitoring changes in spatial tree distribution patterns is a more powerful and fast indicator of the development of formally managed forests towards more naturalness compared to commonly used parameters such as diameter distribution and species composition.

3.6 Conclusion

We analyzed densities and characteristics of very large trees (VLT: DBH ≥ 80 cm) in a 10 ha secondary old-growth lowland beech stand in Belgium. Recorded densities, increasing from 31.5 to 34.3 trees ha^{-1} over the last 25 years, are distinctly higher than for other primary and secondary old-growth beech forests in Europe, where densities of 5-20 trees ha^{-1} are prevalent. Also the average size and size range of the VLT is clearly larger, with mean DBH of 99 cm and the largest tree attaining a DBH of 159 cm. Notwithstanding their size, these trees still present high growth rates (DBH increment of 4.75 mm.year^{-1}) and low mortality figures (0.89%.year^{-1}), indicating that they are still vital.

Favorable soil and climate conditions are important explanatory factors, but also the management history of the stand. As it originates from a large-scale regeneration at the end of the 18th century, the stand shows a rather even-aged structure with a high share of late-successional stage, explaining the current high densities of VLT.

Contrary to primary old-growth beech stands, where young trees are often submitted to long periods of suppression, the trees at the study site were regularly thinned before the establishment of the strict reserve in 1983, so they could grow in continuous released conditions. This explains their more regular spatial distribution pattern and their exceptional tree sizes at relatively low age, compared to trees of similar size in primary old-growth stands (e.g. Trotsiuk et al., 2012; Di Filippo et al., 2012; 2015).

Although derived from a very specific case with particular site conditions and baring the legacy of past management which unintentionally supported the remarkable development of the VLT, our observations may still be relevant to other beech forests, as they tend to reset certain baseline assumptions for growth, longevity and dimensional capacity of European beech in productive lowland forest conditions.
The trees indeed appeared to combine longevity and continuous high growth rates, resulting in remarkable tree sizes.

Our results indicate that potential tree dimensions in secondary old-growth beech forests and managed forests, because of their continuous released growth conditions before reaching the upper canopy, may be much higher than the figures commonly derived from the primary old-growth forests that are normally used to provide reference for close-to-nature silviculture. In this context, applicable diameter classes and distributions for selection forests could be extended to larger sizes, in order to include the full size spectrum. Also it places the commonly applied target diameters and rotation periods in shelterwood systems in a somewhat new perspective, as these standards only correspond to 1/3 and not ½ of the natural potential of beech trees under these conditions. Finally, the results demonstrate the importance of continuous release growth through regular thinning at younger stages on the future growth and size potential of beech trees.

The largest beech tree in the forest reserve: 159 cm DBH and a total tree height of 46.30 m. It has a tree volume of approximately 60 m³ and probably is one of the largest beech trees (in volume) of the world *(Photograph by Peter Van de Kerckhove)*

Chapter 4

“Wohl bin ich ein Wald und eine Nacht dunkler Bäume:
doch wer sich vor meinem Dunkel nicht scheut,
der findet auch Rosenhänge unter meinen Zypressen. “

Friedrich Nietzsche (1844-1900), Also sprach Zarathustra (1885)

Ombra mai fu	*Never was a shade*
di vegetabile,	*of any plant*
cara ed amabile,	*dearer and more lovely,*
soave più.	*or more sweet.*

Xerxes (G.F. Händel – 1738 - libretto: Nicolò Minato, 1654.)

Chapter 4: Development of the herbal layer in previously managed forests left for free development: case study for four strict forest reserves on loamy soils in Flanders (Belgium)

To be submitted as:

Vandekerkhove, K., Thomaes, A., De Keersmaeker, L., Leyman, A., Van de Kerckhove, P., Van Calster, H., Onkelinckx, T., Verheyen, K. (2019.) Enjoying tranquility: development of ground vegetation after cessation of management in forests on loamy soils in Flanders (Belgium).

4.1 Abstract

Centuries of forest management have drastically altered forests, in most areas of Europe. These forests may consist of forest stands with a more homogeneous age structure and range compared to untouched forests, but also with a higher share and frequency of sun-exposed conditions due to wood harvest or grazing. Frequent, small-scaled traditional forestry operations, such as coppicing, may be considered as moderate disturbance events and, in line with the Intermediate Disturbance Hypothesis, often lead to elevated species richness, compared to undisturbed forests. When non-intervention is introduced in formerly managed forests, this may lead to a loss in species richness of vascular plant species, as species related to light or soil disturbance disappear. According to some, even typical shade-tolerant species may eventually be jeopardized due to prolonged deep shade.

We studied the development of ground vegetation in four recently installed strict forest reserves on fertile loamy soils that developed in quarternary loess deposits in Flanders (Belgium) by comparing two surveys in a grid of permanent vegetation plots. We indeed registered a significant decline is species richness both at site and at plot level. This decline was not random, but strongly depending on the ecological traits and strategies of the different species. We discern strong declines in frequency of typical species of compacted, disturbed and bare soils such as *Juncus effusus, Carex remota* and *Persicaria hydropiper* and light-demanding forest species associated to gap phases like *Lonicera periclymenum, Silene dioica* and

Deschampsia cespitosa, but also shade-tolerant species such as *Polygonatum multiflorum, Convallaria majalis, Carex sylvatica* and *Maianthemum bifolium,* that require thin litter layers or bare soil for their recruitment. Many of the species that were no longer found in the second survey, were also very scarce during the first survey and only found in one or two plots. On the other hand, species like *Anemone nemorosa, Allium ursinum, Dryopteris spp., Milium effusum, Melica uniflora* and *Hedera helix* are clearly increasing in frequency and cover. This is remarkable, especially for species like *A. nemorosa,* as earlier studies in the same region and forests indicated also strong declines for these species.

We relate the observed changes to changes in disturbance frequency and canopy cover, but also to climate change and trends in atmospheric deposition. The combined effect of lower disturbance frequency and slowly improving soil conditions apparently support the development of a less species rich, but more characteristic vegetation of typical and diagnostic species of mesic lowland oak and beech forests.

4.2 Introduction

Over the last decades, nature conservation and biodiversity have become increasingly important in forests in many countries. Both integrative and segregative approaches are applied to safeguard the natural values of forests. Integrated approaches focus on protection of elements of high conservation value such as habitat trees, dead wood and rare species within the framework of a regular production forest (e.g. Parviainen et al., 2000; Kraus & Krumm, 2013; Schulz et al., 2014). Segregative approaches concentrate conservation efforts in smaller or larger protected areas, where different levels of management restrictions or targets can be applied. In forest protected areas, strict protection (non-intervention) is often applied as the main conservation strategy: forests are left for free development (Parviainen et al., 2000; Frank et al., 2007). This is an evident choice when protecting the scarce remnants of primary old-growth forest in Europe (Sabatini et al., 2018; but see also Schulze et al., 2014). However, many of the newly protected areas are established in formerly managed forests. Centuries of forest management have often drastically altered these forests, both in species composition and structural features. These forests may consist of forest stands with a more homogeneous age structure and range compared to primary old-growth (due to cohort-like age structure) but also with a higher share of sun-exposed conditions related to wood harvest or grazing (wood pasture) (Brunet et al., 1996; Von Oheimb & Brunet, 2007; Heinrichs & Schmidt, 2017).

According to the Intermediate Disturbance Hypothesis (IDH), (Connell, 1978) the effect of disturbance on species diversity is not necessarily negative towards species richness. Connell (1978) observed that high diversity of trees in tropical rain forests and corals on tropical reefs was related to a non-equilibrium state due to infrequent moderate-scale or frequent small-scale disturbances. If not disturbed further, these ecosystems progress toward a lower diversity equilibrium community sustained by niche diversification. Highest species richness is reached when intermediate levels in frequency and intensity of disturbances occur.. Small-scaled, frequent disturbances of traditional forestry operations, such as coppicing, may be considered as moderate disturbance (at the scale of a larger forest complex) and indeed often lead to elevated species richness, compared to undisturbed forests, particularly for heliophylous and disturbance-related species (e.g. Hédl et al., 2010; Boch et al., 2013; Petzold et al. 2018; Lelli et al., 2019).

This leads to discussion among conservationists what is the best conservation strategy for forests that have been subject to management for many centuries, leading to specific species-rich non-equilibrium forest communities (in line with Connell, 1978). Also in these areas, non-intervention is often selected as management type. This will allow the forests stands to steadily develop towards their climax condition, with gradual buildup of living and dead biomass, and diversification of structural composition (e.g. Vandekerkhove et al., 2009; Müller et al., 2010). This is beneficial to many, mostly late-successional species, that require undisturbed soils and microclimate, dead wood or microhabitats in overmature trees (Larrieu et al., 2018). On the other hand, the elevated share of sun-exposed conditions related to former management regimes, especially those with a long tradition and continuity such as wood pastures and coppicing, have developed a rich associated biodiversity of often thermophilous and heliophilous species (e.g. Buckley, 1992). When included in strict reserves, such areas may go through a phase of increased canopy closure and continued deep shade, before the forest further develops towards ageing and overmature phases, where natural disturbances are more frequent and open up the canopy, restoring more diverse light conditions and a more diverse vegetation (Scherzinger, 1996). This dark transition phase may be detrimental to many of these light-demanding and disturbance associated species. These species may temporarily but sometimes also permanently disappear. This is particularly evident for thermophilous invertebrates (butterflies, beetles) (e.g. Franc & Götmark, 2008; Merckx, 2015), but also for ground vegetation.

In their comparative analysis of biodiversity in managed vs. unmanaged forests, Paillet et al. (2010) indicated the group of vascular plants as one of the groups where non-intervention may result in lower species richness than in managed forests, although the signal is not unequivocal. This is especially true for forests that are halfway between managed and old-growth forest, and where the response to cessation of management depends on site-specific characteristics, type of past management and length of time since last disturbance (Burrascano et al., 2017).
Several studies indeed show a loss of species richness of ground vegetation with the abandonment of traditional management, such as coppicing (e.g. Van Calster et al., 2007; Hédl et al., 2010) or introduction of non-intervention (e.g. Boch et al., 2013; Mölder et al., 2014); other studies (Burrascano et al., 2017; Kaufmann et al., 2017) do not detect a lower species richness in unmanaged forests, but significant differences between both plant communities. However, it is often highlighted that when species richness decreases, mainly indicators of disturbance are lost, but characteristic forest species remain present, be it sometimes with lower frequencies and cover, especially for the species related to gaps and disturbance phases (Brunet et al., 1996; Decocq et al., 2004; Verheyen et al., 2012; Sabatini et al., 2016). Yet, some authors assert that even characteristic shade-tolerant plant species may eventually disappear from these forests, as they undergo an unnatural, prolonged period of deep shade, due to the man-made, uniform age structure of the original forest stands (Plue et al., 2013) or a pulse succession of shade-casting climax tree

species such as beech, that were for centuries suppressed by human interventions (Mölder et al., 2008; 2014). Plue et al. (2013) state that even the shade-tolerant species of closed canopy conditions need recurrent light phases to maintain viable populations in order to assure their long-term survival notwithstanding their numerous morphological and physiological adaptations to cope with low light levels (Neufeld and Young, 2003).

In this study, we focused on ground vegetation development in four formerly managed, recently established strict reserves in Atlantic and Subatlantic lowland beech and oak-hornbeam forests on fertile loamy soils that developed in quarternary loess deposits in Flanders (Belgium). Five to ten years after the cessation of management, a network of permanent plots was established in these sites, where dendrometric surveys and vegetation relevés were performed. These measurements were repeated ten years later. We examined development of ground vegetation and assessed if indeed species richness declined, and especially, how species composition in relation to shade-tolerance, or different ecological plant-traits and strategies changed over time, and if indeed also shade-tolerant species were negatively influenced by prolonged canopy closure. Similar analyses of the development of ground vegetation after cessation or extensification of management were already performed in continental and Mediterranean regions of Europe (e.g. Heinrichs et al., 2012; Burrascano et al., 2017), but only few studies are available for Atlantic lowland Europe (e.g. Baeten et al., 2009; Van Calster et al., 2008a; Lelli et al., 2019; Von Oheimb & Brunet, 2007; Peterken & Mountford; 2017), and none combining several sites and a high number of genuine permanent plots on fertile soils. The Atlantic climate may lead to subtle differences in vegetation developments, compared to continental regions, with certain species like *Pteridium aquilinum* and *Rubus fruticosus* approaching their climatic optimum thus being more predominant. Also strong winter frosts and late spring frosts are less frequent, yet windstorm events more frequent, which may lead to different developments of tree and ground vegetation.

4.3 Material and methods

4.3.1 Study sites

The study was performed in four strict forest reserves, located in ancient woodland sites on fertile loamy soils in Central Belgium, South-West and East of Brussels (Fig. 4.1, Table 4.1).

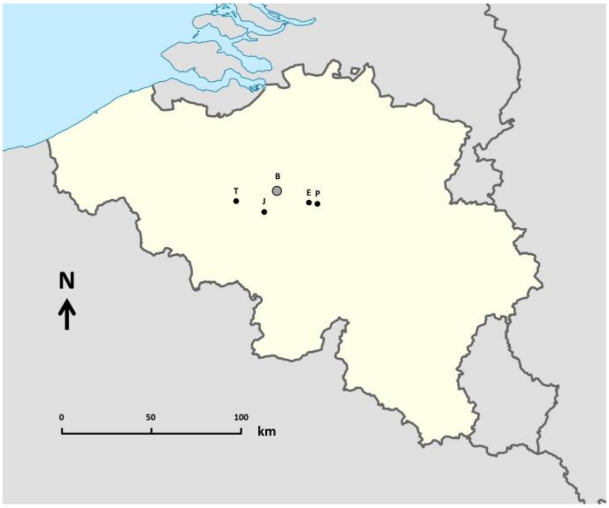


Fig. 4.1. Location of the 4 study sites in Belgium: T = Terrijst; J = Jansheideberg; E= Everzwijnbad; P = Pruikenmakers (B = Brussels)

The prevailing climate in the four sites is characterized as Atlantic to sub-Atlantic with total annual precipitation of ca. 850 mm, uniformly distributed over the year, and average yearly temperature of 10.5 °C, with minimum and maximum average monthly temperatures of 3 °C and 18 °C, respectively. All sites are located on the plateau of Brabant with heights above sea level between 50 and 120 m. Soils at all sites are characterized by slightly lessivated fertile loamy soils (Luvisols) that developed in 2-20m thick Pleistocene aeolian loess deposits on top of tertiary base-rich sandy formations.

Vegetation at all sites is characterized by a well-developed and characteristic ground vegetation of ancient woodlands on fertile loamy soils. The two sites south-west of Brussels have a more explicit Atlantic vegetation, including dominant vegetations of *Hyacinthoides non-scripta (*L.) Chouard ex Rothm. and are characterized as

Endymio-Carpinetum and *Endymio-Fagetum* (Noirfalise, 1984). The two sites east of Brussels are lacking the typical Atlantic species, and are categorized as Sub-Atlantic forms of *Stellario-Carpinetum* and *Milio-Fagetum* (Noirfalise 1984).

All sites have a long and well-described management history. Up to 50-100 years ago, all these forests were managed as coppice-with-standards, with rotation periods of 12-14 years. Standards mainly consisted of oak (*Quercus robur* L. and *Quercus petraea* (Matt.) Liebl.), and the coppice layer was a mixture of primarily hazel (*Corylus avellana* L.) and sycamore (*Acer pseudoplatanus* L.). Since the beginning of the 20th century, the stands were converted to high forest of oak or beech (*Fagus sylvatica* L.) and locally also poplar (*Populus x euramericana* Dode (Guinier)). This process was slightly different in the four sites. In Everzwijnbad and Pruikenmakers (both located in Meerdaal Forest), transformation to oak high forest was a gradual process, in which the coppice was no longer cut and the share and volume of standards gradually increased. These stands now comprise of uneven-aged oak-dominated stands with former standard trees up to 250 years old (Vandekerkhove et al., 2016a). A few patches (in total 3-4 ha) were clearcut in the beginning of the 20th century and planted with beech. Over the last decades, the stands were all regularly thinned, and a few small-scaled (0.1 to 1 ha) final fellings with replanting of oak and beech were performed. Terrijst has a very similar management history, only here, also a larger young stand of beech (30 years old) and some poplar-dominated stands are present. Jansheideberg (located in Hallerbos) was completely pillaged during World War I and regenerated by replanting of uniform oak and beech stands in the 1920’s. Under the oak canopy, a mixed subcanopy of mainly hazel and sycamore has developed, while the beech stands remained uniform. Strict reserve status (non-intervention) was introduced at all sites between 1995 and 1997.

4.3.2 Field measurements

At all sites, a systematic grid of permanent plots (mesh size 70m) was installed and first measured between 2003 and 2005, and resampled 10 years later. Location of the plot center in local UTM-coordinates (X,Y) was registered, and the plot center was marked with a topographic permanent survey marker (FENO-marker), so exact relocation was guaranteed.

Excluding the plots on sandy outcrops, this resulted in a total of 183 plots on fertile loamy soils over the four sites that can be used in the analysis (Table 4.1).

At every plot, vegetation relevés and dendrometric measurements were performed between 2002 and 2005, and repeated 10 years later. Vegetation relevés were carried out on 16x16m squares, oriented with the corners in the cardinal directions. Two samplings were performed at every plot, one in late April and one in June, in order to register both spring and summer species at their optimal development. Species presence and coverage was recorded using the extended decimal scale of Londo (1984). Both records are integrated to one result, taking into account the record with the highest cover (cfr. Mölder et al., 2014). In the vegetation relevé, also overall coverage of tree and shrub layer are registered. Like Van Calster et al. (2008a) and Baeten et al. (2009a) we excluded the woody seedlings from the analysis to keep irregular mast events from clouding the trends in the vegetation composition.

Table 4.1. Short description of the study sites, and the larger forest complex they are located in.

Name	Code	Size (Ha)	Location	Vegetation type	Forest complex	Complex size (ha)	Number of plots
Everzwijnbad	E	27.5	50°47'54"N 4°40'40"E	*Stellario-Carpinetum* *Milio-Fagetum*	Meerdaal-woud	1200	47
Jansheideberg	J	26.5	50°42'21"N 4°16'38"E	*Endymio-Fagetum* *Endymio-Carpinetum*	Haller- bos	650	32
Pruikenmakers	P	38.7	50°47'57"N 4°42'54"E	*Stellario-Carpinetum*	Meerdaal-woud	1200	55
Bos Terrijst	T	28.6	50°43'04"N 4°05'08"E	*Endymio-Fagetum* *Endymio-Carpinetum*	Terrijst-Strihoux	150	49

Dendrometric surveys were done at the same plots using nested circular plots of 9 and 18m radius. Tree species, position and diameter are registered with DBH threshold of 40 cm (large circle) and 10 cm (small circle). Overall basal area per ha, and share of the different major tree species to the basal area are derived.

During the first sampling cycle, also soil samples were taken and analyzed. Mineral soil was sampled using a 3cm diameter auger, taking 5 subsamples within each plot. Those subsamples were aggregated to one soil sample, dried to constant weight at

40°C. Samples were analyzed on texture (Sand, Loam, Clay fraction), pH-$CaCl_2$, CEC and Kjelldal-N using the Standardized Operation Procedures described by Cools & Devos (2016).

4.3.3 Data processing and statistics

Cumulative species richness for each reserve and all sites combined is calculated for each sampling period. Rarefaction curves with 95% confidence intervals providing interpolated and extrapolated species richness for each site and survey are constructed using 999 replicated bootstraps using the package iNext in R (Hsieh et al., 2015). Differences are considered significant if confidence intervals do not overlap.

Based on the plot data, for all recorded species, frequencies and average characteristic cover (= average cover excluding zero-records) are calculated for both periods. For this purpose, Londo cover classes for all plant species were transformed into percentage values using the median of the respective class (Annex 4).

For all herb species, a set of indicator values and characteristics are compiled and assigned. Ellenberg indicator values for light (L), soil reaction (R), soil moisture (F) and nitrogen (N) were assigned to each herb species using the values according to Ellenberg et al. (2001) and Hill et al. (1999). When different values are given for a species in both publications, the average value is assigned.

Ancient Woodland Indicator species are assigned according to Hermy et al. (1999) and forest affinity classes are attributed to each species according to Schmidt et al. (2011). Five classes of forest affinity are applied:

1.1 = closed canopy forest
1.2 = gaps and edges in forests
2.1 = forest as well as open countryside
2.2 = also in forests, but mainly open countryside
O = no forest affinity, species of open countryside

A subset of ‘vernal geophytes’ is selected combining the Raunkiaer life forms classification according to Ellenberg et al. (2001), and flowering period March to May according to Florabank (Van Landuyt et al., 2012). Based on the functional signature scores according to the CSR-strategies of Grime (1979) assigned to each species according to Hunt et al (2004), a set of ‘stress-tolerant’ species and ‘competitors’ are derived (scores $S>0.33$ and $C \geq 0.5$ respectively). Species with Ellenberg L-indicator values of 6 and higher are clustered as ‘light demanding species’.

Furthermore, following calculations are performed on the dataset at plot level and for both surveys:

- Total species richness per plot and Shannon index (H’)
- Ellenberg average indicator values (AIV) for light (L), soil reaction (R), soil moisture (F) and nitrogen (N) per plot and for both periods using weighted averages, based on percentage cover and indicator scores of all species
- species richness and cumulative cover for different characteristic groups (woodland affinity, ancient woodland indicators, vernal geophytes, stresstolerant, competitor and light-demanding species) based on the species presence and cover data.
- Cumulated canopy cover (CCC) is calculated as a combined value for tree layer and shrub layer cover excluding double count for overlap, as used by Mölder et al. (2014) and Heinrichs & Schmidt (2017)
- Litter Quality (LQ) for each plot is calculated as weighted average of litter quality scores of the main tree species (*Quercus spp.* and *Fagus sylvatica* = 1, *Populus* = 4; other species = 3) and their relative share in the basal area at each plot

4.3.4 Statistics

First, we controlled for heterogeneity of site conditions between the reserves by comparing different soil variables (sand fraction, pH-CaCl2, Kj-N, organic matter and CEC-BaCl2) and canopy variables (cover, Basal Area and Litter Quality) recorded at the first survey across the four forest reserves by ANOVA and Tukey test with adjusted Bonferroni p-value. We further examined the difference in cover, basal area and Litter Quality as canopy variables between the four forest reserves and two surveys with ANOVA.

Analysis of changes in species richness at plot level are calculated using absolute species richness per plot and Shannon index (H') and tested for statistical significance using resp. non-parametric Wilcoxon Rank Sign test and paired t-test.

Overall changes in species composition were compared for the two survey periods. Based on the number of shared species, extinctions and colonizations per plot, dissimilarity indices are calculated using package 'betapart' in R (Baselga et al. 2018). Sörensen dissimilarity index is computed for every plot as:

$$\beta s\ddot{o}r = \frac{b + c}{2a + b + c}$$

with b and c number of exclusive species in first and second survey, and a = number of shared species between both surveys. As described by Baselga (2010) and Baeten et al. (2012), this dissimilarity measure can be subdivided in two components for species turnover and nestedness. Turnover refers to the replacement of some species by other species from site to site (or between two surveys), the nestedness component accounts for compositional differences due to richness differences between sites resulting in a nestedness pattern, for instance when species are lost from the first to the second survey. Turnover is expressed by the Simpson-index:

$$\beta sim = \frac{\min(b, c)}{a + \min(b, c)}$$

with min(b,c) being the minimum number of exclusive species for both surveys, and nestedness as the difference between both previous indices:

$$\beta nest = \beta s\ddot{o}r - \beta sim$$

Plot-level compositional shifts between both surveys are also visualised using non-metric multidimensional scaling analysis (NMDS).

Changes in frequency and cover of selected species and species groups (vernal geophytes, stresstolerant, competitor and light-demanding species; woodland association scores) are evaluated, as well as Ellenberg average indicator values (AIV) between both surveys at site level and for all sites combined, and tested for significance using paired t-test (for normally distributed data) and Wilcoxon Signed Rank tests (for Poisson and Binary data), with p-values of <0.05 considered significant (significance levels * for $p<0.05$; ** for $p<0.01$ and *** for $p<0.001$).

All statistics were performed in R version 3.5.2 (R Developement Core Team, 2019) with packages iNEXT (Hsieh et al., 2015) and betapart (Baselga et al., 2018).

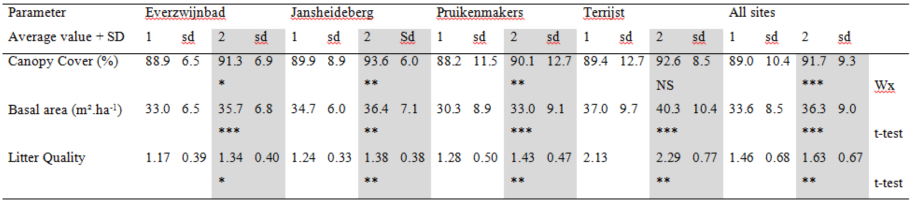
4.4 Results

4.4.1 Environmental variables

The analysis of soil samples revealed important differences on some parameters (like CEC and organic matter content) but showed very similar results on pH, and limited differences on total available nitrogen (Annex 5). On canopy variables, the Combined Canopy Cover (CCC) at first survey was high for all sites (varying between 88 and 90%), with no significant differences between the four sites; for basal area (BA), some differences were significant but all sites showed high average values of 30 to 37 $m^2.ha^{-1}$. Detailed analysis of soil and canopy variables are given in Annex 5.

We also tested canopy variables for significant differences between both surveys (using Wilcoxon and paired t-tests). The results for the paired comparisons are given in Table 4.2. Between surveys both CCC and BA significantly increased, indicating further build-up of growing stock and denser canopy. Indeed, only in 2 out of 183 plots, basal area of living trees decreased by more than 25%, indicating gap disturbance; 17 plots showed BA decreases of 5-15% related to single tree dieback, but all of these plots retained a high canopy cover of over 80% (see also annex 5 for details). Average cover further increased from 89 to 92% on average, and plots that showed a canopy cover of <65%, still numbering 7 at the first inventory closed up and decreased to 4. Finally also LQ values significantly increased between both surveys as shares of poplar and other tree species (mainly Sycamore) increased at the expense of oak and beech.

Table 4.2 Changes in canopy cover, Basal area and litter quality score (LQ) over the two survey periods (significance levels: NS = non-significant; * = p<0.05; ** = p<0.01; *** = p<0.001) – sd = standard deviation



Parameter	Everzwijnbad				Jansheideberg				Pruikenmakers				Terrijst				All sites				
Average value + SD	1	sd	2	sd	1	sd	2	Sd	1	sd	2	sd	1	sd	2	sd	1	sd	2	sd	
Canopy Cover (%)	88.9	6.5	91.3 *	6.9	89.9	8.9	93.6 **	6.0	88.2	11.5	90.1 **	12.7	89.4	12.7	92.6 NS	8.5	89.0	10.4	91.7 ***	9.3	Wx
Basal area ($m^2.ha^{-1}$)	33.0	6.5	35.7 ***	6.8	34.7	6.0	36.4 **	7.1	30.3	8.9	33.0 ***	9.1	37.0	9.7	40.3 ***	10.4	33.6	8.5	36.3 ***	9.0	t-test
Litter Quality	1.17	0.39	1.34 *	0.40	1.24	0.33	1.38 **	0.38	1.28	0.50	1.43 **	0.47	2.13		2.29 **	0.77	1.46	0.68	1.63 **	0.67	t-test

4.4.2 *Species richness, frequency and cover at site level*

On total species richness, we observe a strong overall decrease in species richness (all sites combined) from 86 species to 64 species, with two new species, 62 shared species and 24 species disappeared (full table is given in Annex 6); for every reserve, species richness decreases by 10 to 16 species between the two surveys.

The rarefaction curves (Fig. 4.2) indicate lower species richness for the second survey, with no overlap between confidence intervals for all sites, also in the extrapolated range, indicating that these decreases are significant.

When comparing overall frequency and average characteristic cover of the different species, we discern strong declines in frequency of typical species of compacted, disturbed and bare soils and gap phases (light-demanding species) such as *Urtica dioica, Juncus effusus, Carex remota and C. pallescens, Lonicera periclymenum, Teucrium scorodonia, Silene dioica, Deschampsia cespitosa, Luzula pilosa,* *Pteridium aquilinum, Scrophularia nodosa, Moehringia trinerva,* but also typical shade-tolerant species such as *Lysimachia nemorum, Polygonatum multiflorum, Convallaria majalis, Carex sylvatica* and *Maianthemum bifolium. Persicaria hydropiper* and *Rubus caesius*, during the first survey still present in 10 resp. 6 plots, have completely disappeared in the second survey. All other species that were no longer found in the second survey, were also very scarce during the first survey and only found in one or two plots.

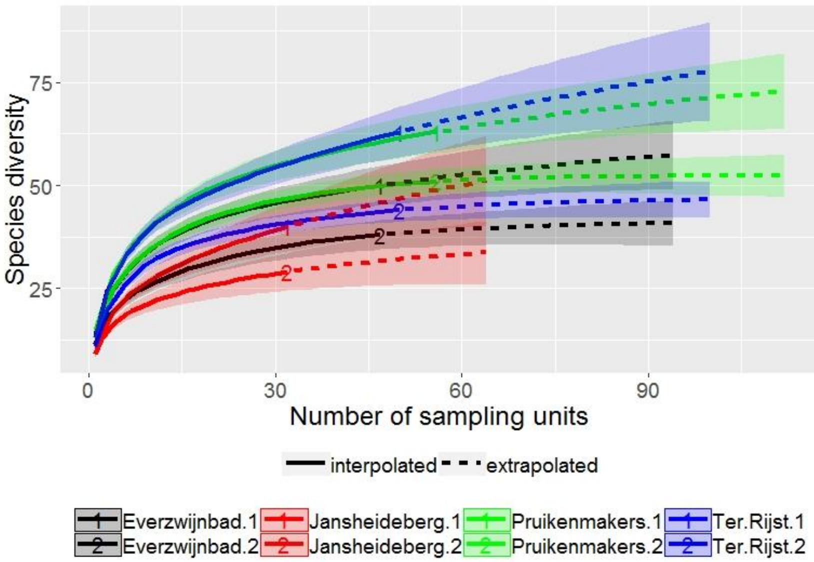


Fig 4.2. Rarefaction curves for species richness for all four sites and for the two surveys (colored zones = 95% confidence interval for 999 replicated bootstraps). None of the confidence intervals of different sampling years are overlapping, indicating significant difference.

On the other hand, species like *Anemone nemorosa*, *Allium ursinum, Dryopteris carthusiana* and *D. dilatata, Milium effusum*, *Melica uniflora* and *Hedera helix* clearly show increasing frequency and average cover. Several other species, like *Lamium galeobdolon, Oxalis acetosella, Hyacinthoides non-scripta, Galium aparine, Narcissus pseudonarcissus, Ficaria verna* and *Adoxa moschatellina* did not show important changes over the two survey periods.

When looking at overall species losses related to the forest affinity classes by Schmidt et al. (2011), we notice a striking difference between the 'closed canopy forest' (class 1.1) species compared to the other species (Table 4.3). Although at each separate site, there were a few species lost between both surveys, the total species pool of closed canopy forest species (37 species) remained unaltered over the two survey periods, while light demanding forest species, and species also associated to open land, all dramatically decreased.

Table 4.3 Species richness per site and for all sites combined, subdividing the recorded species according to the forest affinity classes of Schmidt et al. (2011). 1.1 = closed canopy forest; 1.2 = gaps and edges in forests; 2.1 = forest as well as open countryside; 2.2 = also in forests, but mainly open countryside; O = no forest affinity, species of open countryside

	Everzwijnbad		Jansheideberg		Pruikenmakers		Terrijst		All sites	
survey	1	2	1	2	1	2	1	2	1	2
Class 1.1	28	26	22	22	30	27	27	23	37	37
Class 1.2	3	2	3	1	4	2	4	2	8	3
Class 2.1	14	10	11	5	23	18	23	16	33	21
Class 2.2	2	0	2	1	1	1	3	1	4	2
Class O	1	0	0	0	1	0	2	0	3	0
All	49	38	39	29	59	43	60	47	86	64

4.4.3 Species richness and composition at plot level

Results on changes on plot level are given in Table 4.4. Average species richness per plot, and Shannon diversity index decreased significantly for all sites combined (12.8 to 11.4 and 1.52 to 1.42 resp.) but not for all sites separately: species richness decreases were significant for all sites but J, and Shannon-diversity values were not significantly altered in J and H. Changes in average species richness per plot and per site are visualized in Fig. 4.3.

Trends on species richness are divergent when selected subgroups are analyzed (Table 4.4). The group of Ancient Woodland species (containing both light-demanding and shade-tolerant species) also decreased, but the decrease is less significant, and differs from site to site, with non-significant changes in T and even significant increase in J. The number of light-demanding species very significantly decreased at all sites, while the decline of stress-tolerant species was not significant and showed differing trends in the separate reserves with significant increases in J, non-significant changes in T, and significant decreases in E and P. More specifically, in the group of shade-avoiding vernal geophytes, species numbers did not significantly decrease in any of the sites. The number of competitor species did significantly decline, but not as strong as the light-demanding species. When looking at the combined cover of the selected species groups, we also discern important developments with significant increases of cover by vernal geophytes and stress-tolerant species, while the cover of light-demanding species and competitors was and remained low (no significant decrease).

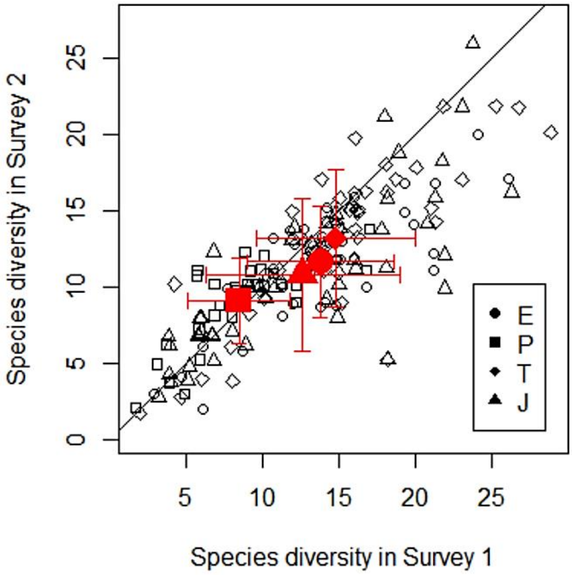


Fig. 4.3 Average species richness (including SD) changes for the four studied sites (for site codes: see Table 4.1), with in the background the results for the individual plots

Regrouping the species according to the forest affinity classes of Schmidt et al. (2011), we noticed no significant changes in numbers of closed-forest species for all sites combined (with divergent results for the separate sites), but very significant declines for species of gaps and edges. The cover of closed-forest species did very significantly increase, while the cover by species of open areas in the forest did not change over all sites combined (with again divergent results for the different sites);

for non-forest species, the numbers and cover values were too low for statistical analysis.

Furthermore, we analyzed (Table 4.4) and visualized (Fig. 4.4) the development of a selection of the most common species, but with divergent developments: five distinctly increasing species, two stable and five decreasing. When comparing average coverages of individual species, the strong expansion of *Anemone nemorosa* is particularly striking, with significant increases in E and P, and also slight (non-significant) increases in the other sites (Fig. 4.5 and Fig 4.6). Other shade-tolerant species like *Dryopteris spp.*, *Milium*, *Allium* and *Hedera helix* also very significantly increased in cover, but *Oxalis acetosella* and *Lamium galeobdolon* did not significantly increase. *Convallaria majalis* on the other hand significantly decreased. The selected light-demanding or disturbance related species *Pteridium aquilinum*, *Urtica dioica*, and *Luzula pilosa* all declined in cover, although not all of these declines could be statistically tested or proven due to insufficient records. Lastly, *Rubus fruticosus*, decreased in frequency but its cover did not significantly change, and remained low in both surveys.

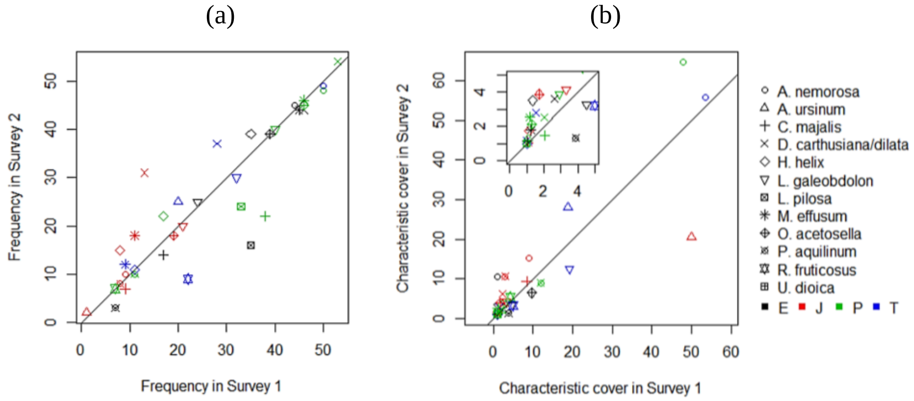


Fig 4.4 Changes in frequency (a) and characteristic cover (b) of selected species for the four different sites – for site codes see Table 4.1.

Table 4.4 Shannon diversity index, average species richness (N) and average cover (C) (%) per plot for all herbaceous species and selected subgroups (aggregated cover) and species and average indicator values according to Ellenberg for the four sites and all sites together; statistical significance of changes between the two surveys are given (paired t-test for normal and gamma distributed data; other: non-parametric Wilcoxon Sign Rank test (W)) '+' = not enough values for statistically relevant outcome – *= p<0.05; ** = p<0.01; ***= p<0.001; SD = standard deviation – forest affinity classes: see Table 4.3

Parameter	Everzwijnbad				Jansheideberg				Pruikenmakers				Terrijst				All sites				
Average + SD	1	SD	2	SD	1	SD	2	SD	1	SD	2	SD	1	SD	2	SD	1	SD	2	SD	
Shannon-index H'	2.13	0.49	1.91	0.44	0.91	0.48	1.01	0.38	1.52	0.59	1.32	0.40	1.34	0.46	1.35	0.45	1.52	0.65	1.42	0.52	
			**				NS				***				NS				*		t-test
N all species	13.8	4.8	11.4	4.0	8.5	3.4	9.1	2.8	14.8	5.2	13.2	4.5	12.6	6.3	10.8	5.0	12.8	5.6	11.4	4.5	
			***				NS				***				**				**		W
Average species richness and aggregated cover for selected subgroups																					
N AW-species	9.2	3.1	7.8	2.8	6.2	2.1	6.7	2.2	9.8	3.2	8.7	3.1	7.1	2.7	6.9	2.3	8.3	3.2	7.6	2.8	
			***				*				***				NS				*		W
N vernal geophytes	1.02	0.39	1.06	0.44	1.88	0.79	1.91	0.78	1.25	0.97	1.22	1.01	3.14	1.44	3.20	1.31	1.82	1.31	1.84	1.30	
			NS				NS				NS				NS				NS		W
N Competitors	4.94	1.99	4.17	1.79	3.22	1.84	2.94	1.68	5.20	2.08	4.67	1.95	4.72	2.49	4.08	2.17	4.66	2.23	4.08	2.00	
			*				NS				*				*				*		W
N light-demanding spp	2.7	2.2	2.0	1.5	2.1	1.8	1.3	0.9	1.7	1.4	1.5	1.0	2.8	1.9	2.3	1.5	3.8	2.8	2.5	1.8	
			**				NS				*				***				***		W
N stress-tolerant spp	10.5	3.0	9.3	3.0	6.5	2.1	7.7	2.2	11.3	3.3	10.2	3.2	7.5	3.2	7.2	2.8	9.2	3.6	8.7	3.1	
			**				***				***				NS				NS		W
C vernal	1.0	0.4	10.5	19.7	54.8	34.9	63.2	35.0	45.4	29.6	59.9	31.4	110.	52.7	102.	42.4	53.4	53.1	59.4	46.8	
			***				*				***				*				**		W
C competitors	11.6	9.7	12.1	9.4	7.5	7.0	11.5	13.5	16.0	17.1	16.3	15.9	23.9	26.6	29.6	27.8	15.5	18.5	18.0	19.7	
			NS				NS				NS				NS				NS		W
C light-demanding	2.6	3.0	1.7	1.2	2.5	3.6	5.9	12.5	6.3	13.3	4.8	9.7	16.2	26.2	15.5	22.4	7.4	16.5	7.1	14.8	
			NS				NS				NS				NS				NS		W
C stress-tolerant	21.3	15.8	30.7	26.9	64.1	34.6	80.9	36.2	60.7	31.8	75.8	36.4	130.	51.4	118.	39.7	70.3	54.0	77.0	47.3	
			*				*				***				***				**		W

Average species richness and aggregated cover for all species according to forest affinity classes of Schmidt et al. (2011)																					
N closed-f. sp.(1.1)	9.51	2.82	8.50	2.75	6.19	2.02	6.75	2.18	9.53	3.13	8.80	3.14	7.14	2.78	6.96	2.50	8.29	3.10	7.86	2.85	
			**				*				***				NS				NS		W
N open f. sp. (1.2	4.09	2.15	3.09	1.52	1.75	1.48	1.88	0.98	5.07	2.50	4.25	1.96	5.04	3.81	3.52	2.67	4.23	2.96	3.34	2.11	
			***				NS				**				***				**		W
N non-f. sp. (2.2 +	0.15	0.51	0.00	0.00	0.50	0.57	0.47	0.51	0.04	0.19	0.04	0.19	0.44	0.58	0.30	0.46	0.26	0.51	0.17	0.38	
			+				+				+				+				+		W
C closed-f. sp.	22.5	17.1	34.3	33.0	67.3	37.8	82.5	38.2	61.9	34.8	78.4	39.0	137.	59.0	129.	49.7	73.2	58.5	82.1	53.3	
			**				***				***				NS				**		W
C open f.sp. (1.2	8.2	7.9	4.7	3.6	2.2	2.4	5.5	8.2	11.6	14.2	11.5	16.7	18.6	27.9	17.1	23.3	11.0	17.8	10.2	16.3	
			***				***				NS				NS				NS		W
C non-f. sp. (2.2 + O)	0.1	0.5	0.0	0.0	0.5	0.6	0.5	0.6	0.0	0.2	0.0	0.2	0.6	0.8	0.6	1.3	0.3	0.6	0.3	0.8	
			+				+				+				+				+		W
Average cover for selected species																					
C *Anemone nemorosa*	0.9	0.2	10.0	19.1	2.6	12.3	4.8	17.1	43.5	30.6	56.5	32.6	53.4	38.1	55.6	36.7	28.2	35.2	35.3	37.3	
			***				NS				***				NS				***		W
C *Allium ursinum*	+	+	+	+	+	+	+	+	+	+	+	+	7.5	21.6	14.0	28.3	+	+	+	+	
															***				+		W
C *Dryopteris* spp.	2.6	2.0	3.4	3.5	0.9	1.3	5.9	7.0	1.9	0.9	2.5	1.2	0.9	0.9	2.1	3.2	1.6	1.5	3.2	4.0	
			NS				***				***				***				***		W
C *Hedera helix*	1.0	1.3	2.9	4.2	0.3	0.5	0.8	1.6	0.3	0.5	0.5	0.7	+	+	+	+	0.5	0.8	1.1	2.5	
			***				**				NS								***		W
C *Milium effusum*	1.2	1.1	1.7	1.3	0.4	0.6	0.6	0.6	1.0	1.0	2.1	3.6	0.2	0.4	0.3	0.5	0.7	0.9	1.2	2.2	
			**				*				***				NS				***		W
C *Lamium galeobdolon*	2.3	4.9	1.7	3.3	2.2	4.0	2.6	4.2	2.1	2.7	2.8	3.2	12.3	21.5	7.5	13.9	4.9	12.4	3.8	8.1	
			NS				NS				NS				*				NS		W
C *Oxalis acetosella*	8.1	12.8	5.3	6.8	1.0	1.6	2.2	3.9	1.1	0.7	1.7	1.7	+	+	+	+	2.6	7.2	2.3	4.4	
			NS				NS				**								NS		W
C *Rubus fruticosus*	0.9	0.5	1.1	0.8	0.9	1.4	2.7	7.3	1.5	3.0	0.9	0.6	4.3	14.0	6.2	17.2	2.0	7.6	2.7	9.7	
			NS				*				NS				NS				NS		W

C *Convallaria majalis*	0.4	0.5	0.3	0.6	2.4	7.5	2.0	8.9	1.4	2.4	0.6	0.9	+	+	+	+	0.9	3.5	0.6	3.8	
			NS				NS				***				+				**		W
C *Luzula pilosa*	0.7	0.4	0.3	0.5	+	+	+		0.6	0.5	0.4	0.5	+	+	+	+	0.4	0.5	0.2	0.4	
			***				+				*				+				***		W
Ellenberg Average indicator values																					
Ellenberg L	4.25	0.53	4.30	0.41	4.84	0.31	4.84	0.35	4.92	0.27	4.85	0.26	4.80	0.45	4.66	0.52	4.70	0.48	4.66	0.45	
			NS				NS				*				***				NS		t-test
Ellenberg F	5.78	0.27	5.80	0.32	5.20	0.27	5.28	0.22	5.59	0.22	5.62	0.22	5.52	0.27	5.68	0.26	5.55	0.32	5.62	0.31	
			NS				**				NS				***				*		t-test
Ellenberg R	4.73	0.54	5.06	0.39	5.84	0.23	5.68	0.33	4.96	0.48	4.99	0.51	5.76	0.43	5.73	0.50	5.27	0.65	5.33	0.57	
			***				***				NS				NS				NS		t-test
Ellenberg N	4.84	0.43	4.97	0.33	5.76	0.47	5.66	0.47	4.38	0.51	4.41	0.53	5.50	0.61	5.52	0.72	5.04	0.74	5.07	0.74	
			NS				NS				NS				NS				NS		t-test

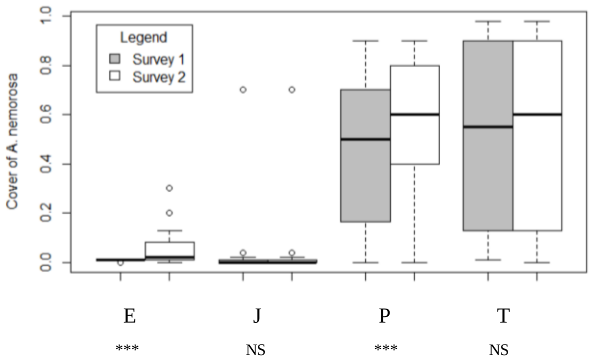


Fig 4.5 Boxplots showing the changes in cover range for *Anemone nemorosa* for the four sites over the two survey periods. Changes were very significant for E and P, not significant for the other two sites (Site codes: see Table 4.1).

Finally, when looking at the Ellenberg-AIV, we do not discern important changes between both surveys. Only the F-value increase was marginally significant, due to decrease or disappearance of species of dry conditions; the R-value appears to converge towards an average value of 5.60; other changes over all sites combined were not significant, though individual reserves may produce significant signals. Although canopies further closed-up, no significant differences for Ellenberg L-value were discerned, as the average value was already low at the first survey. Changes in Ellenberg-N-value were not significant and divergent between sites.

4.4.4 Dissimilarity: Sörensen and NMDS

Dissimilarity indices for all four reserves produced very comparable low figures, fluctuating around 0.2 for Sörensen-index and evenly distributed between turnover (Simpson index – approximately 0.1) and nestedness (also 0.1) (Fig. 4.7).

Fig. 4.6 Paired photographs illustrating the striking increase in cover of *Anemone nemorosa* between both surveys under dense canopy of young beech trees in the forest reserve of Pruikenmakers (plot 931). In the background a grey poplar that died between the two surveys

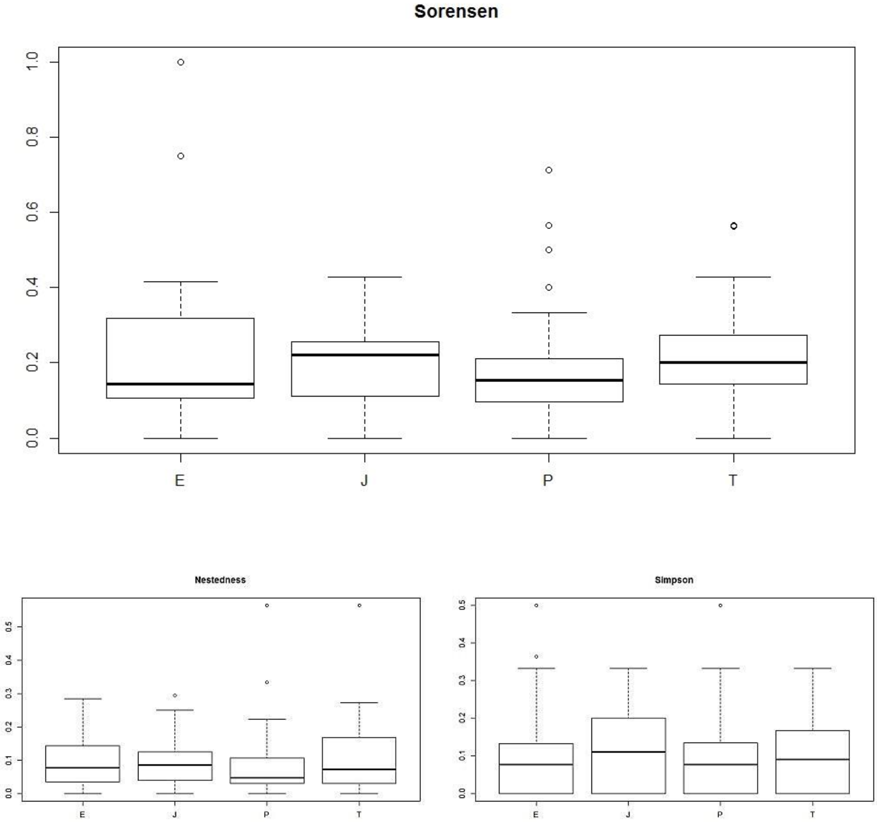


Fig. 4.7 Dissimilarity between species communities between two surveys for the four sites. Boxplots for nestedness and species turnover (Simpson index) and the resulting Sörensen dissimilarity (site codes: see Table 4.1).

The NMDS-plots (Fig. 4.8) clearly indicate a strong convergence over the two surveys towards the middle of the plot, indicating a trend towards homogenization of the vegetation between different reserves and both surveys. Based on the positioning of the species, we notice a convergence of the different plots towards a typical vegetation of closed-canopy mesic oak and beech forests, with species like *Anemone nemorosa*, *Athyrium filix-femina* and *Dryopteris spp.*, and away from indicator species of both eutrophic and oligotrophic sun-exposed and disturbed conditions (*Luzula pilosa*, *Lonicera periclymenum*, resp. *Urtica dioica*, *Silene dioica*).

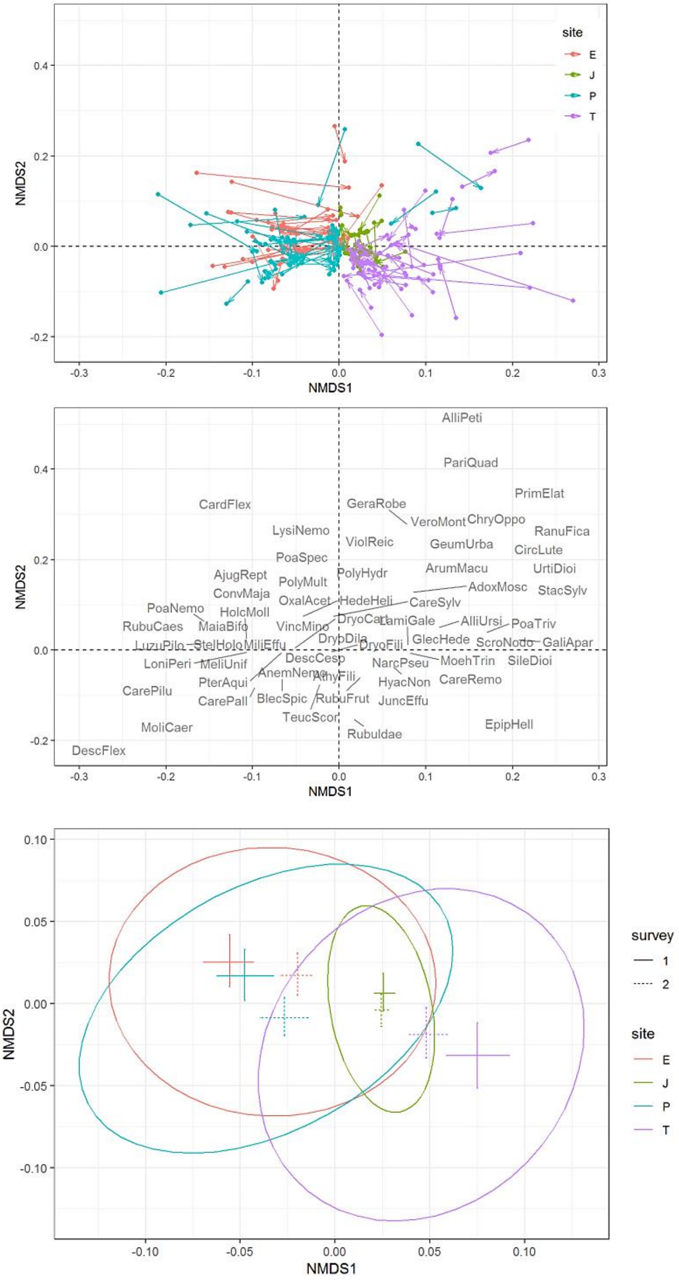


Fig. 4.8. NMDS-plots showing the shifts and convergence of the 183 plots (upper figure) and combined figures for the four sites (lower figure) towards the center of the plot, where the typical species of closed-canopy mesic oak and beech forests are located (middle figure) - site codes: see Table 4.1.

4.5 Discussion

Over a period of ten years, we noticed significant changes in the vegetation, with an overall loss in species richness, but divergent trends for species with different ecological strategies. In this section, we discuss these trends, relate them to the overall trend in the studied reserves with continued and enhanced canopy closure, and confront them to similar cases in literature. Finally, we focus on environmental developments that could further explain and amplify some of the recorded changes.

4.5.1 Short time interval, little canopy disturbance, still relevant changes

Although the time interval between both surveys was limited (10 years), significant changes of vegetation were observed. Most other studies on vegetation changes have a longer timespan or use space-for-time chronosequences. Only Brunet et al. (1996) used a similar time interval. Still, Petzold et al. (2018) state that species assemblages can shift within decadal scales in response to changes in management regime.

The recorded turnover in species composition was limited: Sörensen dissimilarity rates of 0.2 are rather low (compared to e.g. Baeten et al., 2012). This is explained by the limited time interval (10 years) between the two surveys, but can also be related to the large size of the sample plots (256 m²), which makes new appearance and disappearance due to stochastic events less probable. Dissimilarity at plot level was evenly distributed between turnover and nestedness, which means that half of the change is related to plot-level extinctions, while the other half is linked to plot-level influx of species. Although the level of species turnover is not high, we are confident that recorded changes indeed reflect real changes in vegetation, as they result from comprehensive paired observations in genuine permanent plots with both surveys performed by the same people. Many forest understorey resurvey studies are based on semi-permanent plots (e.g. Lameire et al., 2000, Van Calster et al., 2007; 2008a; Heinrichs et al., 2012; Naaf & Wulf, 2011; Jantsch et al., 2013). Relocation and observer errors in such studies are often underestimated and can strongly affect and bias results (Verheyen et al., 2018). Due to a shift in plot location between the surveys in these studies, a part of the observed temporal turnover may actually quantify spatial turnover, the degree of which is generally unknown. The use of genuine permanent plots thus excludes the occurrence of ‘pseudo-turnover’ inflating observed rates of local colonization and extinction in resurvey studies, especially among rare species (Beck et al., 2017; Verheyen et al., 2018).

Many resurvey studies exploring the possible causes of temporal understorey changes often have to rely on indirect measures of soil conditions and light availability based on the understorey composition itself, typically using the Ellenberg indicator values (e.g. Thimonier et al., 1992, Keith et al., 2009, Verstraeten et al., 2013), as tree layer metrics and soil sampling are lacking. We could confront our observations on herb layer development with direct dendrometric data for both survey periods and (limited) soil sampling data from the first survey. Our results on dendrometric data and canopy cover clearly illustrate the aggradation phase where all four reserves can be associated with, characterized by closed canopies with low gap frequency and steady but significant buildup of basal area and growing stock (Bormann & Likens, 1979; Leibundgut, 1978; Korpel', 1995; Saniga & Schütz, 2001). Only in two out of 183 plots, a significant decrease in basal area of living trees was recorded, indicating gap disturbance; less than 10% of the plots showed slight decreases related to single tree dieback, but retained a high canopy cover of over 80%. These results are fully in line with most studies in secondary non-intervention forest, but also other studies in managed forests with increasing Basal Area or crown coverage and less frequent canopy disturbances (e.g. Kirby et al., 2005; Becker et al., 2017; Heinrichs and Schmidt, 2017 , Peterken & Mountford; 2017). Some authors (e.g. Plue et al., 2013) perceive a problem of unnatural prolonged canopy closure in secondary non-intervention forests. Due to the more uniform age structure of the original stands, gap formation may be more infrequent than in natural forests, leading to unnatural long periods of deep shadow, and loss of species, even shade-tolerant species. Disturbance frequency is indeed much lower in strict forest reserves than in managed forests, where 10-15% of the forest area may be subject to management interventions on a yearly basis (6-12 yearly thinning rotations, final harvest rotations of 120-150 years). Nonetheless, the registered disturbance rate in the studied sites does not appear to be very different from reference sites. A large-scale study in the primary old-growth beech forest of

Uholka (Ukraine) revealed disturbance frequencies and canopy gap occurrence in natural beech forests covering less than 1 % of the surface area (Hobi et al., 2014; 2015). The recorded gap frequency is also in line with figures from other primary old-growth forests where gaps also cover less than 5% of the forest area (Meyer et al., 2003; Kenderes et al., 2008).

