Groupings of life-history traits are associated with distribution of forest plant species in a fragmented landscape

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Abstract

Questions: 1. Do relationships among forest plant traits correspond to dispersability-persistence trade-offs or other inter-trait correlations found in the literature? 2. Do species groups delineated by trait similarity, differ in occurrence in ancient vs. new forests or isolated vs more continuous forest patches? 3. Are these patterns consistent for different forest types?

Location: Central Belgium, near Leuven.

Methods: We investigate the distributions of a large set of plant traits and combinations among all forest species occurring in patches with varying forest continuity and isolation. Through calculation of Gower's similarity index and subsequent clustering, 'emergent' species groups are delineated. Then, the relative occurrence of these different groups in forest patches of different age and size, sustaining different forest types (alluvial vs. *Quercion*), and having different isolation status is compared through multivariate GLM analysis.

Results: Correlations among several life history traits point towards trade-offs of dispersability and fecundity vs. longevity. We distinguished three species groups: 1= mainly shrubs or climbers with fleshy or wind dispersed fruits and high dispersal potential; 2 = dominated by small, mainly vegetatively reproducing herbs; 3 = with spring flowering herbs with large seeds and mainly unassisted dispersal. Relative occurrence of these groups was significantly affected by forest age, area, isolation and forest type. Separate analyses for alluvial and *Quercion* forests indicated that the relative importance of these factors may differ, depending on forest type and species group. Both forest continuity and isolation are important in restricting the relative occurrence of forest species in alluvial forests, whatever their group membership. In *Quercion* forests forest patch area was the primary determinant of relative occurrence of species groups.

Conclusions: It is very important to preserve the actual forest area including the spatial setting and the dispersal infrastructure within the landscape. Next, forest connectivity may be restored, but it is inherently a long process.

Keywords: Dispersal; Ecoinformatics; Species group; Forest age; Isolation; Persistence; Reproduction.

Nomenclature: Lambinon et al. (1998).

Abbreviation: GSC = Gower's Similarity Coefficient.

Introduction

The effects of temporal interruptions in forest continuity on species diversity and composition have been studied extensively, especially in mosaic landscapes in Northwest Europe (e.g. Hermy & Stieperaere 1981; Peterken & Game 1984; Dzwonko & Loster 1989; Honnay et al. 1999; Graae & Sunde 2000) and North America (e.g. Glitzenstein et al. 1990; Matlack 1994). Independent of geographic region, recently established forests or forests that have experienced intermittent, intensive agricultural transformation differ significantly in vegetation composition from ancient forests. The resulting local presence-absence patterns of plant species are assumed to originate from population colonizations and extinctions, but these processes are very difficult to demonstrate given the long time-frames involved (but see Verheyen et al. (2004) for demonstration of metapopulation dynamics in a mosaic of forest patches).

All plant characteristics (traits) that influence the capacity of individual species to colonize patches and to persist within these patches are, therefore, important for community diversity (Ehrlén & van Groenendael 1998). However, trade-offs may exist between, for instance, dispersability and longevity or between longevity and fecundity, and these may limit the potential of forest species – evolutionarily adapted to relatively stable environments – to persist in current, man made landscapes where effects of highly dynamic land use are greater than those of natural disturbances such as fire or storms (Hermy et al. 1999; Honnay et al. 2002a, b).

During the past few decades ecological interest has shifted gradually from classical phylogenetic classification to species classifications that relate directly to function based on shared life-history traits (Lavorel et al. 1997; Semenova & van der Maarel 2000). Growing awareness that functional diversity, rather than species numbers *per se*, strongly determines ecosystem processes such as resource dynamics and biomass production (Díaz & Cabido 2001) has accelerated this process. Moreover,

these plant functional classifications may be useful in predicting dynamics of plant communities subjected to disturbances (Noble & Gitay 1996). This higher level of abstraction in comparison with species based analyses is essential for comparing vegetation dynamics and ecosystem processes over different biogeographical regions (Diaz & Cabido 1997).

