

Research article

Landscape factors and regional differences in recovery rates of herb layer richness in Flanders (Belgium)

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Abstract

The recovery of understory plants in recent forests is critical for evaluating the overall capacity of landscapes to maintain plant biodiversity. Here we used a large data set of vegetation plots from the Flemish Forest Inventory in combination with maps of forest history and soil-based Potential Natural Vegetation to evaluate regional differences in the rate of recovery of understory plant diversity in three regions of Flanders, Belgium. We expressed the degree of recovery in recent forests using the species richness of ancient forests as a reference point, and found strong differences among regions in the average level of recovery. These differences appeared to be due to regional variation in average patch connectivity and age (ultimately stemming from differences in land use history) and – to a lesser extent – environmental conditions. We also found an increase in the proportional representation of vertebrate dispersed species and species with short-distance dispersal with increasing levels of recovery. Our results highlight the potential drivers of inter-regional variation in the process of recovery of plant diversity during restoration, and they emphasize the importance of historical and spatial context in the recovery process.

Introduction

Next to the protection of habitats, their restoration on sites from which they disappeared sometime in the past is increasingly recognized as an important tool for conserving biodiversity (Dobson et al. 1997). However, recovery success is often highly variable among regions and the species richness at restored sites is typically considerably lower than in reference sites. Local habitat

factors such as hydrological conditions or soil nutrient status (e.g., Brown et al. 1997; Honnay et al. 2002) in restored sites are important in determining recovery success (e.g., Bakker and Berendse 1999), but landscape factors may also have an influence.

In forests of the north-temperate zone an increasing number of studies demonstrate that differences in herb layer species diversity and composition between ancient and recent forests

may persist for hundreds of years (reviewed by Hermy et al. 1999; Flinn and Vellend 2005). Ancient forests are defined as forests that have been continuously forested since the date of the earliest land-use maps, while recent forests have originated some time after that date, mostly on abandoned agricultural land, including extensively grazed areas such as heathlands. Important factors influencing the colonization of forest herbs in recent forests include spatial and temporal isolation from other forest habitat patches (e.g., Jacquemyn et al. 2003), and also the nature of the intervening matrix. For instance, Petit et al. (2004) found that the species richness in forests was higher when networks of hedgerows were present in the surrounding landscape. In accordance with the importance of connectivity on recovery, studies of species' life-history traits have demonstrated that recent forests may be especially impoverished in species characterized by poor dispersal capacities (Matlack 1994; Brunet and von Oheimb 1998; Graae 2000; Verheyen et al. 2003a; Takahashi and Kamitani 2004).

To date, almost all studies have reported results from particular landscapes or regions while only a few studies have focused on variation in recovery rates among landscapes and regions (but see Graae 2000; Vellend 2003). Graae (2000) compared two regions in Denmark and found more pronounced effects of fragmentation in the region with more intensive land use. Comparing 10 landscapes across Europe and North America, Vellend (2003) showed that the degree of recovery of herb layer diversity in recent forests decreased strongly as the fraction of remaining ancient forest in the landscape fell below a threshold of ~10%.

In this paper, we conducted an analysis of recovery rates across three different ecoregions in Flanders (the northern part of Belgium). The regions differ markedly in their present-day forest cover, in the fraction of forest that is ancient and in the dominant natural forest types. Because these regions differ in several characteristics, it is difficult to make specific predictions concerning which regions should show greater or lesser degrees of forest-herb recovery in recent forests. However, we can make the more general predictions that (1) regions will show significant variation in the degree of recovery, and (2) statistically controlling for variation in patch characteristics

(e.g., age, connectivity) should reduce or remove the inter-regional variation. The comparison was made possible due to the availability of a large number of vegetation plots systematically distributed over the entire territory as part of the Flemish Forest Inventory (Waterinckx and Roelandt 2001) and the availability of maps of forest age and Potential Natural Vegetation throughout the region (De Keersmaecker et al. 2001). The latter was important since – apart from landscape characteristics – recovery is expected to increase with increasing secondary forest age and also to vary as a function of differences in abiotic site conditions. For instance, Jacquemyn et al. (2001) and Verheyen et al. (2003b) found recovery to be slower in forest communities on drier and less fertile upland sites than on mesic, rich valley bottom sites. In addition to focusing on variation in recovery among regions, we tested two additional, related hypotheses: (1) Due to dispersal limitation, the relative frequency of species lacking adaptations for long-distance dispersal is lower in recent forests exhibiting a lower overall degree of recovery and vice versa; (2) The age, connectivity, and site fertility of recent forests will all have a positive influence on the degree of recovery herb layer richness.

