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SPATIO-TEMPORAL PATTERNS OF VEGETATION RECOVERY IN POST-AGRICULTURAL FORESTS IN FLANDERS

Thesis submitted in fulfillment of the requirements
For the degree of Doctor (PhD) in Applied Biological Sciences:
Land & Forest Management

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Dutch translation of the title:
Spatio-temporele patronen van vegetatieherstel in bossen op voormalige landbouwgronden in Vlaanderen

Illustrations on the cover:
A species-rich forest path in Muizenbos on calcareous soil with a low phosphorus content. *Primula elatior* and *Anemone nemorosa* are flowering, dark leaves halfway are of *Colchicum autumnale*.

Citation:
De Keersmaeker L (2013) Spatio-temporal patterns of vegetation recovery in post-agricultural forests in Flanders. PhD thesis, Ghent University, Ghent, Belgium

ISBN-number: 978-90-5989-653-6

Woord vooraf

Dit werk is het eindpunt van een lange tocht met vele kleine stapjes en lange tussenstops. Ik kon er maar geraken dankzij heel veel hulp en aanmoediging onderweg. In de eerste plaats wil ik mijn ouders bedanken, die mij alle kansen hebben gegeven om te studeren en die mij ook steeds op het belang ervan hebben gewezen. In het voorlaatste jaar van de bio-ir opleiding trok het onderwerp over de ecologische waarde van populierenbossen mijn aandacht. Het begin van een ontdekkingstocht in het Muizenbos en zijn omgeving en de eerste stapjes in het onderzoek naar vegetatieontwikkeling in beboste landbouwgronden. Ik ben Bart Muys nog altijd erg dankbaar dat hij dit omstreden onderwerp heeft aangereikt en de interesse voor onderzoek heeft aangewakkerd. Enkele jaren later, aan het laboratorium voor bosbouw in bij prof. Lust in Gontrode, werd ik in de biogeochemische cycli en de bosomvorming geworpen en kwam ik tot het besef dat onderzoek ‘mijn ding’ was. Hoog tijd om de medewerkers van toen expliciet te bedanken, om buiten de hokjes te denken en een ‘net-niet-bosbouwer’ binnen te halen. Gontrode was een heel bijzondere en aangename werkomgeving, een ideale opstap van de opleiding naar het ‘gewone’ werk. Ik ben An De Schrijver heel dankbaar dat ze me vanuit Gontrode is blijven aanmoedigen om door te gaan met publiceren en werk te maken van een doctoraat.

Mijn start aan het IBW dank ik aan Bruno De Vos en Jos Van Slycken, die me enkele jaren later het VLINA project over de ecosysteemvisie bos hebben toevertrouwd. Dit voorstel was erg ambitieus en het was alle hens aan dek om de doelstellingen te halen. Samen met Raf Lauriks en Bart Cosyns (de toenmalige GIS coördinatoren van het IBW), Marc Esprit, Nele Rogiers, en een heleboel jobstudenten is er een formidabele prestatie neergezet: het scannen en georefereren van honderden historische kaarten, waarop ruim 42.000 bossen werden gevectoriseerd. Marc verdient een aparte vermelding omdat hij met eindeloos geduld de gaten en correcties in het digitalisatiewerk voor zijn rekening nam en technische oplossingen bedacht om het werk te versnellen. De huidige en vroegere collega’s van het bosecologisch onderzoek bij het IBW/INBO, wil ik bedanken voor ruim 13 jaar samenwerking. De samenwerking met Peter Van de Kerckhove, Bart Christiaens, Marc Esprit, Anja Leyman, Kris Vandekerkhove, Arno Thomaes, Ruben Walleyn, Hans Baeté, Koen Smets, Leen Govaere en Johnny Cornelis was niet alleen efficiënt, maar minstens even belangrijk, ook heel aangenaam. Kris wil ik bedanken omdat hij tijdens het voorbije jaar, twee doctorerende bosonderzoekers uit de wind heeft gezet en een heleboel taken heeft overgenomen. Eén van de voordelen van een relatief groot onderzoeksinstituut, is de mogelijkheid tot specialisatie, van groot belang als je op wetenschappelijk gebied iets wil betekenen. Zonder de expertise en steun van de INBO statistici, Thierry Onkelinx, Pieter Verschelde en Paul Quataert, was dit werk gewoon niet mogelijk geweest. Ik bewonder ook de snelheid waarmee de medewerkers van de bib erin slaagden om een oude publicatie uit een veraf gelegen bibliotheek als pdf te pakken te krijgen: bedankt! Een doctoraat schrijven ‘tussen de soep en de patatten’ is een vrijwel onbegonnen werk. Het is heel mooi dat het management van het INBO mij de mogelijkheid heeft gegeven om er eerst deeltijds, de laatste 6 maanden zelfs voltijds, mee bezig te zijn. De warme aanmoedigingen van Beatrijs Van der Aa, Janine van Vessem en Geert De Blust in de laatste rechte lijn deden echt deugd.

De promotoren Kris Verheyen en Martin Hermy waren steeds bereikbaar om hun inzichten te delen, maar ook voor andere steun. Martin heb ik al een eerste keer lastig gevallen in 1992, met een brief (!) vol vragen over Muizenbos en hij heeft toen de tijd genomen om vanuit het verre Kiewit te antwoorden. Recenter is hij de zaak van onze PNV paper persoonlijk gaan bepleiten bij een editor die dit helemaal niet zag zitten. Ook al heeft dit toen niet geholpen, deze steun was heel belangrijk om er in te blijven geloven en elders te proberen. Kris was een zeer goede promotor, omdat hij als geen ander onvolkomenheden in de verhaallijn kan aanduiden en op het juiste ogenblik een voorzet kan geven die niet meer te missen is. Bedankt allebei! I would like to thank the members of the jury, in particular Frieke Van Coillie, Laurent Bergès and Jörg Brunet, whose thorough reviewing improved the thesis. The contributions of Laurent and Jörg reminded me to the fact that the study area of this PhD research is tiny. Forests in France and Sweden together cover approximately 300 times the area of forests in Flanders.

Er is nog een leven naast het werk en gelukkig hielpen Veerle, Gert en Rik me om de knop (meestal) snel om te draaien. Veerle deed er alles aan om het mij makkelijk te maken, zodat ik de tijd die voor het doctoraat beschikbaar was, zo goed mogelijk kon gebruiken. Heel erg bedankt, ik zie jullie graag!

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DEFINITION OF SOME TERMS USED IN THE THESIS

List of abbreviations and symbols

Abbreviations and symbols

A_c	consumer's accuracy
AF	ancient forest
AFS	ancient forest species
A_p	producer's accuracy
CCA	canonical correspondence analysis
DTM	digital terrain model
FC	forest continuity
GAM	generalized additive model or model
GLMM	generalized linear mixed model
ISA	indicator species analysis
mL	mean of the species indicator value for light
mF	mean of the species indicator value for soil humidity
mN	mean of the species indicator value for the soil trophic level
mR	mean of the species indicator value for soil acidity
n	number of plots or samples
N	nitrogen
NN	nearest neighborhood
P	phosphorus
P	significance of statistical test
PNV	potential natural vegetation
RF	recent forest
S	species number
SD	standard deviation
SE	standard error
TWINSPAN	two-way indicator species analysis
R^2	coefficient of determination

Definition of some terms used in the thesis

AF	ancient forest (AF) in Flanders is a forest continuously present since 1775
AFS	ancient forest species (AFS) are species that occur more in AF than in RF
Connectivity	A measure of the ease of movement of an organism between two patches based on the distance between the two patches and a patch characteristic
Forest continuity	The continuous presence of a forest cover, quantified by forest age. The forest age is the number of years a forest was continuously present since the last conversion from open land to forest
Mesophilous forest	forest on sites with intermediate conditions for soil humidity, soil nutrients, and soil acidity
PNV	Potential Natural Vegetation is the most mature vegetation that can develop on a site, without consideration of the required time
RF	recent forest in Flanders is a forest not continuously present since 1775, but converted to other land use for some time

1 Introduction

Forest organisms depend to a certain degree on the continuity of the forest cover in space or time, or even in both dimensions. Disruptions in any of those dimensions will most likely result in a loss of forest biodiversity, as patterns of habitat availability and suitability are affected by spatio-temporal forest cover changes. This is first illustrated by means of a hypothetical landscape that is dynamic, meaning that the landscape configuration is changing in time.

We will then discuss the processes that explain the occurrence or abundance of herbaceous forest plant species in forests affected by spatio-temporal disruptions. The magnitude of the disruptions explains the species-specific response and consequently also the variable recovery level of forest vegetation. Processes that affect vascular forest plant species and forest vegetation have been studied thoroughly during the past decades. The findings of this research will be related to the patterns of habitat availability and suitability illustrated in the first section.

The final section of the introduction specifies the objectives and the outline of the thesis. This work has the ambition to quantify and map the impact of spatio-temporal forest cover changes on availability and suitability of habitat for herbaceous forest plant species in Flanders. Patterns of herbaceous forest plant species composition, in particular on mesophilous sites, are revealed, quantified and explained at multiple scale levels. Factors that influence the rate of forest plant species recolonisation and vegetation recovery are identified, which results in recommendations for landscape planning and forest management.

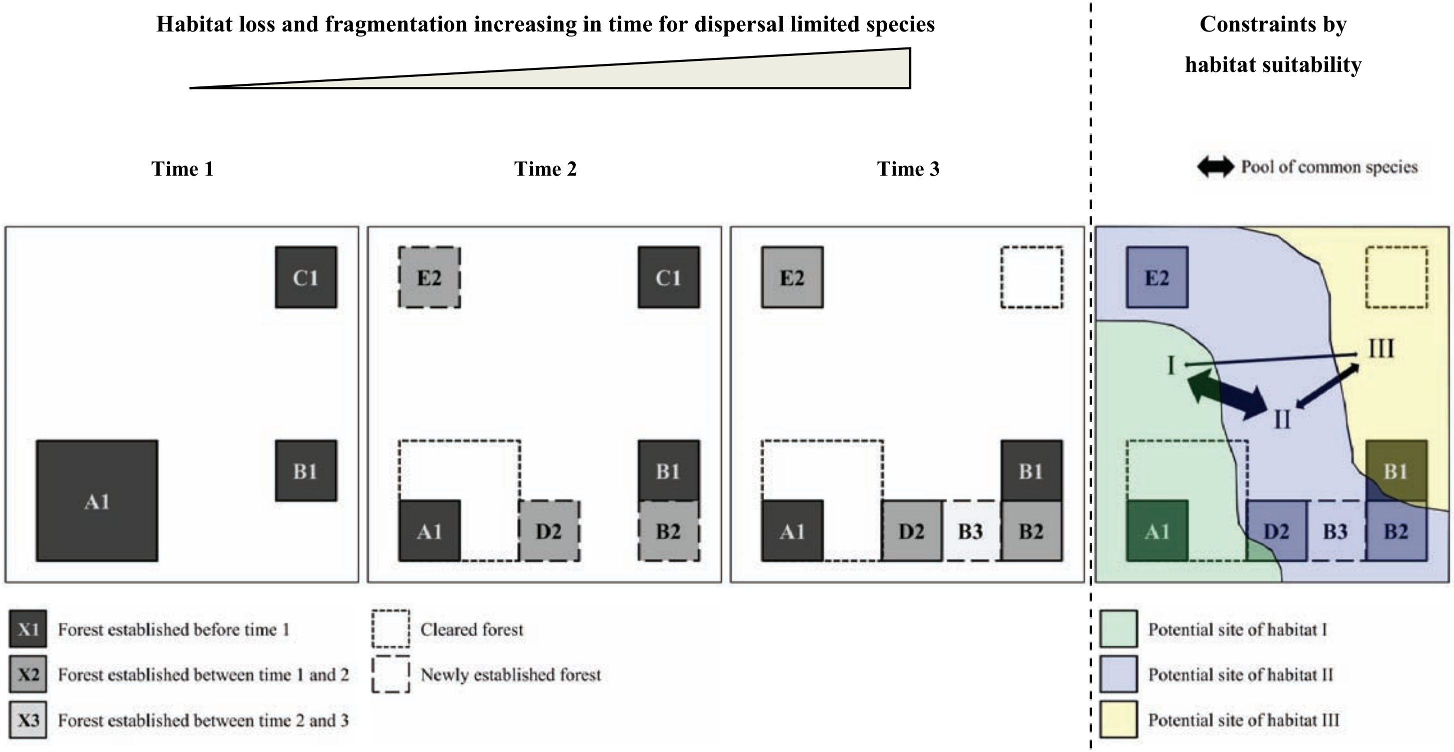

Fig. 1.1 Spatio-temporal forest cover changes in a hypothetical dynamic landscape, at three consecutive times. The forest patches of time 1 have not been altered for a very long time (e.g. centuries) before time 1. The landscape at time 3 is further specified for three potential forest habitat types, to illustrate the additional habitat loss and fragmentation experienced by habitat specialists. The codes of the forest patches and habitat types are used throughout the introduction.

1.1 Impact of spatio-temporal disruptions on habitat availability and suitability

1.1.1 Impact of fragmentation

Fragmentation is a spatial process that occurs when a habitat patch is broken apart into smaller patches (Fahrig 2003). Fragmentation can result into a decline of habitat interior, and into an increase of perforated habitat, habitat edge, transitional habitat, and habitat patchiness (Riitters *et al.* 2000).

In the hypothetical case illustrated in Fig. 1.1, the total area of forest habitat, without specification of its suitability, is less fragmented at time 1 and 3 than at time 2. As opposed to this hypothetical landscape where the total area is constant in time, progressive fragmentation often also results into a decline of the total habitat area, i.e. habitat loss. The term fragmentation is sometimes used to cover both aspects. Further on in this work, the strict definition proposed by Fahrig (2003) is applied and fragmentation therefore does not refer to habitat loss.

Habitat fragmentation is a process that affects connectivity. Connectivity is defined as the interaction between a species and the landscape in which it occurs (Moilanen & Hanski 2001). The definition of connectivity is somewhat different in metapopulation ecology than in landscape ecology (Moilanen & Hanski 2006). In landscape ecology, connectivity is the degree to which the landscape facilitates or impedes species movement among resource patches (Taylor *et al.* 1993). In metapopulation ecology, which is based on the island theory (MacArthur & Wilson 1967, Levins 1969), connectivity measures the rate of species immigration and extinction in a habitat patch. This process-oriented approach requires a simplification of the landscape matrix (Moilanen & Hanski 2001). The matrix in between habitat patches is often qualified as unsuitable and movement of species outside habitat patches is assumed as more or less random (Moilanen & Hanski 2001). By contrast, landscape ecology often disregards the fundamental process of immigration and extinction (Moilanen & Hanski 2001); it focusses on patterns of species, using habitat patches as well as the surrounding landscape matrix with a heterogeneous suitability (Tischendorf & Fahrig 2000). This thesis is not a study of fundamental processes, but aimed at studying landscape, vegetation and species patterns at variable spatial and temporal scales (see 1.3).

As connectivity is species-dependent, measures that are used for quantification should be appropriate to estimate the interaction of a species and a landscape under study (Fagan & Calabrese 2006). A simple and frequently used connectivity measure is the nearest neighbourhood (NN) measure that is calculated as the Euclidean distance between a focal habitat patch and the nearest neighbourhood patch. This can be a useful measure for species that rely on short-distance dispersal modes (e.g. many forest plant species, see 1.2).

In the hypothetical dynamic landscape in Fig. 1.1, connectivity of forest patch A1 (time 1) is lower than connectivity of the equal-sized forest patch D2B3B2B1 (time 3) if calculated as an NN connectivity measure. There are, however, other connectivity measures, e.g. based on the shape of a habitat patch, that can provide other results (Fagan & Calabrese 2006). In the hypothetical dynamic landscape of Fig. 1.1, forest patch A1 is more compact than forest patch D2B3B2B1. By consequence, the perimeter to area ratio (PAR) of A1 is lower than the PAR of D2B3B2B1, which means that patch D2B3B2B1 has more forest edge than patch A1. Forest edges can have another species composition than forest interior, as further explained in section 1.2.

1.1.2 Impact of temporal disruption

Whereas fragmentation refers to the spatial disruption of habitat, it does not apply directly to the dimension of time, although temporal disruption can result into a further habitat fragmentation. In a dynamic landscape, fragmentation of habitat is often accompanied by temporal disruption. In the hypothetical dynamic landscape of Fig. 1.1, the total forest cover remains constant. One patch reduces in size (A1) and another disappears (C1), but a third patch increases in size (B1) and a new patch is created, isolated from the other forest patches (E2). As a result, only 33% of the total forest area was continuously present between time 1 and time 3. Of the forest cover at time 3, 50% established between time 1 and time 2 and 17% between time 2 and 3.

Sites that have been permanently covered by forest for as long as we know (e.g. patches A1 and B1 at time 3 in Fig. 1.1) by convention are called ancient forest (AF). Forest patches converted to other land use for a certain period of time are called recent forest (RF) (patches D2, B3, B2, and E2 at time 3 in Fig. 1.1). In Flanders, the maps drawn by de Ferraris (1771-1778) are mostly used as the oldest reference to identify AF (e.g.

Hermy *et al.* 1999). The maps by de Ferraris are the first detailed maps that cover most of present-day Flanders. Older sources only cover a small area (e.g. land books) or are not detailed enough for the purpose of this study (e.g. the map of the Netherlands drawn in 1573 by Ortelius). Elsewhere in Europe, pragmatic choices based on the available maps resulted in other threshold dates, e.g. 1600 (England, Peterken 1974), 1747-1789 (France, Vallauri *et al.* 2012), 1767-1787 (Prussia in Germany, Wulf & Gross 2004), 1789 (Denmark, Lawesson *et al.* 1998), 1850 (the Netherlands, Grashof-Bokdam 1997), 1900 (the Netherlands, Daamen 2008).

Herbaceous forest vegetation in AF and RF can be very different, as further explained in section 1.2. Vascular plant species that are found more frequently or more abundantly in AF than in RF are called ancient forest species (AFS) (Peterken 1974). At time 3 in the hypothetical landscape (Fig. 1.1), certain forest plant species are probably more frequent or more abundant in the AF (A1 and B1) than in the RF patches and temporal disruption could have resulted into a progressive loss and fragmentation of habitat of AFS. Survival of forest species in open habitat after forest clearance is rare but not impossible (e.g. Rackham 2003). Survival of AFS in linear landscape elements that are relics of the cleared forest is frequently reported (e.g. Peterken 1974, Honnay *et al.* 1999a). These linear landscape elements are not always represented on forest cover maps. If forest species survived along the historical border of patch A1, which was mostly cleared between time 1 and 2, they could have colonized forest patch D2 that was created at that time (Fig. 1.1).

1.1.3 Constraints by habitat suitability

The previous section indicated that temporal disruption can result in loss and fragmentation of habitat of slow colonizing forest species, e.g. AFS. The effects of spatio-temporal isolation on species populations, caused by on-going habitat loss and fragmentation, can be difficult to quantify as a consequence of such a slow response (Gu *et al.* 2002; further explained in 1.2). Studying patterns of spatio-temporal forest cover changes and the effects on forest biodiversity is further complicated by the habitat specificity of species. Many forest species can be called habitat specialists, based on their preference for forest habitat and scarcity outside forest. AFS are in many cases stress-tolerant species according to Grime *et al.* (1988): they are adapted to low light levels

(Hermy *et al.* 1999) but can be outcompeted by fast-growing species (competitors according to Grime *et al.* 1988) when light availability increases (Ash & Barkham 1976, Kirby 1990).

1.1.3.1 Natural habitat heterogeneity

Within forests, most plant species are restricted to certain abiotic habitat conditions as e.g. expressed by the species indicator values for light, soil acidity, soil humidity and soil trophic level (Ellenberg *et al.* 1992, Hill *et al.* 1999). Plant species with a broad ecological amplitude can be present in several forest habitat types, whereas habitat specialists are mostly found in only one suitable forest habitat type (Cornelis *et al.* 2009). Habitat loss and fragmentation experienced by habitat specialists can thus be different than the level experienced by generalists. As a consequence, the pool of forest plant species that can be exchanged between patches of different habitat types is constrained. This assumption was applied to explain the variable recovery level of forest vegetation in Flanders (Butaye *et al.* 2001, Verheyen *et al.* 2006). In the hypothetical landscape of Fig. 1.1., the potential areas of three forest habitats (I, II, III) are determined by specific natural soil conditions. We assume that well-developed forest vegetation of habitats I and II has many common species, but that vegetation of forest habitats II and III shares less species. Vegetation of forest habitats I and III shares only few species and the potential areas are also separated from each other by the area that is potentially suitable for habitat II.

Certain habitat types can be affected more by spatio-temporal disruptions than other types (Fig. 1.1). Although the total forested area remained constant, the area of forest habitat II increased, whereas the areas of forest habitats I and III declined. Most of forest habitat II is RF, whereas other habitat types mostly consist of AF (Fig. 1.1).

1.1.3.2 Impact of fragmentation on habitat suitability

An increased level of habitat fragmentation, e.g. forest habitat at time 2 compared to time 1 (Fig. 1.1), often provokes habitat degradation (Harrison & Bruna 1999). As illustrated above, fragmentation leads to reduced patch size and increased perimeter to area ratio. The proportion habitat interior declines, whereas the proportion of habitat edges increases (Laurance & Yensen 1991, Ries *et al.* 2004, Fletcher *et al.* 2007). Small forests are climatically altered by edge proximity (Matlack 1993). Light availability, temperature, vapor pressure deficit, and soil humidity can be affected up to 50 m from the forest edge. The magnitude of the edge effects depends on orientation, canopy closure, forest development phase and the quality of the neighboring open land (Matlack 1993, Gehlhausen *et al.* 2000, Wright *et al.* 2010).

Forest edges are more vulnerable than the forest interior for external pressures that can reduce habitat suitability, e.g. eutrophication and acidification caused by atmospheric deposition of nitrogen and sulphur. Atmospheric deposition can be much higher at the forest edge than in the forest interior (De Schrijver *et al.* 1998, De Schrijver *et al.* 2007, Wuyts *et al.* 2008). Forest edges can be affected by fertilizers blown in from the neighboring agricultural fields and by biotic invasions (Honnay *et al.* 2002a).

1.1.3.3 Impact of temporal disruption on habitat suitability

Many habitat features are modified by the conversion of forest to other land use. After reforestation, some features can recover relatively fast whereas other features need a long time to restore. The light and microclimate conditions in forests are controlled by the canopy of tree species (Canham *et al.* 1990, Chen *et al.* 1993). Restoration of the high levels of shade and air humidity characteristic of a forest microclimate can be promoted by planting fast-growing species, e.g. poplar cultivars (Boothroyd-Roberts *et al.* 2013). Other habitat features such as soil conditions are modified for a long time, if not permanently. Many studies assessed long-term effects of former use as agricultural land or heathland on soil phosphorus (P) concentrations, pH, and organic matter content (Koerner *et al.* 1997, Leuschner 1997, Wilson *et al.* 1997, Verheyen *et al.* 1999, Dupouey *et al.* 2002, Plue *et al.* 2008, see also a compilation in Baeten 2010). As soil conditions are essential for terrestrial vascular plant species, spatio-temporal forest cover changes as illustrated by Fig. 1.1 can further reduce suitable habitat for specialists. The RF patch B2 is located next to AF on a site potentially suitable for the same habitat type, which is an ideal configuration for recovery of forest vegetation (Fig. 1.1). However, the soil conditions of patch B2 could be modified in such a way that recolonization by species that are specialists of forest habitat II is hampered.

1.2 Impact of spatio-temporal disruptions on herbaceous forest vegetation

1.2.1 Impact of fragmentation

Metapopulation models were successfully applied on vascular plant species occupancy in forest patches affected by spatio-temporal changes (Jacquemyn *et al.* 2003a, Vellend 2003, Verheyen *et al.* 2004). The incidence of many plant species was positively related to connectivity and area of forest patches in central Belgium (Jacquemyn *et al.* 2003b) and in central Lincolnshire (Verheyen *et al.* 2004). Other studies concluded that the positive relationship between forest species number and patch size was primarily explained by reduced habitat suitability or habitat diversity in small forest patches, and that the effect of increased extinction, as suggested by the metapopulation concept, was of minor importance (Peterken & Game 1984, Honnay *et al.* 1999a, Dupré & Ehrlén 2002). Negative effects of fragmentation can be difficult to assess (Harrison & Bruna 1999). Many forest plant species respond slowly to changes in changed landscape structure. Long-lived plants for which clonal propagation is important, as many forest plant species are, rather show remnant population dynamics instead of metapopulation dynamics (Eriksson 1996). The slow response of forest plant species to a changed landscape structure can result in an extinction debt, i.e. species populations continue to decline for some time after habitat loss and fragmentation have stopped (Vellend *et al.* 2006), but also in a colonization credit that indicates that species have not yet colonized newly created, suitable habitat (Vellend 2003; further explained in 1.2.2). Negative effects of fragmentation on species diversity can also be masked by an increase of forest edge species (Honnay *et al.* 1999a, Ewers & Didham 2006).

1.2.2 Impact of temporal disruption

The effect of habitat loss by temporal disruption on forest species diversity has been demonstrated many times. Many forest organisms are indicators of ecological continuity and are therefore sensitive to temporal disruption, e.g. lichens (Rose 1993, Coppins & Coppins 2002, Fritz *et al.* 2008), springtails (Ponge *et al.* 2006), beetles (Assmann 1999, Desender *et al.* 1999, Buse 2012), and vascular plants, which is the best studied species group (Peterken 1974, see also 22 studies compiled by Hermy *et al.* 1999).

The concept of ecological continuity refers to the continuous presence of suitable habitat, and in the case of forests, the term ‘forest continuity’ is often used (Nordén & Appelqvist

2001). Further on in this work, forest continuity refers to the continuous presence of a forest cover, not to the continuous presence of certain structural elements, e.g. old-growth trees or coarse dead wood. These elements can be habitat for certain species, e.g. specialized fungi or invertebrates, but are less important for vascular plant species. In this thesis, forest continuity is quantified by forest age, i.e. the number of years a forest was continuously present since the last conversion from open land to forest.

As explained in section 1.1.3., shade-tolerant AFS suffer from competitive exclusion by light-loving species when the tree cover is removed. Other mechanisms that explain the dependency of AFS on forest continuity are their poor seed dispersal capacity and low recruitment success (Flinn &Vellend 2005, Hermy & Verheyen 2007). Many AFS rely on short-distance dispersal modes (Matlack 1994b, Hermy *et al.* 1999), e.g. seed dispersal by ants. Rare long-distance dispersal events can explain higher-than-expected colonization rates (Clark 1998, Higgins & Richardson 1999). Most seeds of AFS are short-lived and are therefore scarce in the soil (Brown & Oosterhuis 1981, Bossuyt & Hermy 2001). However, this low frequency of viable seeds is relevant when a large area is considered (Plue *et al.* 2012). Long-term seed survival and long-distance seed dispersal can promote forest vegetation recovery when fragmentation of forest cover is low and ample space is available in suitable unoccupied habitat. An empirical study confirmed that the dispersal limitation of forest species is aggravated by forest fragmentation (Jamoneau *et al.* 2012). The relative importance of dispersal limitation and recruitment limitation, which indicates that species establishment is limited by habitat suitability (Verheyen & Hermy 2001b, Baeten *et al.* 2009b), will be further discussed in section 1.2.3.

The aforementioned processes and species traits explain the inability of AFS to survive even a relatively short period of forest clearing and the importance of spatial and temporal habitat continuity for AFS diversity. By consequence, conservation of the remaining AF is generally seen as a priority (Peterken 1974, Peterken 1977, Peterken & Game 1984, Spencer & Kirby 1992, Wulf 2003, De Frenne *et al.* 2011). The proportion of AF in a dynamic landscape is highly explanatory for the incidence of forest species in RF patches, and therefore also for the recovery rate of RF vegetation (Honnay *et al.* 2002b, Vellend 2003). RF in physical contact with AF can be colonized by AFS, albeit slowly, whereas AFS are rarely found in isolated RF (Peterken & Game 1984, Jacquemyn *et al.* 2003b). Linear landscape elements can also be important for the recovery of herbaceous forest vegetation. They can be relics of AF that still contain AFS (Peterken 1974, Honnay *et al.* 1999a). Hedgerows and tree rows can also function as habitat corridors, increasing connectivity between forest patches (Petit *et al.* 2004, Wehling & Diekmann 2009), and support vegetation recovery when included in RF (Endels *et al.* 2004).

In the hypothetical dynamic landscape illustrated by Fig. 1.1, RF patch B2 is located adjacent to AF patch B1, and for this reason, B2 has the highest recovery potential. RF patch D2 is connected with AF patch B1 from time 3 onwards. However, the distance to the AF patch B1 is relatively large and therefore recovery may take a long time. As most AFS depend on short-distance colonization and survival outside forest is exceptional, recovery of patch B3, established after D2, is necessary before D2 can be accessed by AFS. Patch D2 also shares a border with the historical perimeter of patch A1 and can be colonized faster by AFS if relic populations are still present along this historical border, e.g. in a hedgerow. If not connected by hedgerows, RF patch E2 is completely isolated from other forest patches and is expected to have the lowest recovery potential.

1.2.3 Constraints by habitat suitability

1.2.3.1 Natural habitat heterogeneity

The AFS listed by 22 European studies avoid wet and very dry soils and prefer weakly acid to neutral soils with an intermediate trophic level, i.e. mesophilous soils (Hermy *et al.* 1999). Forest plant communities of mesophilous soils thus potentially contain a high number of AFS, whereas communities on waterlogged peat soils and nutrient-poor, acid sand soils contain very few AFS (Hermy *et al.* 1999)

Forest communities of mesophilous sites, classified as *Fagetalia* in Ellenberg *et al.* (1992), contain 56% (74 species) of the AFS of Europe, and 25% (157 species) of typical forest species (Hermy *et al.* 1999). *Fagetalia* forests are subdivided into *Fagion sylvaticae* and *Carpinion betuli* communities, both located on soils with a high silt loam content, and the *Alno-Ulmion* community, located on alluvial soil (Ellenberg *et al.* 1992). These forest communities are named ash-alder, elm-ash, maple-ash, ash-oak and partially also oak-beech forest in Flanders (Cornelis *et al.* 2009).

The hypothetical landscape configuration in Fig. 1.1 illustrates that habitat specialists can experience much higher levels of habitat loss and fragmentation caused by spatio-temporal disruptions than generalist species. The natural variability of habitat suitability (habitat heterogeneity) implicates that the distribution of specialist AFS is not uniform in the AF patches, sources for colonization of AFS into the RF parches. Let us assume that sites I and II are silt loam soils and gleysols, respectively, and that site III is an acid sand soil. This would mean that AF of habitat I (patch A1) and II (a small area of patch B1) can contain many AFS, whereas AF of habitat III (most of patch B1) can contain only few AFS. By consequence, the recovery of RF patch B2, most of which is located on a site potentially suitable for habitat II, depends on the small area of AF patch B1 located on a similar site.

1.2.3.2 Impact of fragmentation on habitat suitability

Long-established forests, in particular AF, are considered reservoirs of biodiversity (Rackham 2003), but anthropogenic disturbances, internal or external, can cause a shift in species composition or a loss of species diversity in AF. A highly fragmented forest cover with many small patches has a high proportion of forest edge and is therefore more sensitive to degradation caused by external abiotic and biotic pressures than a less fragmented forest cover with large forest patches (Honnay *et al.* 2002a).

Atmospheric depositions that cause acidification and eutrophication, measured in forest interiors in Flanders, declined with approximately 50% over the past 17 years (Verstraeten *et al.* 2012). However, the average deposition loads of nitrogen and sulphur in 2011 still equaled 24 kg/ha and 9.4 kg/ha, respectively (Verstraeten *et al.* 2012). The critical values for nitrogen in mesophilous forests are comprised between 20 and 34 kg/ha/yr (van Dobben *et al.* 2012). As the deposition loads at the forest edge can be much higher than in the forest interior where depositions are measured, critical loads are mostly exceeded at the forest edge (De Schrijver *et al.* 2007). In that case effects on the vegetation, e.g. an increase of grasses (van Dobben *et al.* 1999), are expected. Soils of loess plateaus are very sensitive to acidification (Brahy *et al.* 2000). The decline of sensitive species, e.g. *Primula elatior* and *Paris quadrifolia*, observed in a *Carpinion betuli* forest community on silt loam soil within 46 years was attributed to acidification (Baeten *et al.* 2009a). Mesophilous alluvial soils, potentially suitable for the *Alno-Ulmion* (Ellenberg *et al.* 1992), can be affected by dessication that causes a shift towards a

Quercion community without vernal AFS (Frambach & Meulman 1988). A 30-year comparison of herbaceous vegetation development in AF and RF on alluvial soil in the western part of Flanders revealed an impoverishment that included a decline of AFS and an increase of competitive species, whereas an increase of AFS in RF would be expected. This opposite development was attributed to negative environmental drivers, e.g. the intensification of the land use surrounding the fragmented forest patches (Baeten *et al.* 2010a).

Other studies indicated no causal relationship between habitat fragmentation and habitat degradation (Adriaens *et al.* 2009, Jamoneau *et al.* 2012). Small undisturbed habitat fragments can be suitable for rare habitat specialists (Adriaens *et al.* 2009). In landscapes with a similar level of forest fragmention, the species diversity of forest patches was determined by the quality of the surrounding landscape matrix (Jamoneau *et al.* 2012).

1.2.3.3 Impact of temporal disruption on habitat suitability

The recovery of the herbaceous vegetation in RF patches in Fig. 1.1 could also be hampered by modified habitat suitability as a consequence of former land use. Many soil characteristics are modified for a very long time when forest is converted to another land use, e.g. heathland, grassland, or arable field (see review by Baeten 2010). Former Roman settlements still have altered soil conditions and are marked by a specific forest vegetation, more than 1500 years after reforestation (Dupouey *et al.* 2002, Plue *et al.* 2008, Etienne *et al.* 2013).

In the course of succession from heathland to forest, litter production by trees triggers a gradual recovery of the degraded heathland soil by nutrient accumulation in the organic topsoil. The time necessary for a full recovery of forest soil and vegetation was quantified at 350 years (Leuschner 1997). By contrast, the soil of forest formerly used as fertilized grassland or arable field, is often eutrophicated, in particular with P. The persistence of P in post-agricultural forest soils has been demonstrated many times (Koerner *et al.* 1997, Verheyen *et al.* 1999, Dupouey *et al.* 2002, Falkengren-Grerup *et al.* 2006, Dambrine *et al.* 2007, Plue *et al.* 2008). Eutrophication with P stimulates competitive species, e.g. *Urtica dioica* (Pigott 1971). Increased P availability can also strengthen the differential colonization capacities of forest species. As opposed to a fast-colonizing species (*Geum* *urbanum*), a slow colonizer (*Primula elatior*) lacked the plasticity to benefit from the increased P level (Baeten *et al.* 2009b).

Forests that originated on heathland are mostly located on acid sand soils in northeastern Flanders (Fig. 1.2). Mesophilous sites with a high silt loam content that are the focus of this thesis, are located more to the south of Flanders. If not covered by forest for a long time, forests on mesophilous sites were mostly used as grassland or arable land before conversion to forest (Fig. 1.2).

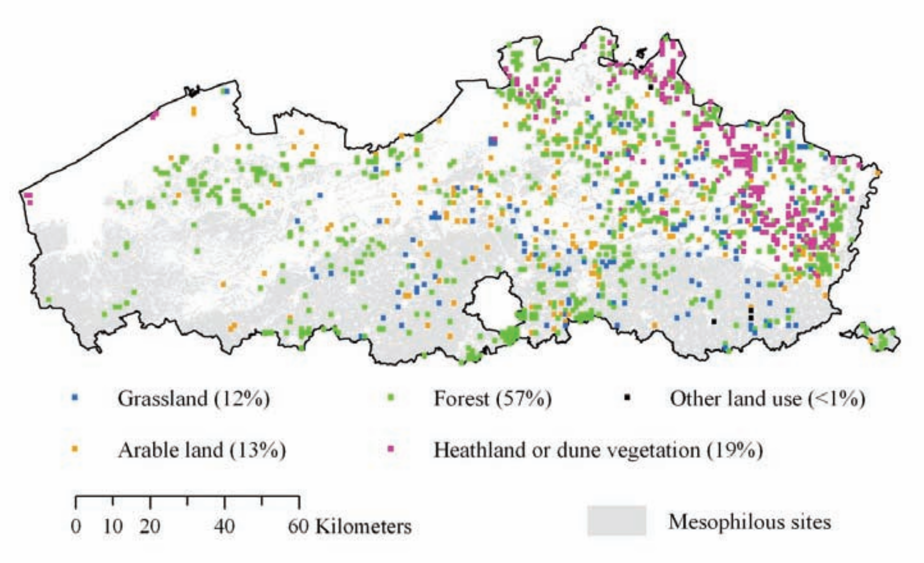

Fig. 1.2 Specification of the dominant land use between 1775 and 2000 (color code) of forests of Flanders in 2000, represented by forest inventory points (n = 1296). For this survey forest vegetation was systematically inventoried in 256 m^2 plots set out at the nodes of a 1 km x 1 km grid. The colors represent land use categories that occupied sample points for the longest time in the past 225 years, with the proportions of the total forest cover in 2000 between brackets.

1.2.4 The relative importance of dispersal and recruitment limitation

Many forest plant species, but AFS in particular, are scarce in RF. This can be caused by the high rate of land use changes, which exceeds the colonization capacities of AFS (Matlack 2005). If the frequency or abundance of a species is affected, this species is classified as dispersal limited (Primack & Miao 1992, Verheyen & Hermy 2001b). On the other hand, land use conversions can also result in long-term or even permanent modifications of the habitat suitability, in particular for the soil compartment. Species that are hampered by modified habitat features are called microsite- or recruitment-limited species (Eriksson & Ehrlén 1992, Verheyen & Hermy 2001b). When both processes are involved, a species is recruitment and dispersal limited (Verheyen & Hermy 2001b, Baeten *et al.* 2009b). Recent research indicated that the colonization rate in RF is highly variable among AFS: some species listed as AFS are fast colonizers whereas other are very slow colonizers (Brunet *et al.* 2012). The relative importance of dispersal and recruitment limitation could explain the heterogeneous behavior among AFS colonizing RF.

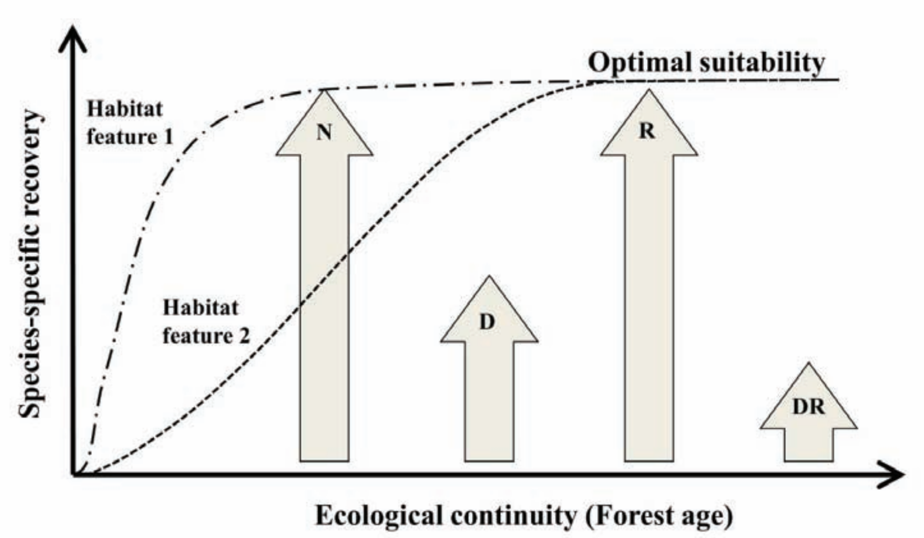

Fig. 1.3 The suitability of habitat features can increase fast (feature 1, e.g. canopy cover) or slowly (feature 2, e.g. certain soil conditions) with increasing ecological continuity, in this case the age of a post-agricultural forest. Based on the rate of the response to the increasing habitat suitability, plant species can be qualified as dispersal limited (D, e.g. *Anemone nemorosa*), recruitment limited (R, e.g. *Paris quadrifolia*), dispersal and recruitment limited (DR, e.g. *Primula elatior*), or not limited by dispersal or recruitment (N, e.g. *Ranunculus ficaria*). The graph is inspired by Nordén & Appelqvist (2001) but modified for vascular plant species based on the qualification by Verheyen & Hermy (2001b).

The specific recovery rate in RF of four species, classified by Verheyen & Hermy (2001b), can be depicted in relation to the recovery rate of the required habitat features and the ecological continuity of forest habitat, i.e. the time that is available for recolonization (Fig. 1.3). This graph does not represent the distance to a colonization source, e.g. the adjacent AF, as it was assumed that connectivity was equal for all four species types.

A habitat feature such as canopy cover can recover relatively fast after reconversion of open land to forest (habitat feature 1 in Fig. 1.3). Species with good dispersal capacities that benefit from a closed canopy cover and that are not specialists for other habitat features (N in Fig. 1.3) can increase fast after conversion from open land to forest, e.g. *Ranunculus ficaria*, a species that was not dispersal or recruitment limited in the forest studied by Verheyen & Hermy (2001b). *Paris quadrifolia* was limited by recruitment but not by dispersal (R in Fig. 1.3) in the same study. As an endozoochorous species, which can be dispersed via digestion by animals (Hermy *et al.* 1999), it is capable of long-distance dispersal. However, *P. quadrifolia* requires soil with a high pH and a low soil P content (habitat feature 2 in Fig. 1.3). These specific habitat features were not (yet) in an optimal condition in the forest stands recently planted on agricultural land studied by Verheyen & Hermy (2001b). By contrast, *Anemone nemorosa* is a species with a wide amplitude for many soil conditions, e.g. soil pH. Although habitat was already suitable in the post-agricultural forest, the species was still scarce as a consequence of its poor dispersal capacity (D in Fig. 1.3). *Primula elatior* was classified as dispersal and recruitment limited (DR in Fig. 1.3). A long time is needed to achieve the required optimal suitability of habitat feature 2 (high soil pH, low soil P availability), but even when the RF habitat is at this point, species frequency or abundance are still relatively low as a result of dispersal limitation.

Species that are confined to AF suffer from dispersal limitation, from recruitment limitation, or from both (Eriksson & Ehrlén 1992, Verheyen & Hermy 2001b). Furthermore, there are indications that habitat loss and fragmentation alter the relative importance of both processes. In landscapes with an intact forest cover, habitat heterogeneity explained species assemblages better than in landscapes with a fragmented forest cover, where stochastic extinction and dispersal limitation prevailed (Jamoneau *et al.* 2012).

1.3 Objectives and outline of the thesis

As demonstrated in the previous section, spatio-temporal disruptions can result into a progressive loss and fragmentation of forest habitat and the processes that explain the impact on forest plant diversity are well studied. As a result of spatio-temporal disruptions, forest cover can be composed of a variable proportion of RF patches, with a specific habitat continuity (age), connectivity and suitability that determine forest vegetation composition (e.g. see Verheyen *et al.* 2006). Spatial explicit data (maps) on these three aspects, at a scale that is relevant for landscape planning, are not available for our study area. By consequence, the relative importance of habitat continuity, connectivity, and suitability is unknown. It is the objective of this thesis to map and quantify the impact of habitat continuity, connectivity, and suitability on different scales. The example of the hypothetical dynamic landscape (Fig. 1.1) illustrated that it is highly relevant to do so, in order to develop and implement strategies of forest habitat conservation and restoration.

Table 1.1 Outline of the thesis, with the number and title of the successive Chapters. The spatial and temporal resolution of the input data increase throughout the thesis, whereas the area and time period that are covered diminish.

Chapter number and title	Space		Time	
	Range (km^2)	Resolution (qualitative)	Range (yr)	Resolution (yr)
2 Natural habitat heterogeneity: a map of Potential Natural Vegetation (PNV)	Flanders (~13500)	Medium	>200	+/-75
3 Forest habitat loss and fragmentation by spatio-temporal disruptions (based on Chapter 2)	Flanders (~13500)	Medium	>200	+/-75
4 A map of potential AFS diversity on mesophilous sites (based on Chapters 2 and 3)	Flanders (~13500)	Medium	>200	+/-75
5 Impact of soil and light conditions on vegetation recovery in a mesophilous forest	Forest patch (0.33)	High	>200	+/-25
6 Impact of clear-felling on colonization of forest plants into a post-agricultural forest stand	Forest stand (0.003)	Very high	10	5

In Chapters 2, 3, and 4 habitat continuity, connectivity, and suitability, were studied for a whole region with a uniform forest and nature policy (Flanders, northern Belgium) (Table 1.1). Chapter 2 presents a map of natural forest habitat heterogeneity in Flanders. This map depicts the Potential Natural Vegetation (PNV), which is the most complete forest vegetation, including slow colonizing AFS, that can develop on a site. This is, as far as we know, the first time that the AFS concept is included into PNV construction. Also sites, presently not covered by forest, are represented by the PNV map and for this purpose the dimension of the time that is necessary for a PNV to develop, is disregarded. In Chapter 3, the PNV map is used to quantify the loss and fragmentation of five forest habitat types (PNV types), caused by spatio-temporal disruptions. This landscape study at the level of Flanders, additionally included maps of the forest cover at four times between 1775 and 2000. Mapping forest cover changes at such an extent is a methodological challenge and has been rarely done before. We applied an innovative accuracy analysis, using land use history assessed on forest inventory points, to validate the quantified impact on habitat loss and fragmentation. Natural habitat suitability, derived from the PNV map in Chapter 2, and maps of forest cover at four times between 1775 and 2000 (Chapter 3) served to predict the AFS richness of present-day forest and the recovery potential of open land (Chapter 4). For this purpose, we had to calculate new landscape metrics and such an operational landscape model has not been constructed before. This spatial explicit model focussed on mesophilous sites, where the highest AFS diversity can be found and, according to the results of Chapter 3, the need for conservation and restoration is the highest.

The results of Chapters 2, 3, and 4 indicate that several variables that explain vegetation recovery, are not available for the whole region or are only available with a low resolution at this range. For this reason, forest vegetation recovery was also studied in smaller areas, where additional explanatory information was sampled at the scale of cadastral parcels or forests stands (Chapters 5 and 6, see Table 1.1). In Chapter 5 the impact of chemical soil conditions and light intensity on herbaceous forest vegetation were studied within a single forest, for which land use change in the past 225 years was mapped with a high resolution (Table 1.1). Spatial and temporal resolution further increase in Chapter 6, where the effect of forest management was monitored on vegetation recovery in a single post-agricultural forest stand (Table 1.1).

In Chapter 5, vegetation recovery is studied at the level of a single mesophilous forest. The Muizenbos forest reserve (33 ha) was an ideal study site for this purpose as it consists of a mosaic of RF stands adjacent to AF, which is an optimal layout for vegetation recovery. The land use history of this forest since 1775 was mapped with a high resolution (see Verheyen & Hermy 2001a). In Chapter 5, a systematic 50 m x 50 m grid was used for representative sampling of vegetation and explanatory variables. By doing so, vegetation recovery at the scale of this single forest was related to variables that are not available for the whole of Flanders, e.g. soil eutrophication level, soil pH, or light conditions. By doing so it was revealed that, in this forest, habitat quality (in particular the level of eutrophication with P) is explained by land use history. In the final Chapter 7 forest inventory data confirmed that these findings apply to Flanders in general. Chapter 6 investigates in detail a single forest stand in the same forest, Muizenbos. The studied stand was planted on agricultural land in 1952 and inventoried three times between 1997 and 2007, by means of 5 m x 5 m grid. By doing so, the effect of forest management (clear-felling) on vegetation recovery was monitored for a single stand. The impact of clear-felling on forest vegetation was studied several times before, which is also the case for colonization patterns of forest plants in post-agricultural forest. The impact of clear-felling on colonization patterns in post-agricultural forest, however, has not been studied before.

The final Chapter 7 is a general conclusion and a generalization of the results in Chapters 2-6, followed by recommendations for landscape planning, and nature and forest management. The final section gives perspectives for further research based on the identified knowledge gaps.