Finally, overall species composition and developments of the herbaceous layer were analogous in all sites, notwithstanding the apparent significant differences for several soil characteristics (see annex). Apparently, the recorded differences are outside of the ranges where they become of high relevance to the vegetation. The only factor that was within the critical range of several species was the soil pH, but this parameter was very similar in all sites.

4.5.2 Decline in species richness: less is more ?

We recorded a significant loss in species richness, both at site and at plot level. This is in line with several other studies where previously managed forests with frequent canopy cover disturbances evolve towards continued high canopy cover due to abandonment of management (e.g. Paillet et al., 2010; Boch et al., 2013; Lelli et al., 2019) or extensification of former forest management practices, e.g. when coppice-with-standard forests are replaced by more extensively managed high forest (e.g. Van Calster et al., 2007; Hédl et al., 2010; Kopecký et al., 2013; Müllerová et al., 2015; Becker et al., 2017). This is in accordance with the Intermediate Disturbance Hypothesis (IDH) of Connell (1978) and is especially true for forest stands with a legacy of past use due to the immigration of non-forest plant species and the higher frequency of taxa related to disturbance that were promoted by frequent management interventions, reduced canopy cover, litter removal, activation of seed bank and soil disturbance by logging trails (Brunet et al., 1996; Boch et al., 2013).

However, not all studies record a lower species richness in unmanaged forests. According to Kaufmann et al. (2017), it is a question of scale: often comparisons are made on plot-level data. In their study, production forests indeed appeared richer in species when small sampling numbers are considered (20 plots of 500 m²).

However, this relation tended to reverse for 40 plots and beyond, and extrapolated species number/plot number curves of unmanaged forests further increased and crossed the production forest curves. Gap-related, light demanding species that are frequently found and rather evenly distributed in managed forests may still be present in the unmanaged forest stands but with much lower occurrence due to lower frequency of gap disturbance, and therefore be missed when standard sampling efforts are involved (Lelli et al., 2019). Also Burrascano et al. (2017) compared managed and unmanaged mesic beech stands in Italy and concluded that the species richness and beta-diversity did not differ between managed and unmanaged stands, but the species composition was significantly different. Šebesta et al. (2017) also did not find significant differences in species richness but a different composition when comparing coppice forests and high forests in Romania. Herb species with various environmental demands (both semi-shade and light-demanding species and grassland-related species) were more frequent in coppices whereas high forests had more vernal species and shade-tolerant species. They conclude that intensification of management (like coppice restoration) may be especially beneficial for populations of thermophilous and non-forest species with generalist dispersal strategies. Also Brunet et al. (1996) recorded a higher species richness in heavily disturbed managed plots, but mainly consisting of non-forest species; in the unmanaged plots, species richness remained constant with typical forest herb species enduring well. In managed forests, typical specialist forest taxa are increasingly replaced by species with broader ecological niche, that tolerate higher disturbance levels, disperse more rapidly and often are more competitive (Kaufmann et al., 2017).

Several authors therefore conclude that a loss in species richness due to non-intervention not necessarily is detrimental to the overall conservation status of the forest: close-to-nature composition of the herb layer is more important than maximum species richness (Schmidt, 2009; Paillet et al., 2010; Mölder et al., 2014).
Moreover, a decline of species richness of vascular plants not necessarily indicates a global decline in species richness, as this development may coincide with strong opposite developments of other species groups such as saproxylic beetles or fungi (Paillet et al., 2010; Sabatini et al., 2016; Burrascano et al., 2018).

Boch et al. (2013), Sabatini et al. (2016), Burrascano et al. (2017) and Lelli et al. (2019) therefore all conclude that the total herbal species richness is not suited as an indicator for the conservation status of forests, but rather indicates disturbances, as decline in species richness mainly relates to typical disturbance-related and ruderal species, and that their abundance in managed forests is an artifact of anthropogenic disturbances. Their decline can be interpreted as a succession and recovery to a more natural, original species pool and relative abundances and frequencies of species of natural forest types. They suggest that relative share of trait-based functional groups and sets of typical and diagnostic species (cfr. Schmidt et al., 2011; Scolastri et al., 2017) are to be considered as better indicators of ecological quality of the vegetation than species richness itself.

4.5.3 Non-random losses

As in many other studies, we noticed strong differences in the development of species groups with differing ecological strategies. Strongly declining and disappearing were species with low affinity to forests (Schmidt et al., 2011) and typical light-demanding gap-related species (Class 1.2 according to Schmidt et al., 2011). Many of the species that disappeared from the survey already had low frequencies and cover at the first survey (1-2 plots on a total of 183). With such low frequencies, losses due to random population fluctuations and stochastic events are expected (Peterken & Mountford, 2017). Some of the lost species are not characteristic for forest ecosystems and their presence in the forest was clearly anthropogenic (such as *Poa trivialis, P compressa, Taraxacum,…*). Other species are specifically related to, or promoted by disturbance and soil compaction related to harvest operations such as *Persicaria hydropiper, Juncus effusus, Moehringia trinerva, Carex remota* and *Scrophularia nodosa* (Brunet et al., 1996; Mölder et al., 2014; Petzold et al., 2018).

We also see important losses both in frequency and cover of light-demanding forest species and competitors, the typical gap-dwelling species. These species clearly prospered due to (unnaturally) high shares and frequency of disturbances by former management. Unmanaged and primary old-growth forests commonly exhibit strong dominance of the closed-canopy developmental stages, with associated low species richness of very specific shade-tolerant and vernal species (Petzold et al., 2018) but with swift development to high abundances of gap-dwelling species in natural disturbance gaps (Naaf & Wulf, 2007; Kelemen et al., 2012). Standovár et al. (2017) studied the dynamics of the vegetation in a primary old-growth beech forest in Hungary, focusing on vegetation development in recent and three year old closing gaps. Colonization events and increasing species richness and herbaceous layer cover prevailed in the newly created gaps, but a swift decrease in species richness and herbaceous layer cover, as well as high species turnover, characterized the closing gaps. A steady but pronounced decrease in the total cover, but low species turnover was detected in the continued closed-canopy stands with survival of the majority of the closed forest specialists. These gaps, and the associated species are indeed infrequent and ephemeral, but are steadily available at larger scale, allowing for a stable species pool, including gap-related species, in a cyclic pattern (Ujházy et al., 2005; 2007; Šamonil & Vrška, 2008; Standovár et al., 2017; Tinya & Ódor, 2016; Kaufmann et al., 2017; 2018).

The declining disturbance-related species in unmanaged forests are good dispersers (anemochores or endochores) or produce long-lived seed banks (cfr. Thomson et al., 1997), thus can rapidly re-emerge when canopy disturbance occurs. Kelemen et al. (2012) focused on species composition and dynamic response of herb vegetation over a period of eight years in newly established (small and medium sized) artificial gaps in a closed-canopy managed beech forest. They recorded an overall low herbaceous cover and low species richness before gap creation, that increased dramatically after gap formation. This total species richness remained high over the next six years, while species turnover decreased slightly. By the end of the observation period, colonization and extinction rates became equal. New colonization following gap creation primarily consisted of species with both long distance dispersal and long-term persistent seed banks. Later on, not only did the number of new occurrences in this group decline, but their relative importance became smaller. Also Naaf & Wulf (2007) and Van Calster et al. (2008b) came to the same conclusion: colonization of forest gaps mainly comes both from an in situ soil seed bank and through long distance seed dispersal.

Results for Ancient woodland indicator species (Hermy et al., 1999) were not significant, or even decreasing. This may be surprising on first glance, but as Lelli et al. (2019) point out, this list is primarily based on characteristics of land-use continuity and connectivity, and not on canopy conditions, so includes both light-demanding species related to forest gaps and species of closed-canopy forests.

4.5.4 Flourishing in the shade: vernal geophytes and shade-tolerant summer- and wintergreen species

Species performing well under the conditions of increased canopy cover and decreased disturbance frequency are mainly shade-tolerant hemicryptophytes (*Athyrium, Dryopteris*,…) or evergreen (*Hedera helix*) and shade-evading vernal geophytes (*Anemone, Allium,…*). They are increasing both in frequency and cover. Other typical ancient woodland indicating vernal geophytes (*Hyacinthoides non-scripta, Paris, Narcissus, Arum, Oxalis,…)* managed to remain. They are defined as 'herbaceous Dryad species' by Decocq & Hermy (2003), having comparable plant-ecology-strategy schemes (PESS) characterized by a K-strategy, slow growth rates but high longevity, late sexual maturity, a low production of seeds and low dispersal ability due to heavy barochoreous or myrmecochoreous diaspores, a lack of persisting seed banks and a capacity for vegetative multiplication and clonality.

These results are in line with many other studies that also showed an overall loss of species, except for vernal geophytes and other typical shade-tolerant closed-canopy forest plant species that manage to persevere in continuous closed-canopy conditions and even show a distinct increase in cover. Particularly, the strong expansion of *Anemone nemorosa* and *Allium ursinum* after abandonment of management or extensification to low frequency canopy openings was also recorded in many other studies (Barkham, 1992; Van Calster et al., 2008a; Müllerová et al., 2015; Becker et al., 2017; Heinrichs & Schmidt, 2017; Vojík & Boublík, 2018; Nagel et al., 2019). Also Peterken & Mountford (2017) and Kirby et al. (2005) register a decrease in total species richness but an increase in vernal geophytes like *Anemone nemorosa, Allium ursinum, Hyacinthoides non-scripta, Narcissus pseudonarcissus and Millium effusum* in abandoned coppice forests in the UK.

Some studies do, however, register a decline of shade-tolerant vernal geophytes with transition from coppice to high forest or non-intervention. Decocq et al. (2004) registered lower presence and cover of vernal geophytes and shade-tolerant perennials in selectively harvested continuous cover high forests (SC) as compared to coppice-with-standards (CWS). However, the SC forest stands showed a much higher disturbance frequency of 4-8 years, while the CWS-stands were harvested every 30 years. Cutting intervals in SC appear to be shorter than recovery times, so that early successional species-dominated communities are maintained. Vernal geophytes and shade-tolerant perennials seem to be limited by the frequency of disturbance rather than by the severity of disturbance, with canopy cover density thus playing a subordinate role. Indeed, also Godefroid et al. (2005) recorded that the frequency and cover of several herb layer species, including *Anemone nemorosa*, was reduced for at least thirteen years following a clear cut. De Keersmaeker et al. (2011) studied the development of forest plants on a clearcut area: they noticed that most shade-tolerants decline in cover shortly after the clearcut, due to competition with typical competitors (gap-species), and take about a decade to recover. On the other hand, Plue et al. (2013) also recorded a lower cover of *A. nemorosa* in the ‘urwald’-area of the Hasbruch forest, as compared to 120 year old beech stands, and relate this to prolonged continuity of deep shade. However, the so-called ‘urwald’ was a wood pasture with half-open canopy up to 1930 (Pott & Hüppe, 1991), so has a shorter deep shade continuity than the 120 year old beech stands, where the geophytes performed best.

Also other authors state that these vernal geophytes may be declining due to increased forest cover (e.g. Van Dort et al., 1999). Baeten et al. (2010a) observed a decline in frequency of several ancient woodland indicators, including vernal geophytes like *Anemone nemorosa, Polygonatum multiflorum* and *Primula elatior* in a number of ancient woodland patches in Flanders, and see a correlation with increased shade but also with the desiccation and eutrophication associated with the intensification of the land use in the surrounding landscape. Lameire et al. (2000) recorded a significant decrease in mean cover of *Anemone nemorosa* and also assumed this was related to an increased tree cover and lowering groundwater table. In both studies, species relaxation after historical forest fragmentation, i.e. paying off the extinction dept, may also have contributed to the losses in these highly fragmented forests (Baeten et al., 2010a). Baeten et al. (2009a) recorded significant changes in species composition in their study resurveying 50 year old relevés in Meerdaal forest, covering both managed and unmanaged stands, but excluding recently disturbed sites. Especially strong decrease in cover of vernal geophytes like *Anemone nemorosa* was striking. Redundancy analysis pointed to increased shade as main factor, but also soil acidity increased and a majority of plots entered the aluminium buffer range, which potentially affected herb layer composition. We now see a clear recovery of vernal geophytes in the unmanaged reserves (E and P) in the same forest, although shading has further increased. This indicates that former decline of shade-tolerant species was most probably due to acidification because of N-deposition, and not increased shadow pressure. Indeed, what all these studies with decreasing cover of vernal geophytes have in common is that they are all located in forests that were exposed to high deposition loads of Nitrogen, thus combining increased shadow pressure with acidification. Several authors of the referred studies (e.g. Van Dort et al., 1999; Lameire et al., 2000; Baeten et al., 2009a) pointed out that they could not disentangle both effects.

When species such as *Anemone nemorosa* do disappear under closed canopy conditions, this is often due to acidification and Al-toxicity (Falkengren-Grerup & Tyler 1993). When pH levels reach the aluminium-buffer range, aluminium is released in the soil solution, resulting in toxicity to many plants, including *Anemone*. This pH threshold is regarded as a critical point for the successful establishment and growth of forest herbs in deciduous forests (Falkengren-Grerup & Tyler 1993). Wittig (2008) introduced rhizomes of *Anemone* into three different soil types in a beech forest and showed that soil acidification resulting from industrial air pollution inhibited the successful establishment of a population over the course of nine growing seasons. Contrary to the assumption of Baeten et al. (2009a), our results indicate that with reduced deposition pressure, recovery still appears possible (see below).

4.5.5 Development of specific species

Specific species that perform particularly well in the secondary non-intervention sites are *Anemone nemorosa, Allium ursinum, Hedera helix,* the different *Dryopteris* species and *Milium effusum.*

Anemone nemorosa showed an overall strong increase though different among sites. There was a very significant increase in cover in E and P, but non-significant increases in T and J. In T, the species already had a high cover during first inventory, explaining why the further increase was no longer statistically significant. In J, vernal vegetation is highly dominated by *Hyacinthoides non-scripta*, directly competing *A. nemorosa* and preventing this species to develop high cover. A similar phenomenon was also observed by Heinrichs & Schmidt (2017) with *A. ursinum* outcompeting *A. nemorosa*, leading to a local decline of the latter.

As stated before, our result is fully in line with other studies where increased canopy cover leads to increased cover by *A. nemorosa* (e.g. Kirby et al., 2005; Heinrichs et al., 2012; Van Calster et al., 2007; 2008a; Nagel et al., 2019). In order to evaluate whether this development is specific for unmanaged stands, or is just part of a general trend, we compared our results to the regional forest inventory, where similar vegetation relevés are performed and repeated (semi-permanent plots). We selected inventory plots in managed, ancient woodland sites on loess. Only 56 plots met these requirements, so the sample is very limited but also indicated a moderate increase of *A. nemorosa,* be it much less explicit than in the studied unmanaged reserves. This increase could not be statistically substantiated.

Allium ursinum is now still absent at the sites in Meerdaalwoud (E and P), but is rapidly expanding in the forests of T and J. We analysed the expansion of dominant ranges of *A. ursinum* in T and recorded expansions up to 30 m after ten years (Van de Kerckhove & Vandekerkhove., 2016). A strong expansion of *A. ursinum* was also observed by Heinrichs & Schmidt (2017). According to these authors, the species appears to benefit from early spring warming and a prolongation of the vegetation period. *Allium* also benefits from increased availability of phosphorous and nitrogen and may therefore also be promoted by moderate levels of nitrogen deposition (Heinrichs et al., 2012).

The expansion of *Hedera helix* is also in line with other studies. A spread of *H. helix*. into Central European forests has been observed during the last 20 years (Heinrichs & Schmidt, 2015). As this species is susceptible to intensive frost, and is evergreen, allowing for photosynthetic activity also in autumn and winter when temperatures are high enough, it is believed that climate change with mild winters will be beneficial to this species (Iversen, 1944; Dierschke, 2005; Diekmann, 2010). Also Naaf & Wulf (2011) and Becker et al. (2017) demonstrated a distinct increase in the distribution of winter-green species and species with more oceanic distributions such as *H. helix* (and *Ilex aquifolium*). The spread of *H. helix*, however, also goes along with higher nitrogen availability and a reduction in browsing pressure. A fertilization experiment underlined a positive impact of N and P on the *H. helix* abundance (Heinrichs & Schmidt, 2015). Due to its high shade-tolerance, this species also thrives in the closed-canopy conditions of unmanaged forests.

Strong increase of shade-tolerant fern species was observed in *Dryopteris carthusiana, D dilatata, D filix-mas and Athyrium filix-femina.* They all clearly increased both in frequency and cover. Several elements play a role here: all these ferns species are known to grow in deep humus rich soils and germinate and develop well on decaying logs and branches (Seifert, 1992; Page, 1997; Waal et al., 2001; Zielonka & Piątek, 2004; Rünk et al., 2012). Due to litter and deadwood accumulation (see Annex 5 for details), regeneration and growing conditions for these species have significantly improved. These species, especially *D. carthusiana*, require high air humidity conditions (Rünk et al., 2012), associated with closed canopy forests. Finally, these species are also considered to benefit from N-deposition (Thimonier et al., 1992; Verheyen et al., 2012).

The trends for other typical shade-tolerant species like *Milium effusum, Oxalis acetosella and Lamium galeobdolon* were divergent. Where *Milium* clearly increased in cover, the other two species did not significantly change. Some shade-tolerant species such as *Maianthemum bifolium, Polygonatum multiflorum* and *Convallaria majalis* even remarkably decreased in frequency (but limited change in cover) over the two survey periods. This was also observed by other studies (e.g. Van Calster et al., 2008a). Both *C. majalis* and *M. bifolium* mainly reproduce vegetatively, and require soil disturbance for successful recruitment of seedlings (Kosiński, 2008; Vandepitte et al., 2010). Vandepitte et al. (2010) also found very low genotypic diversity and sexual reproduction for *C. majalis* in the Meerdaal Forest complex, leading to almost monoclonal populations with very low or even absent fruit set. Populations consisting of multiple genotypes mainly occurred in locations with a thin litter layer. Baeten et al. (2009b) registered a significant effect of litter removal on the recruitment success of seedlings of *Polygonatum multiflorum*. As leaf litter tends to accumulate in non-intervention forests, the negative interaction between genotypic diversity and reproductive success in all three species may result in abandonment of sexual reproduction and a lack of recruitment. Due to stochastic events, growing sites may disappear and are not compensated by new establishments if soil disturbance becomes infrequent compared to managed conditions, thus leading to declined frequency of these species. Also Van Calster et al. (2008a) indicate sensitivity to increased litter amounts as possible explanation for the decline of these species. The combined effect of litter accumulation and increased shade explains the strong decline of species like *Luzula pilosa*. Other species are not hindered or even promoted by thick leaf litter layers. The stable and increasing shade-tolerant species *Milium effusum, Oxalis acetosella* and *Lamium galeobdolon* combine a high tolerance to heavy shading and thick litter layers (Packham, 1978; De Frenne et al, 2017), giving them a competitive advantage to the previous species. The increased leaf litter cover may even promote geophytes like *A. nemorosa* and *H. non-scripta* as it is not hindering their development, but even protect the belowground plant parts to late spring frost events (Baeten et al., 2010b; Baltzinger et al., 2012). The reason why *O. acetosella* and *L. galeobdolon* are not increasing in the unmanaged forests is unclear, but may be related to competitive exclusion by other species (like *Anemone nemorosa*) that increased in cover (Van Calster et al., 2008a).

Finally, the development of the light-demanding species of gaps, like *Urtica dioica, Pteridium aquilinum* and *Rubus fruticosus* are evidently linked to the overall high canopy cover. The declines of *Urtica* and *Pteridium* could not be statistically substantiated due to too low frequencies and cover at both surveys. *Rubus* remains omnipresent but shows low cover rates at both surveys, explaining why developments were not significant. All these species however remain present as persistent relic populations or in the seed bank, stand-by to promptly respond to canopy disturbances. For *Pteridium,* it is known that it can survive periods of heavy shade, up to relative light levels of 4%, quickly developing to dense vegetations when fully exposed to daylight (Marrs & Watt, 2006).

4.5.6 Environmental developments that may support the recovery of certain species.

The recorded important expansion of species like *A. nemorosa* in the Meerdaal forest sites is remarkable when compared to previous studies in this forest complex, reporting strong decreases (e.g. Baeten et al., 2009). We assume that this remarkable recovery can be mainly explained by soil recovery due to decreased N-deposition load (cfr Verstraeten et al., 2012; 2018). Current levels of deposition are still high and within the range of the critical loads of nitrogen deposition reported by Bobbink et al. (1998; 2010), that can still cause loss of understorey species diversity and alter the species composition of forest understoreys. Still, deposition loads appear to have decreased to a level that can lead to recovery of forest soils (Baeten et al., 2010b ; Dirnböck et al., 2018; Schmitz et al., 2019). Johnson et al. (2018) and Verstraeten (2018) found that the Acid Neutralizing Capacity of the soil at 10–20 cm indeed increased in acid-sensitive soils indicating a recovery of the soil. This may subsequently result in recovery of understory vegetation.

Recovery from N-deposition was also described by Riofrio-Dillon et al. (2012) for France. Based on a very large set of country-wide vegetation data covering several decades, they concluded that floristic reconstructed pH trends demonstrate a gradual cessation and recovery from acidification of French forests after a period of intense atmospheric pollution. Vanhellemont et al. (2014) also recorded some indications of recovery from soil acidification in an ash forest stand where N-deposition distinctly decreased. Moderate levels of N-input may even be beneficial to specific species and has been demonstrated for *A. ursinum, A. nemorosa* and *H.helix* (cfr resp. De Frenne et al., 2018 and Heinrichs et al., 2012; Heinrichs & Schmidt, 2015).

4.5.6.1 Enjoying the shade, avoiding the N-time bomb.

Being well adapted to a specific habitat, diagnostic shade-tolerant forest herb species are generally sensitive to habitat variations and share characteristics such as lower dispersal ability or limited seedling recruitment, along with the need for long-term undisturbed habitats for colonization (Brunet & Von Oheimb, 1998; Hermy et al., 1999). Vild et al. (2013), Scolastri et al. (2017) and de Lombaerde et al. (2018) all refer to the risk that canopy opening increases soil surface temperature and therefore microbial activity and litter decomposition may result in increased nutrient availability. This process limits the abundance of shade-tolerant species and favors the spread of light- and nutrient-demanding, competitively strong species.

The risk of characteristic shade-tolerant species to be outcompeted by ruderal and light-demanding tall competitive species in disturbance gaps is especially high in areas with increased nitrogen availability due to atmospheric deposition (Bobbink et al., 2010; Dirnböck et al., 2014; De Frenne et al., 2015). Becker et al. (2017) and Verheyen et al. (2012) both emphasize that the competitive advantage of ruderals and competitors is enhanced by N-accumulation in the litter layer after decades of N-deposition. The effects of N-accumulation however are currently not strongly expressed in vegetation developments due to concurrent increases in canopy cover, holding back the decomposition of litter, and maintaining the competitive advantage of shade-evading and shade-tolerant species. However, a swift and massive release of the accumulated N is expected upon canopy opening and litter decomposition (described as the N-time bomb), which may lead to massive development of nitrophilous competitive and ruderal species outcompeting the diagnostic forest species, including oligothrophic light-demanding forest gap species. A strong community reordering and possible species loss could be expected (Verheyen et al., 2012). The high canopy cover pressure and low frequency of canopy gaps in unmanaged forests prevent these processes to occur and therefore supports the conservation and development of shade-tolerant characteristic forest species.

4.5.6.2 (Positive) effects of climate change?

Climate change may also have a positive effects on performance of certain vernal geophytes. This is especially true under continued closed-canopy conditions, as they are prevailing in unmanaged forests. Higher average soil temperature in spring increased both seed production, rhizome and shoot growth of *Anemone* (Phillip & Petersen, 2007; De Frenne et al., 2010a; 2010b;), and may also lead to longer growing season in spring (cfr Kirby et al., 2005; Heinrichs & Schmidt, 2017). According to Jantsch et al. (2014) positive effects of increased temperature can be expected for *A. nemorosa, Convallaria majalis, Melica uniflora* and *H. Helix*, but negatieve effects are expected for species like *Maianthemum bifolium, Paris quadrifolia, Sanicula europaea* and *Viola riviniana*. This advantage though may also be subdued by earlier tree leaf phenology (Phillip & Petersen, 2007; Bigler & Bugmann, 2018). Menzel et al. (2006) found an evident signal of advancing leaf unfolding, flowering and fruiting in wild plants in almost 80% of the records averaging 2.5 days per decade between 1970 and 2000.

On the other hand, decreased soil moisture due to severe drought events in spring may negatively influence the performance of species like *A. nemorosa* (Lameire et al., 2000; Phillip & Petersen, 2007) or *D. carthusiana* (Rünk et al., 2012). In closed-canopy forests, however, this risk is strongly reduced after leaf unfolding by the specific microclimate with higher relative air humidity, soil moisture and buffered air temperatures (e.g. Schmidt et al., 2017). An extensive world-wide analysis by De Frenne et al. (2019) shows that closed-canopy forests can function as a thermal insulator, cooling the understory when ambient temperatures are hot (on average with 1.7°C; for maximum temperature even up to 4°C) and warming the understory when ambient temperatures are cold (+ 1.1°C). This may prove to be essential for the survival of closed-canopy forest species. De Frenne et al. (2013) already demonstrated that microclimatic effects brought about by forest canopy closure can buffer biotic responses to macroclimate warming, thus explaining an apparent climatic lag. The thermophilization of ground-layer plant communities is attenuated in forests whose canopies have become denser, as is the case in most strict forest reserves. Conversely, increases in harvesting that open forest canopies can accelerate thermophilization of temperate forest biodiversity, and lead to loss of species requiring cooler conditions.

4.6 Conclusion

Our study revealed an overall loss of species richness at all sites, and a trend towards homogenization of the vegetation. This can be considered as a loss of natural value and diversity with a trend towards mesic forests (cfr Van Calster, et al., 2007; Hédl et al., 2010, Heinrichs & Schmidt, 2017). However, it can also be regarded as a natural succession and restoration of a more genuine ‘characteristic vegetation’ where species richness is generally low and light demanding species are rare and ephemeral. High species richness in this context indicates management-related disturbances rather than conservation status of forests (cfr. Boch et al., 2013, Sabatini et al., 2016; Burrascano et al., 2017; Lelli et al., 2019).

Secondary strict reserves may go through a longer period of deep shade on larger area due to lower heterogeneity of habitats compared to natural woodlands, due to the cohort-like age structure. This may involve a risk of irreversible loss of species. On the other hand, the dense closed canopy of unmanaged forests also provides the necessary buffer against release of accumulated nutrients due to atmospheric deposition, and more frequent summer droughts and temperature extremes due to climate change. Risk of loss of certain herb species should not be a pretext to refrain from establishing new strict reserves in formerly managed forests. These reserves are often embedded in larger, managed forests and open countryside where the species that are jeopardized by the cessation of management should be able to survive. Moreover, many of these species have long lasting seed bank and good dispersal abilities, making them well adapted to the infrequent and ephemeral disturbance events in unmanaged forests.

It is evident that rare light-demanding vegetations with high conservation value (e.g. Hédl et al., 2010; Müllerová et al., 2015; Heinrichs & Schmidt, 2017) or containing shade tolerant species that need recurrent light phases to maintain viable populations in order to assure their long-term survival, such as *Orchis mascula* or *Primula vulgaris* (Jacquemyn et al., 2008; Valverde and Silvertown, 1998) should not be included in these unmanaged areas. Like the species related to them, active and passive (non-intervention) conservation strategies are complementary (Vandekerkhove et al., 2016b). In regions with long history of active forest management, a combined approach with sufficiently large unmanaged areas and areas with active management (specific conservation management or integrated in regular multifunctional management) give the best assurance for overall conservation and development of forest biodiversity.

Veniet tempus quo ista quae nunc latent in lucem dies extrahat et longioris aevi diligentia (...) Quam multa animalia hoc primum cognouimus saeculo, quam multa negotia ne hoc quidem! (...) Rerum natura sacra sua non semel tradit; initiatos nos credimus: in vestibulo eius haeremus.

The time will come when diligent research over very long periods will bring to light things which now lie hidden. (…) How many animals we have learned about for the first time in this age; how many are not known even now! (…). Nature does not reveal her mysteries once and for all. We believe that we are her initiates but we are only hanging around the forecourt.

Lucius Annaeus Seneca (4 BC -, 65 AD) Quaestiones Naturales, Liber VII, 25-30

Look deep into nature, and then you will understand everything better.

Albert Einstein (1879-1955)

Chapter 5: Development of fungi and a selection of faunal groups as a consequence of greater presence of elements of late successional stages – the case for Flanders

---

After: Vandekerkhove, K., De Keersmaeker, L., Walleyn, R., Köhler, F., Crevecoeur, L., Govaere, L., Thomaes, A., Verheyen, K., 2011. Reappearance of old-growth elements in lowland woodlands in northern Belgium: do the associated species follow? Silva Fennica 45, 909-935.

5.1 Abstract

The forest cover of the western European lowland plain has been very low for centuries. Remaining forests were intensively managed, and old-growth elements like veteran trees and coarse woody debris became virtually absent. Only over the last decades, these old-growth elements progressively redeveloped in parks, lanes and forests, and have now reached their highest level over the last 500-1000 years. Biodiversity associated with these old-growth elements makes up an important part of overall forest biodiversity. The ability of species to recolonize the newly available habitat is strongly determined by limitations in their dispersal and establishment. We analyse the current status and development of old-growth elements in Flanders (northern Belgium) and the process of recolonization by means of specific cases, focusing on saproxylic fungi and saproxylic beetles. Our results show that 'hotspots' of secondary old-growth, even isolated small patches, may have more potential for specialized biodiversity than expected, and may provide important new strongholds for recovery and recolonization for an important share of late-successional species.

5.2 Introduction

5.2.1 A long history of low forest cover and fragmentation

Flanders (Northern Belgium) is a highly industrialised, densely populated area with over 450 people per km² (FPS Economy, SMEs Self-employed and Energy, 2009). Its countryside has been intensively used and altered by humans over centuries. This is clearly reflected in the area and characteristics of forest cover. The present forest area is about 146.000 ha (i.e. 11% of the total area) and together with Ireland (10%), the Netherlands (11%) and the UK (12%), Flanders ranks among the least forested regions of Europe (MCPFE, 2007). This low forest cover is not a recent phenomenon. As early as the first century BC, forest cover had gradually decreased to about 50% of the total land cover, followed by a slight recovery during the Dark Ages (4th-8th century AD) (Verhulst, 1995). Especially during the Full Middle Ages (12th-13th century AD) a steep decline of forest cover took place: demographic pressure led to woodland clearance to create more farmland. Around 1250 less than 10% of forest cover was left (Verhulst, 1995; Tack and Hermy, 1998,). Since that time, total forest cover has remained at a similar figure, with a slight increase in the 18th century to about 12%, and a minimum of about 9% halfway through the 19th century. Although total forest area remained relatively stable during the last centuries, the spatial distribution of the forests dramatically changed with deforestation on fertile loamy soils (30-50% decrease) and new afforestation on former heathlands and alluvial meadows (De Keersmaeker et al., 2001; Vandekerkhove et al., 2005; Hermy et al., 2008). As a result, the current forest is severely fragmented both in space and time. Only a small fraction (15 %) of the current forest cover is considered to be ancient woodland, which is defined as having remained continuously forested between the end of the 18th century and now (De Keersmaeker et al., 2001; Hermy and Verheyen, 2007; Hermy et al., 2008). Most forests are 19th and 20th century afforestations, in particular even-aged poplar (*Populus x euramericana* and *Populus x interamericana*) and conifer plantations (primarily Scots pine, *Pinus sylvestris*). They contain trees of less than 80 years old and are now gradually being transformed into mixed stands (Afdeling Bos en Groen, 2001b; Vandekerkhove et al., 2005).

Moreover, the remaining forests were used very intensively over the past centuries in order to maximise the production of resources like firewood, utensils and construction wood (Tack et al., 1993; Tallier 2004). Until the 18th century, most forests were managed as coppice systems, and coppice with standards in the larger estates of nobelty and monasteries on richer soils in the south. High forest was exceptional (Tack et al., 1993; Tack and Hermy, 1998; Tallier, 2004).

This history of low forest cover, shifts through recent deforestations and afforestations, and continuous intensive use is comparable with other regions in the Northwest-European lowlands (the Netherlands, northwest Germany, southern England) (Buis, 1985; Rackham, 1986; Peterken, 1993; Watts, 2006).

5.2.2 Old-growth elements: reappearance after centuries of absence

Large quantities of dead wood and a high density of very large trees are characteristic elements of the late-successional phase of natural forests (Harmon et al., 1986). They are often referred to as ‘typical’ elements for natural forests, that are absent or rare, even in forests under close-to-nature commercial management (e.g. Christensen and Emborg, 1996; Korpel', 1997; Bobiec, 2002). An important share of forest biodiversity is strictly or primarily dependent on these elements for their survival (e.g. Harmon et al., 1986; Kirby and Drake, 1993; Samuelsson et al., 1994; Økland et al., 1996; Esseen et al., 1997; Siitonen, 2001; Heilmann-Clausen and Christensen, 2003; Vandekerkhove et al., 2003; Ódor et al., 2006). For instance, Siitonen (2001) calculated that a decline of the total amount of coarse woody debris by 90-98%, may lead to the disappearance of at least 22-32%, and more probably over 50%, of all saproxylic species. If this habitat loss is combined with habitat fragmentation, this proportion is expected to be even larger. The situation in Flanders (and other regions in the western European lowlands) has even been worse, with very fragmented forests and virtually no large trees and dead wood as a result of the traditional management regime. Indeed, except for some corner trees marking the border between two properties, no standard trees were left to reach sizes over 60-80 cm DBH, as they were too heavy to manipulate and had higher risks of defects. Even in the forest of Meerdaal, famous for its high quantity and quality of standard oak trees, only a few trees were selected to grow to sizes over 80 cm DBH: at the end of the 19th century, the forest only contained about 30 such trees on an area of over 1500 ha (Vandekerkhove et al., 2009b). Century-old user rights involved the right to remove all dead and dying trees both in private and public forests (Tack et al., 1993; Tallier, 2004). Decadent and dead trees and even dead branches on trees were promptly removed. Even the smallest branches were sought after. Older coppice stools that became less productive were entirely taken out, including the root bole. The same was done with the standard trees: they were not cut down, leaving dead stumps, but felled by digging and cutting over of the roots. The root bole was a too precious resource to be left in the forest (Tack et al., 1993; Vandekerkhove et al., 2009b). In the 19th and 20th century, traditional management systems were replaced by high forest management and plantation forestry. These management systems also excluded dead wood and large trees (Branquart et al., 2004). Large tree dimensions were economically not desired (no specific market, difficult to transport, risk of hidden defects like discoloration and rotten core) and forest management was tailored to this. Dead wood was considered a potential source of disease outbreaks, and waste of resource or an indication of negligence.

Only over the last 30 to 40 years, the ecological value of dead wood and veteran trees progressively gained attention in forest management. Over the last two decades, the conservation of a certain amount of dead wood and old trees has been fully integrated in principles and practices of sustainable forest management, together with smaller scale forest operations, longer rotations and transformation of plantations to more mixed stands (Ammer 1991; Burschel, 1992; ONF, 1993; Hodge and Peterken, 1998; Afdeling Bos en Groen, 2001a; Harmon, 2001; Kappes and Topp, 2004). This has lead to a gradual increase of the average stand age and structural diversity of forest stands, and a significant increase of dead wood and large trees.

Regional forest policies, including the Flemish policy, frequently have the explicit goal to further increase both quantity and quality of dead wood and conserve old and large trees, through a two-way approach. In multifunctional forests, the aim is to gradually improve both quality and quantity of dead wood by leaving some of the dead and dying trees during forest operations. For large trees, 5-10 trees per ha should be selected to be left uncut (Afdeling Bos en Groen, 2001a). At the same time, a network of strict forest reserves (SFR) is being developed, covering up to 5% of the forest area. In these, a spontaneous build-up of dead wood and veteran trees to natural levels is taking place (so-called 'secondary old-growth'). Analyses of this process have shown for dead wood an average net accumulation of about 1.5 $m^3.ha^{-1}$ $year^{-1}$ but there is wide variation around this mean (Vandekerkhove et al., 2009a). It is expected to take about one century, on average, to reach natural levels of dead wood estimated at 100-150 $m^3.ha^{-1}.year^{-1}$ (Kraigher et al., 2002; Meyer et al., 2003; Müller-Using and Bartsch, 2003; Christensen et al., 2005; von Oheimb et al., 2005; Vandekerkhove et al., 2009a). As most sites already contain mature and old forest stands, the same time horizon to reach natural densities of large trees (e.g. Nilsson et al., 2002) is expected. It is believed that the combination of these two approaches is necessary and complementary to reach the overall goal of biodiversity conservation and restoration in forests (Parviainen et al., 2000; Frank et al., 2007).

5.2.3 Is recolonization by old-growth-associated species possible ?

Due to the long history of absence of old-growth elements, species typically associated to them are likely to have disappeared completely, or may be restricted to rare relictual fragments of old-growth elements. Nowadays, the availability of redeveloped habitat offers important possibilities for recolonization by old-growth associated species.

Colonization is the joint result of successful dispersal and successful establishment (e.g. Jonsson et al., 2005). In Flanders, studies on colonization and recolonization have primarily been focused on dispersal and recruitment limitations for vascular plants (e.g. Butaye et al., 2001; Verheyen and Hermy, 2001; 2004; Verheyen et al., 2003a; 2003b; Hermy and Verheyen, 2007). These studies show wide ranges in dispersal and recruitment capacities, with particularly low dispersal and recruitment figures for so-called ancient woodland indicator species.

We analysed this potential for recolonization by saproxylic fungi and beetles, two groups with a strong link to old-growth elements, covering a wide range of dispersal limitation and habitat requirements (Kallio, 1970; Solbreck, 1980; Nilsson, 1984; Ranius and Hedin, 2001; Edman et al., 2004a, 2004b). Their response was analysed both using nationwide distribution data (if available) and specific cases from sites with high potential for recolonization: ancient semi-natural woodlands with large amounts of dead wood and very large trees in strict forest reserves. In the discussion, we also linked the development of old-growth characteristics to literature and published trends on cavity-nesting birds.

5.3 Materials and Methods

5.3.1 Quantification of the amount of dead wood and large trees in Flemish forests

We summarised the actual status of dead wood quantity and quality in Flemish forests from data of the forest inventory of the Flemish Region. This inventory uses a systematic sample resulting in 2665 plots (Waterinckx and Haelvoet, 1997). The first inventory of all plots was performed between 1997 and 2000. Since 2009 a second inventory has been conducted, switching to a continuous inventory in which every year about 1/10 of the plots is measured (Wouters et al., 2008). Our calculations are based on the datasets of the first inventory (2665 plots) updated with preliminary results from a selection of plots from the second inventory. Standing trees (both alive and dead) with DBH between 7 cm and 40 cm are sampled in circular plots with a radius of 9 meter; trees with DBH ≥ 40 cm are sampled in a larger circle (R=18 m). Species, status (alive/dead), DBH and height are recorded. Volume calculations for living and intact standing dead trees used regional tariffs based on DBH and height measurements (Dagnélie et al., 1985). Volumes of standing wood fragments (snags) were calculated using formulas of truncated cones. In the first forest inventory, no quantitative data for lying dead wood are available. In the second inventory, additional sampling of lying dead wood is performed using Line Intersect Sampling (Warren and Olsen, 1964), with 3x15 m lines sampled in every plot in 3 fixed directions from the plot centre (Wouters et al., 2008; Govaere et al., 2010). This ‘fan-design’ is also used in other countries (e.g. Böhl and Brändli, 2007). Volumes are calculated using the formula of van Wagner (1968).

An estimate of the density of large and very large trees (over 80 and 95 cm DBH respectively) was derived from the sample of the first forest inventory (total sampled area 271 ha). Because of the very low incidence of occurrence, the sampled population in the forest inventory was very small, allowing no further detailed analysis. Additional inventories were therefore performed in a selected set of ‘hotspot’ sites (Table 5.1). These are ancient woodlands that are known for their relatively high densities of very large trees. A full survey of these sites was done in parallel strips. Every tree surpassing the threshold diameter of 95 cm DBH was registered, and marked in the field (in order to avoid double counts). Tree species, DBH and health status were recorded. In total over 5.000 ha of forest were surveyed in this way.

5.3.2 Saproxylic fungi

Data on fungi are derived from the centralised database on fungal distribution in Belgium (FUNBEL, database of the Royal Flemish Mycological Society - KVMV, before Royal Antwerp Mycological Circle - KAMK). This database contains over 500.000 records on more than 5300 taxa. All records are also geographically positioned based on the national 4x4 km floristic atlas grid. Annual relative occurrences (this is the number of records of one species as a share of the total number of records for all species for that year in the database) were calculated for a selection of wood-decaying fungi: 4 currently widespread species (*Fomes fomentarius, Ganoderma lipsiense, Piptoporus betulinus and Trametes versicolor)* and a group of 21 highly selective and rare species that require a very specific substrate (wood mould in senescent trees and large dead wood) and high spatio-temporal continuity of this habitat (Christensen et al., 2005b). Trends of both groups were analysed by comparing average relative occurrences over the last 5 decades (Kruskal-Wallis rank sum test and paired comparisons with Wilcoxon rank-sum test). Trends in spatial distribution are derived from the comparison of number of occupied 4x4 km grid cells over the last 5 decades.

5.3.3 Saproxylic Beetles

Recent information on distribution and status of saproxylic beetles in Flanders is very limited. An analysis for the entire region based on existent centralised data is therefore not possible. This study compiles the existent recent information from a pilot study on saproxylic invertebrates (Versteirt et al., 2000; Heirbaut et al., 2001) together with a more thorough inventory of one specific site.

The pilot study was performed on 8 locations using a set of standardised sampling techniques: 3 pitfall traps, 3 colour traps, one stem-eclector, a large window-trap and a decoy-window-trap. All sites were ancient woodland sites with a moderate to high potential for saproxylic beetles, covering a wide range of dead wood volumes (8-140 $m^3.ha^{-1}$) and forest patch size (15-4500 ha). Dominant tree species were beech (*Fagus sylvatica*) or pedunculate oak (*Quercus robur*). Investigated sites were: Beiaardbos (beech), Wijnendalebos (oak-beech), Meerdaalwoud (beech), Kolmont (oak+beech), Rodebos (oak+beech) and three sites in Sonian forest (one oak stand, two beech with high resp. low amounts of dead wood) (location of the sites is given in Fig. 1.6).

In 2008 and 2009 a detailed and elaborate inventory was made at one site from the previous set, Kolmont forest reserve (Köhler et al., 2011). This is an isolated forest patch of 17 ha containing an exceptionally high density and variability of habitat for saproxylic organisms, located in the south-east of Flanders (50°47'56.6"N 5°25'28.3"E; see site 29 on the map in Fig. 1.6). It is located in a countryside area with very low forest cover (<5%). In this context it is a suitable site to study the potential for survival and recolonization of saproxylic beetles in a landscape context that is representative for an important share of forest in Flanders. It is a very diverse and well structured mixed forest, on a hilly terrain, covering a wide range of soil conditions (from hydromorph rich alluvial soils to acid dry sandy loam). The forest is dominated by beech (*Fagus sylvatica*), with an important admixture of other tree species like oak (*Quercus robur*), ash (*Fraxinus excelsior*), birch (*Betula pendula*), gray poplar (*Populus canescens*), and sycamore maple (*Acer pseudoplatanus*). The site harbours a relatively high amount of dead wood in all forms and decay stages, and a high density of overmature trees: the amount of dead wood exceeds 40 $m^3.ha^{-1}$, including very large logs and snags, and a total of over 90 living trees with a DBH over 95 cm occur, almost all beech trees (density >5 trees ha^{-1}). The sampling was spread over two years, and was done using window traps (3 normal traps and one decoy trap) 4 glue-rings, light traps and active catch by sifting of wood mould and hand catches on shrub vegetation and fungi. All coleoptera were identified to species level.

Recorded species were attributed to different substrate classes according to Köhler (2000), and their conservation status was assessed based on the Red Lists for Great-Britain, Germany and for Europe (Hyman and Parsons, 1992;1994; Geiser 1998; Nieto and Alexander, 2010), since no Red List for Coleoptera in Belgium exists (except for Carabid beetles; Desender et al., 2008). Indicator species for old-growth continuity were derived from the list developed by Müller et al. (2005) and the Saproxylic Quality Index (SQI) and Index of Ecological Continuity (IEC) developed for the UK for evaluation of the conservation value of sites for saproxylic beetles (Fowles et al., 1999; Alexander, 2004) were calculated.

The results for Kolmont on total species number, number of red-listed species and share of different substrate classes were compared to a diverse set of beech-dominated strict forest reserves in Germany and Luxemburg that were sampled in an identical way (Köhler, 2010a). Furthermore, Hurlbert's modified rarefaction curves (Hurlbert, 1971; Simberloff, 1972) were generated using BioDiversity-Pro software (McAleece, 1997), on original datasets of Kolmont forest and 14 forest reserves in the west of Germany (Köhler, 1996; 2000; 2009) in order to provide a further comparison that is not affected by differences in sample size.

5.4 Results

5.4.1 Dead wood and large trees in Flemish forests

The average volume of dead wood (threshold diameter 7cm) in Flemish forests derived from the first forest inventory was estimated at 7 $m^3.ha^{-1}$. As no concrete data were available for lying dead wood, this figure involved a very conservative estimate of the lying volume (about 3.5 $m^3.ha^{-1}$), based on the average volume of standing dead wood and the ratio of lying to total fractions derived from data in strict forest reserves. Preliminary results from the second inventory (on 221 plots) indicate that the total amount is now surpassing 13 $m^3.ha^{-1}$, with the lying fraction making up more than 70% of the volume. The estimate also indicates that trees with DBH over 40 cm contribute for only 20% in this volume, while trees smaller than DBH 20 cm make up half of the volume.

Based on the first Regional Forest Inventory (NFI), the density of trees over 80 cm DBH is estimated at 0.656 trees per ha (95% confidence interval: 0.564-0.757). Extrapolated over the total forest surface (146 000 ha) this corresponds to approximately predicted 96 000 trees (82 000-110 000). The density of very large trees (DBH>95 cm) is estimated at 0.132 trees per ha (95% confidence interval: 0.094-0.181) corresponding to 19 000 trees (13 700-26 300). About half of the registered trees (both at 80 and 95 cm DBH threshold) are beech trees, and one quarter are oaks (both *Quercus robur* and *Quercus petraea*). This is quite remarkable, as beech and oak stands only make up for about 5 and 15% of the total forest surface area respectively. The remaining quarter are mainly poplars and northern red oaks (*Quercus rubra*).

Detailed full surveys of selected sites showed that the very large trees are not equally distributed over the Flemish forest area but are mainly concentrated in ‘hotspot’ locations. On an area of less than 5000 ha (3% of the total forest area) we registered over 9000 trees over 95 cm DBH, corresponding with more than half of the total number of very large trees estimated in the forest inventory. An overview of trees over 95 cm DBH for the 12 selected locations is given in Table 5.1. This shows that the site ‘Zoniënwoud’ contains more than 1/3 of the estimated total number of very large trees (DBH> 95 cm) in Flanders. Densities are 20 times higher than the average. The forest complexes of Meerdaalwoud and Heverleebos also contain high amounts and densities of such trees. Over 500 of the recorded trees here are oaks, meaning that 10% of all monumental oaks are concentrated in these two ancient woodlands. Other investigated sites sometimes have very high densities of very large trees, but are all much smaller. This is in line with the findings of Götmark and Thorell (2003) for reserves in southern Sweden.

Table 5.1 Overview of monumental trees in 12 selected ancient woodland sites, both in absolute numbers and densities (number of trees per ha) for different DBH thresholds (in cm).

Site	Area (ha)	N >95	N >110	N >125	$N.ha^{-1}$ >95	$N.ha^{-1}$ >110	$N.ha^{-1}$ >125
Zoniënwoud	2475	7069	1867	288	2.86	0.75	0.12
Meerdaalwoud	1320	1230	270	35	0.93	0.20	0.03
Heverleebos	650	230	50	5	0.35	0.08	0.01
Veursbos	156	113	17	2	0.73	0.11	0.01
Neigembos	69	112	7	2	1.62	0.10	0.03
Kluisbos	57	109	19	3	1.91	0.33	0.05
Kolmont	18	95	38	12	5.28	2.11	0.67
Beiaardbos	17	93	15	1	5.45	0.88	0.06
Bellebargiebos	78	59	4	0	0.76	0.05	0.00
Wijnendale	65	53	14	3	0.82	0.22	0.05
Teuvenerberg	40	38	18	13	0.95	0.45	0.32
Bos Ter Rijst	29	35	10	2	1.22	0.35	0.07
Total	**4974**	**9236**	**2329**	**366**	**1.86**	**0.47**	**0.07**

5.4.2 Saproxylic fungi

The comparison of FUNBEL-records shows a clear increase in the registrations for saproxylic species. As shown in Fig. 5.1, the relative occurrence of common and widespread species like *Fomes fomentarius, Ganoderma lipsiense, Piptoporus betulinus* and *Trametes versicolor* have significantly increased over the last five decades (Kruskal-Wallis rank sum: $p<0,001$ for all species separately and the 4 species together), although the trend already starts to level out for several decades. Fomes shows a steady increase over time, while *Ganoderma* and *Piptoporus* appear to have stabilized over the last 40 years. A pairwise comparison over the periods 1970-89 and 1990-2009 for these two species and for all 4 species together show no further significant increase (Welch modified two sample t-test and one sided Wilcoxon rank-sum test: $p>0.05$). Still, comparing the last two decades, all 4 species again showed a renewed increase (one sided Wilcoxon rank-sum test: $p < 0.05$). The number of occupied grid cells also strongly expanded over time. Before 1970, these species were known from less than 3% of all 4x4 grid cells. They now occur in 15 to

30% of all grid cells. This means that they occur in the majority of grid cells containing forest, and can be considered widespread in all forests.

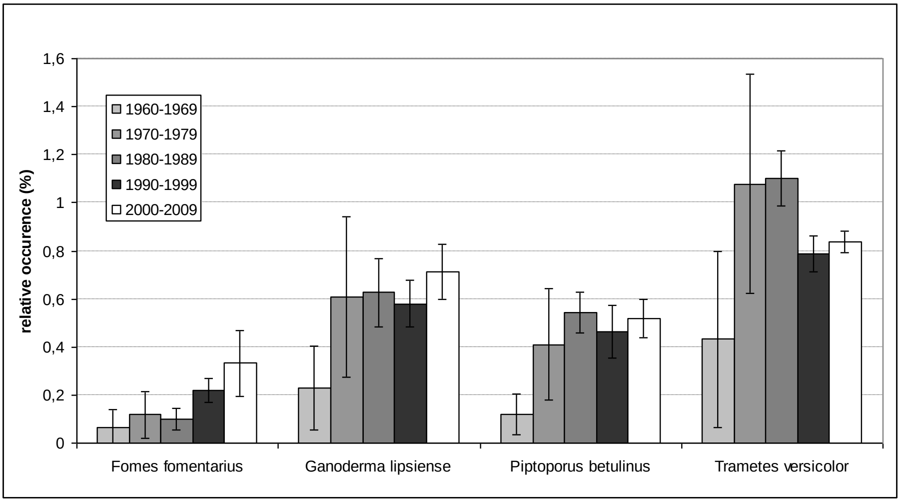


Fig. 5.1 Relative occurrence (= annual number of records of a species as a share of the total number of records that year) of four common and widespread saproxylic fungi in Flanders over the last 5 decades.

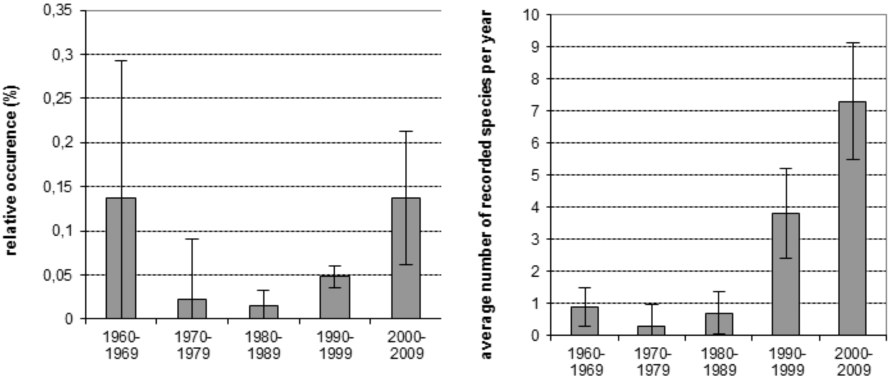


Fig. 5.2 Occurrence of European indicator species of saproxylic fungi with high substrate requirements (Christensen et al., 2005b) in Flanders over the last 5 decades. Left: relative occurrence of all 21 species combined; right: average number of recorded species per year.

The trend for the group of species with high substrate requirements (21 species) is even more explicit (Fig. 5.2). Relative occurrence and average number of recorded species per year have significantly increased over time (Kruskal-Wallis rank-sum; $p<0.001$). The higher values for the first decade are entirely related to one species

(*Inonotus cuticularis*), that was relatively often recorded in the 1960's. Pairwise comparisons over the last two decades and the periods 1970-89 and 1990-2009 show very strong increases both in number of recordings and yearly reorded number of species (one sided Wilcoxon rank-sum test: $p < 0.001$). Until the 1980's, species from this group occurred in less than 1% of all 4x4 km grid cells, while in the last decade, over 7% of all grid cells contained at least one species, with several cells containing 4 species or more.

5.4.3 Saproxylic beetles

The pilot study revealed between 50 and 90 species per site, which is quite limited compared to other inventories (Köhler, 1996; 1999; 2000). Still, between 20 and 30% of the recorded species at every site are considered rare or red-listed in Germany and the UK (Hyman and Parsons, 1992; 1994; Geiser, 1998). Although these inventories probably did not reveal the complete species richness of the sites, they indicated that the species composition did not entirely consist of common fast colonisers, but also included more sensitive species that are susceptible to habitat decline (as shown by their Red List status). Some of the recorded species are known to require a high spatio-temporal continuity of dead wood (e.g. *Elater ferrugineus, Stictoleptura scuttellata)* and are included in the list of indicator species for sites of European importance for saproxylic invertebrates (Speight, 1989).

The additional study of Kolmont forest in 2008-2009 was the first detailed inventory of saproxylic beetles in Flanders. It resulted in a much more complete picture of the total species richness with a total number of 824 species of Coleoptera identified (Köhler et al., 2011). Of these, 315 species are listed on the catalogue of xylobiontic beetles of Germany by Köhler (2000). At least 10 new species for Belgium were recorded. Results of the comparison with other beech forest reserves in Germany and Luxemburg that were surveyed in a similar way (Köhler, 2010) are given in Table 5.2. The total species richness is quite high, placing Kolmont among the most species rich sites (average over 24 sites: 256 species).

This is also clearly illustrated in the rarefaction curves comparing Kolmont with 14 sites in the west of Germany (Fig. 5.3). The estimated species diversity and the steep inclination of the curve for Kolmont indicate a distinctively higher than average species richness.

The distribution of the recorded species over different substrate classes shows a well balanced saproxylic beetle community, including an important share of species living in wood mould, nests and saproxylic fungi, and is in line with the results from other sites in Germany and Luxemburg (Table 5.2).