Methods

Study area

For this study, the three largest ecoregions (the Kempen region, the Flemish Sandy Region and the Sandy Loam Belt) in Flanders were selected, covering 11,585 km² or 85% of the Flemish territory (Figure 1). Ecoregions are defined as regions with similar geological and geomorphological properties (Sevenant et al. 2002). The soils in the Kempen, Flemish Sandy Region and Sandy Loam Belt are characterized by a sandy soil, a combination of sand and sandy loam, and a sandy loam soil, respectively. In accordance with the variation in site conditions, large differences in the frequency of the potential forest community types are apparent among regions (Figure 2). While the potential natural vegetation in the Kempen region is dominated by birch-oak forests, the percentage of this forest type decreases from the Flemish Sandy Region to the Sandy Loam Belt. The

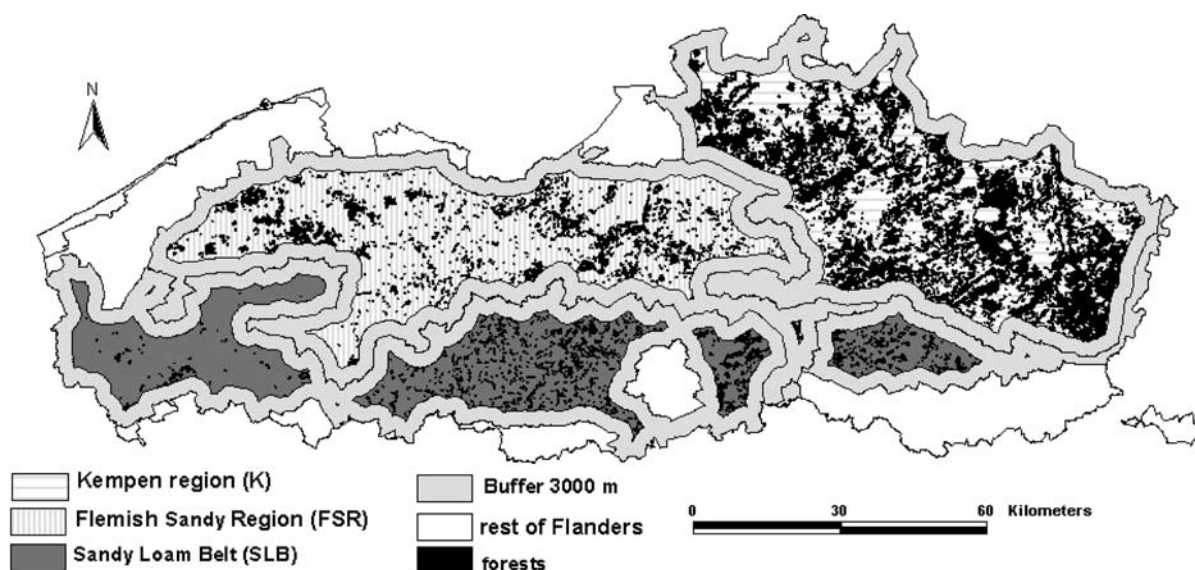


Figure 1. Map of Flanders and the forest cover in the three selected ecoregions according to Seventant et al. (2002).

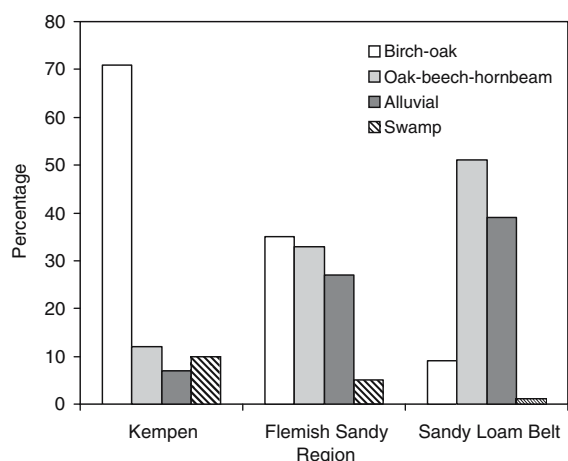


Figure 2. Relative importance of the four forest types per region as percentage of the total regional forest cover.

