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## Understory succession in post-agricultural oak forests: Habitat fragmentation affects forest specialists and generalists differently

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### ABSTRACT

The herbaceous understory forms the richest stratum in temperate broadleaved forests in terms of plant diversity. Understanding the process of understory succession is thus of critical importance for the development of management guidelines for biodiversity restoration in post-agricultural plantation forests.

We studied effects of stand age, forest fragmentation, and soil and canopy conditions on species richness and abundance of four species groups in the understory of post-arable oak plantations in southern Sweden: herbaceous forest specialists, habitat generalists and open-land species, and woody species.

The group of forest specialists may approach the richness of continuously forested sites after 60–80 years in non-fragmented plantations, but many forest species were sensitive to habitat fragmentation. Open-land species richness decreased during succession, while the richness of woody species and of generalists remained stable, and was not affected by fragmentation. Abundance of generalists gradually decreased in non-fragmented plantations, probably due to competition from colonizing forest specialists. Soil pH in post-arable stands remained consistently higher than in continuously forested stands, which maintained differences in species composition. The development of a shrub layer seemed to imply a competitive advantage for forest specialists compared to generalist species.

For successful recovery of a rich understory, we suggest that post-arable plantations should be established on loamy soils of intermediate to high pH proximate to older forest with source populations, and that a continuous overstory canopy cover of 70–80% is maintained by regular light thinnings and promotion of a shrub layer.

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### 1. Introduction

Temperate forests are the global biome that has been most influenced by human activities through history (Hannah et al., 1995). In northern Europe, the once widespread mixed oak (mainly *Quercus robur*) forests have been subjected to extensive clearance since the early medieval period, with the rate of loss accelerating during the 18th and 19th century (Lindbladh and Foster, 2010). This decline was initially caused by conversion of forest into farmland, and the unsustainable use of oak stands for fuel and construction timber. During the past century, many of the previously spared oak-dominated woodlands were also converted into production forests of Norway spruce (*Picea abies*), Scots pine (*Pinus syl-*

*vestris*) and European beech (*Fagus sylvatica*) (Nilsson et al., 2006; Emanuelsson, 2009).

Mixed oak forests provide habitat for a rich biodiversity and their decline in abundance has endangered a large number of species (Berg et al., 1994). Until now, related conservation efforts have mainly focussed on the continued preservation of the few remaining stands with ancient trees (Nilsson et al., 2006). However, from a conservation perspective, these efforts must be supplemented by the establishment of new oak forest, in order to substantially increase the availability of oak habitat in Northern Europe (Lindbladh and Foster, 2010). Plantations established on abandoned arable land are an important source of newly created oak habitat. Planting ecologically valuable, indigenous tree species, such as oak, on extremely disturbed land (arable fields) may result in a high long-term gain of biodiversity (Bremer and Farley, 2010).

The herbaceous understory plays a key role during restoration of biodiversity in plantations. It forms the richest stratum in tem-

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perate forests in terms of plant diversity, and it influences the development and diversity of higher forest strata (Gilliam, 2007). Understanding the process of understory succession is thus of critical importance for the development of management guidelines for biodiversity in plantation forests. Generally, the development of understory diversity and composition in new plantations is controlled by a combination of niche-based processes at local scale, and dispersal-based processes operating at both local and landscape scale (Ehrlén and Eriksson, 2000; Ozinga et al., 2005).

The availability of species-specific niches in plantations is influenced by the legacy of former agricultural use, which changes important soil properties. Long-term effects may include increased soil P levels and soil pH, combined with lower C/N ratios due to depleted soil organic matter (Honnay et al., 2002; Flinn and Vellend, 2005; Falkengren-Grerup et al., 2006; Valtinat et al., 2008). Furthermore, the fine-scale heterogeneity of soil characteristics present in natural forests is often lost in post arable soils. This has potentially large effects on environmental sorting, and may result in floristic homogenization (Gilliam, 2007; Vellend et al., 2007).

Many shade tolerant forest herbs possess life history traits such as unassisted seed dispersal, low fecundity and short-lived seed banks (Verheyen et al. 2003). These traits suggest a low dispersal capacity in space and time, making the majority of forest herbs sensitive to habitat loss and fragmentation (Hermy and Verheyen, 2007). Arable weeds and generalist plants, on the other hand, may be expected to be common in young post-arable forests due to recruitment from soil seed banks and dispersal from the agricultural matrix (Motzkin et al., 1996). These results suggest that the degree of soil alteration and the connectivity with older forests are critical factors for determining the process of understory recovery in post-arable plantations.

While many studies have investigated vegetation succession in secondary forests, no study has analysed the relative importance of dispersal- and niche-based processes for understory development in post-arable oak plantations. In this study, we use an 80-year chronosequence of oak plantations established on former agricultural land in southern Sweden, to analyse the process of long-term understory restoration along gradients of spatial isolation, forest age, and important soil and overstory characteristics. Specifically we hypothesized that: (1) Understory species richness increases with stand age in oak plantations on former arable land, (2) Forest specialist plant species are more strongly influenced by habitat fragmentation than generalists, (3) Understory species composition is influenced by canopy closure and persistent agricultural legacies on soil properties.

## 2. Materials and methods

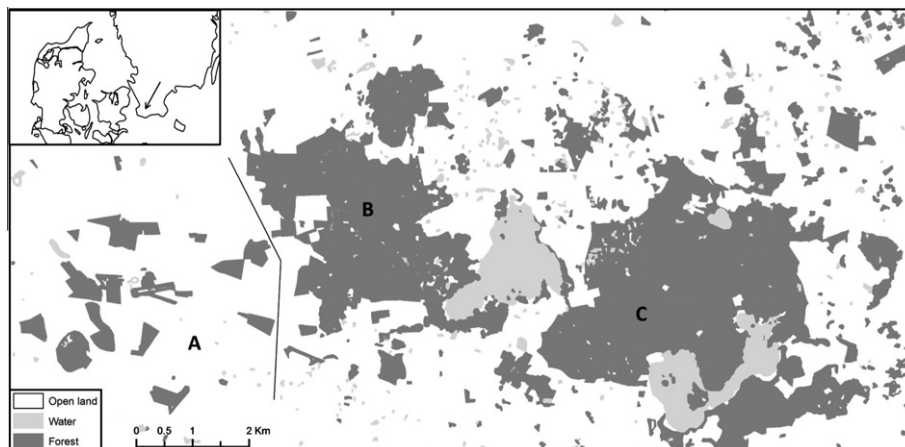
### 2.1. Study area

The study was conducted in Pedunculate oak (*Q. robur*) plantations within the hilly forest landscape of the Skabersjö and Torup estates in Skåne county, southernmost Sweden (55°32'N, 13°11'E, Fig. 1). During the mid-Holocene this part of Sweden was dominated by mixed oak forests (Berglund, 1991). A pollen analysis and historical documents show that oak forests continued to play a major role in our study area up unto more recent history, but experienced a rapid decline in the 17th–19th centuries (Brunet, 2007a; Hultberg et al., 2010). The establishment of plantations on arable land, pastures, and clear-cut forest land since ca 1920 has led to a considerable increase in the total area of oak forest (Brunet, 2007a).