Many authors have studied the specifics of plant species mainly restricted to ancient forest patches (reviewed by Hermy et al. 1999 and Verheyen et al. 2003a). While species indicative of ancient forest vary between countries (Hermy 1994; Wulf 1997), between regions within a country (Peterken & Game 1984; Graae 2000a) and between soil types (Dzwonko & Loster 1990), some general patterns emerge as to their characteristics and requirements. Regarding habitat requirements, Hermy et al. (1999) concluded that: "Ancient forest plant species tend to be more shade tolerant than the other forest plant species; dry and wet sites are avoided. They are typical of forest sites with an intermediate pH and nitrogen availability". Together with Verheyen et al. (2003a) and Wulf (2003) they also found that a complex of interacting variables may explain the poor ability of these species to colonize new forest sites: they all show low dispersability (i.e. large seeds, low fecundity, unassisted dispersal). Long life spans and limited dispersal in space and time can be seen as an adaptive response to relatively low disturbance regimes and high reliability of opportunities for local recruitment (Strykstra et al. 2002).

Here we investigate differences in distribution of many plant traits over all forest species occurring in forest patches of two community types and of various ages in Belgium. We analyse the correlation structure of the plant traits associated with these species. After delineating 'emergent' groups (cf. Lavorel et al. 1997) based on a large range of vegetative and reproductive traits, we compare their relative occurrence in the different forest patches. Three groups of research questions are addressed:

1. What is the relationship between life history traits of species found in a set of forest patches of various age and with various abiotic conditions? Are life-history traits distributed among species such as to allow differentiation of groups of species with coherent life-history syndromes, e.g. the seed size/shape - seed longevity trade-off noted in grasslands (Bekker et al. 1998) and forests (Moles et al. 2000)?

2. Do patterns of life-history traits occurrence differ between ancient forests and newly established forests or isolated vs. more continuous forest patches? Which traits are mainly 'responsible' for these differences in occurrence?

3. The effects of spatial arrangement of forest patches and/or forest age on plant species composition of differ-

ent forest types have been studied extensively (e.g. Graae 2000b; Verheyen et al. 2003), but impact of these factors on the occurrence of life history-based species groups has seldom been compared among forest community types. In particular, we investigate whether the relative impact of forest age, isolation and patch size differs between alluvial forests and upland *Quercion* forests.

Initially, to assess the impact of forest age, patch area, isolation and forest type on relative occurrence of species groups, these factors are incorporated into one analysis, using an ecoinformatics approach. Ultimately, species diversity is analysed separately for alluvial and *Quercion* forests because abiotic conditions differ considerably, resulting in communities being drawn from the same regional species pool through a different environmental filter. This study may contribute to a better understanding of mechanisms governing species assemblages in fragmented forests and, with earlier studies of Butaye et al. (2001) and Jacquemyn et al. (2003) in the same area, help predict colonization of newly established forest patches by forest plant species on the basis of their life-history traits. Finally, they can help to establish remedial measures to enhance colonization of newly established forests.

Material and Methods

Study area

The study area of 42 km² is in the central part of Belgium (Vlaams-Brabant) between Leuven, Diest and Tienen (for a map see Butaye et al. 2001). Due to a long history of logging and plantation activities this region is characterized by a complex land-use history (Butaye et al. 2001), resulting in a highly fragmented forest landscape with numerous small forests of different ages (Jacquemyn et al. 2003). Nowadays, forests cover only 6% of the investigated area. The study area partly covers the valley of the Velpe river and consists largely of alluvial soils, characterized by a silty texture, poor drainage, rich nutrient status and a weakly acid pH (mean = 4.9; SD = 0.9; $n = 60$). Close to the river, soils have no profile development, which suggests recent alluvial deposits. The most recent forests were established on former grasslands and are planted with *Populus* cultivars (63% of the total forest area). Older forests have affinity with the *Alno-Padion*. Apart from the planted *Populus*, *Alnus glutinosa* is the dominating tree species and is mainly found in coppice stands or coppice with standards. More recently established forests, often planted in *Arrhenatheretum elatioris* or sometimes *Calthion palustris* grasslands, show different successional stages with the youngest forests still displaying clear affinities to the *Filipenduletea*. Species