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2 Natural habitat heterogeneity: a map of Potential Natural Vegetation (PNV)

After: De Keersmaeker L, Rogiers N, Vandekerkhove K, De Vos B, Roelandt B, Cornelis J, De Schrijver A, Onkelinx , Thomaes A, Hermy M, Verheyen K (2013) Integrating the concept of ancient forest plant species into a Potential Natural Vegetation map - a case study from Flanders, northern Belgium. Folia Geobotanica 48, 137-162

2.1 Abstract

Construction of potential natural vegetation (PNV) poses particular challenges in landscapes heavily altered by human activity and must be based on transparent, repeatable methods. We integrated the concept of ancient forest (AF) and ancient forest species (AFS) into a four-step procedure of PNV mapping: 1) Classification of forest vegetation relevés; 2) Selection of those vegetation types that can serve as PNV units, based on AF and AFS; 3) merging of selected vegetation types to five PNV units that can be predicted from a digital morphogenetic soil map; 4) mapping of three additional PNV units based on additional environmental data. The second step, concerning the selection of reference forest vegetation, is of particular interest for PNV construction in Flanders (northern Belgium), where forest cover has been subject to temporal disruption and spatial fragmentation. Among the variety of extant forest recovery states, we chose those vegetation types as PNV units, of which a high proportion of relevés had been located in AF and that contained many AFS. As the frequency of AFS depends on site conditions, we only compared and selected vegetation types that are found on similar sites according to average Ellenberg indicator values. While succession is irrelevant for the definition of PNV, colonization rates of AFS can be used to estimate the time required for PNV to be restored in a site.

2.2 Introduction

The PNV concept, introduced by Tüxen (1956), is defined as the hypothetical vegetation, that would be installed instantaneously in equilibrium with the ruling site conditions, if human interference ceased. PNV units can be derived from existing actual vegetation, its relationship with site conditions and observation of competition (Mueller-Dombois & Ellenberg 2002). PNV maps present an effect-oriented site classification for nature-oriented silviculture, nature conservation and landscape planning (Tüxen 1956). They serve as a baseline to project shifts of natural vegetation caused by climate change (Brzeziecki *et al.* 1995, Wang *et al.* 2011). They can also be very useful as a reference for restoration of terrestrial ecosystems in anthropogenic landscapes (Moravec 1998). Integrating abiotic constraints and competition in the absence of management, PNV maps are an alternative for neutral landscape models, that aim to differentiate random patterns from patterns generated by ecological processes (Ricotta *et al.* 2002). Combining PNV map and neutral landscape model allows to analyze the recovery level of forest vegetation (e.g. Verheyen *et al.* 2006).

PNV was introduced as an alternative to the climax concept, where succession was excluded to overcome discussions regarding the time required for climax vegetation to install (Härdtle 1995). The PNV concept was adjusted to include persistent and irreversible anthropogenic changes of site conditions (Kowarik 1987, Härdtle 1995, Zerbe 1998). It has recently been proposed to preserve the original, static PNV concept as a baseline and cover estimations of potential successional outcomes by the extended concept of potential future natural vegetation (PFV) (Somodi *et al.* 2012).

Paradoxically, the need for PNV maps is highest for landscapes with a low degree of 'naturalness', where PNV construction is most problematic. An essential and critical step in PNV construction in cultural or semi-natural landscapes is the selection of reference vegetation. Thus, in constructing forest PNV alterations of tree species composition by former management pose considerable challenges (Leuschner 1997, Zerbe 1998). Herbaceous forest vegetation usually develops without intentional human manipulation, but is indirectly influenced by forest management (e.g. Becker 1979, Decocq *et al.* 2004, Van Calster *et al.* 2008). In landscapes dominated by recent forests land use history and landscape configuration are important explanatory factors, too (e.g. Verheyen *et al.* 1999, Flinn & Vellend 2005, Verheyen *et al.* 2006). Many forest species, so called ancient forest species (AFS), are slow colonizers (Matlack 1994b, Brunet & von Oheimb 1998a, Bossuyt *et al.* 1999b). They depend on a long and continuous forest cover and are scarce or missing in recently established forest (Peterken 1974, Hermy & Stieperaere 1981). AFS are therefore considered as quality indicators of forest biodiversity (Peterken 1974). When several AFS are present, succession is more or less completed and forest vegetation is ‘saturated’ in the sense of Kopecký & Hejný (1974). Their presence can thus be used as a criterion to select reference forest vegetation for PNV construction, while excluding ‘unsaturated’ forest vegetation.

The present study integrates the AFS concept into PNV construction. Flanders (northern Belgium) is an ideal study area for this purpose since it is characterized by a very dynamic land use history that includes successive phases of deforestation and reforestation (e.g. Tack *et al.* 1993, Verheyen *et al.* 1999, see Chapter 3 and 5).

2.3 Materials and methods

2.3.1 Study area

The Flemish region in the North of Belgium covers ca. 13.500 km^2. The climate is temperate oceanic with some geographical variation, as indicated by average values for climate data calculated on the time period 1981-2010 by the Royal Meteorological Institute of Belgium. From the North Sea shore towards the eastern border, the annual average of monthly maximum temperatures increases from 12.5 °C to 14.3° C, and the annual number of frost days increases from 55 to 95. Annual sunshine hours decrease from 1723 to 1541 and annual precipitation increases from 660 mm to 1015 mm along this gradient.

Altitude gradually increases from sea level to ca. 290 m in the Southeast. The North of Flanders is flat or undulating, but steep slopes can be found locally in the South. Some relic hills up to 150 m are present in the Southwest, originating from a plateau which is less eroded towards the Southeast. In the Northeast, a periglacial gravel plateau deposited by the river Meuse with an altitude of up to 100 m, creates specific edaphic conditions.

The basins of the rivers Scheldt, Yser and Meuse, which all flow to the North Sea, determine the hydrology. Topsoils mainly consist of pleistocene aeolian sand and loess deposits. The silt loam content gradually increases from the North to the South. Heathland or forest soils on sand are mostly Podzols (IUSS Working Group WRB 2006). Silt loam soils covered by forest have a clay illuviation horizon and are classified as Albeluvisols or Luvisols (IUSS Working Group WRB 2006). Alluvial soils in valleys without profile development, classified as Gleysols, and peat soils, classified as Histosols, frequently occur in valleys in the Northeast. Outcroppings of tertiary deposits (sand, clay or sandstone) or secondary marlstone are scarce but locally determine topsoil conditions.

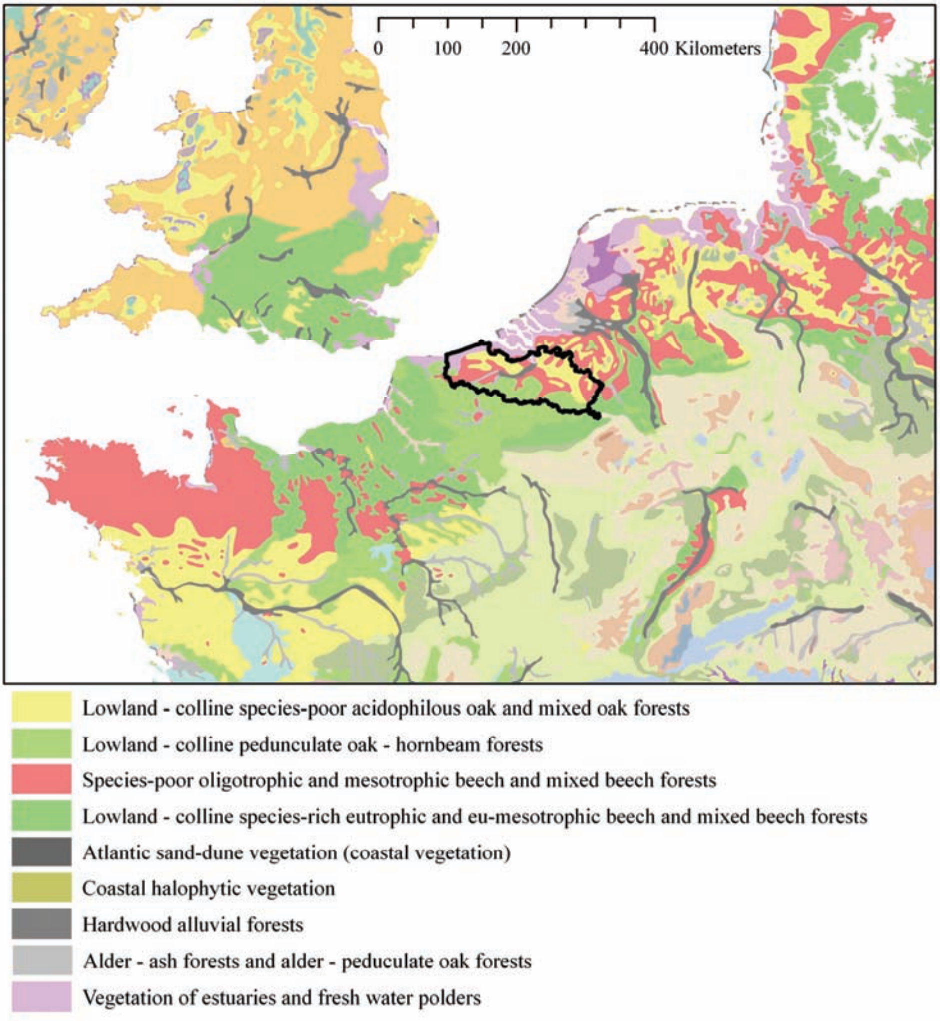


Fig. 2.1 Snap shot of the Natural Vegetation Map of Europe (Bohn *et al.* 2003), representing NW-Europe with Flanders (northern Belgium) indicated by the black outline. Vegetation units that occur in Flanders are explained by the legend.

11% of the total area is covered by forest, half of which is concentrated on sandy soils that are mainly former heathlands afforested with conifer species (*Pinus sylvestris* and *P. nigra*). Approximately 16% of the forest cover has been permanently present since 1775, at which time the oldest, systematic map covering the whole region was drawn (see Chapter 3). These forests are henceforth referred to as ancient forest (AF), whereas all other forests are called recent forest (RF). The natural vegetation map of Europe (Bohn *et al.* 2003) indicates that most of Flanders would be covered by lowland or colline forest vegetation, classified as acidophilous oak and mixed oak forests on sand soils, oak-hornbeam forest on silt loam soils, and oligotrophic, mesotrophic or eutrophic beech or mixed beech forests on soils with an intermediate silt loam content. Hardwood alluvial forests and ash-alder forests mark the main river valleys, whereas the coastal plain is not covered by forest vegetation (Fig. 2.1). A further subdivision of forest vegetation on silt loam soils into Atlantic (West) and Subatlantic (East) phytogeographical regions is based on the distribution of *Hyacinthoides non-scripta* and *Tamus communis* (Van Landuyt *et al.* 2006).

2.3.2 Methodological framework

We share the point of view expressed by Peterken (1996), who stated that the definition of ‘natural’ is not a matter of right or wrong, but of arriving at something useful for a particular purpose. PNV will serve its purposes best when constructed in an unambiguous, repeatable manner (Härdtle 1995, Somodi *et al.* 2012). The PNV map of Flanders was therefore constructed within following methodological framework:

1) PNV mapping must be based on a consistent pedological basis, the digital soil map of Belgium (AGIV 2001a). The digital soil map is the result of a morphogenetic soil classification and displays robust properties resulting from long-term pedogenic processes. Soil properties that change rapidly as a consequence of human occupation, e.g. pH, organic matter and eutrophication are not represented by the digital soil map, and are considered less appropriate for PNV construction. Ponds or lakes, and marine polders were excluded as these sites would not be covered by forest vegetation without further human interference. This is in agreement with the Natural Vegetation Map of Europe (Bohn *et al.* 2003, see Fig. 2.1). Soil information of disturbed sites, built up areas and military areas is missing and therefore these sites were not mapped either.

2) Temporal continuity and spatial isolation are disregarded in PNV mapping, since the PNV concept explicitly excludes a time component.

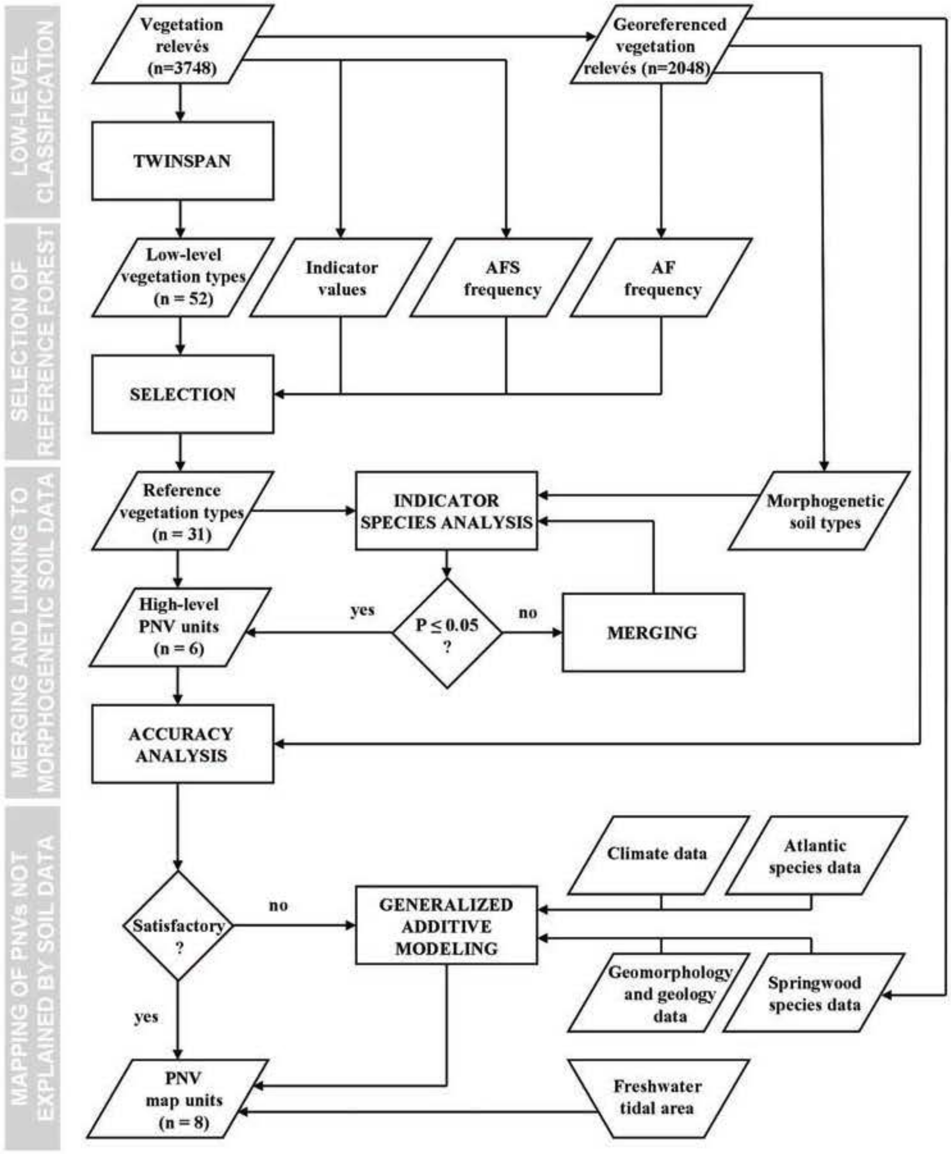


Fig. 2.2 Flow diagram of data and operations for PNV construction. Parallelograms indicate input or output data; rectangles are operations; diamonds are decisions; the trapezoid is a manual operation.

3) With no pristine forests available, vegetation relevés that served as a reference for PNV construction were mostly collected in forest ecosystems under traditional management, which includes a reduction or control of natural dynamics, e.g. by timber extraction and grazing. As some ecosystem types such as alluvial forests may be restored by re-introducing dynamics, we considered removal of river embankments as a scenario for freshwater and oligohaline tides, which may serve to counteract negative effects, e.g. increased inundation risk observed during the past decades (Van Braeckel *et al.* 2006).

The methodology applied for PNV construction included four successive phases, that will be explained in following sections (Fig. 2.2): 1) Preliminary fine-scale classification of herbaceous forest vegetation relevés into vegetation types; 2) selection of reference vegetation types by evaluation of AF and AFS frequencies, in relation to edaphic conditions represented by species indicator values (Ellenberg & Leuschner 2010); 3) Merging of selected reference vegetation types to PNV units linked to morphogenetic soil types, thus converting the digital soil map into a PNV; 4) mapping of PNV units that are floristically well defined, but not accurately explained by the digital soil map according to an error analysis, using additional environmental data.

2.3.3 Floristic data and classification

PNV construction was based on 3748 vegetation relevés of the herbaceous layer of forests that also served for a new typology of forest vegetation of Flanders (Cornelis *et al.* 2009, see Table 2.1). The plot sizes were variable (Table 2.1), which is often the case in phytosociological studies, but large enough to include most specific species of the studied forest vegetation types and therefore suitable for a vegetation classification. Coordinates that are necessary for PNV mapping were available for a subset of 2048 relevés. The 3748 relevés were classified by the TWINSPAN algorithm (Hill 1979), considering eight levels of division to obtain a fine-scale classification with high resolution (Annex 2.1). The resulting groups of vegetation relevés are henceforth referred to as vegetation types. Three pseudospecies cutlevels (limits: 0, 5 and 50% cover) were applied. These threshold values are compatible with both the Braun-Blanquet and Londo sampling scales. All species and relevés were given an equal weight for classification, in order not to manipulate the results by a priori assumptions, e.g. concerning the presence of AFS.

Table 2.1 Origin of the data and the number of relevés used in the classification (Nc), the number of georeferenced vegetation relevés (Ng), the plot size, the time of sampling and the applied scale.

Sources with reference	Nc	Ng	Plot size (m^2)	Time	Scale
Van Den Meersschaut et al. (1999)	56	55	256	1998-1999	Londo
Waterinckx and Roelandt (2001)	1400	1296	256	1997-1999	Braun-Blanquet
Hermy (1985) and Godderis (1976), incorporated in Hermy (1985)	638	0	Variable	1975-1983	Braun-Blanquet
Faculté Universitaire des Sciences Agronomiques de Gembloux	571	0	Variable	1942-1980	Braun-Blanquet
Information Centre of the Zoniën Forest (ICZO)	139	0	Variable	1989-1999	Braun-Blanquet
Institute for Nature Conservation	161	0	Variable	1982-1998	Londo
Herrier (1989)	20	0	Variable	1987-1988	Londo
De Keersmaeker (unpublished)	42	41	250	1997	Londo
Vanmechelen et al. (1997); Van Den Meersschaut et al. (1996); Geudens et al. (1997); Viaene et al. (1997)	721	656	250	1996-1997	Londo
Total	3748	2048			

Trees and shrubs were not used for classification, as their species composition is usually directly manipulated by forest management. Although not used for classification, regeneration of tree and shrub species (height < 1.3 m) was included in the synoptic table of PNV units (Annex 2.2) to give an indication of future composition of the woody layer without human interference.

2.3.4 Selection of reference vegetation

The TWINSPAN classification was interpreted by means of indicator values of herbaceous plant species listed by Ellenberg & Leuschner (2010). These indicator values provide an indication of edaphic site conditions, i.e. nutrients (N), reaction (R) and moisture (F). Averages of the indicator values were calculated at vegetation relevé level (mR, mN, and mF) using presence/absence species data (qualitative data) as described by Diekmann (2003). The mR, mN, and mF values calculated at vegetation relevé level, were used to calculate average values and standard deviations at vegetation type level, by means of the included vegetation relevés. The mN x mR value, which is a quantification of the humus quality according to Rogister (1978), was calculated analogously. The humus quality value and the mF value for humidity form the axes of an ecogram that was used for vegetation-based site classification (Muys & Granval 1997). We used the same approach to construct an ecogram to characterize the retained vegetation types.

AFS frequency was calculated based on the floristic composition at relevé level (n = 3748). The number of herbaceous species listed as AFS by Hermy *et al.* (1999) was divided by the total species number of the same relevé and expressed as a percentage (AFS frequency). An average value of AFS frequency was calculated at vegetation type level, to serve for comparison of vegetation types. Areas of ancient forest (AF) were defined as forest permanently present on 7 historical maps distributed by the Belgian National Geographic Institute, and approximately drawn at: 1775, 1850, 1865, 1890, 1909-1940, 1960 and 1980. AF frequency was calculated at vegetation type level on the subset of georeferenced relevés (n = 2048), as the number of relevés of a vegetation type located in AF, divided by the total number of relevés included into a vegetation type, expressed as a percentage.

AFS frequency and AF frequency were used as criteria for selection of reference vegetation, in combination with the mN x mR, and mF values of vegetation types. We did not use threshold values for selection of reference vegetation, but compared AFS frequency and AF frequency of vegetation units that occupy similar positions in the ecogram. When more than one vegetation type was present on a similar place in the ecogram (indicating similar edaphic conditions of these vegetation types), the vegetation type with the highest AFS frequency and AF frequency was retained as the reference vegetation. In that case the other vegetation types with lower values of AF frequency and AFS frequency were not included into PNV construction. Although the AFS and AF ratios assisted with the selection procedure, it was still an evaluation procedure.

2.3.5 Merging and linking to soil types

PNV mapping was mainly based on soil characteristics represented by the digital Belgian soil map at a scale of 1: 20,000 (AGIV 2001a). The digital soil map corresponds to the original analogue map that resulted from the National Soil Survey, carried out between 1947 and 1971. This field survey applied a morphogenetic soil typology based on ordinal classes of texture, drainage, and profile development (Table 2.2). The digital soil map combines these ordinal classes into a three-character code, further referred to as soil series.

The low-level vegetation types that were selected as reference vegetation for PNV construction, were merged in agreement with the TWINSPAN hierarchy until all the resulting PNV units were significantly ($P<0.05$) related with groups of soil series, according to Indicator Species Analysis (ISA: Dufrêne & Legendre 1997). ISA determines the indicator value of a species in a classification (IndVal score), which is the association between a species and a group of sites, and tests the significance of the association by permutation. In this study, the selected reference vegetation types were treated as species and the soil series, on which at least 5 relevés were found, were treated grouping variables.

Table 2.2 Explanation of the soil series of the Belgian soil map, composed by three characters representing ordinal texture, drainage and profile development classes.

CLASS	TEXTURE CODE AND DESCRIPTION		DRAINAGE CODE AND DESCRIPTION			PROFILE DEVELOPMENT CODE AND DESCRIPTION	
				Textures Z, S, P	Textures L, A, E, U		
1	X Z	Sand dunes (Coarse sandy soils) Sand	a	No mottling in upper 120 cm	not distinguished	h	Discontinuous humus and / or iron B horizon (Postpodsols)
2	S	Clayey and silty sand	b	Mottling at 90-120 cm depth	no mottling	g	Podsolized soils
3	P	Light sandy silt	c	Mottling at 60-90 cm depth	Mottling at 80-120 cm	f	Weakly podzolized: developed humus and or iron B horizon
4	L	Sandy silt	d	Mottling at 40-60 cm depth	Mottling at 50-80 cm	c	Discontinuous textural B horizon
	G	Sandy silt xith more than 5% coarse fragments (> 2 mm)				m	Thick antropogenic humus A horizon
5	A	Silt	e	Mottling at 20-40 cm depth	Mottling at 30-50 cm and reduction horizon at 80-120 cm depth	a d	Textural B horizon Textural B horizon
			h	Mottling at 20-40 cm depth, no permanent water table (pseudogley)	Mottling at 30-50 cm and no permanent water table (pseudogley)	x	Undefined profile development
6	E	Clay	f	Mottling at <20 cm depth and reduction horizon at 40-80 cm depth	Mottling at <30 cm and reduction horizon at 40-80 cm depth	b	Structural B or colour B horizon
			i	Mottling at <20 cm depth and no permanent water table (pseudogley)	Mottling at <30 cm and no permanent water table (pseudogley)		
7	U	Heavy clay	g	Reduction horizon <40 cm	Reduction horizon <40 cm	e p	Chernozemic A horizon No B horizon
8	V	Soils with > 30% organic matter in the upper 40 cm					

The ISA procedure resulted in significant associations of 5 PNV types with 12 soil series groups, that included 79 soil series (from a total of 426) and covered 44.1% of the total area of Flanders. The number of georeferenced relevés classified to a PNV unit and located on a soil series group, was divided by the total number of georeferenced relevés classified to all PNV types, located on the same soil series group. This ratio (expressed as a percentage) was used as a measure for the association between soil series and PNV units. To determine association measures of the 301 soil series not included into ISA (covering 33.1% of the total area of Flanders), the three ordinal texture, drainage, and profile development classes that form a soil series were split off. The association measures were interpolated for each of these three soil characteristics separately, based on the values determined on the 79 soil series that were included into ISA. The association measure of a soil series not included into ISA was calculated as an average value of the values interpolated for the texture, drainage, and profile development classes. Special soil series not represented by a three-character code (e.g. complex outcroppings of tertiary soils, totaling 39 soil series that cover 0.9% of Flanders), were assigned to PNV units based on best professional judgement. Areas that were not mapped (see methodological framework) covered 21.9% of Flanders.

Based on the association between soil series and PNV units, a PNV synthesis map was created by assigning soil series to the PNV with the highest measure of association. The accuracy of the PNV synthesis map was assessed on the subset of geographically located relevés (n=2048), by comparing the PNV units that are the result of the TWINSPAN classification, with the units they were assigned to by the PNV synthesis map. This is a confrontation rather than an independent validation since there were not enough vegetation relevés to set aside for this purpose. The classification results can be regarded as ‘ground truth’, which enabled us to perform a kappa analysis. The producer’s, consumer’s, and overall accuracies are calculated as follows (Jensen 1996):

1) The producer’s accuracy (in %), is a score indicating the number of relevés classified to a PNV that are found within the map unit of the same PNV, divided by the total number of relevés classified to this PNV.

2) The consumer’s accuracy (in %), is a score indicating the number of relevés classified to a PNV that are found within the map unit of the same PNV, divided by the total number of relevés found within this PNV map unit.

3) The overall accuracy is computed by dividing the overall correct number of relevés by the total count.

2.3.6 Mapping of PNVs not explained by morphogenetic soil data

The results of the error analysis indicated that three floristically very well identified PNV units, were not, or not accurately, explained by morphogenetic soil data. Two of them were modeled using additional environmental data: an Atlantic type, only found in the West of Flanders as a subtype of the PNV on silt loam soils, and the vegetation of spring wood forest that is a subtype of the PNV on alluvial soil. Mapping of the Atlantic PNV was based on presence/absence data of *Hyacinthoides non-scripta* and *Tamus communis*, in a selection of 398 grid cells (4 km x 4 km) represented by the flora atlas of Flanders (Van Landuyt *et al.* 2006). The selected grid cells are at least partially located on silt loam soils and mineral alluvial soils that are potentially suitable for both Atlantic species, and completely cover the species distribution. The potential area of the springwood forest PNV was determined by modeling the number of species that are indicators of this PNV according to the TWINSPAN classification (totaling nine; see Annex 2.2). We used the number of these species observed within a selection of georeferenced relevés (n = 358), classified to forest vegetation of fertile sites by the first TWINSPAN division, but without dune forest and scrub vegetation.

Relationships of Atlantic and springwood species number with potential explanatory variables were analyzed with generalized additive models (GAMs) in R version 2.14.1 (R Development Core Team 2011). Evaluation and reduction of model complexity followed Wood (2006), using the MGCV package in R for mixed modeling (Wood 2011). A logistic regression was applied to model the area of the two Atlantic species and a Poisson regression to model the area of the nine springwood forest species. The upper model on the Atlantic species number included four climate variables described in the study area section and the cover (%) by AF as represented by De Keersmaeker *et al.* (2001). Mean values of these explanatory variables were calculated for 4 km x 4 km grid cells of the flora atlas (Van Landuyt *et al.* 2006) that also contain Atlantic species data. The estimated values of the selected climate variables were calculated on a fixed cover of 40% AF, to eliminate the effect of the present-day variable AF cover. The upper model on the spring wood forest species included five explanatory variables determined on 358 selected georeferenced relevés: slope (degrees); altitude (m above sea level); nearest distance to the border of alluvium on the digital soil map (m; negative values within and positive values outside alluvium); nearest distance to a watercourse (m); first appearance of a forest, not reclaimed ever since, on one of the 7 historical maps used for the historical analysis (see above; included as a factor variable). Slope and altitude were determined on DTM grids with 25 m x 25 m resolution (Digital terrain model of Flanders 2001-2004) and all other variables were calculated for similar grids.

A third PNV not explained by morphogenetic soil series was a forest vegetation restricted to the freshwater and oligohaline tidal zone in the basin of the river Scheldt. Most relevés of this PNV were not georeferenced, and the digital soil map does not represent the hydrodynamics that are essential for this vegetation. The potential area of this PNV was based on the delineation by Van Braeckel *et al.* (2006) along the river Scheldt itself, but completed with information on the tidal amplitude (at least 1 m) along the Rupel, Dijle, Nete and Zenne rivers that belong to the basin of the river Scheldt. Lock weirs that eliminate the tides upstream and high salinity that inhibits tree growth downstream were set as limits to the potential area.

All GIS operations were performed with ArcMap 9.3 (ArcInfo license type).

2.4 Results

2.4.1 Selection and identification of PNVs

The low-level TWINSPAN classification resulted in 52 vegetation types (see dendrogram in Annex 2.1). 31 vegetation types were selected as reference vegetation types and merged to seven PNV units, whereas 21 low-level vegetation types not selected for PNV construction were assembled to six vegetation types of a similar classification level, for comparison with PNV units. These 13 vegetation types were given technical names based on a characteristic combination of two herbaceous species (Table 2.3). The TWINSPAN output table was summarized to a synoptic table, that expresses a gradient in edaphic conditions and groups diagnostic herbaceous species and characteristic regeneration of shrub and tree species of PNV units (see Annex 2.2).

Table 2.3 Frequencies of ancient forest (AF) and ancient forest species (AFS), both calculated as percentages on 13 forest vegetation types evaluated for PNV construction. AF frequency is the ratio of the number of plots in AF (NAF), to the total number of relevés included into a vegetation type, which is the sum of the number of relevés in ancient forest (NAF) and in recent forest (NRF). AFS frequency is the ratio of AFS to the total species number in a relevé (S), calculated as an average value for a forest vegetation type. AFS frequency and the total species number (S) per relevé were calculated on subsets of relevés in ancient forest and in recent forest (RF). Abbreviations in capitals indicate vegetation types selected as PNVs, other abbreviations are vegetation types not selected as PNVs. Standard deviations are mentioned between brackets.

Forest vegetation type (+ abbreviation)	AF (%)	Relevés in ancient forest					Relevés in recent forest				
		N_{AF}	S_{AF}		AFS (%)		N_{RF}	S_{RF}		AFS (%)	
Molinia caerulea – Vaccinium myrtillus (MCVM)	38.5	70	3.6	(2.2)	43.5	(5.9)	112	3.8	(2.1)	31.3	(4.3)
Athyrium filix-femina – Pteridium aquilinum (AFPA)	71.1	189	4.9	(2.8)	53.0	(3.6)	77	4.2	(2.3)	37.3	(5.5)
Molinia caerulea – Deschampsia flexuosa (mcdf)	8.2	62	5.8	(3.4)	23.0	(5.3)	697	5.9	(3.3)	21.3	(1.5)
Luzula pilosa – Oxalis acetosella (LPOA)	73.6	128	8.8	(4.4)	66.4	(4.2)	46	8.4	(5.6)	45.8	(7.2)
Rubus fruticosus – Holcus lanatus (rfhl)	22.8	44	4.2	(3.5)	37.1	(7.3)	149	4.8	(4.9)	19.1	(3.1)
Carex elongata – Scutellaria galericulata (CESG)	7.1	7	19	(10.4)	18.8	(14.8)	92	18.8	(7.4)	9.9	(3.0)
Circaea lutetiana – Hedera helix (clhh)	23.1	3	6.7	(6.1)	27.1	(25.7)	10	5.4	(4.3)	36.0	15.2)
Chrysosplenium – Equisetum telmateia (CSET)	57.1	12	26.4	(7.2)	51.0	(14.4)	9	22.3	(8.2)	28.0	(14.2)
Adoxa mosschatellina – Primula elatior (AMPE)	51.5	50	19.1	(9.6)	48.4	(7.1)	47	18.9	(6.9)	32.1	(6.7)
Urtica dioica – Galium aparine (udga)	5.6	11	12.5	(8.4)	6.1	(7.2)	185	18.3	(7.8)	6.2	(1.7)
Anemone nemorosa – Geranium robertianum (angr)	23.1	3	15	(10.6)	31.2	(26.7)	10	8.4	(5.6)	23.7	(13.4)
Claytonia perfoliata – Cynoglossum officinale (cpco)	0.0	0					28	11.6	(6.8)	1.5	(2.3)
Impatiens glandulifera – Cardamine amara (IGCA)	0.0	0					7	9.6	(5.1)	3.1	(6.6)
Overall	28.3	579	7.7	(6.9)	49.5	(26.8)	1469	8.7	(7.4)	20.8	(19.9)

It was not possible to apply fixed threshold values of AFS or AF frequencies for the selection of reference vegetation types. This approach would be possible if only the proportion of relevés located in AF, included into a vegetation type, would determine the mean AFS frequency at vegetation type level. Separating relevés in AF from relevés in RF confirmed that there was a higher ratio of AFS in the first subset than in the latter (Table 2.3). However, this subdivision also revealed that the ratio of AFS depended on the vegetation type, also within the subset of relevés located in AF (Table 2.3).

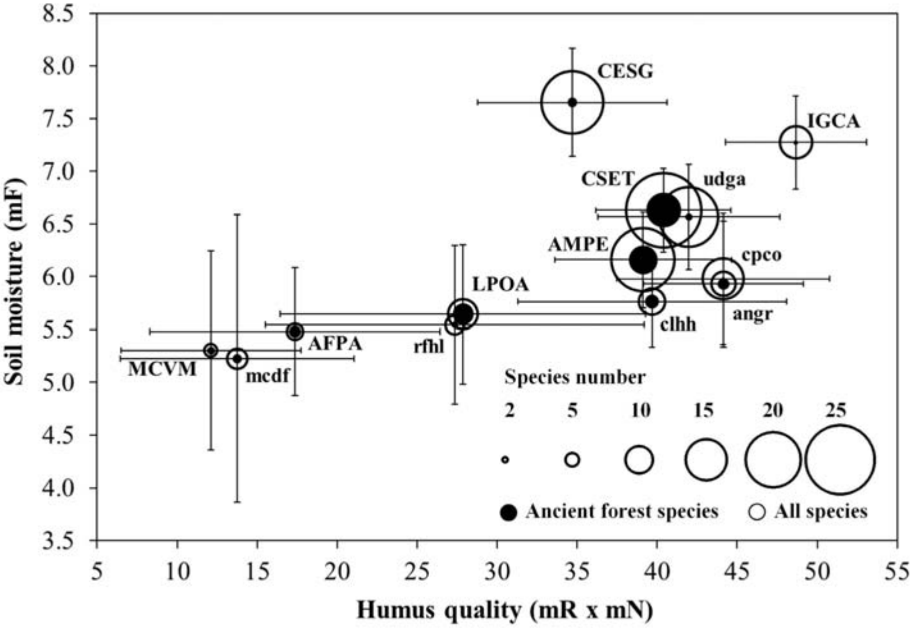


Fig. 2.3 Ecogram positioning PNV units (abbreviations in capital) and vegetation types not selected as PNV unit (other abbreviations) along axes representing the humus quality (mR x mN) and the mean indicator value for soil moisture (mF). Abbreviations are explained in Table 1. Flags indicate standard deviations calculated at relevé level. Symbol size is a function of species number, with filled and open circles representing the number of ancient forest species and the total species number, respectively.

We assumed that edaphic conditions could also be explanatory, and therefore displayed the vegetation types in an ecogram with the average mR x mN and mF values as axes (Fig. 2.3). As clarified in the next paragraphs, forest vegetation types at similar positions in the ecogram (Fig 2.3) were compared for AFS and AF ratios (Table 2.3), to select reference vegetation that can serve for PNV construction.

The *Athyrium filix-femina – Pteridium aquilinum*, *Molinia caerulea – Vaccinium myrtillus*, and *Molinia caerulea – Deschampsia flexuosa* indicate poor humus quality (Fig. 2.3) and mean total species number is relatively low (Table 2.3). The number of plots in AF and AFS ratio of the latter type, not selected as PNV, are low compared to values of the first two that were selected as PNV units (Table 2.3). The *Molinia caerulea – Vaccinium myrtillus* and *Athyrium filix-femina – Pteridium aquilinum* belong to the *Quercion robori-petraeae* alliance sensu Noirfalise (1984). Vernal geophytes are not present and the first PNV unit contains more species restricted to acid, nutrient-poor soils (e.g. *Vaccinium myrtillus* and *Calluna vulgaris*) than the second. Most frequently regenerating shrub and tree species typical for these PNV units are *Ilex aquifolium*, *Prunus serotina*, *Frangula alnus*, *Quercus spp.*, *Betula spp.*, and *Pinus sylvestris* (Annex 2.2). The *Luzula pilosa – Oxalis acetosella* and the *Rubus fruticosus – Holcus lanatus* types occupy similar intermediate positions with respect to the mR x mN value (Fig. 2.3), but the first type selected as PNV has much higher values of AFS frequency and number of relevés in AF than the latter that was not selected as PNV (Table 2.3). The *Luzula pilosa – Oxalis acetosella* PNV unit corresponds to the *Fagion sylvaticae* or *Carpinion betuli* syntaxa (Noirfalise 1984). Regeneration of *Acer pseudoplatanus*, *Fagus sylvatica*, and *Carpinus betulus* is found with the highest frequency in this PNV unit (Annex 2.2). The *Luzula pilosa – Oxalis acetosella* occupies an intermediate position as it contains herbaceous species that indicate slightly acid or near-neutral soils (e.g. *Stellaria holostea*), as well as species indicating acid soils (e.g. *Pteridium aquilinum*). Only few herbaceous species (e.g. *Milium effusum*, *Oxalis acetosella*, and *Luzula pilosa*) have an optimum in the *Luzula pilosa – Oxalis acetosella* type and contrary to other PNV units it was composed of vegetation types separated by the first TWINSPAN division. This manipulation aimed to keep low-level vegetation types that contain vernal species (e.g. *Anemone nemorosa*) united into one PNV.

The other vegetation types listed in Table 2.3 all indicate sites with an intermediate or high humus quality, and a variable soil humidity (Fig. 2.3). The proportion of relevés in AF and the frequency of AFS are higher in the *Chrysosplenium – Equisetum telmateia* and *Adoxa moschatellina – Primula elatior* than in the other vegetation types (Table 2.3) and therefore both were selected as PNV. The *Chrysosplenium – Equisetum telmateia* type corresponds to the association of spring woods (*Carici remotae-Fraxinetum*; Noirfalise 1984) and contains specific AFS not present in the *Adoxa moschatellina – Primula elatior* type, which was identified as the *Alno Padion* alliance (Noirfalise 1984). Most frequently regenerating tree and shrub species of the *Chrysosplenium – Equisetum telmateia* and *Adoxa moschatellina – Primula elatior* PNV units are *Fraxinus excelsior*, *Viburnum opulus* and *Cornus sanguinea* (Annex 2.2). All relevés of the *Claytonia perfoliata – Cynoglossum officinale* type are located in woodland and scrub of coastal dunes. Since none is located in AF and AFS were scarce (Table 2.3), this type was not selected as a PNV. The *Impatiens glandulifera – Cardamine amara* and *Carex elongata – Scutellaria galericulata* types are species-rich and floristically well characterized vegetation types of wet sites (Fig. 2.3). Although both have low AFS frequencies, with none and seven georeferenced relevés in AF (Table 2.3), they were selected as PNV units and identified as the *Salicion albae* and the *Alnion glutinosae alliances* (Noirfalise 1984), respectively (see discussion). The tree layer of the *Impatiens glandulifera – Cardamine amara* PNV unit is dominated by *Salix spp.*, but regeneration of these species was scarce and Sambucus nigra was the most frequently regenerating woody species (Annex 2.2). Regeneration of *Alnus glutinosa* is characteristic for the *Carex elongata – Scutellaria galericulata*, but regeneration of *Quercus robur* and *Betula spp.* is frequent in this PNV unit as well (Annex 2.2).

2.4.2 PNV mapping

The selection and ISA procedure yielded seven PNV units, but left the Atlantic subtype of the *Luzula pilosa – Oxalis acetosella* type unexplained by soil data. Calculated accuracies for the PNV units that resulted from assigning a soil series to a PNV unit with the highest association are listed in Table 2.4.

Five PNV units with satisfactory accuracies, were included into the PNV synthesis map (Fig. 2.4). Accuracies of the *Impatiens glandulifera – Cardamine amara* were not calculated, as there were only seven georeferenced relevés and its potential area was delineated as an overlay, that represents a scenario for which removal of embankments is necessary, whereas other PNV units can develop without removal of embankments (Fig. 2.4).

Table 2.4 Error matrix summarizing similarities between classification units (horizontal) and PNV synthesis map units (vertical). The classification unit, a georeferenced relevé is assigned to by TWINSPAN, was compared to the unit where it was located on according to the PNV synthesis map (Fig 2.4). Vegetation relevés that were correctly mapped, are found on the diagonal. 0 indicates vegetation relevés not included into PNV classification, or located on areas not covered by the PNV map. AP is the producer's accuracy (%), AC is the consumer's accuracy (%). Accuracies that were not calculated, are indicated by /. The overall accuracy equaled 53%. For the meaning of abbreviations see Table 2.3.

		Map unit								A_P(%)
		0	MCVM	AFPA	LPOA	CESG	CSET	AMPE	IGCA	
	0	114	747	140	40	46	20	80	15	/
Classification unit	MCVM	5	112	49	8	3	0	5	0	63
	AFPA	15	37	99	93	4	1	17	0	39
	LPOA	4	11	33	99	6	11	9	1	58
	CESG	14	8	11	0	55	0	7	4	65
	CSET	0	0	2	3	2	8	6	0	38
	AMPE	3	3	19	13	8	4	47	0	50
	IGCA	1	1	0	0	2	0	2	1	/
A_C (%)		/	65	46	46	69	33	51	/	53

The area of the *Chrysosplenium – Equisetum telmateia* type was not accurately mapped using the digital soil map (Table 2.4). From a phytosociological point of view this PNV unit is part of the *Adoxa moschatellina – Primula elatior* type (e.g. see Noirfalise 1984), but it is floristically very well characterized with a high number of preferential AFS (Annex 2.2). Based on the low accuracies of this PNV, we decided not to use the digital soil map, but to model its potential area by including additional environmental data (see below). The *Carex elongata – Scutellaria galericulata* type is found on peat soils (Histosols) or on waterlogged soils without profile development (Gleysols) and these specific soil conditions explain the high accuracies (Table 2.4). The *Adoxa moschatellina – Primula elatior* type is assigned to humid or wet silt loam soils without profile development (Gleysols), and mapped with average accuracies (Table 2.4). The *Luzula pilosa – Oxalis acetosella* PNV unit is only found on silt loam soils with a B horizon of particular texture or color that are classified as Albeluvisols or Luvisols (IUSS Working Group WRB, 2006), respectively. The producer's accuracy of this PNV is higher than its consumer's accuracy, indicating that most of the area where it could be found is assigned to this PNV unit, but also that other PNV units are frequently found within the same area (Table 2.4). The *Athyrium filix-femina – Pteridium aquilinum* is almost equally frequent on silt loam soils as the *Luzula pilosa – Oxalis acetosella* (Table 2.4) but this PNV is also present on soils with a higher sand content, north of the silt loam belt (Fig. 2.4). The *Molinia caerulea – Vaccinium myrtillus* is dominant on sand soils (Fig. 2.4) and accurately mapped (Table 2.4).

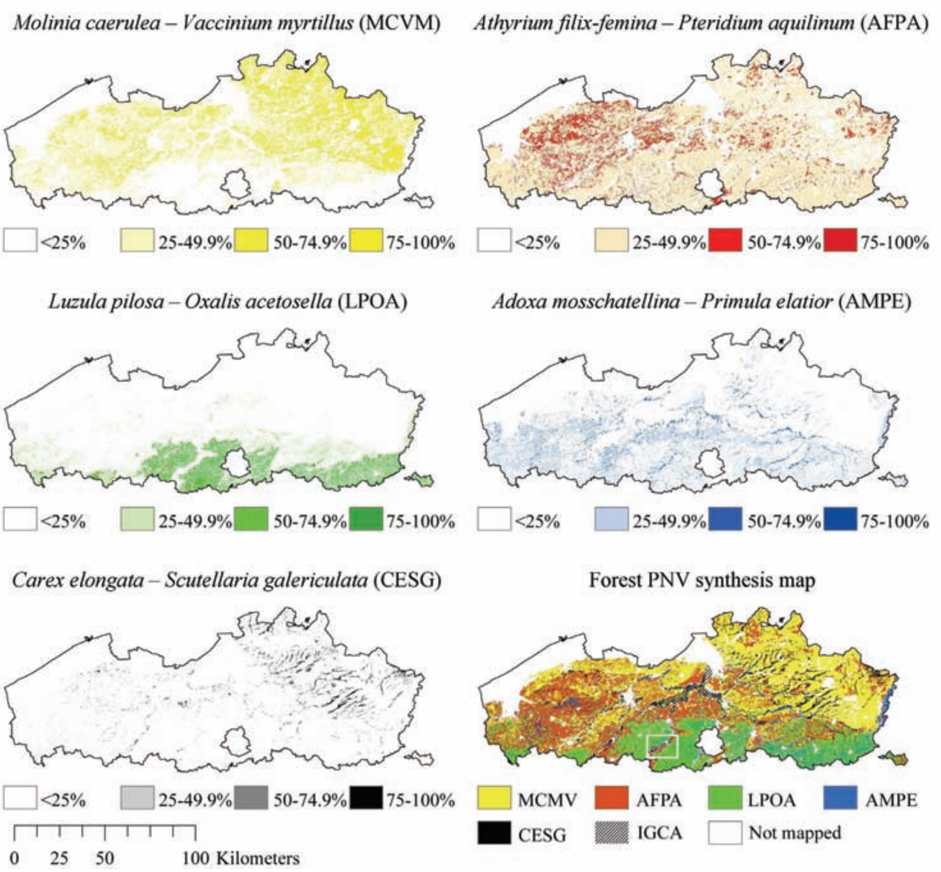


Fig. 2.4 Maps of five units of forest PNV that are related to morphogenetic soil series, and a forest PNV synthesis map (below right). The legend of the first five maps represents an association measure based on the number of relevés on a soil series, classified to a PNV type by TWINSPAN, as a percentage of the total number of relevés of all PNV types located on that soil series. Selection of the PNV with the highest association measure resulted in the PNV synthesis map. The hatched overlay on the PNV synthesis map indicates the potential area of the *Impatiens glandulifera – Cardamine amara* (IGCA), when embankments are removed. The white box on the PNV synthesis map is illustrated by Fig. 2.6.

Table 2.5 Parametric coefficients and approximate significance of the smooth terms of the GAM on the number of characteristic species of the *Chrysosplenium – Equisetum telmateia* PNV unit, on a total of nine characteristic species, expressed by the formula: SPECIES NUMBER ~ s(DISTAL500) + s(SLOPE) + s(ALTITUDE). Names of variables are explained in Fig. 2.5. Edf: estimated degrees of freedom for the model terms; Ref.df: estimated residual degrees of freedom. The GCV score equaled 1.5191 and the model explained 15.1% deviance (n= 358).

	Estimate	Std. Error	t-value	Pr(>|t|)
Intercept	-0.10295	0.07026	-1.465	0.144
Smooth term	edf	Ref.df	F-value	*P*
s(DISTAL500)	4.194	5.024	5.543	<0.001
s(SLOPE)	3.211	3.715	2.526	0.045
s(ALTITUDE)	4.553	5.450	2.570	0.023

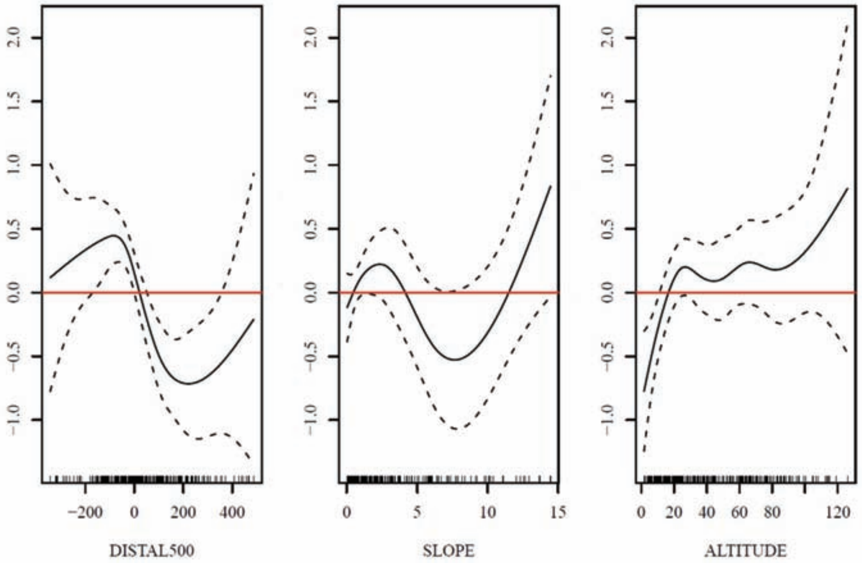


Fig. 2.5 Estimated partial effects (solid lines) of 3 variables included into the GAM of the number of springwood species, with the 95% confidence interval indicated by dashed lines. The red line is the overall mean species number and the values of the Y-axis indicate the relative effect in the natural log scale (0: no effect; 1: 2.72 times the species number of the overall mean; -1: 0.37 times times the species number of the overall mean). Tickmarks on the x-axis show the location of observations. DISTAL500: distance to the border of alluvial soils (m; values > 500 m are not included), negative values are located within , positive values outside alluvium; SLOPE: average slope in degrees determined on 25 m x 25 m grid cells of a DTM; ALTITUDE: average elevation above sea level (m) determined on 25 m x 25 m grid cells of a DTM.