The forests of the study area grow on well-drained dystric and eutric cambisols derived from glacial till (Weichselian glaciation), and vary in altitude from 25 to 75 m.a.s.l. The mean temperature in January is  $-0.5^{\circ}\text{C}$ , with a mean of  $16.5^{\circ}\text{C}$  in July. Mean annual precipitation is 650 mm. The average vegetation period in the study area is 210 days.

The western part of the study area (A, Fig. 1) is an open agricultural landscape with small isolated forest patches, while the central and eastern parts are dominated by two large contiguous forests (B and C, Fig. 1). Detailed historical maps and forest management plans (scale 1:4000–1:10000) are available from 1769 (area A), 1694–1812 (area B) and 1703 (area C), till the present time, and allow for stand-wise reconstruction of the forest history, including precise information regarding the year of stand establishment.

“Core forest” is defined as areas with continuous forest cover during the past 198–316 years, with the variation due to the age of the oldest maps available. Pollen analysis from area B (Torup) indicates that at least part of the core forest consists of primary forest, which has never been cleared for agriculture (Hultberg et al., 2010). Until ca 1840, core forests in the study area had irregular selective cuttings taken, and were grazed by domestic livestock. After 1840, shelterwood and clear-cut management systems were introduced and grazing gradually ceased (Brunet, 2007a). The management history of the core forests in the study area is representative of the broadleaved forests of southern Sweden. The species pool found in the core forest contains most forest plant species that can be expected to occur within the range of soil and topographical conditions present (Tyler et al., 2007).



**Fig. 1.** Map over the study area (large picture) and its situation in the province of Skåne, southernmost Sweden (indicated in the small picture). A to the left of the line indicates the western, fragmented part, B and C indicate the central and eastern large contiguous forests. The latter forests contain large areas of core forest, with most post-arable plantations along the margins.

Previous studies from the area have shown that differences in soil properties (pH, P, C, N) between post-arable oak stands and oak stands in core forest decrease with increasing soil depth and tend to vanish below the tilling horizon (Falkengren-Grerup et al., 2006; Valtinat et al., 2008). Together with evidence from soil maps, this pattern suggests that differences in top soil characteristics mainly are a result of historical land use, and not of initial differences of the parent material. Hence, the study area offers the opportunity for investigating long-term effects of land-use history on both soil conditions and plant distributions.

## 2.2. Site selection

Based on the available land-use history, 58 stands of a size >0.5 ha were studied. All 58 stands had a canopy dominated by planted oak, sometimes containing individuals of beech and European sycamore (*Acer pseudoplatanus*). All stands are managed for timber production and are subjected to regular thinnings, usually every 5 years up to an age of 60 years, and every 10 years in older stands. After the first pre-commercial thinnings, stem density is ca 400–600 ha<sup>-1</sup>, which is reduced by further commercial thinnings to a stem density of 50–70 ha<sup>-1</sup> at final harvest (tree age 120–180 years).

The study stands were divided into three categories based on land-use prior to stand creation, and the matrix within which the stand is situated (Table 1):

- (1) *Core forest*: stands established on continuously forested land, and located within a forest-dominated matrix.
- (2) *Proximate*: stands established on former arable land, and located along the margins of the two large contiguous forest areas (area B: 780 ha, and area C: 900 ha, respectively, Fig. 1). These stands were either directly adjacent to core forest or connected with core forest by older post-agricultural forest.
- (3) *Isolated*: stands established on former arable land and located in the heavily fragmented western part of the study area (area A, Fig. 1). Most forest patches in that area consist of several planted stands, are of post-agricultural origin, and were established after 1800.

## 2.3. Data collection

In each of the 58 oak stands, a well-drained sample plot of 25 × 20 m was selected in the interior part of the stand, at least 20 m from any stand margins, and marked at the corners. Within this sample plot, vegetation surveys were conducted in ten subplots of 1 × 1 m. Within each 1 m<sup>2</sup> subplot, all species of herbaceous vascular plants, and woody plants lower than 1 m, were recorded as herb layer vegetation (understorey). Percentage ground cover for each species was estimated visually on a scale from 0.5% to 100%. Cover estimates were averaged over the ten subplots to give plot means for each species. Presence of additional species in the 20 × 25 m plots was also recorded during extensive 15 min searches. Additional species were given a plot-level cover value of 0.05%. Furthermore, all woody species of 1–5 m height were recorded separately in each subplot. Canopy cover of woody

species was estimated vertically above each 1 m<sup>2</sup> subplot separately for the height classes 1–5 m (shrub layer cover) and >5 m (tree layer cover), and averaged to obtain plot means. Subplots were placed systematically but without overlap with subplots for soil samples (see below). The vegetation of each plot was surveyed twice to include both spring (vernal) and summer species. When the same species was encountered during both survey periods, the higher of the two cover values was used. The vegetation of 41 plots was sampled during the 2004 summer (July and August) and the 2005 spring (April), and the remaining 17 plots were sampled during April and July of 2010. Species names are according to Mossberg and Stenberg (2003). Weather conditions may have induced some inter-annual variation in species cover (Brunet and Tyler, 2000), but we do not believe that this has a significant influence on the general results of this study, as there were no periods with extreme weather conditions during the sampling seasons.

After providing for a four m margin along the borders of each vegetation plot, five soil sampling subplots were marked, one in the plot's centre and four in each corner. Soil samples were taken from 0 to 5 cm depth below the litter layer and mixed into one composite sample. For measurement of soil pH, 10 g of sieved soil were extracted in 50 ml deionised water. The pH (H<sub>2</sub>O) was measured using a microprocessor ion analyzer. For a random subset of 36 sample plots, organic matter content was measured as % weight loss by burning the samples at 600 °C.

The year of stand establishment was obtained from 2001 forest management plans, and cross-checked using management plans and maps from 1915 to 1992 (see Brunet, 2007a). For the 43 post-arable stands, the distance (m) from the sample plot to the nearest core forest edge was measured using forest maps at a scale of 1:10 000.

## 2.4. Data analysis

All herbaceous species were divided into three categories of primary habitat preference according to Schmidt et al. (2002); (1) Forest specialists, mainly found in closed forest, (2) Generalist species found in both closed forest and open land, and (3) Species mainly found in open land. In addition, we treated woody species in the herbaceous layer (<1 m) as an additional group. Group 1 (forest specialists) was further divided into vernal species which flowered and unfolded their foliage in early spring and wilted before summer; and species with green leaves which persist at least into July.

Linear regression was used to compare the relationship between stand age and the richness and abundance of species by habitat group in the core, proximate and isolated stands. Linear regression was also used to analyse the relation between stand age and soil pH and organic matter content. Six post-arable stands were planted after a first generation of forest with Norway spruce. These second-rotation plantations were excluded from regression of soil pH against stand age, due to the likely influence that spruce stands would have on soil acidity. The three categories of oak plantations were compared using ANOVA (after Normality testing) with post-hoc Tukey test. A two-sample *t*-test was applied when comparing the core forest plots with proximate plots older than 70 years (*n* = 11). These analyses were computed in Minitab 16.1.1 (Minitab Inc., 2011).

**Table 1**

Stand age (range) and mean values (SD) of total canopy cover (tree and shrub layer), soil pH and organic matter in oak plantations in core forest, post-arable proximate plantations and isolated post-arable plantations. Means that do not share a letter are significantly different (*p* < 0.05) according to ANOVA and Tukey-test.