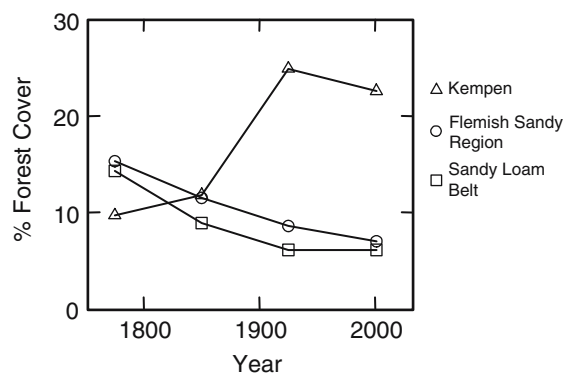


Figure 3. Changes in the forest cover in each region derived from De Keersmaecker et al. (2001), expressed as the percentage of the total area of the region.

percentages of oak-beech-hornbeam and alluvial forests show an opposite trend, and are highest in the Sandy Loam Belt (Figure 2).

Partially related to these site and forest community characteristics, the extent and history of forest cover also vary among the three regions (De Keersmaecker et al. 2001). While the Kempen was the least forested region in 1775 (~10% forest cover), it now has a forest cover of ~23%, which is the highest of the three regions in Flanders (Figure 3). Forest expansion in the Kempen mainly took place at the end of the 19th century,

when there was a high demand for pine wood to be used in coal mining. Today, ancient forests are very rare in the Kempen region (4% of the current forest area). The two other regions exhibit very different trends: forest cover decreased from ~15% in 1775 to ~6% in 2001 (Figure 3) and ancient forests constitute, respectively, 23% and 33% of the current forest area in the Flemish Sandy Region and the Sandy Loam Belt. However, a large fraction of the ancient forests in the Flemish Sandy Region probably originates from heathland afforestations in the early 18th century (Tack et al. 1993), while the ancient forests in the

Sandy Loam Belt probably originated much earlier or are even primary (i.e., were never cleared).

Data sources

We started with the 1383 vegetation plots that were recorded as part of the first Flemish Forestry Inventory between 1997 and 1999 (Waterinckx and Roelandt 2001). The vegetation plots are systematically distributed over Flanders on points of a 1 km × 1 km grid that were situated within a forest. In spring and summer, the cover of all plant species in the herb layer was estimated in 16 m × 16 m plots using the Braun–Blanquet scale. Of the 1383 plots, 1096 plots containing 472 species were located in the three selected ecoregions.

Based on a simplified version of the Potential Natural Vegetation map (De Keersmaecker et al. 2001; Appendix 1), one of four potential climax forest types was assigned to all 1096 plots. The four types are: birch-oak forest (on dry to moist poor soils; BO), oak-beech-hornbeam forests (on moist and relatively rich soils; OBH), alluvial forests (on temporarily wet and rich soils; All) and swamp forests (on permanently wet sites). The PNV map represents a reclassification of the 1:20,000 Belgian Soil Map based on known relationships between naturally occurring forest and soil types. The soil types synthesize information on soil texture, soil drainage and soil profile development. This information thus provides an independent source of 'environmental' data that are independent of the forest inventory data.

Next, the age of the forest containing each vegetation plot was determined from the forest history map of Flanders by De Keersmaecker et al. (2001). This map was constructed by making an overlay between the present-day (i.e., 2001) forest map and three historical land-use maps with scales varying between 1:12,500 and 1:40,000 and dating from 1775, 1850 and 1910–1930. Although historical maps are available for additional time periods, digitizing these maps for all of Flanders is extremely laborious, and these are the only time periods for which maps have been digitized to date. The age of ancient forests, i.e., forests that originated before 1775, was arbitrarily set at 250 years, while the other forest ages were calculated based on the midpoint between the dates of

two consecutive maps, resulting in ages of 189 years (between 1775 and 1850), 116 years (between 1850 and 1910–1930) and 41 years (between 1910–1930 and 2001). In reality, however, very few forests originated during the last few decades of the 20th century.