As a consequence of the low accuracy of the *Chrysosplenium – Equisetum telmateia* unit's area, as represented by the digital soil map, the number of characteristic species of this PNV was modeled using explanatory variables on hydrography and topography. Only slope, altitude, and nearest distance to alluvium were significant (Table 2.5). Springwood forest species were typically found on moderate slopes (<5°), on alluvium but close to the border with other soil types and above an altitude of 20 m (Fig. 2.5 and Fig. 2.6). The GAM only explained 15% deviance, indicating that several variables that influence the presence of this PNV are not or not very accurately included.

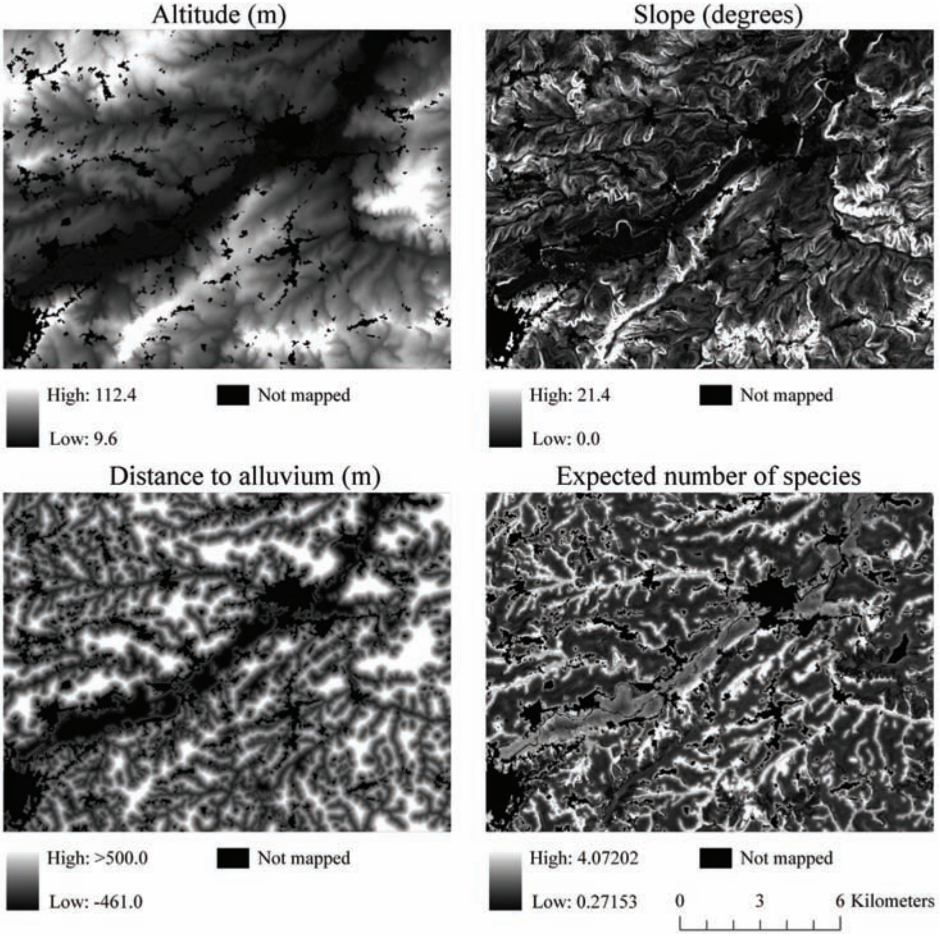


Fig. 2.6 Expected number of springwood forest species (down right) that are characteristic for the *Chrysosplenium – Equisetum telmateia*, as compared to altitude (m), slope (degrees), and distance to alluvium (m) that are explanatory variables in the GAM. The mapped area is indicated by the white box on the PNV synthesis map of Flanders (Fig. 2.4).

The area of the Atlantic PNV, not explained by soil data, was modeled using the presence of the number of Atlantic species as dependent variable and climate data as explanatory variables. All 4 tested climate data were included (Fig. 2.7) and the GAM explained 58% deviance (Table 2.6). The northern limit of both Atlantic species corresponded very well with the belt of silt loam soils that was assigned to the *Luzula pilosa – Oxalis acetosella* type on the PNV synthesis map. Only one isolated patch of silt loam soils in the Northwest, that is potentially suitable for Atlantic species according to the GAM, has no occurrences of diagnostic species (Fig. 2.8). The eastern limit was mostly explained by climate data, in particular the annual number of frost days (Fig. 2.7).

Table 2.6 Parametric coefficients and approximate significance of the smooth terms of the GAM on the two characteristic species of the Atlantic subtype of the *Luzula pilosa – Oxalis acetosella* PNV unit, expressed by the formula: cbind(TOTAL, 2 - TOTAL) ~ s(MEAN_TEMP) + s(MEAN_PREC) + s(MEAN_SUN) + s(MEAN_FROST) + s(sqrt(AF_I)). Names of variables are explained in Fig. 2.7. Edf: estimated degrees of freedom for the model terms; Ref.df: estimated residual degrees of freedom. The GCV score equaled 0.70 and the model explained 58.7% deviance, on 398 observations.

	Estimate	Std. Error	t-value	Pr(>|t|)
Intercept	-23.47	16.75	-1.401	0.162
Smooth term	edf	Ref.df	F-value	*P*
s(MEAN_TEMP)	8.950	8.996	3.226	<0.001
s(MEAN_PREC)	1.000	1.000	25.818	<0.001
s(MEAN_SUN)	8.911	8.993	6.508	<0.001
s(MEAN_FROST)	7.636	7.878	7.461	<0.001
s(sqrt(AF_I))	6.619	7.683	5.780	<0.001

2.5 Discussion

2.5.1 Classification level and map resolution

PNV construction for Flanders resulted in 8 units, mostly corresponding to alliances in Braun-Blanquet's phytosociological system. The classification level is similar to Bohn *et al.* (2003, see Fig. 2.1), but the PNV map of Flanders yielded a much higher spatial resolution. The PNV maps of Ireland (Cross 1998) and Switzerland (Brzeziecki *et al.* 1993), also display a similar classification level, but this results in a higher number of

PNV units since climatic, topographical, and edaphic variation is much higher in both countries. Tichý (1999) mapped 10 PNV units that corresponded with the level of association, but for a study area that covered a relative small area (110 km2) in the Czech republic. The PNV map of NE China, covering a much larger area, discerned 16 types mostly corresponding to formations or subformations (Liu *et al.* 2009). Zampieri & Lionello (2010) used climate data to map 12 high-level PNV units (formations) on a global scale.

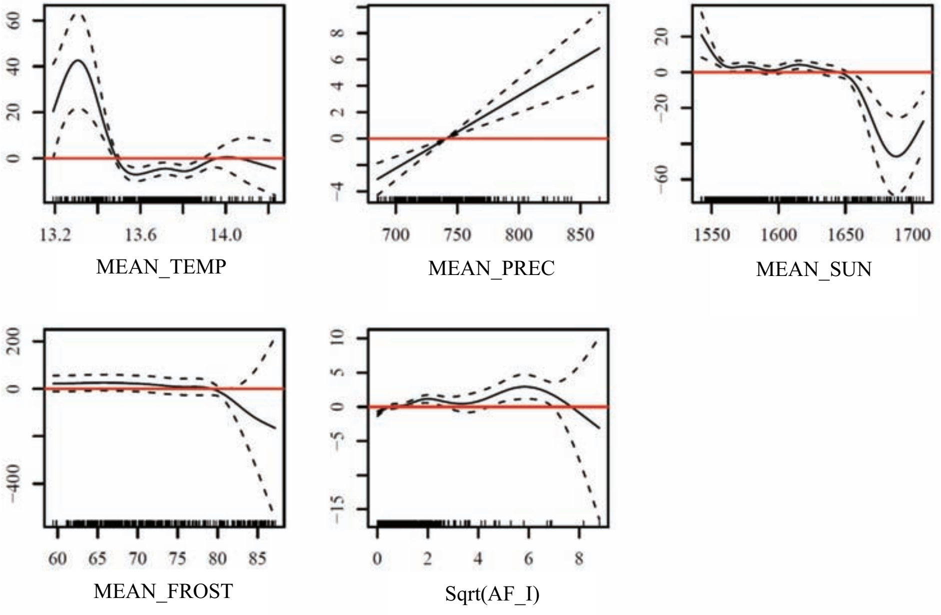


Fig. 2.7 Estimated partial effects (solid lines) of 5 predictor variables included into the GAM of the number of Atlantic species, with the 95% confidence interval indicated by dashed lines, and 0 values indicating no effect in the logit scale. Tickmarks on the x-axis show the location of observations. MEAN_TEMP: daily maximum temperature as an annual mean (°C); MEAN_PREC: mean annual precipitation (mm); MEAN_SUN: mean annual sunshine (hours); MEAN_FROST: mean annual frost days (days); AF_I: ancient forest cover (% of 16 km2 squares).

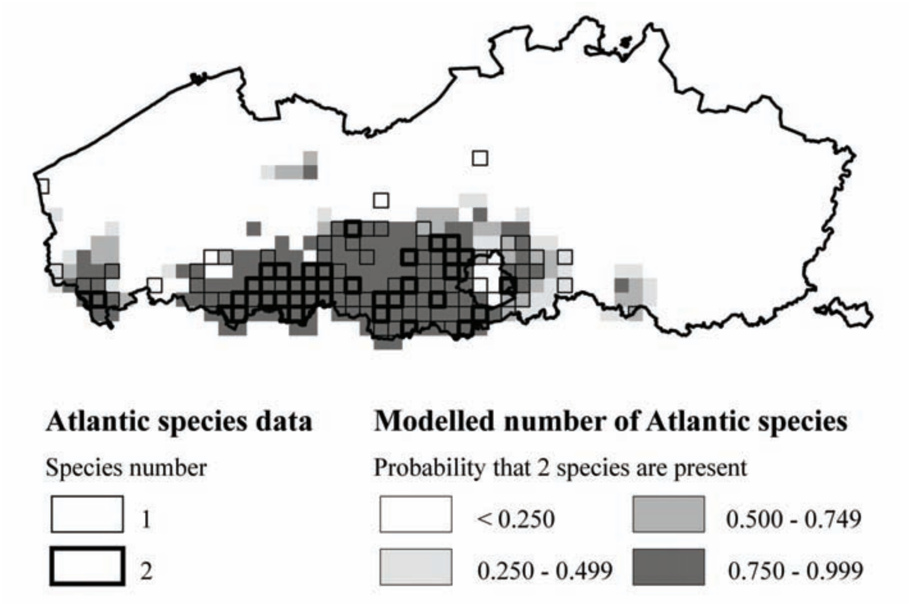


Fig. 2.8 Estimated probability of the presence of two Atlantic species (filled squares), *Hyacinthoides non-scripta* and *Tamus communis*, based on GAM, as compared to species distribution (outlines) according to Van Landuyt *et al.* (2006).

Accuracy of the PNV map of Flanders was restricted by the quality of explanatory environmental data, more than by the quality of floristic data, which is also what Brzeziecki *et al.* (1993) experienced. This was most obvious for the vegetation of spring woods (*Carici remotae-Fraxinetum association*), which is floristically well characterized. The environmental conditions that determine this PNV are complex and not completely represented by GIS data. Quality and dynamics of groundwater are necessary for a further subdivision of the *Alnion glutinosae* (cf. Döring-Mederake 1990), but these data are not available for the whole area of Flanders.

The accuracy analysis indicated that PNV units with and without vernal species, sensitive to acidification (e.g. *Stellaria holostea* and *Lamiastrum galeobdolon*), were found with similar frequencies on silt loam soils of plateaus in the South of Flanders. We assume that variation in soil pH or light conditions, not given by the morphogenetic soil data used for PNV mapping, can determine vegetation patterns. The acid silt loam soils in the South of Flanders have a poor buffer capacity and are very sensitive to further acidification, either natural or man-made (Brahy *et al.* 2000). Within the pH range observed by Brahy *et al.*

(2000), establishment and growth of *Stellaria holostea* and *Lamiastrum galeobdolon* is hampered (Falkengren-Grerup & Tyler 1993). On silt loam soils, tree species (e.g. *Fagus sylvatica* vs. *Acer pseudoplatanus*, Neirynck *et al.* 2000, Thomaes *et al.* 2011), and forest management in general (Decocq *et al.* 2004, Van Calster *et al.* 2008, Baeten *et al.* 2009a) determine herbaceous forest vegetation composition, mainly through soil and light conditions. Remnants of pristine forest or reference forest with a woody vegetation that is unmanaged for a very long time, are missing in our study area and therefore natural tree species composition is not clear. The uncertainty is high for silt loam soils, that are suitable for a high number of tree species and where *Acer pseudoplatanus* is expanding, but also for sand soils, where Fagus sylvatica is successfully regenerating in woodland dominated by *Quercus spp.* or *Pinus sylvestris* (see Leuschner 1997). We excluded tree species composition from PNV construction since it is manipulated by forest management, but this also implicates that future tree species effects on composition of herbaceous forest vegetation are not forecasted.

Some PNV maps are based on expert judgement (e.g. Stumpel & Kalkhoven 1978; Cross 1998) whereas others are the result of a quantification of relationships between PNV units and GIS-based environmental variables (e.g. Brzeziecki *et al.* 1993, Tichý 1999, Liu *et al.* 2009, Zampieri & Lionello 2010, Vaca *et al.* 2011). All these studies used an existing vegetation classification to create or refine a PNV map. The approach of first classifying vegetation without any reference to the environmental data, followed by a quantification of relationships with environmental data, is called ‘assembling first and predicting later’ (Ferrier & Guisan 2006). By contrast, the strategy of ‘community-level modeling with a simultaneous assembling and predicting strategy’ is not yet applied for PNV construction. Only Zampieri & Lionello (2010) pursued an optimal classification level by varying the number of clusters. PNV construction for Flanders followed a hybrid strategy: we started from a low-level classification, but not from vegetation sampling units (relevés) as the ‘simultaneous assembling and predicting’ strategy would require. The low level vegetation types were first sorted out for PNV construction (see below), and then assembled until significant relationships were assessed with a morphogenetic soil typology, as we assumed it contained the most relevant explanatory variables for our study area. In a final step we included additional explanatory variables to enhance mapping of PNV units that were floristically well identified, but not properly explained by morphogenetic soil data. In conclusion, the classification level of our PNV typology was mostly determined by the explanatory power of environmental variables, a feature our methodology has in common with the simultaneous assembling and predicting strategy (cf. Ferrier & Guisan 2006).

2.5.2 Integrating the AFS concept into PNV construction

PNV can be seen as a baseline or null model, representing the vegetation that would persist under the current conditions if it was already there (Somodi *et al.* 2012). It should be based on the most mature vegetation stage that can currently be observed on a certain site type (Farris *et al.* 2010, Loidi *et al.* 2010). Criteria for selecting reference vegetation that serves for PNV construction, are often not clearly proposed. This should not be a problem for PNV construction in regions with enough remnants of natural vegetation. However, when constructing PNV units for a landscape with a long and often opaque history of intensive human occupation and cultivation, careful selection of vegetation that can serve for PNV construction is essential.

We used forest vegetation composition (AFS frequency) and land use history data (AF frequency) as we think these are appropriate criteria that can be applied to all areas where the relation between forest vegetation and land use history has been studied. We were able to use AFS as quality indicators to decide which forest vegetation has recovered closest to its mature stage and can be regarded as a PNV. In most cases land use history data were used to create regional lists of AFS (e.g. Hermy 1985, Wulf 1997, Rackham 2003, Cornelis *et al.* 2009). Combining both criteria is the most appropriate way to select reference forest vegetation in an area such as Flanders, where forests in all stages of recovery or degradation are present. In a considerable part of our study area, reforestation following medieval reclamation already started before 1775 (Tack *et al.* 1993), i.e. the time when the first map was drawn for the whole study area. Forest vegetation in this area can still be impoverished, in spite of reforestation centuries ago. By contrast, colonization of AFS into recent forest that originated after 1775, can already be completed when landscape factors and soil conditions are favorable (Verheyen & Hermy 2001a, see Chapter 5). Degraded site conditions on the other hand, can also result in a loss of AFS in AF (Baeten *et al.* 2010a). For these reasons, and because of the higher risk of a selection bias, we consider evaluation of land use history and AFS frequency at the level of individual relevés less appropriate than an evaluation of low-level vegetation types. By doing so, groups of relevés that are located in degraded AF and immature RF, can be separated from of groups of relevés with mature vegetation, either located in AF or in RF.

The use of AFS frequency as a selection criterion is complicated by the fact that this variable is dependent on natural site conditions, i.e. edaphic conditions. Thus, AFS frequency is low in *Alnion glutinosae* forest on waterlogged soil, also in the few relevés of this type located in AF. Only one AFS, *Carex laevigata*, is characteristic for this vegetation type (Hermy *et al.* 1999). AF of the Salicion albae is missing in Flanders (Van Braeckel *et al.* 2006), but it can be assumed that its development is determined by hydrodynamics and morphodynamics, not so much by site history (Wolf *et al.* 1997). Dynamic site conditions of the *Alnion glutinosae* and *Salicion albae*, particularly frequent flooding, seem to be incompatible with the stress-tolerant life strategy of AFS (Hermy *et al.* 1999). By contrast, the vegetation type that comprised dune forest and scrub was not selected as PNV since AF was missing, and AFS were scarce although stabilized dunes could be suitable sites for AFS. Definition of PNV units for coastal dunes is complicated by the fact that these sites by nature can be dynamic and isolated from inland forests, preventing colonization by AFS.

The AFS concept also helps to decide which anthropogenic changes in site quality to include into PNV construction. According to the definition of PNV, irreversible changes in site quality should be taken into account, but it is not clear how they can be differentiated from reversible ones (Härdtle 1995). This lack of clarity is mostly explained by the variable rate at which soils recover after conversion to forest. Thus, forest soils recovered within 100 yr in the Piedmont region (Delaware and Pennsylvania, USA), before forest vegetation had recovered (Matlack 2009). Changes in site quality can also be an inherent part of secondary succession. Nutrient accumulation in spontaneously developing forest on degraded heathland soil in Germany enabled the development of a *Fago-Quercetum*, that includes several AFS, through *Betulo-Quercetum* stages, where AFS are rare or missing, within a time period of 350 yr (Leuschner 1997). Former use as agricultural land or heathland can also have persistent effects on soil characteristics, in particular on soil P, pH, and organic matter content (e.g. Koerner *et al.* 1997, Wilson *et al.* 1997, Verheyen *et al.* 1999). Roman settlements with altered soil conditions in northern France are still marked by a specific vegetation 1600 yr after reforestation (Dupouey *et al.* 2002, Plue *et al.* 2008), with several AFS (e.g. *Euphorbia amygdaloides*) as indicators. We propose that for PNV construction, anthropogenic changes in site quality can be accepted as permanent when soil recovery rate is expected to be (much) lower than the recovery or succession rate of forest vegetation, including AFS, assuming that there are no migration barriers. This is still in agreement with the original static concept, whereas, the potential future natural vegetation (PFV) concept, proposed by Somodi *et al.* (2012) is similar to the 'future naturalness' by Peterken (1996) and both are a forecasting of vegetation succession in the course of time that also takes into account future changes of environmental conditions.

2.5.3 Application of PNV maps for forest restoration projects

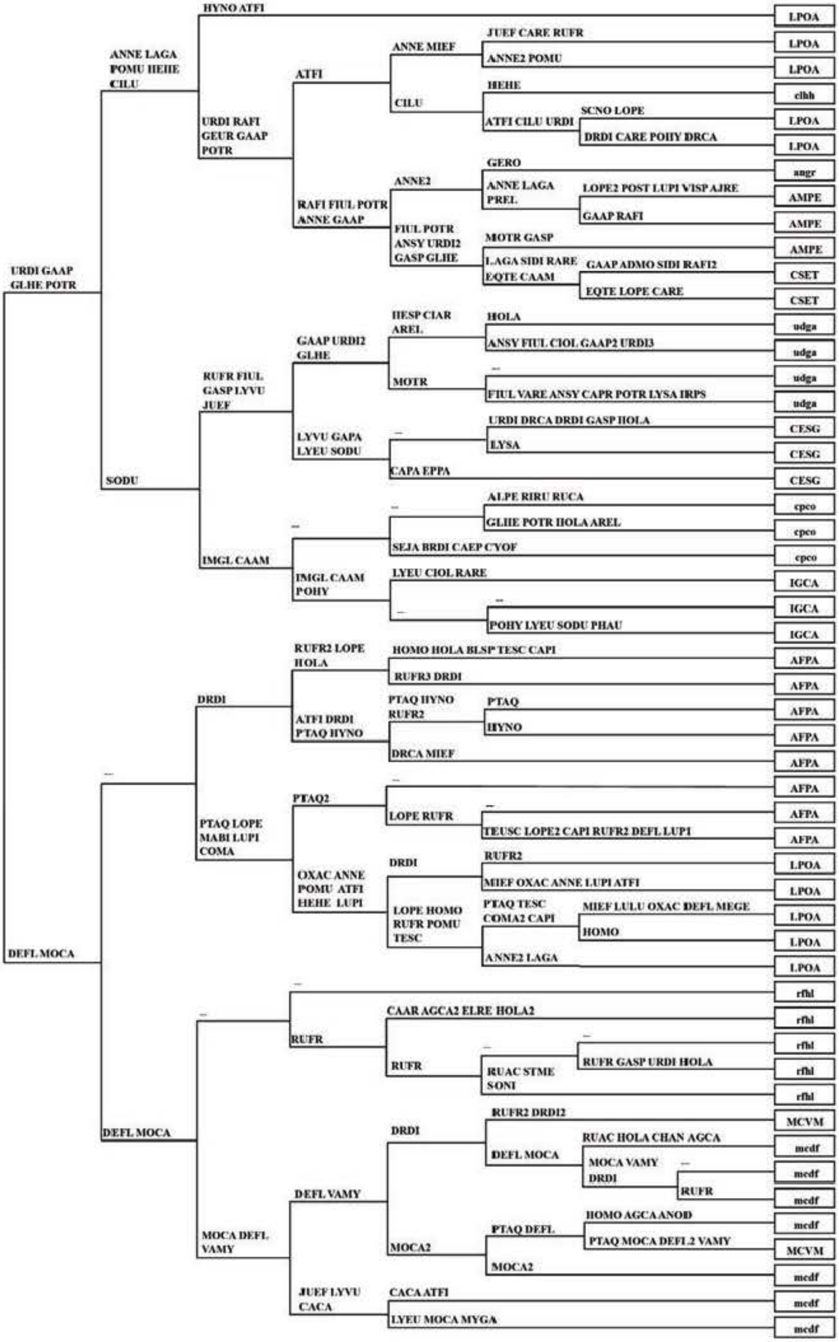
In particular for a region with a low and fragmented forest cover, a forest PNV map is useful as a reference for forest restoration projects. However, the PNV concept is criticized for being unrealistic, since the time that is necessary for a PNV to develop is not specified (Chiarucci *et al.* 2010, Carrión 2010). Even without a dimension of time, the PNV concept is valuable as a null model (Somodi *et al.* 2012), but an integration of the AFS concept into the PNV concept can also facilitate the use of PNV maps for restoration purposes. The time for a forest vegetation to develop to PNV is determined by colonization by AFS and colonization rates of AFS can be quantified (e.g. see Brunet & von Oheimb 1998a, Bossuyt *et al.* 1999b, see Chapter 6). An analysis of landscape factors and environmental quality, that influence the colonization rate by AFS, allows to compare the potentials of sites that are considered for restoration.

Inherent space-for-time substitutions are cited as a problem for PNV construction (Chiarucci *et al.* 2010). We discern two cases in our study area, for which such substitutions can complicate the application of a PNV map for restoration purposes: The P eutrophication level of agricultural land that has changed in time and the distribution of Atlantic species in a changing climate. In our study area, secondary forest that originated after 1945, can be enriched with P to a higher level than farmland converted to forest before that time (see Chapter 5). P eutrophication can accentuate the difference in colonization capacity among forest herbs (Baeten *et al.* 2009b). When using PNV maps for forest ecosystem restoration, the P content of farmland soils should be assessed to compare restoration potentials. The distribution range of Atlantic forest species, e.g. *Hyacinthoides non-scripta*, can be accurately mapped by climate data, in particular by minimum temperature data (see also Kohn *et al.* 2009). However, a 45-year transplantation experiment 70 km beyond the eastern limit of its range indicated that *Hyacinthoides non-scripta* is nowadays primarily limited by poor dispersal capacities (Van der Veken *et al.* 2007). Present-day distribution might thus reflect historical climate limitation. Restoration projects for the Atlantic PNV should therefore primarily focus on landscape factors and environmental quality that determine dispersal and recruitment limitation of both Atlantic species.

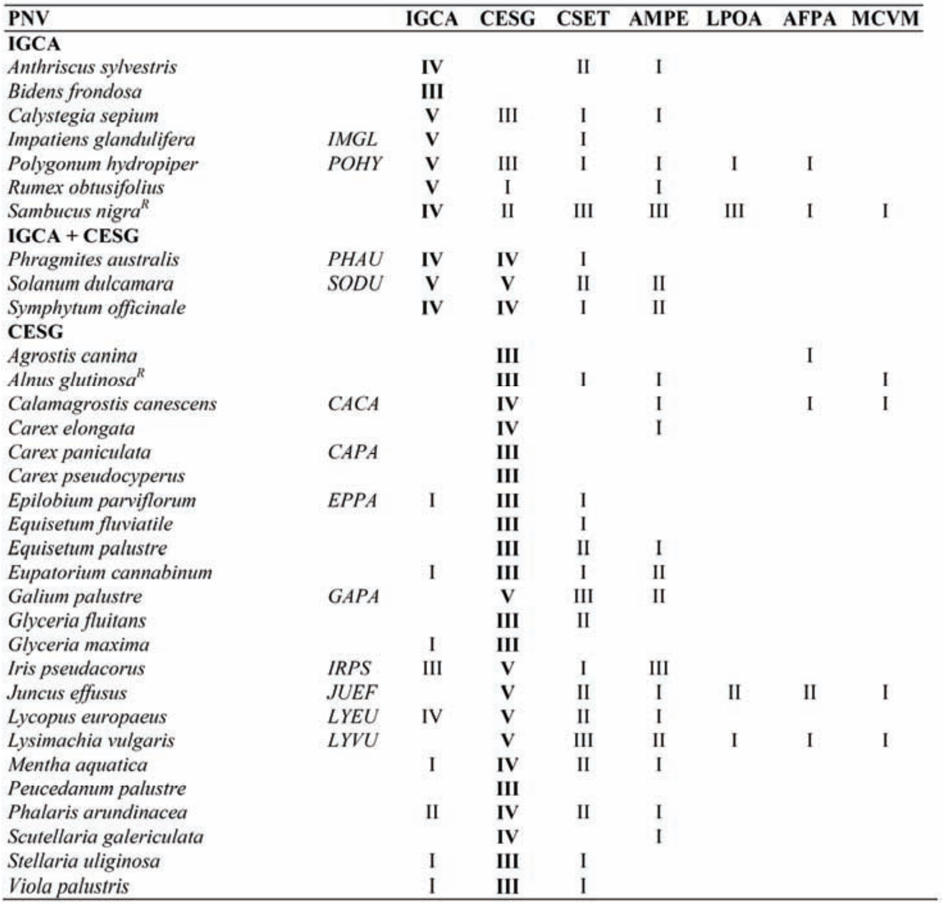
2.6 Conclusions

The methodological framework we proposed for PNV construction can be applied to all fragmented landscapes with a forest cover of a variable recovery or succession level, provided that the necessary data are available. Apart from the GIS-based environmental data that are traditionally used for PNV construction, a regional list of AFS and information on land use history are required to select reference forest vegetation. The recovery or succession of forest vegetation can be considered completed when characteristic AFS - if there are any - have colonized recent forest. The selection of reference forest is an assessment that should also take into account that AFS frequency is dependent on ‘natural’ site conditions (edaphic factors). Recovery rate of forest vegetation to PNV is primarily determined by colonization of characteristic AFS. Restoration projects that use PNV maps as a reference, should therefore also include data on environmental quality and landscape factors that determine the colonization rate of AFS. By including such information, the potentials of sites to develop towards a PNV unit can be compared, within the area of this PNV unit delimited by the PNV map.

Annex 2.1 TWINSPAN dendrogram, with 52 vegetation types, merged to 7 PNV units (abbreviations in capitals: see Table 2.1) and 6 other vegetation types not selected as PNV (abbreviations not in capitals; explained in Table 2.1). Species abbreviations are explained in Annex 2.2, abbreviations followed by "2" indicate species with at least 5% cover.



Annex 2.2 Synoptic table of PNV units with species frequencies in 5 classes: no symbol: 0≤ x <1%; I: 1%≤ x <5%; II: 5≤ x<10%; III: 10≤ x <20%; IV: 20≤ x <40%; V: 40≤ x <100%; Species observed less than 4 times were not listed; between brackets: species restricted to the Atlantic region; in bold: preferential species; * ancient forest species according to Hermy *et al.* (1999); + species selected for the model on springwood forest vegetation; ^{R} regeneration of shrub and tree species with height below 1.3m. Italic four letter codes are species abbreviations used in the TWINSPAN dendrogram (Annex 2.1). Four letter PNV abbreviations are explained in Table 2.1.



PNV		IGCA	CESG	CSET	AMPE	LPOA	AFPA	MCVM
IGCA								
Anthriscus sylvestris		**IV**		II	I			
Bidens frondosa		**III**						
Calystegia sepium		**V**	III	I	I			
Impatiens glandulifera	*IMGL*	**V**		I				
Polygonum hydropiper	*POHY*	**V**	III	I	I	I	I	
Rumex obtusifolius		**V**	I		I			
Sambucus nigra^R		**IV**	II	III	III	III	I	I
IGCA + CESG								
Phragmites australis	*PHAU*	**IV**	**IV**	I				
Solanum dulcamara	*SODU*	**V**	**V**	II	II			
Symphytum officinale		**IV**	**IV**	I	II			
CESG								
Agrostis canina			**III**				I	
Alnus glutinosa^R			**III**	I	I			I
Calamagrostis canescens	*CACA*		**IV**		I		I	I
Carex elongata			**IV**		I			
Carex paniculata	*CAPA*		**III**					
Carex pseudocyperus			**III**					
Epilobium parviflorum	*EPPA*	I	**III**	I				
Equisetum fluviatile			**III**	I				
Equisetum palustre			**III**	II	I			
Eupatorium cannabinum		I	**III**	I	II			
Galium palustre	*GAPA*		**V**	III	II			
Glyceria fluitans			**III**	II				
Glyceria maxima		I	**III**					
Iris pseudacorus	*IRPS*	III	**V**	I	III			
Juncus effusus	*JUEF*		**V**	II	I	II	II	I
Lycopus europaeus	*LYEU*	IV	**V**	II	I			
Lysimachia vulgaris	*LYVU*		**V**	III	II	I	I	I
Mentha aquatica		I	**IV**	II	I			
Peucedanum palustre			**III**					
Phalaris arundinacea		II	**IV**	II	I			
Scutellaria galericulata			**IV**		I			
Stellaria uliginosa		I	**III**	I				
Viola palustris		I	**III**	I				

Annex 2.2 (Continued)

PNV		IGCA	CESG	CSET	AMPE	LPOA	AFPA	MCVM
CSET								
Caltha palustris		III	III	**V**	II			
*Carex pendula**$^{+}$				**III**	I			
*Carex strigosa**$^{+}$				**III**				
*Chrysosplenium alternifolium**$^{+}$				**IV**	I			
*Chrysosplenium oppositifolium**$^{+}$			I	**IV**				
Cirsium oleraceum	*CIOL*	II	II	**IV**	II			
Equisetum telmateia^{+}	*EQTE*		I	**V**	I			
Geranium robertianum^{+}	*GERO*	I	I	**V**	III			
*Lysimachia nemorum**$^{+}$			I	**III**		I		
Lysimachia nummularia		I	II	**III**	II			
Ranunculus repens	*RARE*	II	IV	**V**	III			
Silene dioica^{+}	*SIDI*	I	II	**V**	III	I		
*Veronica montana**$^{+}$				**IV**	I			
IGCA + CSET								
Cardamine amara	*CAAM*	**V**	I	**V**	I			
AMPE								
Acer campestre^{R}					**I**			
Cornus sanguinea^{R}			I	II	**III**	I		
Deschampsia cespitosa			III	IV	**V**	III	I	I
*Listera ovata**			I	I	**III**			
Rubus caesius	*RUCA*	I	II	II	**III**			
*Vinca minor**				II	**III**	I		
AMPE + CSET								
*Adoxa moschatellina**	*ADMO*			**V**	**V**	II		
Aegopodium podagraria			I	**IV**	**IV**			
Ajuga reptans	*AJRE*		II	**V**	**IV**	I		
Arum maculatum	*ARMA*			**IV**	**IV**	I		
*Carex sylvatica**	*CASY*			**IV**	**IV**	II		
*Circaea lutetiana**	*CILU*		II	**V**	**IV**	II	I	
*Festuca gigantea**				**III**	**II**			
Geum urbanum	*GEUR*		I	**V**	**V**	I		
Glechoma hederacea	*GLHE*	II	III	**V**	**V**	II		
*Paris quadrifolia**			I	**III**	**III**	I		
*Primula elatior**	*PREL*		I	**V**	**V**	I		
Ranunculus ficaria	*RAFI*	I	I	**V**	**V**	I		
Rumex sanguineus			I	**IV**	**IV**			
*Stachys sylvatica**			I	**V**	**IV**	I		
Ulmus spp.^{R}				**I**	**I**			
Viburnum opulus^{R}			III	**IV**	**IV**	II		I
CESG + AMPE + CSET								
Carex acutiformis			**III**	**III**	**II**			
Cirsium palustre			**V**	**III**	**IV**			
Filipendula ulmaria	*FIUL*		**IV**	**V**	**V**			
Humulus lupulus		II	**IV**	**III**	**IV**		I	
Ribes rubrum	*RIRU*		**III**	**III**	**IV**	I		
Valeriana repens	*VARE*		**III**	**IV**	**IV**			

Annex 2.2 (Continued)

PNV		IGCA	CESG	CSET	AMPE	LPOA	AFPA	MCVM
LPOA								
Acer platanoides^R						**I**		
Acer pseudoplatanus^R			I	III	III	**IV**	I	I
*Athyrium filix-femina**	*ATFI*		IV	IV	IV	**V**	IV	II
Carpinus betulus^R					I	**II**		
*Dryopteris filix-mas**		I	II	II	II	**III**	I	I
Fagus sylvatica^R				I	I	**III**	I	I
*(Hyacinthoides non-scripta)**	*HYNO*			III	III	**V**	III	
*Luzula pilosa**	*LUPI*			I	II	**V**	II	II
Mespilus germanica^R						**I**		
*Milium effusum**	*MIEF*			III	II	**IV**	II	
*Oxalis acetosella**	*OXAC*			II	II	**IV**	II	
CSET + AMPE + LPOA								
*Anemone nemorosa**	*ANNE*		I	**V**	**V**	**V**	II	
Fraxinus excelsior^R			II	**IV**	**IV**	**IV**	I	
Hedera helix	*HEHE*		I	**V**	**V**	**IV**	II	I
*Lamiastrum galeobdolon**	*LAGA*		I	**V**	**V**	**IV**	I	
*Polygonatum multiflorum**	*POMU*		I	**IV**	**V**	**V**	III	I
Populus canescens^R				**I**	**I**	**I**		
*Stellaria holostea**			I	**IV**	**III**	**III**		
AMPE + LPOA								
Corylus avellana^R				I	**II**	**II**		I
MCVM								
Calluna vulgaris							I	**III**
Castanea sativa^R				I		I	I	**II**
Deschampsia flexuosa	*DEFL*					III	I	**V**
Frangula alnus^R			II			I		**V**
Ilex aquifolium^R				I		I	I	**III**
Molinia caerulea	*MOCA*		II			I	II	**V**
Pinus sylvestris^R								**III**
Prunus serotina^R			I		I	II	I	**V**
Quercus petraea^R						I	I	**II**
Quercus rubra^R			I	I	I	II	I	**V**
*Vaccinium myrtillus**	*VAMY*					II	I	**V**
CESG + MCVM								
Betula pendula^R			**II**		I	I		**III**
Betula pubescens^R			**II**				I	**III**
Quercus robur^R		I	**IV**	I	III	III	I	**V**
LPOA + AFPA + MCVM								
Carex pilulifera	*CAPI*					**III**	**III**	**III**
*Convallaria majalis**	*COMA*				I	**IV**	**III**	**III**
*Maianthemum bifolium**	*MABI*				I	**IV**	**II**	**III**
*Pteridium aquilinum**	*PTAQ*				I	**IV**	**IV**	**IV**
Teucrium scorodonia	*TESC*		I		I	**IV**	**IV**	**III**

Other species mentioned in Annex 2.1, without preference for a PNV: *Agrostis capillaris (AGCA), Alliaria petiolata (ALPE), Angelica sylvestris (ANSY), Anthoxanthum odoratum (ANOD), Arrhenatherum elatius (AREL), Blechnum spicant (BLSP), Brachypodium sylvaticum* (BRSY), Bryonia cretica subsp. dioica (BRDI), Calamagrostis epigeios CAEP), Cardamine pratensis (CAPR), Carex arenaria (CAAR), Carex remota* (CARE), Cirsium arvense (CIAR), Crataegus monogyna*^{R}*, Cynoglossum officinale (CYOF), Dryopteris carthusiana* (DRCA), Dryopteris dilatata (DRDI), Elymus repens (ELRE), Epilobium angustifolium (EPAN), Galeopsis bifida + tetrahit (GASP), Galium aparine (GAAP), Heracleum sphondylium (HESP), Hieracium murorum (HIMU), Holcus lanatus (HOLA), Holcus mollis (HOMO), Lonicera periclymenum* (LOPE), Luzula luzuloides* (LULU), Lythrum salicaria (LYSA), Moehringia trinervia (MOTR), Myrica gale (MYGA), Poa trivialis (POTR), Potentilla sterilis* (POST), Prunus avium*^{R}*, Rubus fruticosus (RUFR), Rumex acetosella (RUAC), Scrophularia nodosa* (SCNO), Senecio jacobaea (SEJA), Solanum nigrum (SONI), Sorbus aucuparia*^{R}*, Stellaria media (STME), Urtica dioica (URDI), Viola reichenbachiana* + V. riviniana (VISP)*

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3 Forest habitat loss and fragmentation caused by spatio-temporal disruptions

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After: De Keersmaeker L, Onkelinx T, De Vos B, Rogiers N, Vandekerkhove K, Thomaes A, De Schrijver A, Hermy M, Verheyen K. Habitat loss and fragmentation as a result of spatio-temporal forest cover changes (1775-2000) in Flanders (northern Belgium). Landscape Ecology, *submitted*

3.1 Abstract

Many forest species need forest continuity so reconstruction of historical forest cover is essential to understand present-day forest biodiversity. We quantified loss and fragmentation of five forest habitat types in Flanders (~ 13,500 km², northern Belgium), caused by spatio-temporal forest cover changes. For this purpose, forest cover at four time slices between 1775 and 2000 was digitized and combined into a forest continuity (FC) map. Undetected land use changes and positional errors limited the accuracy of the FC map. We therefore performed an error analysis, using forest inventory sample points as a reference, and achieved an accuracy of 82% after selecting patches with a low perimeter to area ratio. The comparison of forest cover at four time slices indicated that fragmentation increased slightly over time, with forest cover ranging between 9.7% and 12.2% of the total area. However, temporal disruption was high since as little as 16% of the forest cover in 2000 was ancient forest (AF), being forest continuously present at least since 1775. Furthermore, only 14% of the recent forest (RF), being forest that originated after 1775, was embedded into patches that included AF. Forest habitat on silt loam soils declined, whereas forest habitat on sandy soils and on waterlogged soils, increased. We conclude that the analysis of spatio-temporal forest cover changes, in combination with a site classification of forest habitat types, reveals high levels and specific patterns of habitat loss and fragmentation.

3.2 Introduction

Habitat loss has negative effects on biodiversity and its impact can be exacerbated by fragmentation, i.e. the spatial arrangement of remaining habitat patches (Ewers & Didham 2006). However, negative effects of this landscape process can be masked by an increase of species of habitat edges (Honnay *et al.* 1999a) and by the slow response of species to a changed landscape structure (Vellend *et al.* 2006). Many forest organisms with a slow response depend on ecological continuity. The association of these species with a continuous forest cover can be explained by the slow formation of suitable habitat (e.g. old-growth structures) or by poor dispersal capacities (Nordén & Appelqvist 2001). Such an association with ecological continuity was observed for certain lichens (Fritz *et al.* 2008), springtails (Ponge *et al.* 2006), beetles (Assmann 1999, Desender *et al.* 1999), and vascular plants (Hermy *et al.* 1999). Vascular plant species, called ancient forest plants (AFS), are mostly found in ancient forest (AF), that as far as known has been continuously present (Hermy *et al.* 1999, Rackham 2003).

When quantifying potential forest habitat loss and fragmentation, it is relevant to pay attention to the most vulnerable species, that depend on forest continuity (FC) and that also are habitat specialists. Several studies explained substantial forest cover changes, observed in NW Europe and NE America during the past centuries, by site characteristics (Foster 1992, Hall *et al.* 2002, Wulf *et al.* 2010). Studies that adopt the perspective of forest species habitat, however, are rare (but see Wulf & Rujner 2011).

Our study aimed to map spatio-temporal forest cover changes, in combination with a site classification of potential forest habitat. We focused on potential effects on vascular plant species, more specifically on ancient forest plant species (AFS), for which all the necessary information was available. Mapping spatio-temporal forest cover changes is complicated by error propagation, that can have a large impact when using information extracted from old maps (Leyk *et al.* 2005, De Clercq *et al.* 2009, Burnicki 2012). As we aimed to map forest cover changes for a time period of 225 years and for a relative large area, it was also a methodological challenge to obtain an adequate spatial and temporal resolution.

3.3 Materials and methods

3.3.1 Study area

This study covered most of Flanders (northern Belgium, 13.500 km²). The climate is mild with little regional variation. Average monthly minimum and maximum temperatures equal 2.5 °C and 17.0°C, respectively, and annual precipitation amounts to 852 mm according to the Royal Meteorological Institute (www.meteo.be). The altitude increases from sea level in the West to ca. 290 m in the East. The north of Flanders is flat or undulating and relic hills up to 150 m are present in the southwest and the center. Topsoils mainly consist of pleistocene aeolian sand and loess deposits. The silt loam content gradually increases from the north to the south. Heathland or forests soils on sand mostly are Arenosols or Podzols (IUSS Working Group WRB 2006, Dondeyne *et al.* 2012). Soils with a high silt loam content that are covered by forest, have a clay illuviation horizon and are classified as Albeluvisols or Luvisols (IUSS Working Group WRB 2006, Dondeyne *et al.* 2012). Alluvial soils without profile development are classified as Gleysols or Fluvisols and peat soils as Histosols (IUSS Working Group WRB 2006, Dondeyne *et al.* 2012). Forests covered 11% of the surface area in 2000. According to the delivered permissions, approximately 2600 ha (1.8% of the total forest cover) was cleared between 2000 and 2012, whereas 1800 ha of the open land was afforested (Bos+ 2012). Flanders has been subdivided in 12 ecoregions that are characterized by more or less homogeneous geological, geomorphological, and hydrological conditions (Sevenant *et al.* 2002).

3.3.2 Digitization of the historical forest cover

Forest cover was digitized on three historical maps (Table 3.1): the cabinet maps by de Ferraris, the topographical maps by Philippe Vandermaelen, and the third edition of military topographical maps by Dépôt de la Guerre, which is the precursor of the National Geographic Institute (NGI). Further on we refer to the mean time of the drawing. The maps by de Ferraris and by Vandermaelen were selected as they are the oldest maps, drawn in an era when systematic mapping at a detailed scale had just started. The legends of all three historical maps clearly distinguish forests from other land use categories, e.g. heathland, meadows, arable fields, water bodies, or orchards. Semi-open land use classes (e.g. wood pastures or wooded meadows) were not represented and were probably very scarce in Flanders. However, we can assume that the edge between forest and some open land use categories (e.g. heathland or meadow) nowadays is sharper than it was in the 18th and 19th century. Linear landscape elements containing trees, e.g. tree rows, were not digitized. The digitization only quantified the forest cover at successive time slices. Changes in species composition and structure of forests in Flanders, caused by a changed forest management since 1775, could not be studied by this GIS-analysis.

Table 3.1 Information on eight series of maps included into this study: map name, drawing scale, time at which the drawing started and ended, the mean time further used to refer to, and an indication if the forest cover of the map was digitized and included into the forest continuity map.

Map name	Drawing scale	Drawing time			Forest cover digitized
		Start	End	Mean	
De Ferraris	1:11.520	1771	1778	1775	Yes
Vandermaelen	1:20.000	1846	1854	1850	Yes
Dépôt de la Guerre 1	1:20.000	1860	1873	1867	No
Dépôt de la Guerre 2	1:20.000	1863	1897	1883	No
Dépôt de la Guerre 3 West	1:20.000	1879	1911	1904	Yes
East	1:20.000	1922	1938	1931	Yes
NGI 1	1:25.000	1949	1969	1959	No
NGI 2	1:25.000	1970	1988	1979	No
Forest reference layer	1:5.000			2000	Yes

The cabinet maps by de Ferraris (1775) cover the Austrian Netherlands, which comprised all of present-day Flanders except three municipalities. These municipalities account for 0.8% of the total surface area of Flanders and they were excluded from further analysis. The relative accuracy of the cabinet maps by de Ferraris is low, as a basis for triangulation was missing and distances were often measured by counting steps (illustrated by Annex 3.1). By convention, AF is forest that was already present on these maps and never was deforested afterwards. The maps by de Ferraris originally were drawn at a scale of 1:11,520. We scanned a 1:25,000 reproduction at 600 dpi and reprinted it at 1:10,000 for interpretation (see below). The maps by Vandermaelen (1850) are based on joined and updated cadastral plans that originate from the beginning of the 19th century and that were reduced to a scale of 1:20,000. As these cadastral plans are based on triangulation, accuracy of the Vandermaelen maps is higher than the maps of de

Ferraris (illustrated by Annex 3.1). The Vandermaelen maps were also scanned and reprinted at 1:10,000 for interpretation (see below).

Forest cover on the 1775 and 1850 maps was digitized by manual interpretation to moderate the large positional errors. Forests on the 1:10,000 prints were located by means of topographical maps printed at the same scale on transparency film. When located, forest perimeter was delineated on an empty film that was attached to the transparency film with the topographical map. When all forests of a topographical map sheet were drawn, the film with the forest perimeters was scanned and georeferenced, using the edge points of the topographical map sheet that were also marked on this film. Finally, the forest perimeters on the georeferenced raster image were vectorized by autotracing.

Forest cover at the third time slice was extracted from the third edition of topographical maps (illustrated by Annex 3.1). The drawing of this map was interrupted by World War I and for this reason the mean drawing time of the western part of Flanders was 1904, whereas the mean drawing time of the eastern part was 1931. The map sheets were first scanned and georeferenced and pixels in forest patches were selected by a supervised image classification. In a first step, land use classes with a distinct color were selected on the georeferenced maps (arable land and grassland: white; water: blue; roads and buildings: red; forests: green). The characteristic color palettes of the selected areas were written to signature files, that were used to perform the classification in ArcGrid, by means of an AML (Arc Macro Language) file. Not all map sheets could be classified using only one signature file. Sheets that were not processed properly, were grouped and processed again with another signature file. This process was repeated and resulted into the successful processing of 90% of the map sheets. A manual digitization was applied to the remaining map sheets. After the image classification, the land use class ‘forest’ was selected and the image was converted to a binary file. We applied a despeckle to remove small groups of misclassified pixels and a median filter by means of a moving window that was 7 x 7 pixels wide, to simplify the forest perimeter. After that, the grid was converted to a vector file.

It took approximately 800 working days between 1998 and 2001 to digitize the forest cover on the three aforementioned historical maps. We used for this purpose ArcInfo 7, including the ArcScan and ArcGrid extensions.