Site group	No. plots	Stand age (years)	Canopy cover (%)	pH H <sub>2</sub> O	Organic matter (%)
Core forest	15	49–78	77 (20) a	4.73 (0.33) a	10.9 (2.5) a
Post-arable, proximate	25	14–82	75 (16) a	5.50 (0.44) b	7.1 (3.0) b
Post-arable, isolated	18	13–75	72 (12) a	5.40 (0.60) b	6.9 (5.1) b

To reveal their relative importance, explanatory variables were fitted to various species metrics (all species, forest specialists, generalist, open land species, and woody species, respectively) for the 43 post-arable plantations using General Linear Models (GLM) with Poisson error distribution and logarithmic link function. Models were built applying backwards elimination, entering all variables and subjecting the resulting model to model simplification until the most parsimonious model had been identified. Percentage cover of the herbaceous layer (all species) and cover sums for habitat-defined groups were modelled in the same way, except that ordinary GLM (Gaussian error distribution and identity link) was applied. Variables used in GLM included stand age, distance to nearest core forest, soil pH, tree layer cover and total canopy cover (tree and shrub layer). Distance to nearest core forest (m) was used as a continuous explanatory variable in GLM instead of stand type (proximate, isolated).

The two large forest patches (areas B and C) and also some of the smaller patches in the fragmented area A contained more than one oak stand with sample plots. The GLM applied does not provide specific information on spatial autocorrelation. Spatial autocorrelation between stands of the same forest patch may occur, but probably not as a result of an underlying difference in regional species pools. All stands in the study area share the same regional species pool, as the study area is not very large (4000 ha) and climatic and edaphic gradients are small (Tyler et al., 2007). Therefore, differences in herb layer vegetation between stands are likely to primarily result from factors related to land use history, forest age and fragmentation.

Indicator species analysis was performed to assess the strength of association between species and the three groups of oak planta-

tions (Dufrêne and Legendre, 1997). We applied an improved method of indicator species analysis, Multilevel Pattern Analysis (MPA, De Cáceres et al., 2010). This method allows combination of groups of sites, and identifies species which indicate either one group only, or a combination of several groups, respectively. GLM and MPA were performed in R 2.12.2 (R Development Core Team, 2010).

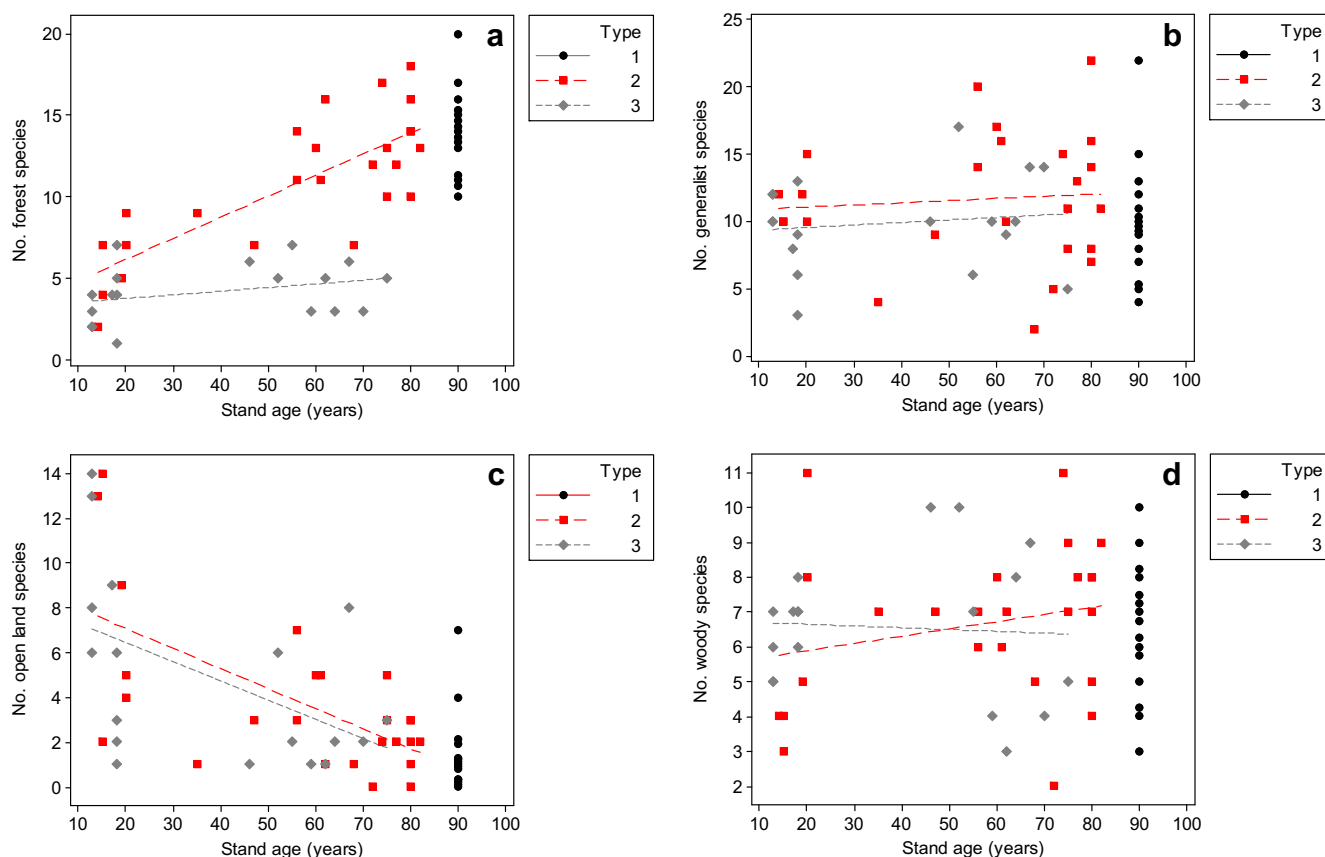
### 3. Results

#### 3.1. Stand characteristics

There were no significant differences in mean canopy cover between post-arable plantations and oak plantations in core forest, but soil pH was significantly lower and organic matter content significantly higher in core forest (Table 1). There were no significant differences in canopy cover, soil pH or organic matter between proximate and isolated post-arable plantations (Table 1). Soil pH did not change significantly with stand age ( $r^2 = 0.040$ ,  $p = 0.234$ ,  $n = 43$ ), but organic matter content increased with stand age in post-arable plantations ( $r^2 = 0.606$ ,  $p < 0.001$ ,  $n = 26$ ). In general, organic matter content was negatively correlated with soil pH (Pearson  $r = -0.853$ ,  $p < 0.001$ ,  $n = 36$ ).