A modified version of the Incidence Function Model (IFM) connectivity measure of Hanski (1994) was used to calculate the connectivity of the patches containing a vegetation plot. Here we defined a patch as a forest of a single PNV type and with a similar land use history. Moilanen and Nieminen (2002) stressed that significant effects of connectivity in highly fragmented landscapes are more likely to be found with the IFM measure compared to simple connectivity measures, such as nearest neighbour, buffer measures, etc. However, a modification of the original formula was necessary, since we had to take into account the differential contribution of different forest types to the connectivity of each focal patch (the original formula assumes environmental homogeneity). For instance, situations occur where alluvial forest is adjacent to dry non-alluvial forest, and these two forest types share very few species in common. Therefore, the higher the (potential) similarity in vegetation composition between target and source patches, the more important the latter should be as colonization source. To achieve this, we weighted the area of the source patch (A_j) by the mean Czekanowsky similarity (sim_{ij}) between the species composition of the forest types of the target patch i and source patch j . Connectivity of each patch i (C_i) was thus calculated as:

$$C_i = \sum_{j \neq i} \exp(-\alpha d_{ij}) A_j^b \text{sim}_{ij} \quad (1)$$

where d_{ij} is the distance between patch i and j . The parameter b scales the effect of patch size to emigration and α scales the effect of distance to migration. Parameter values were taken from Moilanen and Nieminen (2002): $b = 0.5$ and $\alpha = 0.002 \text{ m}^{-1}$. Distances were in metres, areas in m^2 . The computation of the Czekanowsky similarity coefficients was based on a random selection of 40 plots from each forest type. To avoid biases due to uneven distribution of plots over the four types (cf. Chao et al. 2005), we use a fixed number of plots per type. The coefficient was thus calculated as follows:

Table 1. Czekanowsky similarity coefficients between the four forest types based on the frequency of the field layer species in a random selection of 40 plots per forest type.

Forest type	Birch-oak	Oak-beech-hornbeam	Alluvial	Swamp
Birch-oak	1			
Oak-beech-hornbeam	0.40	1		
Alluvial	0.14	0.29	1	
Swamp	0.29	0.35	0.5	1

$$\text{sim}_{ij} = \frac{2 \sum_{k=1}^n \min(x_{ki}, x_{kj})}{\sum_{k=1}^n (x_{ki} + x_{kj})} \quad (2)$$

where sim_{ij} is the similarity in forest floor species composition between forest type i and forest type j , x_{ki} is the percent cover of species k in forest type i , x_{kj} is the percent cover of species k in forest type j and n is the number of species. Pairwise coefficients are shown in Table 1.

Finally, two connectivity measures were calculated for each patch (using equation 1): the connectivity in the current landscape and the connectivity taking into account only ancient forest patches. As ancient forests are considered the main sources for colonization of forest herbs, it may be possible that the latter measure performs better than the former (Lindborg and Eriksson 2004; Van Ruremonde and Kalkhoven 1991; Vellend 2003). In each ecoregion, reliable connectivity calculations could only be obtained for patches that were located >3000 m from the boundaries of a region. For patches closer to the boundaries, connectivity was underestimated by neglecting forest fragments outside the region. Hence, the number of useful vegetation plots was further reduced to 712. All GIS-analyses were performed in ArcView 3.2[®] and the connectivity measures were calculated using Matlab 7.0.1[®].

Data analysis

Previous studies have demonstrated that idiosyncratic results are obtained when the total species richness is used as a response variable (Flinn and Vellend 2005) and therefore only typical forest species (i.e., mostly shade-bearing species that

predominantly occur in forests) were selected for further analysis, based on a list proposed by Stieperaere and Franssen (1980). Next, to account for the large differences in (potential) alpha diversity among forest types, the recovery of forest plant species richness in each recent forest plot was calculated by dividing the number of forest species present by the mean number of forest species in ancient forest plots of the same forest type (cf. Vellend 2003). We thereby assumed that ancient forest plots serve as a reference for herb layer diversity. Though there is evidence that some of the ancient forests, particularly in the Flemish Sandy Region, actually represent heathland afforestations dating from the early 18th century (Tack et al. 1993), using ancient forests as a reference to evaluate recovery is the only viable option throughout Europe and North America; indeed ancient forests are the closest to true primary forests in terms of herb layer richness and composition (Peterken 1996). Twenty-nine ancient forest plots were available for the birch-oak forests, 31 for the oak-beech-hornbeam forests, 11 for the alluvial forests and only one for the swamp forest type, which was therefore excluded from further analyses. Before adopting this measure of recovery, we first verified that the species richness in ancient forests of each forest type did not differ between the three regions, as this could bias the recovery measure we adopted. The results of one-way ANOVA's confirmed that this was the case (BO: $p = 0.243$; OBH: $p = 0.785$; All: $p = 0.587$).