frequently occurring in the herb layer are: *Ranunculus ficaria*, *Cirsium oleraceum* and *Filipendula ulmaria*. The soils on the hills bordering the valley have a more sandy loam texture and are well drained and more acid (mean pH = 3.4; SD = 0.4; n = 40). These drier, elevated hills were frequently cultivated in the past and the forests are generally classified as *Quercion* forests. The tree layer mainly consists of *Quercus robur* and *Betula pendula*, but here 22% of the forest area is also planted with *Populus* cultivars. In this forest type common herb layer species are: *Teucrium scorodonia*, *Luzula pilosa*, *Poa nemoralis* and *Holcus mollis*.

Historical forest patches as sample units

The land-use history of the study area was reconstructed for all forests using nine historical maps from 1775 to 1991 (scale 1:20 000). All historical maps were digitalized and a Geographical Information System (GIS; Anon. 1998) was used to compare them, resulting in identification of 239 'forest patches', each with a homogeneous land-use history and a unique forest age (Butaye et al. 2001; Jacquemyn et al. 2003). Using forest patches as the sampling unit allowed us to distinguish easily between source and target patches. An older patch is considered as a potential source of plant species for a more recent forest patch, which is the target for potential colonization of plant species. This procedure only accounts for migrations from ancient to recently established forest patches and disregards migration in the opposite direction. However, earlier studies in this area pointed out that the latter may be rare since the species assemblages of recently established patches are nested subsets of those of ancient forests (Butaye et al. 2001).

Data collection

In 1998, the forest plant community was sampled twice, once in early spring and a second time during summer. Presence or absence was determined for 206 plant species occurring predominantly in forests (Tack et al. 1993; Honnay et al. 1999). Forest patches were systematically surveyed by walking transects of 5 m width. Special attention was given to ditches, ponds, forest borders and other microhabitats where more species could be expected. Therefore, sampling effort linearly increased with forest area (for more details see Butaye et al. 2001). For shrubs and trees, only species that were not planted were recorded. This procedure excludes almost all trees in the highest canopy layer whereas the shrub layer developed spontaneously in these forests. In total, 139 species were found. Species that could be determined only to genus level (*Sphagnum* spp. and *Hieracium* spp.) were omitted from the dataset because it would be inap-

propriate to use mean trait values in these cases. Hence we worked with a species list of 137 forest plants (see App. 1).

Data on plant traits of all species found in these forest patches were gathered from five plant databases: BIOLFLOR (Klotz et al. 2002), BIOPOP (Poschlod et al. 2003), the electronic version of 'Comparative plant ecology' (Hodgson et al. 1995), the soil seed bank database of Thompson et al. (1997) and the 'Biological traits of vascular plants' database (Kleyer 1995). These data were supplemented with information on long distance dispersal capacity from Tamis et al. (2004), unpublished data from the Rijksuniversiteit Groningen and our own measurements on seed weight and release height. Based on the trait standards of LEDA (Knevel et al. 2005) and the available data for the selected set of species, 24 plant traits were included in this study (Table 1). Some traits incorporated in the LEDA database (Knevel et al. 2003) were omitted either because data for our species was too scarce (seed number, digestion survival and attachment capacity) or the trait was not relevant for the case study (buoyancy and tissue density). Several other traits were included in the analysis based on their presumed importance in the specific context of finding differences in traits between forests of various ages (established strategy, life form and season of seedling emergence). An overview of traits compiled from the various data sources used to construct the final trait matrix is given in Table 1.

Data analysis

In a first exploratory phase, general correlations between the ordinal and numerical traits (n = 15) were examined using Spearman rank correlations. The relationships between ordinal and nominal traits were assessed by means of Kruskal-Wallis tests (Mann-Whitney for the binary variable 'branching') and the association between nominal traits was determined with the Pearson χ^2 test-statistic (Siegel & Castellan 1988). Our research was mainly directed towards ecological issues and since no specific evolutionary questions were addressed, we did not perform phylogenetically independent contrasts (Felsenstein 1985).