#### 3.2. Species richness

In total, we found 155 herbaceous vascular plants in the herbaceous layer, of which 42 were forest specialists, 57 were generalist species and 56 were classified as open land species. In addition, 37 woody species were found in the herbaceous layer. Six of the forest



**Fig. 2.** Relations between number of species and stand age in oak plantations. Stand types are plantations in core forest (1, placed at stand age 90 years for comparison, some dots slightly moved to distinguish plots with the same values), proximate post-arable plantations (2) and isolated post-arable plantations (3).  $R^2$ -values are given for statistically significant ( $p < 0.05$ ) linear regressions. (a) Forest specialists: Type 2,  $r^2 = 0.611$ . (b) Generalist species. (c) Open land species: Type 2,  $r^2 = 0.391$ . Type 3,  $r^2 = 0.254$ . (d) Woody species.

specialists were vernal species (*Adoxa moschatellina*, *Anemone nemorosa*, *Anemone ranunculoides*, *Corydalis intermedia*, *Gagea lutea*, *Gagea spathacea*) and one generalist species was vernal (*Ranunculus ficaria*).

Linear regression showed that the number of forest specialists increased significantly with stand age in the proximate stands, but not in the isolated plantations (Fig. 2a). Species richness in older proximate stands was similar to that of stands in core forest (Fig. 2a). There was no effect of stand age or isolation on species numbers of generalists or woody species (Fig. 2b,d). For woody species, this pattern remained unchanged also when including woody species of the shrub layer (1–5 m height, results not shown). The number of open land species decreased with increasing stand age in both proximate and isolated stands (Fig. 2c).

According to the GLM analysis, total species richness in the herb layer of all post-arable stands ( $n = 43$ ) was positively related to stand age, soil pH and tree layer cover, but negatively with total canopy cover (i.e. including the shrub layer, Table 2). Stand age (+) and distance to the nearest core forest (–) explained the majority of variation in species richness of forest specialists in post-arable plantations, but soil pH also had a slight positive effect (Table 2). The number of generalist species increased significantly with stand age and tree layer cover, but total canopy cover (tree and shrub layer) was negatively related to richness of generalists. Stand age had a strong negative effect on open land species richness. None of the explanatory factors in GLM significantly accounted for variation in woody species richness (Table 2).

### 3.3. Species abundance

According to linear regression, total ground cover of forest specialists increased significantly with stand age in proximate plantations, and slightly, but still significantly, in isolated plantations (Fig. 3a). There was no significant difference in the ground cover of summer-green forest species between the oldest proximate stands (>70 years,  $n = 11$ ) and the 15 plantations in core forest ( $t$ -test). In contrast, the mean cover of vernal species was significantly higher in core forest than in the oldest post-arable stands (mean cover 47% vs 11%,  $p < 0.001$ ,  $t$ -test). This difference was mainly caused by a generally higher abundance of *A. nemorosa* in core forest, while this species was rare in all but two of the post-arable plantations (Fig. 3b). Ground cover of generalists declined in older proximate stands but increased with stand age in isolated plantations (Fig. 3c). There were no significant relationships between stand age and the cover of open land species or woody species in the herbaceous layer.

GLM analysis of all post-arable sample plots ( $n = 43$ ) revealed that cover of all species was best explained by stand age (+), soil

pH (+) and total canopy cover (–). Stand age (+) and distance to the nearest core forest (–) were significant explanatory factors for forest specialist abundance. Abundance of generalist species increased with soil pH, and stand age had a positive effect on the abundance of woody species in the herbaceous layer (Table 2).

### 3.4. Species distributions in relation to stand type

Forest specialists were a heterogeneous group with respect to their capacity to colonize post-arable stands (Table 3). Several species had a low colonization capacity and were indicative of core forest according to Multilevel Pattern Analysis (e.g., *A. nemorosa*, *Lamium galeobdolon*). However, all species indicative of core forest had colonized at least some of the proximate plantations (results not shown). Another subgroup of forest specialists was found to regularly colonize proximate stands, but was rarely encountered in isolated stands (Core + Proximate, e.g., *Mercurialis perennis*, *Stellaria holostea*). A few forest species were indicators of proximate stands (e.g., *A. moschatellina*, *Circaea lutetiana*). The occurrence of several forest specialists was either not influenced by stand type (e.g., *Milium effusum*, *Poa nemoralis*) or they were even indicators of post-arable plantation (Proximate + Isolated, e.g., *Festuca gigantea*, *Moehringia trinervia*).

With few exceptions (e.g., *Deschampsia flexuosa*), generalist species and open land species were either common in all stand types or indicated post-arable plantations (Table 3). The distribution of most woody species was not influenced by stand type (Table 3).

## 4. Discussion

### 4.1. Dispersal-based processes

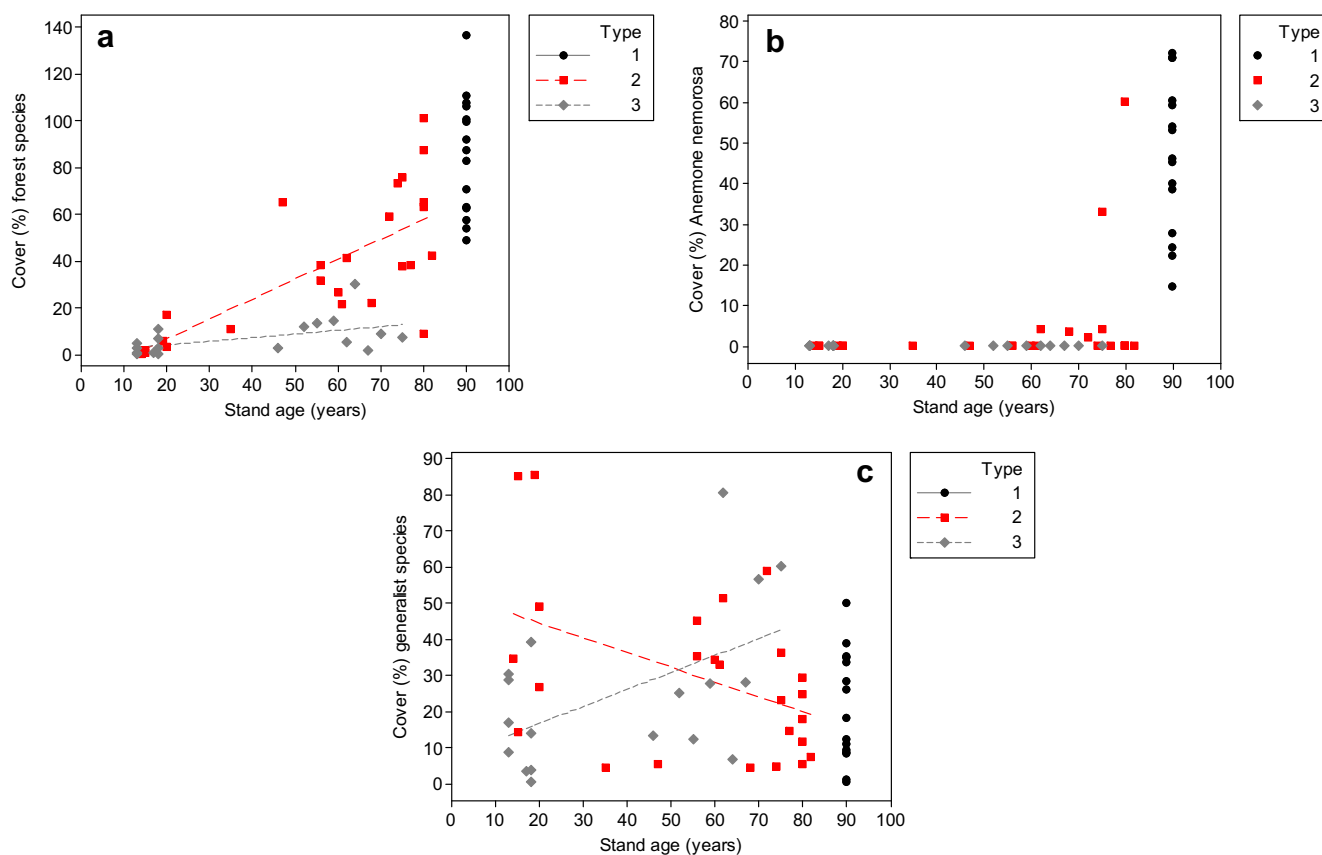
Our results demonstrate that habitat fragmentation has a large impact on the colonization patterns of forest specialists in post-arable oak plantations. Importantly, members of this species group showed large variation in their distribution pattern within the three stand categories. In general, proximate post-arable plantations can be colonized by most forest species by gradual, diffusion-like colonization (Matlack, 1994; Brunet and von Oheimb, 1998a; Bossuyt et al., 1999b; Singleton et al., 2001; Verheyen and Hermy, 2001). The species specific rates of colonization of proximate stands are likely influenced by a combination of several factors, including size and distance of source populations, seed production, seed size and morphology of the species considered, and dispersal vectors (Graae and Sunde, 2000; Verheyen et al., 2003; Kolb and Diekmann, 2005).