To test for differences in recovery among regions we first conducted a one-way ANOVA. Next, the combined effects of region, forest type, secondary forest age and connectivity on recovery of species richness were assessed using General Linear Modelling (GLM). For this analysis, region and forest type were considered random factors, while age and the two (ln-transformed) connectivity measures were used as covariates. Significant interactions ($p < 0.05$) between region and the other variables were also included in the model.

To assess the relationship between recovery and the relative frequency of dispersal modes, we first used the compilation by Biesbrouck et al. (2001) to classify the forest species as wind or water dispersed, vertebrate dispersed, or lacking adaptations for long-distance dispersal. When several adaptations for dispersal occurred, species were

assigned to more than one dispersal mode. The relative frequencies of the three dispersal modes were then calculated as the fractions of the total number of forest species in the plots. Finally, Spearman Rank correlations were calculated between these relative frequencies and the recovery variable, both for all plots together and separately for each forest type.

Ancient forest plots were excluded from all above-mentioned analyses as we were only interested in the recovery of richness in recent forests. Whenever necessary, the recovery variable was ln-transformed to meet the assumptions for statistical analysis and all analyses were performed using SPSS 12.0.

Results

Strong differences in recovery were found among the regions ($F_{2,587} = 10.598$, $p < 0.001$; Figure 4) with the Sandy Loamy Belt exhibiting higher recovery rates than the Kempen region, which in turn exhibited higher recovery rates than the Flemish Sandy Region (Figure 4). The results of the GLM-analysis (Table 2) no longer indicated a significant effect of region on recovery of herb layer richness, but strong effects of age and current

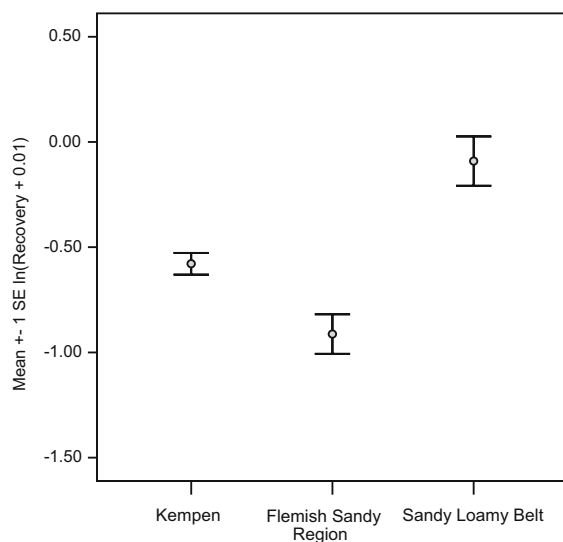


Figure 4. Mean \pm Standard Error (SE) of the ln-transformed forest plant species recovery in the three regions. All Bonferroni-corrected pairwise-comparisons are statistically significant ($p \leq 0.001$).

Table 2. Results of the General Linear Model-analysis with the (ln-transformed) recovery of herb layer richness as dependent variable. Only significant ($p < 0.05$) interactions were included in the model.

Variable	d.f.	F	p-value
Region ^a	2, 16.1	0.439	0.652
Forest type ^a	2, 5.6	1.580	0.286
Age ^b	1, 571	7.758	0.006
Connectivity (current) ^b	1, 571	5.178	0.023
Connectivity (ancient forest) ^b	1, 571	1.764	0.185
Region \times forest type	4, 571	3.069	0.016
Region \times connectivity (ancient forest)	2, 571	3.234	0.040

^a Random factor.

^b Covariate.

connectivity instead (see also Figure 5b and c). The effects forest type and connectivity to ancient forest were weaker, but these variables showed significant interactions with region (Table 2; Figure 5a and d). These interactions were caused in large part by the limited recovery of the alluvial forests in the Kempen region compared to the other regions and by the weak effect of connectivity to ancient forest in the Sandy Loam Belt.

Significant relationships were found between recovery and the relative frequencies of the three dispersal modes, and these relationships were consistent across forest types (Table 3). Wind or water dispersed species were relatively more frequent in the least recovered plots, while vertebrate dispersed species and species lacking adaptations for long-distance dispersal were relatively more frequent in plots with higher recovery.