'Emergent' groups (*sensu* Lavorel et al. 1997) based on plant trait similarities were identified by calculating Gower's Similarity Coefficients (GSC; Gower 1971). GSC is a general, robust measure of proximity that can cope with mixed data types (nominal, ordinal, interval and ratio) as well as with missing values (Legendre & Legendre 1998) and it has been used by several authors to process trait matrices (Verheyen et al. 2003a; Hérault et al. 2005). For this analysis traits were included only if data were available for more than 50% of the species (see Table 1). The calculated Gower proximity matrices were

Table 1. Overview of all 24 plant traits used in the present study. For full description of trait categories (ordinal and nominal traits) see original references mentioned in the 'source' column. N = number of species with trait data available (max. 137).

Plant trait	Type of data	Unit (if any)	N	Source
Established strategy	Nominal		97 (70.8%)	Hodgson et al. (1995)
Canopy height	Ordinal	m	111 (81%)	Hodgson et al. (1995); Kleyer (1995)
Leaf size	Ordinal	cm^2	52 (38%)	Kleyer (1995)
Leaf distribution	Nominal		50 (36.5%)	Poschlod et al. (2003)
Life form (*sensu* Raunkiær 1937)	Nominal		97 (70.8%)	Hodgson et al. (1995)
Shoot growth form	Nominal		51 (37.2%)	Poschlod et al. (2003)
Woodiness	Nominal		50 (33.6%)	Poschlod et al. (2003)
Branching	binary		46 (33.6%)	Poschlod et al. (2003)
Reproduction type	Nominal		133 (97.1%)	Klotz et al. (2002)
Lateral spread	Ordinal	mm	97 (70.8%)	Hodgson et al. (1995)
Life span	Ordinal		133 (97.1%)	Klotz et al. (2002)
Age at first flowering	Ordinal		34 (24.8%)	Kleyer (1995); Poschlod et al. (2003)
Start of flowering period	Ordinal		133 (97.1%)	Klotz et al. (2002)
End of flowering period	Ordinal		133 (97.1%)	Klotz et al. (2002)
Length of flowering period	Numerical	month	133 (97.1%)	Klotz et al. (2002)
Seed shedding period	Nominal		51 (37.2%)	Kleyer (1995)
Seed weight	Numerical	mg	97 (70.8%)	Klotz et al. (2002); Poschlod et al. (2003); RuG, unpubl. data
Seed length	Numerical	mm	103 (75.2%)	Klotz et al. (2002)
Seed shape	Numerical	-	106 (77.4%)	Klotz et al. (2002)
Seed bank longevity	Numerical	-	119 (86.9%)	Thompson et al. (1997)
Release height	Numerical	m	120 (87.6%)	Poschlod et al. (2003)
Terminal velocity	Numerical	m/s	25 (18.2%)	Poschlod et al. (2003)
Long distance dispersal (LDD) potential	Ordinal		131 (95.6%)	Tamis et al. (2004)
Season of seedling emergence	Nominal		32 (23.4%)	Poschlod et al. (2003)

then used to cluster the species into three groups using the 'Weighted Average Linking' method (Clustangraphics 5.08; Clustan Ltd., 2001). We inspected species groups produced by cluster analyses with differing numbers of 'terminal' groups, and settled on three clusters, judging that other groupings resulted either in heterogeneous clusters showing no interpretable differences in species traits or relative occurrence in different forest patches (in the case of two groups) or in entire clusters consisting of only a few, deviating species (in the case of four and five groups). To check if missing values distorted the results we obtained through clustering the proximity data, we compared their proportions among the three groups. While slightly lower for group 2 (mean = 0.10; SD = 0.10) than for group 1 (mean = 0.19; SD = 0.13) and 3 (mean = 0.16; SD = 0.13) proportions of missing values did not differ significantly (Kruskal-Wallis χ^2 = 3.980; df = 2; P = 0.137).