Forest cover of 2000 was represented by the forest reference layer (AGIV 2001b, see Annex 3.1). A post processing procedure was applied to obtain uniform criteria for forest polygons of the four time slices. Paths and small roads with a width ≤ 10 m that separate forest polygons, were removed by a closing procedure (buffer +5 m; dissolve; buffer -5m). Polygons with an area below 0.5 ha were removed, as this was the threshold value for digitization of the forest reference layer (AGIV 2001b).

3.3.3 Forest continuity

Forest cover at four time slices was combined into an overlay map. The eight overlay classes for sites covered by forest in 2000 were reduced to four classes of FC (Table 3.2). Each FC class represents forest patches that originated in the same time period and never were deforested thereafter, whatever the land use before the final conversion to forest was (Table 3.2 and illustrated by Annex 3.2). The accuracy of the FC map was quantified by comparing FC of the forest patches according to the map, with FC determined on forest inventory sample points only. The forest inventory is a systematic sampling of forests in Flanders. Sample points are located on the intersections of a 1 km x 1 km grid that are covered by forest according to a desk-top interpretation of orthophotographs. All points covered by forest were visited during a field survey, between 1997 and 1999 (Waterinckx & Roelandt 2001).

Table 3.2 Four classes of forest continuity (FC) based on the forest cover at four time slices. One indicates forest, zero is no forest at a time slice. The combination of values at four time slices results into eight overlay classes, that were reduced to four FC classes. FC class 1: continuously covered by forest since 1775 (AF); FC class 2: continuously covered by forest since 1850; FC class 3: continuously covered by forest since 1904-1931; FC class 4: converted from open land to forest after 1904-1931.

2000	1904-1931	1850	1775	Overlay class	FC class
1	1	1	1	1111	1
1	1	1	0	1110	2
1	1	0	0	1100	3
1	1	0	1	1101	3
1	0	0	0	1000	4
1	0	0	1	1001	4
1	0	1	1	1011	4
1	0	1	0	1010	4

The forest inventory points were carefully located and land use was determined on all eight map series listed in Table 3.1. The reconstruction of the land use took approximately 35 working days for 1238 sample points. This analysis did not use the vectorized historical forest maps, but the original maps to assess historical land use. The land use was gradually reconstructed, working back in time from the most accurate maps towards the least accurate, oldest maps. Interpretation of FC based on these eight time slices, for comparison was reduced to four classes that cover the same time periods as the FC map classes (Table 3.2). If, for example, a sample point located in a patch of the FC map with value 2 (Table 3.2) was forest in 1850, but cleared in 1867 and after that time continuously covered by forest, from 1883 up to 2000 (Table 3.1), this resulted into a FC value of 3 according to the sample point analysis. As we included eight historical maps instead of four and as sample points were very carefully relocated, we assumed that FC assessed by this analysis was more accurate than FC according to the map. An error matrix was used to quantify the agreement or disagreement of FC according to the map and according to the land use history assessed on forest inventory sample points. Since the forest inventory is a systematic sampling, results correspond with a proportion of the forest cover in 2000. We also compared the proportion of AF assessed on a variable number of map series that cover the same time period (1775-2000).

A subset of polygons of the FC map was selected for further analyses, based on maximum values of the perimeter to area ratio (PAR) of polygons. The maximum threshold values of the PAR (Annex 3.4) were determined by means of a receiver operating characteristic (ROC) curve (Metz 1978) (Annex 3.5). This methodology resulted into an optimal compromise for sensitivity and specificity, meaning that the accuracy, calculated as a proportion of the total area, increased without losing too much information. This is illustrated by Annex 3.3.

3.3.4 Habitat types

We used the Potential Natural Vegetation (PNV) map of Flanders (see Chapter 2) as a site classification of potential forest habitat types, to combine with the forest cover at four time slices and with the FC map. The five habitat types of the PNV map are the result of significant soil-vegetation relationships and are based on reference forest vegetation samples with a high proportion of AFS (Table 3.3). The PNV map depicts the most mature vegetation that can develop on a specific site covered by forest, if all conditions (landscape factors, habitat quality, management) are favorable. Approximately 20 % of the total area is not classified by the PNV map, comprising disturbed soils (Technosols), military areas, and marine polders and dunes.

Table 3.3 Codes and description of five forest habitat types that correspond with a classification of potential natural forest vegetation (see Chapter 2) and the soil types they are located on (Dondeyne *et al.* 2012).

Habitat code	Potential Natural Forest Vegetation types	Soil types
I	*Alnion* forest with *Carex elongata* and *Scutellaria galericulata*	Waterlogged soils classified as Histosol, Gleysol or Fluvisol
II	*Alno-Padion* forest with *Adoxa moschatellina* and *Primula elatior*	Moderately wet alluvial soils classified as Gleysol, Fluvisol or Cambisol
III	*Fagion* or *Carpinion* forest with *Luzula pilosa* and *Oxalis acetosella*	Soils with a high silt loam content classified as Luvisol, Albeluvisol or Cambisol
IV	*Quercion* forest with *Athyrium filix-femina* and *Pteridium aquilinum*	Soils with an intermediate silt loam content classified as Albeluvisol, Cambisol or Stagnosol
V	*Quercion* forest with *Molinia caerulea* and *Vaccinium myrtillus*	Sandy soils classified as Arenosol, Podsol or Anthrosol

3.3.5 Analyses of habitat loss, fragmentation, and recovery potential

Total cover, patch size, PAR, and the number of habitat types in a patch were determined on the forest cover at four time slices. Landscape metrics calculated on land use change maps, as the FC map is, are affected by positional errors (Burnicki 2012). AF patch size can be reduced by error propagation, but we worked around this problem by comparing sizes of forest patches at four time slices, that intersect with selected AF patches of the FC map. The recovery potential of recent forest (RF), being all FC classes together except AF, was qualified based on the connectivity with AF. We discerned two levels, assuming that RF within a forest patch that includes AF (called aggregated RF), had a higher recovery potential than RF in a forest patch without AF (called nucleated RF). Recovery potential of RF was calculated for the whole of the forest cover, but also for each habitat type separately. A high recovery level of RF of a specific habitat type, not only required that RF and AF were located in the same forest patch, but also that AF and RF were of the same habitat type. The sum of areas of recovery potential classes, determined for habitat types separately, was compared with total areas of recovery potential classes disregarding the habitat typology, and is considered to indicate the increased fragmentation habitat specialists experience, as compared to generalists.

3.4 Results

3.4.1 Forest cover at four time slices

Total forest cover was low between 1775 and 2000, ranging between 9.7% of the total study area in 1850 and 12.2% in 1904-1931 (Table 3.4). In 1775 forest cover was mainly located in the West and South and these areas were gradually deforested afterwards. By contrast, in 1775 forest was scarce in the northeast, but this area was gradually afforested (Fig 3.1).

Whereas a high proportion of the forest cover in 1775 was classified to habitat types III and IV on soils with a high silt loam content, approximately half of the forest cover in 2000 was classified to habitat type V on sandy soils. There was a strong decline of forest classified to habitat types III and IV, whereas forest classified to habitat types I and V increased (Table 3.4). The total forest cover of habitat type II did not change much.

Table 3.4 Forest cover in Flanders at four time slices, subdivided for habitat types and expressed as a surface area (ha) and as a proportion of the total area potentially covered by that habitat type (%). Habitat types are explained in Table 3.3.

Habitat types	1775		1850		1904-1931		2000	
	(ha)	(%)	(ha)	(%)	(ha)	(%)	(ha)	(%)
I	1789	6.6	1659	6.2	3394	12.6	8154	30.3
II	18920	14.0	14901	11.0	13126	9.7	19487	14.4
III	17291	10.0	10464	6.1	9090	5.3	9502	5.5
IV	59629	16.4	40884	11.2	23885	6.6	17486	4.8
V	37324	10.5	48488	13.6	87296	24.5	72991	20.5
Not classified	11700	3.9	14614	4.9	27707	9.4	15172	5.1
Total	146653	10.8	131010	9.7	164499	12.2	143711	10.6

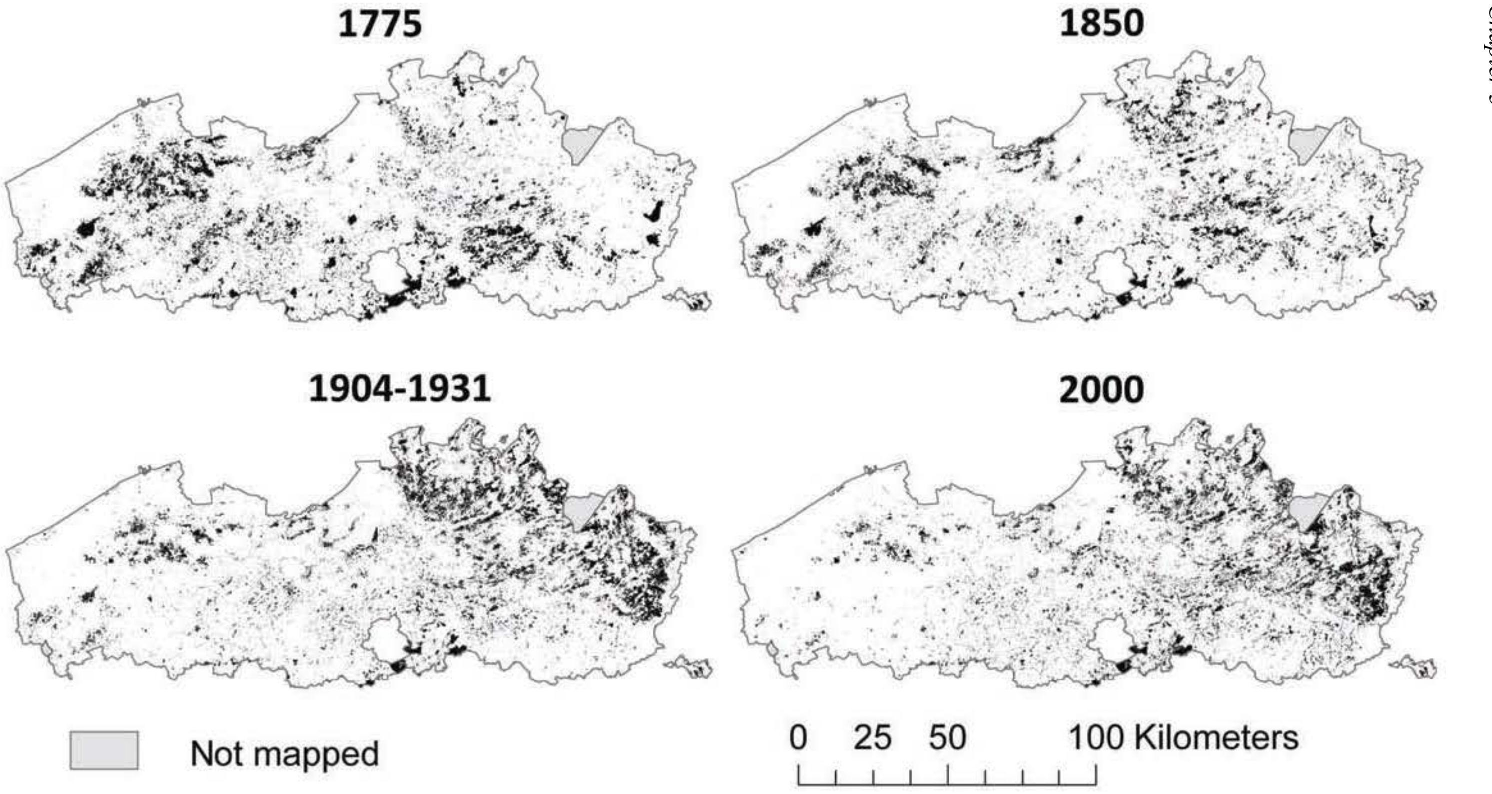


Fig. 3.1 Forest cover in Flanders on four time slices between 1775 and 2000.

Table 3.5 The number (#) and proportion of the total number (%) of forest patches at four time slices, specified for the number of habitat types (maximum totaling 5) included into a single patch.

Habitat types	1775		1850		1904-1931		2000	
	(#)	(%)	(#)	(%)	(#)	(%)	(#)	(%)
1	4392	39.7	5662	42.7	7691	48.3	8963	49.8
2	4784	43.2	5562	41.9	6061	38.1	6472	36.0
3	1518	13.7	1668	12.6	1790	11.2	2069	11.5
4	326	2.9	345	2.6	348	2.2	427	2.4
5	49	0.4	32	0.2	36	0.2	53	0.3
Not classified	637		459		1191		893	
Total	11706	100.0	13728	100.0	17117	100.0	18877	100.0

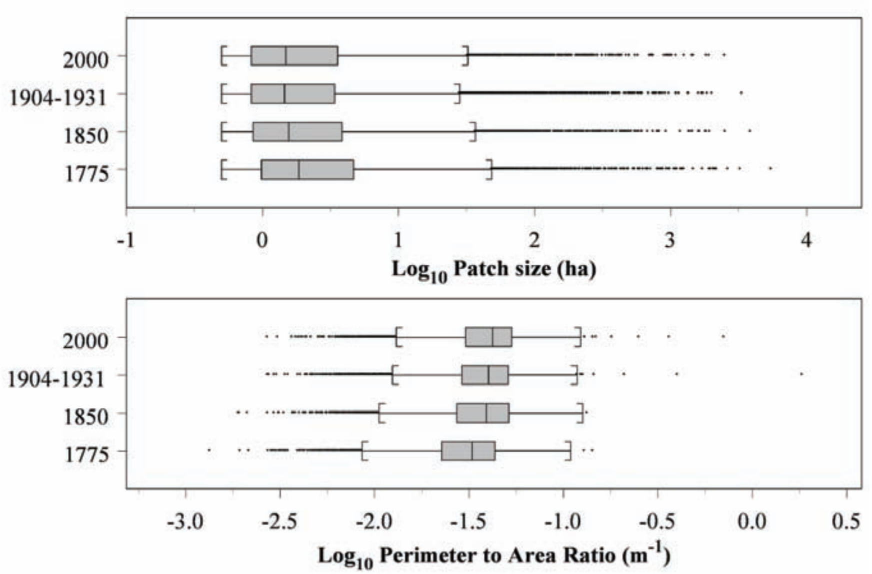


Fig. 3.2 Boxplots that represent the $\log_{10}$ transformed values of size (ha) and the perimeter to area ratio (PAR) of forest patches at four time slices.

The total number of forest patches increased since 1775 (Table 3.5) and median patch size was slightly reduced (Fig 3.2). Median patch size, between 1.5 and 2.0 ha, was low at all four time slices (Fig 3.2). The PAR increased slightly between 1775 and 2000 (Fig. 3.2). The increased number of forest patches since 1775 resulted into an increase of patches with a low number of included habitat types (1 or 2), whereas the number of patches with 4 or 5 included habitat types did not change as much (Table 3.5).

3.4.2 Forest continuity and recovery potential

According to the error matrix 71% of the FC map area was classified correctly (Table 3.6). Accuracy was relatively high for the FC classes representing AF and sites that were afforested after 1904-1931, but very low (33%) for the FC class representing sites afforested between 1775 and 1850. The accuracy of the FC map increased from 71% to 82% by selecting polygons with PAR values below threshold values listed in Annex 3.4. The ROC curve and model characteristics, used to determine maximum PAR threshold values for the four classes of the FC map, are presented in Annex 3.5. The total area of selected polygons amounted to 66.7% of the total forest cover in 2000. Accuracy of the FC class that represents AF increased from 76% to 86% by selecting 463 polygons with a low PAR (Annex 3.4). None of the polygons of FC class 2 that contains, according to the FC map, sites afforested between 1775 and 1850 and continuously covered by forest ever since, was selected, a consequence of the low accuracy of this FC class (see Table 3.6).

Table 3.6 Error matrix on 1238 forest inventory sample points, confronting forest continuity (FC), represented by the FC map based on four time slices, with the interpretation of land use on eight historical map series (see Table 3.1). The four letters refer to the time period at which a sample point was converted to forest and never deforested ever since: before 1775 (ancient forest: A), between 1775 and 1850 (B), between 1850 and 1904-1931 (C), after 1904-1931 (D).

		Map				
		A	B	C	D	Total
Sample points	A	135	25	23	18	201
	B	6	42	19	11	78
	C	29	40	323	73	465
	D	7	19	89	379	494
	Total	177	126	454	481	1238
Accuracy (%)		76	33	71	79	71

The proportion of the total forest cover that was qualified as AF, decreased as temporal resolution increased, by reduction of the proportion of missed land use conversions (Fig 3.3). However, this value was highly dependent of the map series that were selected to include into the analysis (Fig 3.3). Although the 1850 map had a higher positional error than the 1904-1931 map, the 1850 map was more relevant to include for FC assessment, as forest cover was at a minimum at that time (see discussion). The proportion of AF based on the overlay of maps with forest cover at four time slices equaled 14.9%, whereas calculation using the same four time slices but based on the forest inventory sample points, resulted into a value of 19.7%. We can conclude that this difference is a consequence of error propagation that reduced the patch size of AF in the GIS overlay. The proportion of AF, based on forest inventory sample points and using eight map series, equaled 16% (Fig. 3.3). We assumed this was the most accurate assessment of the proportion of AF.

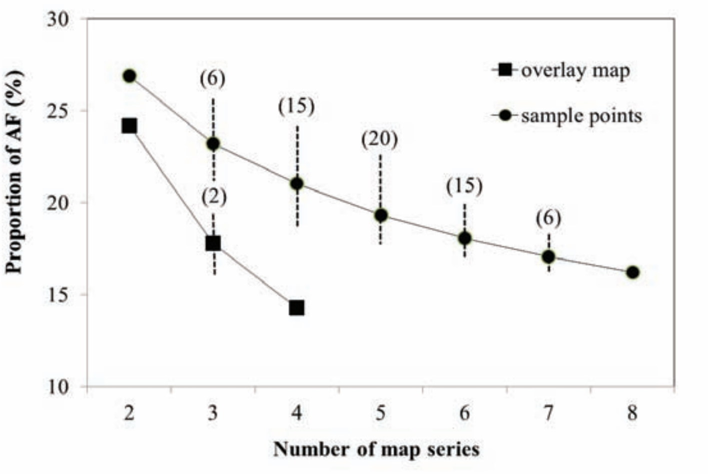


Fig. 3.3 Mean proportion of the forest cover in 2000 (%) classified as ancient forest (AF), based on a variable number of map series that cover the time span between 1775 and 2000. Proportions are determined on the overlay of maps with the digitized forest cover at maximum four time slices and on the land use history of sample points at maximum eight time slices (see Table 3.1). The numbers of possible combinations used to calculate the mean values are mentioned between brackets, the dotted lines connect the minimum and maximum values.

There is a high regional variability in the proportion of the total forest cover that is AF (compare Figs 3.1 and 3.4): it is high in ecoregions in the west of Flanders (except in polders and dunes) and in the ecoregions in the center with an undulating topography. The proportion of the forest cover in 2000 that is AF, is very low in the ecoregion in the southeast and in the ecoregion of the northeast, that comprised 60% of the total forest cover of Flanders in 2000.

The median of selected AF patches in 2000 is embedded into a forest patch that covers twice the area of the AF (Fig 3.5). The size of these enclosing forest patches was reduced through time to approximately 20% of the size in 1775 and the strongest decline was observed between 1775 and 1850 (Fig 3.5).

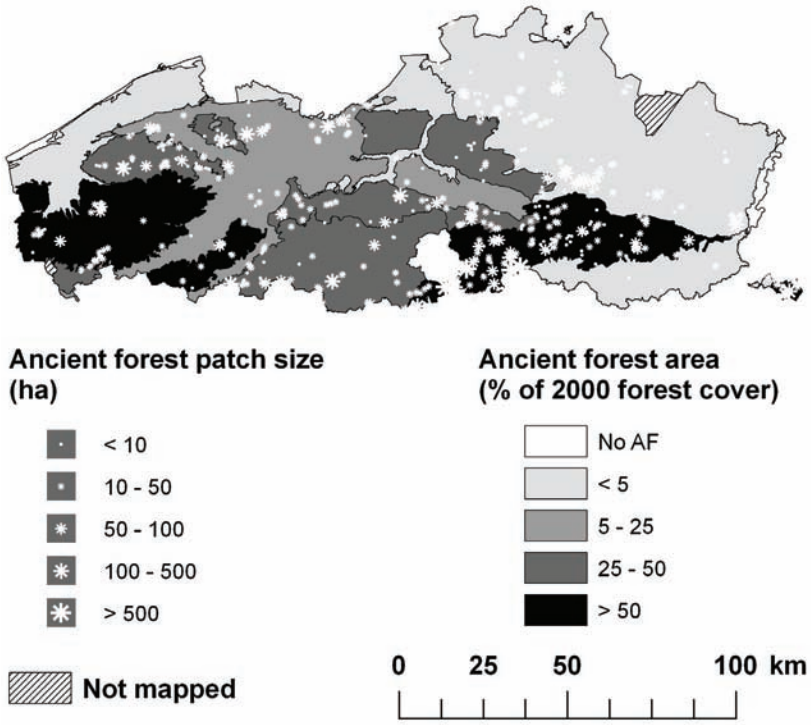


Fig. 3.4 Area covered by ancient forest, expressed as a percentage of the 2000 forest cover, in 12 ecoregions of Flanders. Symbols mark the location and size of 463 selected ancient forest patches (see Annex 3.4).

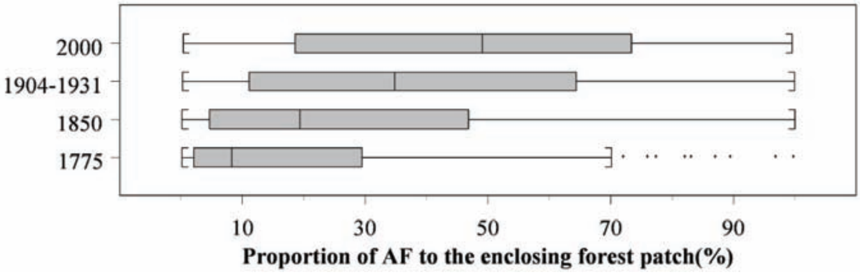


Fig. 3.5 Proportion (%) of the area that is qualified as AF on the overlay of forest cover at four time slices, to the area of enclosing forest patch at each time slice.

The proportion of AF is highly dependent of habitat type (Table 3.7): it is high for types III and IV, intermediate for type II and V, and low for type I. More than 80% of the forest cover of habitat types I and II originated after 1904-1931. The proportion of the forest cover of habitat type V that originated between 1850 and 1904-1931, is of a similar order of magnitude (approximately 45%) as the proportion that originated after that time.

Table 3.7 Area covered in 2000 by five forest habitat types, subdivided over three forest continuity (FC) classes. Habitat types (Roman numerals) are explained in Table 3.3, FC classes (capital letters) in Table 3.6. FC class B was not retained by the ROC analysis (see Annex 3.4 and 3.5).

Habitat type	FC classes					
	A		C		D	
	(ha)	(%)	(ha)	(%)	(ha)	(%)
I	85	1.3	583	9.2	5699	89.5
II	1310	10.4	953	7.6	10358	82.1
III	4485	63.0	377	5.3	2255	31.7
IV	3805	35.8	1741	16.4	5078	47.8
V	4032	8.3	23031	47.2	21718	44.5
Not classified	612	5.9	1531	14.7	8253	79.4
Total	14329	14.9	28217	29.4	53362	55.6

Table 3.8 Connectivity of recent forest in 2000 (classes C and D in Tables 4 and 5) with ancient forest (class A in Tables 4 and 5), specified for five habitat types (Roman numerals explained by Table 3.3). Connected recent forests are included into a forest patch with ancient forest of the same habitat type.

Habitat type	Connected		Not connected	
	(ha)	(%)	(ha)	(%)
I	212	3.4	6070	96.6
II	1107	9.8	10204	90.2
III	577	21.9	2055	78.1
IV	1287	18.9	5532	81.1
V	6596	14.7	38153	85.3
Total	9778	13.6	62015	86.4

Forest cover in 2000 mostly consisted of nucleated RF, meaning that it is not embedded into a patch that also contained AF (Table 3.8). Aggregated RF of habitat types I and II is very scarce, but less so for habitat types III and IV. The sum of RF aggregated to AF of the same habitat site (listed in Table 3.8), amounted to 85% of the total area of RF aggregated to AF, without the condition that both should be of the same habitat type. This finding suggests that habitat specialist AFS did not experience much more isolation than generalist AFS.

3.5 Discussion

3.5.1 Methodological aspects

Land use or land cover change, including its causes and consequences, is a key research topic in landscape ecology, but so is its data quality and accuracy assessment (Hobbs & Wu 2007). Land use changes can be mapped with a high accuracy over a long time period when small areas are studied (Foster 1992, Verheyen *et al.* 1999, Cousins 2001), whereas spatial or temporal resolution are relatively low for large study areas (Iverson 1988, Hall *et al.* 2002, Wickham *et al.* 2007). Achieving a high resolution over a long time period and for a large area is complicated by the relative inaccuracy of old maps. A case study on a single municipality in Flanders using the same historical maps indicated that the positional root mean squared error decreased with time (with 99.9% confidence interval): 43m +/- 0.6m (1775), 31m +/-0.6m (1850), and 16m +/-0.2m (1904-1931), respectively (Onkelinx *et al.* 2004). Several authors applied a rubber sheeting to reduce positional errors of old maps (Cousins 2001, Wulf *et al.* 2010, Andrieu *et al.* 2011, Skalos *et al.* 2012). We applied a manual interpretation using a slide, as Lindbladh *et al.* (2007) did. It is safe to assume that the remaining positional errors after this manual correction were of minor importance for comparison of landscape metrics (total forest area, patch size, PAR) calculated on separate time slices, for a large study area (see also Iverson 1988). However, superimposing historical land use information digitized separately, even with reduced positional errors, can result into a high proportion of false change in the resulting land use change map, e.g. our forest continuity map (De Clercq *et al.* 2009). Landscape metrics calculated on land use change maps indicate a more fragmented and variable landscape under error (Burnicki 2012). The proportion of false land use change is determined by the positional error of the included maps, but is also positively correlated with the number of patches, the total forest cover, and the nearest distance between patches, i.e. the level of fragmentation (De Clercq *et al.* 2009). On the other hand, the amount of error of land use change maps is reduced by a high temporal change (Burnicki 2012), which is certainly the case for our study area. If the rate of land use change (e.g. forest vs. other land use) is high between two time slices, the patches on a land use change map that indicate cleared and newly created forest, are large. Large land use change patches are affected less by the error propagation than small land use change patches.

False change by error propagation can be avoided by transferring information of error-perturbed old maps to a reference map, such as accurate cadastral or topographical maps (e.g. applied by Verheyen *et al.* 1999, Skalos *et al.* 2012). When doing so, a regressive interpretation method could be appropriate, working back in time towards the oldest and most difficult to interpret map (e.g. applied by Andrieu *et al.* 2011). Given the scale of our study area we could not apply this labor-intensive method. Instead we digitized historical maps separately but submitted the overlay map to an error analysis. An error analysis of this kind could be based on the buffering of historical maps included into the overlay, using the specific RMSE of each included historical map (e.g. see Leyk *et al.* 2005). This methodology, however, does not take into account the errors that originate from land use conversions missed by the limited number of historical maps included into the overlay. For this reason we preferred the error analysis based on the land use history of the forest inventory points. The ROC analysis resulted into a subset of polygons, with an optimal sensitivity and specificity, selected for further analysis. The error analysis indicated that a high accuracy, expressed as a proportion of the total forest cover, was achieved for three out of four forest continuity classes. The forest inventory sample points used for the error analysis, were interpreted regressively on all available historical maps series, not only the series used to create the overlay. By doing so, not only slivers but also errors that originate from using a reduced number of historical maps were quantified. We applied this methodology a posteriori, but it could also be used a priori, to select maps for digitization that attribute most to an accurate assessment of forest continuity. The low time consumption as compared to the digitization of the whole forest cover on three historical maps (< 4%), emphasizes the usefulness of the sample point interpretation as an exploratory analysis.

3.5.2 Spatio-temporal forest cover changes

Forest cover changes since the 18th century have been studied in NE America (Foster 1992, Hall *et al.* 2002, Matlack 2005) and in central and western Europe (Sereda & Lukan 2009, Wulf *et al.* 2010, Skalos *et al.* 2012). According to most of these studies, forest cover was relatively low in the 19th century. Forest clearance in Flanders and in

Prussia before 1850 is explained by population growth, but also by political, economic, and technological changes (Tack *et al.* 1993, Wulf *et al.* 2010, Vandekerkhove *et al.* 2011). Some studies recorded a forest cover increase towards the end of the 19th century (Hall *et al.* 2002, Skalos *et al.* 2012). Between 1850 and 1931, forest cover of the Campine ecoregion (NE of Flanders) increased from 8% to 26%, mostly by plantation of pine forest on heathland.

Both in NE America and in Europe, forest cover changes were related to environmental conditions (Foster 1992, Hall *et al.* 2002, Wulf *et al.* 2010, Andrieu *et al.* 2011, Skalos *et al.* 2012). In Flanders, forests on silt loam soils were converted to farmland in the 19th century, whereas forest cover increased on soils with a high sand content, a process also observed in Prussia (Wulf *et al.* 2010). Waterlogged soils in Flanders were converted to forest in the 20th century, which was also observed in central Bohemia (Skalos *et al.* 2012). Reforestation of fields in central New England (MA, USA) since the middle of the 19th century, started at poorly drained sites (Foster 1992).

The magnitude of the spatio-temporal forest cover changes explains the low forest continuity in Flanders, as compared to other areas in Europe studied for the same time period. In central Bohemia forest cover ranged between 12% and 18% between 1780 and 2007, but 53% of the total forest cover was continuously present (Skalos *et al.* 2012; based on four time slices), as opposed to 16% in Flanders. Forest cover of the Prignitz region (Germany) amounts to 23%, 35% of which is AF (Wulf & Gross 2004; based on three time slices). Total forest cover is low in England and Wales (8%), but 34% of it is qualified as AF, being forest that was continuously present since 1600 (Spencer & Kirby 1992; based on at least four time slices). Approximately 7% of the AF area in England and Wales was cleared for other land use in the past 50 years (Spencer & Kirby 1992). In Flanders, 37% of the forest that was continuously present between 1775 and 1904-1931 (totaling almost 30,000 ha), was cleared after that period.

3.5.3 Effects on forest species diversity

Landscape metrics calculated at separate time slices and disregarding forest continuity (patch area and PAR), only indicated a slight increase of forest fragmentation in Flanders between 1775 and 2000. Fragmentation, expressed by a high PAR, can be positive for some species groups, e.g. species of edges and clearings, but not for true (inner) forest species. Such diverging effects have been assessed for vascular plant species (Honnay *et al.* 1999a), but also for other organisms, e.g. springtails (Ponge *et al.* 2006). The high but more or less constant level of (spatial) forest fragmentation in our study did not reveal the very high temporal disruption of the forest cover. Many forest organisms depend on a continuous forest cover and are unable to overcome rapid conversions between forest and other land use. Some species e.g. certain beetles (Assmann 1999, Desender *et al.* 1999), springtails (Ponge *et al.* 2006) or vascular plants (Hermy *et al.* 1999) lack the necessary dispersal capacities. Other species, e.g. lichens (Fritz *et al.* 2008), have good dispersal capacities but require specific habitat that is mostly restricted to a continuous forest cover. Hereafter we focus on potential effects of spatio-temporal forest cover changes on vascular plant species, AFS in particular, as these organisms are thoroughly studied. Many forest plant species, but AFS in particular, are slow colonizers and colonization rates can be below 1 $m.yr^{-1}$ (Brunet *et al.* 2011, see Chapter 6). AFS can be dispersal or recruitment limited and the relative importance between both is variable (Verheyen & Hermy 2001b).

Recovery of forest vegetation is lagging behind reforestation for a considerable time even when sources for recolonization are still present (Matlack 2005). The loss of AF has a strong negative influence on the recovery potential of plant species diversity in RF (Vellend 2003). Conservation of the remaining AF therefore is seen as a priority (Peterken & Game 1984, Spencer & Kirby 1992, Wulf 2003, De Frenne *et al.* 2011). Most AFS are associated with mesophilous forest habitat, located on moderately wet soils with a high silt loam content (habitat types II and III), that declined. By contrast, only few AFS are characteristic for habitat types on waterlogged and acid sand soils (habitat types I and V, respectively), that increased (Hermy *et al.* 1999, see Chapter 2). So even if RF vegetation in Flanders can recover, it is mostly located on habitat sites that are suitable only for a few AFS.

According to Jacquemyn *et al.* (2001), area and time cannot be treated independently as predictors of forest plant species richness. There are several relationships between forest continuity (forest age) and landscape variables (level of fragmentation), that have an influence on forest plant species diversity. The recovery level of RF is higher in landscapes with a high connectivity between forest patches (Honnay *et al.* 2002b, Verheyen *et al.* 2006). RF in physical contact with AF (aggregated RF) is richer in species than nucleated RF (Peterken & Game 1984, Jacquemyn *et al.* 2003b). Species number in RF adjacent to AF, increased more as a function of area increase, than in isolated RF, but less so than in AF (Peterken & Game 1984). As only 14% of the area of RF is aggregated, we can conclude that most of the RF in Flanders has a low recovery potential.

Habitat diversity and quality are important explanatory factors of forest species diversity, related to the time dimension as well. Positive species-area relationships in AF mostly were attributed to increased habitat diversity of large forest patches (Peterken & Game 1984, Honnay *et al.* 1999a). Several studies indicated that not only connectivity with AF but also modified habitat quality in RF could explain the interactions between area and time, observed for species-area relationships. Where the historical continuity was high, local environmental characteristics explained a significant amount of species assemblages within metacommunities (Jamoneau *et al.* 2012). Wilson *et al.* (1997) found a higher soil variability in AF than in RF as a result of homogenization of RF soils under agricultural land use. Many RF soils in our study area are eutrophicated with P (see Chapter 5), which can accentuate the difference in colonization capacity among forest herbs (Baeten *et al.* 2009b).

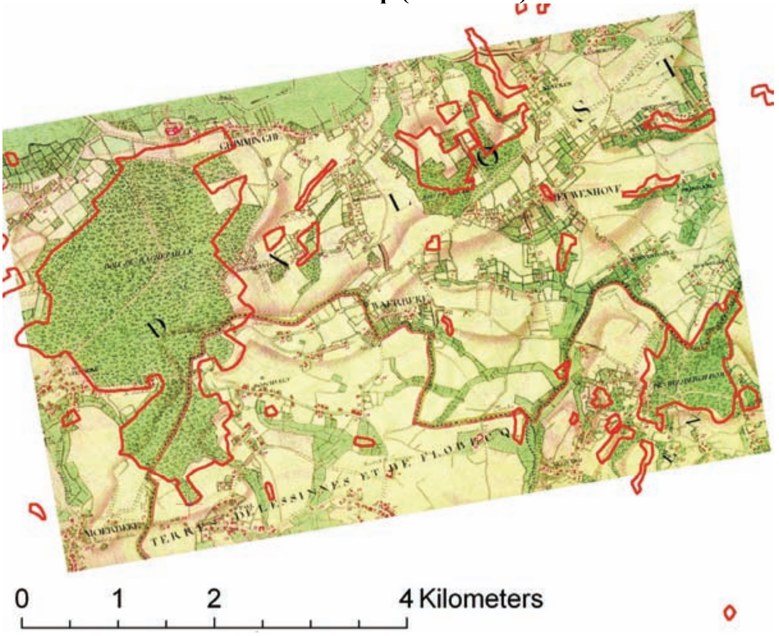
3.6 Conclusions

A GIS-based analysis of spatio-temporal changes, specified for forest habitat type, revealed high and specific levels of temporal disruption of forest cover in Flanders. However, such an analysis faces several methodological challenges and is labor intensive. Compromises have to be made for the temporal and spatial resolution that can be achieved. An accurate analysis of land use history of systematically sampled points, is far less time consuming and could be used to select maps that contribute most to the assessment of forest continuity, and to determine the amount of error of a forest continuity map.

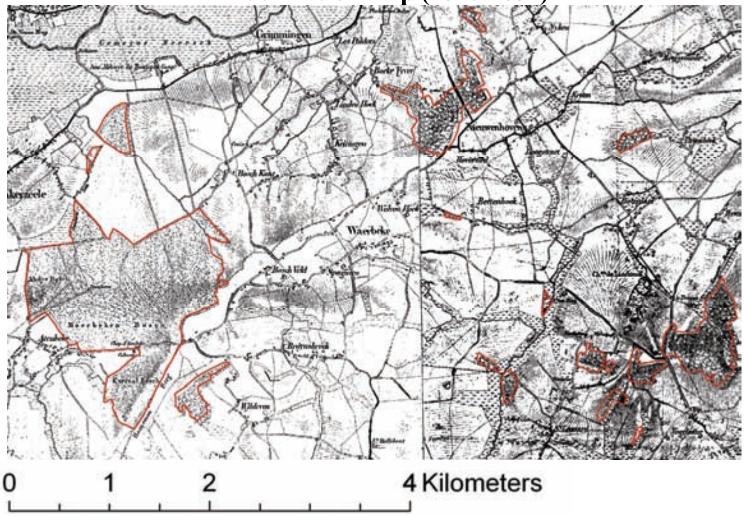
Based on numerous studies on this subject, we can assume that the rate of spatio-temporal forest cover changes in Flanders resulted into massive habitat loss and fragmentation for slowly colonizing forest plant species (AFS). This analysis provided qualitative and quantitative, spatially explicit information on the historical and present-day forest cover. The resulting maps are used for forest conservation, e.g. by identifying AF that are potential biodiversity hotspots (Spencer & Kirby 1992), and for the assignment of Natura 2000 forest habitat in Flanders. Forest continuity maps can also support projects that aim for restoration or defragmentation of forest habitat, as optimal sites can be selected by a relatively simple desk-top analysis.

Annex 3.1 Snaps shots of the historical maps with digitized forest patches represented as red outlines. The Ferraris and Vandermaelen maps were georeferenced for visualization but these georeferenced maps were not used for digitization of forests. This explains the mismatch between the outlines and the forests represented by the maps. The depicted area (Geraardsbergen – Galmaarden) is located within the red box of Fig. 4.6.

Ferraris map (1771-1778)

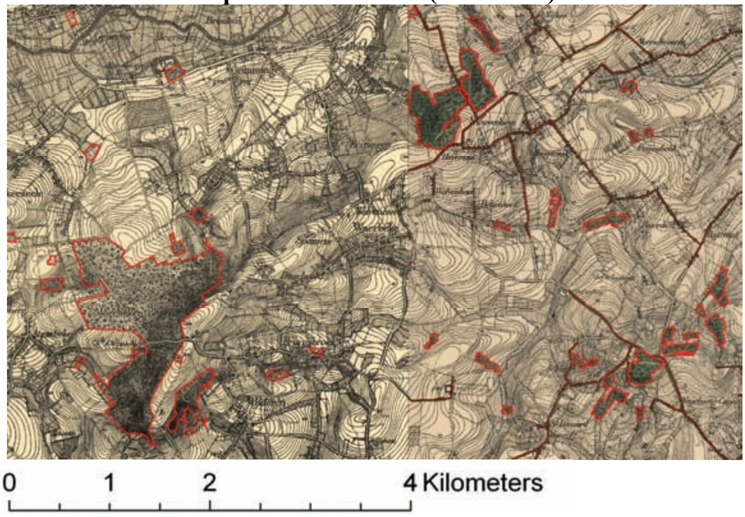


Vandermaelen map (1846-1854)

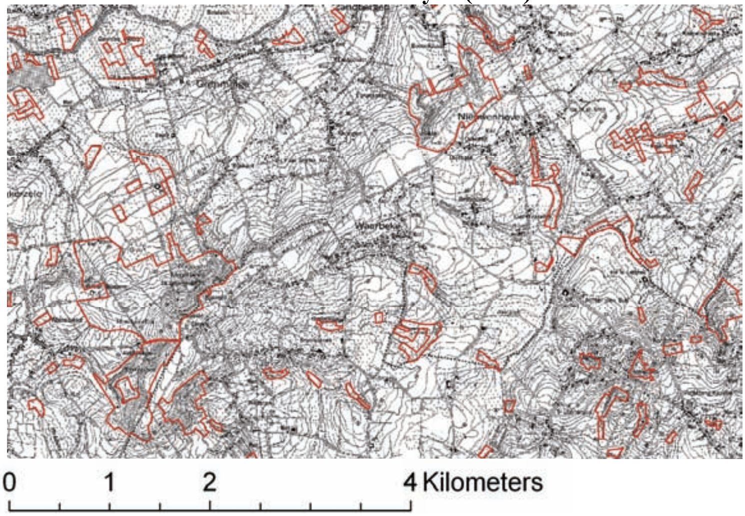


Annex 3.1 (continued) Snaps shots of the historical maps with digitized forest patches represented as red outlines. The western map of Dépôt de la Guerre 3 (1910) was published in black and white and forests were manually digitized for this reason. The eastern map of Dépôt de la Guerre 3 (1911) was digitized by means of image classification. The depicted area (Geraardsbergen – Galmaarden) is located within the red box of Fig. 4.6.

Dépôt de la Guerre 3 (1910-1911)

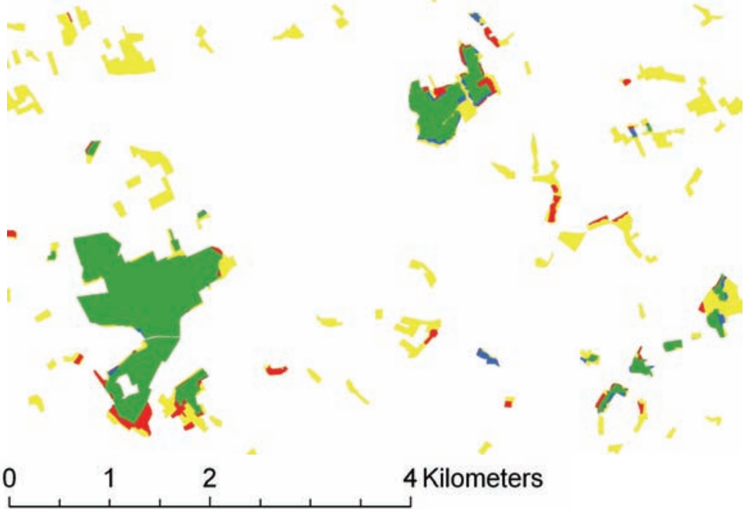


Forest reference layer (2000)



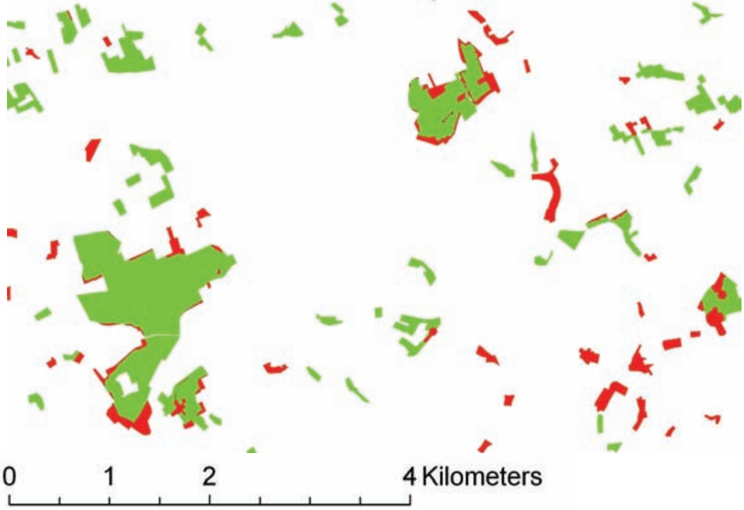
Annex 3.2 The forest continuity map for the area illustrated by Annex 3.1, with four classes of forest continuity of the forest cover in 2000. FC class 1 is green (AF), FC class 2 is blue, FC class 3 is red and FC class 4 is yellow (FC classes are explained in Table 3.2).

Dépôt de la Guerre 3 (1910-1911)



Annex 3.3 Patches of the forest continuity map that were selected for further analysis by the ROC graph (Annex 3.5) are green, patches that were not selected are red.

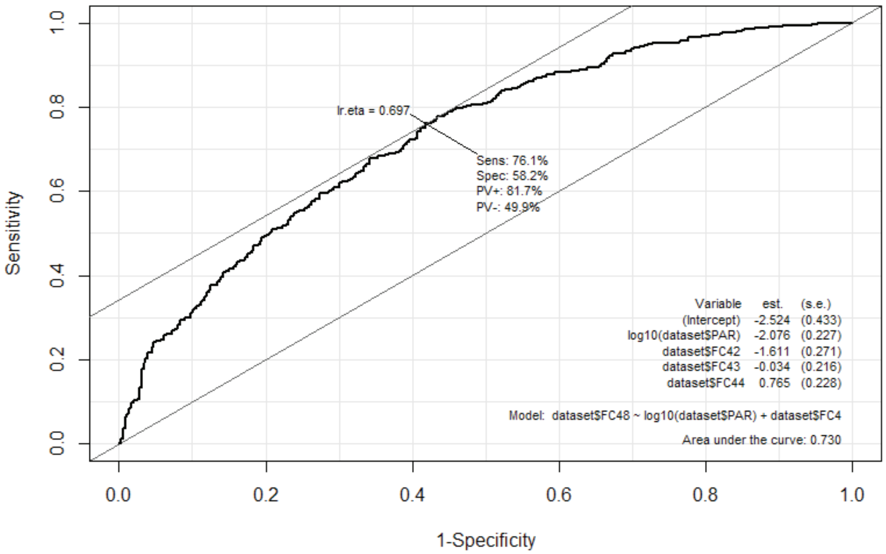
Forest reference layer (2000)



Annex 3.4 The perimeter to area (PAR) threshold values applied to select polygons of four forest continuity classes (FC), and the number and proportion of selected polygons and area. The accuracy calculated on the selected patches is based on an error analysis similar as Table 3.4, using forest inventory sample points..

FC	PAR threshold	Selected polygons (GIS)		Selected Area (GIS)		Accuracy
			(%)		(%)	(%)
1	0.0241	463	8.0	14329	76.1	86
2	0.0040	0	0	0	0	/
3	0.0232	821	3.6	28217	58.9	78
4	0.0562	12373	27.5	53362	84.6	83
Total		13657	16.2	95908	66.7	82

Annex 3.5 ROC curve representing the true positive rate (Sensitivity) as a function of the false positive rate (1-Specificity), for the model constructed on the agreement (FC48 as a binary variable) between FC4 and FC8. FC4 is forest continuity based on the overlay map, FC8 is forest continuity based on forest inventory sample points. The model included the perimeter to area ratio (PAR) of polygons on the map and the 4 forest continuity classes of this map (FC41, FC42, FC43, FC44) as explanatory variables. The threshold values for the PAR are determined by the point of tangency of the ROC curve with the line parallel to the bisector.



Variable	est.	(s.e.)
(Intercept)	-2.524	(0.433)
log10(dataset$PAR)	-2.076	(0.227)
dataset$FC42	-1.611	(0.271)
dataset$FC43	-0.034	(0.216)
dataset$FC44	0.765	(0.228)

Model: dataset$FC48 ~ log10(dataset$PAR) + dataset$FC4

Area under the curve: 0.730

Anemone nemorosa is colonizing an 18-years old post-agricultural forest stand in Muizenbos, where *Ranunculus ficaria* is already dominant.

4 A spatially explicit empirical model on actual and potential ancient forest plant species richness

After: De Keersmaeker L, Onkelinx T, Vandekerkhove K, Thomaes A, Hermy M, Verheyen K. A spatially explicit empirical model on actual and potential ancient forest plant diversity in a fragmented landscape. Landscape and Urban Planning, *submitted*

4.1 Abstract

Spatio-temporal forest cover changes often result into a decline of forest plant species richness. In particular slow colonizing ancient forest plant species (AFS) are affected, as they depend to a certain degree on the continuity of the forest cover in space and time. The implementation of conservation and restoration strategies for AFS can be supported by a map that represents the actual AFS richness of the current forest, as well as the potential AFS richness that open land can achieve when converted to forest. To create such a map for Flanders (northern Belgium), an empirical model was constructed using spatially explicit data on habitat suitability and continuity. The model calculated a high AFS richness for suitable mesophilous sites covered by forest in 1775 and in the early 20th century. Sites near a concave edge of a forest patch in 2000, either inside or outside forest, were also rated high. This is the first operational landscape model on AFS richness that can be used to select hotspots of AFS richness in the present-day forest and sites with a high restoration potential in the open landscapes. Application of the AFS richness map on a local scale should include additional information on linear landscape elements, soil conditions and forest management, as we assume that these factors account for a high proportion of the unexplained deviance.