Discussion

The three regions varied considerably in the mean level of recovery of the understory plant community in recent forests (Figure 4), as expected based on their different environmental conditions, histories of forest cover, and present-day landscape structure. However, when statistically controlling for this variation in forest type, age, and connectivity, these inter-regional differences disappeared (Table 2). At the most general level, these results suggest that the extensive variability observed among studies in terms of the process of recovery of understory plants in recent forests (reviewed in Flinn and Vellend 2005) is likely attributable, in part, to regional variation in environmental conditions and the history and structure of forests.

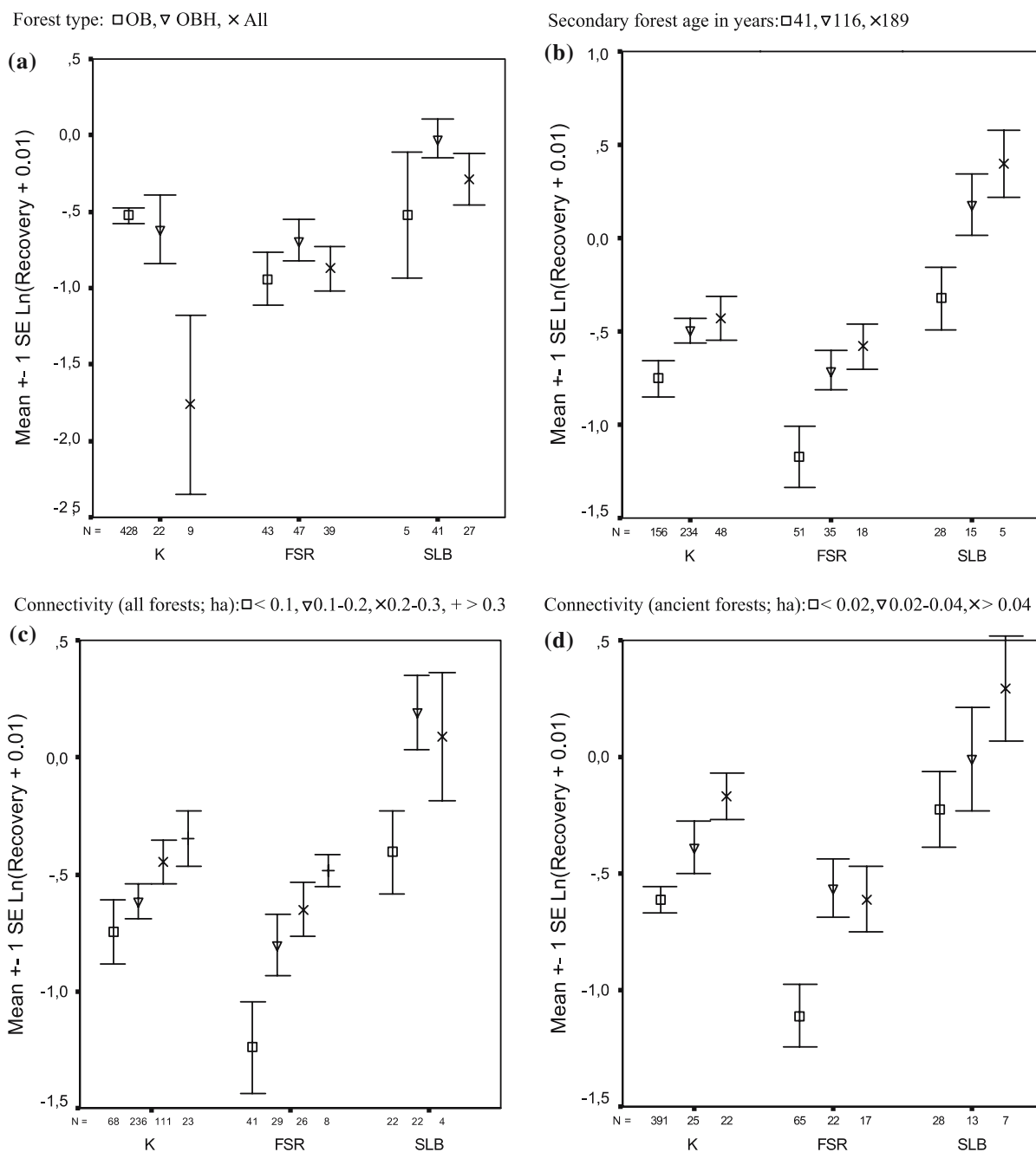


Figure 5. Mean \pm Standard Error (SE) of the ln-transformed forest plant species recovery per region (K, Kempen; FSR, Flemish Sandy Region; SLB, Sandy Loamy Belt) and per forest type (a), secondary forest age classes (b), connectivity classes to all forests (c) and to ancient forests only (d).