The time needed to develop populations to a size similar to that found in core forest varied widely depending on the species in

**Table 2**

Results of General Linear Models including effects of stand age, distance to nearest core forest, soil pH, tree layer cover (%) and total canopy cover (% tree and shrub layer) on species groups in the herbaceous layer of post-arable oak plantations ( $n = 43$ ), a) no. of species, and b) cover (%) of species. Given are  $z$ -/ $t$ -values of statistical significant variables ( $*P < 0.05$ ,  $**P < 0.01$ ,  $***P < 0.001$ ), and variation explained (% deviance explained of null deviance) of the final models.

	Stand age	Distance to core forest	Soil pH	Tree layer	Tree + shrub layer	Variation explained (%)
<i>(a) No. of species</i>						
All species	3.628***		2.461*	2.992**	–2.760**	21.7
Forest species	5.722***	–4.397***	2.091*			69.0
Generalist species	2.536*			2.857**	–3.451***	24.9
Open land species	–6.656***					36.4
Woody species						2.9
<i>(b) Percent cover</i>						
All species	6.222***		2.548*		–2.505*	51.8
Forest species	5.301***	–2.413*				52.2
Generalist species			2.089*			9.6
Open land species						4.0
Woody species	2.062*					9.4



**Fig. 3.** Relations between cover (%) and stand age in post-arable oak plantations. Stand types are plantations on core forest land (1, placed at stand age 90 years for comparison), proximate post-arable plantations (2) and isolated post-arable plantations (3).  $R^2$ -values are given for statistically significant ( $p < 0.05$ ) linear regressions. (a) Forest specialists: Type 2,  $r^2 = 0.528$ . Type 3,  $r^2 = 0.263$ . (b) *Anemone nemorosa*. (c) Generalist species: Type 2,  $r^2 = 0.197$ . Type 3,  $r^2 = 0.269$ .

question. For example, many slow-colonizing species still indicate core forest in the study area (Table 3). A prime example is *A. nemorosa*. This species was common in core forest, and was the only vernal species attaining high cover values. Large carpets of this clonal geophyte are one of the most characteristic features of core forests in the study region and elsewhere in Europe (Baeten et al., 2010). *A. nemorosa* had colonized several sample plots in proximate plantations, but only after 60–80 years. Transect studies across ecotones between core forest and proximate plantations have shown that the advancing edge of *Anemone* carpets moves at an average rate of only  $0.4 \text{ m year}^{-1}$  (Brunet and von Oheimb, 1998b). Several other slow-colonizing forest specialists probably expand within proximate plantations through a combination of recruitment by seeds and clonal propagation (e.g., *L. galeobdolon*, *Melica uniflora*, *M. perennis*, *Oxalis acetosella*, *S. holostea*, *S. nemorum*, cf. Brunet and von Oheimb, 1998a).

In the proximate plantations of this study, a minimum of approximately 60 years was needed to accumulate forest species numbers to a level comparable to core forests, a pattern that is consistent with earlier findings from floristic surveys in our study area (Brunet, 2004, 2007b) and from similar studies carried out elsewhere (Bossuyt and Hermy, 2000; Honnay et al., 2002; Flinn and Marks, 2004).

In the more extensively fragmented western part of our study area, only three forest patches are of ancient origin and contain a rich flora of forest specialists comparable to the two large forest areas. Therefore, the colonization of isolated plantations in this part of the study area is not only inhibited by forest fragmentation *per se*, but also by the very low proportion of core forest with source populations (Vellend, 2003; De Frenne et al., 2011). Most forest specialists remained absent from these stands, and species

richness of this group did not increase in stands older than 20 years. The comprehensive and negating effect of fragmentation on this group is strongly indicative of an inherent limited dispersal capacity (Peterken and Game, 1984; Dzwonko and Loster, 1992; Grashof-Bokdam and Geertsema, 1998; Jacquemyn et al., 2001, 2003). This view is supported by our observations that isolated and relatively young oak stands were quickly colonized by a few forest specialists possessing a high capacity for long-distance dispersal. For example, several shade-tolerant grass species (*F. gigantea*, *M. effusum*, *P. nemoralis*) which are effectively dispersed in animal fur (Heinken, 2000; Graae, 2002), or in the dung of deer (von Oheimb et al., 2005), regularly colonized these stands.

Woody species are often noted as possessing efficient dispersal capacities (Butaye et al., 2001; Wulf and Heinken, 2008; Sciama et al., 2009). Likewise, the forest species which were among the first to colonize the youngest stands in our study, included *Ulmus glabra* and *A. pseudoplatanus*. Their winged seeds are produced in large numbers and are efficiently dispersed. Compared to pioneer trees such as *Betula* or *Salix*, their seeds are also larger, which is likely to have promoted seedling recruitment in the initially dense herbaceous vegetation prior to canopy closure of the planted oaks. Richness of woody species in the understory had already reached levels of core forest sites after 15–20 years in post-arable plantations, regardless of the extent of isolation. However, site-to-site variation in species richness was large. An experimental study in the same area indicates that post-dispersal seed predation may be of importance in explaining spatial variability in woody vegetation (Bruun et al., 2010).

Species richness of generalists remained at a constant level along the chronosequence in both proximate and isolated planta-

**Table 3**

Association between species and stand types according to Multilevel Pattern Analysis. Stand types are Core (oak plantations in core forest), Proximate (proximate post-arable plantations) and Isolated (isolated post-arable plantations). Significance levels are: \*\*\* $p < 0.001$ ; \*\* $p < 0.01$ ; \* $p < 0.05$ . Only species with a frequency of at least 30% in one of the stand types are included in the table. F = forest specialists, G = generalist species, O = open land species, and W = woody species. V = vernal species.