4.2 Introduction

Many forest organisms are slowly colonizing habitat specialists and the best studied species in this respect are vascular plants called ancient forest plant species (AFS) (Hermy *et al.* 1999). AFS are, by definition, found more frequently in ancient forest - sites as far as we know continuously covered by forest - than in recent forest that was converted to other land use for some time (Rackham 2003). AFS depend on a long and continuous forest land use and they suffer from habitat loss and fragmentation at a rate that exceeds the slow colonization capacities of AFS (Vellend 2003, Verheyen *et al.* 2004). Spatio-temporal disruptions can result into a highly fragmented forest cover with a variable recovery level of forest vegetation (Verheyen *et al.* 2006).

The recovery of forest vegetation at former agricultural sites is a slow process and largely depends on the connectivity with source populations of AFS (Brunet 2007, Baeten *et al.* 2009c, Brunet *et al.* 2011). For this reason conservation of remaining ancient forest is seen as a priority (Peterken 1977, Vellend 2003, Wulf 2003). The AFS number in recent forest is positively influenced by physical contact with ancient forest (Peterken & Game 1984, Honnay *et al.* 1999a). However, the quality of the landscape matrix can be important as well. Relic populations of AFS can survive forest clearance in fringe relics, hedges or tree rows, that support vegetation recovery following reforestation (Honnay *et al.* 1999b). Furthermore, hedgerows and tree rows can function to some extent as habitat corridors for AFS (Corbit *et al.* 1999, Endels *et al.* 2004, Wehling & Diekmann 2009).

AFS richness is not only explained by habitat continuity and connectivity, but also by habitat suitability, that can be influenced by natural and by anthropogenic factors. The number of AFS is dependent of habitat type (see Chapter 2, Hermy *et al.* 1999). The highest richness of AFS in NW Europe is found in forest habitat on mesophilous sites (Hermy *et al.* 1999). However, more than other forest habitat types, mesophilous forest was cleared and converted to agricultural land during the past centuries (Wulf *et al.* 2010, Andrieu *et al.* 2011, see also Chapter 3). AFS richness of the remaining mesophilous forest habitat can also decline by anthropogenic habitat degradatation (Decocq *et al.* 2004, Van Calster *et al.* 2008, Baeten *et al.* 2009a, Baeten *et al.* 2010a). As a result of habitat loss and degradation, the recovery of recent forest can be inhibited as well (Vellend 2003, Baeten *et al.* 2010a).

As spatio-temporal forest cover changes and habitat degradation put a high pressure on AFS richness, there is a need for tools that can support conservation and restoration projects. Strategies for conservation of forest plant species richness have been explored several times, e.g. in the framework of the SLOSS (a single large or several small) discussion (Game & Peterken 1984, Honnay *et al.* 1999a, Hokkanen *et al.* 2009). The operationalization of conservation strategies requires thorough species inventories (Hokkanen *et al.* 2009), that are mostly only available for a selected, relatively small number of forest patches. The aim of this study was to build a model using spatial explicit explanatory variables that can predict AFS richness on a scale and resolution that are beyond the limits of what is possible by means of field surveys. As argued above, such a model requires maps on habitat suitability and on forest continuity, both of which are available for our study area (see Chapters 2 and 3). However, we also aimed to create a map that can be used to forecast the recovery potential of open land, when converted to forest. As the historical landscape structure can explain the recovery rate of post-agricultural forest, we wanted to include connectivity measures calculated on separate historical and present-day forest maps instead of measures only calculated on the remaining ancient forest (AF). As we aimed to create a spatial explicit model, explanatory connectivity measures had to be quantified for the whole study area, not only for forests. As far as we know, an operational landscape model of this kind has not been constructed before.

4.3 Methods

4.3.1 Study area

This study covered most of Flanders (northern Belgium, 13.500 km²). The climate is mild with little regional variation. Average monthly minimum and maximum temperatures equal 2.5 °C and 17.0°C, respectively, and mean annual precipitation amounts to 852 mm according to the Royal Meteorological Institute (www.meteo.be). The altitude increases from sea level in the West to ca. 290 m in the East. The north of Flanders is flat or undulating and relic hills up to 150 m are present in the southwest and the center. Topsoils mainly consist of pleistocene aeolian sand and loess deposits that result in soils with a high silt loam content. The silt loam content gradually increases from the north to the south. Flanders has been densely populated for a long time and it is assumed that forest cover was already low in medieval times and in many cases even in the Roman era (Tack *et al.* 1993). At the end of the 18th century, forest cover equalled 10.8% of the total area. Absolute changes were small since that time and the forest cover occupied 10.6% of the total area in 2000. However, after 1775 many forests on mesophilous sites were converted to farmland, which resulted into a decline by approximately 50% of the area covered by forest on these sites. This area loss was compensated by the conversion of heathland and waterlogged soils to forest in the 19th and 20th century. As a result of these spatio-temporal forest cover changes, only approximately 16% of the forest cover in 2000 is ancient forest, i.e. forest continuously present since 1775 when the first maps for the whole area were drawn (see Chapter 3).

4.3.2 Response data

We intended to explain AFS number for a relative large area, counted in grid-based plots that are representative for the total forest cover in our study area. The plot-based inventory data were provided by the Flemish forest inventory, a systematic sampling of forests containing an inventory of vegetation at the intersections of a 1 km x 1 km grid (Waterinckx & Roelandt 2001). Grid points covered by forest were visited between 1997 and 1999 for this purpose. Vegetation was inventoried in 16 m x 16 m (256 m^2) sample plots, using the Braun-Blanquet sampling scale (Waterinckx & Roelandt 2001). Sample points at a distance of less than 200 m from the border of the study area were omitted, as not all explanatory variables could be calculated at closer distance (explained below).

Table 4.1 The median, upper and lower quartiles of the ancient forest species (AFS) count per plot and the number of specialist AFS, in five forest types that are PNV in Flanders (see Chapter 2). Specialist AFS occur much more frequently in one type than in others. PNVs with a code between brackets are mesophilous forest habitat, selected for modeling.

Forest vegetation types		Median AFS count (1st – 3th quartiles)	Specialist AFS
Alnion forest with *Carex elongata* and *Scutellaria galericulata*		2 (1-3)	0
Alno-Padion forest with *Adoxa moschatellina* and *Primula elatior*	(AP)	8 (5-10)	15
Fagion or *Carpinion* forest with *Luzula pilosa* and *Oxalis acetosella*	(FC)	5 (3-7)	6
Quercion forest with *Athyrium filix-femina* and *Pteridium aquilinum*		2 (1-4)	0
Quercion forest with *Molinia caerulea* and *Vaccinium myrtillus*		1 (1-2)	1

We calculated from this vegetation samples (n = 1121) the number of species, that are considered AFS according to a European compilation list (Hermy *et al.* 1999). The number of AFS in forest vegetation is not only determined by forest history, but is also highly dependent of natural site conditions (see above). To reduce zero-inflation of the dataset, we removed samples located on sites that are unsuitable for mesophilous forest habitat according to the Potential Natural Vegetation (PNV) map of Flanders (see Chapter 2). PNV is the most mature forest vegetation that can be expected and the map depicts the suitability of a site for five PNV types (Table 4.1). The two selected PNV types (AP and FC in Table 4.1) are mesophilous forest habitat with a high number of AFS, including several habitat specialists that are frequent in one PNV type but scarce in others. AFS, in particular habitat specialists, are scarce in other PNV types that were not selected (Table 4.1). As a result of this selection, 737 sample points were removed, most of which counted less than four AFS (Fig. 4.1). Seven sample points with extreme values of explanatory variables were also removed, so 377 samples on sites with a potential for mesophilous forest were used for modeling.

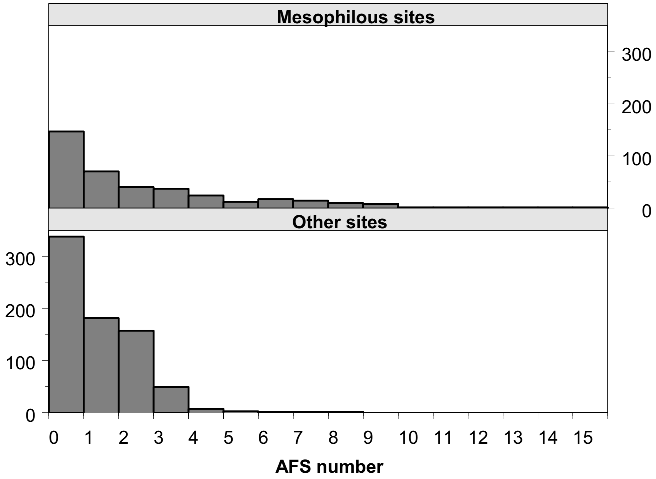


Fig. 4.1 Histograms of the AFS count in forest inventory sample plots located on mesophilous sites (n = 384) and other sites (n = 737).

4.3.3 Explanatory data

The explanatory variables were derived from five types of source data (Table 4.2): eight connectivity measures were calculated on forest cover maps at four time slices, four connectivity measures were calculated on a cadastral map, two habitat suitability indices were extracted from the PNV map, slope was derived from a DTM, and three variables were the result of an interpretation of land use on eight maps that cover the time period between 1775 and 2000. Names of explanatory variables are indicated by capitals hereafter (Table 4.2). Contrary to the other variables that are spatially explicit, the three land use history variables (FOREST AGE, FIELD, GRASSLAND) were assessed on forest inventory sample points only. These three variables were included to compare with a model that only used spatially explicit variables.

Table 4.2 Description, units, and naming (capitals) of 18 explanatory variables included into modeling, derived from five types of source data.

Source data	Variable description, units, and naming (capitals)	
Forest cover at four times	Nearest neighbourhood (m)	Buffer (m)
1775	NN_1775	BUFFER_1775
1850	NN_1850	BUFFER_1850
1904-1931	NN_TOPO3	BUFFER_TOPO3
2000	NN_2000	BUFFER_2000
Cadastral parcel borders	Nearest neighbourhood (m)	Buffer (m)
Unchanged since 1810-1825	NN_CADORI	BUFFER_CADORI
Created after 1810-1825	NN_CADALT	BUFFER_CADALT
Mesophilous forest sites	Site index (≥0 and ≤1, sum indices > 0)	
Alno-Padion (Table 4.1)	SI_AP	
Fagion or Carpinion (Table 4.1)	SI_FC	
Digital Terrain Model (DTM)	SLOPE (degrees)	
Land use interpretation	Time (years between 1775 and 2000)	
Forest continuity	FOREST AGE	
Time used as field	FIELD	
Time used as grassland	GRASSLAND	

The connectivity measures calculated on forest cover maps and on maps with cadastral parcel borders can be classified as nearest neighbourhood variables (NN) and buffer variables (Moilanen & Hanski 2006). The forest cover represented by maps drawn in approximately 1775, 1850, between 1904 and 1931, and in 2000 was digitized for most of Flanders (see Chapter 3). We derived from these four polygon maps with historical forest cover, raster maps with a resolution of 10 m that contain the Euclidean distance (m) of a grid cell to the edge of the nearest forest patch. These variables were named in chronological order: NN_1775, NN_1850, NN_TOPO3, NN_2000 (Table 4.2). Grid cells within forest were given negative values, cells outside forest had positive values (Fig. 4.2), and grid cells on the forest edge were equal to zero.

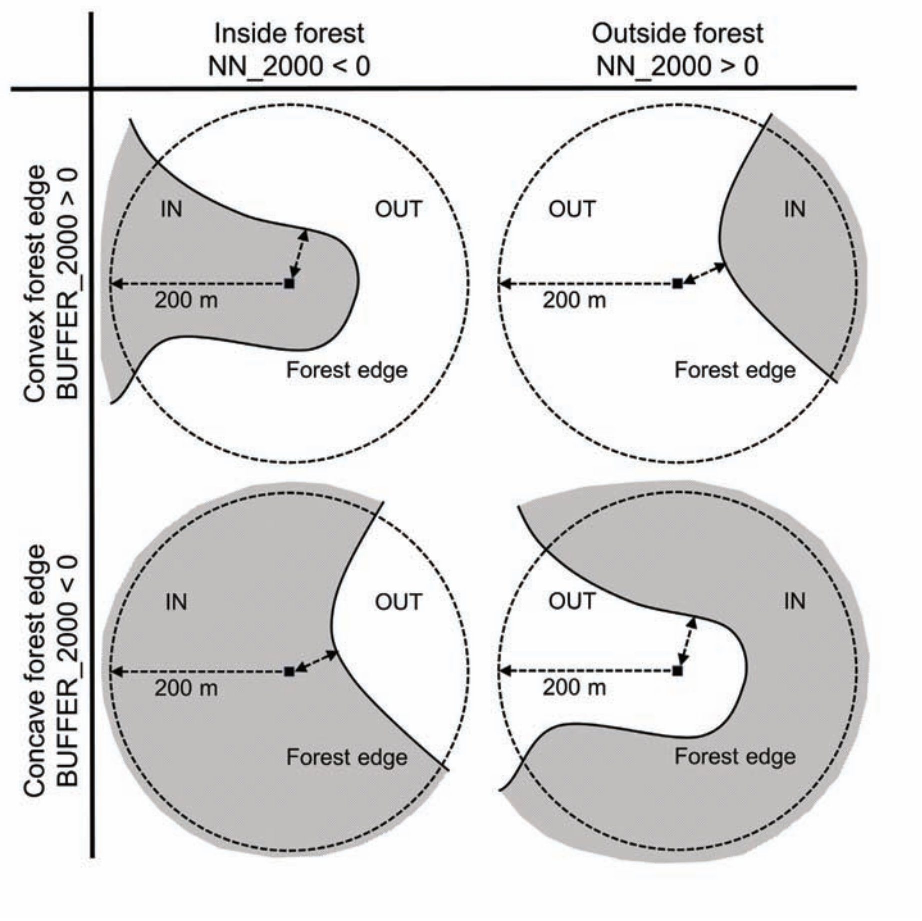


Fig. 4.2 Connectivity measures calculated for raster pixels (black squares) on the forest cover (e.g. in 2000). The grey areas are covered by forest. The NN_2000 measure is indicated by the double arrow and calculated as the nearest distance to the forest edge (solid line), with negative and positive values inside (IN) and outside (OUT) forest, respectively. The BUFFER_2000 measure is calculated as the mean value of the NN_2000 measures within in a radius of 200 m (single arrow) around the focal pixel (black squares), minus the NN_2000 value of the focal pixel itself.

In a similar way, but with only zeros and positive values, the Euclidean distance was determined to cadastral parcel borders represented by the Cadmap layer (AGIV 2013). We discerned parcel borders that were already present when the first cadastral maps were drawn (1810-1825), from borders that were created after that time, assuming that the former had a higher potential to contain AFS, e.g. in linear landscape elements, than the latter.

The raster maps with NN variables served to calculate raster maps that contained BUFFER variables (Table 4.2 and Fig. 4.2). For this purpose the Focalmean_{200} value of a grid cell first was calculated, being the mean value of the NN values in a circular area with a radius of 200 m around the focal grid cell (Fig. 4.2). We assumed that AFS migration since 1775 was mostly restricted to this distance, as many AFS have colonization rates below 1 m/yr (e.g. Hermy & Verheyen 2007, Brunet *et al.* 2012). The Focalmean_{200} values were highly correlated with the NN values and therefore a linear combination of both correlated variables was calculated (Dormann *et al.* 2013), e.g. on forest cover in 2000: $\text{BUFFER\_2000} = \text{Focalmean}_{200}[\text{NN\_2000}] - \text{NN\_2000}$.

The BUFFER variables that are the result of this equation were not correlated with the NN variables and therefore used for modeling instead of the Focalmean_{200} variables. The BUFFER variables are continuous, with negative values indicating that the nearest forest edge to a grid cell is concave, and positive values indicating that the nearest forest edge is convex (Fig. 4.2).

We included two indices (SI_AP and SI_FC) extracted from the fuzzy PNV map of Flanders (see Chapter 2) that quantify the suitability of a site for the two selected mesophilous forest types (AP and FC in Table 4.1). The suitability indices range between 0 (not suitable) and 1 (highly suitable for only one type) and the sum of indices of all five PNV types that can occur on a site is always equal to 1. We only selected 377 samples on sites that have a potential for at least one of both mesophilous types, covering 41% of Flanders, and for this reason the sum of SI_AP and SI_FC was always greater than 0. As the values of both selected site indices are not independent, it is appropriate to include also the interaction term into modeling (Zuur *et al.* 2009).

It was hypothesized that an undulating topography could result into microhabitats for AFS, not explained by the site indices extracted from the PNV map. For this reason the variable SLOPE was included, that indicated the slope (degrees) derived from a DTM grid with 5 m x 5 m resolution (Digital terrain model of Flanders 2001-2004). This grid was resampled to a 10 m x 10 m grid with a similar extent as the other spatial explicit variables. All aforementioned spatial analyses and grid calculations to obtain spatial explicit explanatory variables were performed in Arc/Info 10.

Three variables on land use history were assessed on the forest inventory sample points only, but were not available as digital raster maps: forest age, total time used as grassland since 1775, and total time used as field since 1775. For this purpose, land use was interpreted on eight historical maps, approximately drawn in: 1775, 1850, 1867, 1883, 1904-1931, 1959, 1979, and 2000. FOREST AGE is a quantification of forest continuity and was determined as the time (years) up to 2000, a sample plot was continuously covered by forest, since final conversion from open land to forest. This value was calculated using the mean of the interval between the two successive maps, that preceed and follow on this final land use change. FOREST AGE of sample plots continuously covered by forest, equalled 225 years. The mean values of interval times were also used to calculate the total number of years between 1775 and 2000, sample points were occupied by grassland (GRASSLAND) and field (FIELD). Other land use, e.g. heathland, was only marginally present on mesophilous soils and was therefore not quantified.

4.3.4 Model characteristics

Relationships of AFS with potential explanatory variables were analyzed in R version 2.15.2 (R Development Core Team 2011), with generalized additive models (GAMs), using spline smoothers. Partial effects were illustrated by response shapes of smoothed predictor variables. The number of AFS are over dispersed count data that were modelled with a quasi Poisson distribution. We compared a model that only included spatially explicit data, with a model that also included additional, more detailed information of land use history on forest inventory sample points only, and both followed the same procedure for the selection of explanatory variables. The upper models in both cases included 15 and 18 variables, respectively. Model shrinkage followed the procedure by Wood (2006), using the mgcv package in R for mixed modeling (Wood 2011). Variables selected for the final GAMs were all significant ($P < 0.05$). The calculation of the grid maps with the predicted AFS count and the 95% confidence interval, that had a similar extent and resolution as the maps of explanatory variables, was also performed in R version 2.15.2 (R Development Core Team 2011).

4.4 Results

The final models on AFS richness with and without sample point variables included the same spatially explicit data. The correlation values of the included variables are all below an absolute value of 0.7 (Annex 4.1), which is a commonly applied threshold value (Dormann *et al.* 2013).

When the three variables without spatial dimensions (FOREST AGE, FIELD, GRASSLAND) were also included in model construction, this resulted into a final model that included FOREST AGE and FIELD. Smoothers gave similar, but weaker relationships for spatially explicit variables when FIELD and FOREST AGE were included (compare Figs 4.3 and 4.4).

The model that only used spatially explicit variables explained 18% deviance, whereas the model that also included FOREST AGE and FIELD explained 24% deviance (compare Annex 4.2 and Annex 4.3). A visual control in a GIS indicated that most of the sample plots that were recently converted from field to forest, were located adjacent to ancient forest and already contained several AFS. This could explain the shape of the smoother on FIELD (Fig. 4.3). The forest cover in 2000 was included as a buffer variable (BUFFER_2000), whereas forest cover at other included time slices were NN variables. The smoother on BUFFER_2000 indicated that a concave forest border resulted into more AFS than a convex forest border (see Figs 4.3 and 4.4). SLOPE and variables calculated on the cadastral parcel borders were not retained.

The selection procedure included connectivity measures calculated on forest cover maps at three time slices (1775, TOPO3, 2000). Forest cover in 1850 was not explanatory for AFS count in present-day forest.

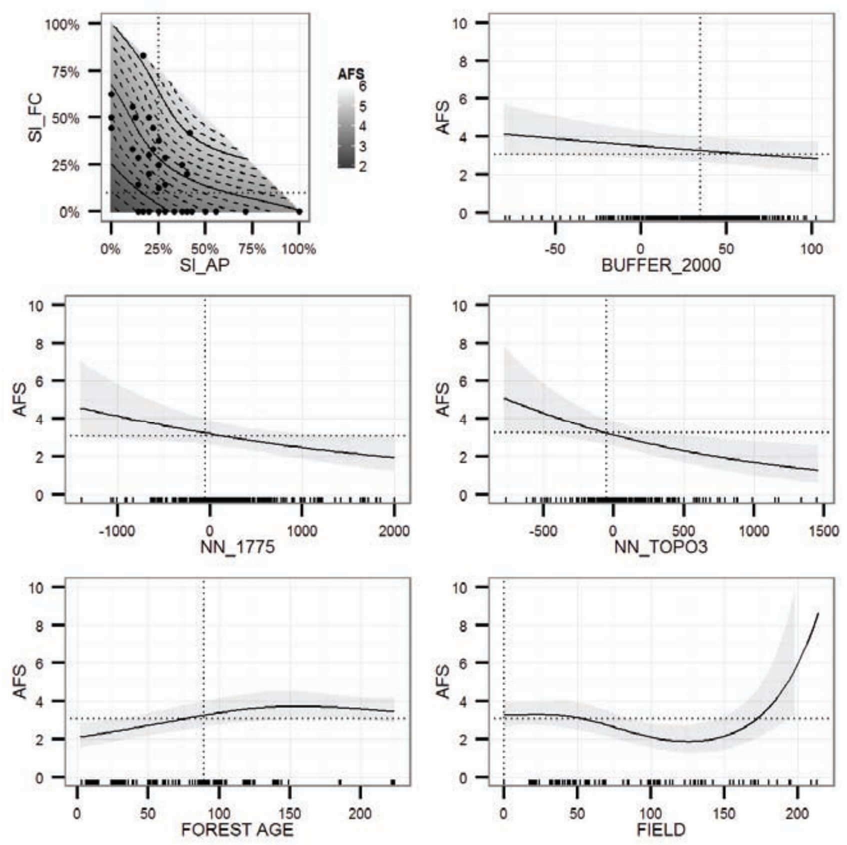


Fig. 4.3 Estimated partial effects of four spatial explicit variables and two variables assessed on forest inventory point samples only, included into the GAM of the ancient forest species (AFS) count. The 95% confidence interval is indicated by the grey area in the 2D plots. Dotted lines represent reference values of the model. Tickmarks on the x-axis (2D plots) and dots (3D plot) show the location of observations. Variable names are explained in Table 4.2.

As illustrated in Fig. 4.3, there was, according to the GAM, no further increase of the AFS number at sites with a FOREST AGE above 150 years. This finding was further explored using the overlay classes of forest history illustrated by Table 3.2 (Fig. 4.5). The relationship between the AFS number and the forest history classes, ranked in order of increasing FOREST AGE, is mostly in agreement with the GAM but there is a wide overlap of the interquartile ranges, as compared to the 95% confidence interval of the smoother (compare Figs 4.3 and 4.5). This could be explained by site quality or landscape factors, not represented by the boxplots but included into the GAM.

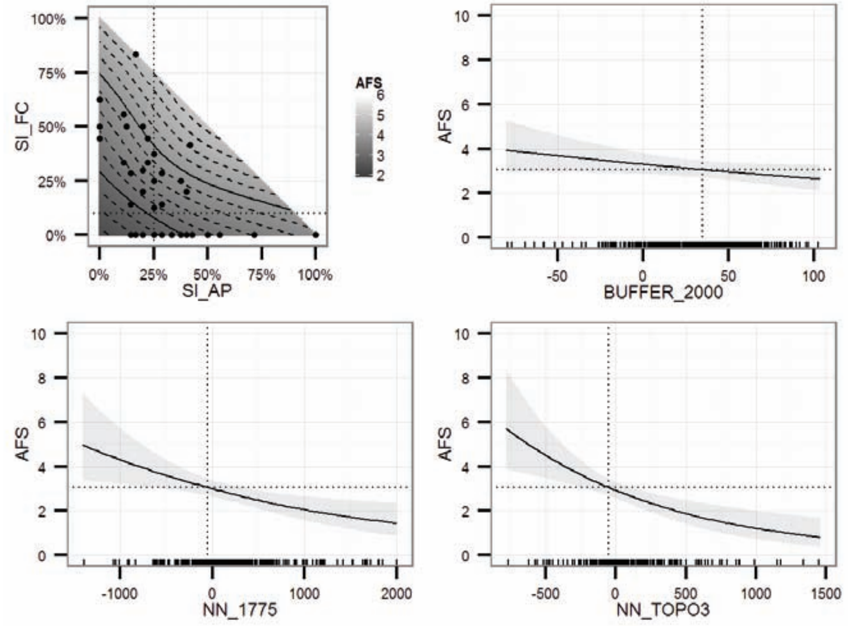


Fig. 4.4 Estimated partial effects of four spatially explicit variables, included into the GAM of the ancient forest species (AFS) count. The 95% confidence interval is indicated by the grey area in the 2D plots. Dotted lines are reference values of the model. Tickmarks on the x-axis (2D plots) and dots (3D plot) show the location of observations. Variable names are explained in Table 4.2.

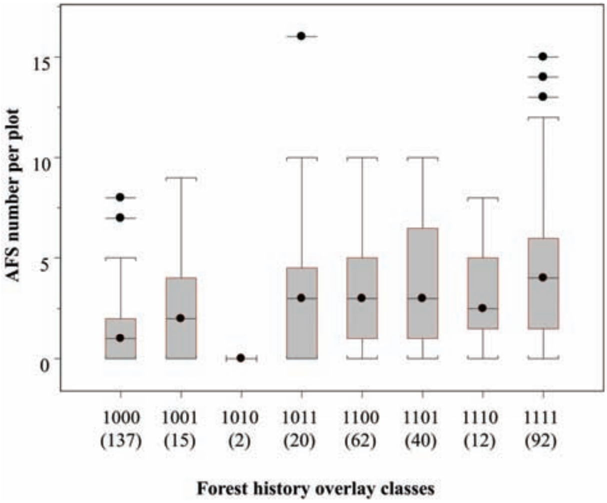


Fig. 4.5 Boxplots of the AFS number per plot (256 m^2) in eight forest history classes (Table 3.2). Classes are based on an interpretation of land use history on eight historical maps, reduced to four time periods (see Table 3.2). The number of plots are between brackets.

The spatially explicit model exhibited a slight autocorrelation of residuals, at a distance between 1 km and 2 km where the semivariance is lower than at distances above 2 km (Fig. 4.6). We did not adjust the modeling for this autocorrelation but assumed that the confidence intervals of the smoothers were somewhat broader than illustrated by Fig. 4.4. For this reason we used the values of the lower confidence limit for mapping (Figs 4.7 and 4.8).

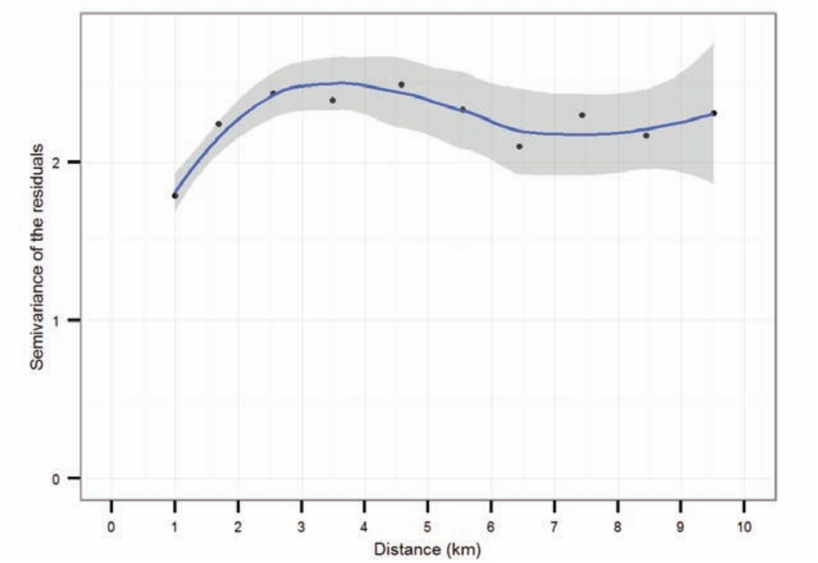


Fig. 4.6 Semivariogram with the semivariance of the residuals of the model illustrated by Fig 4.4, as a function of the distance between forest inventory sample points (represented as dots) that are response data. The grey area depicts the 95% confidence interval.

The map of Flanders with the modelled AFS count illustrates that a high AFS count is forecasted in the south of Flanders (Fig. 4.7). This area is characterized by a high proportion of mesophilous soils and, although forest cover was low in 2000 (between 5% and 15%), many forests are ancient forest. By contrast, suitable mesophilous sites are scarce in NE Flanders (Fig. 4.7), where forest cover in 2000 is high (> 20%). In this area locations with a high potential AFS count are mostly located on alluvial soil along watercourses.

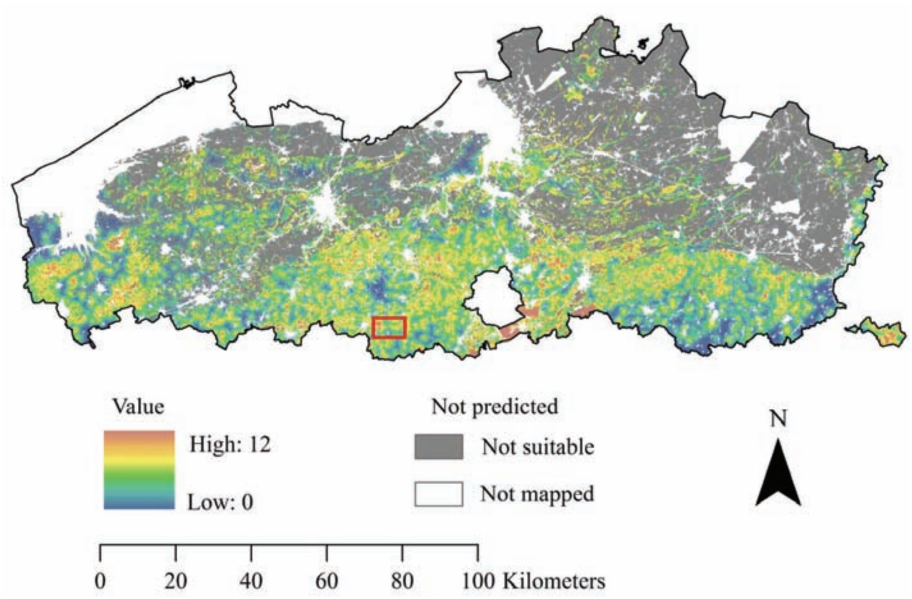
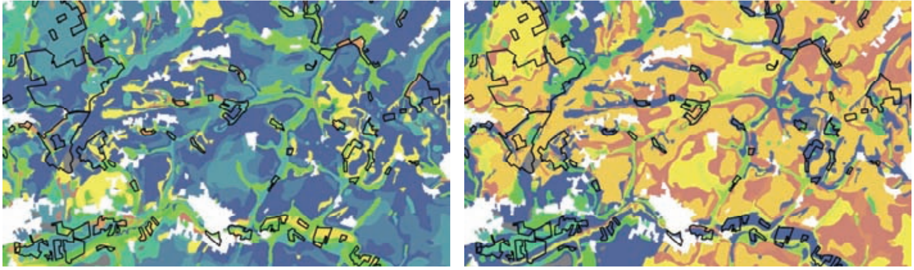
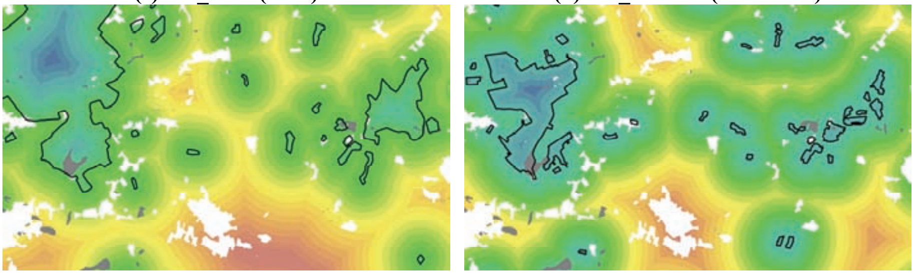
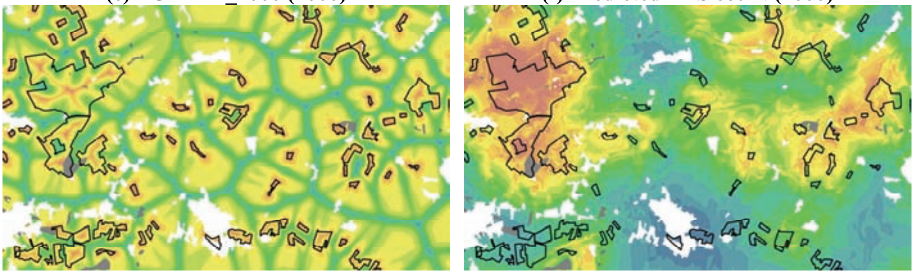


Fig. 4.7 Predicted count of AFS (lower confidence limited) in Flanders by the GAM using spatial explicit variables (see Fig. 4.4). White areas are not mapped as no habitat site index was available (e.g. polders, dunes, military areas, disturbed soils), or as areas were not mapped in 1775. Grey areas are sites that are not suitable for mesophilous forest habitat. The area of the red rectangle is illustrated by Fig 4.7.

The spatial patterns generated by the explanatory variables and by the model on AFS count are illustrated for an area selected in the south of Flanders (Fig. 4.7), where a forest patch on silt loam soil covered approximately 600 ha in 1775 but was reduced to approximately 180 ha in 2000 (Figs 4.8 c, d, e). The north of this forest, located on the most suitable sites where the modelled AFS count is high, was cleared in the 19th century. South of the remaining ancient forest several small forest patches emerged in the 20th century on alluvial soils. Although most patches are located on suitable sites for AFS (Fig. 4.8 a, b), the model predicted a low AFS count due to spatio-temporal isolation (Figs 4.8 c, d). Extrapolation of the model to the open landscape not covered by forest in 2000 resulted into high values for areas that were covered by forest in 1775, on suitable sites (compare Figs 4.8 a, b, c, d, and f). Also open land next to a concave ancient forest edge or within an ancient forest patch, is rated high (compare Figs 4.8 e and 4.8 f).


(a) Site index for AP (2000)
(b) Site index for FC (2000)


(c) NN_1775 (1775)
(d) NN_TOPO3 (1904-1931)


(e) BUFFER_2000 (2000)
(f) Predicted AFS count (2000)

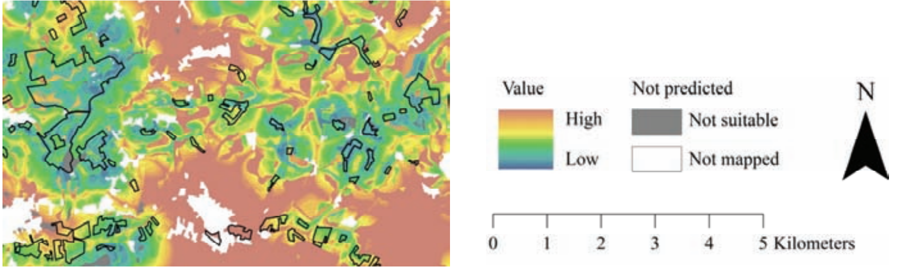

(g) 95% Confidence interval (2000)

Fig. 4.8 Patterns of explanatory variables (a, b, c, d, e) of the spatial explicit model (see Fig. 4.4 and Annex 4.2), predicted ancient forest species (AFS) count (f), and width of 95% confidence interval (g). Black outlines depict forest perimeter at time slices mentioned between brackets. Variable names are explained in Table 4.2.

4.5 Discussion

4.5.1 Model construction

The connectivity of forest patches has been used before to explain occurrence or richness of AFS (Jacquemyn *et al.* 2003a, Verheyen *et al.* 2004). As opposed to our empirical model, these studies applied mechanistic models based on the metapopulation concept, explaining the fundamental processes of species extinction and colonization in habitat patches (Levins 1969). Such a process-oriented approach, mostly based on the Incidence Function Model (IFM), makes it necessary to simplify the description of the landscape matrix for modeling (Moilanen & Hanski 2001). Simplifications are always necessary for modeling. The available data, species characteristics, and the permeability of the landscape matrix for species to migrate determine what kind of simplifications are most helpful (Moilanen & Hanski 2001, Fagan & Calabrese 2006). A drawback of an empirical model is that indirect variables or variables without causation, can be included (Guisan & Zimmerman 2000). The FIELD measure in our model could be an example of such a variable.

Landscape indices can be subdivided into three categories: nearest neighborhood (NN) values, buffer values, and the incidence function model (IFM) connectivity measure (Moilanen & Hanski 2006). We used NN and buffer measures derived from spatial explicit data to explain AFS counts on a set of forest vegetation samples that is representative for the whole present-day forest cover. Such an approach can be successful for matrix-sensitive species, i.e. species that do not tend to wander out of the preferred habitat type (Fagan & Calabrese 2006). For two out of three included forest cover maps, NN measures were significant but not the variables that included additional information calculated for a buffer area. This is in disagreement with the conclusion that NN measures mostly are inferior to buffer and IFM measures (Moilanen & Hanski 2006). Based on the species traits, it can be assumed that most AFS show remnant dynamics instead of metapopulation dynamics (Eriksson 1996). This could explain the effectiveness of NN measures in our study.

As we wanted to calculate a value for the open land too, the use of the extended IFM measure, for which the area of the focal patch is required, was not possible. It can be relevant to calculate a value for the open land, as AFS can also occur in linear landscape elements (Honnay *et al.* 1999b, Endels *et al.* 2004) not represented by the applied forest cover maps. Calculation of NN values for the open landscape is supported by the findings that physical contact of hedgerows with forest patches resulted into an increased species richness (Corbit *et al.* 1999, Roy & de Blois 2008) and that richness of forest species in attached hedgerows declined with increasing distance to the forest patches they were attached to (Wehling & Diekmann 2009). Another advantage of our approach could be that the applied NN measures, calculated as the distance to the forest perimeter, can have either positive or negative values. The variable positional error of the historical maps can be handled this way.

4.5.2 Factors that determine AFS richness

The slight autocorrelation, assessed for sample plots at distances between 1 km and 2 km (Fig. 4.5) can have several causes, e.g. environmental gradients, similar forest management, but also dispersal effects (Bjørnstad *et al.* 1999). The absence of autocorrelation beyond 2 km could indicate that long-distance dispersal events are not highly explanatory for the AFS richness in present-day forests of Flanders. The high level of forest fragmentation for more than 200 years in our study area and AFS traits support this hypothesis. AFS in general are long-lived forest interior species that have poor colonization capacities (Hermy *et al.* 1999).

Colonization of new habitat by AFS is mostly a slow process, although recent studies (e.g. Brunet *et al.* 2012) indicated that the migration rate may vary considerabely among AFS. The high proportion of unexplained deviance could be caused by the heterogeneous behaviour among AFS colonizing RF. A further homogeneization of the response variable, e.g. by defining subgroups based on species traits, could further improve modeling. A drawback could be that the zero inflation of the response variable could further increase by a subdivision.

The age of a recent forest was found to be highly explanatory for its forest plant richness (Jacquemyn *et al.* 2001). Forest age can be derived from land use identified on successive historical maps. When applied to sample plots, such an analysis is relatively simple and accurate as compared to the spatial explicit approach (see Chapter 3). The positional error of old maps can generate false land use changes in an overlay map (De Clercq *et al.* 2009, Burnicki 2012) and by using only four forest cover maps instead of eight that are available for point sample interpretation, some land use changes remained undetected (see Chapter 3). The positional root mean squared error of the three included historical maps was higher than the raster resolution (10 m), and specific for each time slice: 43m (1775), 31m (1850), and 15m (1904-1931) (Onkelinx *et al.* 2004). Calculation of NN measures for separate time slices is more appropriate to handle the variable positional error of the forest cover maps, than calculating similar measures on an overlay map containing false land use change classes. Including more detailed and accurate information on historical land use, assessed on sample points, slightly improved the model but also indicated that a high proportion of deviance remained unexplained.

The NN measures calculated on two historical maps (1775 and TOPO3) indicated that the AFS count increased from the forest edge to the forest interior. Although abiotic and biotic conditions of forest edges differ from the forest interior, no such effects were registered beyond 80 m of the forest edge (Matlack 1994a, Gehlhausen *et al.* 2000, Wuyts *et al.* 2008). Similar long periphery-to-interior gradients, observed for many forest species, were attributed to repeated displacements of the forest edge by successive creation of recent forest at the periphery (Pellissier *et al.* 2013). This conclusion is confirmed here as we found that, when more detailed information was included on historical land use of sample plots, the relationship between the NN measures and AFS count was weaker. The remaining periphery-to-interior gradient in AFS richness is unexplained, but it could be possible that land use conversions before 1775 for which no information was available, were also explanatory. The model also indicated that a concave or interior forest edge, resulted into a higher count of AFS than an external, convex forest edge. We assume that forest edges protruding into farmland suffer more from increased N and S depositions (e.g. Wuyts *et al.* 2008), misplacement of fertilizer and increased competition by light and nutrient demanding species (Honnay *et al.* 2002a) than concave or interior forest edges.

As forest age is regarded to be essential for preserving AFS richness (see, e.g. Wulf 2003), it is a remarkable finding that connectivity measures on the 1850 forest cover did not contribute to the model. Our results indicated that sites that were deforested between 1775 and 1850, but reforested before 1904-1931 (TOPO3), in general had recovered to a level similar as ancient forest. This may be explained by the fact that many of these forests were converted to farmland for a very short time, during a famine (Tack *et al.*

1993, Vandekerkhove *et al.* 2011). Low soil P levels indicated that these clearings probably were not fertilized, as opposed to sites converted from farmland to forest in the 20th century (see Chapter 5). P eutrophication can slow down recovery of forest vegetation, as competitive exclusion of AFS by species with a higher plasticity is promoted (Baeten *et al.* 2009b). Another explanation for the recovery of AFS richness since 1850 could be that AFS survived forest clearing in linear landscape elements (Honnay *et al.* 1999b). Linear landscape elements, also newly created ones, can be suitable habitat for AFS and can function as a colonization source when incorporated in recent forest (Endels *et al.* 2004). We tested connectivity measures on cadastral parcel borders as a substitute for linear landscape elements, but none of these measures explained AFS richness in forest patches. Perhaps the density of linear landscape elements with AFS was too low to detect an effect on the recovery of recent forest at the scale of our study. Moreover, fringe relics of the mid-19th century forest clearing, that enabled recovery of AFS after reforestation, did not necessarily coincide with the border of cadastral parcels (Honnay *et al.* 1999b).

4.5.3 Application of the AFS richness map

The spatial explicit model offered the advantage that it generated information on AFS richness for a very high number of forest patches (19.000) that covered a large total forest area (144.000 ha). Research that compared conservation strategies based on the inventory of forest patches, comprised a smaller total forest area and much less forest patches, selected from study areas that also contained patches that were not inventoried (Peterken & Game 1984, Honnay *et al.* 1999a, Hokkanen *et al.* 2009). When using the prediction map it should be kept in mind that a high proportion of the deviance was not explained. The GIS map can thus be used for prospection of potential richness hotspots, guiding additional field surveys that can provide a more accurate assessment of species richness.

When using the map for local conservation projects, it is recommended to collect additional information on explanatory variables. The unknown connectivity of forest patches through linear landscape elements, discussed above, could attribute to some of the unexplained deviance, particularly in recent forest. The habitat site index is derived from a morphogenetic soil map, that does not represent certain soil characteristics that can explain AFS richness, e.g. the level of eutrophication with P (explained above), and soil pH. Undisturbed soils of the silt loam plateau indeed have a poor buffer capacity and are sensitive to acidification (Brahy *et al.* 2000). Acidification can cause a decline of sensitive species, including many AFS (Baeten *et al.* 2009a). The rate of this process can be influenced by tree species (Thomaes *et al.* 2011, Thomaes *et al.* 2012). Current or historical forest management practices, not included into our models, also can have an important impact on AFS richness (Decocq *et al.* 2004, Van Calster *et al.* 2008).

The map generated by the empirical landscape model can also be used for restoration projects, as an estimated value is calculated for the open land. Suitable sites covered by forest on historical maps, but not anymore in 2000, were also rated high. In such areas, relic populations of AFS could be present in hedgerows and tree lines and the map can be used for the prospection of such linear landscape elements. Not only herbaceous species, but also rare woody species can survive in linear elements that are relics of ancient forest (e.g. *Ulmus laevis* as described by Vander Mijnsbrugge *et al.* 2005). However, linear landscape elements have severely declined in the past decades (Barr & Parr 1994), and for this reason colonization of reforested open land by AFS is probably mostly dependent of source populations in forest. In this case the map can be used to select open sites with a suitable habitat quality, adjacent to a forest with a high predicted AFS richness. The shape of the present-day forest edge can influence the restoration potential as well, as more AFS were found in a concave forest edge than in a convex forest edge. Moreover, a parcel surrounded by forest with a high AFS richness can be colonized from more than one side (e.g. Chapter 6).

4.6 Conclusions

Spatially explicit data on habitat suitability, historical and present-day forest cover can be used to explain AFS richness when spatio-temporal forest cover changes have resulted into a variable recovery level of forest cover. The applied model generated values for the present-day forest, but extrapolation to sites at present not covered by forest can be relevant. Areas that were recently deforested and that have a high potential AFS count according to the prediction map, can contain relic populations of AFS, e.g. in linear landscape elements that are not represented by digitized forest cover maps. In most cases however, recovery of reforested open land will rely on physical contact with present-day forest that still contains AFS. The AFS richness map can be applied for landscape planning at a regional scale, e.g. for selecting biorichness hotspots in present-day forest or for selection of open locations with a high recovery potential. However, the map should be combined with additional information on historical land use, landscape structure, soil characteristics, and forest management history when used for the operationalization of conservation, defragmentation or restoration projects.

Annex 4.1 Correlation matrix of the variables used into the models on AFS richness (see Annex 4.1 and Annex 4.2).

	FOREST AGE	FIELD	NN_1775	NN_TOPO3	BUFFER_2000	SI_AP
FIELD	-0.38					
NN_1775	-0.50	0.11				
NN_TOPO3	-0.53	0.15	0.50			
BUFFER_2000	-0.12	0.13	0.23	0.16		
SI_AP	-0.26	0.04	0.23	0.22	0.12	
SI_FC	0.21	0.05	-0.26	-0.14	-0.15	-0.58

Annex 4.2 Parametric coefficients and approximate significance of the smooth terms of the GAM on ancient forest species (AFS) count, using spatial explicit data only. The model is expressed by the formula: AFS ~ s(SI_AP, SI_FC) + s(NN_TOPO3) + s(NN_1775) + s(BUFFER_2000). Variable names are explained in Table 4.2. Edf: estimated degrees of freedom for the model terms; Ref.df: estimated residual degrees of freedom. The GCV score equaled 2.451 and the model explained 18.3% deviance on 377 observations.

	Estimate	Std. Error	t-value	Pr(>|t|)
Intercept	1.00989	0.04969	20.32	<2e-16
Smooth term	edf	Ref.df	F-value	*P*
s(SI_AP, SI_FC)	2.3832	3	2.931	0.013
s(NN_TOPO3)	0.9258	3	4.573	<0.001
s(NN_1775)	0.9013	3	3.188	<0.001
s(BUFFER_2000)	0.7336	3	1.060	0.034

Annex 4.3 Parametric coefficients and approximate significance of the smooth terms of the GAM on AFS count, using spatial explicit data and forest inventory sample point data. The model is expressed by the formula: AFS ~ s(SI_AP, SI_FC) + s(NN_TOPO3) + s(NN_1775) + s(BUFFER_2000) + s(FOREST AGE) + s(FIELD). Variables names are explained in Table 4.2. Edf: estimated degrees of freedom for the model terms; Ref.df: estimated residual degrees of freedom. The GCV score equaled 2.3536 and the model explained 23.6% deviance on 377 observations.

	Estimate	Std. Error	t-value	Pr(>|t|)
Intercept	0.98048	0.04988	19.66	<2e-16

Smooth term	edf	Ref.df	F-value	*P*
s(SI_AP, SI_FC)	2.5715	3	3.924	0.004
s(NN_TOPO3)	0.8458	3	2.316	0.003
s(NN_1775)	0.7930	3	1.646	0.009
s(BUFFER_2000)	0.7283	3	1.060	0.034
s(FOREST AGE)	1.9324	3	3.568	0.002
s(FIELD)	2.8377	3	4.045	0.005

The shade-casting shrub *Corylus avellana* reduces the cover of light-demanding species (*Rubus* and *Urtica*) and promotes colonization by the shade-tolerant *Ranunculus ficaria*, in a 45-year old post-agricultural forest stand in Muizenbos.