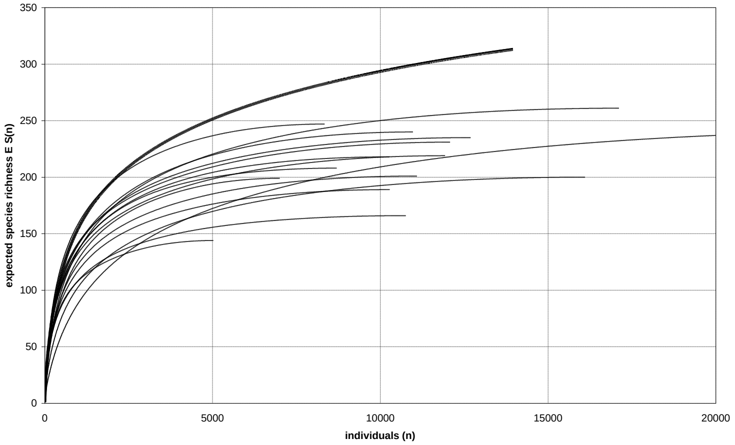


Fig. 5.3 Estimation of species richness using Hurlbert's modified rarefaction curves (Hurlbert 1971; Simberloff 1972) for Kolmont forest (bold line) compared to 14 forest reserves in the west of Germany

Not only the quantity and composition of species surpassed expectations, the list also contains an important share of rare and endangered species (see Annex 7). Almost 30% of all registered saproxylic species in Kolmont (92) occur on the German Red List (average over 24 sites: 24.5%). Seven of these are listed as ‘critically endangered’, 24 as ‘endangered’ and 61 as ‘vulnerable’. More than 100 species are found on the British Red List, most of them in the ‘notable’ categories, but 10 are ‘endangered’(RDB1), 6 ‘vulnerable’ (RDB2) and 15 ‘rare’ (RDB3).

Two species are listed on the new European Red List (Nieto and Alexander, 2010): *Cerophytum elateroides* occurs in the category ‘Vulnerable’ and *Brachygonus megerlei* is on the additional list of ‘Near Threatened’ species. Another species in this category, *Elater ferrugineus* was also found in Kolmont, both in 2000 and in 2011, but not during the two year survey. This species, together with *Allecula* *rhenana, Abraeus parvulus, Micridium halidaii,* and *Batrisodes buqueti* are listed on the German indicator list of species that are considered to be associated with high spatio-temporal continuity of old-growth stand features (Müller et al., 2005).

Table 5.2 Saproxylic beetles: total species number, number of red-listed species and share of species in different substrate classes for the Belgian site of Kolmont compared to a diverse set of beech-dominated strict forest reserves in Germany and Luxemburg that were sampled in an identical way (Köhler, 2010a). Sites are ranked in order of increasing species richness

Reserve	Strict reserve since (year)	Elevation (m asl)	Size (ha)	Average yearly temperature (°C)	Age-range of dominant trees	estimated deadwood share (%)	wood	wood mould	nests	fungi	bark	exsudates	total nr of saprox. beetle species	German Red List 1998	Urwald relic species
Schönbuche	1988	410	27.9	7.8	120-160	4.0	37	30	2	35	63	1	168	23	0
Hohestein	1989	510	26.7	8.0	90-140	0.7	41	30	3	35	63	0	172	30	0
Gold-Ziebachsrück	1988	330	31.3	8.0	120-160	0.5	36	32	1	40	64	2	175	22	0
Eischeid	1982	600	34.0	7.5	100-160	1.5	32	37	1	44	76	4	194	32	0
Niddahänge	1988	560	42.0	6.7	120-240	6.3	33	36	4	55	74	1	203	41	0
Schäferheld	1983	490	23.3	8.0	120-160	1.5	45	35	5	54	73	3	215	41	0
Etscheid	2001	490	40.0	7.9	100-160	1.0	54	34	4	49	74	5	220	33	0
Serrahner Berge	1998	120	73.3	8.0	>200	19.4	47	55	5	50	66	4	227	73	3
Geldenberg	1971	60	22.1	9.8	130-200	2.0	53	44	6	46	73	7	229	44	2
Dohlenwald	2000	50	45.1	8.3	80-120	5.0	61	40	7	56	61	6	231	61	2
Wiegelskammer	1983	410	13.9	8.0	80-120	2.0	54	37	2	54	79	5	231	31	0
Bohnrath	2003	60	34.2	8.2	200-240	5.8	59	58	9	57	75	4	262	79	5
Altwald Ville	1978	135	19.9	9.6	130-180	3.0	68	41	7	53	88	5	262	60	1
Himbeerberg	1991	540	42.0	7.4	140	40.0	60	44	2	52	102	5	265	39	0
Rotenberghang	1991	390	22.0	8.4	100-200	30.0	62	39	5	50	103	6	265	48	0
Stelzenbach	1995	370	74.0	8.6	120-160	3.0	62	51	3	59	86	5	266	41	0
Platte	1978	450	33.9	7.6	100-200	5.0	68	42	5	68	87	2	272	52	1
Heilige Hallen	1998	130	39.2	7.9	280-320	24.6	61	79	11	71	75	3	300	108	13
Laangmuer	2005	400	103.4	9.4	120-180	2.6	76	56	7	72	85	7	302	77	1
Conower Werder	2003	90	49.9	8.2	120-160	13.5	66	68	13	82	81	4	314	115	10
Useriner Horst	1998	60	37.4	8.1	>250	16.2	70	79	10	79	72	4	314	107	8
Kolmont	**1995**	**90**	**17.0**	**9.2**	**140-200**	**9**	**79**	**56**	**16**	**70**	**88**	**6**	**315**	**94**	**5**
Fauler Ort	1938	60	20.8	8.2	>350	27.8	85	93	16	76	80	7	357	149	17
Mummelskopf	1972	300	52.6	8.8	170	20.0	96	71	10	84	116	8	385	105	3
Average value for all 24 sites	**1988**	**296**	**38.6**	**8.2**	**155**	**10.2**	**59**	**49**	**6**	**58**	**79**	**4**	**256**	**63**	**3**

Hotspot sites for saproxylic beetles in Bavaria, Germany contain more than 10 of these species, whereas most investigated sites have two or less (Büssler, 2010).

On the British indices (Fowles et al., 1999; Alexander, 2004), Kolmont has a score of over 800 on the Saproxylic Quality Index (SQI) and 149 on the Index of Ecological Continuity (IEC). Compared to over 150 sites from the UK, the SQI and IEC of Kolmont are only surpassed by Windsor Great Park and New Forest (Alexander 2004; Saproxylic Quality Index… 2009). Sites in the UK with an IEC of over 80 are considered of international importance, deserving special conservation status and management (Alexander, 2004).

5.5 Discussion

The average amount of dead wood in Flemish forests (over 13 $m^3.ha^{-1}$) is not exceptionally high but in line with other European countries: average figures per country in Europe vary from less than 1 to 23 $m^3.ha^{-1}$. (MCPFE, 2007). Nevertheless, we can clearly state that the amount of dead wood has not been as high as it is now over at least 500 years, and probably much longer. The recorded figure, however, is still less than 10% of the amounts to be expected in natural forests in this part of Europe (Kraigher et al., 2002; Meyer et al., 2003; Müller-Using and Bartsch, 2003; Christensen et al., 2005; von Oheimb et al., 2005; Vandekerkhove et al., 2009a). Considering that the climax vegetation in Flanders is forest for over 90% of its territory, the current amount of dead wood represents only 1% of the natural density, is very unevenly distributed, and consists mainly of small diameter material. The same conclusion can be drawn for very large trees: their average density is 10-50 times lower than in natural lowland forests (Nilsson et al., 2002; Bobiec, 2002), and considering the low forest cover, the density of these trees in forest context is 100-500 times lower than in reference conditions. However, this calculation does not take into account the monumental trees in hedgerows, parks and tree rows that occur scattered in the open countryside and that may play an important part in the survival and recovery of old-growth associated species (see below).

Considering the estimates of species loss by Siitonen (2001) – estimated at a minimum of 22-32% and more likely over 50% of all saproxylic species in case of a decline of dead wood habitat by 90-98% - it is expected that forest biodiversity, especially saproxylic communities in Flanders have been decimated in the past and reduced to a small fraction of its original diversity. Due to the very recent increase in old-growth elements, a slow recovery could be assumed, through long distance recolonization - or short distance in case relic populations are still present - of the newly available habitat.

5.5.1 Recolonization: a question of dispersal ability and habitat requirements

As shown in the historic account, old-growth elements have for centuries been completely absent from forests in Flanders. It is therefore assumed that most late-successional species that are strictly related to old-growth elements (dead wood and old trees) completely disappeared from these forests or only managed to survive in very scarce relics.

Over the last decades, conditions for these species have clearly improved in our forests to a level unprecedented over the last centuries, giving perspective for recovery (Ódor et al., 2006; Irmler et al., 2010). The level of recovery is strongly related to the ability of species to recolonize suitable habitat. This colonization is the joint result of successful dispersal and successful establishment (e.g. Jonsson et al., 2005). The success is strongly dependent on the species-dependent dispersal and recruitment potential (e.g. for vascular plants: see Butaye et al., 2001; Verheyen et al., 2003b; 2004; Hermy and Verheyen, 2007). When habitat disappears, species may manage to persist for a period of time -the so called ‘extinction debt- (e.g. Hanski, 1999; 2000). For slow-colonising forest plants in Flemish forests for instance, it was determined that the loss of species due to land use shifts may still be ongoing (Vellend et al., 2006). Similarly, species recolonization of newly established habitat might also be delayed because of lag phases in the dispersal and establishment of populations, the so-called colonization or immigration credit (Hanski, 2000; Jackson and Sax, 2009; Baeten et al., 2010).

Forest birds are a well-studied group of evident good dispersers. Species from the ecological group of cavity-nesting birds, related to mature high forest with dead wood (according to Sierdsema, 1995) are expected to react promptly on the improved condition of the forest habitat. Their response will depend on their reproductive potential and their requirements to the habitat. Woodpeckers (family *Picidae*), especially, have therefore been proposed as good indicators for forest biodiversity (Angelstam and Mikusiński, 1994; Mikusiński et al., 2001). Requirements of the species are diverse with great spotted woodpecker (*Dendrocopos major*) and black woodpecker (*Dryocopus martius)* being less restrictive than others like middle spotted woodpecker (*Dendrocopos medius)* (Rolstad et al., 1998; 2000; Kosiński, 2006; Bocca et al., 2007). Secondary cavity breeders like tits (family *Paridae*), European nuthatch (*Sitta europaea*), and tawny owl (*Strix aluco*) that are dependent on the old cavities provided by the former, are expected to quickly follow.

Trends for Flanders for the period 1990-2002 indeed indicate a significant increase of the breeding population of cavity-nesting birds (Dumortier et al., 2005). Tawny owl showed an increase between 20 and 50%, and European nuthatch, lesser spotted woodpecker (*Dendrocopos minor*) and black woodpecker populations increased by more than 50%. New assessments also confirm this trend for the next 5-6 year period (Van Daele et al., 2010). Comparing the recent population estimates with data covering the period 1973-1977 (Devillers et al., 1988), populations of lesser spotted and black woodpecker apparently have tripled, and those of great spotted woodpecker and European nuthatch quadrupled over the last 40 years. The most critical of this group of species is the middle spotted woodpecker, a species that is very strongly related to old broadleaved forests (Jöbges and König, 2001; Angelstam et al., 2003; Pasinelli, 2007; Müller et al., 2009). Until 1998 this species was not breeding in Flanders. In 1999 the first two breeding pairs were registered in the ancient woodland of Meerdaalwoud, where the population increased to 15 breeding pairs by 2003 (Moreau, 2006). By that time breeding was also confirmed in other ancient woodlands in the southeast and southwest of Flanders (Vermeersch et al., 2004). The Flemish breeding population in 2005 was already estimated at over 50 breeding pairs and is still increasing and extending its breeding range (Vermeersch et al., 2006). More demanding species like middle spotted woodpecker apparently take much longer to react to the improved conditions, but are now also re-establishing and are strongly increasing. Similar trends are also seen for this species in the Netherlands and northwest Germany (Kamp, 2008; van Dijk et al., 2010).

Like birds, fungi are in principle very good dispersers: they produce millions of spores, that can be spread over hundreds of kilometers (e.g. Risbeth, 1959; Kallio, 1970; Hallenberg and Kuffer, 2001; Stenlid and Gustafsson, 2001). However, only a very small fraction of the spores actually spreads over a longer distance (Kirk et al., 2008). Spore dispersal studies indicate that the vast majority of spores fall within a few meters of the fruiting body. The density of spores at 100 m distance is already 1000 times lower than at 1 m distance (Risbeth, 1959; Kallio, 1970). Ecologically effective spore spreading distances might be restricted to a few kilometres (Edman et al., 2004a; 2004b; 2004c). However, given the enormous number of spores, there is still a fair chance for some spores to travel over large distances. This small fraction is crucial to establish new populations in distant localities (Stenlid and Gustafsson, 2001). Such long-distance dispersal events are considered to be crucial to range expansions (e.g. Pakeman 2001; Clark et al., 1998). In contrast to birds and insects, the spores cannot actively search for suitable substrate to germinate, thus depend entirely on coincidence, except for species that are using insects as vector dispersing from dead wood (Seibold et al., 2019).

Moreover, even when a viable spore might reach a new substrate at long distance and be able to germinate, another compatible spore must reach the same substrate in order to mate and produce a dikaryotic mycelium that in its turn is able to produce fruit bodies and new spores (Stenlid and Gustafsson 2001). This process makes the development of a reproductive new mycelium at longer distance much more unlikely than expected from its reproductive and dispersal capacity. The mere occurrence of spores and presence of suitable substrate does not guarantee colonization (Jonsson et al., 2005).

Historic descriptions on saproxylic fungi indicate how impoverished the mycoflora of saproxylic fungi in Flanders and the surrounding areas must have been after many centuries of absence of suitable habitat. Although already described for the area as early as the 17th century (Van Sterbeeck, 1675), species like *Fomes fomentarius* that are now widespread were explicitly mentioned to be rare in 19th century reference works (Kickx, 1835; 1867; Bommer and Rousseau, 1879), and they still were halfway the 20th century. Van der Laan (1972) mentions only 10 known findings of this species for the Netherlands. In his description of the distribution of *Fomes fomentarius*, stretching over the whole temperate zone of the northern hemisphere, Jahn (1962) explicitly describes a 'hole' in the distribution covering northwest Germany, Belgium, The Netherlands and England. Species that live on small branches or stumps, like *Trametes versicolor*, were the only wood decaying fungi that were considered rather widespread in 19th century literature (Bommer and Rousseau, 1879).

With the increased availability of habitat, fungal communities of dead and old trees are expected also to recover. Indeed, over the last decades, mycologists already reported an increase in both species richness and range of saproxylic fungi. Species like *Fomitopsis pinicola*, *Schizopora flavipora*, *Pholiota aurivella*, *Pluteus umbrosus*, *Ischnoderma benzoinum* and *Phleogena faginea* that used to be extremely rare, appeared to have gradually extended their range and were now found throughout the region (Walleyn, 2003; 2004; 2006). Other species (e.g. *Mycena crocata, Plicaturopsis crispa, Hennigsomyces candidus, Hohenbuehelia auriscalpium, Cystoderma simulatum*) that were not recorded before the 1980's now have well established populations at several localities. The lack of records before that time could not simply be explained by a lack of knowledge or inventory, as also very conspicuous species abundantly producing fruitbodies every year (like *Mycena crocata*) were missed and the locations where they are now common were also visited regularly in the past (Walleyn, 2003; 2004; 2006). Similar trends are also reported for the Netherlands (Arnolds and Van den Berg, 2001; Veerkamp and Arnolds, 2008).

In an attempt to quantify and statistically test these trends, we had to rely on the best available information: a centralised database compiled from mycological excursions, research projects, historical records in literature, herbarium collections, etc… These data are not based on standardised inventory protocols or sampling designs and data in the dataset are not equally distributed over time (the dataset contains more records in the last two decades than the decades before). Results were as far as possible standardised by using annual relative occurrences of species (as a weight factor for differences in record numbers) and identical time periods of 10 years. Only the last five decades that contained enough records for reliable analysis (>10.000 records per decade) were taken into account. Over this period of 50 years the specific group of macrofungi related to dead wood has always been well studied and was indeed included in all inventories, although there might have been eras with more or less attention to certain groups of fungi causing some bias to the data. In this sense, the recorded trends are not ‘absolute’, but indicative. However, the trends are so distinctive and significant, that we are confident that they represent real trends.

Our results show that for species that are not too selective in their substrate requirements, the current density of available habitat appears sufficient to allow the steady development of new viable populations and expansion of their range. Some, like *Trametes versicolor* and *Piptoporus betulinus*, are now widespread in all forests, and appear to have reached a point of saturation. Species like *Fomes fomentarius* and *Ganoderma lipsiense*, that are both related to the more uncommon habitat of larger snags and logs, are still increasing. Similar trends are also observed in the Netherlands (Arnolds and Van den Berg, 2001; Veerkamp and Arnolds, 2008). Still, all four species appear to have further increased over the last two decades, which may be related to the further increase of available habitat.

A number of highly selective species though, like the indicators for habitat continuity of Christensen et al. (2005b) are still very rare or absent. They are often related to very specific rare and transient substrates (like wounds or rotholes of old trees), or specific stages of decay of large size logs and snags. On the rare occasions that suitable habitat is available, these species may easily fail to arrive in time, especially if source populations are distant (Christensen et al., 2005b). Only 14 out of 21 species have up to now been recorded in Flanders and most of them are very rare with less than 30 records registered. Individual hotspot sites in France, UK, Denmark and Czech Republic may contain up to 16 species (Christensen et al., 2005b). This indicates the impoverished status of Flanders for these selective species.

This conclusion was also drawn in a comparative study of selected sites with high densities of dead wood in Hungary, Slovenia, Denmark, The Netherlands and Belgium (Ódor et al., 2006). Overall species richness per log or snag in the Belgian site was comparable to other countries, but country level species richness was lower only in the Netherlands. In both Belgium and the Netherlands the proportion of frequent species was higher than in the other countries. Focusing on more demanding species, the differences were even more distinct. The authors developed a list of 99 ‘species of special interest (SSI)’. The total number of SSI’s recorded in the Netherlands (27) and Belgium (24) was much lower than in Hungary (51), Slovenia (43) and Denmark (41). Also the number of records and the proportion of these species were the lowest in the Netherlands and Belgium. For the highly selective species like the SSI-species of Ódor et al. (2006) and the indicator species of Christensen et al. (2005b), the required threshold of temporal and spatial continuity and density of suitable substrate necessary to build up viable populations appears not to have been reached yet. With suitable habitat widely distributed, but occurring at very low density and relatively ephemeral over time, their colonization is strongly determined by stochasticity (Gu et al., 2002).

Still, also on this group of highly selective species, our analysis shows a distinct increase, both in number of species and records. Unlike the less selective species, the expansion does not appear to slow down over the last 20 years, but appears to become even more explicit. Over the last 20 years, 7 of the 21 indicator species of Christensen et al. (2005b) apparently have newly established in Flanders, of which 5 over the last 10 years.

These new establishments of species presumably had to rely on long distance inflow of spores. Sites with a high occurrence and density of suitable substrate not only increase the probability of these spores reaching suitable habitat and thus the chances of successful establishment, but also allow further development of larger local populations, with a lower risk for local extinction (Nordén and Appelquist, 2001; Stenlid and Gustafsson, 2001; Edman et al., 2004a; 2004b; Jonsson et al., 2005; Christensen et al., 2005b). In order to persist as local populations species indeed must be able to colonise new suitable host trees at the same average rate as the old host trees become unsuitable. This requires sufficient suitable trees within dispersal range, thus high densities of potential habitat (Rukke, 2000; Siitonen, 2001). Not surprisingly, the observations of highly demanding species of fungi in Flanders are often concentrated in the rare localities with a high density of their specific habitat, like strict forest reserves, old park areas and landscapes with high densities of old tree rows. These new satellites may in the future develop to become new sources for further expansion (Siitonen, 2001; Stenlid and Gustafsson, 2001; Edman et al., 2004a, 2004b, Jonsson et al., 2005).

For saproxylic beetles, similar aspects of habitat requirements and availability are influencing possibilities for recolonization as for birds and saproxylic fungi (Schiegg, 2000; Jonsson et al., 2005), but the process is complicated by the extremely diverse dispersal potential of the different species (Jonsell et al., 1999). Some species, often linked with highly ephemeral habitats (like bark beetles) have a high dispersal capacity, while species inhabiting stable dead wood microhabitats (like species in wood mould) have low dispersal rates (Nilsson and Baranowski, 1997; Jonsell et al., 1999; Köhler, 2000). This dispersal ability may be a key characteristic for the survival and recovery potential of species (Ranius, 2006). Brunet and Isacsson (2009) found that common species were not affected by isolation from old-growth forest, but for rare and red-listed species there was a significant effect after a few hundred meters, and some species appeared not to be able to cross a section of two km of unfavourable habitat. In a study on saproxylic beetles on beech trees by Weiss and Köhler (2005) the level of isolation of the tree also proved to be a significant factor in the colonisation rate of the trees.

Ips typographus and *Hylobius abietis* are known to be able to travel over distances of 10 km and even up to 80 km and can actively search and detect suitable habitat from long distance (Solbreck, 1980; Nilssen, 1984). They also have high reproduction capacities. These species are very quick colonisers and react promptly to the new availability of suitable habitat. However, many species are limited in their dispersal, rarely spreading over distances more than a few 100 meters. Jonsell et al. (1999) concluded that the fungi-inhabiting species they studied could colonize suitable substrate within 1 km of their point of origin, but noted a reduced colonization over a distance of only 150 meters. Irmler et al. (2010) found an asymptotic decrease of species richness of saproxylic beetles with distances of more than 80 meters from source populations.

For some species, dispersal over distances of as little as 200 m is even unlikely (Speight, 1989; Nilsson and Baranowski, 1997). Moreover some of these non-mobile species are very selective in their habitat. They are dependent on sites with high spatio-temporal continuity of habitat related to natural forests, and are therefore often used as indicator species for habitat continuity (Alexander, 2004; Müller et al., 2005). As a consequence they are often rare or Red Listed in most countries where natural forests are rare or in decline.

Given the highly fragmented forest landscape and its management history in Flanders with the absence of suitable habitat for these species during centuries, it is highly unlikely to find any of these demanding species. What was expected was an impoverished fauna, containing the good dispersers with limited substrate requirements, but lacking the more demanding species, especially the dispersal limited species.

No extensive datasets are available in Flanders to underpin this hypothesis, but existing fragmentary information appears to confirm it. A comparison of the present-day carabid beetle fauna occurring in woods of Flanders with a unique data-set of archaeological carabid remains from a Late and Post-Roman forest at Velzeke (Eastern Flanders), showed a significant loss of stenotopic woodland species, with some of them considered extinct in Flanders (Desender et al., 1999). A study on saproxylic beetles and hoverflies in the south of Belgium (Fayt et al., 2006; Dufrêne et al., 2008) indicated an impoverished fauna with less than half of the expected species number found, and a large part of the species with residual and highly localized populations.

Signs of recovery are also fragmentary but indicate a similar long lag phase as for saproxylic fungi. A species like *Bolitophagus reticulatus* living in fruit bodies of *Fomes fomentarius* only managed to recolonize in the last decade, although suitable substrate was already available for some time. The first recordings of the species in Flanders were made in 2002-2003 (Troukens, 2004; Dufrêne et al., 2008) and by now it has been recorded in several locations all over the territory. In the Netherlands a first specimen was found in 1984 (de Goffau 1984), but only in 2005 populations were found in several locations (Moraal et al., 2007). Studies on this species have shown that it is normally a short distance disperser, moving only up to 100 m (Sverdrup-Thygeson and Midtgaard, 1998; Rukke and Midtgaard, 1998), but with the capacity for incidental long distance dispersal (Jonsell et al., 2003). Like for fungi, sites with high amounts of suitable habitat are considered of high importance both to increase incidence and continuity of suitable resources and possibilities to establish viable populations (Rukke, 2000; Jonsson et al., 2005).

Species depending on even more specific habitat (like old trees with rotholes) with very limited dispersal abilities like *Lucanus cervus* and *Osmoderma eremita* (Ranius and Hedin, 2001; Rink and Sinsch, 2007; Thomaes et al., 2008b) had probably already been lost from most, if not all, forests by the middle ages. They are considered close to extinction or extinct in Flanders (e.g. *Osmoderma*: Ranius et al., 2005) or restricted to a few small relics (e.g. *Lucanus*: Thomaes et al., 2008a).

5.5.2 Relic sites: essential for dispersal limited, selective species

The inventory in Kolmont revealed an unexpected quantity and quality of species richness in saproxylic beetles. The share of German red-listed species is quite remarkable, even taking into consideration the fact that this list contains a few species with a more Atlantic distribution that are considered widespread in Flanders. Both total species richness and number of red listed species are comparable with sites like ‘Heilige Hallen’ or ‘Fauler Ort’. These are reserves that are renowned for their exceptionally old beech stands with high amounts of dead wood in all decay stages, and can be considered as reference sites for beech forest biodiversity in western Europe. Moreover, most of the reserves in Table 5.2 and Fig. 5.3 are embedded in extensive woodland areas, thus much less isolated than Kolmont and therefore expected to be richer in species.

Also, the high scores on SQI and IEC (Fowles et al., 1999; Alexander, 2004) indicate this very small site to be of high importance, although it should be acknowledged that the saproxylic fauna of the British Isles is somewhat poorer than on the European continent, and a few widespread species on the continent are endangered in the UK.

Several explanations for this exceptional result may be given. First of all, although very small, the site contains a large variety of abiotic and biotic conditions, with a high density of very large trees and an amount of dead wood (>40 $m^3.ha^{-1}$) that surpasses the threshold value of 20-30 $m^3.ha^{-1}$ that might be required to safeguard the complete spectrum of species that rely on dead wood (Angelstam et al., 2003; Humphrey et al., 2004; Müller and Büssler, 2008). The admixture of other tree species like pedunculate oak, ash and sycamore may also be higher than in some of the German sites. Also, good conditions for thermophilous species may also be more abundant in south-exposed slopes, gaps and along the forest edge in Kolmont.

Moreover, and contrary to what was expected, the site contains some highy selective, dispersal limited species that are indicative for a high spatio-temporal continuity of their specific habitat like wood mould in tree cavities at the site or its immediate surroundings (Alexander 2004; Müller et al., 2005; Nieto and Alexander 2010).

Indeed, the site may have known an exceptional history of continuity in old-growth characteristics, clearly atypical to the Flemish situation. From the 12th to 15th century, the site supported a castle of high strategic importance, its vicinity covered with protective woodland. Also, in later times, the site never had high economic value to its owner, and was incorporated in a ‘romantic’ park landscape in which old and decaying trees were considered of ornamental value. For at least two decades no interventions were made in the forest, allowing the dead wood amount and density of old and decaying trees to further increase. Moreover, this small forest island (merely 17 ha) used to be surrounded by a traditional landscape with extensive old fruit orchards and hedges with pollarded trees. For old-growth related species this landscape provided very valuable alternative habitat. Speight (1989), Alexander (2004; 2008) and Dubois et al. (2009) already pointed out the importance of these alternative habitats for saproxylic species, especially dispersal limited species of wood mould in hollow trees. In this sense, the site was not as isolated as it appears at first sight. We come to the conclusion that this site had an atypical continuity of old-growth-characteristics in the forest and probably also in the surrounding countryside. Indeed, the matrix context may clearly influence and enhance the functionality of the reserve area (Franklin and Lindenmayer, 2002). The results for the investigated sites of the pilot study were too fragmentary to make similar conclusions, but suggest that some of these sites may also contain species that are indicative of relic habitat and populations. These sites were indeed not randomly selected but involve sites that actually bear good quantities of suitable habitat. Some of them may have known a less intensive management in the past than the average forest, allowing relic populations to survive. Future and ongoing inventories at these and other sites should reveal more relic populations that may prove to be essential for the survival of dispersal-limited species.

In many parts of Flanders, the traditional countryside landscape with old pollard trees and traditional fruit orchards may have played an essential role in extending the survival for many slow colonizing species, especially saproxylic beetles living in wood mould. These very slow colonizers (limited dispersal and specific substrate requirements) may therefore been able to uphold better than expected. This is also the case in other countries, where strongholds of old-growth species are primarily found in ancient wood pastures, royal hunting grounds and deer parks and traditional orchards and pollards in the countryside (e.g. Speight, 1989; Alexander, 2004; 2008; Dubois et al., 2009). In Flanders, similar wood pastures and deer parks were absent, but orchards and pollards frequently occurred in the countryside, providing alternative and relic habitat for at least a specific part of the old-growth related biodiversity. However, these alternative habitats in their turn have been lost during the second half of the 20th century: most of the trees were cut (Deckers et al., 2005), and the few old orchards that were spared were often treated with pesticides. Thus, despite the relative stability in forest area and improvement of saproxylic habitat within, fragmentation and loss of habitat severely increased both on a regional and a local scale, because forest habitats are surrounded by an increasingly hostile environment, where the survival of forest species becomes highly unlikely (Bailey, 2007; Hermy et al., 2008). This may have been the final blow to many species. Exemplary for this situation is *Gnorimus nobilis*, a typical species of rotholes, that was uncommon but widespread in Belgium until the 1950's surviving mainly in fruit orchards (Janssens, 1960). Most of these orchards have since then been cut down or treated with pesticides. As a consequence *Gnorimus nobilis* disappeared from all but three of its localities: it is now at the brink of extinction, with one of the known localities located in the forest reserve Joseph Zwaenepoel (Sonian forest).

5.5.3 Conclusion and future prospects

In Flanders, 'old-growth elements' have been virtually absent from the intensively used, fragmented forests for centuries. They are now slowly but gradually reappearing in our forests, with higher concentrations in non-intervention sites ('secondary old-growth'). Species related to old-growth elements are responding to this improved situation depending on their (re-)colonization capacities. Species with good dispersal potential and moderate habitat requirements often show a remarkably quick and strong response, that is widespread over the whole forest area, wherever suitable habitat is available. Examples are cavity nesting birds related to mature and senescent forest developmental stages, and moderate to low selective saproxylic fungi and beetles. Although no long-term standardised inventories are available in northern Belgium for saproxylic beetles and fungi to underpin this statement, we believe that the trends and results we compiled are so explicit we can assume that they indeed reflect a genuine positive trend for these less selective species.

Species with higher substrate requirements but with the capability of long-distance dispersal (some of the rare saproxylic fungi and beetles, middle spotted woodpecker) also appear to increase, although there appears to be an important lag phase in the establishment of their populations. Some species are still missing although suitable habitat is available, representing an important immigration credit (Hanski, 2000; Jackson and Sax, 2009; Baeten et al., 2010). Stochasticity may play an important role in determining whether these species are able to establish and persist. In this sense, locations with high concentrations of old-growth related habitat (like parks and forest reserves) can play a very important role increasing the chance of establishment of permanent populations, that in their turn can act as new sources for dispersal. Repeated studies in three strict forest reserves in Rhineland (Germany) indeed indicated a clear increase in species richness of saproxylic beetles over the last 20 years. The positive trend is related to both increase in dead wood supply and changed climatic conditions (Köhler, 2010b). Species with high restrictions both in dispersal and substrate requirements are very unlikely to recolonize over longer distances and appear to be restricted to and relying on relic sites. These can be old orchards, parks and pollard landscapes that have escaped from destruction and pesticide influence over the last 50 years, or forest patches like Kolmont that retained or redeveloped suitable habitat before the loss of the alternative habitat took place. An active search for such relic sites, based on historic information and old distribution maps of indicative species, and subsequent inventory of these sites for these species could be of great interest for species conservation. Protection, restoration management of these sites, and extension of small relics are crucial to guarantee the survival and recovery to viable populations of their valuable saproxylic communities.

“What I see in Nature is a magnificent structure that we can comprehend only very imperfectly, and that must fill a thinking person with a feeling of humility. “

Albert Einstein (1879-1955)

“The tree which moves some to tears of joy is in the eyes of others only a green thing that stands in the way. Some see nature all ridicule and deformity... and some scarce see nature at all. But to the eyes of the man of imagination, nature is imagination itself.”

William Blake (1799)

Chapter 6: Conclusions and recommendations

This study focused on the development of previously managed forest towards so-called secondary old-growth forest. Spontaneous developments in these, formerly managed forests are clearly different from primary old-growth sites. The newly established reserves are still developing, in a more unidirectional way towards a dynamic steady state (Vandekerkhove et al., 2009; Meyer and Schmidt, 2011), thus may be considered as a successional pathway, rather than the typical disturbance dynamics of a climax vegetation. As in other successional pathways, these developments may profoundly change these forest stands on structural features and composition, but may also strongly influence the species community of herbal layer, fungi and fauna, promoting late-successional and stress-tolerant species that thrive in closed-canopy forest conditions with infrequent natural disturbance and abundance of dead wood and microhabitat-bearing trees.

In this study, we focused on specific aspects of these developments, and aimed to quantify and analyse the processes of spontaneous succession. For forest structural developments, we focused on the two most prominent characteristics that distinguish old-growth forests from close-to-nature managed forest stands: the presence of large amounts of dead wood, and the share of large, overmature trees. In order to analyse the effects of the introduction of non-intervention on biodiversity, we looked at effects on the herbal layer, but also on the community of late-successional species focusing on the specific species groups of saproxylic fungi and beetles.

In these concluding remarks, we bring together the most important results from previous chapters, the answers to our hypotheses, and complement them with additional information from other datasets on Strict forest reserves at INBO and literature. Subsequently, from these conclusions, we derive some important implications for forest policy and management. We indicate particular points of interest, and make suggestions, mainly on the spatial configuration of management options in order to create forest conditions that allow for multifunctional use, but still provide functional ecological networks for late-successional species. Finally we conclude with some remarks and perspectives for future research an policy.

6.1 A critical review of methods and results in this study

Data available for this study was limited, both in time and space, sometimes fragmentary. Therefore, we had to make some concessions and trade-offs.

<u>A narrow time window, repeated measurements with few repetitions</u>

Analyzing succession, especially in forests, requires very long time series. Such long time series are not evident, and very seldom available. As the Flemish forest reserve programme is only 20 years old, long time-series were simply not available. We could, however, rely on a large set of (published and unpublished) data from a wide range of forest reserves, both primary and secondary old-growth sites, that allowed us to confront and complement our own datasets, in order to draw conclusions over a wider ‘time window’. This space-for-time substitution approach has the advantage that one can relate a short measuring time window to long time developments, and derive successional developments that take place over many decades. Drawback of this method is that there is no full control on site conditions, stand conditions and management history over the different sites at the onset of non-intervention, allowing only to draw conclusions on global trends and solid explanatory factors. Moreover there is the risk that results may be influenced by outlyers due to stochastic events (like stand-replacing windstorms).

For the study on development of very large trees and ground vegetation, genuine resurveys could be applied, that allow to derive genuine changes through paired observations. An important drawback, also here, is the narrow time window covered: for the large trees it covers 25 years, for ground vegetation only 10 years. These time intervals are substantial but limited compared to the total life expectancy of trees, or vegetational changes. Also just one or two resurveys have been performed up to now, so no real time-series are available: it is unclear whether recorded developments can be extrapolated over longer periods, and fit a real trend or just reflect a short temporal divergent development. It is also unclear what happened between two surveys: is this development linear, or non-linear ?

Moreover, due to the high intensity of measurements at every site, the number of sites that can be covered with standardized resurveys in such observational studies is limited. On the development of late-successional species, we did not have large surveys, let alone standardized resurveys to evaluate status and trends of the covered species groups. We had to rely on fragmentary information, general datasets and specific case-studies to derive assumptions and conclusions.

Therefore, it was important not to over-interpret the results, and always critically question in how far these results reflect trends that can be interpreted and extrapolated and not coincidential or anecdotal.

Common risks in long term observational studies

Ecologists and managers of natural resources readily acknowledge the importance of long-term research, which often includes monitoring, for the improved understanding and management of complicated ecological systems, providing baselines to detect and evaluate changes in ecosystem structure and function (Lindenmayer & Likens, 2009).

In observational monitoring or survey programmes, a wide set of response variables and potential explanatory variables is periodically measured on a –whether or not representative- smaller or larger set of sampling areas in order to record, in a standardized way, developments and changes of the response variables, and relate them to a (often) wide set of explanatory variables. Several important risks are involved when dealing with such observational datasets.

Using such large datasets, and the currently readily available statistical analysis tools may involve certain risks. One of the common errors is to confuse correlation and causality: finding related patterns that may be based on coincidence or may be caused by another factor that was not analysed but that influences both factors (confounding factor). Moreover, if this pattern follows expectations, one is also more likely to consider it plausible and adopt it, than if this is not the case (‘assymetric attention’ – cfr. Nuzzo, 2015).

Another important critique to many observational long-term monitoring programmes is that they often don't originate from an explicitly formulated hypothesis or goal (not 'hypothesis-driven'). Or, as Roberts (1991) formulates it, 'planned backwards on the 'collect now (data), think-later (of a useful question) principle'. Explicitly formulated research questions at the outset of a monitoring programme help to pinpoint the data needs, and to effectively design the monitoring set-up. Lindenmayer and Likens (2009) however add to this that research questions and measurements should not be fixed, but can be further developed and reformulated during the programme, as new circumstances, issues or measuring techniques arise, provided that the adoption of new sampling or analytical methods ensure that the integrity of the long-term data record is neither breached nor distorted.

If no explicit research questions are formulated, a common hazard in interpretation of observational data, is to detect developments and construct rational explanations for observed patterns afterwards ('just-so-storytelling' – cfr. Nuzzo, 2015). On the other hand, a too explicitly formulated and advocated hypothesis can also lead to 'hypothesis myopia' (cfr. Nuzzo, 2015), focusing on evidence that supports your hypothesis, neglecting evidence against it and ignoring other explanations.

Also in our study, the research questions and hypothesis are not always explicitly formulated for the investigated topics. Still, the performed measurements and interpretations can be related to a set of hypotheses. They are enumerated in Chapter 1. Based on the results presented in Chapters 2 to 5, we can now provide them with answers, given in short below. In the following paragraphs (6.3 and 6.4) these conclusions are further elaborated and supplemented with additional information.

6.2 An answer to the hypotheses

<u>On dead wood accumulation:</u>

- *In secondary old-growth forests, the average amount of dead wood is lower than in primary old-growth forests*

Yes: the average amount of dead wood found in the sites with secondary old-growth succession (mean time of non-intervention: 35 years) were still significantly lower than in primary old-growth forests. We found average and median values of 75 m3.ha-1 and 53 m3.ha-1 respectively, while primary old-growth forests show amounts of over 100 m3.ha-1, with natural ranges of 50 to 200 m3.ha-1.

- *During secondary succession to old-growth, the input of dead wood is higher than the decay rate, resulting in gradual net accumulation of dead wood.*

Yes: we found a median net accumulation of 1.64 m3.ha-1.year-1. The accumulation is in most cases a very sYeslow and gradual process, due to small-scale disturbances (individual or small group dieback or windthrow); only two out of 109 sites showed figures over 10 m3.ha-1 due to stand-replacing disturbances.

- *Dead wood accumulation rates differ between beech and oak dominated forests*

Yes: dead wood net accumulation was significantly higher in beech forests as compared to oak forests. Accumulation was on average twice as high in beech-dominated forests, although this average is influenced by the few sites with very high accumulation figures (which were all beech dominated). Median values were less divergent (1.89 vs. 1.24 m3.ha-1 year-1). Variance in accumulation rates was significantly larger in beech forests compared to oak forests.

- *Dead wood accumulation rates depend on the average age of the dominant trees at the onset of non-intervention*

Yes: average accumulation rates were significantly higher for stands with an average age of the dominant trees over 125 years at the onset of non-intervention. However, the variance is much higher in the younger stands, as the dataset contained a few middle-aged beech stands in UK that were severely damaged by an exceptional storm event in 1987.

- *Dead wood accumulation rates depend on site fertility (rich vs. poor sites)*

No: surprisingly, our dataset did not show significant differences in dead wood accumulation between richer and poorer sites. However, this result could be distorted again by the presence of a small number of sites, mostly on poorer soils, with stand-replacing disturbances. In theory, the more fertile sites should produce higher growing stock amounts, so higher potential for input of dead wood. Off course, all depends on previous management and the stock levels that were reached at the onset of non-intervention. These data were not available for most sites, making it impossible to test this hypothesis.

- *Dead wood accumulation rates depends on geographical location.*

Yes: the average accumulation rate was slightly higher in Northwest-Europe compared to Central Europe, be it only marginally significant. Also, the interaction with dominant tree species plays an important role: for oak-dominated sites, the difference was not significant, while for beech stands an important difference was noted. Rates could indeed be expected to be higher in Northwest-Europe compared to Central Europe, due to higher windstorm frequency. As beech trees are more sensitive to windthrow than oaks, the effect could be more significant for beech than for oak stands. However, mortality rates and dead wood input can also be expected to be lower, due to milder climate conditions in Northwest-Europe.

- *On the ratio of lying to total dead wood, it is expected that this ratio is higher for beech dominated forests than for oak dominated forests, as beech trees are more prone to windthrow compared to oak trees.*

Yes: also this hypothesis was confirmed by the data: in oak stands, only 50% of the dead wood volume consists of lying dead wood, while in beech stands this is 75%. This conclusion however needs some nuance: this difference is particularly true for sites with short time of non-intervention, but fades out in the long run, averaging at a level of 75% for both oak and beech dominated sites.

On Very Large Trees (Case study of a secondary old-growth lowland beech forest)

- The diameter distribution of the secondary old-growth sites differs from the typical inverse J-curve (or rotated sigmoid curve) of primary old-growth forests

Yes: as secondary old-growth sites to a more or lesser extent originate from even-aged stands (due to management history), they show a typical bell-shaped distribution, or an intermediate shape (bimodal), as they gradually evolve towards the rotated sigmoid curve.

- The density of VLT is higher in the previously managed stand in the SFR Joseph Zwaenepoel as compared to primary old-growth forests, due to the 'overshoot'-effect (more even-aged stand reaching over-mature state).

Yes: the results of the study site show VLT densities that are two to three times higher than in primary old-growth forests (ca. 30 vs. 10 trees.ha-1). This is also reflected in the share of VLT in the stand basal area, reaching over 70% in the study site, while values of 24-50% are noted in the primary old-growth forests.

- Higher growth rates lead to shorter life expectancy, thus higher mortality.

No: tree growth at the study site is exceptionally high, with diameter and tree basal area increment figures significantly higher than in the other studied sites or literature. Trees with average tree ring widths as recorded, have life expectancies well under 200 years (e.g. Di Filippo et al., 2015). The dominant trees at the study site have reached or even surpassed this maximum life expectancy, so elevated mortality rates were expected (well over the average values of 0.7-1.3% per year), as well as a reduction in growth rates in the surviving trees, indicating declining condition. None of these signals were recorded. Instead, very low average mortality rates and continued high diameter increments -even in the largest trees- were registered, indicating good vitality.

- Due to the combined effect of high growth rates and short life expectancy, the size range of VLT is similar in lowland conditions compared to montane and high elevation sites.

No: as stated above, the beech trees at the study site appear to combine high growth rates with higher-than-assumed life expectancy. This results in exceptionally large beech trees, resetting baseline assumptions on tree size and longevity in lowland conditions.

- *Spatial distribution of VLT gradually evolve towards random pattern during secondary succession.*

Yes: spatial pattern of VLT differs between primary and secondary old-growth sites: in primary old-growth sites, the distribution of VLT generally shows a random pattern, while in secondary old-growth sites, the distribution is more regular, due to deliberate spacing of trees during former thinning operations. Over time, this spacing will also become more random due to random or clustered patterns in mortality.

<u>On status and development of the herbal layer after introduction of non-intervention</u>

- *Based on the Intermediate Disturbance Hypothesis, the species richness of vascular plants will decrease if formerly managed forest stands are left unmanaged.*

Yes: we recorded a significant decline in species richness, both at plot level and at site level over a time-interval 10 years in four non-intervention sites.

- *Species loss is not random: especially light-demanding and disturbance-related species will be lost.*

Yes: we registered significant declines in species richness of light-demanding species and competitors. However, species richness of shade-tolerant species like vernal geophytes remained unaltered.

- *This process of non-random species loss leads to homogenization of the vegetation.*

Yes: primarily due to the loss of differentiating species (originally occurring in few sample plots) and converging cover ranges of the remaining species, the vegetation in the different plots shows higher similarity. The plots gradually exhibit a characteristic ground vegetation of closed-canopy broadleaved forests on fertile soils, with high cover of vernal (shade-evading) geophytes and shade-tolerant species.

- Even typical shade-tolerant and -evading species may be jeopardized in unmanaged forests, due to prolonged deep shade, leading to species loss and lower cover rates.

No: our results show stable or increasing figures on frequency and strong significant increases in cover of most shade-tolerant species, particularly of *Dryopteris*-ferns, *Milium effusum, Hedera helix* and vernal geophytes like *Anemone nemorosa* and *Allium ursinum*. Although the time interval is too short to genuinely evaluate long-term effects, the current evolutions are not indicating towards species decline, rather towards expansion. This is also in line with most other studies. The few studies that indicate declines of these species with increased shadow pressure were also affected by acidification. Several authors of the referred studies (e.g. Baeten et al., 2009a) pointed out that they could not disentangle both effects.

On status and development of biodiversity associated to the late-successional stage of old-growth forests: case study for Flanders

- *Species richness of saproxylic fungi and beetles is low in secondary old-growth forests: due to centuries of absence of suitable substrate, the associated species disappeared and are not able to recolonise.*

NO: the overall species richness of wood-decaying fungi and saproxylic beetles at the Flemish study sites is only slightly lower or even comparable to primary old-growth sites and long-existent secondary old-growth sites in Central Europe. The available data on fungi indeed confirm a suspected gradual recovery and recolonization of saproxylic species. Over a period of only a few decades, a surprisingly rich saproxylic community has managed to recover and reclaim the newly available dead wood habitat.

- *Species composition of saproxylic fungi and beetles is different in secondary old-growth forests, lacking highly demanding species with low dispersal abilities.*

Yes: the difference between saproxylic communities in primary vs. secondary old-growth forests is eminent when focusing on highly demanding species, requiring long continuity of dead wood habitat (so-called 'old-growth indicator species'). Recovery can be fast for species with high dispersal capacities and low (i.e. less specific) habitat requirements. Species with higher habitat requirements recolonize slower due to the longer required development time or scarcity of their specific habitat. Species combining low dispersal capacities and high habitat requirements are practically absent due to the high level of fragmentation and isolation (in time and space) of suitable habitat. They will never, or only in the distant future be able to recolonize the secondary old-growth sites (colonization or immigration credit), provided the necessary connective structures are restored or assisted migration is applied.

6.3 Development of old-growth characteristics in secondary old-growth succession: what have we learnt?

On the build-up speed of dead wood amounts, we could conclude that this accumulation takes place at an average pace of 1 to 1.5 $m^3.ha^{-1}.year^{-1}$. We could also derive that the average decay-time for larger logs can vary greatly, from 10-20 years for full decay of large poplar logs and 30-40 years for beech and maple, up to over 100 years for oaks. This result was also confirmed by other sources (e.g. Meyer and Schmidt, 2011). Knowing that in primary old-growth forests the average amounts of deadwood generally fluctuate between 50 and 200 $m^3.ha^{-1}$ (Korpel', 1997; Saniga and Schütz, 2001a), with all decay stages represented, one can conclude that it will take between 50 and 100 years for a formerly managed stand to develop comparable amounts and diversity of dead wood as found in reference conditions.

This deadwood build-up may play an important role in the framework of *in situ* carbon sequestration in forests. Contrary to what is often assumed, old-growth forests do continue to store carbon, even when the overall 'steady-state' level is

reached (Zhou et al., 2006; Luyssaert et al., 2008; Leuschner et al., 2014; Schrumpf et al., 2014). During the process of decomposition of biomass, an important share is not oxidized to CO_2, but humified and semi-permanently, or even permanently incorporated in the soil (the so-called Stable SOC pool). Unlike the upper, labile SOC-pool, mainly consisting of leafs and small branches, this stable organic carbon fraction is not decomposing under undisturbed forest conditions. Radiocarbon-dating of belowground organic carbon in forest soils revealed ages of several hundred up to over 4000 years (Trumbore, 2000; Schöning, 2005; Schöning et al., 2013). An estimated 20% of the labile SOC is not decomposed and oxidized, but ultimately transferred to the stable SOC pool, leading to a considerable net accumulation of SOC (Schöning et al., 2013). However, in intensively harvested forests, all remaining surface organic carbon is oxidized, and even negative balances of SOC are registered (Achat et al., 2015).
Recent studies indicate an underground carbon storage, in undisturbed ancient woodlands, reaching over 1/3 and in wet conditions even over half of the total carbon stock (e.g. Smith et al., 2013). Average figures for Flemish forests, based on 276 soil profiles, are estimated at 170-200 $Mg.ha^{-1}$ of SOC in the upper meter of forest soil (Ottoy et al., 2017).

Also in the framework of nutrient conservation and recycling, the decay of dead wood may play an important, and for scarce (often base) elements, be essential for the ecosystem. The results by Dhiedt et al. (2019) in the strict reserves of Sonian Forest and Wijnendale forest, confirm important and gradual release of chemical elements, especially basic cations like Calcium from the decaying wood to the forest soil.

As stated before, the previously managed forests commence their spontaneous development with living stock figures that are well below the equilibrium values of aboveground biomass in primary old-growth forests. These amounts fluctuate over the different developmental stages within the forest, and may (for mesic beech forests) be as low as 200-300 $m^3.ha^{-1}$ in the aggradation phase, but culminate in the optimal and early senescent stage at 800-1000 $m^3.ha^{-1}$. This means that during the succession of secondary old-growth, there is still an important build-up margin, also for living biomass. We made the analysis for the set of strict reserves with repeated measurements in Flanders (Table 6.1).

Table 6.1 Average figures for Living and Dead Aboveground biomass ($m^3.ha^{-1}$) at first and second survey (interval period 10 years) in a selection of monitored reserves and observed changes between the two surveys ($m^3.ha^{-1}$) (Δ living = difference in living aboveground biomass; Δ dead = difference in dead aboveground biomass; Δ TAB = difference in Total aboveground biomass (= living+dead); %dead = share of dead wood as compared to living biomass (%); KV = Core area; CP = network of circular plots.

Site	Living		Dead		Δ living	Δ dead	Δ TAB	%dead	
	survey1	survey 2	survey1	survey 2				survey1	survey2
Bos Ter Rijst CP	476.8	557.2	29.6	43.5	80.4	13.9	94.3	6.2	7.8
Bos Ter Rijst KV	567.2	618.7	41.5	64.6	51.5	23.1	74.6	7.3	10.4
Coolhembos KV-Alnion	296.0	262.0	70.0	100.0	-34.0	30.0	-4.0	23.6	38.2
Coolhembos KV-A-Q	226.0	214.0	64.0	89.0	-12.0	25.0	13.0	28.3	41.6
De Heirnisse - CP	186.3	237.9	18.6	27.8	51.6	9.2	60.8	10.0	11.7
De Heirnisse - KV	263.2	322.2	11.3	25.1	59.0	13.8	72.8	4.3	7.8
Jansheideberg - CP	404.0	496.4	8.7	18.2	92.4	9.5	101.9	2.2	3.7
Jansheideberg - KV	433.5	540.9	4.0	15.1	107.4	11.1	118.5	0.9	2.8
Everzwijnbad - CP	433.0	507.0	5.8	22.1	74.0	16.3	90.3	1.3	4.4
Everzwijnbad - KV	402.6	451.4	8.0	24.8	48.8	16.8	65.6	2.0	5.5
Pruikenmakers - CP	419.3	482.1	16.8	16.6	62.8	-0.2	62.6	4.0	3.4
Pruikenmakers - KV	472.1	538.6	32.6	26.7	66.5	-5.9	60.6	6.9	5.0
Withoefse heide - CP	238.7	271.7	31.8	25.4	33.0	-6.4	26.6	13.3	9.3
Hannecartbos - TR	118.1	205.4	39.7	58.2	87.3	18.5	105.8	33.6	28.3
Rodebos - KV1	409.3	498.5	25.2	40.9	89.2	15.7	104.9	6.2	8.2
Rodebos - KV2	292.1	351.6	31.9	35.3	59.5	3.4	62.9	10.9	10.0
Walenbos - KV	319.0	336.6	68.1	50.5	17.6	-17.6	0.0	21.3	15.0
Walenbos – KV/ transect	163.4	132.8	32.1	77.8	-30.6	45.7	15.1	19.6	58.6
Wijnendalebos - CP	365.4	444.8	39.7	43.8	79.4	4.1	83.5	10.9	9.8
Wijnendalebos - KV	368.4	424.3	32.3	44.3	55.9	12.0	67.9	8.8	10.4
Zoniën-Kerss.pl.- KV	668.6	740.6	115.7	108.7	72.0	-7.0	65.0	17.3	14.7
Zoniën-Kerss.pl. - CP (excl. KV)	559.1	681.0	24.2	31.2	121.9	7.0	128.9	4.3	4.6

In all these sites, management has ceased roughly over the same period of time, but there is a wide range of baseline situations with some of the areas originating from mid-aged even-aged stands (60-80years old), while others originate from older, uneven aged stands (150-200 year old), or have been subject to mass dieback due to rewetting of the area (e.g. poplars in Walenbos, old willows in Coolhembos). This table is descriptive and illustrative, and does not presume to provide an exact representative sample of the overall development of non-intervention sites in Flanders, but gives us an impression of the global trend and wide variety of situations.

The analysis covers an area of approximately 450 ha, and revealed an average build-up of the total aboveground biomass of 75 $m^3.ha^{-1}$ over a period of 10 years (or 7.5 $m^3.ha^{-1}.year^{-1}$). This accumulation averages approximately 10 $m^3.ha^{-1}.year^{-1}$for productive sites (*Fagion* and *Carpinion* sites), about 6 $m^3.ha^{-1}.year^{-1}$ for forests on sandy moderately poor to poor, acidocline soils (*Fago-Querceta, Querco-Betuleta, Pineta*) and 4 $m^3.ha^{-1}.year^{-1}$ in wet soil conditions (*Alnion, Lysimachio-Querceta*). This last, low score may be related to higher mortality due to raising groundwater-levels, or dieback of large poplar trees and succession towards a younger generation of alder trees. When we extrapolate these results to the total area of strict forest reserves (total area ca. 2400 ha, consisting of 40% productive sites, 30% acidocline dry sites and 30% wet and moist acidocline sites), we reach a weighted average of 7.15 $m^3.ha^{-1}.year^{-1}$, or a total of 16.850 $m^3.year^{-1}$. Converted to CO_2-equivalents, this results in a yearly aboveground carbon sequestration in (only) the strict forest reserves of roughly 17.000 Mg CO_2-eq.$year^{-1}$. This corresponds to the average emission of over 3500 households (average emission of 4.6 Mg CO_2-eq.$year^{-1}$) or the emission of 85 million driven km with an average car (emission 200 g CO_2-eq.km^{-1}).

The case study on large overmature trees illustrates the commonly underestimated dimensional potential of old trees in lowland conditions. We learnt that the <u>conditions in the Atlantic lowland are favorable for the development of exceptionally large trees</u>. We registered sizes of large beech trees that exceed the size ranges that are commonly recorded in primary old-growth conditions. Also the density and share of growing stock was significantly higher than in primary reference areas. We related these exceptional results to the favorable growing conditions (deep, well-drained fertile soils, long growing season, mild climate conditions), but also partly to the legacy of former management, with regular thinning operations and a more uniform age structure. This may lead to an 'overshoot' in the successional development towards the dynamic steady-state (Bormann and Likens, 1979). We can expect a similar development in several other strict reserves that originate from comparable conditions, concluding that <u>secondary old-growth succession may result in (temporary) higher frequency and size of overmature trees.</u>

From the extensive comparison with reference areas all over Europe, we learnt that the <u>density of large overmature trees (DBH >80 cm) varies between 5 and 20 trees per ha, representing a share of 10-30% of the growing stock</u>. In the case study, this density was over 30 trees, representing over ¾ of the growing stock. These results are evidently exceptional, also for Atlantic lowland conditions. When analyzing this for other strict reserves in Flanders, we come to following figures (Table 6.2).

Table 6.2 Density of very large trees (DBH>95 cm) in a selection of SFR in Flanders (note that the threshold DBH is higher than in the case study, due to inventory restrictions) (-1 = first survey; -2 = second survey).

Site	Density ($N.ha^{-1}$)	Largest tree measured (cm DBH)	Share of growing stock (%)
Wijnendale – 1	7.7	140-145	24.0
Wijnendale – 2	12.4	145	31.1
Pruikenmakers – 1	8.8	140-145	29.0
Pruikenmakers – 2	9.8	145-150	28.5
Everzwijnbad – 1	9.4	140-145	29.1
Everzwijnbad – 2	12.7	145-150	33.0
Bos Ter Rijst – 1	3.5	142	10.4
Bos Ter Rijst – 2	6.9	146	15.7
Heirnisse – 1	0	75-80	0
Heirnisse – 2	1.5	90-95	4.6

As these reserves originate from managed forests, where trees are normally harvested when reaching target diameters, it would be logical that these numbers are lower than in natural forests. Still the figures are quite high and rising, indicating that 'natural' levels may be reached in short time, or have been reached already. What is also notable is that mortality in these very large trees has been very limited over the last decade, indicating –fully in line with to the results from the case study- that the large old trees have not reached their age and size limits yet.