Stand type indicated	Indicator value	P-value	Species type
<b>Core</b>			
<i>Anemone nemorosa</i> (V)	0.931	***	F
<i>Athyrium filix-femina</i>	0.878	***	F
<i>Deschampsia flexuosa</i>	0.622	**	G
<i>Gagea lutea</i> (V)	0.564	*	F
<i>Gagea spathacea</i> (V)	0.756	***	F
<i>Lamium galeobdolon</i>	0.795	***	F
<i>Maianthemum bifolium</i>	0.740	***	F
<i>Polygonatum multiflorum</i>	0.712	***	F
<i>Stellaria nemorum</i>	0.798	**	F
<b>Core + Proximate</b>			
<i>Deschampsia cespitosa</i>	0.843	***	G
<i>Dryopteris filix-mas</i>	0.721	*	F
<i>Melica uniflora</i>	0.736	*	F
<i>Mercurialis perennis</i>	0.570	*	F
<i>Oxalis acetosella</i>	0.837	***	F
<i>Quercus robur</i>	0.803	*	W
<i>Stellaria holostea</i>	0.922	***	F
<i>Viola riv./reich.</i>	0.721	***	F
<b>Proximate</b>			
<i>Adoxa moschatellina</i> (V)	0.632	**	F
<i>Circaea lutetiana</i>	0.857	***	F
<i>Geranium robertianum</i>	0.582	*	G
<b>Proximate + Isolated</b>			
<i>Epilobium montanum</i>	0.805	***	G
<i>Festuca gigantea</i>	0.762	**	F
<i>Fragaria vesca</i>	0.649	*	G
<i>Galium aparine</i>	0.944	***	G
<i>Geum urbanum</i>	0.860	***	G
<i>Holcus lanatus</i>	0.571	*	O
<i>Moehringia trinervia</i>	0.740	*	F
<i>Poa trivialis</i>	0.804	***	G
<i>Taraxacum Vulgaria</i>	0.682	**	G
<i>Urtica dioica</i>	0.922	***	G
<b>Isolated</b>			
<i>Elytrigia repens</i>	0.561	**	O
<i>Epilobium angustifolium</i>	0.601	**	G
<i>Sambucus nigra</i>	0.703	**	W
<b>Core + Isolated</b>			
<i>Sorbus aucuparia</i>	0.696	***	W
<b>No preferred types</b>			
<i>Acer pseudoplatanus</i>			W
<i>Agrostis capillaris</i>			G
<i>Arrhenatherum elatius</i>			O
<i>Carex pilulifera</i>			G
<i>Dactylis glomerata</i>			G
<i>Dryopteris carthusiana</i>			F
<i>Crataegus spp.</i>			W
<i>Fagus sylvatica</i>			W
<i>Fraxinus excelsior</i>			W
<i>Galeopsis bif./tetr.</i>			G
<i>Juncus effusus</i>			G
<i>Milium effusum</i>			F
<i>Myosotis arvensis</i>			O
<i>Poa nemoralis</i>			F
<i>Ranunculus ficaria</i> (V)			G
<i>Rubus idaeus</i>			W
<i>Rubus fruticosus</i>			W
<i>Ulmus glabra</i>			W

tions, which suggests that the species of this group generally are fast colonizers. Most of these species are present in the agricultural matrix in the study area, in particular in grasslands and tall herb communities along roads, ditches and forest edges. These relatively abundant source populations provided ample opportunities for

seed dispersal into new plantations. An interesting result of our study was the fact that the ground cover of generalists decreased with stand age in proximate plantations, but increased in isolated stands. Increasing competition from colonizing forest species in the former sites, absence of such competition and a larger seed influx in the isolated stands may explain these contrasting patterns.

As expected, open land species decreased with increasing stand age. This pattern was observed within all post-arable forest stands. Regardless of what is presumably a regular and extensive seed rain from such species emanating from the surrounding open landscape, this has nevertheless not resulted in their persistent occurrence within forest stands. This suggests that open land species are not able to compete with generalist and forest species in the interior parts of plantations, regardless of the suitability of the matrix.

#### 4.2. Niche-based processes

Light is considered as the most important limiting resource for understory plants (Neufeld and Young, 2003). In our study, the number of generalists increased with tree layer cover, but decreased with total canopy cover (tree and shrub layer). This indicates that light demanding generalist species are able to persist under oak canopies, unless a dense shrub layer of shade casting species such as *Acer*, *Carpinus*, *Corylus*, *Fagus*, *Tilia* or *Ulmus* becomes established.

Vernal species use the high light flux prior to leaf flush of the canopy trees. During their short growing period, they maintain higher rates of photosynthesis and respiration than summer species. This may explain their association with eutrophic soils which provide readily available resources for achieving rapid growth (Neufeld and Young, 2003; Burton et al., 2011). This association has also resulted in a disproportionate loss of habitat through the historical cultivation of eutrophic soils. Restoration of broadleaved forest on abandoned fields will thus provide potentially suitable habitat for vernal herb species.

Our results indicate, however, that the colonization by vernal herbs is the most critical part of herb layer restoration in plantations. As colonized proximate stands did not deviate from uncolonized ones in measured soil properties or canopy cover, we suggest further studies to analyse the conditions that favour successful dispersal and recruitment of vernal herbs (cf. Baeten et al., 2010). Considering that all vernal herbs in this study are geophytes, the effects of top soil structure (e.g. porosity) on clonal spread or bulb production in post-arable soils should be explored in more detail.

Soil pH is another key factor controlling plant distributions (Brunet and Neymark, 1992; Tyler, 2003). Previous studies have reported a variable persistence of increased soil pH in post-agricultural forest (Richter et al., 1994; Koerner et al., 1997; Bossuyt et al., 1999a; Honnay et al., 2002; Matlack, 2009). In our study, post-arable soil pH remained higher than soil pH on core forest land throughout the chronosequence. Although oak litter is relatively persistent, oak has been shown to have a less acidifying effect on the topsoil than, e.g. beech (*F. sylvatica*, Nordén, 1994).

The difference in soil acidity partly explains the persistent floristic gradient in the herbaceous layer between old post-arable stands and sites in core forest. Eutrophic and acidifugous species such as *C. lutetiana*, *F. gigantea* and *Geum urbanum* are mostly absent from core forest, but were frequent in post-arable plantations. Small, oligotrophic and calcifugous species such as *Carex pilulifera*, *D. flexuosa* and *Maianthemum bifolium*, on the other hand, rarely recruited in the tall and dense herbaceous layer of post-arable plantations.

In summary, the spatio-temporal stand characteristics explained a larger part of the variation in understory species richness and abundance in post-arable forests than soil pH and canopy cover. Most post-arable stands had a soil pH between 5.0 and 6.0 and a



canopy cover ranging from 60 to 85%. Such intermediate conditions are favourable for almost all herbaceous forest species and represent only a relatively small part of the range in soil acidity and light availability in temperate broadleaved forests (Kolb and Diekmann, 2004; Wulf and Naaf, 2009).

#### 4.3. Forest management and restoration implications

From our results, we conclude that the following three key characteristics should be met for successful recovery of a rich understory of forest species: (1) where possible, locating plantations adjacent to older forest will facilitate colonization from source populations. (2) Maintaining a continuous canopy cover of 70–80% by regular light thinning and promotion of a patchy shrub layer will favour forest specialists in relation to light-demanding generalists. (3) Plantations established on loamy soils of intermediate to high pH will maximize potential understory species richness. In severely isolated post-arable plantations, assisted dispersal from regional source populations will be necessary to enhance diversity of herbaceous forest species. For other organism groups, such as saproxylic beetles or epiphytic bryophytes and lichens, modification of other aspects of forest management (i.e. increased rotation length, dead wood and green tree retention) would be needed to improve the biodiversity value of plantation forests (Hartley, 2002; Brunet et al., 2010; Felton et al., 2010).