5 Impact of soil and light conditions on vegetation recovery in a mesophilous forest

After: De Keersmaeker L, Martens L, Verheyen K, Hermy M, De Schrijver A, Lust N (2004) Impact of soil fertility and insolation on diversity of herbaceous woodland species colonizing afforestations in Muizen Forest (Belgium). Forest Ecology and Management 188:291-304

5.1 Abstract

In a chronosequence of afforestations adjacent to ancient forest, relations between herbaceous forest vegetation and possible explanatory variables, such as soil characteristics, land use history variables and relative insolation on the forest floor, were studied using linear models on species groups and a direct gradient analysis (CCA). An explorative correlation analysis indicated that the moisture, carbon, total nitrogen and phosphorus contents of the soil, were correlated with forest age. Although soil pH was not correlated with forest age, its variability was greater in ancient forest and 19th century afforestations than in recently afforested parcels. The linear models indicated that soil pH positively influenced the diversity and cover of both slow colonizing and fast colonizing forest species. P enrichment, in combination with a high relative insolation, stimulated *Urtica dioica* in recent afforestations. Deep shadow on the forest floor suppressed light-demanding species, such as *Urtica dioica*, and indirectly favored forest species. The multivariate analysis confirmed that floristic diversity was best accounted for by the variables plant-available P, pH (KCl), nitrate (negatively correlated with insolation) and forest age. The discussion focuses on the origin of the observed variability in soil characteristics, natural or anthropogenic, and the impact on vegetation succession. It is concluded that most forest species can colonize recently afforested farmland parcels in Muizen forest, as soil pH is not a limiting factor. However P eutrophication can have an indirect negative effect, increasing competitive exclusion by *Urtica dioica*. Plantation of an understorey can suppress *Urtica dioica* and stimulate colonization of shade-tolerant forest species in afforested farmland.

5.2 Introduction

A large number of European forest plants are associated with ancient forests (Hermy *et al.* 1999), which indicates that forest vegetation is strongly determined by land use history. Several studies have focused on the poor dispersal capacities of ancient forest species and on colonization patterns in secondary forest (Matlack 1994b, Brunet & Von Oheimb 1998a, Bossuyt *et al.* 1999b). The habitat quality of recent forests can also limit the colonization capacities of forest species. The relative importance of recruitment versus dispersal limitation can vary (Verheyen & Hermy 2001b). Dzwonko & Gawronski (1994) found that the vegetation composition of 70-year-old afforestations adjacent to ancient forest was determined more by soil conditions, insolation and the influence of dominant tree species than by dispersal mode.

Following the afforestation of farmland, many soil characteristics gradually change and move towards the levels of ancient forest soils (Goovaerts *et al.* 1990, Muys *et al.* 1992, Catt 1994, Bossuyt *et al.* 1999a, Verheyen *et al.* 1999). However, even after a long period of time, persistent differences between ancient and secondary forest soils can be observed. Former arable land use generally results in increased nutrient levels, especially of P (Koerner *et al.* 1997, Wilson *et al.* 1997, Honnay *et al.* 1999b). P is immobile and the total P content is stable (Binkley 1986), although its availability decreases after the afforestation of farmland (Magid 1993).

High P levels might hamper the establishment of forest species in recent forests by increasing competitive exclusion. *Urtica dioica* benefits from a high P availability (Pigott 1971) and therefore the vegetation in recent forests on former arable land is often dominated by this species. Hermy *et al.* (1993) found a negative relationship between the number of forest species and the cover of *Urtica dioica*. Honnay *et al.* (1999b) mentioned a significant negative correlation between P content and the number of ancient forest species. Both studies faced the problem that P content and the cover of *Urtica dioica* were correlated with secondary forest age, and therefore it is not clear which factor (forest age or P availability) caused the low number of forest species in recent forests.

Using field experiments in coppice woods, Pigott & Taylor (1964) demonstrated that insolation could limit the growth of *Urtica dioica* on fertilized soils. Therefore, a comparison of vegetation succession in afforestations with high soil P levels but varying light conditions, might provide an indication as to the impact of light-demanding, competitive species such as *Urtica dioica* on the colonization rate of forest species in afforested farmland.

We used a field study to investigate the following hypotheses: 1) soil nutrients, in particular the P content, are affected by the land use history; 2) a high soil P availability favors competitive species (*Urtica dioica*) and 3) forest species benefit from shadow that reduces *Urtica dioica* and other light-demanding competitive species.

5.3 Materials and methods

5.3.1 Study area

The Muizen forest is a 34 ha forest reserve, in a flat region at approximately 10 m above sea level, situated 15 km east of Antwerp in northern Belgium (Fig. 5.1).

Fig. 5.1 Location of the study area in Belgium.

The center of the forest is somewhat lower than the periphery, but the difference in altitude does not exceed 2 m. The topsoil is of Quarternary niveo-eolian origin and the silt loam content increases from the periphery to the center of the forest. In the central depression, an impermeable sandy clay layer of Tertiary marine origin, at 0.5 to 1 m depth, impairs water percolation and creates a Gleysol (IUSS Working Group WRB 2006) in the central depression (Fig. 5.2). The local presence of fossils in the sandy clay layer results in these Gleysols having a highly variable soil acidity, with pH (KCl) values that range between +/-3 and +/- 7. The Gleysols are surrounded by Plaggic Anthrosols (IUSS Working Group WRB 2006) in the west and by Albeluvisols (IUSS Working Group WRB 2006) in the east (Fig. 5.2). The soil texture and drainage classes of the Plaggic Anthrosols and Albeluvisols are similar, but the former is discerned from the latter by the presence of a thick antropogenic humus A horizon. This humus A horizon is the result of the use as arable field for a very long time. According to the Belgian soil map the soils are moderately wet, as depth to mottling varies from 30 cm to 90 cm. A frequently flooded area in the north of the forest was not included in this study.

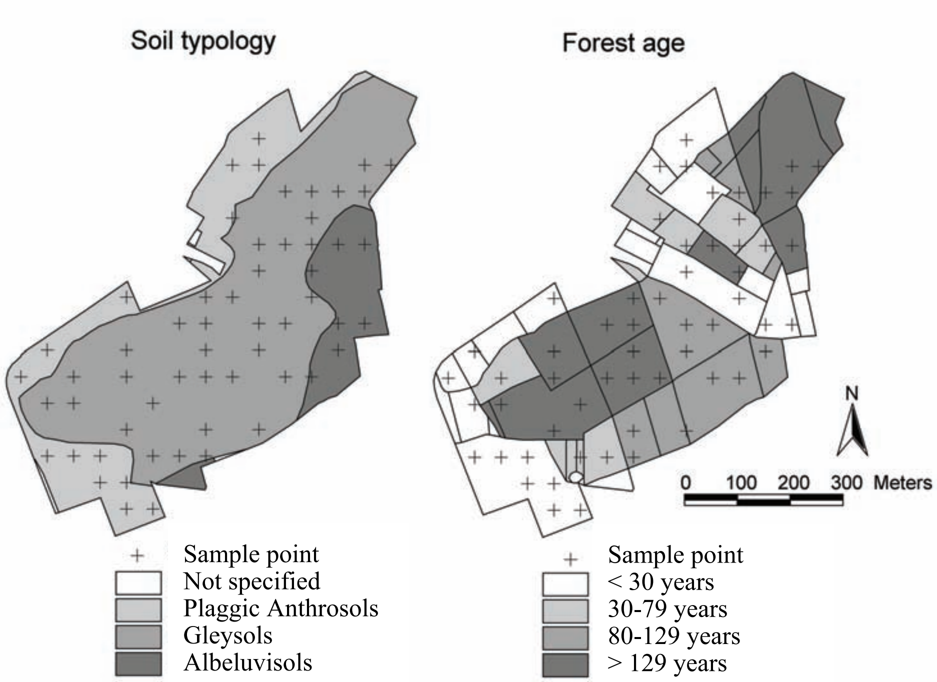


Fig. 5.2 Soil map and forest age map of the Muizen forest with the position of the 57 grid-based sample points.

The Muizen forest consists of a mosaic of small parcels (surface area between 0.5 and 1.5 ha) with a specific land use history. The number of years since afforestation, further referred to as forest age, is illustrated in Fig. 5.2. Approximately 3.5 ha in the NE of the forest, on Gleysols and on Albeluvisols, have always been forest since 1775 when the earliest maps were drawn. This area is therefore referred to as ancient forest. Most of the Gleysols in the SW were forest in 1775 but converted into arable land between 1775 and 1834. These parcels were abandoned and reforested between 1854 and 1892. The parcels that surround the historical core of the forest, were all afforested in the 20th century. The last afforestations, largely on Plaggic Anthrosols, date from 1991.

Most forest stands were planted homogeneously with poplar cultivars on 8 x 8 m or 10 x 10 m spacing. The earliest management notes indicate that poplar cultivars had already been planted before 1928. Some clear-cuts of poplar plantations were reforested with *Fraxinus excelsior*, *Tilia cordata* and *Quercus robur*. In some stands, shrubs and tree species (in particular *Acer pseudoplatanus*, *Alnus glutinosa* and *Corylus avellana*) were planted in between the poplars, while in others shrubs and trees established spontaneously. This resulted in varying levels of shadow on the forest floor of recent afforestations.

A wide variety of forest vegetation is found in the Muizen forest: stands where *Urtica dioica* or *Rubus fruticosus* are dominant neighbor stands with an abundant vernal aspect. Vegetation on acid soils belong to the *Violo-Quercetum roboris* (Oberdorfer 1957) and vegetation on calcareous soils belong to the *Primulo-Fraxinetum excelsioris* (Hermy 1985).

5.3.2 Data collection

Vegetation was sampled in 57 plots of 100 m^2, set out systematically on the nodes of a 50 x 50 m grid that covered the forest (Fig. 5.2). Only plots with a homogeneous vegetation were sampled. The herbaceous layer, including pteridophytes, was inventoried in April and May 1996 and plots were revisited in July 1996. Species cover was estimated by means of the decimal scale of Londo (1984), with 13 cover classes that were converted to mean values for data analysis. For this purpose, only the maximum species cover of both sampling times was selected. Species nomenclature follows Tutin *et al.* (1964–1993).

Parcels with a common land use history since 1775 were delineated to determine the forest age (see Verheyen & Hermy 2001a). The forest age of parcels that have been permanently afforested since 1775 was set at 221 years. The distance of the sample points to the nearest parcel margin that has never been disturbed since 1775 was calculated, assuming that this functioned as a colonization source (see Verheyen & Hermy 2001a).

The insolation on the forest floor was measured with a luxmeter in August 1996, at 36 points systematically distributed over each sample plot. Relative insolation of a plot was calculated as the mean value of 36-point measurements, divided by the insolation recorded in an open field.

The upper 10 cm of the mineral soil was sampled to characterize soil conditions that can determine the herbaceous vegetation. A mixture of 7 samples within each 100 m^2 plot was collected for analysis in August 1996. Soils were analyzed for soil moisture, total P, plant-available P, nitrate, total N, total C and pH (KCl). It was assumed that these variables could detect both natural gradients and anthropogenic influences on soil conditions. Total P and plant-available P were both obtained by extraction with $HClO_4$ (Olsen & Sommers, 1982) and ammonium lactate (Vanderdeelen 1995). Both P extractions were determined according to the colorimetric method of Scheel (1936) with Molybdenum vanadate as the color reagent. For calcareous soils, the H2SO_4 in the Scheel solution II was replaced by HNO_3 (Van Ranst *et al.* 1999). The relative P availability was quantified by the fraction of plant-available P to the total P content. Nitrate concentration was determined potentiometrically with a specific electrode after extraction of the fresh soil with a $KAlSO_4$ solution. The modified Kjeldahl method, using Se as catalyst, was applied for the analysis of total N (Van Ranst *et al.* 1999). The analysis of the C content followed the Walkley and Black method and a correction factor was applied which assumed that this method analyzed 75% of the total C content (Van Ranst *et al.* 1999). Soil pH (KCl) was measured potentiometrically with a glass-calomel electrode in 1 N KCl (Van Ranst *et al.* 1999). The moisture content was determined gravimetrically by drying 5 g of the fresh soil for 48 hours at 105 °C (Van Ranst *et al.* 1999).

5.3.3 Data analyses

Ancient forest species were identified based on Honnay *et al.* (1998). Species that were not indicative for ancient forest according to Honnay *et al.* (1998) were subdivided into shade-tolerant and light-demanding species using Ellenberg's L index (Ellenberg *et al.* 1992). Species not listed as ancient forest species but with an L value below 6, which indicates that they are at least tolerant to moderate levels of shadow, are further referred to as fast colonizing forest species. Species that are not indicative for ancient forest and with an L value equal to or above 6 are further referred to as light-demanding species. The total cover of the species groups in the sample plots was calculated as the sum of the cover of individual species.

Kendall partial rank-order correlations between environmental variables were calculated in an exploratory analysis. The impact of environmental variables on forest vegetation was investigated using direct gradient analysis (CCA) in Canoco for Windows (version 4.0). The automatic forward selection procedure for environmental variables was followed, with 9 variables in the upper model: pH (KCl), forest age, distance to migration source, total N content, soil nitrate, C content, plant-available P, soil moisture, and relative insolation. Total P was not included since it was assumed that the plant-available P fraction better reflected the soil fertility level. Variables significant at the 0.05 level (Monte Carlo test) were included in the model, as prescribed by ter Braak & Smilauer (1998). The triplots were generated in Canodraw 3.1 and Canopost for Windows 1.0.

Stepwise linear regression models were constructed to test the impact of the environmental variables on species number and on the total cover of each species group. The cover of competing species groups was also added to the regression models of ancient forest species and fast colonizing forest species. Distance to migration source and forest age were not included in the models for light-demanding species, since it was assumed that these species are not dispersal limited, but the impact of the interaction between plant-available P and relative insolation on light-demanding species was determined. After an arcsine transformation, which has a normalizing effect on species cover data, the response of *Urtica dioica* was investigated in a similar manner to the total cover of the light-demanding species.

Table 5.1 Significance of correlations between environmental variables, tested with Kendall's tau statistic. The following variables were investigated: Forest age (AGE), C content (C), C/N ratio (CN), C/P ratio (CP), distance to migration source (D), soil moisture content (M), soil nitrate concentration (NI), Total N content (NT), pH (KCl) (PH), plant-available soil P content (PL), Total P content (PT) and relative insolation (RI).

	AGE	C	CN	CP	D	M	NI	NT	PH	PL	PT
C	0.39^{***}										
CN	0.05^{NS}	0.15^{NS}									
CP	0.59^{***}	0.45^{***}	0.12^{NS}								
D	-0.21^{*}	-0.25^{**}	0.05^{NS}	-0.16^{NS}							
M	0.50^{***}	0.49^{***}	-0.01^{NS}	0.44^{***}	-0.37^{***}						
NI	-0.09^{NS}	0.24^{**}	-0.01^{NS}	-0.04^{NS}	-0.10^{NS}	0.12^{NS}					
NT	0.35^{***}	0.55^{***}	-0.30^{***}	0.32^{***}	-0.29^{**}	0.45^{***}	0.23^{*}				
PH	-0.05^{NS}	-0.02^{NS}	0.15^{NS}	-0.07^{NS}	0.10^{NS}	-0.08^{NS}	-0.07^{NS}	-0.13^{NS}			
PL	-0.54^{***}	-0.23^{*}	-0.09^{NS}	-0.56^{***}	0.04^{NS}	-0.31^{***}	0.15^{NS}	-0.15^{NS}	-0.04^{NS}		
PT	-0.55^{***}	-0.29^{**}	-0.08^{NS}	-0.84^{***}	0.13^{NS}	-0.34^{***}	0.13^{NS}	-0.19^{*}	0.06^{NS}	0.60^{***}	
RI	-0.11^{NS}	-0.33^{***}	-0.07^{NS}	-0.18^{*}	0.02^{NS}	-0.19^{*}	-0.26^{**}	-0.27^{**}	-0.07^{NS}	0.10^{NS}	0.08^{NS}

2-sided P values. ***$P \leq 0.001$, ** $P \leq 0.01$, ** $P \leq 0.05$, NS = not significant.

5.4 Results

5.4.1 Relations between forest age and other environmental variables

A large number of significant correlations were recorded between forest age and other environmental variables. Exceptions were the C/N ratio, soil nitrate, pH (KCl) and relative insolation (Table 5.1). The C and total N contents gradually increased, from respectively 3.3% and 2708 mg/kg in the most recently afforested parcels to 4.3% and 3375 mg/kg in ancient forest and 19th century afforestations (Table 5.2). Most of the other significant correlations with the C and N contents were due to the strong correlations of both variables with forest age. Since C and N simultaneously increased, the C/N ratio was constant over all four forest-age classes. By contrast, the C/P ratio was a good indicator for the age of an afforestation (Tables 5.1 and 5.2). In spite of the increasing soil N pool after afforestation, nitrate concentrations measured at the end of the growing season were not correlated with forest age. Nitrate values were correlated with the total N content and to relative insolation (Table 5.1). The negative correlation of nitrate with the relative insolation on the forest floor indicates that concentrations were relatively high in shaded forest soils (Table 5.1).

Table 5.2 Mean values of environmental variables in four forest-age classes (years), with the standard error of each mean between brackets. Abbreviations are explained in Table 5.1.

		<30		30-79		80-129		>129	
C	(%)	3.3	(0.2)	3.9	(0.1)	3.8	(0.2)	4.3	(0.1)
CN		12.4	(0.2)	12.0	(0.4)	11.9	(0.4)	12.7	(0.3)
CP		113.2	(14.9)	267.0	(49.6)	296.0	(23.2)	349.8	(22.4)
D	(m)	33.2	(5.6)	16.4	(3.8)	27.1	(3.8)	18.4	(4.1)
M	(%)	25.5	(1.3)	33.1	(1.9)	31.8	(1.9)	36.9	(1.0)
NI	(mg/kg)	13.5	(2.3)	14.0	(3.6)	4.1	(1.1)	10.4	(2.4)
NT	(mg/kg)	2708.0	(121.0)	3302.0	(179.0)	3202.0	(147.0)	3375.0	(90.0)
PH		4.4	(0.1)	4.7	(0.2)	3.9	(0.3)	5.0	(0.3)
PL	(mg/kg)	89.7	(11.8)	18.3	(3.9)	17.4	(3.5)	12.1	(2.0)
PT	(mg/kg)	359.0	(31.4)	175.3	(20.2)	135.5	(11.6)	128.8	(7.2)
RI	(%)	19.9	(4.9)	8.7	(2.2)	12.9	(4.4)	13.8	(4.8)

Both soil P fractions were negatively correlated with forest age (Table 5.1). Mean values of total P and plant-available P recorded in most recently afforested parcels were respectively 3 and 7 times as high as the values recorded in ancient forest and 19th century reforestations (Table 5.2). In particular Plaggic Anthrosols, most of which were only afforested in 1991, are eutrophicated with P (Fig. 5.3); moreover an increased ratio of plant-available P to total P was determined in these soils (Fig. 5.4).

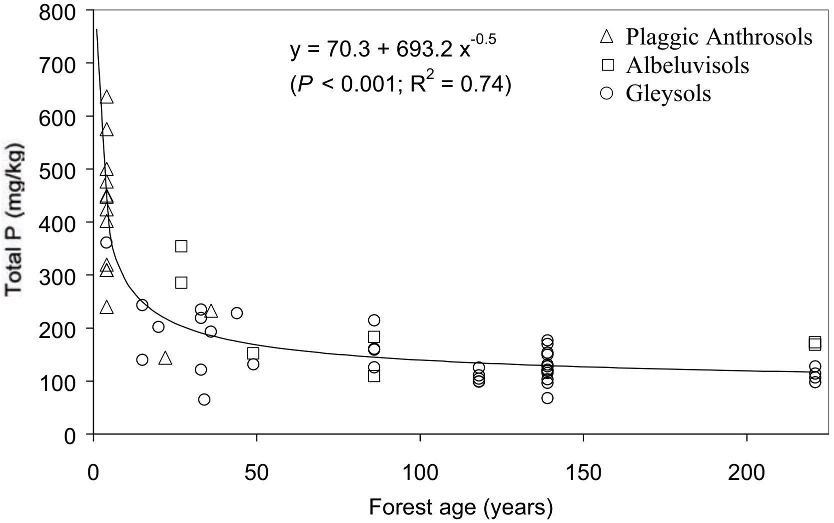


Fig. 5.3 The total P content as a function of the forest age, with a specification of the soil type according to the Belgian soil map.

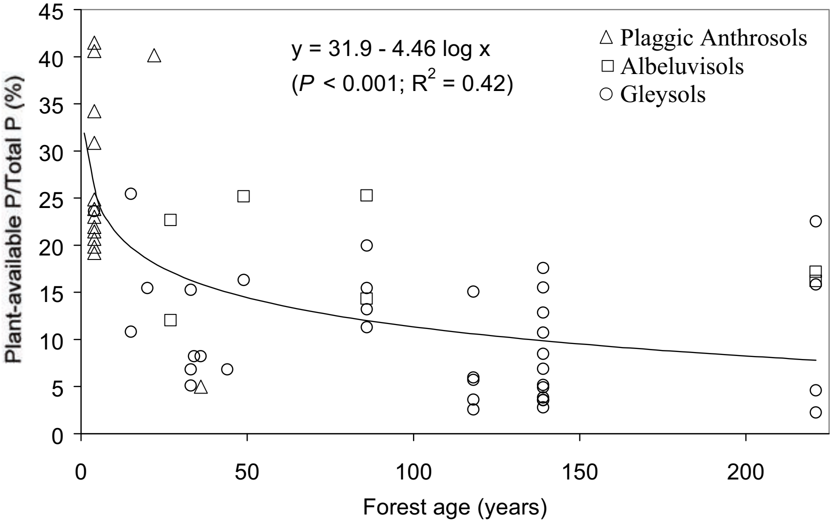


Fig. 5.4 The ratio of plant-available P to total P as a function of forest age, together with a specification of the soil type according to the Belgian soil map.

The positive correlation between soil moisture content and forest age (Table 5.1) is explained by the fact that wet Gleysols of the historical core of the forest (Fig. 5.2) were afforested first, whereas most of the relatively dry Plaggic Anthrosols surrounding the Gleysols were only afforested in 1991. This could also explain the observed correlations between soil moisture and soil P, soil moisture and total N content, soil moisture and C content, and soil moisture and the distance to the nearest migration source (Table 5.1). The pH (KCl) value was not significantly correlated to any other variable, but the variability was higher in older forest parcels than in younger ones (Tables 5.1 and 5.2). The absence of a significant correlation between forest age and relative insolation is due to the plantation of an understorey in some of the recent afforestations.

Table 5.3 Classification of species using the list of ancient forest species of Honnay *et al.* (1998), in combination with Ellenberg's indicator value for insolation (L) (Ellenberg *et al.* 1992). The number of observations on a total of 57 plots is stated between brackets.

Ancient forest species
Arum maculatum (22), Brachypodium sylvaticum (6), Carex sylvatica (2), Convallaria majalis (2), Deschampsia cespitosa (20), Lamiastrum galeobdolon (13), Lonicera periclymenum (6), Maianthemum bifolium (2), Oxalis acetosella (2), Paris quadrifolia (14), Poa nemoralis (1), Polygonatum multiflorum (21), Pteridium aquilinum (2), Viola reichenbachiana+riviniana (7)
Shade-tolerant species ($L < 6$), not indicative for ancient forest
Adoxa moschatellina (12), Aegopodium podagraria (12), Anemone nemorosa (25), Athyrium filix-femina (14), Circaea lutetiana (21), Dryopteris carthusiana (9), Dryopteris dilatata (8), Dryopteris filix-mas (1), Geranium robertianum (1), Geum urbanum (4), Moehringia trinervia (6), Ranunculus ficaria (27), Stachys sylvatica (5), Stellaria holostea (2)
Light-demanding species ($L \geq 6$), not indicative for ancient forest
Agrostis canina (1), Agrostis stolonifera (1), Ajuga reptans (3), Angelica sylvestris (18), Arrhenatherum elatius (2), Cardamine flexuosa (1), Chenopodium polyspermum (1), Cirsium arvense (9), Cirsium oleraceum (13), Cirsium palustre (6), Dactylis glomerata (1), Elymus repens (1), Epilobium angustifolium (1), E. adenocaulon (1), E. parviflorum (1), E. tetragonum (2), Equisetum arvense (1), Eupatorium cannabinum (8), Filipendula ulmaria (15), Galeopsis bifida+tetrahit (7), Galium aparine (31), Glechoma hederacea (19), Glyceria fluitans (2), Heracleum sphondylium (5), Holcus lanatus (12), Humulus lupulus (8), Hypericum maculatum (1), Iris pseudacorus (2), Juncus effusus (2), Listera ovata (8), Lolium perenne (1), Lychnis flos-cuculi (1), Lycopus europaeus (2), Mercurialis annua (1), Ornithogalum umbellatum (8), Poa trivialis (6), Polygonum hydropiper (3), Primula elatior (17), Ranunculus acris (1), R. repens (9), Rubus caesius (11), Rubus fruticosus (33), Rumex acetosa (2), Senecio vulgaris (1), Solanum dulcamara (2), Sonchus oleraceus (1), Stellaria graminea (2), S. media (3), Symphytum officinale (4), Tussilago farfara (1), Urtica dioica (43), Valeriana repens (1), Vicia hirsuta (1)

5.4.2 Colonization of forest species in shaded and illuminated afforestations

Table 5.3 lists all observed herbaceous species, classified as ancient forest species, fast colonizing forest species and light-demanding species with good colonization capacities. The number and total cover of ancient forest species per plot steadily increased with increasing forest age, which is in accordance with their status (Fig. 5.5).

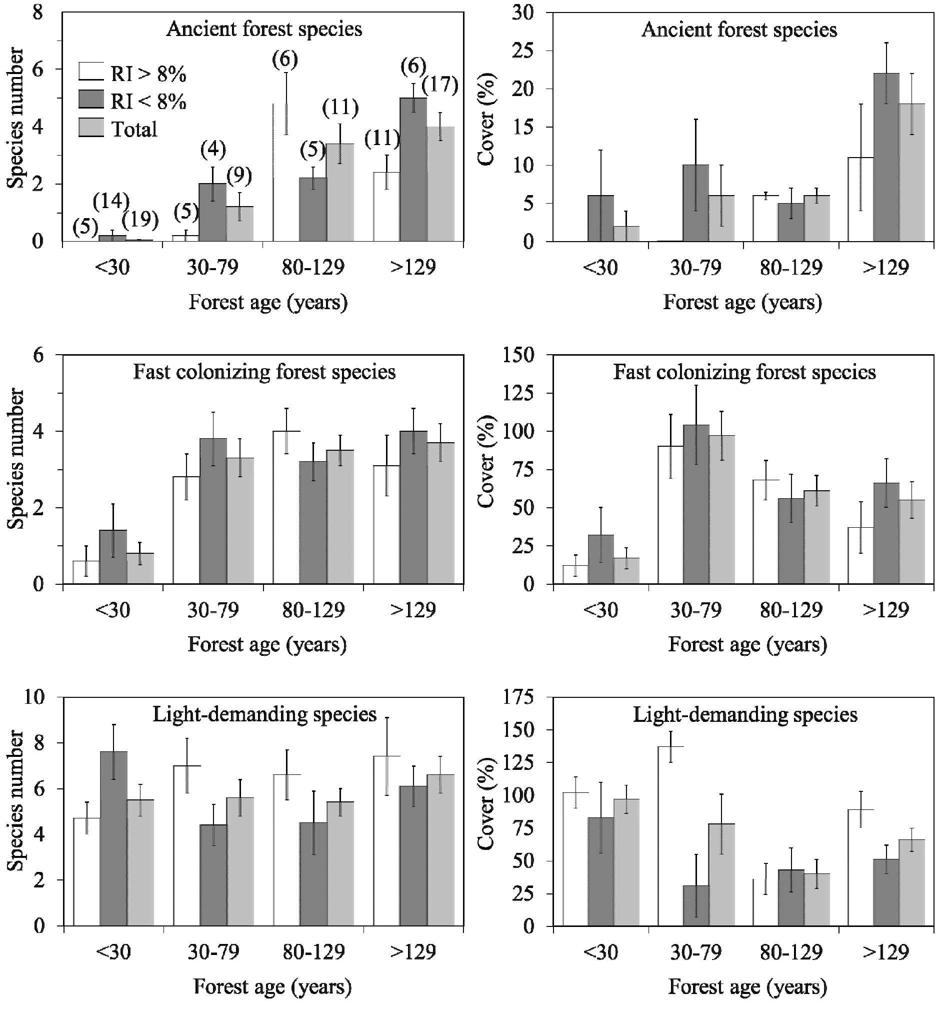


Fig. 5.5 Comparison of mean species number and cover of the three species groups in four forest-age classes, further subdivided into illuminated sample plots (RI ≥ 8%) and shaded sample plots (RI < 8%). The number of observations is stated between brackets.

The stepwise linear regression models indicated that this tendency was highly significant for the species number but somewhat weaker for the total cover (Table 5.4). By contrast, the number of fast colonizing forest species had already reached its optimum in 30 to 79-year-old afforestations and therefore no significant contribution of forest age was found in the regression model (Table 5.4). The total cover of fast colonizing forest species was negatively correlated with forest age (Table 5.4), as it had a maximum of 97% in 30 to 79-year-old afforestations and was lower in older forest age classes (Fig. 5.5). There was no indication that forest age influenced species number and the cover of light-demanding species (Fig. 5.5 and Table 5.4). The cover of light-demanding species was lower in shaded than in illuminated sample plots, but no significant effect on the species number was detected (Fig. 5.5 and Table 5.4).

Species number and the cover of forest species, irrespective of their colonization capacities, were higher in sample plots with a relative insolation below 8%, than in illuminated sample plots with a relative insolation equal to or higher than 8% (Fig. 5.5). This was observed in three of the four forest-age classes. Although no significant direct contribution of relative insolation could be assessed in the regression models on forest species (see further in Table 5.4), there was an indirect effect, as reduced competition by light-demanding species had a positive influence on species number as well as the cover of ancient forest species and fast colonizing forest species.

5.4.3 Direct gradient analysis

The relation between soil types, species groups and environmental variables is visualized by two triplots (Fig. 5.6). The CCA indicated that plant-available P, pH (KCl), nitrate and forest age, in order of decreasing importance, were the variables that contributed significantly to the ordination model. All other variables were eliminated by the forward selection procedure. Although a strong negative correlation between forest age and total soil P content was assessed (Table 5.1), both variables were included. The permutation test indicated that the global species-environment relation was significant (P=0.005). Forest age and plant-available P correlated best with the first canonical axis, pH (KCl) with the second axis and soil nitrate with the third axis. The first three axes explained 19.4% of the variance of the species data and 89.5% of the variance of the species-environment relation.

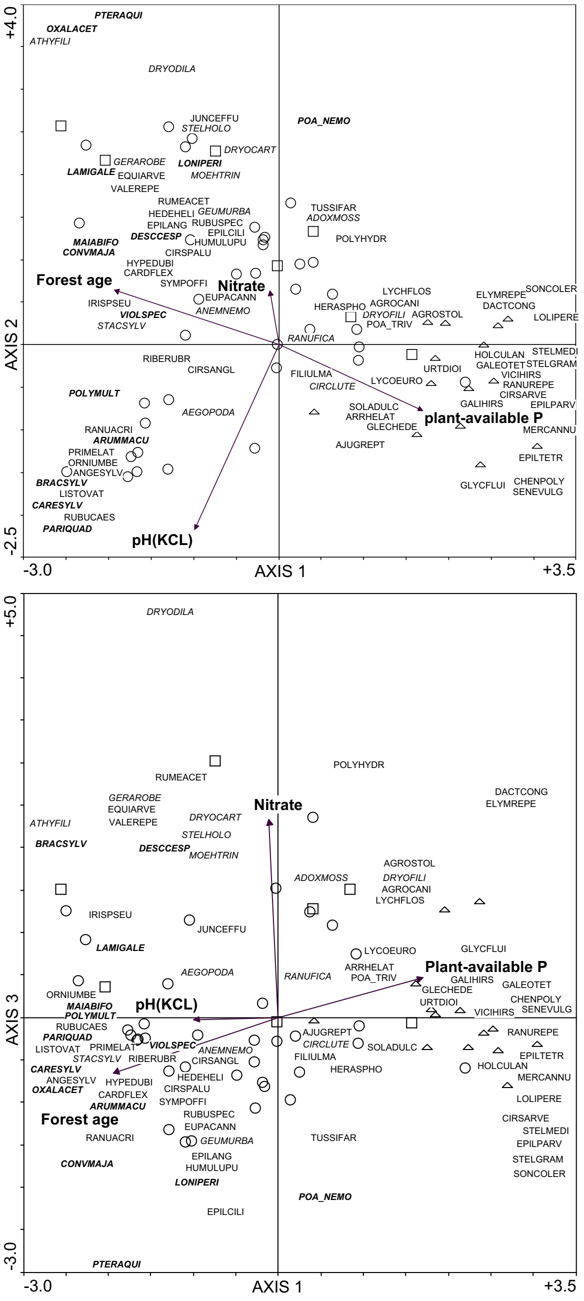


Fig. 5.6 Triplots of the first three axes of the CCA, both illustrating the ordination of species and sample plots in relation to four significant ($P<0.05$) environmental variables. Sample plots are labeled with symbols that indicate soil types (see Fig. 5.3). Bold italics indicate ancient forest species, italics indicate fast colonizing forest species and the standard font type indicates light-demanding species.

The triplots illustrate that Plaggic Anthrosols were only recently afforested and that high soil P values were determined in these soils (compare Figs 5.3 and 5.6). Albeluvisols are characterized by a low pH and a high nitrate concentration. Gleysols are scattered and do not occupy a specific position in the triplots.

The CCA indicated that environmental variables were also correlated with the performance of the three species groups. Ancient forest species were found on the negative side of the first axis, corresponding with a high forest age and a low soil P content (Fig. 5.6). Fast colonizing forest species occupied an intermediate position and the group of light-demanding species with good colonization capacities had no preference towards soil P level or forest age. *Angelica sylvestris*, *Eupatorium cannabinum*, *Humulus lupulus*, *Iris pseudacorus*, *Rubus caesius*, and *Rubus fruticosus* were light-demanding species that preferred older forests with low soil P values, while *Cirsium arvense*, *Galeopsis bifida + tetrahit*, *Galium aparine*, *Ranunculus repens*, and *Urtica dioica* were indicators for recent forests on P-rich soils. The triangular pattern of the species plot confirms that soil pH had a greater influence on forest vegetation in ancient forest and the earliest afforestations than in recently afforested farmland (Fig. 5.6). *Arum maculatum*, *Brachypodium sylvaticum*, *Paris quadrifolia*, and *Polygonatum multiflorum* were indicators of a high soil pH, while *Lonicera periclymenum*, *Oxalis acetosella*, *Pteridium aquilinum* and *Lamiastrum galeobdolon* (weaker) preferred acid soils (Fig. 6).

Grasses (*Brachypodium sylvaticum* and *Deschampsia cespitosa*), ferns (*Athyrium filix-femina*, *Dryopteris carthusiana*, *D. dilatata*), *Adoxa moschatellina* and *Moehringia trinervia* were positively correlated with soil nitrate concentration. The ancient forest species *Lonicera periclymenum*, *Convallaria majalis*, *Pteridium aquilinum* and most of the light-demanding species, which prefer a high forest age and a low soil P content, showed a negative relationship with soil nitrate concentration. Fast colonizing forest species were generally found on nitrate-rich soils (Fig. 5.6).

5.4.4 Linear models on species groups

The impact of soil characteristics, in combination with forest age, distance to migration source and relative insolation, was also studied using regression models (Table 5.4). No significant contributions were detected for total N content, C content and distance to migration source, and the variables are therefore not listed in Table 5.4.

Soil pH was positively correlated with the diversity of all species groups, although the correlation with fast colonizing forest species was relatively weak (Table 5.4). There was also a positive contribution to the regression model on the total cover of both forest species groups, but not on the total cover of light-demanding species. In spite of the highly significant correlation between forest age and soil P content, both factors were included in three of the four regression models for forest species (Table 5.4). These findings are in accordance with the CCA that recorded a significant effect of forest age, additional to plant-available soil P content. A high soil P content was negatively correlated with diversity and total cover of ancient forest species and to the total cover of fast colonizing forest species. Competition by light-demanding species was negatively correlated with the total cover and species number of both forest species groups, irrespective of their colonization capacities (Table 5.4). There was no indication that ancient forest species suffered from competitive exclusion by fast colonizing forest species (Table 5.4).

The regression model confirmed that the total cover of species with good colonization capacities and a high L indicator value, was positively influenced by relative insolation and by P enrichment. This effect of P availability was mainly due to *Urtica dioica*, which was dominant in well-illuminated forests on P-rich soils (Table 5.4). A negative interaction of relative insolation with soil P was assessed for the model on the total cover of light-demanding species and there were no indications that the combination of both factors had a stimulating effect. A negative correlation was observed between the cover of light-demanding species and the soil nitrate concentration (Table 5.4).

Table 5.4 Linear regression models for species number and cover on environmental variables, and on competition by other species groups. RIxPL: interaction between RI and P; CF: total cover of fast colonizing forest species; CL: total cover of light-demanding species; /: not tested; other abbreviations: see Table 5.1.

Species group		R^2	*F*	*P*	AGE	M	NI	PH	PL	RI	PLxRI	CF	CL
Ancient forest species													
Species number	(log)	0.70	30.0	<0.001	+++	NS	NS	++	-	NS	/	NS	--
Total cover	(sqrt)	0.65	15.6	<0.001	+	NS	NS	+++	-	NS	/	NS	---
Fast colonizing species													
Species number	(log)	0.59	18.9	<0.001	NS	+	NS	+	---	NS	/	/	--
Total cover	(sqrt)	0.52	10.9	<0.001	--	NS	NS	++	---	NS	/	/	--
Light-demanding species													
Species number		0.26	4.5	0.003	/	NS	NS	+++	NS	NS	-	/	/
Total cover	(sqrt)	0.40	6.8	<0.001	/	NS	-	NS	++	++	-	/	/
Cover *Urtica dioica*	(arcsine)	0.37	15.6	<0.001	/	NS	NS	NS	+++	+	NS	/	/
Total													
Species number	(log)	0.58	18.3	<0.001	+	NS	NS	++	---	NS	/	/	/
Cover	(sqrt)	0.57	11.4	<0.001	---	+	--	+++	--	+	/	/	/

Positive coefficient: +++ $P \leq 0.001$, ++ $P \leq 0.01$, + $P \leq 0.05$

Negative coefficient: --- $P \leq 0.001$, -- $P \leq 0.01$, - $P \leq 0.05$

NS: not significant

5.5 Discussion

5.5.1 Impact of land use history on forest soil fertility

Both soil P fractions were much lower in the soils of ancient forest and 19th century reforestations than in the most recently afforested farmland soils. Several other studies report similar observations (Dzwonko & Loster 1997, Koerner *et al.* 1997, Honnay *et al.* 1999b). The impact of former agricultural land use on soils can vary, which could explain the opposite findings of Wilson *et al.* (1997), who compared ancient forest soils with soils of 100 to 200- year-old afforestations. Soils of secondary forests established on heathland contained less Ca^{2+}, Mg^{2+}, K^{+} and P than ancient forest soils, but the reverse was observed in forest soils on former arable land (Wilson *et al.* 1997). Froment & Tanghe (1967) also found soil degradation, expressed by a decrease in soil pH, as a consequence of agricultural exploitation. Agricultural crises and famine in the mid 19th century provoked a reclamation of forest, which severely reduced the forest area in Flanders (Tack *et al.* 1993). Most of the infertile and impoverished soils were abandoned in the second half of the 19th century and reforested (Tack *et al.* 1993). A similar phenomenon was observed in Muizen forest. The total soil P contents in afforestations of the 19th century and early 20th century were comparable with the P contents in ancient forests on Gleysols and on Albeluvisols, which indicates that these soils have received little or no fertilization. By contrast, very high P contents were found in Plaggic Anthrosols that had been arable land until 1945 and then grassland until afforestation in 1991. According to the soil map, the field survey for this was performed in circa 1960, these soils are characterized by an anthropogenic Ah-horizon of at least 50 cm thickness. This observation indicates that this is old arable land, with a long history of manuring that can explain high soil P contents.

Fertilization of arable land and grassland results in an accumulation of P in the topsoil (Guggenberger *et al.* 1996) and as P is tightly retained in forest ecosystems (Wood *et al.* 1984, Binkley 1986, Zhang & Mitchell 1995), losses are negligible in afforested farmland. The highest total P values in Muizen forest, amounted to 600-700 mg/kg, which is comparable with values determined in a field on a calcareous clay polder soil, in Flanders (Vanderdeelen 1995). Values recorded in ancient forest soils and 19th century reforestations of Muizen forest ranged between 50 and 200 mg/kg. The use of fertilizers in previous centuries, but in particular after 1945, is deemed to be responsible for the observed accumulation of P in the upper soil of recently afforested parcels. In particular labile inorganic forms of P increase as a result of fertilization (Guggenberger *et al.* 1996). After the afforestation of farmland, P is gradually immobilized by the formation of Ca and Al phosphates. Afforestation often results in a progressive soil acidification (Goovaerts *et al.* 1990, Bossuyt *et al.* 1999a), reducing P availability by formation of Al phosphates (Kuo 1993). On acidic, spruce-covered, sandy soils in Denmark, most of the added fertilizer P had become immobilized 20-30 years after application (Magid 1993). When a calcareous field soil, which had remained uncropped for 6 years, was extracted with ammonium lactate, 30% of the total P content was still recovered (Vanderdeelen 1995). A similar level was found in the Plaggic Anthrosols of Muizen forest which had been afforested for 4 years, while no more than 20% of the total P content was extracted from Gleysols and Albeluvisols that had been afforested for at least 100 years.

The variability in soil pH recorded in Muizen forest was correlated with forest age. Wilson *et al.* (1997) found that soil variability was greater in ancient forest than in recent forests. The liming and fertilization of farmland soils could explain the low soil variability in sites of Muizen forest that were recently converted from farmland to forest. The Plaggic Anthrosols, occupied by farmland for a longer time, had higher soil pH values than the Albeluvisols in Muizen forest, although both have similar soil texture and drainage properties (see section 5.3.1). Fertilization with P can have a leveling effect on soil pH, since P enrichment increases soil negative charge and soil pH in acid soils (Naidu *et al.* 1990). As a consequence, the large pool of plant-available P can slow down acidification of recently afforested Plaggic Anthrosols towards pH (KCl) values recorded in adjacent ancient forest on Albeluvisols, which is a reference situation.

The development of a forest soil after the afforestation of farmland is expressed by a gradual increase of the topsoil organic matter content (Catt 1994, Verheyen *et al.* 1999), a phenomenon also observed in Muizen forest. This accumulation of organic matter is accompanied by an increase in total N content (Muys*et al.* 1992). In spite of the influence of forest age on the total N pool and the significant effect of the total N content on nitrate concentrations, no effect of the forest age was observed on soil nitrate concentrations in Muizen forest. Although soil nitrate was not monitored throughout the year, but determined by a single measurement in the summer, this might indicate that there are other important factors that determine nitrate availability. The impact of forest age on nitrate availability is put into perspective by the following considerations: 1) mean N depositions in Flanders amounted to 39 kg/ha in 1998, causing a general N saturation in forests (Van Gijseghem *et al.* 2000); 2) recently afforested farmland soils are rich in nitrate as a consequence of fertilization and 3) nitrification is optimal in moist soils with a mull humus (Gleysols), which is the dominant soil type in Muizen forest.

5.5.2 Impact of soil fertility and insolation on colonization of forest species

Verheyen & Hermy (2001b) studied the recruitment or dispersal limitation of 16 forest species in Muizen forest. Slow-colonizing species which preferred a high soil pH in our study (*Polygonatum multiflorum*, *Paris quadrifolia*, *Arum maculatum*) were classified as recruitment limited, while *Anemone nemorosa* and *Deschampsia cespitosa*, which were insensitive to soil pH in our study, were classified as dispersal limited. According to Verheyen & Hermy (2001b) *Adoxa moschatellina*, *Circaea lutetiana*, *Dyopteris carthusiana*, *Glechoma hederacea* and *Ranunculus ficaria* were not recruitment or dispersal limited. All these species, except *Glechoma hederacea*, were classified as fast colonizing forest species, with a maximal cover in afforestations with an age of 30-79 years. The relatively low cover of this species group in afforestations older than 79 years, could be due to increased competition with ancient forest species. Verheyen & Hermy (2001b) suggested that the recruitment of fast colonizers was not limited by soil pH. The relatively low variability of pH (KCl) in afforestations younger than 80 years, implies that our data is insufficient to confirm or refute this, as it probably did not cover the complete ecological amplitude of the species. However, according to Taylor & Markham (1978) and Taylor (1997), *Ranunculus ficaria* and *Geum urbanum* respectively can tolerate a wide range of soil pH.

Dzwonko & Loster (1997) observed a strong divergence in the development of secondary woods, as a consequence of differences in N availability and insolation that were determined by tree species. The CCA and the regression models suggest that nitrate also determined secondary succession in Muizen forest. A high cover of light-demanding species (mainly *Urtica dioica*) was associated with a low soil nitrate concentration and shade-tolerant, fast colonizing forest species preferred nitrate-rich soils. This seems to contradict Olsen (1921), who found that *Urtica dioica* has a high nitrate demand. Pigott & Taylor (1964) confirmed this finding but concluded that P availability, and not nitrate, is generally growth- limiting. It is assumed that consumption by light-demanding species, most of which are tall herbs, might have reduced nitrate concentrations at the end of the growing season. At sample points with a dense understorey, high nitrate concentrations were found. The combination of the high N depositions in Flanders, the presence of a clay substrate (which impaired washing out) and the relatively low productivity of the shade-tolerant herbaceous vegetation, resulted in an accumulation of nitrate. Some of the fast colonizing forest species found on nitrate-rich, shaded soils, are indeed known to be N indicators with a high nitrate demand. Van Dobben *et al.* (1999) found that experimental fertilization with N resulted in an increase in *Dryopteris carthusiana* on poor sandy soils.

Koerner *et al.* (1997) found that several forest species sensitive to soil degradation (*Athyrium filix-femina*, *Dryopteris filix-mas*, *Festuca altissima*, *Senecio nemorensis*), occurred more frequently in former cropland and gardens with an elevated P content, than in ancient forest. In Muizen forest, forest species sensitive to acidification might indirectly benefit from P eutrophication, as a large pool of P in Plaggic Anthrosols is a buffer against acidification towards the pH levels observed in Albeluvisols. An introductory experiment by Verheyen (2002) showed that *Primula elatior*, an indicator of a high soil pH, also germinated abundantly on these soils and that seed limitation was the main factor limiting colonization. In spite of this potential positive effect of P eutrophication, the linear models suggested a negative influence on the diversity of forest vegetation. A similar negative effect was found on the floristic diversity of grassland ecosystems (Janssens *et al.* 1998). McKendrick (1996) observed a direct negative influence of P fertilization on the germination of *Dactylorhiza fuchsiï*, an orchid species that is also present on calcareous soils with low soil P values of Muizen forest. Research by Pigott (1971) demonstrated that *Urtica dioica* benefits from increased P availability. We assume that the negative effect of P enrichment in Muizen forest mainly is a consequence of stimulated competitive exclusion by *Urtica dioica*. Verheyen (2002) found that the presence of a competing vegetation cover suppressed the growth of introduced species. In this experiment, no indications were found for increased competition across the old-young forest P-gradient, but at all introduction sites a planted second layer was present which reduced light-demanding competitors.

Pigott & Taylor (1964) found that deep shadow can suppress *Urtica dioica* and this is confirmed by the results from Muizen forest. Low insolation reduced light-demanding species, in particular *Urtica dioica*, and stimulated the colonization of recent afforestations by forest species. The understorey of poplar plantations, the dominant forest type in our research, is initially poorly developed and gradually develops with increasing forest age (Lust *et al.* 2001). The case study in Muizen forest indicated that the plantation of an understorey could be an appropriate management tool for stimulating the establishment of shade-tolerant forest species.

5.6 Conclusions

In this case study, many soil characteristics were correlated with forest age. Forest age, soil pH, soil P content and insolation on the forest floor were the most important determinants for forest vegetation. The diversity of forest species in afforestations adjacent to ancient forest was negatively affected by light-demanding species and in particular by *Urtica dioica*, a species that was stimulated by a high soil P level. Two processes that are correlated with forest age can eliminate the dominance of *Urtica dioica* in afforestations on eutrophicated soils: the immobilization of P and the reduction of insolation on the forest floor. The research in Muizen forest indicated that if colonization sources are present, plantation of an understorey could reduce cover of *Urtica dioica* and favor the establishment of shade-tolerant forest species. However, light-demanding species that prefer a soil with a low P availability (such as *Angelica sylvestris*, *Eupatorium cannabinum*, *Filipendula ulmaria* or *Dactylorhiza fuchsii*) do not benefit from this management. The process of P immobilization will eventually determine how long it takes for afforestations on eutrophicated farmland soils to acquire a herbaceous layer similar to that of ancient forests and 19th century afforestations on unfertilized soils. At present, little is known about the immobilization rates in P-enriched forest soils and the possible controlling factors, such as soil texture, soil acidity, soil moisture and tree species. A combination of long-term observational studies with controlled experiments is needed to obtain more detailed information.