6.4 Effects on biodiversity: what is there, what is to come?

6.4.1 Effects of non-intervention on vascular plants: winners and losers

From chapter 4 we learned that the introduction of non-intervention in previously managed forests may not result in a univocally positive effect on vascular plants. Total species richness distinctly decreased after cessation of management. Especially light-demanding and disturbance-related species declined or even disappeared from the sample plots. This is not unexpected, as the cessation of active human intervention leads to lower frequency of canopy and soil disturbance. Only 2 out of 184 sample plots showed strong decline in living biomass, corresponding to gap formation; 10-15 more plots had a slight decline in growing stock, indicating individual tree dieback, but the overall development was a highly significant increase in basal area and growing stock and a continued closed canopy (aggradation phase or ‘optimal’ phase).

It is widely accepted that unmanaged forests in the aggradation phase go through a temporary phase of deep shadow, leading to low species richness in understorey plants (e.g. Scherzinger, 1996). Several authors (Plue et al., 2013; Mölder et al., 2014), however, perceive a problem of unnatural prolonged canopy closure in secondary old-growth succession. Due to the more uniform age structure of the original stands, gap formation may be more infrequent than in natural forests, leading to unnatural long periods of deep shadow, and loss of species, even shade-tolerant species.

Disturbance frequency is indeed much lower in strict forest reserves than in managed forests, where 10-15% of the forest area may be subject to management interventions on a yearly basis (6-12 yearly thinning rotations, final harvest rotations of 120-150 years). Nonetheless, the registered disturbance rate in the studied sites does not appear to be very different from reference sites. A large-scale study in the primary old-growth beech forest of Uholka (Ukraine) revealed disturbance frequencies and canopy gap occurrence in natural beech forests covering only 2-3% of the surface area (Hobi et al., 2014). These gaps have the size of single or several tree canopies, but are rarely larger than 500 m² (Diaci et al., 2001; Rozenbergar et al., 2003; Kenderes et al., 2008). This is fully in line with the mortality patterns for large canopy trees. The background mortality rate of such trees is less than 1% per year, with exceptional peaks at larger scale disturbances (Wolf et al., 2004; Vandekerkhove et al., 2018). In unmanaged forests, this will result in overall canopy gap rates of 2-3%. This is much lower than the figures of 5-15% disturbed areas extrapolated by Koop (1989), from observations in Fontainebleau, Hasbrucher and Neuenburger Urwald. These figures however also included the regeneration phase, and were based on forest areas that originated from unnatural age structures (former wood pastures). In this context, the low disturbance rates recorded in our reserves and related lower presence and share of ruderals and light-demanding species in these forests are therefore much closer to the natural reference that the ‘artefact’ figures in managed forests.

Previous studies analyzing declines of characteristic ancient woodland species (such as *Anemone nemorosa*) in relation to increased canopy cover were often complicated by concurrent processes of acidification (e.g. Baeten et al., 2009a). Our observations clearly showed now that the characteristic shade-tolerant (or better: shade-avoiding) ancient woodland species -often vernal geophytes- appear to withstand the high shadow pressure of closed canopy unmanaged forest, and even expand their cover. These results indeed confirm and subscribe to the assumption that the decline of such species in previous decades should be related to acidification and excessive nitrogen deposition, rather than increased shading (Baeten et al., 2009a). Nonetheless, our results also confirm the observations that light-demanding species may indeed be (temporarily or permanently) lost from unmanaged forests. For species of conservation concern, it is therefore recommended not to focus all conservation efforts in forests on non-intervention, but also to continue active management (conservation of permanent open spaces, coppicing) on selected sites with high potential for conservation of rare light-demanding species (Peterken and Francis, 1999; Vandekerkhove et al., 2018b).

6.4.2 What about other species groups ?

Contrary to primary oldgrowth forests, secondary oldgrowth forests have had a history of (strong) human interference, often leading to the total disappearance of dead wood and old trees, for a long period of time. This may have led to the total disappearance of the related late-successional species that rely for their development on dead wood or specific microhabitats (such as rotholes) that primarily occur in overmature and veteran trees. As shown in Chapter 5, we can conclude that the amounts of dead wood and overmature trees that are currently found in our forests have never been higher over many centuries. Through analysis of existing datasets and specific surveys, we could check in how far the specific late-successional biodiversity is impoverished in the secondary oldgrowth sites, and check whether re-colonisation takes place or shows an immigration credit.

The analysis in chapter 5 focused on specific groups (birds, saproxylic beetles and wood decaying fungi) and indicates that the late-successional communities are indeed impoverished, as compared to the communities of primary old-growth forests, but still appear to be quite diverse, comparable or even exceeding sites in neighbouring regions. The chapter also illustrated that the process of recovery and recolonization is still ongoing, and depends on the dispersal abilities and specific habitat requirements for establishment of species.

The quick response of late-successional forest birds (woodpeckers and other cavity breeders) and several wood-decaying fungi (such as *Fomes fomentarius*) demonstrate the abilities for good dispersers with less specific habitat requirements to colonize newly developed suitable habitat. The re-establishment of species like *Fomes* also allowed for the species-rich communities of related invertebrates to recolonize. A European-wide comparison indeed revealed that the species richness of *Fomes*-related beetles and flies in the forest reserve of Sonian Forest was among the highest of all studied sites (Friess et al., 2018).

The ongoing colonization by species with more critical habitat requirements illustrates the potential for further development of the late-successional community.

This was demonstrated for the group of 21 European indicator species of natural beech forests: their occurrence and frequency clearly increased over the last decades. Whereas only 6 of these species were registered before 1990, this number increased to 14 species by 2009. Since, this figure further increased to 16, as did the number of locations where they were found.

Our results on saproxylic beetles indicated a richer community than expected, considering the legacy of intensive forest management, and even included species with low dispersal abilities and high habitat requirements, so-called Urwald-Relic Species (Müller et al., 2005). These results indicate that even in the dead-wood-poor environment, some of these relic species managed to survive (maybe in old coppice stools, or pollard trees in the open countryside). Moreover, re-inventories in several German reserves display a further increase in species richness as amounts, diversity and continuity of dead wood and overmature trees develop, but also due to climate change (Köhler, 2010) and allows for further optimistic prospects on the saproxylic beetle community, also in our reserves.

Other inventories and recent studies confirm the recorded positive trends also for other species groups. The inventories of bryophytes and lichens on dead wood in two forest reserves for instance revealed a high and increasing species richness (Van Dort and Van Hees, 2002; Vandekerkhove et al., 2003; Ódor et al., 2006; Van Landuyt and De Beer, 2016; Van Parijs et al., 2018). For saproxylic hoverflies a distinct increase in species richness and occurrence was observed in the Netherlands, and is related to aging of forest stands and increasing amounts of dead wood (Reemer 2003; 2005; Van Steenis and Reemer, 2013). Similar trends are also observed in Flanders (Frank Van de Meutter, pers. Comm.). The positive trends in saproxylic invertebrates in our forests are in shear contrast to the overall strong negative trends of invertebrates worldwide (Sanchez-Bayo and Wijckhuys, 2019; Eisenhauer et al., 2019) or Western Europe (Hallmann et al., 2017).

A final remark that should be made considering the late-successional species communities is that, even more than in vascular plants, species may have a strict preference for the shaded, tempered and damp microclimate of closed-canopy forests such as most fungi and related beetles, slugs, woodlice (e.g. Kappes et al., 2009; De Smedt, 2018; 2019) or require sun-exposed, warm conditions that are in natural conditions related to larger-scale disturbances like jewel and longhorn beetles, certain hoverflies.... An explorative analysis on saproxylic beetles in Meerdaalwoud indicated that both communities may be equally rich, but are clearly differing, thus complementary (Vandekerkhove et al., 2016b).

In conclusion, we can state that the community of late-successional species in our study sites is remarkably rich, and confirms the assumptions that these reserves are developing to become specific biodiversity hotspots. Indeed, prospects are good for further development as the amount and diversity of dead and overmature trees will further develop, and new species appear. Like for vascular plants, it is advisable to complement the primarily shade-casted non-intervention forests with actively managed areas with considerable amounts of sun-exposed deadwood in order to provide good conditions for both shade- and light-demanding species.

6.5 Relevance and recommendations for forest management

Flemish forest policy and management guidelines are aiming at sustainable, multifunctional, close-to-nature forestry, with an increasing emphasis on biodiversity conservation, especially in the Special Areas of Conservation (SAC's) under the habitat directive, covering over 1/3 of the total forest area in Flanders (Leyman and Vandekerkhove, 2003; Vandekerkhove, 2013).
For the establishment of benchmark values for criteria of ecological quality, input from strict forest reserves monitoring has already been important at several occasions. The results of this study particularly illustrate the important potential of strict forest reserves for the delivery and further development of scientific knowledge with high relevance to forest and nature policy in Flanders and abroad.

In the context of the development of the 'Criteria for Sustainable Forest Management' and the 'Management Vision for State Forests' (Afdeling Bos &

Groen, 2001a) and also more recently in the criteria for evaluation of the Local State of Conservation for Natura2000 forest habitats (Thomaes et al., 2009), several benchmark values e.g. for dead wood amounts, number of habitat trees and open spaces were derived from results from Flemish and foreign forest reserves.

The presented results confirm that the benchmark of 4% share of deadwood in the aboveground biomass, corresponding to 10-25 m^3/ha, and set as base quality requirement in state forests and Natura2000-forest types, can be easily reached within 10-15 years simply by ‘benign neglect’, not requiring active interventions. Our results also illustrate that even the prerequisit of 10% of dead wood, required for the ‘natural target types’ (*natuurstreefbeelden*) for forests, can be achieved: several Flemish strict reserves have already reached this threshold after 10-30 years of non-intervention; some are even within the range of 15-30% of dead wood characteristic for primary old-growth forests (Korpel', 1997; Saniga and Schütz, 2001a, Christensen et al., 2005; Vandekerkhove et al., 2009). The results in chapter 2, also covering a large number of other European sites (beech and oak dominated forests) resulted in a median value of 8.9 % after about 25 years of non-intervention.

The target of leaving 10 ‘habitat’ trees per ha, is also in line with our findings, indicating that 5-20 large overmature trees commonly occur in natural forests (where site conditions allow their development). It is evident that in managed forests, not all ‘reserved’ trees should be of large size, also other ecologically valuable habitat trees can be selected. The reference paper by Larrieu et al. (2018) gives a good overview of eligible trees and their value for biodiversity.

Another commonly applied benchmark is the target for 5-15% open spaces (both permanent and temporal) in every forest complex. Such open spaces can be very important for the conservation of species of open areas that are threatened in the intensified countryside. Peterken and Francis (1999) indeed recommend to conserve and develop such open spaces to safeguard overall species diversity of woodlands. The figure of 5-15% was originally inspired by the results by Koop (1981). Our results, and recent studies abroad (e.g. Kenderes et al., 2008; Commarmot et al., 2013; Hobi et al., 2014) indicate that, although infrequent larger disturbances may temporarily result in such high shares of collapsed and rejuvenating areas, this figure does not correspond to the average natural situation, where closed-canopy optimal and senescent phases predominate, and gap-ratios rarely exceed 5%.

6.5.1 Guidelines for the development of functional networks of old-growth structures and elements in forests for the conservation and development of late-successional species

In traditionally managed forests, late-successional species are often missing or threatened, due to the ‘harvest shortcut’: final harvests are performed when trees and stands are in the optimal phase, excluding later developmental phases (senescence and eventual collapse) and related structures (dead wood, habitat trees).

Based on above presented results and insights on development of old-growth elements and autecology of late-successional species (dispersal abilities and habitat requirements), guidelines can be derived for integrative forest management in order to remediate for this shortcut and provide functional infrastructure for these late-successional species. They are comprehensively explained in Vandekerkhove et al. (2013). The main conclusions are repeated below, and further elaborated on specific aspects of closed-canopy vs. sun-exposed areas.

1. Apply the triple R-strategy: reserve, retain and restore.
2. Develop functional networks of old-growth elements, based on the concepts of island biogeography, metapopulations and metacommunities
3. For large enough areas: provide zoning for the conservation of inner-wood microclimate in the core of the forest, and mosaics of dense and sun-exposed patches, with gradual edges at the outer borders of the forest

In order to be effective for the conservation of saproxylic biodiversity, these old-growth elements should be arranged in a functional network, that caters for species with different different life-strategies, from fast-colonizing ruderals to stress-tolerant sedentary survivors, from thermophilous ‘gap’-species to species requiring the microclimate or shade pressure of closed-canopy forests.

Management strategies for conservation of old-growth-elements: “the triple R”

Reserve: safeguard existing relics of old-growth (or other patches with high value or potential) from harvest, by conserving them in delineated areas like forest reserves and national parks, but also in smaller delineated patches, often called ‘Set-aside patches’ or ‘key habitats’ or ‘ilôts de scénescence’

Retain: intentionally keep a number of dead, old or other habitat trees in the stand during thinning and final harvests. Such retention trees are key elements in the managed forest ‘matrix’

Restore: even when none such oldgrowth elements are present at the moment, a policy can be applied to allow them to develop in a premeditated pattern and network.

This concept has been originally developed and applied as the ‘Variable Retention Harvest System’ for the oldgrowth forests of North-West America (Franklin et al., 1997; Lindenmayer and Franklin 2002). However, it can also be applied to temperate forests where no oldgrowth elements are remaining, but where a ‘management for oldgrowthness’ is integrated in the silvicultural practice (Bauhus et al., 2009). It is mainly a question of intentionally ‘let things happen’. Indeed, hollow trees and dead wood emerge by themselves, if the manager allows them to develop and build up.

In this context, theoretical concepts of island biogeography and metapopulations can also be applied to the conservation and development of late-successional species. In this context, the old-growth elements (dead wood , overmature trees) can be considered as a transient network of ‘islands’ of in a ‘sea’ of managed forest and open countryside (see box below).

Continuity and connectivity in time and space are essential elements to sustain viable metapopulations and sound and robust metacommunities. Such a network involves smaller and larger non-intervention patches that are interconnected by “corridors” and “stepping stones” of habitat trees in the managed forest matrix. Based on extensive literature, Lachat and Bütler (2007) suggested a spatial design of late-successional forest elements (Fig. 6.1), catering for a large part of late-successional species. The functionality of the design and core elements for their survival will off-course depend on the habitat requirements and dispersal ability of the individual species. For species with low dispersal abilities and high habitat requirement, the ‘hotspot’ strict reserves will be essential, while good dispersers with ephemeral habitats will depend on good connective structures (Lachat and Bütler, 2007; Vandekerkhove et al., 2013).

Theory of island biogeography, metapopulations and metacommunities – applied to old-growth

The principles of island biogeography were developed by MacArthur and Wilson (1967), who examined species diversity on larger and smaller islands, closer and farther away from the mainland.

Their basic conclusion was that species richness is higher on larger islands than on smaller ones, and higher on islands closer to the mainland than on remote ones. It is basically explained by the fact that the influx of species from the mainland (the source population) to an island decreases with the distance to be crossed. On larger islands, more habitat diversity may be present, making the island suitable for more species, and larger, less extinction-prone populations can build up.

Set-aside areas and habitat trees are for old-growth-dependent species like a network of "old-growth islands" and stepping stones in a "sea" of young and mature forest. Like in the typical island biogeography, larger habitat patches may support larger (sub-) populations for longer periods (lower extinction risk), and patches closer to large source populations also have a greater chance of being colonised. This theory however says very little about species composition: not all species have the same potential to colonize or survive, so remote 'islands' may not only have a lower species richness, but also lack the more demanding species that often represent higher conservational value.

The theory of metapopulations was developed by Levins (1969; 1970), and operationalized for applied ecology mainly by Hanski (1999). It states that a population of a species can be composed of a number of separate subpopulations, each living in discrete patches of suitable habitat, but able to swiftly migrate from one site to another. All these subpopulations together form one so-called 'metapopulation'. Individual sites and sub-populations may go extinct, but as long as the sum of interchanging subpopulations is viable, the population of a species may survive. In some cases (for example, an archipelago with breeding cormorants), the discrete sites are stable over time. In some cases, such as for dead trees or a tree cavity, suitable sites will disappear over time and reappear elsewhere. Saproxylic organisms can be considered as populations that live on melting icebergs and that need to be able to reach the next suitable iceberg before the original one is gone. Some individuals (or spores or seeds) may disperse from one site to reach these new sites by chance while others may actively search for new sites (e.g. beetles). In this case, we speak of a "habitat tracking dynamics" version of the metapopulation.

The metacommunity-concept (Leibold et al., 2004) expands the concept of metapopulation to the community level, where the metacommunity consists of a set of local communities that are linked by the exchange of multiple potentially interacting species. This means that there are at least two fairly discrete levels of community integration. At the local level, there are functional interactions between species (like food web interactions). At the regional level, dispersal among local communities occurs and can occur with variable rates, influencing the species composition and structure of the communities at both local and regional scale.

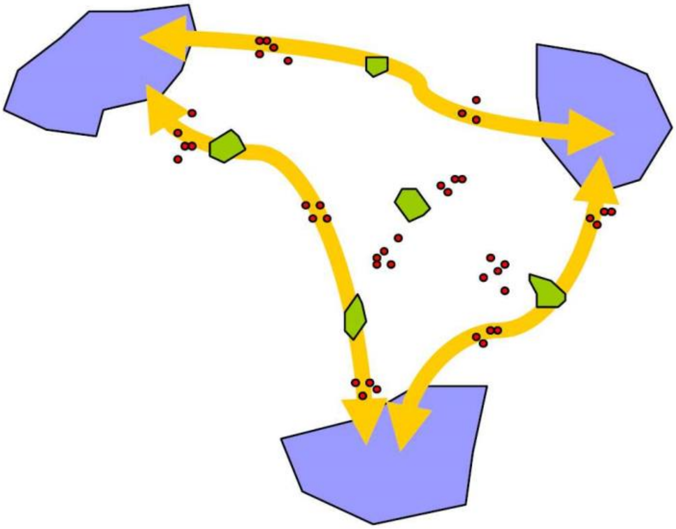


Fig. 6.1 Schematic representation of a functional network of old-growth elements: larger set-asides (reserves >10 ha –blue patches) are interconnected through set-aside patches (1–5 ha - green) and individual habitat trees (red dots). Areas with higher densities of habitat trees can form “corridors” (yellow arrows), but a qualitative “matrix” can also be crossed by most target species. (source: Vandekerkhove et al., 2013 based on Lachat and Bütler 2007).

6.5.2 Importance of closed-canopy core zones vs. sun-exposed areas.

If the functional network needs to cater for both thermophilous and forest microclimate-related species, a specific ‘zoning’ of management strategies and gap-creation is required.

It is commonly known that closed-canopy forests are characterized by a specific microclimate with higher relative air humidity, soil moisture and buffered air temperatures (e.g. Schmidt et al., 2017). An extensive world-wide analysis by De Frenne et al. (2019) shows that forests can function as a thermal insulator, cooling the understory when ambient temperatures are hot (on average with 1.7°C; for maximum temperature even up to 4°C) and warming the understory when ambient temperatures are cold (+ 1.1°C). This difference is magnified as temperatures become more extreme and is of greater magnitude than the warming of land temperatures over the past century. Not only is this conclusion very important in the framework of global warming, it may also prove to be essential for the survival of forest species. De Frenne et al. (2013) already demonstrated that microclimatic effects brought about by forest canopy closure can buffer biotic responses to macroclimate warming, thus explaining an apparent climatic lag. The thermophilization of ground-layer plant communities is attenuated in forests whose canopies have become denser, probably reflecting cooler growing-season ground temperatures through increased shading. As living stocks have increased in many temperate forests in recent decades, local microclimatic effects may commonly be moderating the impacts of macroclimate warming on ground vegetation. Conversely, increases in harvesting that open forest canopies can accelerate thermophilization of temperate forest biodiversity, and lead to loss of species adapted to cooler condition.

Microclimate in closed-canopy forests not only is essential to ground vegetation, but also to many ground-dwelling species such as slugs (Kappes et al., 2009; De Smedt et al., 2019), ectomycorrhizal and wood-decaying fungi (Rayner and Boddy 1988; Boddy 2001; Heilmann-Clausen and Christensen, 2003; Crockatt, 2012), mosses (Ódor et al., 2006; Heilmann-Clausen et al., 2014) and specific groups of arthropods (fungivorous beetles, woodlice, …) (e.g. De Smedt, 2018). Even for many species of canopy dwelling species such as butterflies. Merckx et al. (2012) show that the sheltered, dark, humid, late-successional, deciduous forest biotope is characterized by high numbers of both individuals and species of moth, and is especially important for some scarce and specialist species of conservation concern. Moreover, Slade et al. (2013) demonstrated that species of forest specialists that are restricted to interior forest with undisturbed microclimate require large enough patches of closed-canopy more than 100 m from forest edges and large canopy gaps in order to sustain populations. Indeed the edge-effects for forest microclimate parameters such as relative humidity, air temperature and soil moisture are on average at least 50 to 100 m wide (Schmidt et al., 2017).

The microclimate effect is strongly dependent of canopy structure and density. Von Arx et al. (2013) showed a strong correlation between Leaf Area Index (LAI, as a measure of canopy density). The moderating capacity of dense canopy forests (LAI > 4) on maximum temperature in summer was significantly larger than in sparse canopy (LAI < 4) stands. Anderson et al. (2007) report that mean maximum air temperature were 1 to 4 °C warmer in thinned than unthinned stands. Overstory thinning results in a greater daytime influx of solar radiation with higher near-surface temperature and a greater nighttime loss of longwave radiation with lower near-surface temperatures (Rambo and North, 2009). This in turn results in more extreme diurnal swings of the temperature (Rambo and North, 2009). Dense tree canopies cause not only colder ground-layer temperatures but also increase relative air humidity and shade in the understory (Geiger et al, 2009; Chen et al., 1999; Norris et al., 2012; Von Arx et al., 2013).

Transposed to the Flemish forest situation, closed-canopy broadleaved forests and spruce and Douglas fir plantations may produce strong microclimate buffering, whereas poplar and pine plantations without dense broadleaved sub-canopy perform poorly on the generation of a buffering forest microclimate. In the highly fragmented forest landscape of Flanders, with important shares of pine and poplar stands, closed canopy forest providing a well-established forest microclimate are thus very scarce and should be secured and further developed. In the pine and poplar forests, this can be done by further promoting the development of a dense and diverse sub-canopy of broadleaved species. Creating larger temporal or permanent gaps in the closed-canopy core areas, on the other hand, should be avoided as they will create new edge effects and disturb the microclimate, and thus will be detrimental to the above-mentioned closed-canopy-dependent species. In larger compact broadleaved forest areas we therefore propose, in line with the recommendations by Merckx et al. (2012), Slade et al. (2013), etc… a specific zoning in woodland management and conservation practices to take into account the differential requirements of species and microclimate development. We suggest to concentrate larger non-intervention strict forest reserves, in connection to continuous-cover selection forestry, aiming at gap-ratios of 1-2% in the core areas of deciduous forests, catering for stress-tolerant and other interior forest species, including tree species (beech, maple, lime). Forest management and conservation regimes aiming at larger-scale disturbances, open-canopy forests types (like coppice-with-standards, *futaie claire* sensu Schütz, 1997) and small-to-mid-scaled final harvest systems (e.g. ‘Femelslag’) with sun-exposed forest structures and gradients, catering for light-demanding and thermophilous species should be concentrated in the periphery of the forest (Fig. 6.2).

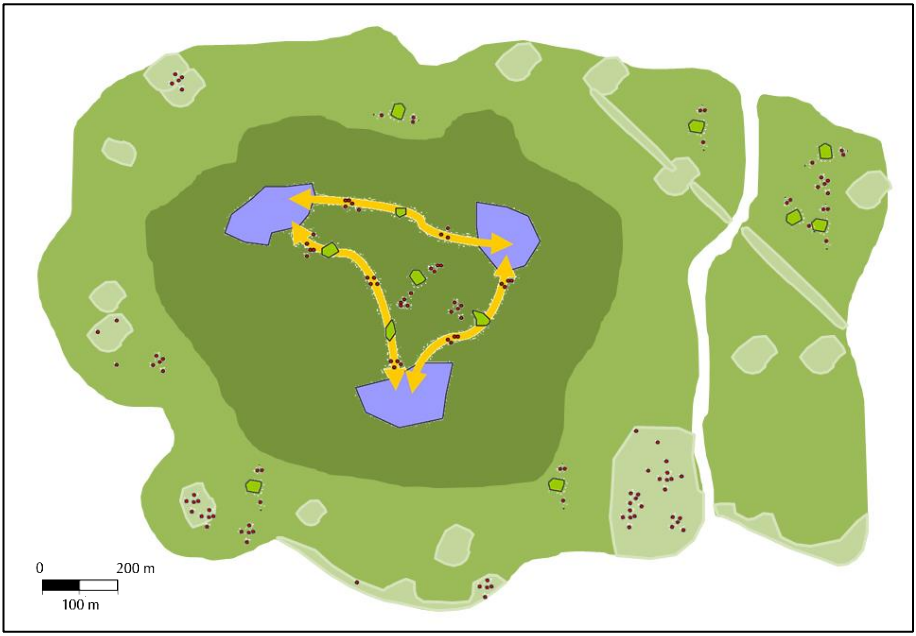


Fig 6.2 Strategic zoning in larger (200-300 ha) forest complex catering for both thermophilous and microclimate-requiring species: network of closed-canopy old-growth elements and continuous cover forestry in the core area (dark green), larger temporal and permanent gaps, sun-exposed habitat trees, open corridors, gradients and open canopy forest types like coppice-with-standards (light green), in a matrix of silviculture with half-shade and light-demanding species (middle-green)

6.6 Perspectives for future policy and research

6.6.1 Need for a regained ambition on process-conservation (Prozeßschutz) in the Flemish nature and forest policy

When the legislation on strict forest reserves was established, (1991; 1993) ambitious goals on the development of a sound and representative network of scientifically monitored unmanaged forests was set, based on inspiring examples in other countries, and opinion papers of leading forest scientists and policy makers (Dua, 1975; Lust, 1982; Van Miegroet, 1977; Hermy, 1992; Van Slycken, 1994). An ambitious target area of 3000 ha was set in the Environmental Policy Plan – 2

(1997) and was reached, be it not by the envisaged year 2002, but only eight years later. The development of a representative network of strict forest reserves, however, is still incomplete, as it does not fully meet the quantitative and qualitative policy targets on representativity and size (Van Elegem, 2006). In order to reach these requirements, at least another 700 ha of strict reserve is needed (De Keersmaeker et al., 2007). New legislation on nature and forest reserves (2014) and the focus on the implementation of the (quantitative and qualitative) conservation targets for habitats and species of the Habitat and Birds directive, however, resulted in a stagnation of the process of selection of new reserves and extension of existing sites. (Fig. 6.3)

Some question the need for further expansion and even continuation of strict reserve areas, as they allegedly not always conform to the habitat directive goals. Yet, the European Commission clearly states in its guidance on Wilderness and 'process-nature' (Technical Report - European Commission, 2013) that such non-intervention areas in climax habitats (such as forests) are fully compatible with the habitats directive. It is an important impediment to the conservation and development of old-growth forests that the EU-directives and interpretation manual do not discern for old-growth characteristics in the definition and evaluation of habitat types: they are entirely focused on botanical composition, not on late-successional structural features. Still, the Technical Report (European Commission, 2013) clearly states that areas with non-intervention can '*significantly contribute to the favorable conservation status of a large set of natural habitat types, i.e. primary habitats, and the species they host. (...) The allowance of natural disturbances, the temporal and spatial variation in environmental conditions and the competition between individuals contribute to a diverse environment at many spatial scales and supports the prevalence of a wide range of their typical species. For instance, many rare and threatened plant, fungi and animal species depend on the natural developmental stages of forests, rich in veteran trees and decaying wood. These can develop only in forests subjected to a long-lasting regime of natural processes. (...) Many other invertebrate species as well, such as saproxylic beetles, are dependent on non-managed forests with large amounts of lying dead wood and standing decaying veteran trees, which they need for their larval stage of their life cycle.*'

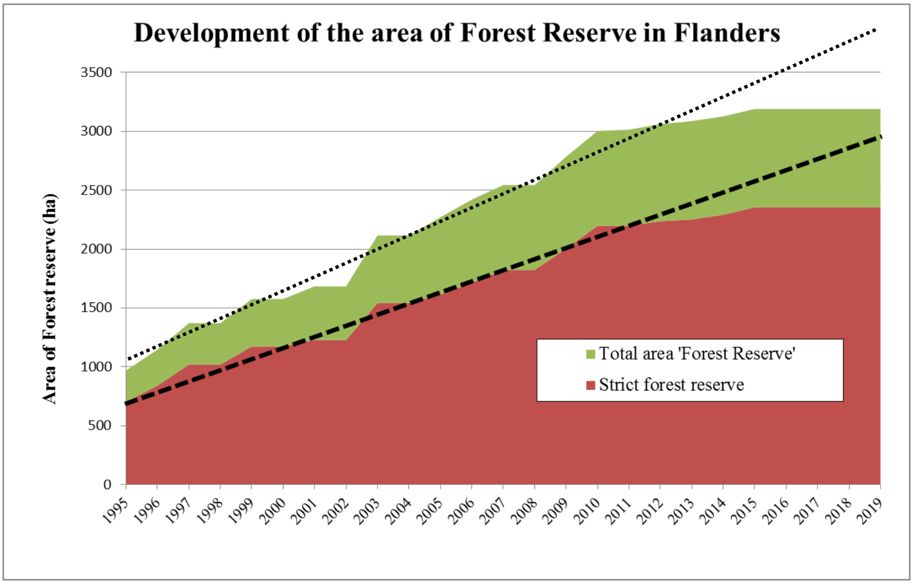


Fig. 6.3 The development of the area of strict forest reserves clearly exhibits a ‘stagnation’ (see black dotted trend-lines) over the last decade, although policy targets require at least another 1000 ha, of which at least 700 ha of strict reserve.

The criteria for evaluation of the Local State of Conservation for forest habitats, implemented in Flemish conservation policy (Thomaes et al., 2009) are also fully compatible with a management regime of non-intervention. Only in case of colonization by invasive non-native species, non-intervention may be in contradiction with the goals on conservation and development of a favorable conservation status of Habitats. Still, research has shown that well-developed structurally rich unmanaged forests, are much less prone to colonization by invasive species (e.g. Vanhellemont et al., 2008) and have much lower frequencies of non-native vascular plant species (e.g. Battles et al., 2001; Schmidt, 2005).

In order to complete the scientific network, procedures for extension and the establishment of new sites and advisory structures under the new legislation are needed in order to restart the stagnated program. This programme should focus on further filling the gaps on representativeness and extending sites that are now to small or fragmented. Additionally, sites can also be specifically selected for conservation of highly demanding and dispersal limited species with high conservation value. For this purpose, a detection of hotspots for late-successional species could be performed, based on the actual distribution of conspicuous and well-known indicator species (such as *Hericium spp., Plagionotus spp., Cerambyx scopolii, Elater ferrugineus, Cucujus cinnaberinus…*).

6.6.2 Need for continued monitoring of spontaneous dynamics

In total about 20 sites are part of the network of intensively monitored forest reserves. First re-measurements have been finalized in 2019 in all of the originally monitored sites, allowing for first comparisons (see chapter 2-4). Further re-measurements are, however, needed in order to confirm the observed trends, and evaluate occurring changes in trends. Analysis of spontaneous dynamics in forests need longer time-windows in order to get the complete picture. Also, the network of intensively monitored sites needs to be further completed: in several forest types that were foreseen in the scientific monitoring programme (De Keersmaeker et al., 2005), no monitored sites are present yet, or monitoring infrastructure is not yet installed.

Continuity of measurements is essential for long-term monitoring programs such as the study of spontaneous forest dynamics. The longer the time-series available, the more valuable, solid and reliable the results will be. Certitude for this continuity is therefore needed. A stable framework provided by a multilevel forest monitoring strategy should allow for better co-operation and better guarantee for continuity. This framework can be based on the concept by Ferretti and Fisher (2013) and consists of four levels of monitoring intensity and longevity (Fig. 6.4). Examples of survey and monitoring programmes for forests in the Flemish context are:

- Level 0: Full-surveys (remote sensing – LiDAR-mapping of high green vegetation, …)
- Level 1: Flemish RFI and N2000-habitat monitoring; Forest health condition network (ICP-Forest Level I)

- Level 2: Forest Reserves Monitoring Network; Forest Ecosystem functioning network (ICP-Forest Level II)
- Level 3: Highly instrumented research sites (e.g. ICOS-sites, measuring tower Brasschaat and Gontrode)

In this framework, the monitoring of strict forest reserves is an important component, delivering detailed information and data-series on unmanaged reference sites.

At the same time, efforts are also being made to enhance the use and accessibility of the acquired data, also by other researchers. For this purpose, derived data will be made available through published data-files or publicly consultable interactive geodatabase. International collaboration with strict forest reserves researchers is already existent be it informally, and should be intensified and officialized. In 2019; a initiative in this context is already taken by Swiss collegues (exploratory workshop 'Joining forces in research on primeval forests and forest reserves').

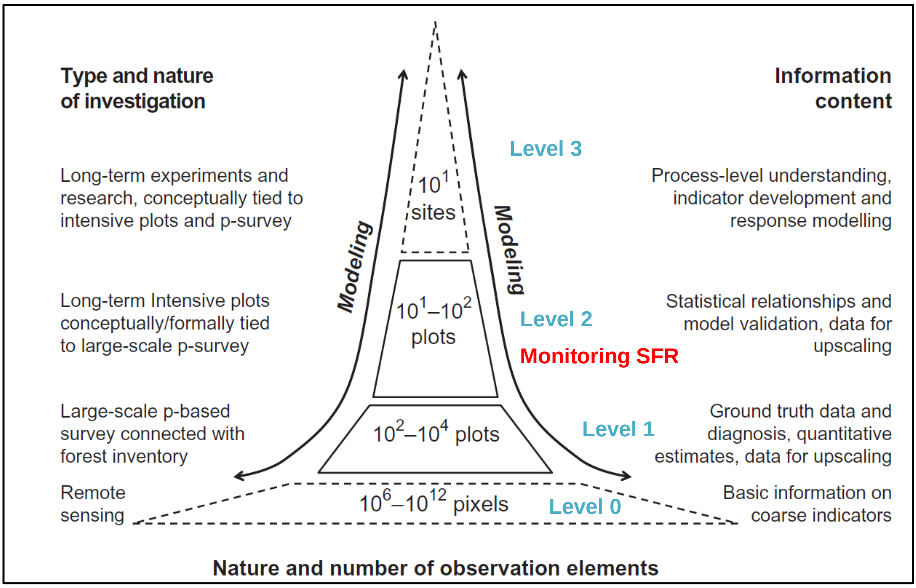


Fig. 6.4 Schematic representation of a four-level hierarchical monitoring framework (Ferretti and Fisher, 2013). The width of the elements is proportional to their sampling density; the height to their data intensity. Arrows represent the modeling for upscale–downscale results.

6.6.3 Forest reserves research and monitoring as a baseline and reference for other complementary and multidisciplinary research

Research in strict forest reserves remains important, not only for the study of natural forest dynamics and biodiversity, these sites and datasets are the baseline and essential ‘blanks’ for studies in functional ecology. Especially, in the framework of global change and environmental pressures, such as the cumulative effect of continued elevated atmospheric depositions, unmanaged forests will provide basic information on resilience and resistance of ecosystems and tree species and resulting fitness and alterations in interspecific competition.

In this context, priorities for future forest research in Flanders (but also in a wider international perspective) were analysed and published by Quataert et al. (2019). Many of the priority research topics and knowledge gaps that were identified have strong links or potential research sites in the strict reserves. A non-exhaustive selection of topics and methods that require our attention and provide important perspectives for future research are given below:

- remote sensing: possibilities of new remote-sensing techniques for characterization of forest stands (such as airborne and ground-based LiDAR. The detailed large-scale inventories in forest reserves can serve as ‘detailed ground-truth’ data for analysis of aircraft-borne hyperspectral and LiDAR-data.

- knowledge gaps on keystone functional ecological groups such as ectomycorrhizal and wood-decaying fungi, community of soil-dwelling and subterrestrial invertebrate decomposers. and their relationship to nutrient cycling and regeneration, using novel techniques of eDNA (next generation sequencing). Due to their undisturbed character, and existing background data and knowledge, strict reserves are the preferential sites for such research.

Furthermore, the standardized re-sampling of specific target groups, will also allow us to evaluate envisaged trends in species richness and composition. Standardization and repeatability have always been important criteria in earlier inventories of species groups in strict reserves. Therefore, these sites are again preferential for resurveys.

First preliminary re-inventories of logs of the NAT-MAN-project (Walleyn and Vandekerkhove, 2002; Ódor et al., 2006), for instance, already reveal interesting new developments (Van Landuyt en De Beer, 2016).
Repeated standardized inventories of saproxylic beetles should also be initiated in order to examine whether observed trends of increased species richness in German reserves also appear in our sites.

For these specific research activities, interdisciplinary co-operation with experts in other disciplines and institutions is required. Such forms of fruitful collaboration should be continued and even enhanced, through joint research projects, MSc and PhD studies,… The strict reserves and their acquired datasets still contain high potential for both fundamental and applied future research.

Experto crede: aliquid amplius invenies in silvis, quam in libris. Ligna et lapides docebunt te, quod a magistris audire non possis.:

‘believe me, you will find more lessons in the woods than in books. Trees and stones will teach you what you cannot learn from masters’

Bernardus van Clairvaux – 1090-1153 - Epistola CVI, sect. 2;

“Laissons faire un peu à nature: elle entend mieux ses affaires que nous”.

Michel de Montaigne (1533-1592)

References

Adam, D., Vrška, T., 2009. Important localities of old-growth forests. In: Hrnčiarová, T., Mackovčin, P., Zvara, I. (Ed.), Landscape atlas of the Czech Republic. Průhonice, Czech Republic: Ministry of Environment and Silva Tarouca Research Institute, Prague, Czech Republic.

Achat, D., Fortin, M, Landmann, G., Ringeval, B., Augusto, L., 2015. Forest soil carbon is threatened by intensive biomass harvesting. Scientific Reports 5, 15991.

Aertsen, W., Janssen, E., Kint, V., Bontemps, J.D., Van Orshoven, J., Muys, B., 2014. Long-term growth changes of common beech (Fagus sylvatica L.) are less pronounced on highly productive sites. Forest Ecology and Management 312, 252-259.

Afdeling Bos & Groen, 2001a. Beheervisie voor openbare bossen. Ministry of the Flemish Community, Brussels, Belgium.

Afdeling Bos & Groen, 2001b. De bosinventaris van het Vlaamse Gewest. Resultaten van de eerste inventarisatie 1997-2000. Ministry of the Flemish Community, Brussels, Belgium.

Ahas, R., 1999. Long-term phyto-, ornitho- and ichthyophenological time-series analyses in Estonia. International Journal of Biometeorology 42, 119–123.

Alessandrini, A., Biondi, F., Di Filippo, A., Ziaco, E., Piovesan, G., 2011. Tree size distribution at increasing spatial scales converges to the rotated sigmoid curve in two old-growth beech stands of the Italian Apennines. Forest Ecology and Management 262, 1950-1962.

Alexander, K.N.A., 2004. Revision of the Index of Ecological Continuity as used for saproxylic beetles. English Nature Research Reports 574. English Nature, Peterborough. UK.

Alexander, K.N.A., 2008. The special importance of traditional orchards for invertebrate conservation, with a case study of the BAP priority species the Noble Chafer Gnorimus nobilis. Landscape Archaeology and Ecology 7, 12-17.

Althoff, B., Hocke, R., Willig, J., 1993. Naturwaldreservate in Hessen. Waldkundliche Untersuchungen, Grundlagen und Konzept. Mitteillungen der Hessischen Landesforstverwaltung, Band 25. Hessische Landesforstverwaltung, Wiesbaden, Germany.

Amanzadeh, B., Sagheb-Talebi, K., Sotoudeh Foumani, B. Fadaie, F., Camarero, J.J., Linares, J.C., 2013. Spatial Distribution and Volume of Dead Wood in Unmanaged Caspian Beech (Fagus orientalis) Forests from Northern Iran. Forests 2013, 4, 751-765. doi:10.3390/f4040751

Ammer, U., 1991. Konsequenzen aus den Ergebnissen der Totholzforschung für die forstliche Praxis. Forstwissenschaftliches Centralblatt 110, 149-157.

Anderson, P. D., Larson, D. J., Chan, S. S., 2007. Riparian buffer and density management influences on microclimate of young headwater forests of western Oregon. Forest Science 53, 254-269.

Angelstam, P., 1998. Maintaining and restoring biodiversity in European boreal forests by developing natural disturbance regimes. Journal of Vegetation Science 9, 593–602.

Angelstam, P., Mikusiński, G., 1994. Woodpecker assemblages in natural and managed boreal and hemiboreal forest - a review. Annales Zoologici Fennici 31, 157-172.

Angelstam, P.K., Butler, R., Lazdinis, M., Mikusiński, G., Roberge, J.M., 2003. Habitat thresholds for focal species at multiple scales and forest biodiversity conservation – dead wood as an example. Annales Zoologici Fennici 40, 473-484.

Ariya, U., Hamano, K. Y., Makimoto, T., Kinoshita, S., Akaji, Y., Miyazaki, Y., Hirobe, M., Sakamoto, K., 2016. Temporal and spatial dynamics of an old-growth beech forest in western Japan. Journal of Forest Research 21, 73-83. doi:10.1007/s10310-015-0514-1

Arnolds, E., van den Berg, A., 2001. Trends in de paddestoelenflora op basis van karteringsgegevens. Coolia 44, 139-152.

Baddeley, A., Rubak, E., Turner, R., 2015. Spatial Point Patterns: Methodology and Applications with R. Chapman and Hall/CRC Press, London, UK.

Baeten, L., Bauwens, B., De Schrijver, A., De Keersmaeker, L., Van Calster, H., Vandekerhove, K., Roelandt, B., Beeckman, H., Verheyen, K., 2009a. Herb layer changes (1954–2000) related to the conversion of coppice-with-standards forest and soil acidification. Applied Vegetation Science 12, 187–197.

Baeten, L., De Frenne, P., Verheyen, K., Graae, B.J., Hermy M., 2010b. Forest herbs in the face of global change: a single-species-multiple-threats approach for Anemone nemorosa. Plant Ecology and Evolution 143, 19–30.

Baeten, L., Hermy, M., Van Daele, S., Verheyen, K., 2010a. Unexpected understorey community development after 30 years in ancient and post-agricultural forests. Journal of Ecology 98, 1447-1453.

Baeten, L., Jacquemyn, H., Van Calster, H., Van Beek, E., Devlaeminck, R., Verheyen, K., Hermy, M., 2009b. Low recruitment across life stages partly accounts for the slow colonization of forest herbs. Journal of Ecology 97, 109-117.

Baeten, L., Vangansbeke, P., Hermy, M., Peterken, G., Vanhuyse, K., Verheyen, K., 2012. Distinguishing between turnover and nestedness in the quantification of biotic homogenization. Biodiversity and Conservation 21, 1399-1409.

Bailey, S., 2007. Increasing connectivity in fragmented landscapes: an investigation of evidence for biodiversity gain in woodlands. Forest Ecology and Management 238, 7-23.

Baltzinger, M., Archaux, F., Dumas, Y., 2012. Tree litter and forest understorey vegetation: a conceptual framework to understand the effects of tree litter on a perennial geophyte, Anemone nemorosa. Annals of Botany 109, 1175-1184.

Barkham, J.P., 1992. The effects of coppicing and neglect on the performance of the perennial ground flora. In: Buckley G.P. (ed.) Ecology and management of coppice woodlands. Chapman & Hall, London, 115–146.

Barthod, C., Trouvilliez, J., 2002. La protection des forêts dans la politique forestière française, le cas particulier des réserves intégrales. Revue Forestière Française 54, 7-16.

Barton, A.M., Keeton, W.S., 2018. Ecology and Recovery of Eastern Old-Growth Forests. Island press, Washington, USA.

Baselga, A., 2010. Partitioning the turnover and nestedness components of beta diversity. Global Ecology and Biogeography 19, 134–143.

Baselga, A., Orme, D., Villeger, S., De Bortoli, J., Leprieur, F., Logez, M., Henriques-Silva R., 2018. Package ‘betapart’- Partitioning Beta Diversity into Turnover and Nestedness Component. version 1.5.1.

Battles, J., Shlisky, A., Barrett, R., Heald, R., Allen-Diaz, B., 2001. Effects of forest management on plant species diversity in a Sierran conifer forest. Forest Ecology and Management 146, 211-222.

Bauhus, J., Puettmann, K., Messier, C., 2009. Silviculture for old-growth attributes. Forest Ecology and Management 258, 525–537.

Beck, J.J., Larget, B., Waller, D.M., 2017. Phantom species: adjusting estimates of colonization and extinction for pseudo- turnover. Oikos 127, 1605-1618.

Becker, T., Spanka, J., Schröder, L, Leuschner, C., 2017, Forty years of vegetation change in former coppice-with-standards woodlands as a result of management change and N deposition. Applied Vegetation Science 20, 304-313.

Bédéneau, M., 2003. Evolution des différentes strates dans le peuplement ligneux de la réserve biologique de la Tillaie en Forêt de Fontainebleau entre 1968 et 2000. Revue Forestière Française 55, 323-332.

Bédéneau, M., 2005. Evolution du peuplement ligneux de la réserve biologique du Gros Fouteau en Forêt de Fontainebleau entre 1971 et 2003. Revue Forestière Française 57, 525-535.

Besag, J., 1977. Contribution to the Discussion on Dr. Ripley's Paper. Journals of the Royal Statistical Society B 39, 193-195.

Bianchi, L., Bottacci, A., Calamini, G., Maltoni, A., Mariotti, B., Quilghini, G., Salbitano, F., Tani, A., Zoccola, A., Paci, M., 2011. Structure and dynamics of a beech forest in a fully protected area in the northern Apennines (Sasso Fratino, Italy). iForest 4, 136-144. doi:10.3832/ifor0564-004

Bigler, C., Bugmann, H., 2018. Climate-induced shifts in leaf unfolding and frost risk of European trees and shrubs. Nature – Scientific Reports 8, 9865.

Bílek, L., Remeš, J., Zahradník, D., 2011. Managed vs. unmanaged. Structure of beech forest stands (Fagus sylvatica L.) after 50 years of development, Central Bohemia. Forest Systems 20, 122-138.

Biondi, F., 1993. Climatic signals in tree-rings of Fagus sylvatica L. from the central Apennines, Italy. Acta Oecologica 14, 57-71.

Biris I.-A., Veen P., 2005. Virgin Forests in Romania. ICAN & KNNV, The Netherlands.

Blicharska, M., Mikusiński, G., 2014. Incorporating social and cultural significance of large old trees in conservation policy. Conservation Biology 28, 1558–1567.

Bobbink, R., Hicks, K., Galloway, J., Spranger, T., Alkemade,R., Ashmore, M., Bustamante, M., Cinderby, S., Davidson, E., Dentener, F., Emmett, B., Erisman, J-W., Fenn, M., Gilliam, F., Nordin, A., Pardo, L., De Vries, W., 2010. Global assessment of nitrogen deposition effects on terrestrial plant diversity: A synthesis. Ecological Applications 20, 30–59.

Bobbink, R., Hornung, M., Roelofs, J.G.M., 1998. The effects of air-borne nitrogen pollutants on species diversity in natural and semi-natural European vegetation. Journal of Ecology 86, 717–738.

Bobiec, A., 2002. Living stands and dead wood in the Białowieża Forest: suggestions for restoration management. Forest. Ecology and Management 165, 125-140.

Bobiec, A., 2012. Białowieża Primeval Forest as a remnant of culturally modified ancient forest. European Journal of Forest Research 131, 1269-1285

Bocca, M., Carisio, L., Rolando, A., 2007. Habitat use, home ranges and census techniques in the Black Woodpecker Dryocopus martius in the Alps. Ardea 95, 17–29.

Boch, S., Prati, D., Müller, J., Socher, S., Baumbach, H., Buscot, F., 2013. High plant species richness indicates management-related disturbances rather than the conservation status of forests. Basic and Applied Ecology 14, 496–505.

Boddy, L., 2001. Fungal community ecology and wood decomposition processes in angiosperms: from standing tree to complete decay of coarse woody debris. Ecological Bulletins 49, 43–56.

Böhl, J., Brändli, U.-B., 2007. Deadwood volume assessment in the third Swiss National Forest Inventory: methods and first results. European Journal of Forest Research 126, 449–457.

Bommer, E., Rousseau, M., 1879. Catalogue des champignons observés aux environs de Bruxelles. Bull.Soc. Roy. Bot. Belgique 18, 61-219.

Boncina, A., Kadunc, A., Robic, D., 2007. Effects of selective thinning on growth and development of beech (Fagus sylvatica L.) forest stands in south-eastern Slovenia. Annals of Forest Science 64, 47-57.

Borlea G.F., 1999. Forest Reserves and their Research in Romania. In: Diaci, J. (ed.) Virgin forests and forest reserves in Central and East European Countries: history, present status and future development. Proceedings of the invited lecturers' reports presented at the COST-E4 Management Committee and Working Groups meeting in Ljubljana, Slovenia 25-28 April 1998. Department of Forestry and Renewable Forest Resources, Biotechnical University, Ljubljana, Slovenia, 67-86.

Bormann, F.H., Likens, G.E., 1979. Pattern and process in a forested ecosystem: disturbance, development and the steady state based on the Hubbard Brook Ecosystem Study. Springer Verlag, New York, USA..

Borrmann, K., 1993. Sturmschäden im Naturwaldreservat. Der Wald 43, 304-307.

Bourquin-Mignot, C., Girardclos, O., 2001. Construction d'une longue chronologie de hêtres au Pays Basque. La forêt d'Iraty et le Petit Age Glaciaire Sud-Ouest Européen. Rev. Géogr. Pyrénées Sud-Ouest 11, 59-71.

Brahy, V., Deckers, J., Delvaux, B., 2000. Estimation of soil weathering stage and acid neutralizing capacity in a toposequence Luvisol-Cambisol on loess under deciduous forest in Belgium. European Journal of Soil Science 51, 1–13.

Brändli, U.-B., Abegg, M., Duc, P., Ginzler, C., 2010. Biologische Vielfalt. In: Brändli, U.-B., Eidgenössische Forschungsanstalt für Wald Schnee und Landschaft WSL, Bundesamt für Umwelt BAFU (Eds.), Schweizerisches Landesforstinventar. Ergebnisse der dritten Erhebung 2004-2006. Eidgenössische Forschungsanstalt für Wald Schnee und Landschaft WSL, Birmensdorf, 187–228.

Brang, P., Heiri, C., Bugmann, H., 2011. Waldreservate. 50 Jahre natürliche Waldentwicklung in der Schweiz. Ed. Haupt, Bern.

Branquart, E., Vandekerkhove, K., Bourland, N., Lecomte, H., 2004. Les arbres sur-âgés et le bois mort dans les forêts de Flandre, de Wallonie et du Grand-Duché de Luxembourg. In: Vallauri, D., André, J., Dodelin, B., Eynard-Machet, R., Rambaud, D. (Eds.). Bois morts et à cavités - une clé pour des forêts vivantes. Lavoisier, Paris, France, 19-28.

Brown, S., Schroeder, P., Birdsey, R., 1997. Aboveground biomass distribution of US eastern hardwood forests and the use of large trees as an indicator of forest development. Forest Ecology and Management 96, 37-47.

Brunet, J., Isacsson, G., 2009. Restoration of beech forest for saproxylic beetles—effects of habitat fragmentation and substrate density on species diversity and distribution. Biodiversity and Conservation 18, 2387–2404.

Brunet, J., Diekmann,M., Falkengren-Grerup, U., 1998. Effects of nitrogen deposition on field layer vegetation in south Swedish oak forests. Environmental Pollution 102, 35–40.

Brunet, J., Falkengren-Grerup, U, Tyler, G., 1996. Herb layer vegetation of south Swedish beech and oak forests – Effects of management and soil acidity during one decade. Forest Ecology and Management 88, 259-272.

Brunet, J., Fritz, Ö., Richnau, G., 2010. Biodiversity in European beech forests – a review with recommendations for sustainable forest management. Ecological Bulletin 53, 77–94.

Brunet, J., Von Oheimb, G., 1998. Colonization of secondary woodlands by Anemone nemorosa. Nordic Journal of Botany 18, 369–377.

Brunet. J., Fritz, Ö., Richnau, G., 2010. Biodiversity in European beech forests: a review with recommendations for sustainable forest management. Ecological Bulletins 53, 77–94.

Brustel, H., 2004. Biological value of French forests assessed with saproxylic beetles: a way to conserve this natural heritage. Proceedings of the 3rd European Symposium and Workshop on the Conservation of Saproxylic Beetles. Riga, Latvia.

Brustel, H., Dodelin, B., 2005. Coléoptères saproxyliques: exigences biologiques et implications de gestion. In: Vallauri, D., André, J., Dodelin, B., Eynard-Machet, R., Rambaud, D. (eds.) Bois mort et à cavités: une clé pour des forêts vivantes. Editions Tec & Doc Lavoisier, Paris, France, 127-135.

Brzeziecki, B., Pommerening, A., Miścicki, S., Drozdowski, S., Żybura, H., 2016. A common lack of demographic equilibrium among tree species in Białowieża National Park (NE Poland): evidence from long- term plots. Journal of Vegetation Science 27, 460-469.

Buchwald, E., 2005. A hierarchical terminology for more or less natural forests in relation to sustainable management and biodiversity conservation, Proceedings: Third expert meeting on harmonizing forest-related definitions for use by various stakeholders Food and Agriculture Organization of the United Nations, Rome, 17-19 January 2005

Buchwald, K., 1958. Die Bedeutung von Waldnaturschutzgebieten für Forstwissenschaft und –wirtschaft. Früne Farbe 10, 10-11.

Bücking, W., 1994. Ziele und Auswahl von Naturwaldreservaten in Deutschland. AFZ 49, 561-562

Bücking, W., 1996. Faunistische Untersuchungen in Bannwäldern. Agrarforschung in Baden-Württemberg 26, 147-159.

Bücking, W., 1998. Faunistische Untersuchungen in Bannwäldern - Holzbewohnende Käfer, Laufkäfer und Vögel. Mitteilungen der Forstlichen Versuchs- und Forschungsanstalt Baden-Württemberg Heft 203, Freiburg, Breisgau, Germany

Bücking, W., 2007. Naturwaldreservate in Europa. Forstarchiv 78, 180-187.

Bücking, W., Schmidt, W., 1999. Germany. In: Parviainen, J., Little, D., Doyle, M., O'Sullivan, A., Kettunen, M., Korhonen, M. (Eds.) Research in forest reserves and natural forests in European countries—country reports for the COST Action E4: Forest Reserves Research Network. EFI Proceedings, 16, Joensuu, Finland, 109-119.

Buckley, G.P. (ed.), 1992. Ecology and Management of Coppice Woodlands. Chapman & Hall, London, UK.

Buis, J., 1985. Historia forestis: Nederlandse bosgeschiedenis. Studia Historica XIV. HES, Utrecht, Netherlands.

Burrascano, S., de Andrade, R.B., Paillet, Y., Ódor, P., Antonini, G., Bouget, C., Campagnaro, T., Gosselin, F., Janssen, P., Persiani, A.M., Nascimbene, J., Sabatini, F.M., Sitzia, T., Blasi, C., 2018. Congruence across taxa and spatial scales: Are we asking too much of species data? Global Ecology and Biogeography 27, 980–990.

Burrascano, S., Keeton, W.S., Sabatini, F.M., Blasi, C., 2013. Commonality and Variability in the Structural Attributes of Moist Temperate Old-growth Forests: a Global Review. Forest Ecology and Management 291, 458-479.

Burrascano, S., Lombardi, F., Marchetti, M., 2008. Old-growth forest structure and deadwood: are they indicators of plant species composition? A case study from central Italy. Plant Biosystems 142, 313-323.

Burrascano, S., Ripullone, F., Bernardo, L., Borghetti, M., Carli, E., Colangelo, M., Gangale, C., Gargano, D., Gentilesca, T., Luzzi, G., Passalacqua, N., Pelle, L., Rivelli, A.R., Sabatini, F.M., Schettino, A., Siclari, A., Uzunov, D., Blasi, C., 2017. It's a long way to the top: Plant species diversity in the transition from managed to old- growth forests. Journal of vegetation science 29, 98-109,

Burschel, P., 1992. Totholz und Forstwirtschaft. Allgemeine Forst Zeitschrift 21, 1143-1146.

Büssler, H., 2010. Hotspot-Gebiete xylobionter Urwaldreliktarten aus dem Reich der Käfer. LWF Aktuell 76, 10-12.

Butaye, J., Jacquemyn, H., Honnay, O., Hermy, M., 2001. The species pool concept applied to forests in a fragmented landscape: dispersal limitation versus habitat limitation. Journal of Vegetation Science 13, 27-34.

Buxton, E.N., 1898. Epping Forest. 5th edition. Stanford, London.

Carbonnelle, S., Lezaca-Rojas, S., 2016. Plaidoyer pour une grande réserve intégrale en Wallonie. Forêt & Naturalité 2016 (1), 1-8.