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#### References

- Baeten, L., De Frenne, P., Verheyen, K., Graae, B.J., Hermy, M., 2010. Forest herbs in the face of global change: a single-species-multiple-threats approach for *Anemone nemorosa*. *Plant Ecology and Evolution* 143, 19–30.
- Berg, Å., Ehnström, B., Gustafsson, L., Hallingbäck, T., Jonsell, M., Weslien, J., 1994. Threatened plant, animal, and fungus species in Swedish forests—distribution and habitat associations. *Conservation Biology* 8, 718–731.
- Berglund, B.E. (Ed.), 1991. The cultural landscape during 6000 years in southern Sweden – the Ystad project. *Ecological Bulletins*, 41.
- Bossuyt, B., Deckers, J., Hermy, M., 1999a. A field methodology for assessing man-made disturbance in forest soils developed in loess. *Soil Use and Management* 15, 14–20.
- Bossuyt, B., Hermy, M., Deckers, J., 1999b. Migration of herbaceous plant species across ancient–recent forest ecotones in central Belgium. *Journal of Ecology* 87, 628–638.
- Bossuyt, B., Hermy, M., 2000. Restoration of the understorey layer of recent forest bordering ancient forest. *Applied Vegetation Science* 3, 43–50.
- Bremer, L.L., Farley, K.A., 2010. Does plantation forestry restore biodiversity or create green deserts? A synthesis of the effects of land-use transitions on plant species richness. *Biodiversity and Conservation* 19, 3893–3915.
- Brunet, J., 2004. Colonization of oak plantations by forest plants: effects of regional abundance and habitat fragmentation. In: Honnay, O., Verheyen, B., Bossuyt, B., Hermy, M. (Eds.), *Forest Biodiversity: Lessons from History for Conservation*. CAB International, Wallingford, UK, pp. 129–141.
- Brunet, J., 2007a. From Wood Pasture to Pillar Hall – Changes in Forest Area and Stand Structure after Introduction of Regular Forest Management at Skabersjö Estate 1838 (in Swedish). Working report No. 35. Southern Swedish Forest Research Centre, Alnarp.
- Brunet, J., 2007b. Plant colonization in heterogeneous landscapes – an 80-year perspective on restoration of broadleaved forest vegetation. *Journal of Applied Ecology* 44, 563–572.
- Brunet, J., Fritz, Ö., Richnau, G., 2010. Biodiversity in European beech forests – a review with recommendations for sustainable forest management. *Ecological Bulletins* 53, 77–94.
- Brunet, J., Neymark, M., 1992. Importance of soil acidity to the distribution of rare forest grasses in South Sweden. *Flora* 187, 317–326.
- Brunet, J., Tyler, G., 2000. Interannual variability in abundance of field layer species in a south Swedish deciduous wood. *Flora* 195, 97–103.
- Brunet, J., von Oheimb, G., 1998a. Migration of vascular plants to secondary woodlands in southern Sweden. *Journal of Ecology* 86, 429–438.
- Brunet, J., von Oheimb, G., 1998b. Colonization of secondary woodlands by *Anemone nemorosa*. *Nordic Journal of Botany* 18, 369–377.
- Bruun, H.H., Valtinat, K., Kollmann, J., Brunet, J., 2010. Post-dispersal seed predation of woody forest species limits recolonization of forest plantations on ex-arable land. *Preslia* 82, 345–356.
- Burton, J.L., Mladenoff, D.J., Clayton, M.K., Forrester, J.A., 2011. The roles of environmental filtering and colonization in the fine-scale spatial patterning of ground-layer plant communities in north temperate deciduous forests. *Journal of Ecology* 99, 764–776.
- Butaye, J., Jacquemyn, H., Hermy, M., 2001. Differential colonization causing non-random forest plant community structure in a fragmented agricultural landscape. *Ecography* 24, 369–380.
- De Cáceres, M., Legendre, P., Moretti, M., 2010. Improving indicator species analysis by combining groups of sites. *Oikos* 119, 1674–1684.
- De Frenne, P., Baeten, L., Graae, B.J., Brunet, J., Wulf, M., Orczewska, A., Kolb, A., Jansen, I., Jamoneau, A., Jacquemyn, H., Hermy, M., Diekmann, M., De Schrijver, A., De Sanctis, M., Decocq, G., Cousins, S.A.O., Verheyen, K., 2011. Interregional variation in the floristic recovery of postagricultural forests. *Journal of Ecology* 99, 600–609.
- Dufrêne, M., Legendre, P., 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecological Monographs* 67, 345–366.
- Dzwonko, Z., Loster, S., 1992. Species richness and seed dispersal to secondary woods in southern Poland. *Journal of Biogeography* 19, 195–204.
- Ehrlén, J., Eriksson, O., 2000. Dispersal limitation and patch occupancy in forest herbs. *Ecology* 81, 1667–1674.
- Emanuelsson, U., 2009. *The Rural Landscapes of Europe – How Man has Shaped European Nature*. Formas, Stockholm.
- Falkengren-Grerup, U., ten Brink, D.-J., Brunet, J., 2006. Land use effects on soil N, P, C and pH persist over 40–80 years of forests growth on agricultural soils. *Forest Ecology and Management* 225, 74–81.
- Felton, A., Lindbladh, M., Brunet, J., Fritz, Ö., 2010. Replacing coniferous monocultures with mixed-species production stands: an assessment of the potential benefits for forest biodiversity in northern Europe. *Forest Ecology and Management* 260, 939–947.
- Flinn, K.M., Marks, P.L., 2004. Land-use history and forest herb diversity in Tompkins County New York, USA. In: Honnay, O., Verheyen, K., Bossuyt, B., Hermy, M. (Eds.), *Forest Biodiversity: Lessons from History for Conservation*. CAB International, pp. 81–95.
- Flinn, K.M., Vellend, M., 2005. Recovery of forest plant communities in post-agricultural landscapes. *Frontiers in Ecology and the Environment* 3, 243–250.
- Gilliam, F.S., 2007. The ecological significance of the herbaceous layer in temperate forest ecosystems. *BioScience* 57, 845–858.
- Graae, B.J., 2002. The role of epizoochorous seed dispersal of forest plant species in a fragmented landscape. *Seed Science Research* 12, 113–121.
- Graae, B.J., Sunde, P.B., 2000. The impact of forest continuity and management on forest floor vegetation evaluated by species traits. *Ecography* 23, 720–731.
- Grashof-Bokdam, C.J., Geertsema, W., 1998. The effect of isolation and history on colonization patterns of plant species in secondary woodland. *Journal of Biogeography* 25, 837–846.
- Hannah, L., Carr, J.L., Lankerani, A., 1995. Human disturbance and natural habitat: a biome level analysis of a global data set. *Biodiversity and Conservation* 4, 128–155.
- Hartley, M.J., 2002. Rationale and methods for conserving biodiversity in plantation forests. *Forest Ecology and Management* 155, 81–95.
- Heinken, T., 2000. Dispersal of plants by a dog in a deciduous forest. *Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie* 122, 449–467.
- Hermy, M., Verheyen, K., 2007. Legacies of the past in the present-day forest biodiversity: a review of past land-use effects on forest plant species composition and diversity. *Ecological Research* 22, 361–371.
- Honnay, O., Bossuyt, B., Verheyen, K., Butaye, J., Jacquemyn, H., Hermy, M., 2002. Ecological perspectives for restoration of plant communities in European temperate forests. *Biodiversity and Conservation* 11, 213–242.
- Hultberg, T., Brunet, J., Broström, A., Lindbladh, M., 2010. Forest in a cultural landscape – the vegetation history of Torup in southernmost Sweden. *Ecological Bulletins* 53, 141–153.
- Jacquemyn, H., Butaye, J., Hermy, M., 2001. Forest plant species richness in small, fragmented mixed deciduous forest patches: the role of area, time and dispersal limitation. *Journal of Biogeography* 28, 801–812.
- Jacquemyn, H., Butaye, J., Hermy, M., 2003. Impacts of restored patch density and distance from natural forests on colonization success. *Restoration Ecology* 11, 417–423.
- Koerner, W., Dupouey, J.L., Dambrine, E., Benoit, M., 1997. Influence of past land use on the vegetation and soil of present day forest in the Vosges mountains, France. *Journal of Ecology* 85, 351–358.
- Kolb, A., Diekmann, M., 2004. Effects of environment, habitat configuration and forest continuity on the distribution of forest plant species. *Journal of Vegetation Science* 15, 199–208.
- Kolb, A., Diekmann, M., 2005. Effects of life-history traits on responses of plant species to forest fragmentation. *Conservation Biology* 19, 929–938.
- Lindbladh, M., Foster, D.R., 2010. Dynamics of long-lived foundation species: the history of *Quercus* in southern Scandinavia. *Journal of Ecology* 98, 1330–1345.