6 Impact of clear-felling on colonisation rates of forest plant species into a post-agricultural forest stand

After: 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 shadetolerant forest herbs into a post-agricultural forest adjacent to ancient forest. Applied Vegetation Science 14, 75-83

6.1 Abstract

The effect of clear-felling on plant species in long-established forests is studied several times before, but the effect on species colonizing a post-agricultural forest is still unknown. We studied the case of a poplar stand with a dense understorey of *Acer pseudoplatanus* in Muizen forest (northern Belgium), planted in 1952 on farmland adjacent to ancient forest and clear-felled in 1997. Forest herbs that are shade-tolerant according to the indicator value for light, were surveyed in 112 grid-based sample plots: just before clear-felling, and 5 and 10 years afterwards. These herbs were subdivided into ancient forest species (AFS) and other shade-tolerant species (OSS). The effects of clear-felling on species number per plot, total cover per plot, and colonization rate of species groups were compared using non-parametrical tests. The species number per plot was modeled by means of generalized linear mixed models (GLMM), with inventory time, distance to the nearest parcel edge, and cover of light-loving species (LS) as explanatory variables. The shift of the C-S-R signature of sample plots was calculated on the selected shade-tolerant species. Frequency of most species increased during the 10 year period, but the number of OSS increased more and faster than number of AFS. The number of OSS increased to the level of the adjacent forest, but was lower, where LS cover remained high. There was a positive correlation between the change of the colonization rate and the competitive plant strategy. We assume that clear-felling stimulated generative reproduction of shade-tolerant herbs, whereas quickly emerging woody species controlled competitive exclusion by LS. A succession of dark and light phases, e.g. provided by an understorey managed as a coppice, could promote colonization of shade-tolerant herbs into post-agricultural forest.

6.2 Introduction

Many forest plant species are slow, short-distance colonizers that are shade-tolerant and dependent on a long and continuous cover of woodland (Matlack 1994b, Brunet & von Oheimb 1998b, Bossuyt *et al.* 1999b, Hermy *et al.* 1999). These species, called 'ancient forest species', are scarce in forests that have been established during the past decades on agricultural land throughout Europe and eastern North America (Peterken & Game 1984, Matlack 1994b, Rackham 2003). They are particularly rare in stands of *Populus x canadensis*, which are typically planted in wide spacings, whereas a limited number of light-loving, highly competitive herbs have a preference for poplar plantations (Hermy 1985). Such an enhanced competition by light-loving species can hamper the establishment and growth of shade-tolerant forest herbs (Baeten *et al.* 2009b). Conversely, reducing the level of insolation by promoting a shrub layer can suppress light-loving competitors and promote the establishment of shade-tolerant forest herbs into poplar plantations (see Chapter 5).

As poplar plantations mainly serve for wood production, they will be cut at some point in time. Felling breaks up the canopy and suddenly cancels out light limitation, which could have adverse effects on herb layer diversity. Felling can favour light-loving, highly competitive or ruderal herbaceous species (Kirby 1990). Clear-felling in particular can have persistent negative effects on herbaceous forest species (Moola & Vasseur 2004, Godefroid *et al.* 2005). However, several authors demonstrated that the impact on forest vegetation is not consistently negative (Halpern & Spies 1995, Brunet *et al.* 1996, Battles *et al.* 2001, Bergès 2004). Recurring short phases of high light availability (e.g. resulting from coppicing or small scale fellings) are expected to promote plant diversity at the stand scale as they enable light-loving species to survive within a forest habitat and simultaneously promote generative reproduction of shade-tolerant herbs (Peterken 1981, Mason & MacDonald 2002). All these studies were performed in ancient forests, without nutrient enrichment by former agricultural land use, and in which many ancient forest species were already present. Studies on the direct impact of felling on colonization of shade-tolerant forest herbs into forest recently planted on agricultural land are lacking. We studied such a scenario by monitoring the establishment of shade-tolerant herbs before and up to a decade after clear-felling of a well-documented poplar plantation on former agricultural land. This field study aimed to discriminate the effect of clear-felling from the time and distance effects, which are key factors of vegetation succession. We hypothesised that clear-felling would promote light-loving, fast-growing herbs and that this would have an indirect negative effect on colonization by shade-tolerant herbs as competitive exclusion would be enhanced.

6.3 Materials and methods

6.3.1 Study area

This study presents results of temporal vegetation patterns in a 0.73 ha forest parcel located in the SW of Muizen forest, a 34 ha forest reserve situated 15 km east of Antwerp in northern Belgium (Fig. 6.1). The forest consists of a central core area of ancient forest stands surrounded by stands established on agricultural land during the past decades.

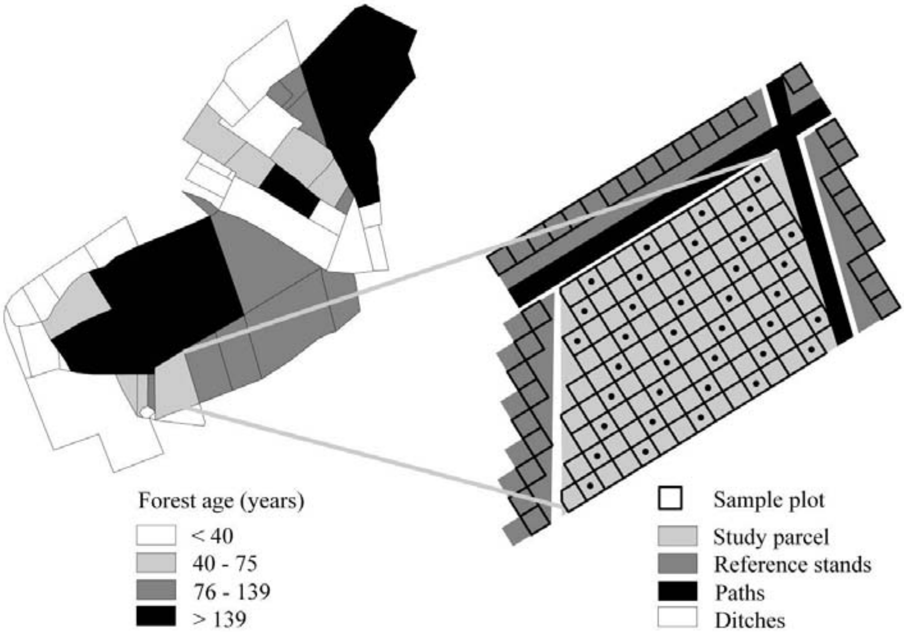


Fig. 6.1 Map of Muizen forest (left) with the grid-based 5 m x 5 m sample plots on the study parcel (n = 112) and the adjacent forest (n = 33) (right). Forest age classes indicate the number of years a parcel was continuously covered by forest in 2007. Sample plots marked with a dot (n = 38) were inventoried for woody species.

The soil has a high silt loam content and, without the formation of a clear profile, is classified as a Gleysol (IUSS Working Group WRB 2006). The soil is slightly acidic; average pH($CaCl_2$) equalled 5.0. Total P, extracted with $HClO_4$, amounted to 228 mg/kg, which is intermediate between the values recorded in ancient forest and old reforestations (100-150 mg/kg) and in most recently afforested agricultural land (300-600 mg/kg) in the same forest (see Chapter 5).

According to ancient maps and other land cover information, the studied parcel was not covered by forest between 1775 and 1952. It was used as arable land until World War II and transformed into grassland after 1943. Old management notes indicate that *Populus x canadensis cv. Robusta* was planted in 1952, on an 8.5 m x 8.5 m spacing. *Acer pseudoplatanus*, but also some *Alnus glutinosa* and *A. incana* trees, were planted simultaneously and then managed as coppice. This understorey coppice layer was cut for the last time in 1972. The basal area in 1992 was 44 m^2/ha for the poplar cultivars and 20 m^2/ha for the coppice layer. The poplars were removed by clear-felling in the winter of 1997-1998, as a conversion measure for further spontaneous development towards a mixed broad-leaved stand following the assignment of the forest reserve status. Prior to exploitation of the poplars, most of the coppice was cut as well. Ten years after clear-felling, the study area belonged to the thicket forest stage in which about three saplings or shoots per m^2 were counted (Table 6.1). Median diameter of the woody plants was below 0.05 m, but the median height already exceeded 2 m. Some relatively large *Acer pseudoplatanus* and *Alnus glutinosa* trees were coppice shoots spared from clear-felling. *Acer pseudoplatanus* and *Fraxinus excelsior* were the dominant woody species, accounting for 75% of the total stem number. Almost 20% of the *Acer* and 12% of the *Alnus glutinosa* shoots regenerated on coppiced boles, whereas all *Fraxinus* trees naturally regenerated. Several shrub and tree species, not found before, established after clear-felling (Table 6.1). The poplar stand was surrounded by five other parcels, separated by shallow ditches and by two unpaved forest paths in the north and northeast. In the south *Quercus robur* was planted in 1991 on a farmland parcel. The four other adjacent parcels were covered by forest for a much longer time than the studied poplar stand (Fig. 6.1). They had a well-developed forest vegetation with many ancient forest species, classified as a *Primulo-Fraxinetum excelsioris* (Hermy 1985). We assumed that they functioned as colonization sources (cf. Brunet & von Oheimb 1998b, Bossuyt *et al.* 1999b).

Table 6.1 Number of shoots of trees and shrubs (per ha) in 38 sample plots in the study parcel, 10 years after clear-felling. The inventoried sample plots were systematically selected from the grid cells, in which shade-tolerant species were monitored (Fig.1). Regeneration is subdivided in 8 dimension classes, based on diameter (D; in cm) and height (H; in cm). Percentages of coppice shoots are in parentheses.

Species	D < 5				D 5-10	D 10-20	D 20-30	D >30	Total
	H 0-30	H 30-50	H 50-200	H >200					
Acer pseudoplatanus	431 (5)	164 (0)	759 (50)	6851 (15)	472 (17)	185 (6)	10 (0)	0	8872 (17)
Alnus glutinosa	10 (100)	0	51 (0)	154 (27)	226 (9)	113 (0)	31 (0)	0	585 (12)
Alnus incana	21 (0)	31 (0)	31 (0)	21 (0)	10 (0)	10 (0)	10 (0)	0	133 (0)
Betula pubescens	10 (0)	0	0	0	0	0	0	0	10 (0)
Carpinus betulus	10 (0)	0	0	10 (0)	0	0	0	0	21 (0)
Cornus sanguinea	472 (0)	749 (0)	1005 (1)	318 (10)	0	0	0	0	2544 (2)
Corylus avellana	0	0	62 (50)	892 (14)	0	0	0	0	954 (16)
Crataegus monogyna	0	0	10 (0)	10 (0)	0	0	0	0	21 (0)
Fagus sylvatica	10 (0)	0	0	0	0	0	0	0	10 (0)
Frangula alnus	0	0	0	31 (0)	0	0	0	0	31 (0)
Fraxinus excelsior	215 (0)	287 (0)	1282 (0)	4903 (1)	236 (0)	10 (0)	0	0	6933 (0)
*Fraxinus/Acer**	6903 (0)	0	0	0	0	0	0	0	6903 (0)
Populus x canadensis	0	0	0	21 (0)	10 (0)	0	0	0	31 (0)
Prunus avium	21 (0)	0	0	31 (0)	0	0	0	0	51 (0)
Quercus robur	246 (0)	62 (0)	21 (0)	62 (0)	0	0	0	10 (0)	400 (0)
Quercus rubra	0	10 (0)	10 (0)	0	0	0	0	0	21 (0)
Salix alba	0	0	0	0	0	10 (0)	0	0	10 (0)
Salix caprea group	0	0	10 (0)	718 (0)	462 (0)	174 (0)	0	0	1364 (0)
Sambucus nigra	51 (20)	277 (19)	318 (39)	226 (23)	0	0	0	0	872 (27)
Sorbus aucuparia	0	0	0	10 (0)	0	0	0	0	10 (0)
Tilia sp.	10 (0)	0	0	0	0	0	0	0	10 (0)
Viburnum opulus	31 (0)	10 (0)	10 (0)	31 (33)	0	0	0	0	82 (13)
All species	8441 (<1)	1590 (3)	3569 (15)	14287 (9)	1415 (7)	503 (2)	51 (0)	10 (0)	29867 (7)

*Seedlings that were too small to discern *Acer* from *Fraxinus*

6.3.2 Sampling methodology

Herbaceous plant species were inventoried three times in grid-based, 5 m x 5 m sample plots (Fig. 6.1): just before clear-felling in 1997, and 5 and 10 years later during the same period (April – May) in the growing season. To guarantee a constant sampling surface area of 25 m^2, only the 112 grid cells completely located within the parcel were studied. The southern part of the parcel was not sampled, because it showed a gradient towards a more acidic soil type. In order to determine reference values for abundance and diversity of herbs in the forest that functioned as colonization source for the studied parcel, the adjacent forest parcels were inventoried in 2007 by means of 33 similar sample plots (Fig. 6.1).

The cover of herbaceous species was visually estimated within each plot using the decimal scale defined by Londo (1984). For species with a low cover (i.e., < 1 %), we measured species abundance as the number of shoots of a species in a sample plot (Van der Maarel 2005), with six abundance classes (1, 2-4, 5-9, 10-19, 20-40, >40). We estimated the percentage cover by woody species, henceforth referred to as ‘canopy cover’, in each plot using the same methods.

To facilitate field surveys and data analyses, herbs were, analogous to the method applied in Chapter 5, a-priori subdivided into three species groups. Species (25 in total) with an indicator value for light below or equal to five according to Ellenberg *et al.* (1992) and Hill *et al.* (1999) were considered shade-tolerant. When the values for Central Europe (Ellenberg *et al.* 1992) and for Britain (Hill *et al.* 1999) were not equal, the mean value was used, which agrees with the intermediate geographical position of the study area. These 25 shade-tolerant herbs were subdivided into ancient forest species (AFS; n = 8) and other shade-tolerant herbs not listed as ancient forest species (OSS; n = 17) according to the renewed list for Flanders by Cornelis *et al.* (2009). We estimated the cover of each individual species within these two groups and calculated the group-level cover of AFS and OSS as the sum of individual species cover values. We assumed that a third species group of light-loving herbaceous species (LS), with an L-value above five, are potential competitors of AFS and OSS and could be promoted by clear-felling. For practical reasons – numerous species emerged after clear-felling – the cover of LS was estimated for the species group as a whole, i.e., not for each individual species.

Species frequency is defined as the number of plots in which a species occurred (Van der Maarel 2005) and is calculated as a percentage relative to the total number of plots in the clear-felled parcel (n = 112) or in the adjacent forest (n = 33). Furthermore, we calculated the characteristic species cover and abundance per plot, which are mean values excluding zero's. Cover and abundance classes were converted to mean class values for this purpose.

6.3.3 Data analyses

Species frequency, species abundance, species cover, species group cover and species number of a group in the study parcel at three inventory times and in the adjacent stands were compared by means of Wilcoxon rank sum tests. We used the Bonferroni correction for multiple comparisons by dividing the threshold error value of 0.05 by the number of comparisons (Sokal & Rohlf 1995).

A commonly applied method to calculate colonization rate is based on the furthest individual from the colonization source (Brunet & von Oheimb 1998a, Bossuyt *et al.* 1999b). This variable is of limited use for our study as it gives an underestimation if individuals are found at the maximum distance from the colonization source, i.e., colonized from beyond the limits of the study area (Brunet & von Oheimb 1998a). In this study, this was the case for three shade-tolerant species before clear-felling, increasing to eight at the end of the study. The colonization rate based on the furthest individual is also very sensitive to stochastic variability: when studying a grid of sample plots, it is based on a single observation. Matlack (1994b) introduced a more robust measure of colonization rate based on the distance to the peak and half the peak density, which can be either frequency or cover (see also Brunet & von Oheimb 1998a, Bossuyt *et al.* 1999b). Application of these rates to our study was complicated by the fact that several species did not fit to a negative exponential or logarithmic colonization function. Therefore, we calculated a value specific to our study that quantifies the mean rate of 'filling up' of the sample grid, weighted for the distance to the colonization source. We refer to this value as colonization rate (CR) and calculated it as follows for species j:

$$CR_j = \frac{\sum_i^n (F_{ij} \text{ x } d_i)}{\Delta T \text{ x } \sum_i^n d_i}$$

This calculation required a subdivision of sample plots into classes of distance to the nearest parcel edge, which we assumed to be the colonization source. In this case we applied regular intervals of 5 m for subdivision into six distance classes. In the equation, Fij is the frequency (%) of species j in sample plots of distance class i, di is the mean distance (m) of the plot centroids in distance class i to the nearest parcel edge and n is the number of distance classes. ΔT is the number of years since afforestation (1952), i.e. the time when colonization was assumed to have started. CRj was calculated for the period before clear-felling (1952 - 1997) and for the whole study period (1952 – 2007); subtracting the former from the latter quantifies the change of CRj after clear-felling (ΔCRj):

$$\Delta CR_j = [CR_i]_{1952\text{-}2007} - [CR_i]_{1952\text{-}1997}$$

This was done to avoid a bias caused by not exactly knowing the starting point of the colonization at the time of plantation in 1952, whereas species positions in 1997 were exactly known. CR values calculated for the two periods were compared with Wilcoxon signed-rank tests for AFS and OSS.

In order to distinguish an effect of LS cover from effects of time and distance on colonization, we constructed Generalized linear mixed models (GLMM) with the number of OSS and AFS as response variables. We used S-PLUS 8.1 for this purpose and applied a stepwise selection procedure starting from an upper model that included LS cover, distance to the nearest parcel edge, inventory time, and interactions between these variables. The sample plot was included as a random (intercept) effect to take the dependence of multiple observations within a plot into account and thus to correct for autoreplication (Pinheiro & Bates 2009). The Akaike Information Criterion (AIC) was used to evaluate the variance structure model. Since the response variables were all count data, a Poisson regression was appropriate. Restricted penalized quasi-likelihood (REPQL) was applied for parameter estimation, as provided by the GLME function in the Correlated Data library in S-Plus 7 (Pinheiro & Chao 2005).

The C-S-R coordinates are the numerical expression of the competitive, stress-tolerant and ruderal strategies, respectively, and these three coordinates represent the functional type of each plant species as defined by Grime (2001). The strategy of a group of herbaceous species (AFS or OSS) was calculated using the mean C-S-R coordinate value of all herbs. Functional signatures of sampled plots were calculated as average values of the C-S-R coordinates of the present shade-tolerant herbs (L-value ≤ 5). We used the spreadsheet-based tool developed by Hunt *et al.* (2004) for these purposes. Functional signatures were calculated for the whole study parcel at the three inventory times and for the adjacent forest in 2007, as mean values of the functional signatures of sample plots. Shift in functional signature after clear-felling was calculated by subtracting the plot C-S-R coordinate values of 1997 from the values of 2007. Mean values of the functional signature shift were calculated for the distance classes also applied to calculate the CR. Finally, the C-S-R coordinate values of a species were related to ΔCR.

6.4 Results

6.4.1 Cover and species number of species groups

Before clear-felling, 14 shade-tolerant herbs were counted in the study parcel, five AFS and nine OSS. The total number of shade-tolerant herbs had increased to 19 (seven AFS) 5 years after clear-felling, and to 21 (seven AFS) after one decade. In particular, three fern species, *Athyrium filix-femina* (AFS), *Dryopteris dilatata*, and *D. filix-mas*, and two sedges, *Carex remota* and *C. sylvatica* (AFS), successfully colonized after clear-felling. Two species, *Paris quadrifolia* (AFS) and *Poa nemoralis* (OSS) were found in the adjacent forest but not in the study area at any time (Table 6.2).

The number of OSS per sample plot continuously increased after clear-felling and was close to the value in the adjacent forest in 2007 (Table 6.3). The number of AFS per sample plot in 2002 was similar to the value in 1997, but had significantly risen in 2007. This value was still below the species number recorded in the adjacent forest. The cover of OSS, mostly accounted for by *Ranunculus ficaria*, was very high and above the level of the adjacent forest before clear-felling. There was a strong decrease shortly after clear-felling, but in 2007 cover of OSS had rebounded to a similar level as in the adjacent forest. AFS cover, mostly accounted for by *Anemone nemorosa*, did not change significantly by clear-felling and in 2007 was still much below the value in the adjacent forest. Before clear-felling, cover of LS was low compared to the adjacent forest.

Table 6.2 Presence (%), median cover (%) or median abundance class, and colonization rate (CR), of 25 shade-tolerant herbs in sample plots in the study parcel (n = 112) and in the adjacent forest (Adj; n = 33). The cover and abundance classes are explained in the materials and methods section. Species were recorded before clear-felling (1997) and 5 years (2002) and 10 years (2007) afterwards. Ancient forest species are indicated by *. Different superscripted letters within a row indicate significantly (P<0.05) different values.

Species	Presence (%)				Cover (%) or abundance classes				*CR* (%.yr^{-1})	
	1997	2002	2007	Adj	1997	2002	2007	Adj	1952-1997	1952-2007
Adoxa moschatellina	74^{ab}	73^{a}	93^{c}	97^{bc}	5-9%^{c}	1-2%^{a}	1-2%^{a}	3-4%^{c}	1.39	1.57
*Anemone nemorosa**	73^{ab}	63^{a}	69^{a}	94^{b}	3-4%^{b}	5-9%^{b}	1-2%^{a}	15-19%^{c}	1.29	0.86
*Arum maculatum**	88^{ab}	85^{a}	96^{b}	97^{ab}	2-4^{a}	10-19^{c}	5-9^{b}	10-19^{c}	1.90	1.68
*Athyrium filix-femina**	0^{a}	1^{a}	51^{c}	21^{b}	1	1	2-4	2-4	0.00	1.17
Brachypodium sylvaticum	0^{a}	0^{a}	2^{ab}	6^{c}		1	2-4	2-4	0.00	0.04
Carex remota	0^{a}	1^{a}	12^{b}	18^{b}		1	2-4	1	0.00	0.17
*Carex sylvatica**	0^{a}	7^{b}	23^{c}	21^{bc}		2-4	5-9	2-4	0.00	0.39
Circaea lutetiana	29^{a}	69^{b}	86^{c}	76^{bc}	10-19^{a}	10-19^{b}	20-40^{c}	20-40^{bc}	0.55	1.64
Dryopteris dilatata	0^{a}	19^{b}	30^{b}	24^{b}		1	1	1	0.00	0.69
Dryopteris filix-mas	0^{a}	0^{a}	23^{b}	6^{ab}		1	1	1	0.00	0.66
Festuca gigantea	1^{a}	0^{a}	0^{a}	12^{b}				1	<0.01	0.00
Geum urbanum	2^{a}	2^{a}	21^{b}	39^{b}	2-4	10-19	2-4	2-4	0.01	0.28
Hedera helix	1^{ab}	0^{a}	50^{c}	9^{b}	1		2-4	1	0.02	1.05
*Lamiastrum galeobdolon**	4^{a}	3^{a}	11^{a}	48^{b}	1-2%	1-2%	5-9%	10-14%	0.04	0.09
Moehringia trinervia	0^{a}	4^{a}	16^{b}	18^{b}		1	2-4	2-4	0.00	0.20
*Paris quadrifolia**	0^{a}	0^{a}	0^{a}	15^{b}				2-4	0.00	0.00
Poa nemoralis	0^{a}	0^{a}	0^{a}	6^{a}				1	0.00	0.00
*Polygonatum multiflorum**	4^{ab}	3^{a}	13^{b}	52^{c}	5-9^{ab}	10-19^{ab}	2-4^{a}	10-19^{b}	0.06	0.13
Primula elatior	29^{a}	49^{b}	63^{bc}	82^{c}	2-4^{a}	10-19^{b}	5-9^{b}	10-19^{b}	0.38	0.77
Ranunculus ficaria	100^{a}	100^{a}	100^{a}	100^{a}	50-59%^{c}	20-29%^{a}	40-49%^{b}	40-49%^{b}	2.22	1.82
Ribes nigrum	0^{a}	1^{a}	4^{a}	0^{a}				<1%	0.00	0.07
Ribes rubrum	1^{a}	4^{a}	7^{a}	39^{b}	1-2%^{ab}	1-2%^{ab}	<1%^{a}	10-14%^{b}	0.06	0.11
Scrophularia nodosa	1^{a}	1^{a}	0^{a}	0^{a}	1	1			0.01	0.00
Stachys sylvatica	0^{a}	8^{b}	7^{b}	42^{c}		2-4	1	2-4	0.00	0.04
*Stellaria holostea**	3^{a}	1^{a}	4^{ab}	18^{b}	1-2%	1-2%	<1%	1-2%	0.01	0.02

Table 6.3 Mean cover (%) and mean number of species per plot of species groups and of the canopy at three inventory times in the study parcel (n = 112) and in the adjacent forest (n = 33). Different superscripted letters within a row indicate significantly ($P<0.05$) different values. AFS = ancient forest species; OSS = shade-tolerant species not listed as ancient forest species; LS = light-loving species

	1997	2002	2007	Adjacent
AFS				
species number	1.7 ^{a}	1.6 ^{a}	2.7 ^{b}	3.7 ^{c}
Cover	4.2 ^{a}	5.5 ^{a}	3.4 ^{a}	22.7 ^{b}
OSS				
species number	2.4 ^{a}	3.3 ^{b}	5.1 ^{c}	5.8 ^{c}
Cover	62.4 ^{c}	26.8 ^{a}	48 ^{b}	51.3 ^{b}
LS				
Cover	19.4 ^{a}	52 ^{c}	25.3 ^{b}	44.9 ^{b}
Canopy				
Cover	68.2 ^{c}	15.8 ^{a}	66.9 ^{b}	74.7 ^{c}

Clear-felling resulted into a strong reduction of the canopy cover in 2002 and corresponded to a strong increase of LS cover (Table 6.3). As coppice shoots and natural regeneration emerged, canopy cover returned to a level only slightly below the value recorded before clear-felling. Cover of LS declined between 2002 and 2007, but in 2007 it was still above the level recorded before clear-felling (Table 6.3).

Table 6.4 GLMM structure, with parameter values (Value), standard errors (SE), and significance levels (*P*) of the fixed effects in the GLMM for two response variables: number of herbaceous ancient forest species (AFS), and number of herbaceous shade-tolerant species not listed as ancient forest species (OSS). Y2002 and Y2007 are parameters that adjust the reference model on the year 1997 to the years 2002 and 2007, respectively. σ_{plot} is noise modeled by including sample plot as a grouping variable and ε is the unmodeled, independent noise. **** $P\leq0.0001$; *** $P\leq0.001$; ** $P\leq0.01$; * $P\leq0.05$; NS not significant; / not included. Model characteristics:

$$\log(\text{AFS or OSS}) = p0 + p1 * \text{Distance} + p2 * \text{Y2002} + p3 * \text{Y2007} + p4 * \text{LS}$$
$$+ p5 * \text{Distance} * \text{Y2002} + p6 * \text{Distance} * \text{Y2007} + \sigma_{plot} + \varepsilon$$

with $\text{Y2002} = 1$ if year $= 2002$ and $\text{Y2007} = 1$ if year $= 2007$; otherwise 0

Parameter	AFS			OSS		
	Value	SE	*P*	Value	SE	*P*
p0	0.8806	0.0616	****	1.1769	0.0656	****
p1	-0.0236	0.0033	****	-0.0203	0.0042	****
p2	-0.0055	0.0548	NS	0.4771	0.0791	****
p3	0.4382	0.0425	****	0.5659	0.0723	****
p4	-0.0019	0.0009	*	-0.0026	0.0007	***
p5	/	/	/	-0.0053	0.0053	NS
p6	/	/	/	0.0170	0.0048	***

A strong negative relationship between the distance to the nearest parcel edge and AFS number was observed at all three inventory times and there was an overall weak but negative effect of LS cover (Table 6.4 and Fig 6.2).

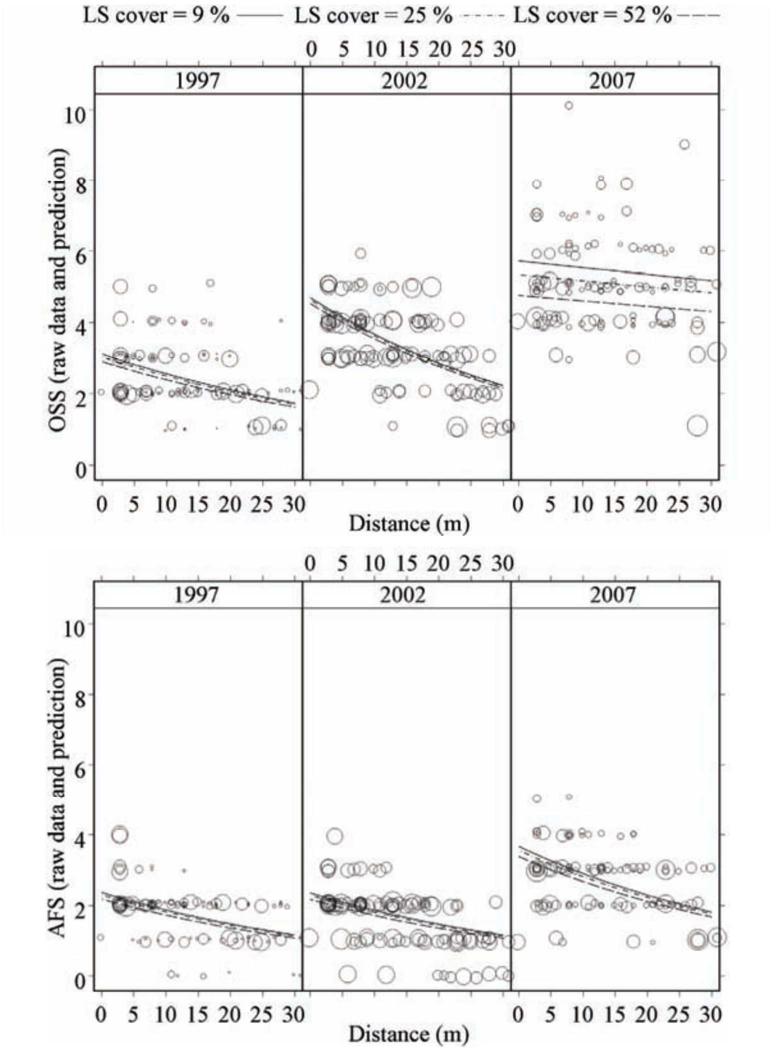


Fig. 6.2 Modeled (lines) and observed (circles) number of herbaceous ancient forest species (AFS) and shade-tolerant herbs not listed as ancient forest species (OSS), as a function of the distance to the nearest parcel edge (Distance) and the cover by light-loving herbs (LS). Overlap of circles is reduced by vertical noise; circle size is a function of the observed LS cover. Predicted values are fixed at median and quartile levels of LS cover.

There were negative relationships between the number of OSS and distance to the nearest parcel edge in 1997 and in 2002, but much less in 2007. In contrast with this finding, there was a persisting negative relationship between LS cover and OSS number (Table 6.4 and Fig. 6.2).

6.4.2 Colonization rates

CR values of 18 shade-tolerant herbs (five AFS) increased after clear-felling, whereas CR values decreased for five shade-tolerant herbs (two AFS) (Table 6.2). For AFS there was no significant difference between the value calculated just before clear-felling (mean value 0.48 %.yr-1) and the value calculated for the whole period (mean value 0.62 %.yr-1), whereas mean CR value of OSS increased from 0.29 %.yr-1 to 0.56 %.yr-1 when the decade after clear-felling was included ($P = 0.004$).

6.4.3 C-S-R signatures

The S-coordinate was more important in the functional strategy of the AFS group (C: 0.27; S: 0.49; R:0.24) than in the strategy of the OSS group (C: 0.38; S: 0.35; R:0.27). The C-coordinate was only marginally represented in the study parcel before clear-felling, but increased strongly afterwards (Fig. 6.3 and Annex 6.1). Ten years after clear-felling the functional signature of the clear-felled area was similar to that of the adjacent forest (Fig. 6.3).

The shift of the functional signature increased with increasing distance to the nearest parcel edge (Fig. 6.4). This is explained by the positive relationship between ΔCR and the magnitude of the C-coordinate in the functional strategy of the studied shade-tolerant herbs (Fig. 6.5): species that increased most after clear-felling are characterized by a predominant competitive strategy. There was no significant relationship between ΔCR and the other coordinates of the functional strategy.

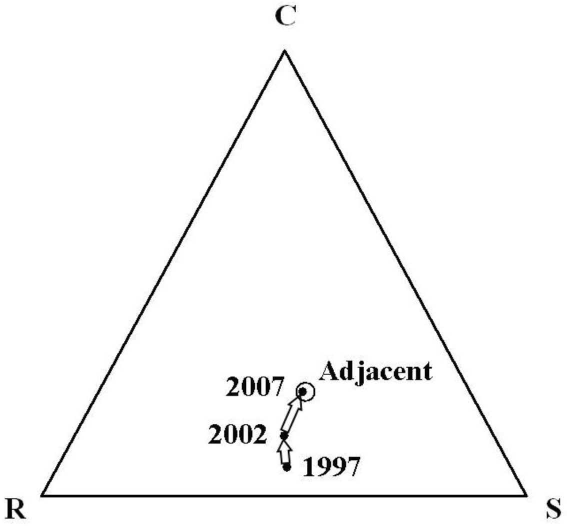


Fig. 6.3 Shift of C-S-R signature calculated for all shade-tolerant herbs in the study area 5 and 10 years following clear-felling in 1997 (black dots), and compared with the adjacent forest (open circle).

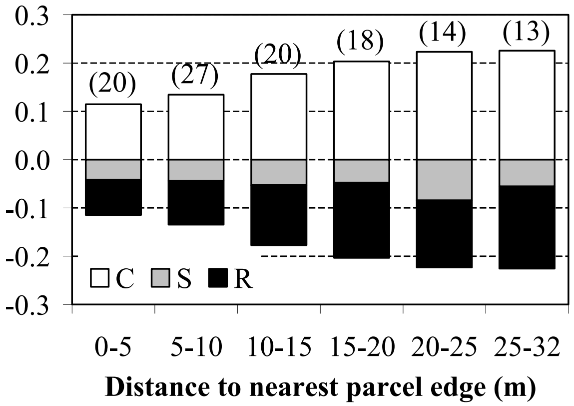


Fig. 6.4 Shift of the C-S-R signature of sample plots between 1997 and 2007 as a function of the distance to the nearest parcel edge. The number of sample plots are in parentheses.

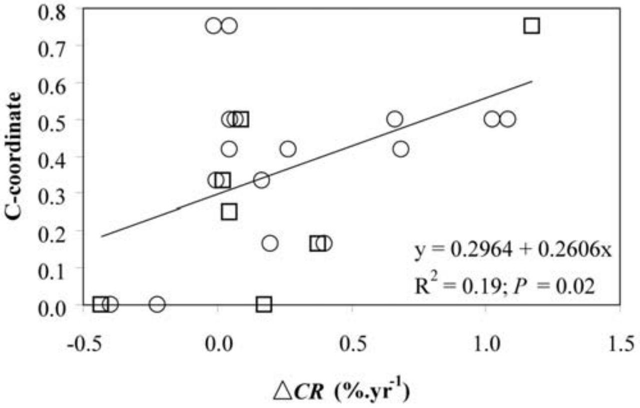


Fig. 6.5 Relationship between the change of the colonization rate after clear-felling (ΔCR) and the C-coordinate of the functional type, for 23 shade-tolerant herbs inventoried in 2007. Squares are ancient forest species, circles represent shade-tolerant herbs not listed as ancient forest species. Overlap of symbols is reduced by a horizontal jitter.

6.5 Discussion

6.5.1 Colonization patterns and rates

The abundance of forest herbs in recent forests mostly follows a negative exponential or negative logarithmic function starting from the colonization source (Matlack 1994b, Brunet & von Oheimb 1998b, Bossuyt *et al.* 1999b). When we aggregated forest herbs into groups based on shade tolerance and fidelity to ancient forests, we found patterns of the same kind, with species number per plot declining from the parcel edges (see Fig. 6.2).

The colonization rate, as we calculated it, is likely to change through time even without management effects. The colonization probability of a patch as a function of time generally is explained by a sigmoid or exponential model, and the former often is more realistic than the latter (Hanski 1994). The sigmoid function implies that the colonization rate of species with initial low frequencies increases, whereas the colonization rate of species with initial high frequencies slows down. Such an intrinsic change interferes with a potential effect of clear-felling, but it is unable to explain following observations: 1) the net species number of shade-tolerant herbs increased by seven within 10 years after clear-felling, whereas only 14 species were present after 45 years of forest cover before clear-felling; 2) several shade-tolerant herbs that established with high frequencies at relatively large distances from the stand edges after clear-felling, were not present before the clear-felling.

6.5.2 Species groups vs. plant strategies

The ancient forest species concept and the concept of a species functional strategy are complementary and both explain observations in our study. The distance to the nearest parcel edge had more impact on the number of herbaceous ancient forest species than on the number of shade-tolerant herbs not listed as ancient forest species, and the latter increased more and faster after clear-felling than the former. Ancient forest plant species are tolerant to stress, low light levels in this case, but generally have poor colonization capacities (Hermy *et al.* 1999). Both could explain the relatively weak response of this species group after clear-felling. Herbs that expanded most after clear-felling had a functional strategy with an important C-coordinate, indicating that they are adapted to a relatively low stress level (Grime *et al.* 1988). These herbs were sensitive to competition by herbs classified as light-loving in our study.

6.5.3 Impact of felling on forest plant species

The impact of felling on forest vegetation can also be explained by the felling size and intensity, by the damage to the understory and by soil disturbances (Brunet *et al.* 1996, Rydgren *et al.* 1998, Buckley *et al.* 2003, Roberts 2004). In this study, the coppice layer was mostly cut before the poplars were removed, except along the parcel borders where some stools of *Acer* and *Alnus* were spared. The impact of felling on the soil was restricted to some tracks but there were no large areas where the soil (an active mull) was compacted. As the impact of felling was quite homogeneous, we do not think that these factors explained the observed revegetation patterns.

Although we have no direct observations, it is very likely that generative reproduction of shade-tolerant forest herbs was stimulated by the altered microclimate after clear-felling. Increased flowering was observed beneath small canopy gaps (Collins & Picket 1988) and after coppicing (Ford & Newbould 1977, Mason & MacDonald 2002, Rackham 2003) in other studies. Hughes & Fahey (1991) observed that seed production of most species was higher in an area where the overstorey was removed than in the surrounding intact forest, and that some unoccupied sites were colonized by these seeds in years following felling.

Not only can flowering and seed production benefit from felling, but the germination of diaspores can be favoured as well. Fellings increase light levels and temperature on the forest floor (Ash & Barkham 1976, Collins & Pickett 1988, Mitchell 1992) and many forest herbs require a certain minimum quantity of light or a minimum temperature to germinate (Grime *et al.* 1988). Three fern species were unable to colonize our study area before clear-felling, but they did rapidly afterwards. Establishment of ferns in recent forests is conditioned by site quality (suitable microhabitats) more than by spore dispersal (Flinn 2007). The successful colonization of two sedges (*Carex sylvatica* and *C. remota*) after clear-felling is another indication that clear-felling altered site conditions. Seeds of both sedges are relatively heavy but can form a persistent seed bank (Kjellsson 1992). The seed bank of both species probably has built up gradually after the conversion from farmland to forest, enabling a successful but postponed colonization after clear-felling.

Light-loving herbs respond strongly to a reduction of the canopy cover, either by clear-felling (Kirby 1990, Bergstedt & Milberg 2001) or by coppicing (Ash & Barkham 1976, Rackham 2003). Light-loving herbs generally have good dispersal capacities or a persistent seed bank (Brown & Oosterhuis 1981, Grime *et al.* 1988). As it can take several years before they become dominant, there is an ecologically significant time-lag between changed site conditions and their expression in the composition and structure of the herbaceous vegetation (Bergstedt & Milberg 2001). We can assume that in this short time of altered site conditions without enhanced competition by light-loving herbs, already established populations of shade-tolerant forest herbs had an opportunity to increase generative reproduction.

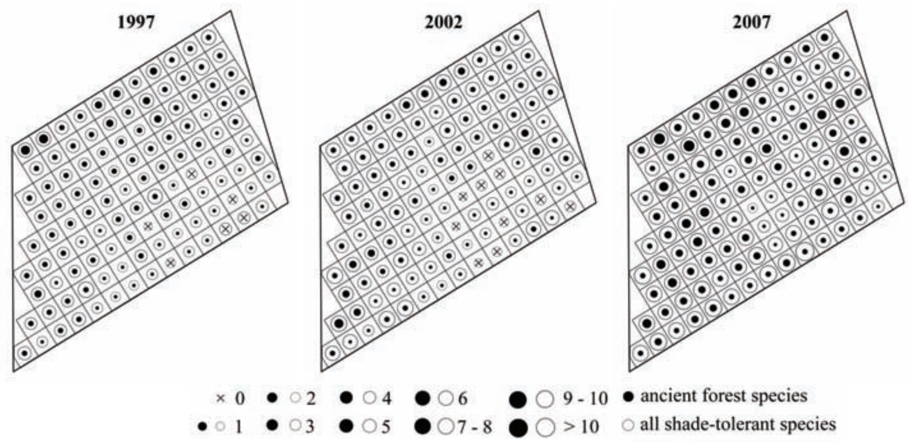
6.6 Conclusions

Coppice management is often considered to have a positive effect on species richness of forest vegetation (Peterken 1981). The impact of clear-felling, on the other hand, often is considered to be negative, although the direct impact of logging is difficult to discern from indirect man-made negative effects (Johnson *et al.* 1993). Canopy can recover faster after coppicing than after clear-felling, as the root system of a coppice is unaffected by felling and coppice shoots already emerge in the first growing season after felling

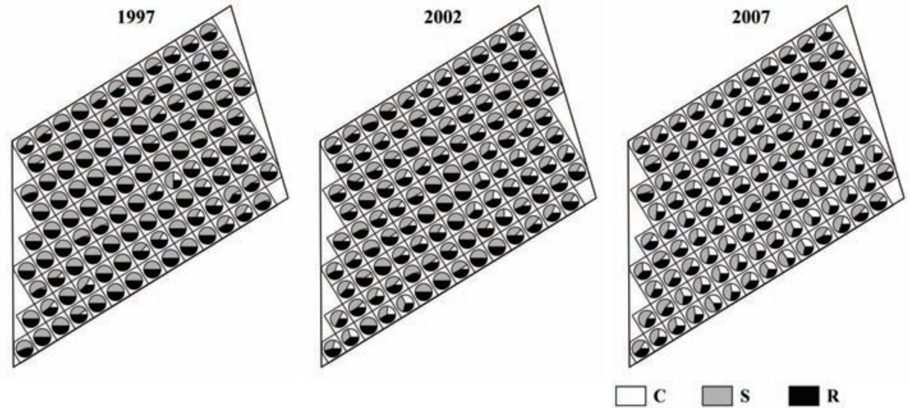
(Mitchell 1992). The successful recovery of the canopy in our study area was mostly (>90%) accounted for by natural regeneration, enabled by the presence of seed trees in the adjacent forest. The recovery rate of the woody vegetation could be a key factor in controlling competitive exclusion of shade-tolerant forest herbs by light-loving species. Tall, light-loving herbs dominated and shade-tolerant herbs were scarce on persistent clearings in a coppice woodland studied by Ash & Barkham (1976). We observed that colonization by shade-tolerant forest herbs lagged behind in plots with a sparse canopy cover, where light-loving herbs were still dominant one decade after clear-felling. In poplar stands that are planted in wide spacings on farmland, the shrub layer is often scarce (Lust *et al.* 2001), and *Urtica dioica* and *Rubus fruticosus* are often dominant (Hermy 1985). Our study suggests that plantation of an understorey managed as a coppice could favour the colonization of shade-tolerant forest herbs into such plantations, on condition that source populations are present in adjacent forest. As this was a case study, the calculated colonization rates and the magnitude of the impact of felling are not generally valid. The results do, however, illustrate that felling can influence the colonization of a post-agricultural forest by herbaceous forest plants and that the canopy recovery rate can have an impact on this process.

Annex 6.1 Number of all shade-tolerant herb species (open circle, size of circle corresponding to number of species as indicated in legend), and ancient forest herb species (closed symbols; see legend), and C-S-R signature of sample plots in the clear-felled area at three inventory times.

Species number



C-S-R signature



Photographs of the area studied in Chapter 6, just before clear-felling (by Leen Martens), five years later (by Arne Verstraeten) and ten years later

7 General discussion & conclusions

7.1 Thesis in short

The impact of spatio-temporal forest cover changes (1775-2000) on forest habitat was first quantified by means of GIS analyses (Chapters 2 and 3). Forest inventory grid points provided representative, high quality data on the floristic composition and on land use history of forest habitat, complementary with the spatial explicit data (GIS maps) generated in Chapters 2 and 3. This was demonstrated in Chapter 4, where both were used to explain AFS diversity in present-day forests and forecast the recovery potential of the open landscape. From this Chapter on, the research focused on mesophilous forest vegetation, where AFS diversity can be much higher than in other forest types. Chapters 2-4 covered most of Flanders and generated results for use at landscape scale, e.g. landscape planning and regional surveys. By contrast, Chapters 5 and 6 studied smaller management units, using additional explanatory data not available for the whole region. In this final Chapter 7, the data on forest inventory grid points were used to quantify some of the findings of Chapter 5 that only applied to a single forest, for the whole of Flanders. The forest studied in Chapter 5 is composed of a chronosequence of RF stands and in Chapter 6, a RF stand at an intermediate stage of vegetation recovery was monitored for one decade (Chapter 6). This monitoring revealed that, even for a single forest stand, the recovery rate of RF vegetation is not constant and can be influenced by management.

7.2 Outlines of the discussion and conclusions

In this final Chapter 7, the results of the Chapters 2-6 are used to discuss the impact of spatio-temporal forest cover changes in Flanders between 1775 and 2000 on AFS. As a result, AFS suffered from habitat loss, habitat fragmentation, and modified habitat quality. First we discuss how these three aspects explain the AFS diversity in AF, followed by a similar discussion for the recovery of AFS diversity in RF. This subdivision is relevant as there is a general consensus that AF is essential for the recovery of vegetation diversity in RF (e.g. Peterken & Game 1984, Honnay *et al.* 1999a, Jacquemyn *et al.* 2003a, De Frenne *et al.* 2011, Jamoneau *et al.* 2012). The third section summarizes the main conclusions and formulates priorities for landscape planning and for nature and forest management. The open questions, that are most relevant to answer, are summarized in the final section.

7.3 Impact of spatio-temporal forest cover changes (1775-2000) on AF

7.3.1 Mesophilous AF: hotspots of AFS diversity

PNV is the most mature vegetation that can be expected at a site and that can serve as a reference, e.g. to determine the level of recovery or degradation of other vegetation (Farris *et al.* 2010, Loidi *et al.* 2010). The identification of PNV types of Flanders was mostly based on the proportion of AFS and AF in vegetation samples (Chapter 2). We did not apply an established classification of forest vegetation, but constructed a functional classification to obtain an optimal resolution of both the classification and the map (Chapter 2). The PNV map displays the natural habitat heterogeneity in Flanders, and PNV types represent forest habitat types that can occur on specific morphogenetic soil types (Fig. 2.4).

Three PNV types were identified as mesophilous forest vegetation (Table 4.1): 1) the *Adoxa moschatellina – Primula elatior* community on Gleysols and Fluvisols (IUSS Working Group WRB 2006; Dondeyne *et al.* 2012), i.e. moderately wet mineral soil without profile development, mostly found along watercourses; 2) the *Chrysosplenium – Equisetum telmateia* community of springwoods; 3) the *Luzula pilosa – Oxalis acetosella* community on Albeluvisols and Luvisols (IUSS Working Group WRB 2006; Dondeyne *et al.* 2012), which are mostly relatively dry loess deposits affected by clay illuviation in the south of Flanders. The area of the *Chrysosplenium – Equisetum telmateia* community was not used for further analyses, since the specific hydrological conditions of springwoods were not accurately enough predicted by means of GIS data. The three PNV types of mesophilous forest are grouped in the *Fagetalia* by most syntaxonomical classifications (see, e.g. Ellenberg *et al.* 1992). AFS richness in the mesophilous PNV types is higher than in the three PNV types not qualified as mesophilous forest (Annex 2.2 and Table 4.1). This is in agreement with an analysis of 22 European AFS lists (Hermy *et al.* 1999). In Flanders, 21 AFS are specialists of mesophilous forest, meaning that they are rarely found in other forest vegetation (Table 4.1). By contrast, only one

AFS, *Vaccinium myrtillus*, has a preference for a PNV not qualified as mesophilous forest vegetation (Annex 2.2 and Table 4.1).