Čermak, L., 1910. Einiges über den Urwald von waldbaulichen Gesichtspunkten. Zentralblatt für das gesamte Forstwesen 36, 340-370.

Chen, J., Saunders, S. C., Crow, T. R., Naiman, R. J., Brosofske, K. D., Mroz, G. D., Franklin, J. F., 1999. Microclimate in forest ecosystem and landscape ecology: variations in local climate can be used to monitor and compare the effects of different management regimes. BioScience, 49, 288-297.

Christensen, M., Emborg, J., 1996. Biodiversity in natural versus managed forest in Denmark. Forest Ecology and Management 85, 47-51.

Christensen, M., Hahn, K., Mountford, E.P., Ódor, P., Standovár, T., Roženbergar, D., Diaci, J., Wijdeven, P., Meyer, P., Winter, S., Vrška, T., 2005a. Dead wood in European beech (Fagus sylvatica) forest reserves. Forest Ecology and Management 210, 267-282.

Christensen, M., Heilmann-Clausen, J., Walleyn, R., Adamčik, S., 2005b. Wood-inhabiting fungi as indicators of nature value in European beech forests. In: Marchetti, M. (ed.) Monitoring and indicators of forest biodiversity in Europe—from ideas to operationality. EFI Proceedings 51, 229-237.

Chursky, M., 2006. Age structure and diameter distribution in a southern Swedish beech dominated landscape. SLU master thesis 2006/78. SLU, Uppsala.

Chylarecki, P., Selva, N., 2016. Ancient forest: Spare it from clearance. Nature, 530, 419.

Clark, J. S., Fastie, C., Hurtt, G., Jackson, S.T., Johnson, C., King, G., Lewis, M., Lynch, J., Pacala, S., Prentice I. C., Schupp, E. W. Webb III, T., Wyckoff, P., 1998. Reid's Paradox of rapid plant migration. BioScience 48, 13-24.

Clark, P.J., Evans, F.C., 1954. Distance to nearest neighbor as a measure of spatial relationships in populations. Ecology 35, 445–453.

Cline, S. P., Spurr, S. H., 1942. The virgin upland forest of central New England: A study of old growth stands in the Pisgah Mountain section of Southwestern New Hampshire. Harvard Forest Bulletin No. 21.

References

Closset-Kopp, D., Schnitzler, A., Aran, D., 2006. Dynamics in natural mixed-beech forest of the Upper Vosges. Biodiversity and Conservation 15, 1063-1093.

Commarmot, B., Abegg, M., Brändli, U.-B., Hobi, M., Korol, M., Lanz, A., 2013. Main results. In: Commarmot, B., Brändli, U.-B., Hamor, F., Lavnyy, V. (eds), 2013, Inventory of the Largest Primeval Beech Forest in Europe. A Swiss-Ukrainian Scientific Adventure. Swiss Federal Research Institute WSL, Birmensdorf, Ukrainian National Forestry University, L'viv, Carpathian Biosphere Reserve, Rakhiv, pp. 41-57.

Commarmot, B., Bachofen, H., Bundziak, Y., Bürgi, A., Ramp, B., Shparyk, Y., Sukhariuk, D., Viter, R., Zingg, A., 2005. Structures of virgin and managed beech forests in Uholka (Ukraine) and Sihlwald (Switzerland): a comparative study. Forest Snow and Landscape Research 79, 45-56.

Connell, J.H., 1978. Diversity in tropical rainforests and coral reefs. Science 199, 1302–1310

Cools, N., De Vos. B., 2016. Part X: Sampling and Analysis of Soil. In: UNECE ICP Forests Programme Coordinating Centre (ed.): Manual on methods and criteria for harmonized sampling, assessment, monitoring and analysis of the effects of air pollution on forests. Thünen Institute of Forest Ecosystems, Eberswalde, Germany.

Corona, P., Köhl, M., Marchetti, M., 2003. Advances in forest inventory for sustainable forest management and biodiversity monitoring. Forestry Sciences series 76. Kluwer Academic Publishers, Dordrecht, The Netherlands.

Crockatt, M.E., 2012. Are there edge effects on forest fungi and if so do they matter? Fungal Biology Reviews 26, 94-101.

Dajoz, R., 1974. Les insectes xylophages et leur rôle dans la dégradation du bois mort. In: Pesson, P. (ed.), Écologie forestière. La fôret: son climat, son sol, ses arbres, sa faune. Gauthier-Villars, Paris, France, 257-307.

Dagnélie, P., Palm, R., Rondeux, J., Thill, A., 1985. Tables de cubage des arbres et des peuplements forestiers. Les presses agronomiques de Gembloux, Gembloux, Belgium.

Daszkiewicz, P., Jędrzejewska, B., Samojlik, T., Bańka, B., 2008. Game management and the last imperial hunts in Białowieża Primeval Forest (1912-1913) in the report of Mitrofan Golenko. Sylwan 152, 47-59

De Frenne, P., Blondeel, H., Brunet, J., Caron, M.M., Chabrerie, O., Cougnon, M., Cousins, S.A.O., Decocq, G., Diekmann, M., Graae, B.J., Hanley, M.E., Heinken, T., Hermy, M., Kolb, A., Lenoir, J., Liira, J., Orczewska, A., Shevtsova, A., Vanneste, T., Verheyen, K., 2018. Atmospheric nitrogen deposition on petals enhances seed quality of the forest herb Anemone nemorosa. Plant Biology 20, 619-626.

De Frenne, P., Brunet, J., Cougnon, M., Decocq, G., Graae, B. J., Hagenblad, J., Hermy, M., Kolb, A., Lemke, I.H., Ma, S., Orczewska, A., Plue, J., Vranckx, G., Wulf, M., Verheyen, K., 2017. Biological flora of the British Isles : Milium effusum. Journal of Ecology 105, 839–858.

De Frenne, P., De Schrijver, A., Graae, B.J., Gruwez, R., Tack, W., Vandelook, F., Hermy, M., Verheyen, K., 2010a. The use of open-top chambers in forests for evaluating warming effects on herbaceous understorey plants. Ecological Research 25, 163–171,

De Frenne, P., Graae, B.J., Kolb, A., Brunet, J., Chabrerie, O., Cousins, S.A., Decocq, G., Diekmann, M., Dhondt, R., Eriksson, O., Heinken, T., Hermy, M., Jogar, U., Saguez, R., Shevtsova, A., Stanton, S., Zindel, R., Zobel, M., Verheyen K., 2010b, Significant effects of temperature on the reproductive output of the forest herb Anemone nemorosa L. Forest Ecology and Management 259, 809–817.

De Frenne, P., Rodríguez-Sánchez, F., Coomes, D. A., Baeten,L., Verstraeten, G., Vellend, M., Bernhardt-Römermann, M., Brown, C.D., Brunet, J., Cornelis, J., Decocq, G., Dierschke, H., Eriksson, O., Gilliam, F., Hédl, R., Heinken, T., Hermy, M., Hommel, P., Jenkins, M.A., Kelly, D., Kirby, K., Mitchell, F., Naaf, T., Newman, M., Peterken, G., Petřík, P., Schultz, J., Sonnier, G., Van Calster, H., Waller, D.M., Walther, G.-R., White, P., Woods, K., Wulf, M., Graae, B., Verheyen, K., 2013. Microclimate moderates plant responses to macroclimate warming. Proceedings of the National Academy of Sciencesof the United States of America, 110(46), 18561–18565. http://dx.doi.org/10.1073/pnas.1311190110

De Frenne, P., Rodríguez-Sánchez, F., De Schrijver, A., Coomes, D. A., Hermy, M., Vangansbeke, P., Verheyen, K., 2015. Light accelerates plant responses to warming. Nature Plants 1 (9), art. 15110.

De Frenne, P., Zellweger, F., Rodríguez-Sánchez, F., Scheffers, B.R., Hylander, K., Luoto, M., Vellend, M., Verheyen, K., Lenoir, J., 2019. Global buffering of temperatures under forest canopies. Nature Ecology & Evolutions. https://doi.org/10.1038/s41559-019-0842-1.

de Goffau, L. J. W., 1984. Bolitophagus reticulatus (Linné, 1767) een nieuwe soort voor Nederland (Coleoptera: Tenebrionidae). Entomologische Berichten 44, 56.

De Keersmaeker, L., Leyman, A., Vandekerkhove, K., 2007. Bepaling van een streefcijfer voor het netwerk van bosreservaten in Vlaanderen. Geactualiseerde versie maart 2007. Advisory report of the Research Institute for Nature and Forest, INBO.A.2007.93.

De Keersmaeker, L., Rogiers, N., Lauriks, R., De Vos, B., 2001. Ecosysteemvisie bos Vlaanderen, ruimtelijke uitwerking van de natuurlijke bostypes op basis van bodemgroeperingseenheden en historische boskaarten. Report VLINA C97/06, AMINAL, Brussels, Belgium.

De Keersmaeker, L., Van de Kerckhove, P., Baeté, H., Walleyn, R., Christiaens, B., Esprit, M., Vandekerkhove, K., 2005. Monitoringprogramma integrale bosreservaten: inhoudelijk programma en basishandleiding. Rapport IBW Bb.R.2005.003. IBW, Geraardsbergen, Belgium.

De Keersmaeker, L., Vandekerkhove, K., Verstraeten, A., Baeten, L., Verschelde, P., Thomaes, A., Hermy, M., Verheyen, K., 2011. Clear-felling effects on colonization rates of shade-tolerant forest herbs into a post-agricultural forest adjacent to ancient forest. Applied Vegetation Science 14, 75–83.

De Lombaerde, E., Verheyen, K., Perring, M.P., Bernhardt-Roemermann, M., Van Calster, H., Brunet, J., Chudomelova, M., Decocq, G., Diekmann, M., Durak, T., Hédl, R., Heinken, T., Hommel, P., Jaroszewicz, B., Kopecký, M., Lenoir, J., Macek, M., Malis, F., Mitchell, F.J.G., Naaf, T., Newman, M., Petrik, P., Reczynska, K., Schmidt, W., Swierkosz, K., Vild, O., Wulf, M., Baeten, L., 2018. Responses of competitive understorey species to spatial environmental gradients inaccurately explain temporal changes. Basic and Applied Ecology 30, 52–64.

De Schrijver, A., De Frenne, P., Ampoorter, E., Van Nevel, L.,Demey, A., Wuyts, K., Verheyen, K., 2011. Cumulative nitrogen input drives species loss in terrestrial ecosystems. Global Ecology and Biogeography 20, 803–816.

De Smedt, P., Baeten,L, Berg, M., Gallet-Moron, E., Brunet, J., Cousins, S., Decocq, G., Diekmann, M., Giffard, B., De Frenne, P., Hermy, M., Bonte, D., Verheyen, K., 2018. Desiccation resistance determines distribution of woodlice along forest edge-to-interior gradients. European Journal of Soil Biology 85, 1-3.

De Smedt, P., Baeten, L., Gallet-Moron, E., Brunet, J., Cousins, S.A.O., Decocq, G., Deconchat, M., Diekman, M., Giffard, B., Kalda, O., Liira, J., Paal, T., Wulf, M., Hermy, M., Verheyen, K., 2019. Forest edges reduce slug (but not snail) activity-density across Western Europe. Pedobiologia 75, 34-37.

Deckers, B., Kerselaers, E., Gulinck, H., Muys, B., Hermy, M., 2005. Long-term spatio-temporal dynamics of a hedgerow network landscape in Flanders, Belgium. Environmental Conservation 32, 20–29.

Decocq, G., Aubert, M., Dupont, F., Alard, D., Saguez, R., Wattez-Franger, A., De Foucault, B., Delelis-Dusollier, A., Bardat, J., 2004. Plant diversity in a managed temperate deciduous forest: understorey response to two silvicultural systems. Journal of Applied Ecology 41, 1065-1079.

Decocq, G., Hermy, M., 2003. Are there herbaceous dryads in temperate deciduous forests ? Acta Botanica Gallica, 150, 373-382.

Dengler, A., 1935. Waldbau auf ökologischer Grundlage: ein Lehr- und Handbuch. Springer Verlag, Berlin, Heidelberg, Germany.

Denis, P., 1998. Arbres morts, arbres à cavités. Pourquoi ? Comment ? Guide. ONF, Fontainebleau, France.

Desender, K., Dekoninck, W., Maes, D., Crevecoeur, L., Dufrêne, M., Jacobs, M., Lambrechts, J., Pollet, M., Stassen, E., Thys, N., 2008. Een nieuwe verspreidingsatlas van de loopkevers en zandloopkevers (Carabidae) in België. INBO Report R.2008.13. Instituut voor Natuur- en Bosonderzoek, Brussels, Belgium.

Desender, K., Ervynck, A., Tack, G., 1999. Beetle diversity and historical ecology of woodlands in Flanders. Belgian Journal of Zoology 129, 139-156.

Devillers, P., Roggeman, W., Tricot, J., del Marmol, P., Kerwijn, C., Jacob, J.P., Anselin, A., 1988. Atlas van de Belgische broedvogels. KBIN, Brussels.

Dhiedt, E., De Keersmaeker, L., Vandekerkhove, K., Verheyen, K., 2019. Effects of decomposing beech (Fagus sylvatica) logs on the chemistry of acidified sand and loam soils in two forest reserves in Flanders (northern Belgium). Forest Ecology and Management 445, 70–81.

Di Filippo, A., Biondi, F., Maugeri, M., Schirone, B., Piovesan, G., 2012. Bioclimate and growth history affect beech lifespan in the Italian Alps and Apennines. Global Change Biology 18, 960-972.

Di Filippo, A., Biondi, F., Piovesan, G., Ziaco, E., 2017. Tree ring-based metrics for assessing old-growth forest naturalness. Journal of Applied Ecology 54, 737-749.

Di Filippo, A., Pederson, N., Baliva, M., Brunetti, M., Dinella, A., Kitamura, K., Knapp, H. D., Schirone, B., Piovesan, G., 2015. The longevity of broadleaf deciduous trees in Northern Hemisphere temperate forests: insights from tree-ring series. Frontiers in Ecology and Evolution 3, 46. doi: 10.3389/fevo.2015.00046.

Diaci, J. (ed.) 1999. Virgin forests and forest reserves in Central and East European Countries: history, present status and future development. Proceedings of the invited lecturers' reports presented at the COST-E4 Management Committee and Working Groups meeting in Ljubljana, Slovenia 25-28 April 1998. Department of Forestry and Renewable Forest Resources, Biotechnical University, Ljubljana, Slovenia.

Diaci, J., Zeibig, A., 2001. Natural gaps in beech forests in Slovenia. In: Mountford, E., 2001. Natural canopy gap characteristics in European beech forests. Nat-Man Working Report 2, FLEC, Kopenhagen, Denmark.

Diaconu, D.; Kahle, H.-P.; Spiecker, H., 2015. Tree- and Stand-Level Thinning Effects on Growth of European Beech (Fagus sylvatica L.) on a Northeast- and a Southwest-Facing Slope in Southwest Germany. Forests 2015, 3256-3277.

Diekmann, M., 2010 Aktuelle Vegetationsveränderungen in Wäldern—Welche Rolle spielt der Klimawandel? Berichte der Reinhardt Tüxen-Gesellschaft 22, 57–65.

Dierschke, H., 2005. Laurophyllisation—auch eine Erscheinung im nördlichen Mitteleuropa? Zur aktuellen Ausbreitung von Hedera helix in sommergrünen Laubwäldern. Berichte der Reinhardt Tüxen-Gesellschaft 17, 151–168.

Diku, A., Shuka L., 2018. Pyjet e vjeter të ahut në Shqipëri. (Old beech forests in Albania). PSEDA-ILIRIA, Tirana, Albania.

Dirnböck, T., Pröll, G., Austnes, K., Beloica, J., Beudert, B., Canullo, R., De Marco, A., Fornasier M.F., Futter, M., Goergen, K., Grandin, U., Holmberg, M., Lindroos A.-J., Mirtl, M., Neirynck, J., Pecka, T., Nieminen, T.M., Nordbakken J.F., Posch, M., Reinds G.-J., Rowe E.C., Salemaa, M., Scheuschner, T., Starlinger, F., Uziębło A.K., Valinia S., Weldon, J., Wamelink W.G.W., Forsius, M., 2018. Currently legislated decreases in nitrogen deposition will yield only limited plant species recovery in European forests. Environmental research Letters 13, 125010.

Dittmar, C., Zech, W., Elling, W., 2003. Growth variations of Common beech (Fagus sylvatica L.) under different climatic and environmental conditions in Europe - a dendroecological study. Forest Ecology and Management 173, 63-78.

Dua, V., 1975. 'Bosreservaten' in 'Standpunten betreffende actuele bospolitieke onderwerpen'. Groene Band 17, 35-41.

Dubois, G., Vignon, V., Delettre, Y.R., Rantier, Y., Vernon, P., Burel, F., 2009. Factors affecting the occurrence of the endangered saproxylic beetle Osmoderma eremita (Scopoli, 1763) (Coleoptera: Cetoniidae) in an agricultural landscape. Landscape and Urban Planning 91, 152-159.

Dufrêne, M., Grootaert, P., Lebrun, P., Rondeux, J., 2008. A research project to study patterns, roles and determinants of wood-dependent species diversity in Belgian deciduous forests (XYLOBIOS): final report. Belgian Science Policy, Brussels.

Dumortier, M., De Bruyn, L., Wils, C., Paelinckx, D., Vander Mijnsbrugge, K., Cox, K., Sioen, G., Roskams, P., Vandekerkhove, K., Hens, M., 2005. Bossen en struwelen. In: Dumortier, M. (Ed.). Natuurrapport 2005 - toestand van de natuur in vlaanderen: cijfers voor het beleid. Mededeling van het Instituut voor Natuurbehoud 24, 115-128.

Edman, M., Gustafsson, M., Stenlid, J., Ericson, L., 2004a. Abundance and viability of fungal spores along a forestry gradient – responses to habitat loss and isolation? Oikos 104, 35–42.

Edman, M., Kruys, N., Jonsson, B.G., 2004b. Local dispersal sources strongly affect colonisation patterns of wood-decaying fungi on experimental logs. Ecological Applications 14, 893–901.

Edman, M., Kruys, N., Gustafsson, M., Stenlid, J., Jonsson, B.G., Ericson, L., 2004c. Spore deposition of wood-decaying fungi: importance of landscape composition. Ecography 27, 103-111.

Edwards, D. M., Jay, M., Jensen, F.S., Lucas, B., Marzano, M., Montagné, C., Peace, A., Weiss, G., 2012. Public preferences across Europe for different forest stand types as sites for recreation. Ecology and Society 17, 27. http://dx.doi.org/10.5751/ES-04520-170127

Eisenhauer, N., Bonn, A., Guerra, C., 2019. Recognizing the quiet extinction of invertebrates. Nature Communications 10, Article 50.

Ellenberg, H., Weber, H.E., Düll, R., Wirth, V., Werner, W., 2001. Zeigerwerte von Pflanzen in Mitteleuropa, 3rd ed. Scripta Geobotanica 18, 1-262. Goltze, Göttingen, DE.

Emborg, J., 2007. Suppression and release during canopy recruitment in Fagus sylvatica and Fraxinus excelsior, a dendro-ecological study of natural growth patterns and competition. Ecological Bulletins 52, 53-67.

Emborg, J., Christensen, M., Heilmann-Clausen, J., 2000. The structural dynamics of Suserup Skov, a near-natural temperate deciduous forest in Denmark. Forest Ecology and Management 126, 173- 189.

Engel, F., Meyer, P., Bauhus, J., Gärtner, S., Reif, A., Schmidt, M., Schultze, J., Wildmann, S., Spellmann, H., 2016. Wald mit natürlicher Entwicklung – ist das 5-%-Ziel erreicht? AFZ-Der Wald 2016/9, 46-48.

Esseen, P.-A., Ehnstrom, B., Ericson, L., Sjoberg, K., 1997. Boreal forests. Ecological Bulletins 46, 16-47.

European Commission, 2011. Our life insurance, our natural capital: an EU biodiversity strategy to 2020. Communication from the Commission to the European parliament, the Council, the economic and social committee and the committee of the regions. E.C. Comm 2011.244. E.C, Brussels.

European Commission, 2013. Guidelines on Wilderness in Natura 2000 - Management of terrestrial wilderness and wild areas within the Natura 2000 Network. Technical Report 2013-069, EU, Brussels.

European Commission-DG-Environment, 2013. Guidelines on Wilderness in Natura 2000 - Management of terrestrial wilderness and wild areas within the Natura 2000 Network. European Union, Brussels, Belgium.

Falinski, J. B. and Mortier, F., 1996. Biodiversité et gestion durable des forêts en Europe. Revue Forestière Française 68, 89-116.

Falkengren-Grerup, U., Tyler, G., 1993. Experimental-evidence for the relative sensitivity of deciduous forest plants to high soil acidity. Forest Ecology and Management 60, 311–326.

FAO, 2015. Global Forest Resources Assessment 2015. Terms and definitions. In: Forest resources Assessment Working Paper 180. FAO, Rome, Italy.

Fayt, P., Dufrêne, M., Branquart, E., Hastir, P., Pontégnie, C., Henin, J.-M., Versteirt, V., 2006. Contrasting responses of saproxylic insects to focal habitat resources: the example of longhorn beetles and hoverflies in Belgian deciduous forests. Journal of Insect Conservation 10, 129–150.

Fedrowitz, K., Koricheva, J., Baker, S.C., Lindenmayer, D.B., Palik, B., Rosenvald, R., Beese, W., Franklin, J.F., Kouki, J., Macdonald, E., Messier, C., Sverdrup-Thygeson A., Gustafsson L., 2014. Can retention forestry help conserve biodiversity? A meta-analysis. Journal of Applied Ecology 51, 1669–1679.

Ferretti, M., Fischer, R. (eds.), 2013. Forest monitoring methods for terrestrial investigations in Europe with an overview of North America and Asia. Developments in Environmental Science Volume 12. Elsevier, Oxford, UK, Amsterdam, the Netherlands.

Ferris-Kaan, R., Lonsdale, D., Winter, T., 1993. The conservation management of dead wood in forests. Research Information Note 241. Research Publication Officer, The Forestry Authority, Research Division, Alice Holt Lodge, UK.

Fitzmaurice, G.M., Laird, N.M., Ware, J.H., 2004. Applied longitudinal analysis. Wiley series in probability and statistics. John Wiley and Sons, New York, USA.

Fowles, A.P., Alexander, K.N.A., Key, R.S., 1999. The Saproxylic Quality Index: evaluating wooded habitats for the conservation of dead-wood Coleoptera. The Coleopterist 8, 121-141.

FPS Economy, SMEs, Self-employed and Energy, 2009. Key figures 2009 - Belgium and the European Union. Brussels. Belgium.

Franc, N., Götmark, F., 2008. Openness in management: hands-off vs. partial cutting in conservation forests, and the response of beetles. Biological Conservation 141, 2310-2321.

Frank, G., Parviainen, J.,Vandekerkhove, K., Latham, J., Schuck, A., Little, D. (Eds)., 2007. COST Action E27 Protected Forest Areas in Europe – Analysis and Harmonisation (PROFOR): Results, Conclusions and Recommendations. Federal Research and Training Centre for Forests, Natural Hazards and Landscape (BFW).Vienna, Austria.

Frelich, L.E., Reich, P.B., 2003. Perspectives on development of definitions and values related to old-growth forests. Environmental reviews 11, 9-22.

Friess, N., Müller, J., Aramendi, P., Bässler, C., Brändle, M., Bouget, C., Brin, A., Bussler, H., Georgiev, K., Gil, R., Gossner, M., Heilmann-Clausen, J., Isacsson, G., Krištín, A., Lachat, T., Larrieu, L., Magnanou, E., Maringer, A., Mergner, U., Mikoláš, M., Opgenoorth, L., Schmidl, J., Svoboda, M., Thorn, S., Vandekerkhove, K., Vrezec, A., Wagner, T., Winter, M.-B., Zapponi, L., Brandl, R., Seibold, S., 2019. Arthropod communities in fungal fruitbodies are weakly structured by climate and biogeography across European beech forests. Diversity and Distributions 25, 783-796

Fritz, Ö., Niklasson, M., Churski, M., 2009. Tree age is a key factor for the conservation of epiphytic lichens and bryophytes in beech forests. Applied Vegetation Science 12, 93-106.

Fuchs, F., 1861. Ungarns Urwälder und das Wesentlichste zur Kenntniß, Beurtheilung und Einführung eines rationellen Forstbetriebs Ungarischen Privatwaldungen. Georg Kilian's Universitäts-Buchhandlung, Budapest, Hungary.

Gayer K., 1868. Der gemischte Wald , seine Begründung und Pflege, inbesondere durch Horst-und Gruppenwirtschaft. Parey, Berlin, Germany.

Gehrhardt, E., 1923. Über Urwaldungen in den Karpathen. Silva 11, 361-363.

Geiger, R., Aron, R. H., Todhunter, P. (2009). The climate near the ground. Rowman & Littlefield, Lanham, USA.

Geiser, R., 1998. Rote liste der Käfer (Coleoptera). In: Bundesanstalt für Naturschutz (ed). Rote Liste gefärdeter Tiere Deutschlands. BfN, Bonn-Bad Godesberg, Germany, 168-230.

Gilg, O., 2005. Old-Growth forests. Characteristics, conservation and monitoring. Technical report 74bis. ATEN, Monpellier, France.

Gillner, S., Rüger, N., Roloff, A., Berger, U., 2013. Low relative growth rates predict future mortality of common beech (Fagus sylvatica). Forest Ecology and Management 302, 372-378.

Godefroid, S., Rucquoij, S., Koedam, N., 2005. To what extent do forest herbs recover after clearcutting in beech forest? Forest Ecology and Management 210, 39–53.

Göppert, H., 1868. Skizzen zur Kenntniss der Urwälder Schlesiens und Böhmens. E. Blochmann & Sohn, Dresden, Germany.

Götmark, F., Thorell, M., 2003. Size of nature reserves: densities of large trees and dead wood indicate high value of small conservation forests in southern Sweden. Biodiversity and Conservation 12, 1271-1285.

Govaere, L., Roelandt, B., Waterinckx, M., 2010. Handleiding tweede bosinventarisatie. Versie 2010.1. Agentschap voor Natuur en Bos, Brussels.

Green, P., Peterken, G.F., 1997. Variation in the amount of dead wood in woodlands of the Lower Wye Valley, UK, in relation to the intensity of management. Forest Ecology and Management 98, 229-238.

Greenberg, C.H., McLeod, D.E., Loftus, D.L., 1997. An old-growth definition for mixed mesophytic and western mesophytic forests. GTR SRS-16, U.S. Department of Agriculture, Forest Service, Southern Research Station, Asheville.

Grime, J.P., 1979. Plant Strategies and Vegetation Processes. Wiley, Chichester, UK.

Grove, S. J., 2002. Saproxylic insect ecology and the sustainable management of forests. Annual Review of Ecology and Systematics 33, 1-23.

Gu, W., Heikilä, R, Hanski, I., 2002. Estimating the consequences of habitat fragmentation on extinction risk in dynamic landscapes. Landscape Ecology 17, 699-710.

Gundersen, V.S., Frivold, L.H., 2008. Public preferences for forest structures: a review of quantitative surveys from Finland, Norway and Sweden. Urban Forestry and Urban Greening 7, 241-258.

Gustafsson, L., Baker, S.C., Bauhus, J., Beese, W.J., Brodie, A., Kouki, J., Lindenmayer, D.B., Löhmus, A., Martinez Pastur, G., Messier, C., Neyland, M., Palik, B., Sverdrup-Thygeson, A., Volney, W.J.A., Wayne, A., Franklin J.F., 2012. Retention Forestry to Maintain Multifunctional Forests: A World Perspective. BioScience 62, 633–645.

Hahn, K., Christensen, M., 2004. Dead wood in European forest reserves—a reference for forest management. In: Marchetti, M. (Ed.), Monitoring and indicators of forest biodiversity in Europe—from ideas to operationality. EFI Proceedings No. 51, Joensuu, Finland, 181-191.

Hallenberg N., Kuffer, N., 2001. Long-distance spore dispersal in wood-inhabiting basidiomycetes. Nordic Journal of Botany 21, 431-436.

Hallmann, C., Sorg, M., Jongejans, E., Siepel, H., Hofland, N., Schwan, H., Stenmans, W., Müller, A., Sumser, H., Hörren, T., Goulson, D., de Kroon, H., 2017. More than 75 percent decline over 27 years in total flying insect biomass in protected areas. PLoS ONE 12(10): e0185809.

Hanski, I., 1999. Metapopulation ecology. Oxford University Press. 313 p.

Hanski, I., 2000. Extinction debt and species credit in boreal forests: modeling the consequences of different approaches to biodiversity conservation. Annales Zoologici Fennici 37, 271–280.

Harmon, M.E., 2001. Carbon sequestration in forests: addressing the scale question. Journal of Forestry 99, 24-29.

Harmon, M.E., Franklin, J.F., Swanson, F.J., Sollins, P., Gregory, S.V., Lattin, J.D., Anderson, N.H., Cline, S.P., Aumen, N.G., Sedell, J.R., Lienkaemper, G.W., Cromack, K., Cummins, K.W., 1986. Ecology of coarse woody debris in temperate ecosystems. Advances in Ecological Research 15, 133-302.

Hartel, T., Plieninger T., 2014. European Wood-pastures in Transition: A Social-ecological Approach. Taylor and Francis, London, UK and New York, USA.

Hartmann T. (1999) Hunderd years of virgin forest conservation in Slovenia. In: Diaci J. (ed) Virgin Forests and Forest Reserves in Central and East European Countries. Proceedings of invited lecturers reports presented at the COST-E4 meeting in Ljubljana, Slovenia. Biotechnical Faculty, University of Ljubljana, Slovenia.

Hayward, G.D., 1991. Using population biology to define old-growth forests. Wildlife Society Bulletin 19, 111-116.

Hédl, R., Kopecký, M., Komárek, J., 2010. Half a century of succession in a temperate oakwood: from species-rich community to mesic forest. Diversity and Distributions 16, 267–276.

Heilmann-Clausen, J., 2001. A gradient analysis of communities of macrofungi and slimemoulds on decaying beech logs. Mycological Research 105, 575-596.

Heilmann-Clausen, J., Aude, E., van Dort, K., Christensen, M., Piltaver, A., Veerkamp, M., Walleyn, R., Siller, I., Standovár, T., Òdor, P., 2014. Communities of wood-inhabiting bryophytes and fungi on dead beech logs in Europe – reflecting substrate quality or shaped by climate and forest conditions? Journal of Biogeography 41, 2269–2282.

Heilmann-Clausen, J., Christensen, M., 2003. Fungal diversity on decaying beech logs-implications for sustainable forestry. Biodiversity Conservation 12, 953-973.

Heinrichs, S., Schmidt, W., 2017. Biotic homogenization of herb layer composition between two contrasting beech forest communities on limestone over 50 years. Applied Vegetation Science 20, 271-281.

Heinrichs, S., Schmidt, W., 2015. Dynamics of Hedera helix L. in Central European beech forests on limestone: results from long-term monitoring and experimental studies. Plant Ecology 216, 1–15.

Heinrichs, S., Winterhoff, W., Schmidt, W., 2012. Vegetation dynamics of beech forests on limestone in central Germany over half a century – effects of climate change, forest management, eutrophication or game browsing? Biodiversity & Ecology 4, 49–61.

Heirbaut, W., Desender, K., Debakker, D., Versteirt, V., Grootaert, P., 2001. Inventarisatie en determinatie van ongewervelden als ecologische indicatoren in Vlaamse integrale bosreservaten. Inventarisatie en determinatie van xylobionte arthropoden in integrale bosreservaten. Rapport ENT.2001.04. Royal Institute for Natural Sciences, Brussels.

Heiri, C., Brändli, U-B., Bugmann, H., Brang, P., 2012. Sind Naturwaldreservate naturnäher als der Schweizer Wald? Schweizerische Zeitschrift für Forstwesen 163, 210-221.

Heiri, C., Brang, P., Commarmot, B., Matter, J.-F., Bugmann, H., 2011. Walddynamik in Schweizer Naturwaldreservaten: Kennzahlen und Trends. In: Brang, P., Heiri, C., Bugmann, H. (eds.), Waldreservate. 50 Jahre natürliche Waldentwicklung in der Schweiz. Haupt Verlag, Bern, pp. 72–89.

Heiri, C., Wolf, A., Rohrer, L., Bugmann, H., 2009. Forty years of natural dynamics in Swiss beech forests: structure, composition and the influence of former management. Ecological Applications 19, 1920–1934.

Hekhuis, H.J., de Molenaar, J.G., Jonkers, D.A., 1994. Het sturen van natuurwaarden door bosbedrijven. Een evaluatiemethode voor multifunctionele bossen. IBN-rapport 078, IBN-DLO, Wageningen, the Netherlands.

Hermy, M., Verheyen, K., 2007. Legacies of the past in the present day forest biodiversity: A review of past land-use effects on forest plant species composition and diversity. Ecological Restoration 22, 361–371.

Hermy, M., 1992. Beschouwingen over integrale reservaten in de bossfeer. Internal Note, Institute for Nature Conservation. Hasselt, Belgium.

Hermy, M., Honnay, O., Firbank, L., Grashof-Bokdam, C., Lawesson, J.E., 1999. An ecological comparison between ancient and other forest plant species of Europe, and the implications for conservation. Biological Conservation 91, 9–22.

Hermy, M., Van Der Veken, S., Van Calster, H., Plue, J., 2008. Forest ecosystem assessment, changes in biodiversity and climate change in a densely populated region (Flanders, Belgium). Plant biosystems 142, 623-629.

Hesmer, H., 1930. Zur frage des aufbaues und der verjüngung Europäischer urwälder. Forstarchiv 6, 265-274.

Hesmer, H., 1934. Naturwaldzellen. Der Deutsche Forstwirt 16, 133–135 and 141–143.

Heyninck, C., 2009. Appel pour un réseau de réserves intégrales de qualité en Région Wallonne. Forêt Wallonne 99, 43-52.

Hilbert, J., Wiensczyk, A.., 2007. Old-growth definitions and management: A literature review. BC Journal of Ecosystems and Management 8, 15–31.

Hill, M.O., Mountford, J.O., Roy, D.B., Bunce, R.G.H., 1999. Ellenberg's indicator values for British plants. ECOFACT Volume 2 Technical Annex. Huntingdon, Institute of Terrestrial Ecology, 46pp. (ECOFACT, 2a).

Hobi, M. L., C. Ginzler, B. Commarmot, and H. Bugmann., 2015. Gap pattern of the largest primeval beech forest of Europe revealed by remote sensing. Ecosphere 6(5), 76.

Hobi, M., Commarmot, B., Bugmann, H., 2014. Pattern and process in the largest primeval beech forest of Europe (Ukrainian Carpathians). Journal of Vegetation Science 26, 323-336.

Hochbichler, E., O'Sullivan, A., Van Hees, A., Vandekerkhove, K., 2000. Recommendations for data collection in forest reserves, with an emphasis on regeneration and stand structure. In: European Community, Directorate General for Research (ed.), Forest Reserves Research Network COST-action E4. EUR19550, European Community, Brussels.

Hodge, S.J., Peterken, G.F., 1998. Dead wood in British forests: priorities and a strategy. Forestry 71, 99-112.

Høiland K., Bendiksen, E., 1997. Biodiversity of wood-inhabiting fungi in a boreal coniferous forest in Sør-Trøndelag County, Central Norway. Nordic Journal of Botany 16, 643-659.

Holeksa, J., Saniga, M., Szwagrzyk, J., Czerniak, M., Staszyńska, K., Kapusta, P., 2009. A giant tree stand in the West Carpathians – An exception or a relic of formerly widespread mountain European forests? Forest Ecology and Management 257, 1577-1585.

Holzwarth, F., Kahl, A., Bauhus, J., With, C., 2012. Many ways to die - partitioning tree mortality dynamics in a near-natural mixed deciduous forest. Journal of Ecology 101, 220-230.

Hoste, I., Diagre-Vanderpelen, D., 2016. Belgian botany in the nineteenth and early twentieth centuries: from plant hunting to nascent nature conservation. Journal for the History of Environment and Society 1, 37–63.

Hsieh, T.C., Ma, K.H., Chao, A., 2015. R-Package ‘‘iNEXT”.

Hülsmann, L., Bugmann, H., Commarmot, B., Meyer, P., Zimmermann, S., Brang, P., 2016. Does one model fit all? Patterns of beech mortality in natural forests of three European regions. Ecological Indicators 26, 2465-2479.

Humphrey, J., Sippola, A.-L., Lempériere, G., Dodelin, B., Alexander, K.N.A., Butler, J., 2004. Deadwood as an indicator of biodiversity in European forests: from theory to operational guidance. In: Marchetti, M. (ed.), Monitoring and Indicators of Forest Biodiversity in Europe - From Ideas to Operationality. EFI Proceedings 51, 193-206.

Hunt, R., Hodgson, J.G., Thompson, K., Bungener, P., Dunnett, N.P., Askew, A.P., 2004. A new practical tool for deriving a functional signature for herbaceous vegetation. Applied Vegetation Science 7, 163–170.

Hunter, M., 1989. What constitutes an old-growth stand ? Journal of Forestry 87(11), 33-35.

Hurlbert, S.H., 1971. The non-concept of species diversity: a critique and alternative parameters. Ecology 52, 577-586.

Hyman, P.S., Parsons, M.S., 1992. A review of the scarce and threatened Coleoptera of Great Britain. Part 1. UK Nature Conservation 3. Joint Nature Conservation Committee, Peterborough. 484 p.

Hyman, P.S., Parsons, M.S., 1994. A review of the scarce and threatened Coleoptera of Great Britain. Part 2. UK Nature Conservation 12. Joint Nature Conservation Committee, Peterborough, UK.

Irmler, U., Arp, H., Nötzold R., 2010. Species richness of saproxylic beetles in woodlands is affected by dispersion ability of species, age and stand size. Journal of Insect Conservation 14, 227–235.

Iversen, J., 1944. Viscum, Hedera and Ilex as climate indicators. A contribution to the study of the post-glacial temperature climate. Geologiska Föreningens Stockholm Förhandlingar 66, 463–483.

Jackson, S.T., Sax, D.F., 2009. Balancing biodiversity in a changing environment: extinction debt, immigration credit and species turnover. Trends in Ecology, Evolution 25, 153–160.

Jacquemyn, H., Brys, R., Honnay, O., Hermy, M., 2008. Effects of coppicing on demographic structure, fruit and seed set in Orchis mascula. Basic and Applied Ecology 9, 392-400.

Jahn, G., 1991. Temperate deciduous forests of Europe. In: Röhrig, E., Ulrich, B. (eds.), Temperate deciduous Forests. Ecosystems of the world 7. Elsevier, Amsterdam, 377-502.

Jahn, H., 1963. Mitteleuropäische Porlinge. Westfälische Pilzbriefe 4, 1-143.

Janík, D., Adam, D., Hort, L., Král, K., Šamonil, P., Unar, P., Vrška, T., 2014. Tree spatial patterns of Abies alba and Fagus sylvatica in the Western Carpathians over 30 years. European Journal of Forest Research 133, 1015-1028.

Janík, D., Král, K., Adam, D., Hort, L., Šamonil, P., Unar, P., Vrška, T., McMahon, S., 2016. Tree spatial patterns of Fagus sylvatica expansion over 37 years. Forest Ecology and Management 375, 134-145.

Janssens, A., 1960. Faune de Belgique. Insectes Coléoptères Lamellicornes. Institut Royal des Sciences Naturelles de Belgique, Brussels. 411 p.

Jantsch, M.C., Fischer, A., Fischer, H.S., Winter, S., 2013. Shift in plant species composition reveals environmental changes during the last decades: a long-term study in beech (Fagus sylvatica) forests in Bavaria. Folia Geobotanica 48, 467–491.

Jantsch, M.C., Fischer, H.S., Winter, S., Fischer, A., 2014. How are plant species in central European beech (Fagus sylvatica L.) forests affected by temperature changes? – Shift of potential suitable habitats under global warming. Annali di Botanica 2014, 97-113.

Jaworski, A., Koodziej, Z., Bartkowicz, L., 2005. Structure and dynamics of stands of primeval character composed of the little-leaf linden (Tilia Cordata Mill.) in the "Las lipowy Obrozyska" reserve (southern Poland). Journal of Forest Science 51, 283-304.

Jöbges, M., König, H., 2001. Urwaldspecht im Eichenwald. LÖBF-Mitteilungen 2, 12–27.

Johnson, J., Pannatier, E.G., Carnicelli, S., Cecchini, G., Clarke, N., Cools, N., Hansen, K.,Meesenburg, H., Nieminen, T.M., Pihl-Karlsson, G., Titeux, H., Vanguelova, E., Verstraeten, A., Vesterdal, L., Waldner, P., Jonard, M., 2018. The response of soil solution chemistry in European forests to decreasing acid deposition. Global Change Biology 24, 3603–3619,

Jones, E.W., 1945. The structure and reproduction of the virgin forest of the north temperate zone. New Phytologist 44, 130-148.

Jonsell, M., Norlander, G., Jonsson, M., 1999. Colonization patterns of insects breeding in wood-decaying fungi. Journal of Insect Conservation 3, 145-161.

Jonsell, M., Schroeder, M., Larsson, T., 2003. The saproxylic beetle Bolitophagus reticulatus: its frequency in managed forests, attraction to volatiles and flight period. Ecography 26, 421-428.

Jonsson, B. G., Kruys, N., Ranius, T., 2005. Ecology of species living on dead wood - lessons for dead wood management. Silva Fennica 39, 289–309.

Kallio, T., 1970. Aerial distribution of thr root rot fungus Fomes annosus in Finland. – Acta Forestalia Fennica 107, 1–55.

Kamp, J., 2008. Bestandszunahme und Ausbreitung des Mittelspechts Dendrocopus medius in NW-Deutschland. Vogelwarte 46, 280.

Kappes, H., Jordaens, K., Hendrickx, F., Maelfait, J.P., Lens, L., Backeljau, T., 2009. Response of snails and slugs to fragmentation of lowland forests in NW Germany. Landscape Ecology 24, 685-697.

Kappes, H., Topp, P., 2004. Emergence of Coleoptera from deadwood in a managed broadleaved forest in Central Europe. Biodiversity and Conservation 13, 1905–1924.

Kartsov, G.P., 1903. Belovezhskaya Pushcha (Białowieża Forest). A.F. Marksa, S-Petersburg, Russia.

Kaufmann, M.R., Moir, W. H., Covington, W.W., 1992. Old-growth forests: what do we know about their ecology and management in the Southwest and Rocky Mountain regions? In: Kaufmann, M.R.; Moir, W. H., Basset, R.L. (eds) Old-growth Forests in the Southwest and Rocky mountain regions. Proceedings of a workshop; Portal, Arizona. USDA Forest Service, General Technical Report RM-213, 1-11. Fort Collins, USA.

Kaufmann, S., Hauck, M., Leuschner, C., 2017. Comparing the plant diversity of paired beech primeval and production forests: Management reduces cryptogam, but not vascular plant species richness. Forest ecology and management 400, 58-67.

Kaufmann, S., Hauck, M., Leuschner, C., 2018. Effects of natural forest dynamics on vascular plant, bryophyte, and lichen diversity in primeval Fagus sylvatica forests and comparison with production forests. Journal of Ecology 106, 2421-2434.

Keith, S.A., Newton, A.C., Morecroft, M.D., Bealey, C.E., Bullock, J.M., 2009. Taxonomic homogenization of woodland plant communities over 70 years. Proceedings of the Royal Society of London, Series B 276, 3539–3544

Kelemen, K., Mihók, B., Gálhidy, L., Standovár, T., 2012.Dynamic response of herbaceous vegetation to gap opening in a central European beech stand. Silva Fennica, 46, 53–65.

Kenderes, K., Mihók, B., Standovár, T., 2008. Thirty years of gap dynamics in a central European beech forest reserve. Forestry 81, 111-123.

Kickx, J., 1835. Flore cryptogamique des environs de Louvain, ou description des plantes cryptogames et agames qui croissent dans le Brabant et dans une partie de la province d'Anvers. Bruxelles, Vandooren.

Kickx, J.J., 1867. Flore cryptogamique des Flandres. Oeuvre posthume de Jean Kickx. Tome I & II. Gand, Librairie Générale de H. Hoste.

Kimmins, J.P., 2003. Old-growth forest: An ancient and stable sylvan equilibrium, or a relatively transitory ecosystem condition that offers people a visual and emotional feast ? Answer- it depends. Forestry Chronicle 79, 429-440

Kint, V., Aertsen, W., Campioli, M., Vansteenkiste, D., Delcloo, A., Muys, B., 2012. Radial growth change of temperate tree species in response to altered regional climate and air quality in the period 1901–2008. Climatic Change 115, 343-363.

Kirby, K.J., Drake, C.M. (eds.) 1993. Dead wood matters: the ecology and conservation of saproxylic invertebrates in Britain. English Nature, Peterborough, UK.

Kirby, K.J., Reid, C.M., Thomas, R.C., Goldsmith, KB., 1998. Preliminary estimates of fallen dead wood and standing dead trees in managed and unmanaged forests in Britain. J. Appl. Ecol. 35, 148-155.

Kirby, K.J., Smart, S.M., Black, H.J., Bunce, R.G.H., Corney, P.M., Smithers, R.J., 2005. Long-term ecological changes in British Woodland (1971–2001). English Nature Research Reports 653, English Nature, Peterborough, UK.

Kirchmeir, H., Kovarovics, A., 2016. Nomination Dossier "Primeval Beech Forests of the Carpathians and Other Regions of Europe" as extension to the existing Natural World Heritage Site "Primeval Beech Forests". E.C.O., Klagenfurt, Austria.

Kirk, P.M., Cannon, P.F., Minter, D.W., Stalpers, J.A., 2008. Dictionary of the Fungi. 10th edition. CABI, U.K. 784 p.

Knapp H.D., Jeschke, L., 1991. Naturwaldreservate und Naturwaldforschung in den ostdeutschen Bundesländern. Schriftenreihe für Vegetationskunde 21, 21-54.

Knohl, A., Schulze, E.-D., Kolle, O., Buchmann, N., 2003. Large carbon uptake by an unmanaged 250-year-old deciduous forest in Central Germany. Agricultural and Forest Meteorology 118, 151-167.

Knorn, J.A.N., Kuemmerle, T., Radeloff, V.C., Keeton, W.S., Gancz, V., Biris, I.-A., Svoboda, M.; Griffiths, P., Hagatis, A., Hostert, P., 2013. Continued loss of temperate old-growth forests in the Romanian Carpathians despite an increasing protected area network. Environmental Conservation 40, 182–193.

Köhler, F., 1996. Käferfauna in Naturwaldzellen und Wirtschaftswald. Vergleichende Untersuchungen im Waldreservat Kermeter in der Nordeifel. Schriftenreihe LÖBF/LAfAO NRW 6. Recklinghausen. Germany.

Köhler, F., 1999. Die Totholzkäferfauna (Coleoptera) der Naturwaldreservate “Möderhäufel” und “Stuttpferch” im Bienwald in der nördlichen Oberrheinebene. Mainzer naturwissenschaftliches Archiv 37, 213-280.

Köhler, F., 2000. Totholzkäfer in Naturwaldzellen des Nördlichen Rheinlandes. Vergleichende Studien zur Totholzkäferfauna Deutschlands und Deutschen Naturwaldforschung. Schriftenreihe LÖBF/LAfAO NRW 18. Recklinghausen, Germany.

Köhler, F., 2009. Die Totholzkäfer (Coleoptera) des Naturwaldreservates Laangmuer. Naturwaldreservate in Luxemburg 5, 48-115.

Köhler, F., 2010a. Die Käfer (Coleoptera) des Naturwaldreservats Goldbachs- und Ziebachsrück (Hessen). Untersuchungszeitraum 1994–1996. In: Dorow, W. H. O., Blick, T., Kopelke, J.-P. (eds.), Naturwaldreservate in Hessen. Band 11/2.2. Goldbachs- und Ziebachsrück. Zoologische Untersuchungen 1994–1996, Teil 2. Mitteilungen der Hessischen Landesforstverwaltung 46, 7-98.

Köhler, F., 2010b. Die klimabedingte Veränderung der Totholzkäferfauna (Coleoptera) des nördlichen Rheinlandes. Analysen zur Gesamtfauna und am Beispiel von Wiederholungsuntersuchungen in ausgewählten Naturwaldzellen. Report for Ministerium für Umwelt und Naturschutz Landwirtschaft und Verbraucherschutz des Landes Nordrhein-Westfalen. Koleopterologisches Forschungsbüro, Bornheim, 184 p.

Köhler, F., Crevecoeur, L., Vandekerkhove, K., 2011. Saproxylic beetles of the Forest Reserve Kolmontbos. Results and analysis of a two-year survey. Report INBO.IR.2011.21. Instituut voor Natuur- en Bosonderzoek, Brussels. 49 p.

Kölbel, M., 1999. Totholz in Naturwaldreservaten und Urwaldern. LWF aktuell 18, 2-5.

Koop, H., de Molenaar, J.G., 1981. Bosreservaten en proefbossen. Nederlands Bosbouwtijdschrift 53, 50-54.

Koop, H., 1981. Vegetatiestructuur en dynamiek in twee natuurlijke bossen: het Neuenburger en Hasbrucher Urwald. Pudoc, Wageningen, Netherlands.

Koop, H., 1989. Forest Dynamics. SILVI-STAR: a comprehensive monitoring system. Berlin, Springer Verlag.

Koop, H., Hilgen, P., 1987. Forest dynamics and regeneration mosaic shifts in unexploited beech (Fagus sylvatica) stands at Fontainebleau (France). Forest Ecology and Management 20, 135-150.

Kopecký, M., Hédl, R., Szabó, P., 2013. Non-random extinctions dominate plant community changes in abandoned coppices. Journal of Applied Ecology, 50(1), 79–87.

Korpel', S., 1992. Ergebnisse der Urwaldforschung fur die Waldwirtschaft im Buchen-Oekosystem. Allgemeine Forst und Jagdzeitung 21, 1148-1152.

Korpel', S., 1995. Die Urwalder der Westkarpaten. Gustav Fischer Verlag, Stuttgart, Germany.

Korpel', S., 1997. Totholz in Naturwäldern und Konsequenzen für Naturschutz und Forstwirtschaft. Forst und Holz 52, 619-643.

Kosiński, I., 2008. Long-term variability in seed size and seedling establishment of Maianthemum bifolium. Plant Ecology 194, 149-156

Kosiński, Z., 2006. Factors affecting the occurrence of middle spotted and great spotted woodpeckers in deciduous forests a case study from Poland. Annales Zoologici Fennici 43, 198-210.

Kraigher, H., Jurc, D., Kalan, P., Kutnar, L., Levanic, T., Rupel, M., Smolej, I., 2002. Beech coarse woody debris characteristics in two virgin forest reserves in southern Slovenia. Zbornik Gozdarstva in Lesarstva 69, 91-134.

Král, K., Valtera, M., Janík, D., Šamonil, P., Vrška, T., 2014. Spatial variability of general stand characteristics in central European beech-dominated natural stands – Effects of scale. Forest Ecology and Management 328, 353–364.

Král, K., Daněk, P., Janík, D., Krůček M., Vrška, T., 2017. How cyclical and predictable are Central European temperate forest dynamics in terms of development phases? Journal of Vegetation Science 29, 84–97.

Kraus, D., Krumm, F. (eds.), 2013. Integrative approaches as an opportunity for the conservation of forest biodiversity. In Focus: managing forest in Europe. European Forest Institute - Central European Office (EFI-CENT), Freiburg, Germany.

Kroiher, F., Bolte, A., 2015. Naturschutz und Biodiversität im Spiegel der BWI 2012. AFZ-DerWald 2015(21), 23-27.

Kucbel, S., Jaloviar, P., Saniga, M., Vencurik, J., Klimaš, V., 2010. Canopy gaps in an old-growth fir-beech forest remnant of Western Carpathians. European Journal of Forest Research 129, 249-259.

Kucbel, S., Saniga, M., Jaloviar, P., Vencurik, J., 2012. Stand structure and temporal variability in old-growth beech-dominated forests of the northwestern Carpathians: A 40-years perspective. Forest Ecology and Management 264, 125-133.

Lameire, S., Hermy, M., Honnay, O., 2000. Two decades of change in the ground vegetation of a mixed deciduous forest in an agricultural landscape. Journal of Vegetation Science 11, 695–704.

Lamprecht, H., Göttsche, D., Jahn, G., Peik, K., 1974. Naturwaldreservate in Niedersachsen. Aus dem Walde - Mitteilungen aus der Niedersächsischen Landesforstverwaltung - Heft 23, 1-233.

Langohr, R., Sanders, J., 1985. The Belgian loess belt in the last 20 000 years: Evolution of soils and relief in the Zonien Forest. In: Boardman (Ed.). Soils and Quaternary Landscape evolution. John Wiley and Sons Ltd., New York, pp. 359-371.

Larrieu, L., Cabanettes, A., 2012. Species, live status, and diameter are important tree features for diversity and abundance of tree microhabitats in subnatural montane beech-fir forests. Canadian Journal of Forest Research 42, 1433–1445.

Larrieu, L., Cabanettes, A., Brin, A., Bouget, C., Deconchat, M., 2014. Tree microhabitats at the stand scale in montane beech–fir forests: practical information for taxa conservation in forestry. European Journal of Forest Research 133, 355-367. doi:10.1007/s10342-013-0767-1

Larrieu, L., Paillet, Y., Winter, S., Bütler, R., Kraus, D., Krumm, F., Lachat, T., Michel, A., Regnery, B., Vandekerkhove, K., 2018. Tree related microhabitats in temperate and Mediterranean European forests: A hierarchical typology for inventory standardization. Ecological Indicators 84, 194-207.

Larsson, T.-B., 2001. Biodiversity Evaluation Tools for European Forests. Ecological Bulletins 50, 1-236.

Latte, N., Perin, J., Kint, V., Lebourgeois, F., Claessens, H., 2016. Major changes in growth rate and growth variability of Beech (Fagus sylvatica L.) related to soil alteration and climate change in Belgium. Forests 7, 174. doi:10.3390/f7080174

Lebourgeois, F., Bréda, N., Ulrich, E., Granier, A., 2005. Climate-tree-growth relationships of European beech (Fagus sylvatica L.) in the French Permanent Plot Network (RENECOFOR). Trees 19, 385-401.

Leibold, M.A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J.M., Hoopes, M.F., Holt, R.D., Shurin, J.B., Law, R., Tilman,D., Loreau, M., Gonzalez, A., 2004. The metacommunity concept: a framework for multi-scale community ecology. Ecology Letters 7, 601–613.

Leibundgut, H., 1959. Über Zweck und Methodik der Struktur- und Zuwachsanalyse von Urwäldern. Schweizerische Zeitschrift für Forstwesen 110, 111-125.

Leibundgut, H., 1978 .Über die Dynamik Europäischer Urwälder. Allgemeine Forst Zeitschrift 33, 686-690.

Leibundgut, H., 1982. Europäische Urwälder der Bergstufe. Verlag Paul Haupt, Bern, CH and Stuttgart, Germany.

Leibundgut, H., 1966a. Die Waldpflege.: Haupt Verlag, Bern, Switzerland.

Leibundgut, H., 1966b. Waldreservate. Schweizerische Zeitschrift für Forstwesen 117, 900-907.

Leibundgut, H., 1978. Über die Dynamik Europäischer Urwälder. AFZ 33, 686-690.

Leibundgut, H., 1982. Europaische Urwalder der Bergstufe. Verlag Paul Haupt, Bern, Switzerland and Stuttgart, Germany.

Leibundgut, H., 1993. Europäische Urwälder. Wegweiser zur naturnahen Waldwirtschaft. Haupt Verlag, Bern, Stuttgart, Wien.

Leibundgut, H., 1993. Europäische Urwälder.Wegweiser zur naturnahen Waldwirtschaft. Verlag Paul Haupt, Bern, Switzerland

Lelli, C., Bruun, H.H., Chiarucci, A., Donati, D., Frascaroli, F., Fritz, Ö., Goldberg, I. Nascimbene, J.,Tøttrup, A.P., Rahbek, C., Heilmann-Clausen J., 2019. Biodiversity response to forest structure and management: Comparing species richness, conservation relevant species and functional diversity as metrics in forest conservation. Forest Ecology and Management 432, 707-717.

Leuschner, C., Wulf, M., Bäuchler, P., Hertel, D., 2014. Forest Continuity as a Key Determinant of Soil Carbon and Nutrient Storage in Beech Forests on Sandy Soils in Northern Germany. Ecosystems 17, 497-511.

Levins, R., 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. Bulletin of the Entomological Society of America 15, 237–240.

Levins, R., 1970. Extinction. In: Gerstenhaber (ed.) Some mathematical problems in biology. American Mathematical Society, Providence, USA, 75–107.

Leyman, A., Vandekerkhove, K., 2003. Bosbeleid: oppervlakte bos in Vlaanderen die is opgenomen in verschillende beschermingsstatuten: enkele statistieken. Silva belgica 110(6), 32-37.