Consistent with earlier studies (e.g., Brunet and von Oheimb 1998; Jacquemyn et al. 2001, 2003), we found that forest patch age and connectivity had positive effects on the degree of recovery in the understory plant community of recent forests.

These results were consistent across regions (Figure 5b–d), emphasizing the importance of the spatial and temporal context of a forest patch for understanding its potential for recovery of biodiversity during restoration. Revealing the generality

Table 3. Spearman Rank Correlations between the recovery of forest species richness and the relative frequency of three main dispersal modes in the plots.

Dispersal mode	All types ($n = 567$)	Oak-birch ($n = 429$)	Oak-beech-hornbeam ($n = 77$)	Alluvial ($n = 61$)
Wind and water	−0.38***	−0.44***	−0.43***	−0.27*
Vertebrate	0.48***	0.50***	0.41***	0.48***
Short distance dispersal	0.18***	0.18***	0.54***	0.12ns

*** $p \leq 0.001$; * $0.01 < p \leq 0.05$; ns not significant.

of these patterns across landscapes was facilitated by using forest-type specific ancient forests as reference points. Although the mean number of species was different in the three forest types (BO < OBH < All), the fraction of species that recovered, appeared to be approximately constant among the three types (Figure 5a). Hence, if recovery is expressed as the absolute number of recovered species or as the number of recovering species per year, then we do find the numbers or rates increasing with increasing site productivity (e.g., 0.04; 0.06; 0.08 recovering species/year in the BO, OBH and Alluvial forests, respectively). When expressed in absolute terms, our results thus confirm the earlier findings of Bellemare et al. (2002), Jacquemyn et al. (2001) and Verheyen et al. (2003b) that recovery was faster in forests on more fertile soils.

We found significant and consistent relationships between dispersal mode and degree of recovery, despite that many authors (e.g., Vander Wall 1992; Heinken et al. 2001; Pakeman et al. 2002; Bullock et al. 2003; Vellend et al. 2003; Myers et al. 2004) have shown that the relationships between diaspore morphology and a species' actual means of dispersal do not always hold. As expected, wind and water dispersed species were relatively more frequent in the least recovered forests, while the opposite was true for the poorly dispersed species (Table 2). Less expected was the strong positive relationship between the degree of recovery and the relative frequency of vertebrate dispersed species, given that vertebrate-mediated seed movement is generally considered an effective means of long-distance dispersal (e.g., Couvreur et al. 2005). It may be the case that fleshy fruits (and dispersal traits in general) are correlated with unmeasured traits (e.g., physiology) that also have an important influence on the rate of population recovery in recent forests (Verheyen et al. 2003a; Kolb and Diekmann 2004). These hypotheses are in need of further testing.

In conclusion, we found that the process of recovery of understory plant communities in recent forests is clearly non-random in that dispersal limited species are only added in the final stages of recovery and that forest connectivity, age and – to a lesser extent – forest type can account for regional differences in recovery rate. Thus, landscape context appears to be a critical consideration when planning restoration projects or when evaluating restoration success.

Acknowledgements

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Appendix A1. Relationships between the four aggregated forest types used in this study and the forest types used for the Flemish Potential Natural Vegetation map (PNV, De Keersmaecker et al. 2001).

Forest type (this study)	Forest type (PNV-map)
Birch-oak (BO)	<i>Quercion robori-petraeae</i> <i>Betulo-Quercetum roboris</i>
Oak-beech-hornbeam (OBH)	<i>Quercion robori-petraeae</i> <i>Fago-Quercetum</i> <i>Fagion sylvatica</i> <i>Milio-Fagetum</i> <i>Endymio-Fagetum</i> <i>Carpinion betuli</i> <i>Stellario-Carpinetum</i> <i>Endymio-Carpinetum</i> <i>Primulo-Carpinetum</i>
Alluvial (All)	<i>Alno-Padion</i> <i>Fraxino-ulmetum</i> <i>Pruno-Fraxinetum</i>
Swamp	<i>Alnion glutinosae</i> <i>Carici elongatae-Alnetum</i> <i>Filipendulo-Alnetum</i> <i>Cirsio-Alnetum</i>

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