Chapters 2-3 studied forest vegetation of all sites, but indicated that mesophilous forest vegetation has the highest diversity of slow colonizers (AFS), whereas habitat loss and fragmentation, as well as habitat degradation, were higher on mesophilous sites than elsewhere (discussed further). These findings indicate that conservation and restoration of mesophilous forest vegetation is a priority. For this reason Chapters 4-6 focused on patterns of vegetation recovery in this forest type.

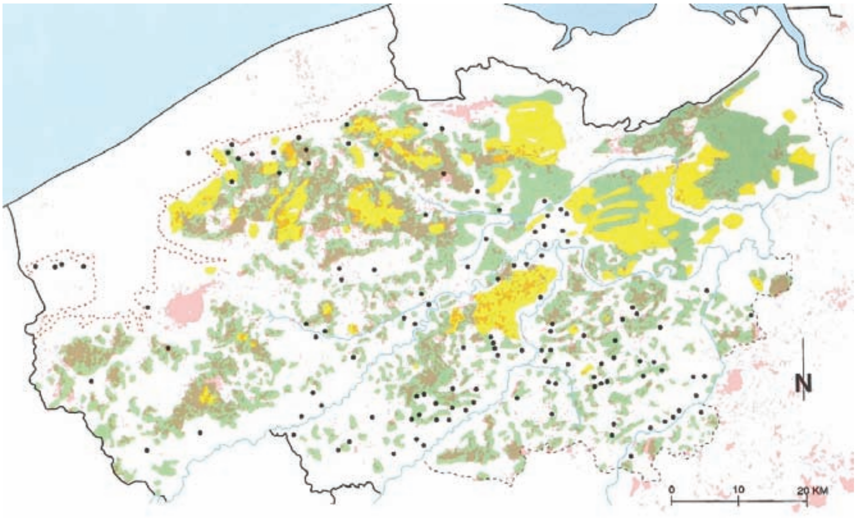
7.3.2 Habitat loss

It is assumed that the impact on forest vegetation of land use changes since 1775 was higher than before, as a result of the intensification of open land use (Baeten 2010 and Box 8.2). Moreover, the rate of forest cover changes exceeded the colonization capacities of many forest plant species (see also Matlack 2005). The causes of these vast land use changes are political, socio-economic, and technological changes in western and central Europe that started at the end of the 18th century (Tack *et al.* 1993, Wulf *et al.* 2010). In the aftermath of the French revolution (1789), many forests owned by monasteries were sold and cleared (Tack *et al.* 1993, Verheyen *et al.* 1999). At that time, coal increasingly replaced wood and charcoal (Gale 2003) and consequently the importance of forests for the supply of fuel, declined. A succession of failing potato, wheat and rye harvests caused a famine between 1845 and 1850 (Vanhaute *et al.* 2006), further stimulating the conversion of forest to arable land (Tack *et al.* 1993). The maps by Vandermaelen (approximately drawn in 1850) show that many forests were cleared between 1775 and 1850, in particular on mesophilous sites. Already before 1850, forest area on sandy soils increased and partially compensated for the loss of forest area on mesophilous sites. As a result, the total forest area in Flanders only declined slightly, from 10.8% to 9.7%, between 1775 and 1850 (Table 3.4). Heathland and other low-productive common grounds gradually lost significance for agriculture in the 19th century. A 1847 law forced the conversion of heathland to agricultural land and pine forest, particularly in the northeast of Flanders where forest cover increased from 8% to 26% between 1850 and 1931 (De Keersmaeker *et al.* 2005). Forests in the southwest of Flanders were destroyed in World War I and many were converted to agricultural land (Tack *et al.* 1993).

Box 7.1 On the impact of forest clearing before 1775

The maps by de Ferraris approximately drawn in 1775 are the first detailed maps that cover most of Flanders and for this reason they are used to identify AF. This does not implicate that ancient forests were also continuously present before that time. Three documented examples of the contrary are: 1) Schriekbos in Zoersel was converted from heathland to pine forest between 1725 and 1729 (Adriaenssen & Verheyen 2013); 2) Harras is a part of the Sonian forest near Brussels that was used as a stud farm between 1613 and 1678 (Baeté *et al.* 2002); 3) Parts of Meerdaal forest were arable fields in the Roman era (Vanwalleghem *et al.* 2004).

Verhulst (1995) published an impression of the area covered by heathland (yellow) and forest (green) in the western part of Flanders in the 12th-13th century (see below). This map is based on the history of settlements (black dots), but also on the maps by de Ferraris drawn much later. Red patches in overlay are forests on the map by de Ferraris (see also Fig. 3.1). This overlay suggests that some areas were completely deforested between the 12th-13th century and 1775 and conversely also that some forests in 1775 were open land in medieval times. Careful interpretation of the overlay is necessary, as the map by Verhulst (1995) is based on expert judgement combined with the maps by de Ferraris, by consequence, there is a risk of circular reasoning.



It is assumed that the use as open land had less impact on the recovery of forest vegetation before 1775 than after that time (Baeten 2010). The vast area of heathland and other common grounds (colored yellow on the map above) was mostly used for grazing and had a variable tree cover. As a consequence common grounds were to some extent also suitable habitat for AFS species (Tack *et al.* 1993). Another argument for this assumption, is that most resources and technology, necessary to intensify agriculture, only became available after 1775 (see Wulf *et al.* 2010). There are, however, regional differences as agriculture intensified earlier in the west, where most common grounds had disappeared at the end of the 18th century, than in the northeast, where the reclamation of common grounds continued in the 20th century (Verhulst 1995 and Fig. 1.2).

In the 20th century, grassland on wet soils was abandoned and converted to forest, a process also observed in the Czech Republic by Skalos *et al.* (2012). The urbanized area in Flanders increased at the end of 20th century to 27% of the total area in 2011, at the expense of agricultural land an forest (MIRA 2012).

It is remarkable that, as a result of all these changes, almost no net loss of the area covered by forest compared to 1775 was observed in the year 2000. By contrast, only 16% of the forest cover in 2000 was never deforested in the past 225 years, as far as the time resolution of the land use reconstruction allowed (Chapter 3). Spatio-temporal forest cover changes since the 18th century were larger in Flanders than other regions in Europe (Spencer & Kirby 1992, Wulf & Gross 2004, Skalos *et al.* 2012).

The PNV map that displays the natural habitat heterogeneity, served to quantify the habitat-specific impact of spatio-temporal forest cover changes, as demonstrated in Chapter 1 with the hypothetical dynamic landscape (Fig. 1.1). For this purpose, an overlay was created of the potential area of five habitat types (PNV types) with the forest cover at four times between 1775 and 2000 (Chapter 3). This analysis indicated that forest cover on sites potentially occupied by the *Luzula pilosa – Oxalis acetosella* community decreased with 45% since 1775 (Table 3.4). More than 60% of the remaining forest on sites that are suitable for this community is AF (Table 3.7). By contrast, forest cover on sites that are suitable for the *Adoxa moschatellina – Primula elatior* community did not change much since 1775 (Table 3.4). However, only 10% of the forest in 2000 located at these sites is AF (Table 3.7).

The number of forest inventory samples that served for the identification of both PNV types, can be used to quantify the present-day area of mesophilous forest vegetation with a high AFS diversity. This calculation indicated that the *Luzula pilosa – Oxalis acetosella* and the *Adoxa moschatellina – Primula elatior* communities only covered 7700 ha and 6200 ha, i.e. 5.3% and 4.2% of the total forest cover in 2000, respectively. The proportion of AF in both communities equaled 74% and 52%, respectively (Table 2.3). As a high AFS diversity is mostly found on mesophilous sites where forest continuity was high, we can conclude that AFS suffered from massive habitat loss since 1775.

7.3.3 Habitat fragmentation

Whereas the total forest cover did not change much between 1775 and 2000, the level of fragmentation increased (Chapter 3). The total number of forest patches in Flanders increased from approximately 12.000 to 19.000. Consequently, the patch size declined and the PAR increased (Table 3.5 and Fig. 3.2). Based on the nearest neighborhood connectivity measures included in the empirical models of Chapter 4, one could conclude that fragmentation had an adverse effect on α diversity of AFS, i.e. the mean number of AFS at habitat level counted in forest inventory plots (Figs. 4.3 and 4.4). AFS diversity increased towards the interior of forest patches in 1775 and in 1904-1931, also beyond the range affected by positional errors of both maps. The models also indicated that the shape of forest patches in 2000 was important: convex (protruding) edges of forest patches had a slightly reduced AFS diversity as compared to concave forest edges. The nearest distance to the edge of forest patches explained AFS diversity better than the shape of the forest edge in 2000 (Figs. 4.3 and 4.4).

It is not clear if the observed relationships between the α diversity and connectivity measures are explained by the increased extinction that fragmentation can cause, as could be expected based e.g. on the island equilibrium theory (MacArthur & Wilson 1967) and the metapopulation concept (Levins 1969, Hanski 1999). AFS diversity was explained by the distances to historical forest edges (1775 and 1904-1931), not the forest edge in 2000. If the size of the historical forest patch is more explanatory than the size of the forest patch in 2000, this implicates that there is an extinction debt, as also observed by Vellend *et al.* (2006).

It is also possible that fragmentation exacerbated habitat degradation: protruding (convex) forest edges can be exposed from more than one side to external pressures than concave forest edges. Forest edges can suffer from eutrophication by misplaced fertilizer, biotic invasions (Honnay *et al.* 2002a) and increased atmospheric depositions (De Schrijver *et al.* 2007, Wuyts *et al.* 2008). Another explanation could be that undetected historical forest clearings, mostly located at the forest edges, caused long-distance gradients of species composition from the forest edge to the interior (Pellissier *et al.* 2013). When a model was constructed that included the most detailed information on historical land use derived from maps, available for the whole of Flanders, this resulted indeed into a weaker effect of the connectivity measures. But also when doing so, connectivity measures were still significant and included into the model on AFS diversity.

Based on the research in Chapter 4, it can be concluded that fragmentation has an adverse effect on AFS diversity, also measured at the level of sample plots (α diversity). It is, however, not clear if this effect is caused by increased extinction, and/or indirectly by increased habitat degradation and/or undetected temporal habitat disruption near forest edges.

7.3.4 Reduced habitat quality

The impact of habitat degradation on mature forest vegetation, mostly found in AF, was not the main focus of this work. However, as AF are biodiversity hotspots and the recovery of RF mostly depends on the remaining AF, it is important to discuss results that give an indication on the extent of habitat degradation. Moreover, we can assume that mesophilous forest vegetation is more sensitive to habitat degradation than many other forest vegetation. As a consequence of the high diversity of AFS, recovery of mesophilous forest vegetation is a very slow process when typical AFS have declined or even have disappeared. By contrast, Alder forests (the *Carex elongata – Scutellaria galericulata* community in Chapter 2) that are sensitive to habitat degradation caused by desiccation (Czerepko 2008), can develop and disappear in a cyclic process. Recovery of Alder forest was observed within 70 years (Pokorny *et al.* 2000, Barthelmes *et al.* 2010). The dynamic site conditions could explain the low frequency of AFS in this community (Hermy *et al.* 1999).

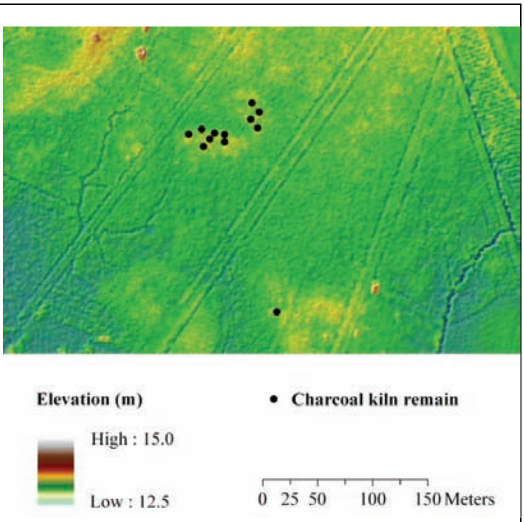
Mesophilous forest vegetation is particularly threatened by acidification, often in combination with eutrophication or desiccation. Atmospheric depositions in combination with unfavorable forest management can threaten the *Luzula pilosa – Oxalis acetosella* community, whereas desiccation is an important threat for the *Adoxa moschatellina – Primula elatior* and the *Chrysosplenium – Equisetum telmateia* communities. Acidification can be caused by atmospheric depositions of N and S (Bredemeier 1989, de Vries *et al.* 1991, Diekmann *et al.* 1999). Acidification can also be influenced by forest management, in particular tree species composition (Neirynck *et al.* 2000, De Schrijver *et al.* 2004, Van Oijen *et al.* 2005, Van Calster *et al.* 2007, Hermy *et al.* 2009, Verstraeten *et* *al.* 2013). Desiccation that results into a lowered groundwater level, can also cause acidification (Frambach & Meulman 1988, van Tol *et al.* 1998, Czerepko 2008).

The loess belt in the south of Flanders was qualified as suitable for the *Luzula pilosa – Oxalis acetosella* community that includes many vernal AFS, e.g. *Anemone nemorosa* (Figure 2.4). However, the error matrix (Table 2.4) indicated that approximately 50% of the retained mature forest vegetation samples of this area are classified to the *Molinia caerulea – Vaccinium myrtillus* and *Athyrium filix-femina – Pteridium aquilinum* communities, both without vernal AFS. This implicates that approximately 50% of the area located on silt loam soils cannot support the complete recovery of mesophilous forest vegetation in RF. Soil pH of most silt loam soils is low and these soils are very sensitive to further acidification, either by natural or anthropogenic causes (Brahy *et al.* 2000). Acidification can result into a decline of vernal AFS (Falkengren-Grerup & Tyler 1993, Falkengren-Grerup *et al.* 1995, Thomaes *et al.* 2011). A case study in an AF on silt loam soil in Flanders confirmed that soil acidification below a pH (H_2O) value of 4.2 resulted into a loss of sensitive vernal AFS, e.g. *Primula elatior* and *Paris quadrifolia* (Baeten *et al.* 2009a). Elsewhere in Europe, a simultaneous acidification and eutrophication with N also resulted into vegetation shifts in mesophilous forest (Falkengren-Grerup 1986, Thimonier *et al.* 1994, Verheyen *et al.* 2012). A shift of forest management can further accelerate this process (Van Calster *et al.* 2007, Baeten *et al.* 2009a).

The *Adoxa moschatellina – Primula elatior* and *Chrysosplenium – Equisetum telmateia* communities depend on suitable hydrological conditions and are therefore sensitive to desiccation. Desiccation could be an explanation for the decline of vernal AFS in alluvial AF in the west of Flanders, within 30 years (Lameire *et al.* 2000, Baeten 2010a). A lowered groundwater table can result into acidification, and an increase of acid-tolerant species, e.g. *Pteridium aquilinum* (Frambach & Meulman 1988, see also Box 7.2).

Contrary to the *Luzula pilosa – Oxalis acetosella* community, no bias was assessed between classification and map for the *Adoxa moschatellina – Primula elatior* and *Chrysosplenium – Equisetum telmateia* communities (Table 2.4). Sites that are suitable for both communities, were not occupied more by vegetation samples classified to PNV communities without vernal species than the other way round.

Box 7.2 Are charcoal kiln remains in Zoersel forest testimonies of an extinct alluvial forest?



The multidisciplinary research of charcoal kiln remains by Deforce *et al.* (2013) in the ancient forest of Zoersel indicated that mesophilous forest vegetation could have declined by desiccation. A cluster of kiln remains in the east of this forest is surrounded by alluvial soil, suitable for the *Adoxa moschatellina* – *Primula elatior* community (Chapter 2). By contrast, present-day ancient forest vegetation is a *Molinia caerulea* – *Vaccinium myrtillus* community (Chapter 2). The kiln remains originate from 1297-1426 AD and contain fragments of woody species, not found in the present-day forest surrounding the kiln remains. Fragments of *Alnus sp.* were most frequently found and the kilns also contained tree and shrub species that are sensitive for acidification: *Viburnum sp.*, *Euonymus europaeus*, *Carpinus betulus*, *Corylus avellana*, and *Populus sp.* A detailed digital elevation model revealed natural water courses, that are connected to the anthropogenic drainage system along the forest roads and in the forest stands. The morphogenetic soil type, the species composition of the kiln remains, and the microtopography are indications that this part of the forest could have been affected by desiccation a long time ago, which resulted into a shift in forest vegetation.

Increased availability of P, e.g. by flooding with contaminated water or by mineralization of organic matter, can result into an increase of *Urtica dioica* and other nutrient-demanding competitive species in AF. Approximately 3% of all forest inventory samples that are AF (n = 6), were classified to the *Urtica dioica* – *Galium aparine* community, where competitive species are dominant and AFS are scarce. The applied PNV classification can be used to detect this kind of extreme vegetation degradation, but it is probably too rough to detect more subtle changes as observed by Baeten *et al.* (2010a).

7.4 Recovery of a high AFS diversity in post-agricultural forest

7.4.1 Can RF become new habitat for AFS?

Whereas the loss of AF, particularly mesophilous AF, directly resulted in habitat loss for AFS, RF established on open land can become new habitat for AFS. Forests that were established after 1775, accounted for 84% of the total forest cover in Flanders in 2000. RF can be colonized by AFS if habitat connectivity and habitat quality are appropriate. The forest stand, monitored in Chapter 6, is an example of a successful recovery as it was colonized by seven AFS, 55 years after conversion of agricultural land to forest.

However, an analysis of the forest inventory plots (n = 1296) indicated that only 7% of the RF (n = 75) in Flanders was classified to both PNV types that are mesophilous forest with a high AFS diversity. This low AFS diversity could be caused by the limited time that was available for recovery, but also by the low connectivity and habitat suitability of RF patches. Habitat connectivity and habitat suitability of the RF in Flanders will be discussed in the next two sections. The relative impact on AFS of low habitat connectivity (described in section 7.4.2) that can result into dispersal limitation, versus low habitat quality (described in section 7.4.3) that can result into recruitment limitation, is species-specific (see Verheyen & Hermy 2001b).

7.4.2 Habitat connectivity

As explained in the introduction (Chapter 1) and summarized by Verheyen *et al.* (2003), colonization capacities of AFS are low as AFS mostly depend on short-distance dispersal modes (see e.g. Matlack 1994b, Hermy *et al.* 1999) and most seeds of AFS do not survive for a long time (Brown & Oosterhuis 1981, Bossuyt & Hermy 2001). The monitoring of vegetation patterns in a post-agricultural forest stand, adjacent to AF, confirmed these outlines (Chapter 6).

It was assumed that RF patches at a distance of more than 100 m from AF patches with source populations are seldom colonized by AFS (Jacquemyn *et al.* 2003b). Other studies indicated that RF patches in physical contact with AF patches, recovered faster than isolated RF patches (Peterken & Game 1984, Honnay *et al.* 1999a). The forest cover in Flanders was low and highly fragmented throughout the past 225 years (see Chapter 3), it is therefore assumed that the recovery potential of RF in physical contact with AF, was much higher than the potential of RF separated from AF by open land.

The GIS analysis on spatio-temporal forest cover changes between 1775 and 2000 indicated that only 14% of the RF in 2000 was embedded into a forest patch that also contained AF (Chapter 3). The level of connectivity was habitat specific: it amounted to approximately 22% of the RF on sites suitable for the *Luzula pilosa – Oxalis acetosella* community, versus only 10% of the RF on sites suitable for the *Adoxa moschatellina – Primula elatior* and *Chrysosplenium – Equisetum telmateia* communities (Table 3.8). We can therefore assume that as a result of this low connectivity, most RF in Flanders has a low recovery potential.

7.4.3 Habitat quality

7.4.3.1 Natural habitat suitability

The spatio-temporal forest cover changes summarized in section 7.1.2 resulted into massive loss of mesophilous forest since 1775, by temporarily or permanent conversion to agricultural land. As a result 84% of the forest cover in 2000 was RF and most of it is not in physical contact with AF (sections 7.2.1 and 7.2.2). Moreover, approximately 80% of the RF is located on waterlogged soils and sandy soils that are unsuitable for mesophilous forest vegetation with a high AFS diversity (Table 3.7). We can thus conclude that the potential to restore a high AFS diversity in RF is low, as connectivity is low and the site conditions in newly created forest habitats are mostly unsuitable.

7.4.3.2 Habitat degradation: focus on P eutrophication

Soil chemistry and light conditions can influence performance of herbaceous species in post-agricultural forest (Dzwonko & Loster 1997, Baeten *et al.* 2010b, Thomaes *et al.* 2012). As these data were not available for the whole region of Flanders, they were collected in a mesophilous forest (Muizenbos) that is composed of a chronosequence of post-agricultural forest stands adjacent to AF (Chapter 5, see Fig 5.2). Based on the summary above it can be concluded that a study area of this kind is rare in Flanders, as most RF is isolated from AF and not located on a mesophilous site.

This case study indicated that soil chemistry is modified and homogenized by the use as agricultural land, as also reported by many other studies (see compilation in Baeten 2010). Soil pH was not correlated with forest age, but less variable in post-agricultural forest younger than 80 years, than in older forests, where both high and low values were measured (Table 5.2). There was a strong correlation between forest age and the total C, total N, total P and plant-available P contents (Table 5.1). This could either indicate that they gradually changed after the conversion of farmland to forest, or that the impact of farmland use has changed in time.

Chapter 5 indicated that the total N and C contents are positively correlated with the age of post-agricultural forest, which is explained by the litter production of trees that results into a gradual increase of the organic matter content in the topsoil of farmland converted to forest (Muys *et al.* 1992, Catt 1994, Verheyen *et al.* 1999). We assumed that N availability did not explain vegetation patterns in Muizenbos, as N deposition is high in Flanders and nitrification is optimal in mesophilous soils of Muizenbos (see Chapter 5). Contrary to the positively correlated total N and total C contents of the soil, the total and plant-available P contents were negatively correlated with the age of the RF (Figs 5.3 and 5.4). The total P content is a legacy of the use as farmland. Fertilization results into an accumulation of P (Guggenberger *et al.* 1996) and P is tightly retained in forest ecosystems (Wood *et al.* 1984, Binkley 1986, Zhang & Mitchell 1995). Forest stands in Muizenbos that were used as farmland in the 19th century, had a similar total P content as AF stands (Fig. 5.3), which indicates that they have received little or even no fertilization.

It was assumed that P availability was highly explanatory for the vegetation patterns in Muizenbos (Fig 5.6). P fertilization can have a direct negative effect, e.g. on the germination of *Dactylorhiza fuchsii* (McKendrick 1996), an orchid species occasionally found in Muizenbos on unfertilized calcareous soil. The indirect effect of eutrophication with P is that it modifies the competition between species and consequently that AFS can suffer from competitive exclusion. Fast-colonizing forest species with a high plasticity, e.g. *Geum urbanum*, can be promoted more by increased P availability than AFS that have a lower plasticity, e.g. *Primula elatior*. As a result, the difference in colonization capacity can be promoted (Baeten *et al.* 2009b). Research by Pigott (1971) demonstrated that *Urtica dioica* is promoted by a high P availability, and therefore an excellent indicator species. Colonization of RF can be hampered by competitive exclusion when competitives are abundant, e.g. *Urtica dioica*, (Verheyen & Hermy 2004). This was confirmed by the monitoring of a post-agricultural forest in an intermediate stage of recovery (Chapter 6), where forest plant species diversity increased faster in areas with a low cover of light-demanding competitors (Fig. 6.2).

Table 7.1 Contingency table representing the distribution of forest inventory plots (n = 1296) with the *Urtica dioica – Galium aparine* community and other vegetation, on mesophilous sites and on other sites (*P*<0.001 based on a Chi-squared test).

Vegetation	Mesophilous sites		Other sites	
Urtica dioica –Galium aparine	84	(35%)	95	(9%)
Other forest vegetation	153	(65%)	964	(91%)
Total	237	(100%)	1059	(100%)

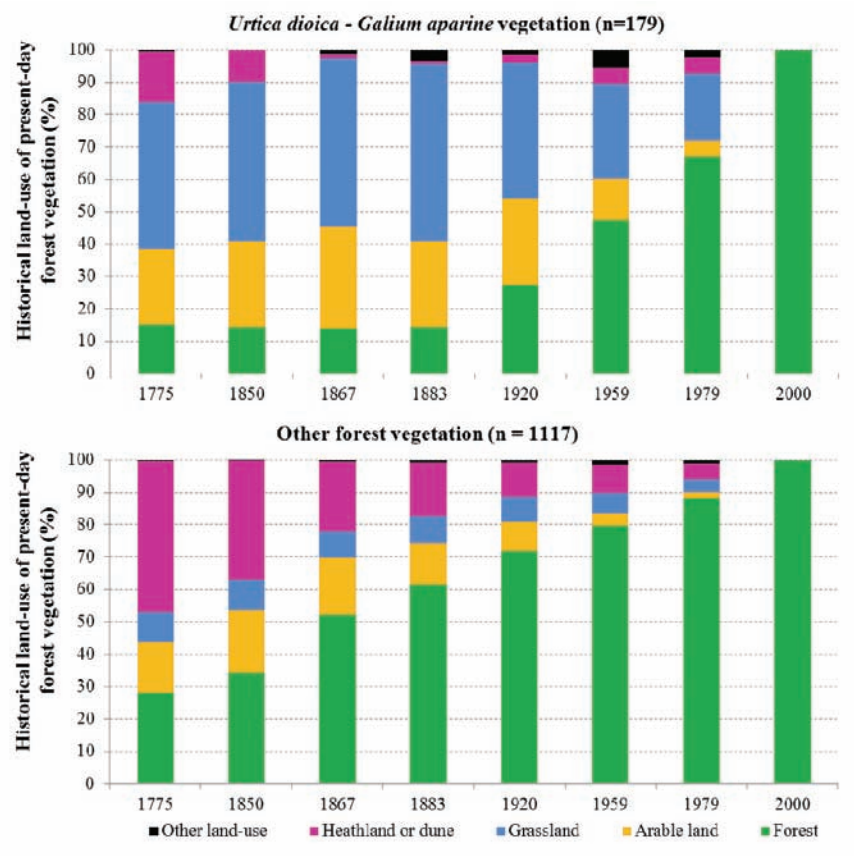


Fig. 7.1 Development of the land use between 1775 and 2000 of forest inventory plots with an *Urtica dioica – Galium aparine* vegetation (see Chapter 2) (n=179), versus other forest vegetation (n=1117).

The vegetation patterns studied in Muizenbos to some extent can be up scaled to Flanders, by comparison with vegetation of the systematically sampled forest inventory plots. The *Urtica dioica – Galium aparine* vegetation, not retained as a PNV as it did not contain many AFS and mostly was located in RF (Table 2.3), is present in RF stands of Muizenbos younger than 30 years, where P availability and light levels were high. This forest vegetation type accounts for one third of the forest vegetation on mesophilous sites, whereas it is scarce in forest on other sites (Table 7.1). The *Urtica dioica – Galium aparine* vegetation is typically found in forest that was until a few decades ago used as grassland or arable field (Fig. 7.1). The long use as grassland or arable field, until the mid-20th century or later when agriculture had intensified, probably has resulted into an accumulation of P as also observed in Muizenbos (Figs. 5.3 and 5.4).

7.4.3.3 Light conditions

Many forest plant species and AFS in particular, are tolerant to stress, i.e. the low light levels that are typical of forests (Hermy *et al.* 1999). In RF, light-demanding competitors are often dominant (see vegetation types with *Urtica dioica*, *Galium aparine*, and *Rubus fruticosus* in Table 2.3). This observation is explained by the fact that in RF planted with tree species that have a low shade-casting ability, e.g. poplar plantations, an understorey initially is poorly developed (Lust *et al.* 2001, Boothroyd-Roberts *et al.* 2013). In most RF stands in Muizenbos with a dense planted understory, cover of light-demanding species was lower and the number of shade-tolerant forest species (AFS and fast colonizers) was higher than in RF stands of a similar age without a dense understory (Fig. 5.5). It was hypothesized that felling would have an adverse effect on the colonization of forest plants into a post-agricultural forest with a dense planted understory, as light levels would increase and light-demanding competitors would be promoted (Chapter 6). However, the monitoring of species diversity for one decade after clear-felling, indicated that increased light levels stimulated colonization by forest plant species (AFS and other shade-tolerant species). The results also indicated that it is important for AFS that the woody vegetation recovers fast. In areas where canopy had not closed within a decade after felling, colonization by forest plant species lagged behind as a result of the persistent dominance of light-demanding competitors. A succession of dark phases and short disturbances with increased light levels, resembles a coppice or coppice-with-standards management, that can promote AFS diversity in long-established forests (Ash & Barkham 1976).

7.5 Priorities and recommendations for conservation and restoration of AFS diversity

The high rate of spatio-temporal forest cover changes in Flanders in the past 225 years, resulted in habitat loss, habitat fragmentation, and reduced habitat quality for AFS. As a result, forest vegetation with a high diversity of AFS, mostly AF on mesophilous sites, is rare and in 2000 only accounted for approximately 10% of the total forest area of Flanders. Conservation of hotspots of AFS diversity, mostly located in AF, should be a priority, not only for biodiversity conservation in se but also to facilitate restoration of AFS diversity in RF.

Most of the forest area in Flanders is RF located on sites that are unsuitable for a high AFS diversity, e.g. acid sandy soils and very wet soils. The recovery of forest vegetation in RF on suitable mesophilous sites is hampered by isolation from forests that contain source populations of AFS and by unfavorable environmental conditions. From the perspective of AFS diversity, forest restoration should focus on the selection of suitable sites adjacent to AF. The highest potential gain is obtained by conversion of suitable open land to forest that connects isolated RF with AF. This defragmentation and area increase can also result into a better buffer against external pressures that can reduce habitat quality. The empirical landscape model on AFS diversity (Chapter 4) can be used for the operationalization of conservation and restoration strategies. It can serve for landscape studies, to select forests with a high AFS diversity and open land that has a high restoration potential.

This map should be complemented with additional data, e.g. on soil chemistry, land use history, and forest management, that are not available as digital maps for the whole of Flanders. The case studies in this work included such additional information and indicated that soil P content and light intensity on the forest floor also determine the recovery rate of vegetation in RF adjacent to forest containing source populations of AFS. Most RF on mesophilous soils was used as fertilized grassland or arable field before conversion to forest and for this reason it is still eutrophicated with P. This eutrophication can promote competitive species (particularly *Urtica dioica*) that hamper colonization by AFS. These forests, however, can be managed in a way that competition by light-demanding species is reduced and shade-tolerant AFS are promoted. The monitoring of AFS colonizing an eutrophicated post-agricultural forest stand indicated that short disturbances, temporarily reducing the canopy cover, can stimulate AFS on condition that light-demanding competitors (*Urtica dioica*, *Rubus fruticosus*) have not enough time to dominate.

7.6 Suggestions for further research

Many aspects on forest plant species and forest vegetation have been studied in the past decades, yet several factors that determine AFS diversity in AF and RF are not completely understood. The most relevant ones for conservation and restoration of forest vegetation are listed hereafter.

The long-term forest vegetation succession on soils that are eutrophicated with P is still unclear. The total P content in agricultural land is nowadays much higher than in RF that was used as grassland or arable field in the 19th and early 20th century. Whereas P is tightly retained in most forest ecosystems (Wood *et al.* 1984), the availability can change in time (De Schrijver *et al.* 2012). This process is determined by physico-chemical soil properties (e.g. the calcium and iron concentration), and also by tree species that are drivers of soil development in post-agricultural forest (e.g. see Magid 1993). Several strategies could be explored to reduce eutrophication by P and promote a diverse forest vegetation: 1) reduce the total soil P content by mining 2) apply a management that can reduce the availability of P for plant species. The first strategy is mostly applied before conversion to forest, but phytoextraction after plantation of trees could also be explored. The second strategy could be based on the plantation of tree species that reduce P-availability relatively fast, or could focus on the soil conditions that reduce P availability regardless of the presence of trees (e.g. by creating specific hydrological conditions).

Many explanatory variables studied in Chapters 5 and 6, are not available for the whole of Flanders. If accurate GIS layers would be developed on the P eutrophication level, hydrology, the soil pH, land use history, or the forest structure, the predictive power of an empirical model on AFS diversity (Chapter 4) could be further improved. AFS could be further subdivided based on species traits, to deal with the high variability of the colonization rate that is observed within this species group.

The AGIV green map (‘hoog groen kaart’) is a land cover map based on remote sensing that also represents linear landscape elements with trees. It could be used to quantify the connectivity between forest patches and explain the forest plant species diversity at landscape level, using systematically sampled Florabank data (see Van Landuyt *et al.* 2006). These Florabank data could also be highly suitable to study a potential extinction deficit or immigration credit, by comparing the present-day AFS richness (e.g. sampled in 4 km x 4 km or 1 km x 1 km grid cells) with present-day and historical landscape structure.

It is unlikely that all relevant data will soon become available as GIS layers with a resolution that is adequate for a complete desk-top analysis of projects that aim conservation and restoration of forest vegetation. A decision support system could be created, integrating GIS analyses that serve for prospection at landscape level, with additional information locally collected by means of field surveys, archive research, local groundwater modeling, etc. Such an integrative, hierarchical decision support system could assist the selection of locations with the highest conservation value and restoration potential.

Habitat continuity and habitat suitability or quality also determine species diversity of grassland, heathland, and other open habitat (see e.g. Cousins *et al.* 2007, Munzbergova *et al.* 2013). Similar quantitative research on the historical and present-day area of open habitat, e.g. heathland or grassland, could be used for the conservation and restoration of open habitat. However, many species that are nowadays restricted to open habitat in Flanders, e.g. *Pedicularis sylvatica*, also occurred in forests as forest management was much more intensive in the 18th and 19th century than it is today. Most forests were managed as a coppice or a coppice with standards and this management often also included root extraction, litter raking and occasional foraging by cows or pigs (Tack *et al.* 1993). The quality of forest edges has also changed: nowadays most forest edges in Flanders are sharp and exterior edges are often degraded by the surrounding farmland. As a result not only plant species of open habitat, but also plant species that prefer open forest and forest edges have declined (see e.g. the red-listed *Solidago virgaurea* that is also listed as AFS by Hermy *et al.* 1999). Compositional changes of forests caused by a shift of forest management (see, e. g., Van Calster *et al.* 2008, Baeten *et al.* 2009a) cannot be studied using historical maps only. Historical maps do not give much qualitative information about the management of forest and open habitat but they can be used to relocate areas with a high restoration potential for open habitat within forest, e.g. areas converted from open habitat to forest in recent history, or historical edges between forest and open habitat (see e.g. De Keersmaeker *et al.* 2011). As opposed to farmland, the abiotic conditions in forests are often still suitable for high-quality open habitat and there is a specific regulation in Flanders that stimulates the restoration of open habitat in forests. When spatial information on the historical area of open habitat and forest habitat is included into a decision support system, conflicts of interest between goals for both could be avoided. Moreover, such an analysis could support the restoration of high-quality gradients between forest and open habitat.

Summary

Many forest organisms depend on a continuous forest cover in space and time and consequently, biodiversity is affected by disruptions in any of those dimensions. Spatio-temporal forest cover changes generate patterns of habitat loss, habitat fragmentation, and reduced habitat suitability. This thesis quantified the impact on forest vegetation in Flanders, more specifically on ancient forest plant species that are mostly found in ancient forest, i.e. forest that has been continuously present as long as we know (since 1775).

As the diversity of ancient forest plant species is also determined by natural site conditions, we first mapped the natural heterogeneity of forest vegetation in Flanders (PNV map) as a baseline. In a next Chapter, the historical forest cover of Flanders at four times was digitized and compared with the PNV map. These GIS analyses revealed that the total forest cover in Flanders was more or less constant, but that only approximately 16% of the forest cover in 2000 is ancient forest. Moreover, the impact of spatio-temporal forest cover changes is habitat-specific, as mesophilous forest vegetation that has the highest diversity of ancient forest species, was affected most. Forests that were established after 1775, i.e. recent forest, have a low potential to obtain a high diversity of ancient forest plant species, as they are mostly isolated from ancient forst and located on unsuitable sites. As a result of the habitat-specific spatio-temporal forest changes, only approximately 10% of the forest cover of Flanders in 2000 has a high diversity of ancient forest plant species.

The GIS analyses in the first three Chapters covered the whole of Flanders but also indicated that important information that can explain the diversity of ancient forest plant species, was not available at this scale. For this reason the following Chapters focussed on vegetation patters in a mesophilous forest composed of ancient forest stands and stands that resulted from the successive conversion of agricultural land to forest. Vegetation patterns in this forest were explained using additional information on land use history, soil chemistry, and light intensity regulated by the canopy of trees and shrubs. The recovery of forest vegetation in post-agricultural forest stands was explained by the level of eutrophication with phosphorus, a consequence of a former use as farmland, and

by the forest structure that determines the light level on the herbaceous layer. It was found that vegetation of post-agricultural forest with high light levels on the forest floor and eutrophicated with phosphorous, is dominated by competitive species, particularly *Urtica dioica*, that hamper the colonization by forest plan species. The forest vegetation dominated by *Urtica dioica* accounts for 14% of all forest vegetation in Flanders.

We monitored the impact of increased light levels by felling on the colonization of forest plant species into a forest stand, planted on moderately eutrophicated farmland and in an intermediate stage of vegetation recovery. As opposed to the expectations, colonization rates of forest plant species increased by felling. However, this only applied to sites where the canopy of woody species restored within a decade and where light-demanding competitive species, e.g. *Urtica dioica* and *Rubus fruticosus*, had not become dominant.

Our results can be used for landscape planning and management aimed at the conservation and restoration of mesophilous forest vegetation with a high diversity of ancient forest species. The GIS layers can be used for the prospection of present-day forest with a high diversity (hotspots). They can also be used to select open land with a high recover potential when converted to forest, e.g. as it connects isolated recent forest on a suitable site with nearby ancient forest. It is indicated what additional information, not available in a GIS, is relevant to collect at a local scale for the operationalization of forest conservation and restoration projects. Finally, this work also indicated that the recovery rate of forest vegetation in post-agricultural forest is not constant, but can be influenced by forest management.

Samenvatting

Heel wat soorten uit bossen zijn afhankelijk van een continue aanwezigheid van bos, in de tijd en in de ruimte. Bijgevolg kan de biodiversiteit van bossen sterk worden aangetast door onderbrekingen in één van deze dimensies. Veranderingen van het bosareaal in tijd en/of ruimte zorgt voor verlies, versnippering en degradatie van boshabitat. Deze thesis spitst zich toe op de impact op de vegetatie van bossen, meer bepaald op oud bosplanten. Oud bosplanten zijn soorten met een binding aan oud bos, dit is bos dat voor zover we weten (sinds 1775) steeds bos gebleven is.

De diversiteit van oud bosplanten wordt ook bepaald door natuurlijke omstandigheden en om deze reden is in eerste instantie de natuurlijke variabiliteit van bosvegetatie in Vlaanderen gekarteerd. Deze PNV kaart diende als een referentie voor verdere analyses. In een volgend onderdeel werd het bosareaal in Vlaanderen op drie tijdstippen gekarteerd en vergeleken met het areaal in 2000 en met de natuurlijke geschiktheid volgens de PNV kaart. Deze ruimtelijke analyses toonden aan dat de totale bosoppervlakte in Vlaanderen sinds 1775 min of meer gelijk bleef, maar dat de ligging van de bossen sterk is gewijzigd. Als gevolg daarvan is slechts 16% van de bosoppervlakte in 2000 oud bos. Bovendien is vooral bos verdwenen op mesofiele bodem, die geschikt is voor een bosvegetatie met een hoge diversiteit van oud bosplanten. Daar staat tegenover dat recente bossen, dit zijn bossen die onstonden na 1775, een geringe potentie hebben om een soortenrijke vegetatie te ontwikkelen omdat ze liggen op locaties die van nature niet geschikt zijn en omdat ze bovendien ook geïsoleerd zijn van oud bos. Als gevolg van de ingrijpende en habitatspecifieke veranderingen in het bosareaal heeft slechts 10% van het bos in 2000 een vegetatie met een hoge diversiteit van oud bosplanten.

De GIS analyses in de eerste drie hoofdstukken beslaan geheel Vlaanderen maar wezen ook uit dat heel wat factoren die de diversiteit van bosvegetatie verklaren, niet beschikbaar zijn op dit niveau. Daarom werden in de daarop volgende hoofdstukken vegetatiepatronen bestudeerd in één mesofiel bos, dat is samengesteld uit oud bospercelen, en percelen met een uiteenlopende bosleeftijd die voorheen een gebruik als landbouwgrond hebben gekend. De vegetatiepatronen in dit bos konden goed verklaard worden met bijkomende, gedetailleerde informatie over het historisch landgebruik, de

bodemchemie en de lichtintensiteit die bepaald wordt door struiken en bomen. De vegetatie van lichtrijke, recente bospercelen op een bodem die is aangerijkt met fosfor, wordt gedomineerd door competitieve soorten, vooral Grote brandnetel (*Urtica dioica*). Dit vegetatietype komt voor in 14% van alle Vlaamse bossen. De verhoogde competitie door Grote brandnetel en andere lichtminners remt de kolonisatie van recente bossen door schaduwtolerante oud bosplanten af.

Een perceel recent bos op matig aangerijkte bodem en in een intermediair stadium van vegetatieontwikkeling, werd gevolg om de invloed van een eindkap te bepalen. Er werd verondersteld dat de invloed daarvan op schaduwminnende bosplanten negatief zou zijn, omdat competitie door lichtminnende soorten zou toenemen. Dit was evenwel enkel zo voor locaties waar de overscherming door bomen en struiken na 10 jaar nog niet was hersteld en forse lichtminnende soorten, zoals bramen (*Rubus fruticosus*) of Grote brandnetel (*Urtica dioica*) tot langdurige dominantie waren gekomen.

De resultaten van dit werk kunnen gebruikt worden voor landschapsplanning en beheer, dat tot doel heeft om mesofiele bossen met een hoge diversiteit van oud bosplanten te behouden of the herstellen. De GIS kaarten kunnen gebruikt worden voor prospectie van bossen met een hoge diversiteit of van open terrein dat een groot potentieel heeft om na bebossing een hoge diversiteit te ontwikkelen. Dit onderzoek geeft aan welke infiormatie, niet beschikbaar als een GIS, relevant is om bijkomend te verzamelen als projecten voor behoud of restoratie geoperationeliseerd worden. Tenslotte wijzen de resultaten ook uit dat het herstel van een diverse bosvegetatie kan versnellen of vertragen en dat het bosbeheer invloed heeft op de snelheid van dit proces.

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Professional experience

May 2000–present	Scientific worker at the Institute for Forestry and Game Management, since 2006 transformed to the Research Institute for Nature and Forest (INBO). The research covered different aspects of spontaneously developing unmanaged forests, and recovery of post-agricultural forest .
Februari 1998–April 2000	Scientific worker at the Institute for Forestry and Game Management on project VLINA/C97/06b: met als titel: ‘Ecosystem concept for forests in Flanders based on PNVs and historical forest cover’
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Scientific activities

Participation in congresses, symposia or workshops

21 February 1998. De betekenis van de ouderdom van bossen en chemische eigenschappen van de bodem voor de diversiteit van bosplanten: een gebiedsstudie te Ranst (Muizenbos). Studiedag 'Inheemse bomen en struiken', Antwerp, Belgium (poster presentation)

11 February 1999. Diversiteit van bosplanten in relatie tot ouderdom en bodemeigenschappen in het Muizenbos (Ranst, B.) Themanamiddag Biodiversiteit en Biometrie,'s Graveland, the Netherlands (poster presentation)

3 March 2001. Veranderingen in de vegetatie van het Meerdaalwoud tussen 1954 en 2000 door verdonkering en verzuring. Bossendag met als thema 'licht in het bos', Leuven, Belgium (oral presentation)

20 October 2004. Bodemverzuring en bosbeheer. Uitreiking van de getuigschriften voor bosgids, Eeklo, Belgium (oral presentation)

20 November 2004. Prioriteiten voor het behoud van bosgemeenschappen in de Kempen: een analyse op basis van boshistoriek en bodemeigenschappen. Studiedag 'bos en heide', Turnhout, Belgium (oral presentation)

2-4 December 2004. Monitoring of species diversity and vegetation development in strict forest reserves as important reference tools for nature-based forest management. European Platform for Biodiversity Research Strategy, Brussels, Belgium (poster presentation)

13-15 January 2005. Forest history related to a PNV site classification: a GIS analysis for the Flemish region. History and forest biodiversity – challenges for conservation, organized by the Laboratory for Forest, Nature & Landscape Research (KULeuven) in cooperation with IUFRO and Flanders Forest Service, Leuven, Belgium (oral presentation)

18-21 October 2005. Monitoring research in Flemish forest reserves: an outline of the methodology. Best practices for measuring and mapping of forest reserves, Kašperské Hory, Czech Republic (oral presentation)

22-26 August 2006. The importance of strict forest reserves for the conservation of saproxylic invertebrates and fungi in Flanders (Belgium). First European Congress of Conservation Biology, Eger, Hungary (oral presentation)

16 November 2010. Populieren: geschikte pioniers voor ecologisch waardevolle bosuitbreiding. Studiedag 'Populier in het Vlaamse bos en Landschap', Brussel, Belgium (oral presentation)

15 June 2011. Mogelijkheden en beperkingen voor de ontwikkeling van schrale graslanden en zomen in een bosomgeving. Studiedag: Ontwikkeling van schrale graslanden en zomen in een bosomgeving (oral presentation)

23 September 2011. Versnippering van het Vlaamse bos in ruimte en tijd. Studiedag: Ecologische bosuitbreiding op sterk bemeste gronden: van wetenschap naar praktijk (oral presentation)

20-21 June 2012. Biogeographic seminar of the Atlantic region. Session Rivers and Lakes. The Hague, The Netherlands

18 December 2012. Impact van verhoogde biomassaoogst op nutriëntenvoorraad. KOBE Workshop: Draagkracht van bossen voor verhoogde biomassaoogst, Groenendaal, Belgium (oral presentation

Supervision of thesis students

1996-1997 Leen Martens. Bosvegetatie in relatie tot historiek en chemische bodemeigenschappen in het Muizenbos te Ranst. MSc thesis, Ghent University, promotor: N. Lust.

1996-1997 Wim Jacobs. De relatie tussen de collembola, de historiek en bodemparameters in populierenbossen te Ranst. MSc thesis, Ghent University, promotor: N. Lust.

1997-1998 Thomas Dossche. Ecologische effecten van bladstrooisel van loofboomsoorten op de ontwikkeling van recent beboste landbouwgronden (Mortagnebos – Zwevegem). MSc thesis, Ghent University, promotor: N. Lust.

1997-1998 Jurgen Samyn. Invloed van begreppeling in bossen op fysische, chemische en floristische parameters. MSc thesis, Ghent University, promotor: N. Lust.

1997-1998 Tineke Kongs. Studie naar natuurlijke verjonging van boom- en struiksoorten in recente aanplantingen met populier. MSc thesis, Ghent University, promotor: N. Lust.

1998-1999 Gert Van Hoydonck. Evaluatie van bosomvorming als effectgerichte maatregel om verzuring en vermesting van bossen op zandgronden tegen te gaan. MSc thesis, Ghent University, promotor: N. Lust.

1999-2000 Katleen Rogiers. Bosevolutie in Vlaanderen sedert Ferraris aan de hand van digitale kaartbestanden en GIS. MSc thesis, Ghent University, promotor: M. Antrop.

2000-2001 Bram Bauwens. Stuurvariabelen voor vegetatiedynamiek in het Meerdaalwoud (Vlaams-Brabant) over de periode 1954-2000. MSc thesis, Ghent University, promotor: N. Lust.

2000-2001	Arno Thomaes. Verspreiding van oud-bosplanten in jonge bossen: invloed van bodem en competitie. MSc thesis, Ghent University, promotor: N. Lust.
2001-2002	Dieter Cuypers. Invloed van habitatkwaliteit op bosplantenrijkdom in oud Kempens bos en karakterisering van oud zuurminnend eikenbos. MSc thesis, Ghent University, promotor: N. Lust.
2004-2005	Maximilien Fontaine. Verspreiding van bosplanten als spiegel van de voorgeschiedenis van het bosareaal van Vlaanderen: een gebiedsdekkende analyse. MSc thesis, KULeuven, promotor: M. Hermy.
2005-2006	Lander Baeten. Veranderingen in de kruidlaag (1967-2005) door een gewijzigd bosbeheer in het domeinbos Tournibus (Houtvesterij Philippeville). MSc thesis, Ghent University, promotor: K. Verheyen.
2006-2007	Bert Schamp. Integrale bosreservaten: selectiecriteria en monitoring met Field-Map. BSc thesis, Hogeschool Gent, dep. Biowetenschappen en Landschapsarchitectuur, promotor: B. Mouton.