Lindenmayer, D.B., 2016. The importance of managing and conserving large old trees: a case study from Victorian mountain ash forests. The Royal Society of Victoria 128, 64-70.

Lindenmayer, D.B., Franklin, J.F., 2002. Conserving forest biodiversity: a comprehensive multiscaled approach. Island Press, Washington DC. 351 p.

Lindenmayer, D.B., Laurance, W., Franklin, J.F., 2012. Global decline in Large Old Trees. Science 338, 1305-1306.

Lindenmayer, D.B., Likens, G., 2009. Adaptive monitoring: a new paradigmfor long-term research and monitoring. Trends in Ecology & Evolution 24, 482-486.

Lingua, E., Garbarino, M., Mondino, E.B., Motta, R., 2011. Natural disturbance dynamics in an old-growth forest: From tree to landscape. Procedia Environmental Sciences 7, 365–370.

Londo, G., 1984. The decimal scale for relevés of permanent quadrats. In: Knapp, R. (Ed). Sampling methods and taxon analysis in vegetation science. Junk Publishers, The Hague, The Netherlands, 45-49.

Lorimer, C.G., 1980. Age structure and disturbance history of a southern appalachian virgin forest. Ecology 61, 1169-1184.

Lorimer, C.G., Dahir, S.E., Nordheim, E.V., 2001. Tree mortality rates and longevity in mature and old-growth hemlock– hardwood forests. Journal of Ecology 89, 960–971.

Luick, R., 2017. The situation of virgin and old- growth forests in Romania seen from an outside perspective. Presentation at the 4th Edition of IMER, Integrated Management of Environmental Resources Conference. November 3- 4th 2017, Suceava, Romania.

Lust, N., 1982. Vergelijkende studie van bosreservaten in Europa. Groene Band 47.

Lust, N., 1982. Vergelijkende studie van bosreservaten in Europa. Groene Band nr. 47, 1-20.

Luyssaert, S., Schulze, E.D., Börner, A., Knohl, A., Hessenmöller, D., Law, B., 2008. Old-growth forests as global carbon sinks. Nature 455, 213-215.

Manning, R.E., 1989. The Nature of America: Visions and Revisions of Wilderness. Natural resources Journal 29, 25-40.

Manso, R., Morneau, F., Ningre, F., Fortin, M., 2015. Effect of climate and intra- and inter-specific competition on diameter increment in beech and oak stands. Forestry 88, 540 –551.

Mansourian, S., Rossi, M., Vallauri, D., 2013. Ancient Forests in the Northern Mediterranean: Neglected High Conservation Value Areas., Marseille, France.

Marchetti, M., Blasi, C., 2010. Old-growth forests in Italy: towards a first network. Italian Journal of Forest and Mountain Environments 65, 679-698.

Marchetti, M., 2004. Monitoring and indicators of forest biodiversity in Europe—from ideas to operationality. EFI Proceedings No. 51, Joensuu, Finland.

Markgraf, F., Dengler, A., 1931. Aus den Waldern Albaniens. Zeitschrift für Forst- und Jagdwesen 63, 1-31.

Marrs R.H., Watt, A.S., 2006. Biological Flora of the British Isles: Pteridium aquilinum(L.) Kuhn. Journal of Ecology 94, 1272–1321.

Maser, C., Trappe, J.M., 1984. The seen and unseen world of the fallen tree. General Technical Reports PNW-164, Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station, Portland, Oregon, USA.

Mauve, K., 1931. Über Bestandesaufbau, Zuwachsverhältnisse und Verjüngung im Galizischen Karpathen-Urwald. Mitteilungen aus Forstwirtschaft und Forstwissenschaft 2, 257-311.

Mayer, H., 1966. Analyse eines urwaldnahen, subalpinen Lärchen-Fichtenwaldes im Lungau. Cbl. ges. Forstwesen 83(3), 129-151

Mayer, H., 1987. Urwald Dobra. Das Buchen-Naturwaldreservat Dobra/Kampleiten im niederösterreichischen Waldviertel. In: Mayer, H., Zukrigl, K., Schrempf, W., Schlager, G. (eds.), Urwaldreste, Naturwaldreservate und schützenswerte Naturwälder in Österreich. Universität für Bodenkultur, Institut für Waldbau, Wien.

Mayer, H., Neumann, M., Schrempf, W., 1979. Der Urwald Rothwald in den Niederösterreichischen Kalkalpen. Jahrbuch 44 des Vereins zum Schutz der Bergwelt, 79-117.

Mayr, H., 1909. Waldbau auf naturgesetzlicher Grundlage. Eine Lehr- und Handbuch. Paul Parey, Berlin.

McAleece, N., 1997. BioDiversity 1997 NHM & SAMS. Available at: http://www.sams.ac.uk/research/software/

MCPFE, 2002. Improved Pan-European Indicators for Sustainable Forest Management, MCPFE Liaison Unit Vienna, Austria.

MCPFE, 2003. State of Europe’s Forests 2003. The MCPFE report on sustainable forest management in Europe. Jointly prepared by the MCPFE Liaison Unit Vienna and UNECE/FAO. MCPFE liaison Unit, Vienna, Austria.

MCPFE, 2007. State of Europe’s forests 2007. The MCPFE report on sustainable forest management in Europe. Jointly prepared by the MCPFE Liaison Unit Warsaw, UNECE and FAO. MCPFE Liaison Unit Warsaw, Poland.

MCPFE, 2015. State of Europe’s Forests 2015. MCPFE Liaison Unit Madrid, Spain.

Menzel, A., Sparks, T. H., Estrella, N., Koch, E., Aasa, A., Ahas, R., Alm- Kübler, K., Bissolli, P., Braslavská, O., Briede, A., Chmielewski, F. M., Crepinsek, Z., Curnel, Y., Dahl, Å., Defila, C., Donnelly, A., Filella, Y., Jatczak, K., Måge, F., Mestre, A., Nordli, Ø., Peñuelas, J., Pirinen, P., Remišová, V., Scheifinger, H., Striz, M., Susnik, A., Van Vliet, A. J., Wielgolaski, F., Zach, S., Zust, A., 2006. European phenological response to climate change matches the warming pattern. Global Change Biology 12, 1969-1976.

Merckx, T., 2015. Rewilding: Pitfalls and Opportunities for Moths and Butterflies. In: Pereira, H., Navarro, L. (eds) Rewilding European Landscapes. Springer, Cham, Switzerland.

Merckx, T., Feber R., Hoare, D. Parsons, M., Kelly C. Bourn, N., Macdonald D., 2012. Conserving threatened Lepidoptera: Towards an effective woodland management policy in landscapes under intense human land-use. Biological Conservation 149, 32-39.

Merino, A., Real, C., Álvarez-González, J.G., Rodríguez-Guitián, M.A., 2007. Forest structure and C stocks in natural Fagus sylvatica forest in southern Europe: The effects of past management. Forest Ecology and Management 250, 206–214.

Meyer, P., 1999. Totholzuntersuchungen in nordwestdeutschen Naturwäldern: Methodik und erste Ergebnisse. Forstwissenschaftliches Centralblatt 118, 167 - 180.

Meyer, P., Bücking, W., Gehlhar, U., Schulte, U., Steffens, R., 2007. Das Netz der Naturwaldreservate in Deutschland: Flächenumfang, Repräsentativität und Schutzstatus im Jahr 2007. Forstarchiv 78, 188-196.

Meyer, P., Schmidt, M., 2011. Accumulation of dead wood in abandoned beech (Fagus sylvatica L.) forests in northwestern Germany. Forest Ecology and Management 261, 342-352.

Meyer, P., Tabaku, V., von Lüpke, B., 2003. Die Struktur Albanischer Rotbuchen-Urwälder - Ableitungen fur eine naturnähe Buchenwirtschaft. Forstwissentschaftliches Centralblatt 122, 47-58.

Meyer, P., Wevell von Krüger, A., Steffens, R., Unkrig, W., 2006. Naturwälder in Niedersachsen - Schutz und Forschung Band 1. NW-FVA, Göttingen, Germany.

Mikusiński, G., Gromadzki, M., Chylarecki, P., 2001. Woodpeckers as indicators of forest bird diversity. Conservation Biology 15, 208–217.

Mitchell, F., Cole E., 1998. Reconstruction of long-term successional dynamics of temperate woodland in Białowieża Forest, Poland. Journal of Ecology 86, 1042-1059

Mlinšek, D., 1976. Zur Ausscheidung von neuen Wald- und Urwaldreservaten (am Beispiel von Slowenien). Proceedings of the IUFRO World Congress Oslo 1976, Group S1, 1-3.

Mölder, A., Bernhardt-Römermann, M., Schmidt, W., 2008. Herb-layer diversity in deciduous forests: Raised by tree richness or beaten by beech? Forest Ecology and Management, 256, 272–281.

Mölder, A., Gürlich, S., Engel, F., 2014. Die Verbreitung von gefährdeten Holz bewohnenden Käfern in Schleswig-Holstein unter dem Einfluss von Forstgeschichte und Besitzstruktur. Forstarchiv 85, 84-101.

Mölder, A., Streit, M., Schmidt, W., 2014. When beech strikes back: How strict nature conservation reduces herb-layer diversity and productivity in Central European deciduous forests. Forest Ecology and Management 319, 51–61.

Moning, C., Müller, J., 2009. Critical forest age thresholds for the diversity of lichens, molluscs and birds in beech (Fagus sylvatica L.) dominated forests. Ecological Indicators 9, 922–932.

Moraal, L., Veerkamp, M., Jagers op Akkerhuis, G., Cuppen, J., Heijerman, T., 2007. Echte tonderzwam geeft bijzondere kever volop kansen. Vakblad Natuur Bos Landschap 4, 20-21.

Moreau, K., 2006. De Middelste Bonte Specht (Dendrocopus medius) in Meerdaalwoud. Natuur.oriolus 72, 4-13.

Mountford E.P., Peterken G.F., Burton E.N., 1998. Long-term monitoring and management of Langley Wood. English Nature Research Reports no. 302, English Nature, Peterborough, UK.

Mountford, E.P., 2001. Natural canopy gap characteristics in European beech forests. Nat-Man Working Report 2. FLEC, Kopenhagen, Denmark.

Mountford, E.P., 2002. Fallen dead wood levels in the near-natural beech forest at La Tillaie reserve, Fontainebleau, France. Forestry 75, 203-208.

Mountford, E.P., 2004. Long term patterns of mortality and regeneration in near-natural woodland. PhD. Thesis, Harper Adams University College, Oxford, UK.

Mountford, E.P., Ball, D., 2004. Storm-damage and vegetation change in East Hampshire beechwoods. I. Ashford Hangers National Nature Reserve. English Nature Research Reports 603. English Nature, Peterborough, UK.

Mountford, E.P., Groome G., 2004. Storm-damage and vegetation change in East Hampshire beechwoods II. Noar Hill Hanger. English Nature Research Reports 604, English Nature, Peterborough, UK.

Mountford, E.P., Peterken, G.F., Edwards, P.J., Manners, J.G., 1999. Long-term change in growth, mortality and regeneration of trees in Denny Wood, an old-growth wood-pasture in the New Forest (UK). Perspectives in Plant Ecology, Evolution and Systematics 2, 223-272.

Müller, J., Büssler, H., 2008. Key factors and critical thresholds at stand scale for saproxylic beetles in a beech dominated forest, southern Germany. Rev. Écol. (Terre Vie) 63, 73-82.

Müller, J., Bütler, R., 2010. A review of habitat thresholds for dead wood: A baseline for management recommendations in European forests. European Journal of Forest Research 129, 981-992.

Müller, J., Büssler, H., Bense, U., Brustel, H., Flechtner, G., Fowles, A., Kahlen, M., Möller, G., Mühle, H., Schmidl, J., Zabransky, P., 2005. Urwald relict species - Saproxylic beetles indicating structural qualities and habitat tradition. Waldökologie Online 2, 106-113.

Müller, J., Noss, R. F., Bussler, H., Brandl, R., 2010. Learning from a "benign neglect strategy" in a national park: Response of saproxylic beetles to dead wood accumulation. Biological Conservation, 143, 2559–2569.

Müller, J., Pöllath, J., Moshammer, R., Schröder, B., 2009. Predicting the occurrence of Middle Spotted Woodpecker Dendrocopos medius on a regional scale, using forest inventory data Forest Ecology and Management 257, 502-509.

Müller, K.M., 1929. Aufbau, Wuchs und Verjüngung der südosteuropäischen Urwälder (eine waldbauliche Studie über den Urwald unserer Zone Überhaupt.) M. & H. Schaper, Hannover, Germany.

Müllerová, J., Hédl, R., Szabó, P., 2015. Coppice abandonment and its implications for species diversity in forest vegetation. Forest Ecology and Management 343, 88–100.

Müller-Using, S., Bartsch, N., 2003. Totholzdynamik eines Buchenbestandes (Fagus sylvatica L.) im Solling. Nachlieferung, Ursache, und Zersetzung von Totholz. Allgemeine Forst und Jagdzeitung 174, 122-130.

Naaf, T., Wulf, M., 2007. Effects of gap size, light and herbivory on the herb layer vegetation in European beech forestgaps. Forest Ecology and Management 244, 141–149.

Naaf, T., Wulf, M., 2011. Traits of winner and loser species indicate drivers of herb layer changes over two decades in forests of NW Germany. Journal of Vegetation Science 22, 516-527.

Nagel, T.A., Iacopetti, G., Javornik, J., Rozman, A., De Frenne, P., Selvi, F., Verheyen, K., 2019. Cascading effects of canopy mortality drive long-term changes in understory diversity in temperate old-growth forests of Europe. Journal of Vegetation Science, https://doi.org/10.1111/jvs.12767

Nuzzo, R, 2015. Fooling ourselves - Humans are remarkably good at self-deception. But growing concern about reproducibility is driving many researchers to seek ways to fight their own worst instincts. Nature 256, 182–18

Neufeld, H.S., Young, D.R., 2003. Ecophysiology of the herbaceous layer in temperate deciduous forests. In: Gilliam, F.S., Roberts, M.R. (eds.) The Herbaceous Layer in Forests of Eastern North America. Oxford University Press, New York, USA, 38-90.

Nieto, A., Alexander, K.N.A., 2010. European Red List of Saproxylic Beetles. Publications Office of the European Union, Luxembourg. 48 p.

Niklasson, M., Zin, E., Zielonka, T., Feijen, M., Korczyk, A.F., Churski, M., Samojlik, T., Jędrzejewska, B., Gutowski, J.M., Brzeziecki, B.M., 2010. A 350-year tree-ring fire record from Białowieża Primeval Forest, Poland: Implications for Central European lowland fire history. Journal of Ecology 98, 1319 - 1329

Nilssen, A.C., 1984. Long-range aerial dispersal of bark beetles and bark weevils (Coleoptera, Scolytidae and Curculionidae) in northern Finland. Annales Entomologici Fennici 50, 37-42.

Nilsson, S.G., Baranowski, R., 1997. Habitat predictability and the occurrence of wood beetles in old-growth beech forests. Ecography 20, 491–498.

Nilsson, S.G., Niklasson, M., Hedin, J., Aronsson, G., Gutowski, J.M., Linder, P., Ljungberg, H., Mikusiński, G., Ranius, T., 2002. Densities of large and dead trees in old-growth temperate and boreal forests. Forest Ecology and Management 161, 189–204.

Nilsson, S.G., Niklasson, M., Hedin, J., Aronsson, G., Gutowski, J.M., Linder, P., Ljungberg, H., Mikusiński, G., Ranius, T., 2003. Densities of large and dead trees in old-growth temperate and boreal forests. Forest Ecology and Management 161, 189-204.

Noirfalise, A., 1984. Forêts et stations forestières en Belgique [Forests and forest site types in Belgium]. Presses Agronomiques, Gembloux.

Nordén, B., Appelqvist, T., 2001. Conceptual problems of ecological continuity and its bioindicators. Biodiversity and Conservation 10, 779–791.

Norris, C., Hobson, P., Ibisch, P. L., 2012. Microclimate and vegetation function as indicators of forest thermodynamic efficiency. Journal of Applied Ecology 49, 562-570.

Ódor , P., Heilmann-Clausen, J., Christensen, M., Aude, E., van Dort, K.W., Piltaver, A., Siller, I., Veerkamp, M.T., Walleyn, R., Standovár, T., 2006. Diversity of dead wood inhabiting fungi and bryophytes in semi-natural beech forests in Europe. Biological Conservation 131, 58-71.

Ódor , P., Heilmann-Clausen, J., Christensen, M., Aude, E., van Dort, K.W., Piltaver, A., Siller, I., Veerkamp, M.T., Walleyn, R., Standovár, T., 2006. Diversity of dead wood inhabiting fungi and bryophytes in semi-natural beech forests in Europe. Biological conservation 131, 58-71.

Ódor , P., Standovár, T., 2001. Richness of bryophyte vegetation in a near-natural and managed beech stands, the effects of management-induced differences in dead wood. Ecological Bulletins 49, 219–229.

Ohser, J., 1983. On estimators for the reduced second moment measure of point processes. Mathematische Operationsforschung und Statistik, series Statistics, 14, 63-71.

Økland, B., Bakke, A., Hågvar, S., Kvamme, T., 1996. What factors influence the diversity of saproxylic beetles? A multiscaled study from a spruce forest in Southern Norway. Biodiversity and Conservation 5, 75–100.

ONF, 1993. Instruction et guide sur la prise en compte de la diversité biologique dans l'aménagement et gestion forestière. ONF, Paris.

Ottoy, S., De Vos, B., Sindayihebura, A., Hermy, M., Van Orshoven, J., 2017. Assessing soil organic carbon stocks under current and potential forest cover using digital soil mapping and spatial generalisation. Ecological indicators 77, 139-150

Packham, J.R., 1978. Biological Flora of the British Isles – Oxalis acetosella L. Journal of Ecology 66, 669-693.

Page, C.N., 1997. The Ferns of Britain and Ireland. Cambridge University Press, Cambridge, UK.

Paillet, Y., Archaux, F., Boulanger, V., Debaive, N., Fuhr, M., Gilg, O., Gosselin, F., Guilbert, E., 2017. Snags and large trees drive higher tree microhabitat densities in strict forest reserves. Forest Ecology and Management 389, 176–186.

Paillet, Y., Bergès, L., Hjältén, J., Ódor, P., Avon, C., Bernhardt-Römermann, M., 2010. Biodiversity differences between managed and unmanaged forests: meta-analysis of species richness in Europe. Conservation Biology 24, 101–112

Pakeman, R. J., 2001. Plant migration rates and seed dispersal mechanisms. Journal of Biogeography 28, 795–800.

Paluch, J., 2007. The spatial pattern of a natural European beech (Fagus sylvatica L.)–silver fir (Abies alba Mill.) forest: a patch-mosaic perspective. Forest Ecology and Management 253, 161–170.

Parker, G.R., Leopold, D.J., Eichenberger, J.K., 1985. Tree dynamics in an old growth deciduous forest. Forest Ecology and Management 11, 31-57.

Parviainen, J., Bücking, W., Vandekerkhove, K., Päivinen, R., Schuck, A., 2000. Strict forest reserves in Europe: efforts to enhance biodiversity and research on forests left for free development in Europe (EU-COST-action E4). Forestry 73, 107-118.

Parviainen, J., Little, D., Doyle, M., O'Sullivan, A., Kettunen, M., Korhonen, M. (Eds.), 1999. Research in forest reserves and natural forests in European countries—country reports for the COST Action E4: Forest Reserves Research Network. EFI Proceedings, 16, Joensuu, Finland.

Pasinelli, G., 2007. Nest site selection in middle and great spotted woodpeckers Dendrocopos medius & D. major: implications for forest management and conservation. Biodiversity and Conservation 16, 1283–1298.

Peck, J.E., Zenner, E.K., Hobi, M.L., Commarmot, B., 2015. Should reference conditions be drawn from a single 10 ha plot? Assessing representativeness in a 10,000 ha old-growth European beech forest. Restoration Ecology 23, 927–935.

Peel, B., Finlayson, L., McMahon, T., 2007. Updated world map of the Köppen-Geiger climate classification. Hydrology and Earth System Sciences 11, 1638–1643.

Penninckx, V., Meerts, P., Herbauts, J., Gruber W., 1999. Ring width and element concentrations in beech (Fagus sylvatica L.) from a periurban forest in central Belgium. Forest Ecology and Management 113, 23-33.

Peterken, G.F., 1993. Woodland Conservation and Management - 2nd Edition. Chapman and Hall, London.

Peterken, G.F., 1996. Natural woodland. Ecology and conservation in northern temperate regions. Cambridge University press, Cambridge, UK.

Peterken G.F., Francis, J., 1999. Open spaces as habitats for vascular ground flora species in the woods of Central Lincolnshire, UK. Biological Conservation 91, 55-72.

Peterken, G.F., Mountford, E., 1996. Effects of drought on beech in Lady Park Wood, an unmanaged mixed deciduous woodland. Forestry 69, 125-136.

Peterken, G.F., Mountford, E., 2017. Woodland Development - A Long-term Study of Lady Park Wood. CABI, Wallingford, UK.

Petriţan, A., Biris, I., Merce, O., Turcu, D., Petriţan I.C., 2012. Structure and diversity of a natural temperate sessile oak (Quercus petraea L.) –European Beech (Fagus sylvatica L.) forest. Forest Ecology and Management 280, 140–149.

Petriţan, I.C., Commarmot, B., Hobi, M.L., Petriţan, A.M., Bigler, C., Abrudan, I.V., Rigling, A., 2015. Structural patterns of beech and silver fir suggest stability and resilience of the virgin forest Sinca in the Southern Carpathians, Romania. Forest Ecology and Management 356, 184-195.

Petriţan, I.C., Marzano, R., Petriţan, A., Lingua, E., 2014. Overstory succession in a mixed Quercus petraea–Fagus sylvatica old growth forest revealed through the spatial pattern of competition and mortality. Forest ecology and management 326, 9-17.

Petzold, J., Dittrich, S., Fichtner, A., Härdte, W., Naumann, B., Von Oheimb, G., 2018. Effects of forest management intensity on herb layer plant diversity and composition of deciduous forest communities in Northern Germany. Tuexenia 38, 79–96.

Philipp, M., Petersen, P.M., 2007. Long-term study of dry matter allocation and rhizome growth in Anemone nemorosa. Plant Species Biology 22, 23–31

Piovesan, G., Bernabei, M., Di Filippo, A., Romagnoli, M., Schirone, B., 2003. A long-term tree ring beech chronology from a high-elevation old-growth forest of central Italy. Dendrochronologia 21, 1-10.

Piovesan, G., Biondi, F., Bernabei, M., Di Filippo, A., Schirone, B., 2005b. Spatial and altitudinal bioclimatic zones of the Italian peninsula identified from a beech (Fagus sylvatica L.) tree-ring network. Acta Oecologica 27, 197–210.

Piovesan, G., Biondi, F., Di Filippo, A., Alessandrini, A., Maugeri, M., 2008. Drought driven growth reduction in old beech (Fagus sylvatica L.) forests of the central Apennines, Italy. Global Change Biology 14, 1265–1281.

Piovesan, G., Di Filippo, A., Alessandrini, A., Biondi, F., Schirone, B., 2005a. Structure, dynamics and dendroecology of an old-growth Fagus forest in the Apennines. Journal of Vegetation Science 16, 13-28.

Plue, J., Van Gils, B., De Schrijver, A., Peppler-Lisbach, C., Verheyen, K., Hermy, M., 2013. Forest herb layer response to long-term light deficit along a forest developmental series. Acta oecologica 53, 63-72.

Podhorsky, J., 1929. Die Bedeutung von Naturbanngebieten (Naturschutzparks) für die Forstwirtschaft. Forstarchiv 5, 25-29.

Pontailler, J.-Y., Faille, A., Lemée, G., 1997. Storms drive successional dynamics in natural forests: a case study in Fontainebleau forest (France). Forest Ecology and Management 98, 1-15.

Pott, R., Hüppe, J., 1991. Die Hudelandschaften Nordwestdeutschlands. Abhandlungen aus dem Westfälischen Museum für Naturkunde 53, 1-328.

Pretzsch, H., Bauerle, T., Häberle, K.H., Matyssek, R., Schütze, G., Rötzer, T., 2016. Tree diameter growth after root trenching in a mature mixed stand of Norway spruce (Picea abies [L.] Karst) and European beech (Fagus sylvatica [L.]). Trees 30, 1761–1773.

Projektgruppe Naturwaldreservate 1993. Empfehlungen für die Einrichtung und Betreuung von Naturwaldreservaten in Deutschland. des Arbeitskreises Standortskartierung in der AG Forsteinrichtung. Forstarchiv 64, 122-129.

Průša, E., 1985. Die böhmischen und mährischen Urwälder—ihre Struktur und Ökologie. Academia Verlag, Prague. Czech Republic.

Quataert, P., Vandekerkhove, K., De Vos, B., Simoens, I., Verheyen, K., Ceulemans, R., Muys, B., Van Acker, J., 2018. Het bosonderzoek in Vlaanderen. Stand van zaken en toekomstverkenning: Conclusies en aanbevelingen naar aanleiding van het Bossymposium "Kennis voor het bos van de toekomst" op 12 mei 2017 in Brussel. Mededelingen van het Instituut voor Natuur- en Bosonderzoek INBO.M.2018.02. Instituut voor Natuur- en Bosonderzoek, Brussels, Belgium.

R Development Core Team (2019). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. (URL: https://www.R-project.org/.)

Rackham, O., 1986. The History of the Countryside. J.M. Dent, London, UK.

Rackham, O., 1995. Trees and woodland in the British landscape: the complete history of Britain's trees, woods and hedgerows. Weidenfeld and Nicolson, London. UK.

Rademacher, C., Neuert, C., Grundmann, V., Wissel, C., Grimm, V., 2001. Was charakterisiert Buchenurwälder? Untersuchungen der Altersstruktur des Kronendachs und der räumlichen Verteilung der Baumriesen mit Hilfe des Simulationsmodells BEFORE. Forstwissenschaftliches Centralblatt 120, 288_302.

Rademacher, C., Winter, S., 2003. Totholz im Buchen-Urwald: Generische Vorhersagen des Simulationsmodells BEFORE-CWD zur Menge, räumlichen Verteilung und Verfügbarkeit. Forstwissenschaftliches Centralblatt 122, 337-357.

Radtke, A., Ambraß, S., Zerbe, S., Tonon, G., Fontana, V., Ammer, C., 2013. Traditional coppice forest management drives the invasion of Ailanthus altissima and Robinia pseudoacacia into deciduous forests. Forest Ecology and Management 291, 308–317.

Raev I., Veen P., 2005.Virgin forests of Bulgaria. Inventory and strategy for sustainable management and protection of virgin forests. FRI-BAS – KNNV, the Netherlands

Rambo, T. R., North, M. P., 2009. Canopy microclimate response to pattern and density of thinning in a Sierra Nevada forest. Forest Ecology and Management 257, 435-442.

Ranius, T., 2006. Measuring the dispersal of saproxylic insects: a key characteristic for their conservation. Population Ecology 48, 177-188.

Ranius, T., Aguado, L.O., Antonsson, K., Audisio, P., Ballerio, A., Carpaneto, G.M., Chobot, K., Gjurašin, B., Hanssen, O., Huijbregts, H., Lakatos, F., Martin, O., Neculiseanu, Z., Nikitsky, N.B., Paill, W., Pirnat, A., Rizun, V., Ruicănescu, A., Stegner, J., Süda, I., Szwałko, P., Tamutis, V., Telnov, D., Tsinkevich, V., Versteirt, V., Vignon, V., Vögeli, M., Zach, P., 2005. Osmoderma eremita (Coleoptera, Scarabaeidae, Cetoniinae) in Europe. Animal Biodiversity and Conservation 28, 1–44.

Ranius, T., Hedin, J., 2001. The dispersal rate of a beetle, Osmoderma eremita, living in tree hollows. Oecologia 126, 363–370.

Rauh, J., 1993. Faunistisch-ökologische Bewertung von Naturwaldreservaten anhand repräsentativer Tiergruppen. Naturwaldreservate in Bayern Band 2, IHW-Verlag, Eching, Germany.

Rayner, A.D.M., Boddy, L., 1988. Fungal Decomposition of Wood; its Biology and Ecology. John Wiley and Sons, Chichester, UK.

Read, H., 2000. Veteran Trees: A Guide to Good Management. English Nature, Peterborough, UK.

Read, H., Cornelis, J., Troch, E., Geerts, P., Thomaes, A., Vandekerkhove, K., Verlinde, R., Joye, T., 2012, Het beheer van veteraanbomen. Vertaling en herwerking van: Read, H. Veteran trees: a guide to good management. Inverde & Agentschap voor Natuur en Bos.

Reczynska, K. , Swierkosz, K., 2017. Compositional changes in thermophilous oak forests in Poland over time: do they correspond to European trends? Applied Vegetation Science 20, 293–303.

Reemer, M., 2005. Saproxylic hoverflies benefit by modern forest management (Diptera: Syrphidae) Journal of Insect Conservation 9, 49–59.

Reemer, M., 2003. Zweefvliegen en veranderd bosbeheer in Nederland (Diptera, Syrphidae). EIS-report 2003-1. Stichting European Invertebrate Survey (EIS), Leiden, Nederland

Reemer, M., Van Helsdingen, P.J., Kleukers, R., 2003. Changes in ranges: invertebrates on the move. Proceedings of the 13th International Colloquium of the European Invertebrate Survey, Leiden, 2-5 September 2001

Regnery, B., Paillet, Y., Couvet, D., Kerbiriou, C., 2013. Which factors influence the occurrence and density of tree microhabitats in Mediterranean oak forests? Forest Ecology and Management 295, 118-125.

Remeš, J., Bílek, L., Novák, J., Vacek, Z., Vacek, S., Putalová, T., Koubek, L., 2015. Diameter increment of beech in relation to social position of trees, climate characteristics and thinning intensity. Journal of Forest Science 61, 456-464.

Ribe, R.G., 1989. The aesthetics of forestry: what has empirical preference research taught us? Environmental Management 13, 55-74.

Rink, M, Sinsch U., 2007. Radio-telemetric monitoring of dispersing stag beetles: implications for conservation. Journal of Zoology 272, 235-243.

Riofrio-Dillon, G., Bertrand, R., Gégout, J.-C., 2012. Toward a recovery time: forest herbs insight related to anthropogenic acidification. Global Change Biology 18, 3383–3394.

Ripley, B.D., 1988. Statistical inference for spatial processes. Cambridge University Press, Cambridge.

Ripley, B.D., 1976. The second-order analysis of stationary point processes. Journal of Applied Probability 13, 255–266.

Risbeth, J., 1959. Dispersal of Fomes annosus and Peniophora gigantea. Transactions of the British Mycological Society 42, 243–260.

Roberts, K.A., 1991. Field monitoring: confessions of an addict. In: Goldsmith, F.B. (ed). Monitoring for Conservation and Ecology, Chapman & Hall, London, UK, 179–212.

Roekaerts, M., 2002. The Biogeographical Regions Map of Europe. Basic principles of its creation and overview of its development. European Environmental Agency, European Topic Centre Nature Protection and Biodiversity, Paris, France.

Rohner, B., Bigler, C., Wunder, J., Brang, P., Bugmann, H., 2012. Fifty years of natural succession in Swiss forest reserves: changes in stand structure and mortality rates of oak and beech. Journal of Vegetation Science 23, 892-905.

Rolstad, J., Majewski, P., Rolstad, E., 1998. Black woodpecker use of habitats and feeding substrates in a managed Scandinavian forest. Journal of Wildlife Management 62, 11-23.

Rolstad, J., Rolstad, E., Sæteren Ø., 2000. Black woodpecker nest sites: characteristics, selection, and reproductive success. Journal of Wildlife Management 64, 1053-1066.

Rozas, V., 2006. Structural heterogeneity and tree spatial patterns in an old-growth deciduous lowland forest in Cantabria, northern Spain. Plant Ecology 185, 57-72.

Roženbergar, D., Konecnik, K., Zaplotnik, V., Diaci, J., 2003. Stand structure, gap formation, and regeneration in virgin forest remnant Strmec—Slovenia. NatMan Working Report 17, FLEC, Kopenhagen, Denmark.

Rubner, K., 1920. Die waldbaulichen Folgerungen des Urwaldes. Naturwissenschaftliches Zeitschrift für Forst- Landwirtschaft 18, 201–214.

Rüffer O., 2007. Entwicklungen in den Naturwäldern Brandenburgs. Eberswalder Forstliche Schriftenreihe Band 28, 50-62.

Rugani, T., Diaci, J., Hladnik, D., 2013. Gap dynamics and structure of two old-growth beech forest remnants in Slovenia. PlosOne 8, 1-13.

Rukke, B. A., Midtgaard, F., 1998. The importance of scale and spatial variables for the fungivorous beetle Bolitophagus reticulatus (Coleoptera: Tenebrionidae) in a fragmented forest landscape. Ecography 21, 561–572.

Rukke, B. A., 2000. Effects of habitat fragmentation: increased isolation and reduced habitat size reduces the incidence of dead wood fungi beetles in a fragmented forest landscape. - Ecography 23, 492-502.

Rünk, K., Zobel, M., Zobel, K., 2012. Biological Flora of the British Isles: Dryopteris carthusiana, D. dilatata and D. expansa. Journal of Ecology 100, 1039–1063.

Runkle, J.R., 1985. Disturbance regimes in temperate forests. In: Pickett, S.T.A., White, P.S. (eds.), The ecology of natural disturbance and patch dynamics. Academic Press, New York, pp.17-33.

Rüther, C. and Walentowski, H., 2008. Tree species composition and historic changes of the Central European oak/beech region. In: Floren, A. and Schmidl, J. (eds) Canopy arthropod research in Europe. Bioform Entomology, Nuremberg, Germany, 61-88.

Sabatini, F. M., Burrascano, S., Keeton, W. S., Levers, C., Lindner, M., Pötzschner, F., Verkerk, P.J., Bauhus, J., Buchwald, E., Chaskovsky, O., Debaive, N., Horváth, F., Garbarino, M., Grigoriadis, N., Lombardi, F., Duarte, J.M., Meyer, P., Midteng, R., Mikac, S., Mikolas, M., Motta, R., Mozgeris, G., Nunes, L., Panayotov, M., Ódor, P., Ruete, A., Simovski, B., Stillhard, J., Svoboda, M., Szwagrzyk, J., Tikkanen, J.-P., Volosyanchuk, R., Vrška, T., Zlatanov, T.M., Kuemmerle, T., 2018. Where are Europe’s last primary forests? Diversity and Distributions 24, 1426–1439.

Sabatini, F.M., Burrascano, S., Azzella, M.M., Barbati, A., De Paulis, S., Di Santo, D., Facioni, L., Giuliarelli, D., Lombardi, F., Maggi, O., Mattioli, W., Parisi, F., Persiani, A., Ravera, S., Blasi, C., 2016. One taxon does not fit all: Herb-layer diversity and stand structural complexity are weak predictors of biodiversity in Fagus sylvatica forests. Ecological Indicators 69, 126–137

Samojlik, T., 2010. Traditional utilisation of Białowieża Primeval Forest (Poland) in the 15th to 18th centuries. Landscape Archaeology and Ecology 8, 150-164.

Šamonil, P., Doleželová, P., Vašíčková, I., Adam, D., Valtera, M., Král, K., Janík, D., Šebková, B., 2013. Individual- based approach to the detection of disturbance history through spatial scales in a natural beech- dominated forest. Journal of Vegetation Science 24, 1167-1184. doi:10.1111/jvs.12025

Šamonil, P., Vrška, T., 2008. Long-term vegetation dynamics in the Sumava Mountains natural spruce-fir-beech forests. Plant Ecology 196, 197–214.

Samuelsson, J., Gustafsson, L., Ingelog, T, 1994. Dying and dead trees - a review of their importance for biodiversity. Swedish Threatened Species Unit, Swedish University of Agricultural Sciences, Uppsala, Sweden.

Sánchez-Bayo, F., Wyckhuys, K., 2019. Worldwide decline of the entomofauna: A review of its drivers. Biological Conservation 232, 8-27.

Saniga, M., Schütz, J.P., 2001a. Dynamics of changes in dead wood share in selected beech virgin forests in Slovakia within their development cycle. Journal of Forest Science 47, 557-565.

Saniga, M., Schütz, J.P., 2001b. Dynamiek des Totholzes in zwei gemischten Urwäldern der Westkarpaten im pflanzengeographischen Bereich der Tannen-Buchen- und der Buchenwälder in verschiedenen Entwicklungsstadien. Schweizerische Zeitschrift für Forstwesen 152, 407-416.

Saproxylic Quality Index: evaluated sites ranked by SQI. 2009. [internet site]. Available at http://yrefail.net/Coleoptera/sqi.htm. [cited 30 oct 2010].

Schenck, C. A., 1924. Der Waldbau des Urwalds. Allgemeine Forst- und Jagd-Zeitung, 100, 377-388.

Scherzinger, W., 1996. Naturschutz im Wald: Qualitätsziele einer dynamischen Waldentwicklung. Ulmer Verlag, Stuttgart, Germany.

Schiegg, K., 2000. Effects of dead wood volume and connectivity on saproxylic insect species diversity. Ecoscience 7, 290–298.

Schmaltz, J., Lange, A., 1999. Untersuchungen in der Zerfalls- und Verjüngungsphase eines Buchennaturwaldes auf der Insel Vilm. Forstarchiv 70, 66-73.

Schmidt M., Jochheim, H., Kersebaum K.-C., Lischeid, G., Nendel, C., 2017. Gradients of microclimate, carbon and nitrogen in transition zones of fragmented landscapes – a review. Agricultural and Forest Meteorology 232, 659–671.

Schmidt, M., Kriebitzsch, W.-U., Ewald, J. (eds.) 2011. Waldartenliste der Farn- und Blütenpflanzen Deutschlands. BfN-Skripten 299, pp. 53–107. Bundesamt für Naturschutz, Bonn-Bad Godesberg, DE.

Schmidt, W., 2009. Vegetation. In: Brumme, R., Khanna, P.K. (Eds.) Functioning and Management of European Beech Ecosystems, Ecological Studies 208. Springer, Berlin and Heidelberg, Germany, 65–86.

Schmitt, U., Möller, R, Eckstein, D., 2000. Seasonal wood formation dynamics of beech (Fagus sylvatica L.) and black locust (Robinia pseudoacacia L.) as determined by the “pinning” technique. Journal of Applied Botany 74, 10-16.

Schmitz, A., Sanders, T, Bolte, A., Bussotti, F., Dirnböck, T., Johnson, J. Penuelas, J., Pollastrini, M., Prescher, A.-K., Sardans, J., Verstraeten, A., De Vries, W., 2019. Responses of forest ecosystems in Europe to decreasing nitrogen deposition. Environmental Pollution 244, 980-994

Schöning, I., 2005. Organic matter stocks in temperate forest soils: Composition, radiocarbon age and spatial variability. PhD dissertation, Lehrstuhl für Bodenkunde, TUMünchen, Germany.

Schöning, I., Grüneberg, E. Sierra, C., Hessenmöller, D., Schrumpf, M., Weisser, W., Schulze, E.D., 2013.Causes of variation in mineral soil C content and turnover in differently managed beech dominated forests. Plant Soil 370, 625–639.

Schowalter, T. D., Zhang, Y. L., Sabin T. E., 1998. Decomposition and nutrient dynamics of oak (Quercus spp.) logs after five years of decomposition. Ecography 21, 3-10.

Schrumpf, M., Kaiser, K., Schulze, E.-D., 2014. Soil Organic Carbon and Total Nitrogen Gains in an Old Growth Deciduous Forest in Germany. PLoS ONE 9(2): e89364.

Schuck, A.; Parviainen, J. and Bücking, W., 1994. A review of approaches to forestry research on structure, succession and biodiversity of undisturbed and semi-natural forests and woodlands in Europe. Working paper 3. European Forest Institute, Joensuu, Finland.

Schulz, T., Krumm, F., Bücking, W., Frank, G., Kraus, D., Lier, M., Lovric, M., Vander Maaten, M., Paillet, Y., Parviainen, J., Vacchiano, G., Vandekerkhove, K., 2014. Comparison of integrative nature conservation in forest policy in Europe: A qualitative pilot study of institutional determinants. Biodiversity and Conservation 23, 3425-3450.

Schulz, T., Krumm, F., Bücking, W., Frank, G., Kraus, D., Lier, M., Lovric, M., Vander Maaten, M., Paillet, Y., Parviainen, J., Vacchiano, G., Vandekerkhove, K., 2014. Comparison of integrative nature conservation in forest policy in Europe: A qualitative pilot study of institutional determinants. Biodiversity and Conservation 23, 3425-3450.

Schulze E.D., Bouriaud, L., Bussler, H., Gossner, M., Walentowski, H., Hessenmöller, D, Bouriaud, O., von Gadow, K., 2014. Opinion paper: Forest management and biodiversity. Web Ecology 14, 3-10.

Schütz, J.-F., 1997. Sylviculture 2: jardinages des forêts. La gestion des forêts irrégulières et mélangées. Presses Polytechniques et Universitaires Romandes, EPFL, Lausanne, Switzerland.

Schütz, J.-P., 2006. Modelling the demographic sustainability of pure beech plenter forests in Eastern Germany, Annals of Forest Science 63, 93–100.

Scolastri, A., Bricca, A., Cancellieri, L., Cutini, M., 2017. Understory functional response to different management strategies in Mediterranean beech forests (central Apennines, Italy). Forest Ecology and Management 400, 665–676,

Šebesta, J., Maděra, P., Řepka, R., Matula, R., 2017. Comparison of vascular plant diversity and species composition of coppice and high beech forest in the Banat region, Romania. Folia Geobotanica 52, 33-43.

Šebková, B.; Šamonil, P.; Janík, D.; Adam, D.; Král, K.; Vrška, T.; Hort, L.; Unar, P. Spatial and volume patterns of an unmanaged submontane mixed forest in Central Europe: 160 years of spontaneous dynamics. Forest Ecology and Management 262, 873–885.

Sefidi, K., Esfandiary Darabad, F., Azaryan, M., 2016. Effect of topography on tree species composition and volume of coarse woody debris in an Oriental beech (Fagus orientalis Lipsky) old growth forests, northern Iran. Iforest 9, 658-665. doi: 10.3832/ifor1080-008

Seibold, S., Müller, J., Baldrian, P., Cadotte, M., Štursová, M., Biedermann, P.,Krah, F.-S., Bässler, C., 2019. Fungi associated with beetles dispersing from dead wood – Let's take the beetle bus! Fungal Ecology 39, 100-108.

Seidel, A., 1848. Beitrage zur Kenntnis des Urwaldes. Tharandt. Forstl. Jh. 5, 158-81

Seifert, M., 1992. Populationsbiologie und Aspekte der Morphologie zweier Wurmfarne, Dryopteris carthusiana und Dryopteris dilatata. PhD Thesis, University of Zürich (UZH), Zürich, Switzerland.

Sierdsema, H., 1995. Broedvogels en beheer. Het gebruik van broedvogelgegevens in het beheer van bos- en natuurterreinen. SBB-rapport 1995-1, SOVON-onderzoeksrapport 1995/04. SBB/SOVON, Driebergen/Beek-Ubbergen. 99 p.

Siitonen, J., 2001. Forest management, coarse woody debris and saproxylic organisms: Fennoscandian boreal forests as an example. Ecological Bulletins 49, 11-41.

Siitonen, J. and Martikainen, P., 1994. Occurence of rare and threatened insects living on decaying Populus tremula: a comparison between Finnish and Russian Karelia. Scandinavian Journal of Forestry Research 9, 185-191.

Simberloff, D., 1972. Properties of the rarefaction diversity measurement. The American Naturalist 106, 414-418.

Slade, E. Merckx, T., Riutta, T., Bebber, D., Redhead, D., Riordan, P., Macdonald D., 2013. Life-history traits and landscape characteristics predict macro-moth responses to forest fragmentation. Ecology 94, 1519-1530.

Smith, J., Heath, L., Hoover, C., 2013. Carbon factors and models for forest carbon estimates for the 2005–2011 National Greenhouse Gas Inventories of the United States. Forest Ecology and Management 307, 7–19.

Solbreck, C., 1980. Dispersal distances of migrating pine weevils, Hylobius abietis, Coleoptera, Curculionidae. Entomologia Experimentalis et Applicata 28, 123-131.

Sparks, T.H., Menzel, A., 2002. Observed changes in seasons: an overview. International Journal of Climatology 22, 1715–1725.

Speight, M., 1989. Saproxylic invertebrates and their conservation. Nature and Environment Series nr. 42. Council of Europe, Strasbourg, France.

S-PLUS 6.2 for Windows Professional edition. S-PLUS: Copyright 1988, 2003 Insightful Corp. S: Copyright Lucent Technologies, Inc. Portions Copyright 1994-1996 McRae Software Int'l, Inc. Portions Copyright 1990-1994 Halcyon Software, Inc.

Standovár, T., Horváth, S., Aszalós, R., 2017. Temporal changes in vegetation of a virgin beech woodland remnant: stand-scale stability with intensive fine-scale dynamics governed by stand dynamic events. Nature Conservation 17, 35–56.

Standovár, T., Kenderes, K., 2003. A review on natural stand dynamics in beechwoods of East Central Europe. Applied Ecological and Environmental Research 1, 19-46.

Štefančík, I., 2013. Development of target (crop) trees in beech (Fagus sylvatica L.) stand with delayed initial tending and managed by different thinning methods. Journal of Forest Science 59, 253–259.

Steinfath, M., 2007. Erste Bilanz nach dem Orkan „Kyrill“: 25 Mio m³ Sturmholz in Deutschland. AFZ-der Wald 62, 152-153.

Stenlid, J., Gustafsson M., 2001. Are rare wood fungi threatened by inability to spread ? Ecological Bulletins 49, 85-91.

Stokland, J.N., 2001. The coarse woody debris profile: an archive of recent forest history and an important biodiversity indicator. Ecological Bulletins 49, 71-83.

Stokland, J.N., Siitonen, J., Jonsson B.G., 2012. Biodiversity in dead wood. Cambridge University Press, Cambridge, UK.

Straussberger, R., 2003. Buchen-Naturwaldreservate - Perlen im Oberpfälzer Wald. LWF-Wissen 43, 47-77.

Sturm, K., 1993. Prozeßschutz – ein Konzept für naturgerechte Waldwirtschaft. Zeitschrift für Ökologie und Naturschutz 2, 181–192.

Sverdrup-Thygeson, A., Midtgaard, F., 1998. Fungus infected trees as islands in boreal forests: Spatial distribution on the fungivorous beetle Bolitophagus reticulatus (Coleoptera: Tenebrionidae). Écoscience 5, 486–493.

Szwagrzyk, J., Czerwczak, M., 1993. Spatial Patterns of Trees in Natural Forests of East-Central Europe. Journal of Vegetation Science 4, 469-476.

Szwagrzyk, J., Szewczyk, J., 2001. Tree mortality and effect of release from competition in an old-growth Fagus-Abies-Picea stand. Journal of Vegetation Science 12, 621–626.

Tabaku, V., 2000. Struktur von Buchen-Urwälder in Albanien im Vergleich mit Deutschen Naturwaldreservaten und Wirtschaftswäldern. PhD-thesis, Göttingen, Germany.

Tabaku, V., Meyer, P., 1999. Lückenmuster in Buchenwäldern unterschiedlicher Nutzungsintensität. Forstarchiv 70, 87-97.

Tack, G., Hermy, M., 1998. Historical ecology of woodlands in Flanders. In: Kirby K., Watkins C. (Eds.), The ecological history of European forests. CAB International, New York, USA, 283-292.

Tack, G., van den Bremt, P., Hermy, M., 1993. Bossen van Vlaanderen. Een historische ecologie. Davidsfonds, Leuven, Belgium.

Tallier, P.-A., 2004. Forêts et propriétaires forestiers en Belgique de la fin du XVIIIe siècle à 1914. Histoire de l'évolution de la superficie forestière, des peuplements, des techniques sylvicoles et des débouchés offerts aux produits ligneux. Académie Royale de Belgique, Brussels.

Thimonier, A., Dupouey, J.L., Timbal, J., 1992. Floristic changes in the herb-layer vegetation of a deciduous forest in the Lorraine Plain under the influence of atmospheric deposition. Forest Ecology and Management 55, 149–167.

Thomaes, A., Kervyn, T., Beck O., Cammaerts, R., 2008. Distribution of Lucanus cervus in Belgium: surviving in a changing landscape (Coleoptera: Lucanidae). Revue d'Ecologie (Terre & Vie) 63, 139-144.

Thomaes, A., Vandekerkhove, K., De Keersmaeker, L., Cornelis, J., Van Elegem, B., Roelandt, B., 2009. Bossen. In: T'jollyn, F., Bosch, H., Demolder, H., De Saeger, S., Leyssen, A., Thomaes, A., Wouters, J., Paelinckx, D., Hoffmann, M., 2009. Ontwikkeling van criteria voor de beoordeling van de lokale staat van instandhouding van de Natura 2000 habitattypen. Versie 2.0. INBO.R.2009.46, 223-290.

Thompson, K., Bakker, J., Bekker, R., 1997. The soil seed banks of North West Europe: methodology, density and longevity. Cambridge University Press, Cambridge, UK.

Thünen-Institut, 2012. Dritte Bundeswaldinventur – Ergebnisdatenbank. https://bwi.info (accessed 22 november 2017).

Tinya, F., Ódor, P., 2016. Congruence of the spatial pattern of light and understory vegetation in an old-growth, temperate mixed forest. Forest Ecology and Management 381, 84-92.

Tkatschenko, M., 1929. Urwald und Plenterwald in Nordrussland. In: Proceedings of the 7th International Congress of Forestry Experimental Stations, Stockholm, 124-128.

Trautmann, W., 1969. Zur Einrichtung von Naturwaldreservaten in der Bundesrepublik Deutschland. Natur und Landschaft 44, 88-89.

Trotsiuk, V., Hobi, M.L., Commarmot, B., 2012. Age structure and disturbance dynamics of the relic virgin beech forest Uholka (Ukrainian Carpathians). Forest Ecology and Management 265, 181–190.

Troukens, W., 2004. Bolitophagus reticulatus aan de westrand van Brussel (Coleoptera: Tenebrionidae). Phegea 32, 151-152.

Trumbore, S., 2000. Age of soil organic matter and soil respiration: radiocarbon constraints on belowground C dynamics. Ecological Applications 10, 399–411.

Tüxen, R., 1970. Zur Einrichtung von Naturwald-Reservaten in der BRD. Natur und Landschaft 45, 170.

Uhlig, P., A. Harris, G. Craig, C. Bowling, B. Chambers, B. Naylor and G. Beemer., 2001. Old growth forest definitions for Ontario. Ont. Min. Nat. Res., Queen's Printer for Ontario, Toronto, ON. 53 p

Ujházy, K., Križová, E., Vančo, M., Freňáková, E., Ondruš, M., 2005. Herb layer dynamics of primeval fir-beech forests in central Slovakia. Herb layer dynamics of primeval fir-beech forests in central

Slovakia. In: Commarmot, B.; Hamor, F. D. (eds.) Proceedings of the international conference 'Natural Forests in the Temperate Zone of Europe–Values and Utilisation', 13–17 October 2003, Mukachevo, Ukraine, 193–202.

Ujházy, K., Krizová, E., Ondruš, M., Vigoda, M., 2007. Short-term vegetation change in the fir beech primeval forest (Badinsky prales, Central Slovakia). In: Abrudan V.I. (Ed.) Forest and sustainable development. Proceedings of the biennial international symposium (2007). Editura Universităţii Transilvania, Braşov, Romania, 213–218

UNEP/CBD/SBSTTA, 2001. Main Theme: Forest Biological Diversity. Report of the Ad Hoc Technical Expert Group on Forest Biological Diversity. Subsidiary Body for Scientific, Technical and Technological Advice, Seventh Meeting, Montreal, 12-16 November 2001. http://www.biodiv.org/programmes/areas/forest/definitions.asp.

University of Padova, 2008. Report on Current State of Forest Resources in the Carpathians, Carpathian Project. Padova, Italy.

USDA Forest service, 1992. Interim old growth definition for Douglas fir, grand/white fir, interior Douglas fir, lodgepole pine, Pacific silver fir, ponderosa pine, Port-Orford cedar/tanaok (redwood), subalpine fir and western hemlock series. USDA forest service, Region 6, Portland, Or. Journal of Forestry 92(1), 22-25.

Utschig, H., Küsters, E., 2003. Wachstumsreaktionen der Buche (Fagus sylvatica (L.)) auf Durchforstungen—130-jährige Beobachtung des Durchforstungsversuches Elmstein 20. Forstwissenschaftliches Centralblatt 122, 389–409.

Vacek, K., Matějka, S., 2003.Vegetation changes in beech and spruce stands in the Orlické hory Mts. in 1951–2001. Journal of Forest Science, 49, 445–473.

Vallauri, D., André, J., Blondel, J., 2003. Le bois mort, une lacune des forêts gérées. Revue Forestière Française 55, 3-16.

Valverde, T., Silvertown, J., 1998. Variation in the demography of a woodland understorey herb (Primula vulgaris) along the forest regeneration cycle: projection matrix analysis. Journal of Ecology 86, 545-562.

Van Calster, H., Baeten, L., De Schrijver, A., De Keersmaeker, L., Rogister, J.E., Verheyen, K., Hermy, M., 2007. Management driven changes (1967–2005) in soil acidity and the understory plant community following conversion of a coppice-with-standards forest. Forest Ecology and Management 241, 258–271.

Van Calster, H., Baeten, L., Verheyen, K., De Keersmaeker, L., Dekeyser, S., Rogister, J.E., Hermy, M., 2008a. Diverging effects of overstorey conversion scenarios on the understorey vegetation in a former coppice-with-standards forest. Forest Ecology and Management 256, 519–528.

Van Calster, H., Chevalier, R., van Wyngene, B., Archaux, F.,Verheyen, K., Hermy, M., 2008b. Long-term seed bank dynamics in a temperate forest under conversion from coppice-with-standards to high forest management. Applied Vegetation Science 11, 252–260.

Van Daele, T., Van Reeth, W., Dumortier, M., Peymen, J., 2010. Natuurindicatoren 2010. Toestand van de natuur in Vlaanderen: cijfers voor het beleid. Mededeling van het Instituut voor Natuur- en Bosonderzoek, INBO.M.2010.2, Brussels.

Van de Kerckhove, P., Vandekerkhove, K., 2016. 10 jaar FieldMap in de bosreservaten, een evaluatie en een voorbeeldcase: facieskartering van daslook in Bos Ter Rijst. [Ten years of FieldMap in the forest reserves, an evaluation and exemplary case: facies mapping of Allium ursinum in Terrijst]. Bosreservatennieuws 15, 4-9.

Van Den Berge, K., Roskams, P., Verlinden, A., Quataert, P., Muys, B., Maddelein, D., Zwaenepoel, J., 1990a. Structure and dynamics of a 215-years old broadleaved forest stand recently installed as a total forest reserve. Silva Gandavensis 55, 113-152.

Van Den Berge, K., Roskams, P., Verlinden, A., Quataert, P., Muys, B., Maddelein, D., Zwaenepoel, J., 1990b. Analyse van een bosreservaat in een 215-jarig bestand in het Zoniënwoud. Rapport 17. Werkgroep Sociale en Economische Betekenis van het Bos. Laboratorium voor Bosbouw, Universiteit Gent.

van der Jagt, J. L., 1980. Bosreservaten: doelstellingen, inrichting en beheer. Nederlands Bosbouwtijdschrift 52, 64-69.

Van der Laan, H.F., 1972. Is Fomes fomentarius minder zeldzaam aan het worden ? Coolia 15, 156-158.

Van der Veken, S., Bossuyt, B., Hermy, M., 2004. Climate gradients explain changes in plant community composition of the forest understorey: an extrapolation after climate warming. Belgian Journal of Botany 137, 55–69.

van Dijk, A., Hustings, F., Boele, A., Koffijberg, K., Zoetebier, D., Plate, C., 2010. Kolonievogels en zeldzame broedvogels in Nederland in 2006 en 2007. Limosa 83, 1-20.

Van Dort, K., Van Hees, A., 2002. Mossen en vaatplanten op dood beukenhout in bosreservaat Kersselaerspleyn (Zoniënwoud, Vlaanderen). Alterra-report 418. Alterra, Wageningen, NL.

Van Dort, K., Bouwma, I, Broekmeyer, M., Koop, H., 1999. Veranderingen in de kruidlaag in bosreservaten. De Levende Natuur 100, 154-157.

Van Elegem, B., 2006. Bosreservaten in Vlaanderen, de beleidsvisie. Bosrevue 15, 2-7.

Van Landuyt, W.& De Beer, D., 2016. Mossen en lichenen op dood hout in de bosreservaten van het Zoniënwoud en Wijnendalebos. Research Report INBO.R.2016.11823501. INBO, Brussels, Belgium.

Van Landuyt, W., Vanhecke, L., Brosens, D., 2012. Florabank1: a grid-based database on vascular plant distribution in the northern part of Belgium (Flanders and the Brussels Capital region). PhytoKeys 12, 59–67.