- Matlack, G.R., 1994. Plant species migration in a mixed-history forest landscape in eastern North America. *Ecology* 75, 1491–1502.
- Matlack, G.R., 2009. Long-term changes in soils of second-growth forest following abandonment from agriculture. *Journal of Biogeography* 36, 2066–2075.
- Minitab Inc., 2011. Minitab statistical software, release 16.1.1. Minitab Inc., State College, PA.
- Mossberg, B., Stenberg, L., 2003. Den Nya Nordiska Floran. Wahlström & Widstrand, Stockholm.
- Motzkin, G., Foster, D., Allen, A., Harrod, J., Boone, R., 1996. Controlling site to evaluate history: vegetation patterns of a New England sand plain. *Ecological Monographs* 66, 345–365.
- Neufeld, H.S., Young, D.R., 2003. Ecophysiology of the herbaceous layer in temperate deciduous forests. In: Gilliam, F.S., Roberts, M.R. (Eds.), *The Herbaceous Layer in Forests of Eastern North America*. University Press, Oxford, pp. 38–90.
- Nilsson, S.G., Niklasson, M., Hedin, J., Eliasson, P., Ljungberg, H., 2006. Biodiversity and sustainable forestry in changing landscapes-principles and Southern Sweden as an example. *Journal of Sustainable Forestry* 21, 11–43.
- Nordén, U., 1994. The influence of broad-leaved tree species on pH and organic matter content of forest topsoils in Scania, south Sweden. *Scandinavian Journal of Forest Research* 9, 1–8.
- Ozinga, W.A., Schaminée, J.H.J., Bekker, R.M., Bonn, S., Poschlod, P., Tackenberg, O., Bakker, J., van Groenendael, J.M., 2005. Predictability of plant species composition from environmental conditions is constrained by dispersal limitation. *Oikos* 108, 555–561.
- Peterken, G.F., Game, M., 1984. Historical factors affecting the number and distribution of vascular plant species in the woodland of central Lincolnshire. *Journal of Ecology* 72, 155–182.
- R Development Core Team, 2010. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.
- Richter, D.D., Markewitz, D., Wells, C.G., Allen, H.L., April, R., Heine, P.R., Urrego, B., 1994. Soil chemical change during three decades in an old-field loblolly pine (*Pinus taeda* L.) ecosystem. *Ecology* 75, 1463–1473.
- Sciama, D., Augusto, L., Dupouey, J.L., Gonzalez, M., Domínguez, C.M., 2009. Floristic and ecological differences between recent and ancient forests growing on non-acidic soils. *Forest Ecology and Management* 258, 600–608.
- Schmidt, M., von Oheimb, G., Kriebitzsch, W.-U., Ellenberg, H., 2002. Liste der im norddeutschen Tiefland typischen Waldgefäßpflanzen. *Mitteilungen der Bundesforschungsanstalt für Forst- und Holzwirtschaft* 206, 1–37.
- Singleton, R., Gardescu, S., Marks, P.L., Geber, M.A., 2001. Forest herb colonization of postagricultural forests in central New York State, USA. *Journal of Ecology* 89, 325–338.
- Tyler, G., 2003. Some ecophysiological and historical approaches to species richness and calcicole/calcifuge behaviour – contribution to a debate. *Folia Geobotanica* 38, 419–428.
- Tyler, T., Olsson, K.-A., Johansson, H., Sonesson, M. (Eds.), 2007. *Floran i Skåne–Arterna och deras utbredning*. Lunds Botaniska Förening, Lund.
- Valtinat, K., Bruun, H.H., Brunet, J., 2008. Restoration of oak forest: effects of former arable land use on soil chemistry and herb layer vegetation. *Scandinavian Journal of Forest Research* 23, 513–521.
- Vellend, M., 2003. Habitat loss inhibits recovery of plant diversity as forests regrow. *Ecology* 84, 1158–1164.
- Vellend, M., Verheyen, K., Flinn, K.M., Jacquemyn, H., Kolb, A., Van Calster, H., Peterken, G., Graae, B.J., Bellemare, J., Honnay, O., Brunet, J., Wulf, M., Gerhardt, F., Hermy, M., 2007. Homogenization of forest plant communities and weakening of species–environment relationships via agricultural land use. *Journal of Ecology* 95, 565–573.
- Verheyen, K., Hermy, M., 2001. The relative importance of dispersal limitation of vascular plants in secondary forest succession in Muizen Forest, Belgium. *Journal of Ecology* 89, 829–840.
- Verheyen, K., Honnay, O., Motzkin, G., Hermy, M., Foster, D.R., 2003. Response of forest plant species to land-use change: a life-history trait-based approach. *Journal of Ecology* 91, 563–577.
- von Oheimb, G., Schmidt, M., Kriebitzsch, W.-U., Ellenberg, H., 2005. Dispersal of vascular plants by game in northern Germany. Part II: Red deer (*Cervus elaphus*). *European Journal of Forest Research* 124, 55–65.
- Wulf, M., Heinken, T., 2008. Colonization of recent coniferous versus deciduous forest stands by vascular plants at the local scale. *Applied Vegetation Science* 11, 307–316.
- Wulf, M., Naaf, T., 2009. Herb layer response to broadleaf tree species with different leaf litter quality and canopy structure in temperate forests. *Journal of Vegetation Science* 20, 517–526.