Van Loy, K., Vandekerkhove, K., Van Den Meersschaut, D., 2003. Assessing and monitoring the status of biodiversity-related aspects in Flemish forests by use of the Flemish forest inventory data. In: Corona P., Köhl M., Marchetti M. (eds.), Advances in forest inventory for sustainable forest management and biodiversity monitoring. Forestry Sciences series 76. Kluwer Academic Publishers, Dordrecht, The Netherlands, 405-430.

Van Miegroet, M., 1977. Het belang van wetenschappelijke ervaring en sociale evolutie voor het huidig bosbouwbeleid. Groene Band nr. 28.

Van Parijs, S., Van Landuyt, W., De Beer, D., Vandekerkhove, K., De Keersmaeker, L., Hoffmann, M., 2018. Species diversity and composition of vascular plants and bryophytes on decomposing logs of beech (Fagus sylvatica) in two forest reserves in Flanders (Belgium). 11th international beech symposium – Viterbo, Italy, 18-21 sept. 2018.

Van Slycken, J., 1994. Nota inzake de inrichting van bosreservaten in het Vlaamse gewest. Internal note. Institute for Forestry and Game Management (IBW), Geraardsbergen, Belgium.

van Steenis, W., Reemer, M., 2013. Zweefvliegen houden van oude bossen. De Levende Natuur 114, 177-181.

Van Sterbeeck, F., 1675. Theatrum fungorum oft het tooneel der Campernoelien. Antwerpen, Ioseph Iacobs. 396 p.

Van Wagner, C. E., 1968. The line intersect Method in forest Fuel Sampling. Forest Science 14, 20-26.

Vandekerkhove, K., 1998. Criteria voor de selectie van bosreservaten in functie van een betere kadering van de vlaamse bosreservaten in een Europees netwerk. Mededelingen van het Instituut voor Bosbouw en Wildbeheer 1998.03. Instituut voor Bosbouw en Wildbeheer, Geraardsbergen, Belgium.

Vandekerkhove, K., 2000. Summaries of Data Collected in Different Countries: an overview of existing methodologies for the monitoring of stand dynamics in Strict Forest Reserves. IN: European Commission Directorate-General for Research: COST Action E4: Forest Reserves Research Network –- EUR 19550, 156-167.

Vandekerkhove, K., 2013. Integration of nature protection in forest policy in Flanders (Belgium): INTEGRATE country report. European Forest Institute - Central European Office (EFI-CENT), Freiburg, Germany

Vandekerkhove, K., Baeté, H., Van der Aa, B., De Keersmaeker, L., Thomaes, A., Leyman, A., Verheyen, K., 2016a. 500 years of coppice-with-standards management in Meerdaal Forest (Central Belgium). iForest – Biogeosciences and Forestry 9, 509-517.

Vandekerkhove, K., De Keersmaeker, L., Baeté, H., Walleyn, R., 2005. Spontaneous re-establishement of natural structures and related diversity in a previously managed beech forest in Belgium after 20 years of non intervention. Forest Snow & Landscape Research 79, 145-156.

Vandekerkhove, K., De Keersmaeker, L., Menke, N., Meyer, P., Verschelde, P., 2009a. When nature takes over from man: dead wood accumulation in previously managed oak and beech woodlands in North-West- and Central Europe. Forest Ecology and Management 258, 425–435.

Vandekerkhove, K., De Keersmaeker, L., Walleyn, R., Köhler, F., Crevecoeur, L., Govaere, L., Thomaes, A., Verheyen, K., 2011. Reappearance of old-growth elements in lowland woodlands in northern Belgium: do the associated species follow? Silva Fennica 45, 909-935.

Vandekerkhove, K., Frank, G., Parviainen, J., Bücking, W., Little, D., 2007. Suggestions for Clarifying Protected Forest Area (PFA) Categories for Reporting Purposes. In: Frank, G., Parviainen, J.,Vandekerkhove, K., Latham, J., Schuck, A., Little, D. (Eds). COST Action E27: Protected Forest Areas in Europe - Analysis and Harmonisation (PROFOR): Results, Conclusions and Recommendations. Federal Research and Training Centre for Forests, Natural Hazards and Landscape, Vienna, 109-133.

Vandekerkhove, K., Thomaes, A., Crevecoeur, L., De Keersmaeker, L., Leyman, A., Köhler, F., 2016b. Saproxylic beetles in non-intervention and coppice-with-standards restoration management in Meerdaal forest (Belgium): an exploratory analysis. iForest – Biogeosciences and Forestry 9, 536-545.

Vandekerkhove, K., Thomaes, A., Jonsson, B.G., 2013. Connectivity and fragmentation: Island biogeography and metapopulation applied to old-growth-elements. In: Kraus, D., Krumm, F. (eds.) Integrative approaches as an opportunity for the conservation of forest biodiversity. In Focus: managing forest in Europe. European Forest Institute - Central European Office (EFI-CENT), Freiburg, 104-115.

Vandekerkhove, K., Van der Aa, B., Baeté, H., Meuleman, B., 2009b. Bakermat van duurzaam bosbeheer. « Pour le plus grand profit de son excellence ». In: Baeté, H., De Bie, M., Hermy, M., Van den Bremt, P. (eds.). Miradal – Erfgoed in het Meerdaalwoud en het Heverleebos. Davidsfonds, Leuven, Belgium, 139-171.

Vandekerkhove, K., van Dort, K., Baeté, H., Walleyn, R., 2003. Species richness of mosses, fungi and vascular plants on coarse woody debris of beech in the Flemish forest reserve ‘Kersselaerspleyn’ (Zoniënwoud). Scripta Botanica Belgica 24, 83-91.

Vandekerkhove, K., Vanhellemont, M., Thomaes, A., Joye, T., Nyssen, B., 2018b. Maatregelen voor natuurwaarden. In: Jansen, P., Boosten, M., Cassaert, M., Cornelis, J., Thomassen, E., Winnock, M. (eds), Praktijkboek Bosbeheer. Inverde, Brussel & Stichting Probos, Wageningen, 400-437.

Vandekerkhove, K., Vanhellemont, M., Vrška, T., Meyer, P., Tabaku, V., Thomaes, A., Leyman, A., De Keersmaeker, L., Verheyen, K., 2018a. Very large trees in a lowland old-growth beech (Fagus sylvatica L.) forest: Density, size, growth and spatial patterns in comparison to reference sites in Europe. Forest Ecology and Management 417, 1-17.

Vandepitte, K., Jacquemyn, H., Roldàn-Ruiz, I., Honnay, O., 2010. Extremely low genotypic diversity and sexual reproduction in isolated populations of the self-incompatible lily-of-the-valley (Convallaria majalis) and the role of the local forest environment. Annals of Botany105, 769-776.

Vanhellemont, M., Baeten, L., Verheyen, K., 2014. Relating changes in understorey diversity to environmental drivers in an ancient forest in northern Belgium. Plant Ecology and Evolution 147, 22-32.

Veen P., Fanta, J., Raev, I., Biriş I.-A., de Smidt, J., Maes, B., 2010. Virgin forests in Romania and Bulgaria: results of two national inventory projects and their implications for protection. Biodiversity and Conservation 19, 1805–1819

Veerkamp, M., Arnolds, E., 2008. Ecological Monitoring Network Newsletter 9. Coolia 51, 97–108.

Vellend, M., Baeten, L., Myers-Smith, I.H., Elmendorf, S.C., Beauséjour, R., Brown, C.D., Wipf, S., 2013. Global meta-analysis reveals no net change in local-scale plant biodiversity over time. Proceedings of the National Academy of Sciences of the United States of America 110, 19456–19459.

Vellend, M., Verheyen, K., Jacquemyn, H., Kolb, A., van Calster, H., Peterken, G.F., Hermy, M., 2006. Extinction debt of forest plants persists for more than a century following habitat fragmentation. Ecology 87, 542–548.

Verheyen, K., Hermy, M., 2001. An integrated analysis of the spatio-temporal colonization patterns of forest plant species. Journal of vegetation science, 12 (4), 567-578.

Verheyen, K., Hermy, M., 2004. Recruitment and growth of herb-layer species with different colonizing capacities in ancient and recent forests. Journal of vegetation science, 15 (1), 125-134.

Verheyen, K., Baeten, L., De Frenne, P., Bernhardt-Römermann, M., Brunet, J., Cornelis, J., Decocq, G., Dierschke, H., Eriksson, O., Hédl, R., Heinken, T., Hermy, M., Hommel, P., Kirby, K., Naaf, T., Peterken, G., Petrik, P., Pfadenhauer, J., Van Calster, H., Walther, G.-R., Wulf, M., Verstraeten, G., 2012. Driving factors behind the eutrophication signal in understorey plant communities of deciduous temperate forests. Journal of Ecology 100, 352–365.

Verheyen, K., Bazany, M., Checko, E., Chudomelova, M., Closset-Kopp, D., Czortek, P., Decocq, G., De Frenne, P., De Keersmaeker, L., Enriquez-Garcia, C., Fabsicova, M., Grytnes, J.A., Hederova, L., Hédl, R., Heinken, T., Schei, F., Horváth, S., Jaroszewicz, B., Jermakowicz, E., Klinerová, T., Kolk, J., Kopecký, M., Kuras, I., Lenoir, J., Macek, M., Máliš, F., Martinessen, T., Naaf, T., Papp, L., Papp-Szakály, A., Pech, P., Petřík, P., Prach, J., Reczyńska, K., Sætersdal, M., Spicher, F., Standovár, T., Świerkosz, K., Szczęśniak, E., Tóth, Z., Ujházy, K., Ujházyová, M., Vangansbeke, P., Vild, O., Wołkowycki D., Wulf, M., Baeten, L., 2018. Observer and relocation errors matter in resurveys of historical vegetation plots. Journal of Vegetation Science, 29, 812-823.

Verheyen, K., Guntenspergen, G., Biesbrouck, B., Hermy, M., 2003a. An integrated analysis of the effects of past land use on forest herb colonization at the landscape scale. Journal of Ecology, 91, 731-742.

Verheyen, K., Honnay, O., Motzkin, G., Hermy, M., Foster, D., 2003b. Response of forest plant species to land-use change: a life-history trait-based approach. Journal of Ecology 91, 563-577.

Verheyen, K., Honnay, O., Motzkin, G., Hermy, M., Foster, D.R., 2003. Response of forest plant species to land-use change: a life-history trait-based approach. Journal of Ecology 91, 563–577.

Verhulst, A., 1995. Landschap en landbouw in middeleeuws Vlaanderen. Gemeentekrediet, Brussels, Belgium.

Vermeersch, G., Anselin, A., Devos, K., 2006. Bijzondere broedvogels in Vlaanderen in de periode 1994-2005: populatietrends en recente status van zeldzame, kolonievormende en exotische broedvogels in Vlaanderen. Mededelingen van het Instituut voor Natuur- en Bosonderzoek, 2006(2). Instituut voor Natuur- en Bosonderzoek, Brussels. 64 p.

Vermeersch, G., Anselin, A., Devos, K., Herremans, M., Stevens, J., Gabriëls, J., Van Der Krieken, B., 2004. Atlas van de Vlaamse broedvogels 2000-2002. Mededelingen van het Instituut voor Natuurbehoud 23, Brussels. 495 p.

Versteirt, V., Desender, K., Geudens, G., Grootaert, P., 2000. Determinatie en bioindicatie van bosgebonden ongewervelden. Verkennend onderzoek naar de potentiële waarde van integrale bosreservaten voor het behoud van xylobionte arthropoden. Rapport ENT.2000.04. Royal Institute for Natural Sciences, Brussels.

Verstraeten, A., 2018. Evolution of soil solution chemistry in temperate forests under decreasing atmospheric deposition in Flanders. PhD-dissertation, University of Ghent, Ghent, Belgium.

Verstraeten, A., Neirynck, J., Genouw, G., Cools, N., Roskams, P., Hens, M., 2012. Impact of declining atmospheric deposition on forest soil solution chemistry in Flanders, Belgium. Atmospheric Environment 62, 50–63.

Verstraeten, G., Baeten, L., Van den Broek, T., De Frenne, P., Demey, A., Tack, W., Muys, B., Verheyen, K., 2013. Temporal changes in forest plant communities at different site types. Applied Vegetation Science 16, 237–247.

Vild, O., Rolečeka, J., Hédl, R., Kopecký, M., Utinek, D., 2013. Experimental restoration of coppice-with-standards: Response of understorey vegetation from the conservation perspective. Forest Ecology and Management 310, 234–241.

Vojík, M., Boublík, K., 2018. Fear of the dark: decline in plant diversity and invasion of alien species due to increased tree canopy density and eutrophication in lowland woodlands. Plant Ecology 219, 749–758.

Volosyanchuk, R., Prots, B., Shparyk, Y., Cherniavskyi, M., Kagalo, A. and Savchyn, V., 2018. Old Growth Forests in the Ukrainian Carpathians: Criteria and Indicators, identification methodology, and results up-to date. 5th European Congress of Conservation Biology. ECCB abstract book. University of Jyväskylä, Finland.

Von Arx, G., Graf Pannatier, E., Thimonier, A., Rebetez, M., 2013. Microclimate in forests with varying leaf area index and soil moisture: potential implications for seedling establishment in a changing climate. Journal of Ecology 101, 1201-1213.

Von Brincken, J., 1828. Mémoire descriptif sur la forêt impériale de Bialowieza en Lithuanie. Glücksberg, Warsawa, Poland.

von Oheimb, G., Brunet, J., 2007. Dalby Söderskog revisited: long-term vegetation changes in a south Swedish deciduous forest. Acta Oecologica 31, 229–242.

Von Oheimb, G., Westphal, C., Hardtle, W., 2007. Diversity and spatio-temporal dynamics of dead wood in a temperate near-natural beech forest (Fagus sylvatica). European journal of forest research 126, 359-370.

Von Oheimb, G., Westphal, C., Tempel, H., Härdtle, W., 2005. Structural pattern of a near-natural beech forest (Fagus sylvatica) (Serrahn, North-east Germany). Forest Ecology and Management 212, 253-263.

Vrška, T., 1998. Prales Salajka po 20 letech (1974–1994). Lesnictvi-Forestry 44, 153-181.

Vrška, T., Hort, L., Adam, D., Odehnalová, P., Horal, D., 2002. Developmental dynamics of virgin forest reserves in the Czech Republic I – The Českomoravská vrchovina Upland (Polom, Žákova hora Mt.). Academia, Prague.

Vrška, T., Hort, L., Adam, D., Odehnalová, P., Horal, D., 2006. Developmental dynamics of virgin forest reserves in the Czech Republic II – The lowland floodplain forests. Academia, Prague, Czech Republic.

Vrška, T., Hort, L., Odehnalová, P., Adam, D., Horal, D., 2000. Prales Mionší – historický vývoj a současný stav. Journal of Forest Science 46, 411-424.

Vrška, T., Hort, L., Odehnalová, P., Adam, D., Horal, D., 2001. The Razula virgin forest after 23 years (1972-1995). Journal of Forest Science 47, 15-37.

Vrška, T., Šamonil, P., Unar, P., Hort, L., Adam, D., Král, K., Janík, D., 2012. Developmental dynamics of virgin forest reserves in the Czech Republic III – Šumava Mts. and Český les Mts. (Diana, Stožec, Boubín virgin forest, Milešice virgin forest). Academia, Prague.

Vuidot, A., Paillet, Y., Archaux, F., Gosselin, F., 2011. Influence of tree characteristics and forest management on tree microhabitats. Biological Conservation 144, 441–450.

Waal, R.W., Bijlsma, R.J., Dijkman, E.M., van der Werff, M.M., 2001. Stekelvarendominantie in bossen op arme zandgronden. De Levende Natuur 102, 118-122.

Walleyn, R., Vandekerkhove, K., 2002. Diversiteit, ecologie en indicatorwaarde van paddestoelen op groot dood beukenhout in het bosreservaat Kersselaerspleyn (Zoniënwoud). Rapport IBW.Bb.R.2002.009, Instituut voor Bosbouw en Wildbeheer, Geraardsbergen, Belgium.

Walleyn, R., 2003. Quelques récoltes intéressantes en Forêt de Soignes (2). Rev. Cercle Mycol. Bruxelles 3, 3-10.

Walleyn, R., 2004. Verspreiding en ecologie in Vlaanderen van enkele houtzwammen met voorkeur voor beukenhout. Meded. Antwerpse Mycol. Kring 2004, 16-22.

Walleyn, R., 2006. Verspreiding en ecologie in Vlaanderen van enkele houtzwammen met voorkeur voor Beuk (2de reeks). Meded. Antwerpse Mycol. Kring 2006, 37-43.

Warren, W.G., Olsen, P.R., 1964. A line intersect technique for assessing logging waste. Forest Science 10, 267-276.

Waterinckx, M., Haelvoet, P., 1997. Operationaliseren en begeleiden van de uitvoeringsfase van de bosinventarisatie van het Vlaamse Gewest. Eindverslag. Afdeling Bosbeheer en Ruimtelijke Informatietechnieken. University of Ghent, Belgium.

Watts, K., 2006. British forest landscapes the legacy of woodland fragmentation. Quarterly Journal of Forestry 100, 273-279.

Weiss, J., Köhler, F., 2005. Erfolgskontrolle von Maßnahmen des Totholzschutzes im Wald. Einzelbaumschutz oder Baumgruppenerhaltung? – LÖBF-Mitteilungen 3, 26-29.

Wells, R.W., Lerzman, K.P., Saunders, S.C., 1998. Old-growth definitions for the forests of British Columbia, Canada. Natural Areas Journal 18, 279-292.

Welzholz, J.C., Johann, E., 2007. History of protected forest areas in Europe. In: Frank, G., Parviainen, J.,Vandekerkhove, K., Latham, J., Schuck, A., Little, D. (Eds), COST Action E27 Protected Forest Areas in Europe – Analysis and Harmonisation (PROFOR): Results, Conclusions and Recommendations. Federal Research and Training Centre for Forests, Natural Hazards and Landscape (BFW),Vienna, Austria, 17-40.

Westphal, C., Tremer, N., von Oheimb G., Hansen, J., von Gadow, K., Härdtle, W., 2006. Is the reverse J-shaped diameter distribution universally applicable in European virgin beech forests? Forest Ecology and Management 223, 75-83.

Winter, S., Möller, G.C., 2008. Microhabitats in lowland beech forests as monitoring tool for nature conservation. Forest Ecology and Management 255, 1251–1261.

Winter, S., Nowak, E., 2001. Totholz in bewirtschafteten und nicht bewirtschafteten Buchen- und Eichen-Hainbuchenwaldern im Biospharenreservat Spreewald. Natur- und Landschaftspflege Brandenburg 10, 128-133.

Wirth, C., Messier, C., Bergeron, Y., Frank, D., Fankhänel A., 2009. Old-Growth Forest Definitions: a Pragmatic View. In: Wirth C., Gleixner, G., Heimann, M. (eds.), Old-Growth Forests - Function, Fate and Value. Ecological Studies 207. Springer Verlag, Berlin, Heidelberg, Germany, 11-33.

Wittig, R., 2008. Experimental research on recolonisation with Anemone nemorosa of the beech forests of the Ruhr district (Germany) floristically impoverished by air pollution. Environmental Science and Pollution Research 15, 492-498.

Wolf, A., 2005. Fifty year record of change in tree spatial patterns within a mixed deciduous forest. Forest Ecology and Management 215, 112–223.

Wolf, A., Møller, P.F., Bradshaw, R.H.W., Bigler, J., 2004. Storm damage and long-term mortality in a semi-natural, temperate deciduous forest. Forest Ecology and Management 188, 197-210.

Wouters, J., Quataert, P., Onkelinx, T. & Bauwens, D., 2008. Ontwerp en handleiding voor de tweede regionale bosinventarisatie van het

Zednik, F., 1938. Über den Aufbau des Urwaldes der Gemässigten Zone [On the structure of virgin forest in the temperate zone]. Zeitschrift für Weltforstwirtschaft 6, 215-229.

Zenner, E., Peck, J., Hobi, M., Commarmot, B., 2015. The dynamics of structure across scale in a primeval European beech stand. Forestry 88, 180-189.

Zhou, G., Liu, S., Li, Z., Zhang, D., Tang, X., Zhou, C., Yan, J., Mo, J., 2006. Old-growth forests can accumulate carbon in soils. Science 314, 1417–1417.

Ziaco, E., Di Filippo, A., Alessandrini, A., D'Andrea, E., Piovesan, G., 2012. Old-growth attributes in a network of Apennines (Italy) beech forests: disentangling the role past human interferences and biogeoclimate. Plant Biosystems 146, 153-166.

Zielonka, T., Piątek, G., 2004. The Herb and Dwarf Shrubs Colonization of Decaying Logs in Subalpine Forest in the Polish Tatra Mountains. Plant Ecology 172, 63-72.

Zielony R., 1999. Natural Forests and Forests protected by Law in Poland. IN: Diaci J. (ed) Virgin Forests and Forest Reserves in Central and East European Countries. Proceedings of invited lecturers' reports presented at the COST-E4 meeting in Ljubljana, Slovenia. Biotechnical Faculty, University of Ljubljana, Slovenia.

Zukrigl, K., 1978. Waldreservate in Deutschland – und in Österreich ? Natur und Landschaft 64, 13-22.

Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A. A., Smith, G. M., 2009. Mixed effect models and extensions in ecology with R. Springer, New York, USA.

Annex 1: Summary details for all sites included in the deadwood accumulation study (chapter 2)

Reserve name	country	survey type	date of recor-ding	Lying dead wood (m^3/ha)	Standing dead wood (m^3/ha)	Total dead wood (m^3/ha)	Ratio lying dead wood (%)	Living volume (m^3)	TAB (m^3)	ratio dead to TAB (%)	accumulation rate (m^3/ha.year)	Geographic location	Domi-nant tree species	Fertility	Elevation (m a.s.l.)	Average age (years)	time of non-interv-ention (years)	Source
Bos Ter Rijst	B	CP	2005	14.8	12.1	26.9	55.0	493	520	5.2	1.13	NW	Q	R	70	128	22	Unpub. data
Bos Ter Rijst	B	CA	2005	31.8	30.9	62.7	50.7	628	690	9.1	2.76	NW	Q	R	70	128	22	Unpub. data
Bos Ter Rijst	B	LT	1996	9.8	16.6	26.4	37.1	267	293	9.0	1.88	NW	Q	R	70	137	13	unpubl. data
Hallerbos-Jansheide	B	CP	2006	2.3	5.5	7.8	29.5	424	431	1.8	0.48	NW	Q	R	100	58	12	unpubl. data
Jongenbos	B	CA	2006	9.0	8.0	17.0	47.1	305	322	5.3	1.15	NW	Q	P	60	147	13	unpubl. data
Kluisbos	B	CA	2006			35.0		500	535	6.5	3.00	NW	F	R	80	109	11	unpubl. data
Kolmont	B	CA	2006	19.0	36.0	55.0	65.5	375	430	12.8	2.04	NW	F	r	60	154	26	unpubl. data
Kolmont	B	LT	1994	16.0	31.9	47.9	33.4	327	375	12.8	3.28	NW	F	R	60	166	14	unpubl. data
Parikebos	B	LT	1993	14.0	3.0	16.8	83.3	360	377	4.5	1.14	NW	F	R	70	107	13	unpubl. data
Rodebos	B	CA	2001	3.0	5.0	8.0	37.5	422	430	1.9	0.46	NW	Q	P	80	87	13	unpubl. data
Wijnendalebos	B	CA	2003	3.6	29.4	33.0	10.9	392	425	7.8	1.55	NW	Q	P	30	130	20	unpubl. data
Wijnendalebos	B	CP	2003	12.2	10.5	22.7	53.7	406	429	5.3	1.04	NW	Q	P	30	130	20	unpubl. data
zonien kernvlakte 1991	B	CA	1991	112.5	6.6	119.1	94.5	634	753	15.8	11.71	NW	F	R	100	220	10	Van den Berge et al., 1990
zonien kernvlakte 2000	B	CA	2001	115.9	22.7	139.0	83.4	792	931	14.9	6.85	NW	F	R	100	205	20	De Keersmaeker et al., 2002
Zonien-Harras	B	LT	1996	2.4	10.2	12.6	19.0	450	467	2.7	0.96	NW	Q	R	80	179	11	unpubl. data
Neunkirch	CH	LT	1999	51.0	6.0	57.0	89.5	470	527	10.8	1.12	C	F	R			49	Christensen et al., 2005
Sihlwald	CH	CA	2000			8.0		516	524	1.5	0.60	C	F	R	650	140	10	Commarmot et al., 2005
Cahnov-Soutok	CZ	CA	1994	93.5	39.5	133.0	70.3	549	682	19.5	1.87	C	Q	R	150	130	70	Vrška et al., 2006
Jirina	CZ	CA	1999	71.0	87.0	158.0	44.9	588	746	21.2	2.36	C	Q	R	165	154	66	Vrška et al., 2006
Ranspurk	CZ	CA	1995	105.3	20.3	125.6	83.8	586	711	17.7	1.93	C	Q	R	150	156	64	Vrška et al., 2006
V kluci	CZ	CA	2000	169.0	54.0	223.0	75.8	681	904	24.7	4.70	C	F	R			47	Christensen et al., 2005
Altes Gehege	D	CP	2003			12.0		494	506	2.4	0.24	C	Q	P	60	59	41	Meyer et al., 2006

Reserve name	**country**	**survey type**	**date of recor-ding**	**Lying dead wood (m^3/ha)**	**Standing dead wood (m^3/ha)**	**Total dead wood (m^3/ha)**	**Ratio lying dead wood (%)**	**Living volume (m^3)**	**TAB (m^3)**	**ratio dead to TAB (%)**	**accumulation rate (m^3/ha.year)**	**Geographic location**	**Domi-nant tree species**	**Fertility**	**Elevation (m a.s.l.)**	**Average age (years)**	**time of non-interv-ention (years)**	**Source**
Bechtaler Wald	D	CP	1995	21.0	46.0	67.0	31.3	314	381	17.6	2.60	C	Q	R	170		25	Bücking, 1996.
Braken	D	CP	2004	8.0	9.0	17.0	47.1	425	442	3.8	1.00	C	Q	R	40	135	15	Meyer et al., 2006
Brand	D	CP	1997			30.0		530	560	5.4	1.22	C	Q	R	40	127	23	Meyer et al., 2006
Buchheide-zechlin	D	CA	2005	59.4	28.3	87.7	67.7	445	533	16.5	2.32	C	F	P	100	233	37	Rüffer, 2007
eisgraben	D	CA	1999	139.0	38.0	177.0	78.5	774	951	18.6	8.33	C	F	R	700	159	21	Kölbel, 1999
Elsbach	D	CA	1999	19.0	10.0	29.0	65.5	562	591	4.9	1.29	C	F	R	600		21	Kölbel., 1999
Fauler Ort	D	CA	2005	126.0	33.0	159.0	79.2	363	522	30.5	1.91	C	F	R	200	238	82	Rüffer, 2007
Franzhorn	D	CA	1997	14.0	31.0	45.0	31.1	529	574	7.8	1.72	C	Q	P	40	115	25	Meyer et al., 2006
Franzhorn	D	CP	1996	10.6	4.0	14.6	72.5	598	613	2.4	0.53	C	F	P	30	136	24	unpubl. data
Friedeholz	D	CA	1997	36.0	17.0	53.0	67.9	387	440	12.0	2.22	C	Q	R	45	177	23	Meyer et al., 2006
Gitschger	D	CA	1999	94.0	41.0	135.0	69.6	640	775	17.4	6.33	C	F	R	650		21	Kölbel, 1999
Gr. Freden	D	CP	2004	7.1	4.8	11.9	59.6	814	826	1.4	0.31	C	F	R	225	98	32	unpubl. data
Grosser Staufenberg	D	CA	2000	18.7	1.5	20.2	92.6	588	608	3.3	0.65	C	F	R	520	112	28	unpubl. data
Grosser Staufenberg	D	CP	1999	25.9	6.8	32.7	79.2	503	535	6.1	1.14	C	F	R	520	113	27	unpubl. data
grubenhau	D	CP	1997	47.0	22.0	69.0	68.1	604	673	10.3	2.48	C	F	R	530		27	Christensen et al., 2005
Hainich	D	CP	2002	42.0	22.0	64.0	65.6	567	631	10.1	5.17	C	F	R			12	Christensen et al., 2005
Hasbruch - altes Res.	D	CA	1994	56.1	61.9	62.0	90.5	401	463	13.4	1.30	C	Q	R	20	94	46	Meyer et al., 2006
Heilige Hallen	D	CP	1999	97.0	88.0	185.0	52.4	506	691	26.8	3.00	C	F	R	130	279	61	Tabaku and Meyer, 1999
Herrenholz	D	CA	2004	14.0	32.0	46.0	30.4	422	468	9.8	1.38	C	Q	R	46	128	32	Meyer et al., 2006
Herrenholz	D	CP	1991	13.0	25.0	38.0	34.2	486	524	7.3	1.89	C	Q	R	46	141	19	Meyer et al., 2006
Hoher Knuck	D	CA	1999	79.0	16.0	95.0	83.2	576	671	14.2	4.43	C	F	R	450		21	Kölbel, 1999
Hoxfels	D	CP	2000	10.0	46.0	56.0	17.9	360	416	13.5	1.93	C	F	R	300		28	Christensen et al., 2005
Hühnstollen	D	CA	1996	13.7	5.3	19.0	72.3	576	595	3.2	0.65	C	F	R	400	109	26	unpubl. data
Junkerwerder	D	CP	2002	16.0	17.0	33.0	48.5	428	461	7.2	1.24	C	Q	R	12	145	25	Meyer et al., 2006
Kalkberg	D	CA	1999	8.0	6.0	14.0	57.1	734	748	1.9	0.57	C	F	R	700		21	Kölbel, 1999

Reserve name	country	survey type	date of recording	Lying dead wood (m^3/ha)	Standing dead wood (m^3/ha)	Total dead wood (m^3/ha)	Ratio lying dead wood (%)	Living volume (m^3)	TAB (m^3)	ratio dead to TAB (%)	accumulation rate (m^3/ha.year)	Geographic location	Dominant tree species	Fertility	Elevation (m a.s.l.)	Average age (years)	time of non-intervention (years)	Source
Karlswörth	D	CP	1990	41.0	18.0	59.0	69.5	623	682	8.7	2.85	C	Q	R	80	160	20	Althoff et al., 1993
Kitschenthalrangen	D	CA	1999	21.0	6.0	27.0	77.8	655	682	4.0	1.19	C	F	R	450		21	Kölbel, 1999
Königsbuche	D	CA	1996	57.5	17.2	74.7	77.0	616	691	10.8	3.03	C	F	R	230	86	24	unpubl. data
Landwehr	D	CP	1996	50.7	23.7	74.4	68.1	434	509	14.6	2.41	C	Q	P	15	110	30	unpubl. data
Leitenwies	D	CA	1999	50.0	21.0	71.0	70.4	737	808	8.8	3.29	C	F	P	400		21	Kölbel, 1999
Limker Strang	D	CA	2003	15.6	5.7	21.3	73.2	500	522	4.1	0.62	C	F	P	400	119	31	unpubl. data
Limker Strang	D	CA	2003	17.1	10.4	27.6	62.1	545	572	4.8	0.82	C	F	P	400	119	31	unpubl. data
Lohn	D	CA	1996	27.9	7.3	35.2	79.2	707	742	4.7	1.38	C	F	R	70	96	24	unpubl. data
Lösershag	D	CA	1999	25.0	16.0	41.0	61.0	651	692	5.9	1.86	C	F	R	650		21	Kölbel, 1999
Lüssberg	D	CA	1996	4.9	1.5	6.4	76.4	337	343	1.9	0.18	C	F	P	130	146	24	unpubl. data
Meinsberg	D	CP	2003	16.3	4.3	20.6	79.0	815	836	2.5	0.62	C	F	R	320	105	30	unpubl. data
Meinsberg	D	CA	2002	20.5	6.4	26.9	76.2	799	826	3.3	0.86	C	F	R	320	106	29	unpubl. data
Neuenburg	D	CA	2000	163.0	46.0	209.0	78.0	488	697	30.0	3.98	C	Q	R	7	128	52	Meyer et al., 2006
Nordahner Holz	D	CA	2003	9.5	29.8	39.2	24.1	609	648	6.1	1.20	C	Q	P	6	109	31	unpubl. data
Nordahner Holz	D	CA	2003	8.6	63.6	72.2	12.0	518	591	12.2	2.27	C	Q	R	6	109	31	unpubl. data
Platzer Kuppe	D	CA	1999	105.0	49.0	154.0	68.2	638	792	19.4	7.24	C	F	R	650	159	21	Kölbel, 1999
ruppiner Schweiz	D	CA	2005	30.3	7.6	37.9	79.9	627	665	5.7	1.80	C	F	R	200	80	20	Rüffer, 2007
Schlossberg	D	CA	1999	4.0	5.0	9.0	44.4	554	563	1.6	0.33	C	F	R	600		21	Kölbel, 1999
Schneetal	D	CA	1999	13.0	2.0	15.0	86.7	655	670	2.2	0.62	C	F	R	550		21	Kölbel, 1999
Seeben	D	CA	1996	7.0	58.0	65.0	10.8	603	668	9.7	3.50	C	Q	R	530	122	18	Kölbel, 1999
Serrahn	D	CA	2002	61.0	33.0	94.0	64.9	603	697	13.5	2.19	C	F	P	100	158	42	Von Oheimb et al., 2007
Sommerberg	D	CP	1995	24.0	7.0	31.0	77.4	333	468	6.6	1.16	C	Q	R	350	145	25	Bücking, 1998
Stechpalmenwald	D	CP	2005	18.7	3.6	22.2	83.9	370	392	5.7	0.61	C	F	P	110	127	33	unpubl. data
Stöberhei	D	CA	2000	36.0	21.0	57.0	63.2	622	679	8.4	1.83	C	F	R			30	Christensen et al., 2005
Süsing	D	CP	1996	4.0	8.0	12.0	33.3	416	428	2.8	0.20	C	F	R	100	70	50	Meyer et al., 2006

Reserve name	**country**	**survey type**	**date of recor-ding**	**Lying dead wood (m^3/ha)**	**Standing dead wood (m^3/ha)**	**Total dead wood (m^3/ha)**	**Ratio lying dead wood (%)**	**Living volume (m^3)**	**TAB (m^3)**	**ratio dead to TAB (%)**	**accumulation rate (m^3/ha.year)**	**Geographic location**	**Domi-nant tree species**	**Fertility**	**Elevation (m a.s.l.)**	**Average age (years)**	**time of non-interv-ention (years)**	**Source**
swartzwihrberg	D	CA	1999	60.0	13.0	73.0	82.2	876	949	7.7	3.38	C	F	R	650		21	Kölbel, 1999
Vilm	D	CP	1997	44.0	109.0	153.0	28.8	561	714	21.4	2.48	C	F	P	5	239	61	Schmalz and Lange, 1999
Vogelherd	D	CA	1999	32.6	2.5	35.1	93.0	480	515	6.8	1.22	C	F	P	490	133	27	unpubl. data
Vogelherd	D	CP	1996	21.4	3.2	24.6	86.9	443	468	5.3	0.94	C	F	P	490	136	24	unpubl. data
Waldhaus	D	CA	1999	115.0	6.0	121.0	95.0	780	901	13.4	5.67	C	F	R	400	159	21	Kölbel, 1999
Wasserberg	D	CA	1999	4.0	8.0	12.0	33.3	518	530	2.3	0.48	C	F	R	400		21	Kölbel, 1999
Weichel	D	CP	2002	8.0	10.0	18.0	44.4	514	532	3.4	1.00	C	F	P	30	124	16	Meyer et al., 2006
Weiherbuchet	D	CA	1999	20.0	6.0	26.0	76.9	646	672	3.9	1.14	C	F	R	600		21	Kölbel, 1999
Fauler Ort	D	CA	1968	53.0	14.0	67.0	79.1	335	402	16.7	1.44	C	F	R	200	235	45	Rüffer, 2007
Knagerne	DK	LT	2003	56.0	31.0	87.0	64.4	449	536	16.2	6.54	NW	F	P	80	237	13	Christensen et al., 2005
Moens klinteskoven	DK	LT	2001	48.0	24.0	72.0	66.7	201	273	26.4	1.06	NW	F	R	90	134	66	Christensen et al., 2005
Stroedam	DK	LT	1983	101.0	38.0	139.0	72.7	490	629	22.1	4.03	NW	F	R	20	166	34	Christensen et al., 2005
Suserup Skov	DK	LT	2002	154.0	9.0	163.0	94.5	674	837	19.5	2.15	NW	F	R	20	155	75	Christensen et al., 2005
Velling	DK	LT	2001	68.0	31.0	99.0	68.7	489	588	16.8	8.82	NW	F	P	75	264	11	Christensen et al., 2005
Fontainebleau	F	CA	2000	165.0	55.0	220.0	75.0	260	480	45.8	1.48	NW	F	R	130	33	147	Christensen et al., 2005
La Massane	F	CA	1998	25.0	8.0	33.0	75.8				1.24	NW	F	R			25	Christensen et al., 2005
Alsohegy	HU	LT	2001	23.0	17.0	40.0	57.5	284	324	12.3	0.62	C	F	R			61	Christensen et al., 2005
Kékes	HU	LT	2001	92.0	14.0	106.0	86.8	454	560	18.9	1.03	C	F	R	700	49	101	Christensen et al., 2005
Öserdö	HU	LT	2001	152.0	23.0	175.0	86.9	765	940	18.6	4.22	C	F	R	700	159	41	Christensen et al., 2005
Dassenberg	NL	LT	2000	43.0	18.0	61.0	70.5	402	463	13.2	5.90	NW	F	R		140	10	Christensen et al., 2005
Gortel	NL	LT	2000	56.0	8.0	64.0	87.5	507	571	11.2	6.20	NW	F	R		140	10	Christensen et al., 2005
Pijpebrandje	NL	LT	2000	32.0	11.0	43.0	74.4	457	500	8.6	1.64	NW	F	R	50	125	25	Christensen et al., 2005
Vijlenerbos	NL	CP	1996			34.8		304	338	10.3	2.52	NW	F	P	250	107	13	Mountford, 2004
Bieszczady	PL	CA	2000	148.0	34.0	182.0	81.3	596	778	23.4	6.67	C	F	R			27	Christensen et al., 2005
Las lipowy Obroż.KV1	PL	CA	2000	32.5	17.5	50.0	65.0	768	818	6.1	0.59	C	Q	R	550	99	81	Jaworski et al., 2005

Reserve name	**country**	**survey type**	**date of recording**	**Lying dead wood (m^3/ha)**	**Standing dead wood (m^3/ha)**	**Total dead wood (m^3/ha)**	**Ratio lying dead wood (%)**	**Living volume (m^3)**	**TAB (m^3)**	**ratio dead to TAB (%)**	**accumulation rate (m^3/ha.year)**	**Geographic location**	**Dominant tree species**	**Fertility**	**Elevation (m a.s.l.)**	**Average age (years)**	**time of non-intervention (years)**	**Source**
Las lipowy Obroż.KV2	PL	CA	2000	50.0	9.0	59.0	84.7	860	919	6.4	0.70	C	Q	R	550	99	81	Jaworski et al., 2005
Las lipowy Obroż.KV3	PL	CA	2000	48.0	9.0	57.0	84.2	761	818	7.0	0.68	C	Q	R	550	99	81	Jaworski et al., 2005
Clairinsh	UK	LT	2000	7.0	12.0	19.0	36.8				0.20	NW	Q	P	10	3	87	Mountford, 2004
Dendles wood	uk	LT	2000	62.0	66.0	128.0	48.4				3.60	NW	F	p	50	115	35	Mountford, 2004
Denny Encl.- Nw Frst	UK	LT	1996	195.0	78.0	273.0	71.4				2.15	NW	F	P	30	124	126	Christensen et al., 2005
Lady Park Wood- OG	UK	LT	1995	67.5	25.5	93.0	72.6				1.01	NW	F	R	50	50	90	Green and Peterken, 1997
Langley wood	UK	LT	1996	15.0	9.0	24.0	62.5				0.39	NW	Q	R	50	24	56	Mountford et al., 1998
Monks Wood	UK	LT	1998	25.0	9.2	37.0	67.6	160	197	18.8	0.45	NW	Q	R	30	12	78	Mountford, 2004
Noar Hill Hanger	UK	CA/LT	2001	300.0	40.0	340.0	88.2	113	453	75.0	16.79	NW	F	R	200	106	14	Christensen et al., 2005
Ridge Hanger	UK	CA/LT	2001	264.0	1.0	265.0	99.6	66	331	80.0	18.79	NW	F	R	200	121	14	Christensen et al., 2005
Scords wood	UK	CA	1998	456.0	30.0	486.0	93.8	50	536	90.7	7.12	NW	F	P	220	52	68	Christensen et al., 2005
The Mens	UK	LT	1998	88.0		115.0	76.5				4.04	NW	F	R	35	142	28	Mountford, 2004

Annex 2. Basic dendrometric data for the forest stands at the study site and the comparison sites of chapter 3 (very large trees)

Basic dendrometric data for the forest stands at the study site and the comparison sites at the different survey times - N_{10} and N_{30} = stem number (trees ha^{-1}) applying threshold diameter of 10 and 30 cm resp.; G_{10} and G_{30}: basal area (m².ha^{-1}) applying threshold diameter of 10 and 30 cm resp; V_{10} and V_{30}: living stock (m³.ha^{-1}) applying the same threshold diameter of 10 and 30 cm resp.; dead wood amounts include both standing and lying dead wood (threshold diameter of 10 cm). NA: not available (no measurements for this threshold)

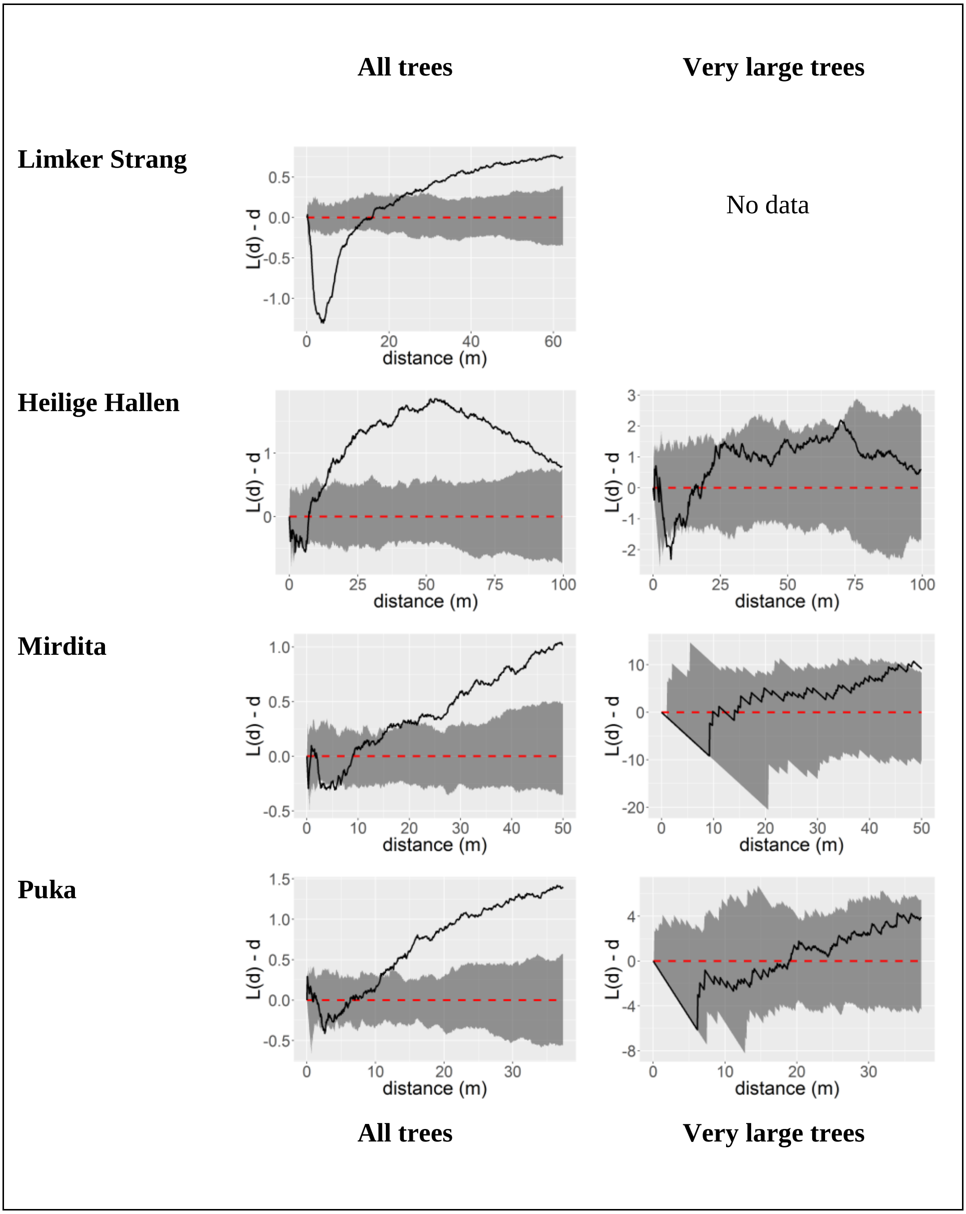
Site - year	**Tree species**	**N_{10}**	**N_{30}**	**G_{10}**	**G_{30}**	**V_{10}**	**V_{30}**	**V_d**
Kersselaerspleyn	*Fagus sylvatica*	NA	49.5	NA	27.2	NA	611.0	26.1
1986	*Quercus robur*	NA	2.9	NA	1.2	NA	23.2	2.5
		NA	**52.4**	NA	**28.4**	**NA**	**634.2**	**28.6**
Kersselaerspleyn	*Fagus sylvatica*	102.9	50.5	28.9	27.6	644.4	632.0	112.2
2001	*Quercus robur*	2.5	2.5	1.3	1.3	24.2	24.2	3.5
		105.4	**53.1**	**30.2**	**28.9**	**668.6**	**656.2**	**115.7**
Kersselaerspleyn	*Fagus sylvatica*	204.7	60.5	33.5	30.0	713.1	680.5	105.2
2011	*Quercus robur*	2.4	2.4	1.6	1.3	27.5	27.5	3.5
		207.1	**63.2**	**35.3**	**31.3**	**740.6**	**708.0**	**108.7**
Razula 1972	*Fagus sylvatica*	67.0	60.7	14.23	14.06	289.5	287.6	32.8
	Abies alba	31.0	30.6	10.8	10.8	208.0	207.8	84.8
	Picea abies	3.4	2.5	1.1	1.07	17.9	17.7	1.6
		101.4	**93.8**	**26.1**	**25.9**	**515.4**	**513.1**	**119.1**
Razula 1995	*Fagus sylvatica*	79.3	53.2	20.2	19.2	441.5	428.5	52.6
	Abies alba	12.3	12.2	6.4	6.4	133.5	132.8	171.8
	Picea abies	2.9	2.4	1.2	1.2	20.4	20.3	5.5
		94.5	**67.8**	**27.9**	**26.8**	**595.4**	**581.6**	**229.9**
Razula 2009	*Fagus sylvatica*	453.4	56.2	27.9	19.9	461.8	382.4	85.5
	Abies alba	9.3	9.1	5.9	5.9	104.7	104.6	140.5
	Picea abies	3.1	2.1	1.4	1.3	20.9	20.6	5.2
		465.8	**67.4**	**35.1**	**27.0**	**587.4**	**507.7**	**231.2**
Salajka 1974	*Fagus sylvatica*	74.5	49.0	10.4	9.8	172.4	167.7	21.4
	Abies alba	58.3	39.6	15.3	14.9	265.9	261.9	151.4
	Picea abies	5.5	4.1	1.4	1.4	19.9	19.6	8.4
	Acer pseudopl.	1.8	0.5	0.1	0.1	1.4	1.2	0.1
		140.1	**93.2**	**27.2**	**26.2**	**459.6**	**450.3**	**181.3**
Salajka 1994	*Fagus sylvatica*	94.8	56.8	17.0	15.3	297.5	279.6	39.6
	Abies alba	27.1	20.3	7.6	7.3	137.5	133.6	308.6
	Picea abies	4.8	3.9	1.5	1.4	20.5	20.0	16.0

	Acer pseudopl.	2.4	1.7	0.3	0.2	4.4	4.0	0.4
		129.1	**82.7**	**26.3**	**24.3**	**459.9**	**437.2**	**364.6**

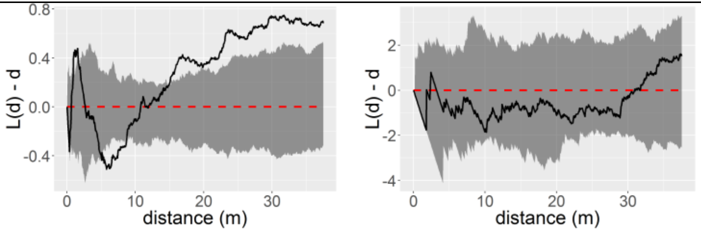
Site - year	**Tree species**	**N_{10}**	**N_{30}**	**G_{10}**	**G_{30}**	**V_{10}**	**V_{30}**	**V_d**
Salajka 2007	*Fagus sylvatica*	386.2	69.5	24.8	17.9	398.4	325.9	40.8
	Abies alba	24.9	20	7.4	7.2	125.3	123.1	240.5
	Picea abies	4.7	3.9	1.6	1.6	23.5	23.1	15.0
	Acer pseudopl.	3.7	2.2	0.4	0.4	5.5	5.0	0.0
		419.5	**95.6**	**34.2**	**27.0**	**552.7**	**477.2**	**296.3**
Žofín 1975	*Fagus sylvatica*	162.4	87.8	25.1	23.6	451.1	438.9	48.5
	Abies alba	9.0	8.9	4.4	4.4	72.9	72.9	23.9
	Picea abies	21.8	19.9	6.9	6.9	103.4	102.9	31.6
	Acer pseudopl.	0.7	0.5	0.1	0.1	3.1	3.1	0
		193.9	**117.1**	**36.6**	**35.0**	**630.4**	**617.7**	**104.1**
Žofín 1997	*Fagus sylvatica*	177.0	83.0	28.7	26.3	535.8	512.3	85.9
	Abies alba	2.7	2.6	1.5	1.5	26.4	26.4	54.8
	Picea abies	18.5	14.6	6.5	6.4	98.22	97.18	55.9
	Acer pseudopl.	0.5	0.3	0.1	0.1	1.9	1.9	2.9
		198.7	**100.5**	**36.8**	**34.3**	**662.3**	**637.8**	**199.5**
Žofín 2008	*Fagus sylvatica*	174.5	80	28.8	26.4	525.1	502.1	140.5
	Abies alba	0.8	0.8	0.3	0.3	5.0	5.0	36.9
	Picea abies	12.3	8.3	3.6	3.5	54.4	53.4	81.9
	Acer pseudopl.	0.5	0.3	0.1	0.1	1.9	1.8	2.5
		188.1	**89.4**	**32.9**	**30.4**	**586.4**	**562.4**	**261.8**
Mirdita	*Fagus sylvatica*	288.0	176.2	36.9	33.7	557.6	523.0	52.8
	Acer pseudopl.	1.0	0.8	0.1	0.1	1.5	1.4	0.0
		289.0	**177.0**	**37.0**	**33.8**	**559.1**	**524.4**	**52.8**
Puka	*Fagus sylvatica*	279.4	162.9	44.0	40.7	759.9	730.5	51.1
	Abies alba	3.8	3.3	1.2	1.2	16.8	16.2	10.4
		283.2	**166.2**	**45.2**	**41.9**	**776.6**	**746.7**	**61.5**
Rajka	*Fagus sylvatica*	280.8	138.3	42.8	39.7	804.0	775.3	65.4
	Abies alba	1.0	0.2	0.1	0.0	0.4	0.2	0.0
	Acer pseudopl.	1.0	0.5	0.1	0.1	1.5	1.4	0.0
		282.8	**139.0**	**42.9**	**39.8**	**805.9**	**776.9**	**65.4**
Heilige Hallen	*Fagus sylvatica*	**NA**	**59.9**	**NA**	**24.3**	**NA**	**482.2**	**182.6**
Limker Strang	*Fagus sylvatica*	163.0	133.7	30.1	28.9	514.3	499.7	13.4
	Quercus robur	0.6	0.6	0.1	0.1	2.0	2.0	0.0
	Picea abies	0.1	0.1	0.1	0.1	1.0	1.0	1.6
		163.7	**134.5**	**30.3**	**29.1**	**517.3**	**502.7**	**15.0**

Annex 3. Ripley’s L functions for comparison sites (chapter 3)

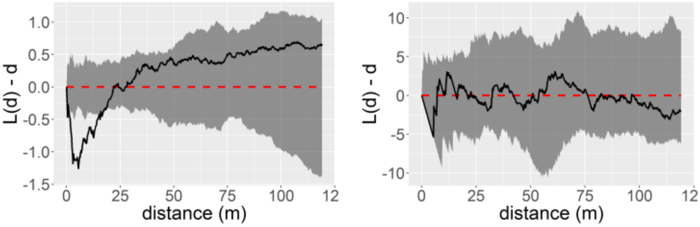
Ripley’s L for all trees (diameter at breast height ≥ 30 cm) and the very large trees (DBH ≥ 80 cm) at the comparison sites of chapter 2. The grey zone is the p = 0.05 confidence interval around the red dotted 0 line (random pattern. Values < 0 indicate a regular pattern; values > 0 a clustered pattern.



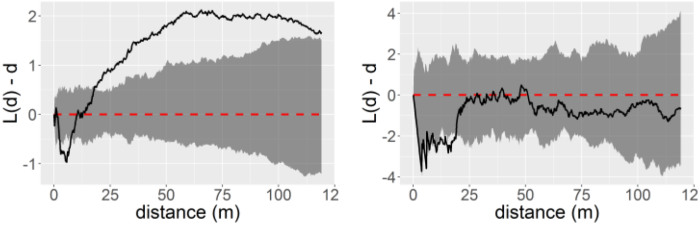
Rajca



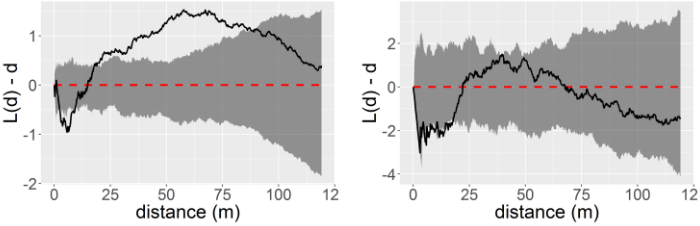
Razula - 1972



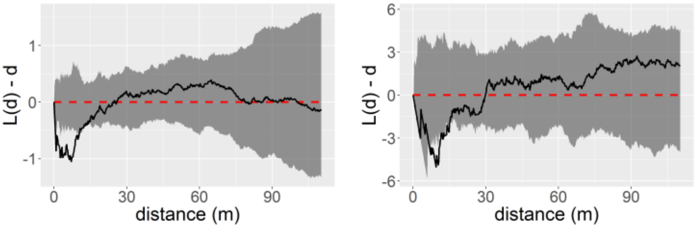
Razula - 1995

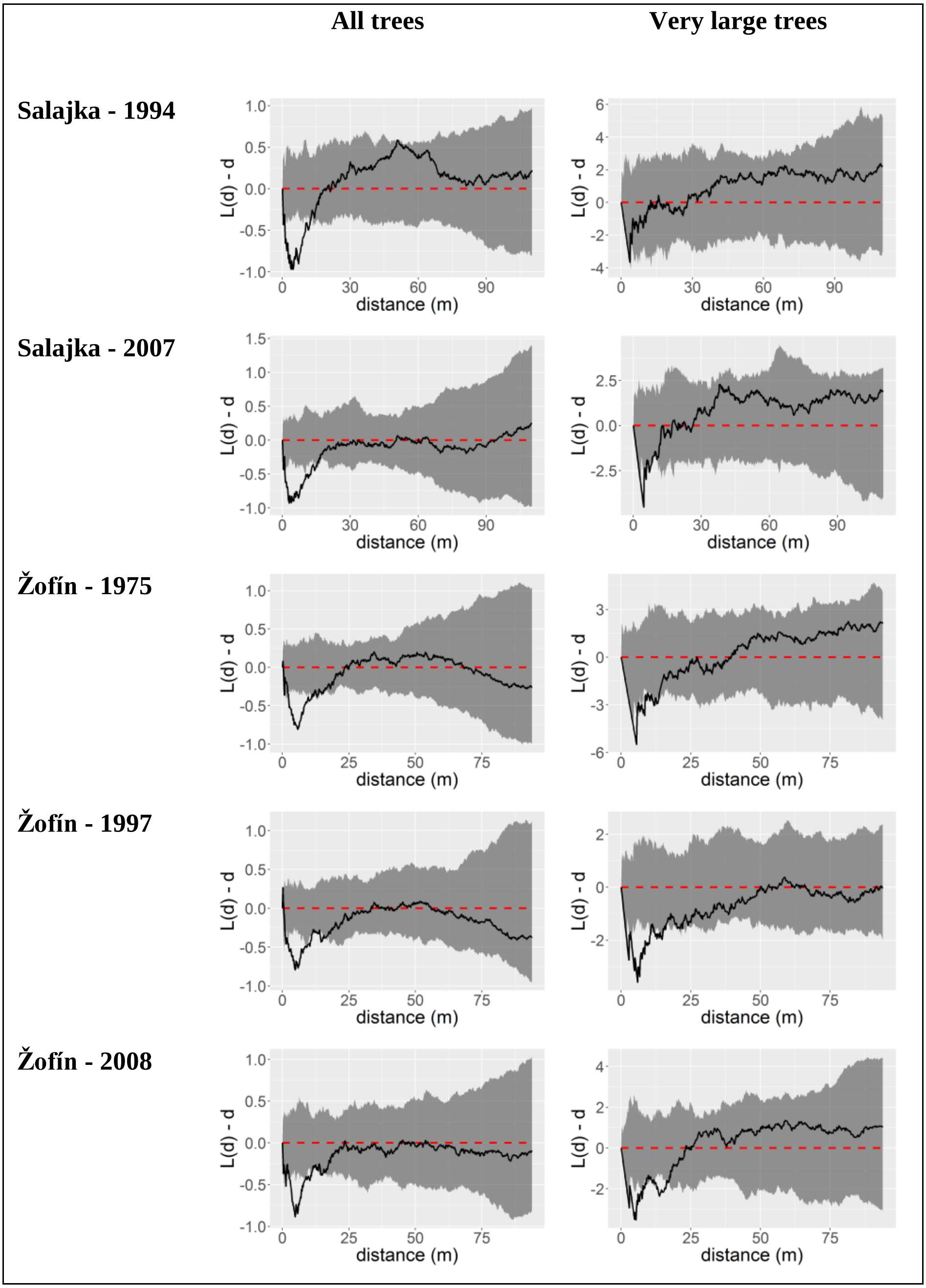


Razula - 2009



Salajka - 1974




All trees
Very large trees
Salajka - 1994
Salajka - 2007
Žofín - 1975
Žofín - 1997
Žofín - 2008
L(d) - d
distance (m)
1.0
0.5
0.0
-0.5
-1.0
1.5
6
4
2
0
-2
-4
2.5
0.0
-2.5
3
0
-3
-6
0
30
60
90
0
25
50
75

Annex 4. Conversion table of Londo-scale cover classes to percentage values

Annotation Londo-scale	% cover	Median value (%)
.1	<1	0.5
.2	1-3	2
.4	3-5	4
1-	5-10	8
1+	10-15	13
2	15-25	20
3	25-35	30
4	35-45	40
5	45-55	50
6	55-65	60
7	65-75	70
8	75-85	80
9	85-95	90
10	95-100	98

Annex 5. Detailed description of canopy variables, soil data and dendrometric data of the sites of Chapter 4.

The analysis of soil and canopy variables taken at the first survey in the four reserves are given in table A1. Significant differences appear between Everzwijnbad and the other three sites for sand-fraction, organic matter content and CEC. These are explained by anomalies in the sampling of site E, where A0 and A1-horizon were sampled and analysed separately, with the reported values being the weighted average between these values. This results in aberrant values that don't reflect real differences, or differences that are not ecologically relevant to the recorded vegetation changes (see below). For nitrogen content, there is a limited but significant gradient from E & P, over J to T. On soil pH, all sites are very similar, with slightly (but not significant) higher values for T. On canopy variables Combined Canopy Cover (CCC) at first survey we registered high values for all sites, with no significant differences between the four sites; for basal area (BA), some differences were significant (with T significantly higher) but all sites showed high values. On Litter Quality (LQ) E, P and J are very comparable, and T has a significantly higher score, due to lower shares of oak and beech, and important shares of poplar. Original data on canopy variables, soil data and dendrometric data for the 183 plots are included in the table A2 below.

Table A1: Soil and canopy variables per forest reserve recorded at the first survey; a, b, c: indicate significant differences between forest reserves based on Tukey test with adjusted Bonferroni p-value (0.05/6). Sand(%) = share of sand fraction (particles > 50 µm) in mass-% of mineral soil – OM(%) = weight % of organic matter in the soil; CEC=Cation Exchange Capacity (cmolc.kg-1) using the BaCl2 method – KJ-N(%) = total available Nitrogen using the Kjeldahl-method; LQ = Litter Quality score – BA = Basal Area ($m^2.ha^{-1}$); VOL = living volume ($m^3.ha^{-1}$); Vol-d = dead volume ($m^3.ha^{-1}$); TAB = Total Aboveground Biomass ($m^3.ha^{-1}$); -1 = first survey; -2 = second survey

	Anova p-value	Mean value			
	Forest reserve	Everzwijnbad	Jansheideberg	Pruikenmakers	Terrijst
Sand (%)	2.72e-11***	19.1^{a}	10.3^{b}	9.4^{b}	7.7^{b}
OM (%)	<2e-16 ***	4.2^{a}	12.4^{b}	10.7^{b}	12.3^{b}
CEC	<2e-16 ***	20.93^{b}	9.96^{a}	8.79^{a}	8.92^{a}
pH-$CaCl_2$	0.522 NS	3.37	3.36	3.37	3.50
Kj-N (%)	1.37e-05***	0.28^{a}	0.36^{b,c}	0.31^{a,b}	0.38^{c}
Cover (%)	0.336 NS	88.9.	89.8	88.2	89.4
Basal Area	1.51e-07 ***	33.0^{a}	34.6^{a,b}	30.3^{a}	37.0^{b}
LQ	<2e-16 ***	1.01^{a}	1.07^{a}	1.12^{a}	1.94^{b}

Table A.2. Detailed site parameters for the individual sample plots. Site codes see Table 4.1 - Sand(%) = share of sand fraction (particles > 50 µm) in mass-% of mineral soil – Kj-N(%) = total available nitrogen using the Kjeldahl-method - OM(%) = weight % of organic matter in the soil – P Plant (ppm): plant available phosphor in mg per kg soil (dry weight) - CEC.$_{\text{BaCl2}}$=Cation Exchange Capacity (cmol$_c$.kg-1) using the BaCl$_2$ method – LQ = Litter Quality score – BA = Basal Area (m².ha^{-1}; VOL = living volume (m³.ha^{-1}); Vol-d = dead volume (m³.ha^{-1}); TAB = Total Aboveground Biomass (m³.ha^{-1}); -1 = first survey; -2 = second survey

Site	IDPlot	Sand(%)	pH CaCl$_2$	Kj-N (%)	OM(%)	P.Plant (ppm)	CEC.BaCl$_2$	LQ-1	Cover-1	BA-1	VOL-1	Vol-d-1	TAB-1	LQ-2	Cover-2	BA-2	VOL-2	Vol-d-2	TAB-2
E	101	20.2	3.18	0.39	5.9	31.5	18.0	1.22	94.0	39.8	579.4	1.9	581.3	1.23	93.0	43.4	655.4	6.9	662.2
E	102	26.2	3.17	0.61	9.7	50.9	26.8	1.55	76.0	29.5	398.9	1.9	400.8	2.40	90.8	35.5	482.1	14.1	496.1
E	103	2.2	3.24	0.38	6.1	22.5	11.0	1.24	91.0	30.6	371.8	3.5	375.3	1.27	82.0	27.6	328.6	97.1	425.7
E	104	17	3.33	0.35	5.5	25.8	15.3	1.02	85.0	34.6	498.0	1.9	499.9	1.29	95.0	34.5	543.3	9.2	552.5
E	105	20.2	3.45	0.24	3	23.9	21.8	0.69	68.0	30.8	428.5	1.9	430.4	0.84	82.0	32.5	493.2	10.3	503.5
E	106	19.7	3.28	0.33	5.2	54.4	37.0	1.79	93.0	21.8	295.6	4.0	299.7	1.77	93.0	25.9	363.2	11.9	375.1
E	107	19.3	3.3	0.38	5.7	24.4	18.2	1.18	96.0	27.8	482.7	4.1	486.8	1.23	94.0	30.1	518.8	25.5	544.3
E	108	17.8	3.32	0.28	3.5	54.4	25.0	1.43	96.0	28.1	399.4	1.9	401.4	1.04	82.0	30.3	464.9	5.6	470.5
E	109	17.6	3.43	0.31	3.9	35.2	19.7	1.40	91.0	25.1	362.1	3.6	365.7	1.90	91.3	31.0	431.2	6.6	437.9
E	110	13.5	3.45	0.36	4.6	16.1	29.6	1.61	91.3	42.0	608.5	6.9	615.4	1.33	92.0	36.9	586.9	37.3	624.2
E	111	21	3.35	0.21	3.4	57.2	21.0	0.90	90.2	33.6	435.3	1.9	437.2	0.98	98.1	37.5	501.6	18.8	520.3
E	113	20.1	3.53	0.38	5.2	7.7	17.6	0.94	88.0	34.2	374.9	101.5	476.4	1.45	93.0	45.5	529.7	82.9	612.6
E	114	14	3.38	0.2	2.4	9.5	9.1	0.30	92.0	23.6	357.1	1.9	359.0	1.48	91.3	25.1	312.9	14.6	327.5
E	115	16.8	3.62	0.23	2.7	9.6	15.3	1.60	82.6	36.3	496.2	3.1	499.3	1.84	90.2	42.8	578.9	23.5	602.5
E	116	23.2	3.5	0.27	4	12.2	23.1	1.34	94.0	26.9	319.7	8.0	327.7	1.62	94.0	36.4	436.9	21.9	458.7
E	117	16.5	3.42	0.26	3.5	10.7	16.7	1.39	97.0	32.4	443.1	2.5	445.6	1.46	93.0	35.7	500.4	6.2	506.6
E	118	18	3.31	0.3	4.5	8.8	18.9	1.17	86.0	39.1	569.6	1.9	571.6	1.34	93.0	41.3	630.5	2.8	633.2
E	119	18.6	3.58	0.21	2.7	15.9	17.7	2.14	88.0	36.8	445.9	4.3	450.2	2.45	93.0	42.2	534.3	12.5	546.8
E	120	18.9	3.42	0.26	3.6	52.9	19.2	1.46	88.0	33.1	444.4	1.9	446.3	1.11	68.0	39.5	556.2	21.2	577.4
E	121	19.7	3.29	0.23	3.7	24.7	23.5	0.90	86.0	34.6	488.7	3.3	492.0	1.01	90.8	36.6	540.1	13.9	554.0
E	122	21.4	3.33	0.26	4.4	13.9	19.8	0.76	75.0	34.7	505.4	1.9	507.3	1.64	98.3	38.7	580.9	3.9	584.9
E	123	19.6	3.39	0.36	4.9	18.7	19.9	1.59	86.0	32.2	458.9	1.9	460.8	1.88	92.0	30.5	450.1	48.9	499.0

Site	IDPlot	Sand(%)	pH $_{CaCl_2}$	Kj-N (%)	OM(%)	P.Plant (ppm)	CEC.B $_{aCl_2}$	LQ-1	Cover-1	BA-1	VOL-1	Vol-d-1	TAB-1	LQ-2	Cover-2	BA-2	VOL-2	Vol-d-2	TAB-2
E	124	17.7	3.2	0.36	5.6	68.5	18.6	1.21	84.0	39.9	567.1	1.9	569.0	1.18	79.0	28.9	392.7	193.8	586.6
E	125	7.8	3.16	0.35	5.4	35.4	17.0	1.08	92.0	31.7	513.0	1.9	514.9	0.85	76.0	36.4	602.0	4.5	606.5
E	126	29.2	3.16	0.32	6.6	9.3	18.9	0.90	90.1	42.7	551.3	2.8	554.2	0.98	98.0	45.8	626.7	5.2	631.9
E	127	17.8	3.68	0.26	3.7	0.3	28.4	0.45	93.0	32.5	427.0	2.0	429.0	1.39	96.0	37.9	503.3	6.1	509.4
E	128	3.1	3.41	0.25	3.6	23.7	19.1	1.05	86.0	35.3	391.6	3.4	395.1	1.05	86.0	41.1	478.5	4.5	483.0
E	129	18.9	3.4	0.25	3.7	16.0	14.5	1.01	90.4	29.8	377.9	1.9	379.8	1.15	98.1	28.0	385.6	23.6	409.2
E	130	39.5	3.27	0.16	2.1	5.6	7.4	1.02	90.2	28.8	362.3	1.9	364.2	1.08	98.0	37.6	521.1	1.8	522.9
E	131	19.4	3.35	0.23	3.1	-	14.7	1.20	92.0	37.5	483.9	3.2	487.1	1.27	95.0	38.8	533.4	23.6	556.9
E	132	41	3.58	0.3	5	7.6	23.5	1.24	73.9	32.6	547.8	1.9	549.7	1.76	98.4	37.3	634.6	11.8	646.4
E	133	26.1	3.39	0.17	3.4	15.7	28.6	0.90	92.0	37.8	776.6	1.9	778.5	0.98	98.3	41.1	871.9	12.8	884.6
E	134	5.8	3.35	0.27	4	8.3	21.7	1.06	90.0	23.7	246.7	1.9	248.6	1.24	95.0	24.2	275.8	29.6	305.5
E	135	23.6	3.23	0.32	5.5	55.2	21.6	1.16	90.2	47.9	682.9	4.0	686.9	1.28	98.0	49.6	737.4	6.4	743.9
E	136	19.1	3.4	0.27	3.8	55.2	22.9	1.44	88.0	37.0	529.1	3.5	532.7	1.49	84.0	41.3	602.2	11.9	614.1
E	137	21.8	3.43	0.22	3.2	7.8	22.5	1.06	97.0	32.4	401.6	1.9	403.5	1.06	96.0	35.6	464.9	46.2	511.0
E	138	18.5	3.23	0.32	4.9	62.9	28.7	1.15	88.0	41.9	672.8	1.9	674.7	1.03	84.0	41.2	700.0	15.2	715.2
E	139	19.5	3.48	0.28	3.9	28.5	23.7	2.16	88.0	19.1	201.9	2.2	204.2	2.37	92.0	25.2	274.2	8.7	283.0
E	140	13.9	3.38	0.28	3.9	24.4	20.6	1.01	97.0	40.7	694.5	2.3	696.8	0.88	92.0	45.0	785.9	23.5	809.4
E	141	15.2	3.5	0.2	3.2	18.4	20.3	1.20	96.0	35.1	404.4	9.0	413.4	1.16	92.0	39.0	471.7	10.5	482.2
E	142	20.4	3.22	0.29	4.7	17.0	21.0	0.92	79.0	42.5	465.0	1.9	466.9	1.08	93.0	39.8	462.7	14.9	477.6
E	143	21.2	3.42	0.22	3.4	27.8	19.7	0.90	92.0	39.0	586.2	3.9	590.1	0.98	98.0	45.8	723.0	11.1	734.1
E	144	21.8	3.28	0.23	3.5	13.3	17.7	1.01	80.0	24.9	303.1	1.9	305.0	1.59	94.0	26.2	336.9	9.6	346.5
E	145	25.5	3.36	0.29	4.3	26.1	25.5	1.09	94.0	33.9	374.5	1.9	376.4	1.10	93.0	35.2	421.5	23.7	445.2
E	146	4.4	3.52	0.22	2.9	21.5	22.4	1.90	96.0	30.1	352.2	21.8	374.0	1.39	76.0	28.7	355.6	45.1	400.7
E	147	21.3	3.51	0.19	2.8	7.2	30.3	0.30	93.0	17.3	253.2	1.9	255.1	0.95	93.0	20.0	259.5	7.2	266.7
E	148	22.8	3.44	0.23	3.8	16.1	30.4	0.90	90.2	29.7	372.4	1.9	374.3	0.98	98.0	29.2	383.2	6.6	389.8
J	801	10.6	3.18	0.33	10.7	20.7	9.1	1.04	98.0	41.2	653.4	0.0	653.4	1.04	98.0	43.0	731.9	4.4	736.3
J	802	11.1	3.2	0.31	11.4	10.9	11.0	0.90	90.1	37.0	559.2	0.0	559.2	0.98	98.0	39.8	643.8	4.2	648.0
J	803	5.6	3.14	0.38	12.1	23.7	8.8	1.22	98.0	34.6	535.6	16.5	552.1	1.23	98.4	37.9	628.0	17.3	645.3

Site	IDPlot	Sand(%)	pH CaCl$_2$	Kj-N (%)	OM(%)	P.Plant (ppm)	CEC.BaCl$_2$	LQ-1	Cover-1	BA-1	VOL-1	Vol-d-1	TAB-1	LQ-2	Cover-2	BA-2	VOL-2	Vol-d-2	TAB-2
J	804	0	3.36	0.39	13.7	8.3	6.3	1.05	90.2	42.2	610.7	0.0	610.7	1.17	98.1	42.6	699.0	10.3	709.3
J	805	10.5	2.98	0.5	16.2	32.0	7.1	1.01	93.0	35.2	403.7	8.8	412.4	1.03	92.0	36.6	499.1	16.9	516.0
J	806	11.1	3.31	0.23	8.2	11.8	6.3	0.98	98.0	33.1	470.8	1.7	472.5	0.98	98.2	32.9	569.7	0.9	570.6
J	807	12.9	3.36	0.38	12.1	52.8	6.7	1.35	86.0	30.2	361.3	22.4	383.7	1.68	98.6	36.0	463.1	10.3	473.3
J	808	2.4	3.09	0.39	13.1	56.8	9.6	1.21	94.0	36.0	395.7	5.1	400.8	1.25	93.0	40.0	495.2	27.5	522.7
J	809	1.9	3.13	0.34	11.4	52.2	9.1	0.89	91.0	32.5	367.7	19.6	387.3	1.18	96.0	37.6	530.3	43.1	573.3
J	810	11	3.29	0.31	10.5	7.1	7.5	1.02	82.6	31.1	334.8	3.2	338.0	1.34	98.2	31.1	317.7	20.1	337.8
J	811	5.8	3.21	0.51	15	65.1	8.8	0.87	65.0	35.4	389.4	0.1	389.5	2.01	79.0	38.2	443.3	25.3	468.6
J	812	12.6	3.46	0.36	13	37.9	9.5	1.07	92.0	46.1	495.6	7.2	502.8	1.51	90.0	46.5	550.3	10.6	560.9
J	813	11.7	3.04	0.45	14.6	43.7	6.2	1.18	84.0	24.3	273.6	16.2	289.8	1.31	93.0	28.4	352.7	5.3	358.0
J	814	14.6	3.4	0.46	15.6	53.4	7.3	2.10	73.9	27.0	316.5	4.9	321.4	2.40	84.0	19.8	283.4	36.4	319.9
J	815	11	3.12	0.39	13.4	25.6	8.9	1.38	93.0	43.2	468.4	5.2	473.6	1.46	94.0	39.3	474.1	28.8	502.9
J	816	12.4	3.12	0.34	13.9	4.6	6.8	1.30	84.0	46.5	554.6	4.6	559.3	1.54	95.0	50.1	669.0	8.1	677.1
J	817	9.5	3.03	0.5	16.8	199.3	13.9	1.46	88.0	30.4	357.4	0.2	357.6	1.92	98.4	31.8	399.6	1.5	401.1
J	818	1.4	3.38	0.28	10	16.5	7.4	1.19	71.2	29.8	378.5	4.0	382.4	1.34	90.8	26.4	385.2	11.1	396.4
J	819	12.3	3.33	0.36	13.3	4.7	7.0	1.68	82.0	35.5	400.5	27.3	427.8	1.93	84.0	35.5	424.4	24.7	449.1
J	820	8.7	3.07	0.46	15.3	57.9	9.8	1.14	88.0	28.6	319.6	5.6	325.3	1.51	91.3	31.4	387.4	19.2	406.6
J	821	1.8	3.3	0.34	11.9	4.5	10.0	1.18	80.4	25.3	316.6	0.7	317.3	1.24	96.0	23.1	294.8	2.9	297.7
J	822	11.3	3.19	0.38	12.3	27.8	11.2	1.39	96.0	38.4	425.0	6.9	431.9	1.48	94.0	38.3	473.0	14.8	487.8
J	823	13.7	3.31	0.22	9.3	2.6	7.0	0.98	98.0	45.3	654.7	4.9	659.6	0.98	98.0	56.1	800.9	6.6	807.4
J	824	5.3	3.15	0.37	11.8	17.9	4.9	1.65	99.0	31.9	324.1	11.8	335.9	1.81	98.4	37.1	440.0	11.8	451.9
J	825	2.6	3.55	0.29	10.6	50.3	5.6	1.64	79.0	27.2	356.1	4.5	360.6	1.58	76.0	33.1	485.1	4.2	489.3
J	826	15.2	3.23	0.25	10.9	4.9	6.8	0.98	98.0	39.0	552.4	0.9	553.3	0.98	98.0	41.0	670.4	28.9	699.3
J	827	13.1	3.69	0.27	8	5.9	10.0	2.05	95.0	33.5	399.4	7.0	406.3	1.97	98.1	35.7	419.1	12.4	431.5
J	828	11.7	3.17	0.22	9.6	23.2	6.9	0.98	98.0	32.0	456.9	19.8	476.7	0.98	98.0	36.6	566.4	21.7	588.1
J	829	29.9	7.02	0.81	22.6	90.7	68.8	1.70	94.0	29.7	306.2	20.9	327.1	1.57	86.0	30.6	375.3	36.8	412.1
J	830	14.3	3.24	0.23	9.2	2.5	6.7	0.98	99.6	40.3	560.6	9.0	569.6	0.90	90.1	37.4	594.2	44.3	638.6
J	831	16.6	3.2	0.27	11.7	2.2	8.6	0.98	98.0	29.7	495.3	2.9	498.3	0.98	98.0	34.6	509.2	9.7	518.9

Site	IDPlot	Sand(%)	pH $CaCl_2$	Kj-N (%)	OM(%)	P.Plant (ppm)	CEC.$BaCl_2$	LQ-1	Cover-1	BA-1	VOL-1	Vol-d-1	TAB-1	LQ-2	Cover-2	BA-2	VOL-2	Vol-d-2	TAB-2
J	832	18	3.36	0.17	9.6	38.8	5.2	1.05	98.0	37.4	541.6	2.6	544.1	1.06	98.0	36.0	601.8	12.9	614.7
T	841	4	3.42	0.37	12.9	12.7	9.7	2.28	86.0	20.2	182.9	0.0	182.9	2.58	90.4	28.0	293.4	2.6	296.0
T	842	18.5	3.36	0.32	11.2	9.0	7.4	1.06	76.0	29.3	448.8	17.0	465.8	2.40	92.0	37.1	570.5	1.8	572.3
T	843	2.2	3.29	0.27	9.3	6.5	9.4	1.81	98.0	27.8	308.2	28.4	336.6	1.98	98.0	36.7	456.4	20.7	477.1
T	844	4.1	3.83	0.49	17	9.4	11.4	1.52	71.2	28.0	359.5	6.8	366.4	1.93	98.2	25.0	346.7	8.7	355.4
T	845	17.4	5.27	0.19	7.1	52.1	11.3	1.59	98.0	21.5	218.2	28.2	246.4	1.40	80.4	26.5	310.7	15.1	325.8
T	846	2.1	3.23	0.34	11.3	2.6	8.3	1.61	98.0	36.6	417.4	27.0	444.5	1.49	98.0	36.6	435.0	28.3	463.3
T	847	2.5	4	0.26	8	1.7	8.0	2.99	90.0	47.7	602.2	45.2	647.4	3.03	88.0	52.1	700.2	42.9	743.1
T	848	6.5	3.36	0.28	9.7	3.2	9.8	1.10	98.0	27.4	273.7	32.8	306.5	1.09	98.0	32.7	352.9	26.2	379.1
T	849	2.2	3.8	0.41	12.7	7.3	9.8	3.23	92.0	29.9	373.5	14.4	387.9	2.58	76.0	33.3	448.2	50.8	498.9
T	850	10.8	3.56	0.42	13.6	24.6	9.4	2.80	90.0	34.0	413.7	50.1	463.7	3.49	99.0	37.0	469.5	51.5	521.0
T	851	3	3.24	0.38	10.2	2.9	7.6	1.56	90.2	29.5	509.5	1.1	510.6	1.74	98.1	32.7	571.1	1.1	572.2
T	852	3.8	3.19	0.38	11.5	5.1	7.7	1.23	98.0	24.7	245.9	19.3	265.2	1.25	98.0	27.9	298.9	17.9	316.8
T	853	2.4	3.36	0.31	9.9	5.7	8.5	1.41	98.0	27.5	291.3	55.0	346.2	1.47	98.0	31.3	368.3	21.6	389.8
T	854	1	3.86	0.29	9	28.5	9.7	3.25	91.3	49.7	589.2	9.2	598.4	2.96	84.0	52.8	663.8	38.3	702.0
T	855	11.7	3.34	0.35	11.8	5.4	9.3	1.90	91.3	34.4	505.8	23.8	529.6	2.08	98.3	40.8	617.3	16.4	633.7
T	856	14.2	3.34	0.3	9.8	7.8	7.6	1.99	98.0	32.0	337.0	41.1	378.2	2.04	98.0	39.5	444.0	31.6	475.7
T	857	3.3	3.19	0.5	15.4	19.7	8.6	0.56	51.0	32.2	520.3	2.3	522.6	1.80	98.1	35.4	577.0	2.2	579.2
T	858	3.2	3.04	0.58	18.2	31.5	9.5	1.77	98.0	30.3	372.1	7.6	379.7	1.82	98.0	32.3	412.4	8.9	421.3
T	859	3.3	3.15	0.45	14.3	6.9	9.1	1.93	98.4	34.7	562.7	49.6	612.3	1.96	98.4	36.3	592.2	72.9	665.0
T	860	1.1	3.38	0.33	9.7	4.8	7.4	1.86	90.4	24.9	365.5	1.9	367.3	1.83	92.0	29.6	434.2	4.2	438.4
T	861	2.6	4.05	0.33	10.2	15.7	9.8	3.65	98.3	44.1	556.1	6.3	562.4	3.70	98.3	49.6	648.0	42.5	690.6
T	862	13.8	3.19	0.57	17.2	8.0	8.6	0.48	23.2	16.3	284.7	0.7	285.3	1.44	60.8	18.3	322.4	0.2	322.7
T	863	14.8	3.14	0.58	18.2	62.3	10.2	1.88	98.0	39.0	629.8	9.5	639.2	1.83	90.2	38.6	649.7	64.3	714.1
T	864	11.4	3.44	0.43	13.4	10.3	9.5	1.75	91.3	37.7	557.5	33.6	591.2	1.99	98.6	40.1	618.7	62.3	681.0
T	865	14	3.29	0.38	13	17.6	9.7	1.61	90.8	28.0	428.5	66.7	495.2	1.28	76.0	31.6	477.4	43.6	521.0
T	866	1.5	3.42	0.38	12.1	5.6	10.2	1.59	90.0	40.2	611.5	56.6	668.1	1.85	93.0	43.2	673.0	88.2	761.2
T	867	12.7	3.06	0.57	18.8	5.5	10.5	1.20	84.0	46.7	789.2	27.3	816.5	1.46	98.2	51.5	897.5	70.8	968.2

Site	IDPlot	Sand(%)	pH $_{CaCl_2}$	Kj-N (%)	OM(%)	P.Plant (ppm)	CEC.B aCl_2	LQ-1	Cover-1	BA-1	VOL-1	Vol-d-1	TAB-1	LQ-2	Cover-2	BA-2	VOL-2	Vol-d-2	TAB-2
T	868	3.1	3.09	0.52	17.9	14.2	10.1	0.94	72.0	42.8	658.6	92.9	751.4	1.07	73.9	37.2	590.3	198.4	788.7
T	869	9.8	3.39	0.23	7.7	1.9	7.8	1.50	93.0	40.1	609.3	108.9	718.3	1.71	98.6	40.9	660.1	79.5	739.7
T	870	13.7	3.45	0.38	11.8	8.6	9.9	1.84	93.0	44.2	724.7	28.7	753.4	1.80	92.0	47.5	810.1	64.3	874.4
T	871	0	3.25	0.47	15.8	9.6	9.9	2.75	90.4	37.8	390.3	14.6	405.0	3.00	98.3	39.1	433.4	59.9	493.3
T	872	12.8	3.47	0.47	14.1	10.3	9.2	2.61	92.0	40.8	489.9	23.3	513.2	2.68	90.4	37.6	492.0	29.0	521.0
T	873	1.1	3.5	0.26	8.3	8.1	8.3	2.54	91.3	55.0	797.5	64.8	862.3	2.88	98.4	55.6	833.1	91.8	924.8
T	875	1	3.29	0.35	12.2	19.9	7.2	2.65	86.0	39.2	460.4	36.3	496.7	3.07	93.0	40.1	505.5	70.9	576.4
T	876	13.7	3.87	0.29	8.9	19.2	7.7	3.45	98.0	52.3	636.2	22.7	659.0	3.49	98.0	59.7	781.8	51.9	833.7
T	877	12.6	3.13	0.44	15.1	39.9	8.4	2.74	90.2	46.1	476.5	19.4	495.9	3.01	98.0	52.1	570.4	39.3	609.7
T	878	14.1	3.26	0.4	13.3	6.3	8.7	2.94	98.0	39.8	485.4	13.8	499.2	2.70	90.2	35.8	453.2	41.9	495.0
T	879	0	3.72	0.42	12.2	33.1	8.7	3.49	91.3	32.7	414.7	81.5	496.2	3.76	98.1	41.8	562.7	85.5	648.2
T	880	1.5	3.6	0.29	9.3	46.3	6.9	2.91	91.3	36.4	364.5	47.2	411.6	3.22	98.1	43.7	489.8	29.2	519.0
T	881	3.5	3.4	0.26	8.2	10.3	6.7	2.21	90.8	19.5	265.9	46.9	312.9	2.18	90.2	20.0	288.2	34.0	322.3
T	882	15.7	4.75	0.25	7.6	8.4	9.4	3.36	92.0	46.0	599.7	8.6	608.3	3.42	93.0	48.9	669.7	46.1	715.8
T	883	1.8	3.46	0.29	9.5	4.4	8.2	2.51	98.2	33.1	442.6	38.5	481.0	2.28	90.2	37.0	513.6	26.7	540.3
T	884	34.5	5.53	0.26	9.1	8.3	10.5	2.67	91.0	56.6	768.8	14.5	783.4	3.78	98.4	63.5	903.5	47.8	951.2
T	885	3	3.13	0.56	21.5	55.9	9.5	1.88	90.4	48.0	662.2	59.0	721.2	2.14	98.1	53.7	754.5	40.5	795.0
T	886	13.7	3.39	0.31	11.7	1.5	9.5	2.93	98.3	45.9	500.0	8.5	508.5	2.39	84.0	56.7	669.1	4.5	673.6
T	887	1.8	3.21	0.46	15	13.6	8.0	2.56	90.2	45.6	662.5	19.5	682.0	2.78	98.3	46.5	720.8	17.7	738.5
T	888	16	3.89	0.28	8.7	4.8	7.9	2.56	88.0	54.9	713.1	4.7	717.8	2.94	94.0	63.8	845.8	76.4	922.1
T	889	10.8	3.18	0.3	9.9	32.8	7.6	1.45	86.0	44.2	688.0	19.1	707.0	1.21	72.4	42.7	672.0	83.7	755.7
T	890	7.1	2.99	0.66	24.1	30.0	12.0	1.49	92.0	38.7	559.0	19.3	578.2	1.49	92.0	40.2	592.1	42.9	635.0
P	901	8.3	3.27	0.22	7.9	18.5	6.2	0.86	82.0	31.5	410.9	16.5	427.4	1.05	94.0	29.4	389.3	20.0	409.3
P	902	2.1	3.11	0.4	13.7	36.2	8.4	1.01	65.0	21.3	276.6	108.2	384.9	1.44	82.0	24.3	294.4	71.4	365.8
P	903	2.2	3.11	0.39	14.1	22.4	8.3	1.35	88.0	40.4	666.2	0.0	666.3	1.47	95.0	44.9	718.7	11.1	729.8
P	905	17.4	3.09	0.2	6.2	19.9	4.8	0.90	90.2	35.4	543.9	15.8	559.7	0.99	98.3	38.0	567.2	10.3	577.5
P	906	2.7	2.97	0.4	14.3	33.1	8.8	1.08	98.0	22.9	357.1	2.4	359.5	1.08	92.0	22.8	362.2	14.7	376.9
P	907	17.9	3.21	0.3	9.6	35.8	7.1	0.76	88.0	36.7	639.5	6.2	645.7	1.24	94.0	42.9	740.6	14.2	754.8

Site	IDPlot	Sand(%)	pH CaCl$_2$	Kj-N (%)	OM(%)	P.Plant (ppm)	CEC.BaCl$_2$	LQ-1	Cover-1	BA-1	VOL-1	Vol-d-1	TAB-1	LQ-2	Cover-2	BA-2	VOL-2	Vol-d-2	TAB-2
P	908	21	3.08	0.34	11.9	27.7	6.9	1.81	91.3	45.0	731.5	5.1	736.6	1.78	91.3	52.0	860.2	5.5	865.7
P	910	38.7	3.1	0.25	9.7	21.9	8.4	2.27	98.0	32.0	421.7	7.7	429.3	2.34	98.0	42.2	533.9	9.3	543.2
P	912	3.9	3.05	0.34	12.1	21.3	10.7	0.80	84.0	25.9	315.0	10.2	325.2	0.90	91.3	31.1	404.5	25.8	430.4
P	913	2.4	3.36	0.29	9.6	34.3	7.9	1.72	86.0	39.5	623.1	4.2	627.2	1.98	95.0	46.4	719.7	2.1	721.8
P	918	4.2	3.28	0.32	11.1	24.8	8.6	1.02	80.0	28.9	445.0	71.4	516.4	1.52	92.0	32.4	496.7	21.0	517.7
P	919	24.1	3.32	0.19	6.8	27.6	6.2	0.90	90.2	26.9	373.3	13.7	387.0	0.90	90.2	31.4	441.3	18.0	459.3
P	920	19.1	3.28	0.26	8.5	32.0	4.6	0.24	92.0	24.8	333.6	5.6	339.2	1.07	92.0	28.0	375.2	21.5	396.6
P	921	1.5	3.06	0.25	8.9	39.3	6.4	0.30	98.6	25.5	417.1	1.1	418.2	0.98	98.0	30.7	492.2	4.6	496.8
P	922	28.3	5.53	0.21	7.3	41.2	12.1	1.43	90.0	15.9	253.7	61.4	315.1	0.42	26.4	14.4	214.0	14.0	228.0
P	924	13	3.19	0.09	8.6	23.7	4.0	0.93	40.6	3.7	45.3	1.4	46.7	0.28	39.1	8.2	76.1	0.0	76.1
P	925	3	3.34	0.19	7.4	15.9	6.1	1.48	98.0	26.5	350.3	1.1	351.4	1.40	98.0	33.0	444.6	8.8	453.5
P	926	18.3	3.35	0.26	9.3	14.9	7.4	1.35	94.0	38.6	677.3	1.5	678.7	1.52	98.6	43.1	672.7	10.3	683.0
P	927	14.9	3.2	0.3	10.7	14.7	8.4	1.34	86.0	52.1	828.5	2.6	831.1	1.31	86.0	50.7	840.9	54.4	895.3
P	928	28.5	7.11	0.22	7.8	52.7	16.0	2.16	91.3	23.9	369.9	6.3	376.2	2.27	92.0	32.8	486.5	24.3	510.7
P	929	3.5	3.19	0.2	7	14.5	8.0	0.98	98.0	42.9	881.4	2.3	883.6	0.60	60.4	45.9	706.5	135.6	842.1
P	930	1.6	3.07	0.27	10.5	16.8	7.1	0.30	58.0	11.8	177.2	163.2	340.4	1.03	98.3	19.0	222.0	24.0	246.0
P	931	1.8	3.24	0.21	7.1	14.6	5.1	0.98	98.0	34.4	531.9	9.0	540.9	0.98	98.0	36.0	486.1	5.3	491.4
P	933	6.6	3.12	0.43	15.8	16.0	11.9	1.05	90.0	22.6	351.7	25.5	377.2	1.25	92.0	21.9	334.9	13.2	348.1
P	934	15.1	3.24	0.28	12.5	14.4	8.6	1.15	85.0	37.2	537.8	104.5	642.2	1.42	86.0	39.0	523.3	55.2	578.5
P	935	2.9	5.06	0.17	6.1	16.8	11.7	2.55	93.0	26.0	372.4	13.1	385.4	2.54	94.0	28.7	422.7	14.5	437.2
P	936	1.1	3.2	0.26	8.9	20.9	7.9	1.15	93.0	35.0	446.0	4.6	450.6	1.21	94.0	33.3	464.8	9.3	474.1
P	937	0.6	3.15	0.37	12.4	14.6	10.1	1.68	92.0	44.2	609.9	0.5	610.4	1.56	90.8	43.8	632.6	1.8	634.4
P	938	22.7	2.92	0.25	8.7	16.0	7.0	0.98	98.1	37.4	570.4	2.6	573.0	0.98	98.0	37.6	580.3	4.3	584.6
P	939	38.1	2.99	0.33	11.7	16.6	12.2	0.75	68.0	36.1	657.0	4.1	661.1	0.88	82.0	38.9	633.8	6.6	640.4
P	940	1.7	3.27	0.45	17.1	32.9	16.3	1.27	98.0	26.4	404.7	2.9	407.6	1.58	96.0	31.5	389.6	4.6	394.2
P	941	3.3	3.39	0.18	7.4	29.0	9.6	1.40	92.0	39.6	610.3	1.0	611.3	1.36	92.0	41.3	646.2	2.8	648.9
P	942	20.5	3.52	0.3	9.5	19.3	8.3	1.89	97.0	26.8	388.5	5.4	393.9	1.87	94.0	30.1	442.1	4.2	446.3
P	943	3.1	3.18	0.47	14.7	57.7	12.1	0.88	58.0	26.9	317.6	44.3	361.9	2.06	92.0	30.4	388.2	25.2	413.4

Site	IDPlot	Sand(%)	pH CaCl_2	Kj-N (%)	OM(%)	P.Plant (ppm)	CEC.BaCl_2	LQ-1	Cover-1	BA-1	VOL-1	Vol-d-1	TAB-1	LQ-2	Cover-2	BA-2	VOL-2	Vol-d-2	TAB-2
P	944	1.2	3.43	0.42	11.4	19.2	12.1	1.42	98.0	28.0	403.9	26.2	430.1	1.59	94.0	32.1	464.6	21.5	486.1
P	945	13	3.4	0.36	11.2	26.2	10.3	1.52	98.0	36.0	482.7	1.5	484.2	1.73	95.0	38.6	528.6	2.1	530.7
P	947	5.8	3.09	0.61	19.1	20.1	15.7	1.35	94.0	35.1	445.6	1.4	447.1	1.56	95.0	34.4	468.3	2.7	471.0
P	948	6.8	3.19	0.44	14.9	14.9	11.4	0.95	94.0	24.1	354.2	2.9	357.1	1.21	95.0	25.9	382.0	1.8	383.7
P	949	17	3.24	0.45	9.2	82.7	8.3	1.45	88.0	22.8	312.9	34.8	347.8	1.89	95.0	25.6	350.8	19.1	369.9
P	950	6.7	3.18	0.34	14.3	73.6	14.4	1.67	90.8	31.7	490.3	100.2	590.5	1.64	90.8	32.7	495.2	59.6	554.7
P	951	1.9	3.16	0.29	11	67.7	8.2	1.31	99.0	23.4	332.9	0.2	333.1	1.50	93.0	19.8	276.4	8.1	284.5
P	952	14.3	3.23	0.27	10.4	43.5	8.5	1.69	90.8	38.1	571.1	4.5	575.5	1.75	92.0	46.3	675.1	6.8	681.9
P	953	2.3	3.23	0.32	11.1	43.6	8.1	1.35	91.0	21.6	259.1	0.7	259.8	1.41	88.0	24.6	297.2	10.3	307.5
P	954	2.2	3.35	0.28	10.5	16.0	5.9	0.75	79.0	26.7	351.2	0.0	351.2	0.81	86.0	29.6	424.3	26.6	450.9
P	955	17.4	3.19	0.29	11	66.5	8.3	2.37	94.0	31.2	501.4	4.3	505.7	2.36	96.0	29.9	437.9	16.1	454.0
P	956	14.9	3.38	0.25	8.2	81.7	6.3	2.03	80.8	36.6	488.7	2.9	491.6	2.32	90.2	44.3	622.0	2.3	624.3
P	958	2.9	3.05	0.5	18.5	71.7	14.3	1.60	86.0	35.3	469.9	2.2	472.1	1.70	92.0	32.0	421.7	15.4	437.1
P	959	0.4	3.36	0.26	8.8	19.5	5.5	0.56	86.0	27.5	331.4	3.9	335.3	1.26	88.0	28.9	361.5	8.1	369.6
P	960	2.6	3.03	0.39	14	74.9	8.3	1.58	92.0	39.9	519.3	20.4	539.8	1.90	95.0	40.4	587.2	22.1	609.3
P	961	1.3	3.26	0.35	11.2	22.4	7.4	1.15	94.0	41.0	634.1	18.2	652.4	1.35	92.0	39.5	617.8	35.9	653.7
P	962	0.3	3.47	0.26	9.7	15.6	7.2	1.50	92.0	37.0	484.6	0.0	484.7	1.61	95.0	35.8	507.6	2.8	510.4
P	963	1.5	3.57	0.4	12.3	16.0	9.8	1.54	96.0	16.8	195.5	21.0	216.5	1.54	96.0	19.0	230.8	27.3	258.1
P	964	8.4	3.38	0.25	7.9	15.0	5.0	0.95	72.4	22.9	255.3	8.4	263.6	1.29	91.3	28.3	362.1	12.4	374.5
P	965	0	3.18	0.38	13.4	100.0	9.4	1.18	94.0	20.0	245.4	44.3	289.7	1.41	94.0	22.0	298.6	18.2	316.8
P	966	0.8	3.5	0.26	8.2	24.0	5.9	1.73	90.4	27.3	327.9	5.0	332.9	1.64	93.0	31.9	369.6	6.1	375.7

Annex 6. frequency (#) and characteristic cover (CC) of all recorded herb species for the 183 plots at first (-1) and second (-2) survey (four sites combined)

NAME	#-1	#-2	CC-1	CC-2
Increasing in frequency and cover				
Anemone nemorosa	153	152	33.9	42.5
Athyrium filix-femina	163	162	6.3	9.8
Dryopteris dilatata	124	153	1.2	2.4
Dryopteris carthusiana	110	135	1.4	1.7
Milium effusum as	111	120	1.2	1.9
Hedera helix	71	87	1.2	2.3
Dryopteris filix-mas	34	39	1.1	1.2
Melica uniflora	26	31	1.6	3.5
Allium ursinum	21	27	20.3	27.4
Circaea lutetiana	42	45	2.3	2.9
Stellaria holostea	30	31	2.0	2.7
stable				
Lamium galeobdolon	117	115	7.8	6.1
Oxalis acetosella	104	102	4.5	4.1
Hyacinthoides non-scripta	80	81	49.8	41.3
Galium aparine	30	27	3.6	3.5
Narcissus pseudonarcissus	30	30	1.2	1.5
Ficaria verna	17	14	8.0	13.1
Adoxa moschatellina	19	19	1.6	2.3
Geum urbanum	18	14	1.0	1.0
Poa trivialis	18	15	1.6	1.3
Poa spec.	11	7	1.0	1.6
Arum maculatum	8	10	1.1	1.2
Blechnum spicant	7	5	1.0	1.0
Vinca minor	6	6	11.3	8.0
Decreasing in frequency and/or cover				
Rubus fruticosus	150	138	2.5	3.6
Luzula pilosa	68	40	1.0	1.0
Convallaria majalis	64	43	2.7	2.6
Lonicera periclymenum	77	61	1.3	1.1
Holcus mollis	74	64	5.8	4.6
Polygonatum multiflorum	72	53	1.0	1.0
Deschampsia cespitosa	58	49	1.1	1.0
Urtica dioica	33	16	4.4	4.2
Carex remota	30	22	2.0	1.0
Moehringia trinerva	29	5	1.0	1.0
Pteridium aquilinum	27	21	6.8	8.5
Silene dioica	27	13	1.0	1.1
Carex sylvatica	26	19	1.0	1.1
Maianthemum bifolium	23	12	1.1	1.1
Juncus effusus	22	7	1.6	1.0
Lysimachia nemorum	18	6	1.0	1.0
Glechoma hederacea	28	22	9.0	13.8
Veronica montana	19	14	1.3	1.4
Rubus idaeus	11	12	3.7	1.2
Teucrium scorodonia	18	5	1.1	1.2
Scrophularia nodosa	16	3	1.0	1.0

Carex pilulifera	12	4	1.0	1.0
Ajuga reptans	10	4	1.0	1.3
Carex pallescens	9	1	1.0	1.0
Cardamine flexuosa	8	1	1.0	1.0
Stachys sylvatica	7	2	1.0	1.5
Poa nemoralis	6	2	1.0	1.0
Persicaria hydropiper	10	0	1.0	0
Rubus caesius	6	0	1.0	0
Species with low frequency and cover				
Paris quadrifolia	5	4	1.2	1.3
Primula elatior	4	5	1.0	1.0
Viola riviniana + reichenbachiana	3	1	1.0	1.0
Chrysosplenium oppositifolium	3	1	5.3	1.0
Molinia caerulea	3	3	1.0	1.0
Deschampsia flexuosa	2	1	1.5	1.0
Epipactis helleborine	2	1	1.0	1.0
Geranium robertianum	2	5	1.0	1.2
Gagea spathacea	1	1	1.0	1.0
Filipendula ulmaria	1	1	1.0	1.0
Equisetum telmateia	1	1	1.0	1.0
Rosa arvensis	2	0	1.0	0
Holcus lanatus	2	0	1.0	0
Alliaria petiolata	3	0	1.0	0
Poa compressa	2	0	1.0	0
Festuca gigantea	2	0	1.0	0
Potentilla sterilis	1	0	1.0	0
Solanum dulcamara	1	0	1.0	0
Vaccinium myrtillus	1	0	1.0	0
Galeopsis tetrahit	1	0	1.0	0
Calamagrostis epigejos	1	0	1.0	0
Digitalis purpurea	1	0	1.0	0
Epilobium angustifolium	1	0	1.0	0
Stellaria graminea	1	0	1.0	0
Plantago major	1	0	1.0	0
Cirsium palustre	1	0	1.0	0
Epilobium tetragonum	1	0	1.0	0
Taraxacum officinale	1	0	1.0	0
Cardamine pratensis	1	0	1.0	0
Phalaris arundinacea	1	0	1.0	0
Senecio ovatus	1	0	1.0	0
Luzula multiflora	1	0	1.0	0
Lycopus europaeus	1	0	1.0	0
Juncus conglomeratus	0	2	0	1.0
Impatiens parviflora	0	1	0	1.0

Annex 7. Overview of Red-listed species (with number of individuals caught) in the Kolmont Strict Forest Reserve.

Overview of all Red-listed species (with number of individuals caught) in the Kolmont Strict Forest Reserve D-RL = German Red list categories (Geiser 1998): 1 = critically endangered, 2 = endangered, 3 = vulnerable; GB-RL = Red list for Great Britain (Hyman & Parsons, 1992, 1994): 1 = endangered, 2 = vulnerable, 3 = rare; EUR-RL = European red list (Nieto & Alexander 2010): NT = near threatened; VU = vulnerable; RELIC = list of European indicator species for old-growth continuity (Urwald relict species, Müller et al., 2005).

family	Species	Number	D- RL	GB-RL	EUR-RL	RELIC
Histeridae	*Plegaderus dissectus (ER., 1839)*	271	3			
Histeridae	*Abraeus granulum (ER., 1839)*	51	3			
Histeridae	*Abraeus parvulus (AUBE, 1842)*	4	2			x
Histeridae	*Aeletes atomarius (AUBE, 1842)*	421	1	3		
Histeridae	*Paromalus flavicornis (HBST., 1792)*	378		1		
Cholevidae	*Nemadus colonoides (KR., 1851)*	1	3			
Leiodidae	*Liodopria serricornis (GYLL., 1813)*	1	3			
Scydmaenidae	*Stenichnus godarti (LATR.,)*	26		3		
Scydmaenidae	*Micoscydmus minimus (CHAUD., 1845)*	20	3			
Scydmaenidae	*Scydmaenus rufus (MULL.KUNZE, 1822)*	30		2		
Scydmaenidae	*Scydmaenus perrisii (RTT., 1881)*	41	2			
Ptiliidae	*Nossidium pilosellum (MARSH., 1802)*	124	3			
Ptiliidae	*Ptenidium gressneri (ER., 1845)*	2	3			
Ptiliidae	*Micridium halidaii (MATTH., 1868)*	1	3			x
Ptiliidae	*Ptinella limbata (HEER, 1841)*	38		K		
Ptiliidae	*Ptinella denticollis (FAIRM., 1857)*	1	1			
Staphylinidae	*Siagonium quadricorne (KIRBY, 1815)*	6	3			
Staphylinidae	*Phyllodrepa nigra (GRAV., 1806)*	1	3	I		
Staphylinidae	*Phloeonomus minimus (Er., 1839)*	1	2			
Staphylinidae	*Xylodromus testaceus (ER., 1840)*	4		1		
Staphylinidae	*Phyllodrepoidea crenata (GRAV., 1802)*	30	3			
Staphylinidae	*Hypnogyra glabra (NORDM., 1837)*	38	3			
Staphylinidae	*Veilleius dilatatus (F., 1787)*	5	3	1		
Staphylinidae	*Quedius brevicornis (THOMS., 1860)*	1	3			
Staphylinidae	*Holobus apicatus (ER., 1837)*	18	3			
Staphylinidae	*Gyrophaena munsteri (STRAND, 1935)*	4		K		
Staphylinidae	*Gyrophaena polita (GRAV., 1802)*	10	3			
Staphylinidae	*Agaricochara latissima (STEPH., 1832)*	50	3			
Staphylinidae	*Autalia impressa (OL., 1795)*	3		3		
Staphylinidae	*Thamiaraea cinnamomea (GRAV., 1802)*	93	3			
Staphylinidae	*Thamiaraea hospita (MARK., 1844)*	2	2			
Pselaphidae	*Plectophloeus nitidus (FAIRM., 1857)*	2		2		
Pselaphidae	*Trichonyx sulcicollis (REICHB., 1816)*	6	3	2		
Pselaphidae	*Batrisodes delaporti (AUBE, 1833)*	6		1		
Pselaphidae	*Batrisodes buqueti (AUBE, 1833)*	1	2	1		x

family	**Species**	**Number**	**D- RL**	**GB-RL**	**EUR-RL**	**RELIC**
Pselaphidae	*Batrisodes unisexualis (BES., 1988)*	3	3			
Pselaphidae	*Batrisodes oculatus (AUBE, 1833)*	2	1			
Cleridae	*Tillus elongatus (L., 1758)*	78	3			
Trogositidae	*Nemosoma elongatum (L., 1761)*	5		3		
Elateridae	*Ampedus sanguineus (L., 1758)*	1		E		
Elateridae	*Ampedus nigroflavus (GOEZE, 1777)*	1	3			
Elateridae	*Brachygonus megerlei (LACORD., 1835)*	1	2		NT	
Elateridae	*Procraeus tibialis (LACORD., 1835)*	10	2	3		
Elateridae	*Elater ferrugineus (L., 1758)*	1	2	1	NT	x
Elateridae	*Stenagostus rhombeus (OL., 1790)*	28	3			
Cerophytidae	*Cerophytum elateroides (LATR., 1804)*	2	2		VU	
Eucnemidae	*Eucnemis capucina (AHR., 1812)*	2	3			
Eucnemidae	*Dromaeolus barnabita (VILLA, 1838)*	2	2			
Eucnemidae	*Dirhagus pygmaeus (F., 1792)*	1	3			
Eucnemidae	*Dirhagus lepidus (ROSH., 1847)*	3	3			
Eucnemidae	*Hylis olexai (PALM, 1955)*	26	3			
Lissomidae	*Drapetes cinctus (PANZ., 1796)*	1	3			
Dermestidae	*Trinodes hirtus (F., 1781)*	1		3		
Nitidulidae	*Epuraea neglecta (HEER, 1841)*	4		I		
Silvanidae	*Silvanoprus fagi (GUER., 1844)*	12		1		
Erotylidae	*Triplax rufipes (F., 1775)*	282	1			
Erotylidae	*Dacne rufifrons (F., 1775)*	42	2			
Biphyllidae	*Biphyllus lunatus (F., 1792)*	1	1			
Cryptophagidae	*Cryptophagus labilis (ER., 1846)*	2	2			
Cryptophagidae	*Atomaria elongatula (ER., 1846)*	3	3			
Latridiidae	*Latridius hirtus (GYLL., 1827)*	11	3			
Latridiidae	*Enicmus brevicornis (Mannh., 1844)*	8	3			
Latridiidae	*Enicmus testaceus (STEPH., 1830)*	116	2			
Latridiidae	*Stephostethus pandellei (Bris, 1863)*	1	3			
Latridiidae	*Corticaria alleni (JOHNS., 1974)*	5	2			
Latridiidae	*Corticaria longicollis (ZETT., 1838)*	1		K		
Mycetophagidae	*Triphyllus bicolor (F., 1792)*	19	3			
Mycetophagidae	*Mycetophagus piceus (F., 1792)*	34	3			
Mycetophagidae	*Mycetophagus populi (F., 1798)*	1	3			
Colydiidae	*Cicones variegatus (Hellw., 1792)*	1	3			
Colydiidae	*Cicones undatus (GUER, 1844)*	1	3			
Colydiidae	*Colydium elongatum (F., 1787)*	6	3	3		
Corylophidae	*Orthoperus nigrescens (STEPH., 1829)*	108	2			
Endomychidae	*Symbiotes gibberosus (LUC., 1849)*	4	2			
Cisidae	*Ropalodontus perforatus (GYLLENHAL, 1813)*	2	3	3		
Cisidae	*Orthocis pygmaeus (MARSH., 1802)*	17	3			
Anobiidae	*Grynobius planus (F., 1787)*	1	3			
Anobiidae	*Ochina ptinoides (MARSH., 1802)*	51	3			
Anobiidae	*Gastrallus laevigatus (OL., 1790)*	1	2			
Anobiidae	*Anobium denticolle (Creutzer, 1796)*	5	3			

family	**Species**	**Number**	**D- RL**	**GB-RL**	**EUR-RL**	**RELIC**
Anobiidae	*Mesocoelopus niger (MULL., 1821)*	2	3			
Anobiidae	*Dorcatoma chrysomelina (STRM.)*	19	3			
Anobiidae	*Dorcatoma dresdensis (HERBST, 1792)*	6	3			
Anobiidae	*Dorcatoma robusta (STRAND, 1938°*	64	2			
Scraptiidae	*Scraptia fuscula (MULL., 1821)*	28	3	1		
Scraptiidae	*Anaspis lurida (STEPH., 1832)*	2	3			
Scraptiidae	*Anaspis garneysi (FOWL., 1889)*	2	1			
Aderidae	*Euglenes oculatus (PAYKULL)*	10	2			
Melandryidae	*Phloiotrya rufipes (GYLL., 1810)*	1	3			
Melandryidae	*Melandrya caraboides (L., 1761)*	24	3			
Tetratomidae	*Tetratoma desmarestii (LATR., 1807)*	2	1			
Tetratomidae	*Tetratoma ancora (F., 1790)*	11	3			
Alleculidae	*Allecula morio (F., 1787)*	4	3			
Alleculidae	*Alleculla rhenana (BACH, 1856*	31	2			x
Alleculidae	*Prionychus ater (F., 1775)*	5	3			
Alleculidae	*Pseudocistela ceramboides (L., 1761)*	8	2			
Tenebrionidae	*Bolitophagus reticulatus (L., 1767)*	42	3	3		
Tenebrionidae	*Diaperis boleti (L., 1758)*	21		2		
Tenebrionidae	*Platydema violaceum (F., 1790)*	1	3	1		
Tenebrionidae	*Pentaphyllus testaceus (HELLW., 1792)*	23	3	U		
Tenebrionidae	*Corticeus unicolor (PILL. Mitt., 1783)*	32		3		
Tenebrionidae	*Corticeus bicolor (OL., 1790)*	5	3			
Scarabaeidae	*Trichius zonatus (GERM., 1794)*	1	3			
Cerambycidae	*Leptura aurulenta (F., 1792)*	3	2			
Cerambycidae	*Obrium cantharinum (L., 1767)*	1	2	E		
Cerambycidae	*Pyrrhidium sanguineum (L., 1758)*	2		2		
Cerambycidae	*Plagionotus detritus (L., 1758)*	1	2			
Cerambycidae	*Exocentrus adspersus (MULS., 1846)*	2	3			
Anthribidae	*Choragus sheppardi (KIRBY, 1818)*	5	3			
Scolytidae	*Kissophagus hederae (SCHMITT., 1843)*	6	3			