Then, species traits were compared between the groups by executing one-way ANOVA for each numerical trait (see Table 1). Since the assumptions for ANOVA were not fulfilled, non-parametric Kruskal-Wallis tests were applied to compare groups for the ordinal traits and χ^2-tests were performed to analyse cross-tabulations of nominal and binary traits with the clusters. A one-way ANOVA was also executed to assess whether the mean number of occurrences in the 239 forest patches diverged for species belonging to different groups. Finally, the Pearson's χ^2-statistic was calculated to test for the distribution of ancient forest plant species, *sensu* Hermy (1994) and Honnay et al. (1998), among the three groups.

To relate the relative occurrence of species groups to forest patch characteristics, we first calculated the proportion of species of each group present in each forest patch (i.e. species of group i found in patch j divided by the total number of species in group i). Among forest characteristics we focused on patch area (as a surrogate for habitat diversity; see also Honnay et al. 1999), isolation, forest age and forest type (alluvial forest vs. *Quercion* forest). For the same study area, Butaye et al. (2001) showed that when all ancient forest patches within 1000 m of any edge of the focal forest patch are taken into account, seed dispersal sources (i.e. ancient forests sustaining populations of a particular species) can be found for 91% of the flora in recent forest (i.e. forests established less than 50 years ago). Therefore, total area of ancient forest within 1000 m of the forest edge was used as a measure for isolation status in our analyses. Both forest patch area and total area of ancient forest within 1000 m of each forest patch were calculated in a GIS (Anon. 1998). Since there were many cases where no ancient forest was found within the perimeter, this measure for isolation was recoded into a binary variable. This procedure neglects the capacity of the agricultural and suburban landscape matrix to sustain populations of the species that are used in our analyses. However, given the intensive agricultural management in this region and the removal of most of the small landscape elements (such as hedgerows) during recent decades we assumed, for purposes of analysis, that forest species or even species that are normally not restricted to forest patches, are not able to survive outside forests.

To test for differences in group occurrences in different forest patches and taking into account that these rela-

tive proportions for the three groups are interdependent, proportional occurrences were simultaneously introduced as dependent variables in a multivariate general linear modelling procedure with forest type and isolation status as fixed factors. To meet the standards for parametric ANOVA, forest area was logarithmically transformed and, together with forest age, it was added to the model as a covariate (General Linear Model procedure (GLM); Anon. 2001). We used Phillai's Trace value as a multivariate measure of association to construct multivariate tests of significance (Finn 1974). Since preliminary analyses had shown significant differences between the two forest types, we subsequently performed multivariate GLM for alluvial and *Quercion* forests separately. Except for the clustering procedure, all statistical analyses were executed in SPSS 11.0 (Anon. 2001).

Results

General relationships among species traits

All intertrait correlations are shown in App. 2a, b. Particularly interesting emergent patterns point to general trade-offs between longevity, dispersal and reproduction. Plants with long life spans have delayed age of first flowering, reduced seed bank longevity and shorter flowering periods. Strategy and life form are also significantly associated with life span. Tall plants have delayed first flowering and produce heavier seeds which are shed over a longer period compared to other plants. In turn, age at first flowering is significantly positively correlated with seed weight. However, delayed age at first flowering also implies having shorter seed bank longevity and flowering period. Plants producing heavy, large seeds generally show short seed bank longevity.

Delineation and description of the species groups

The three 'emergent' species groups, obtained through clustering of a proximity matrix with GSC values, differ significantly in seed weight and seed length (group 1 having significantly heavier and larger seeds than group 2; Fig. 1). For length of the flowering period, seed shape and seed bank longevity, however, no significant differences were detected between the groups. Plants in group 1 have the highest canopy (Table 2) and consequently release their seeds from higher distances above ground level. These species also have lower terminal velocities compared to those of groups 2 and 3 (Fig. 1). Age at first flowering significantly differs between all groups (1 > 3 > 2), while for many other traits no difference between groups 2 and 3 can be found. *Post-hoc* tests shown in Table 2, further indicate that plants in group

Table 2. Comparison of ordinal traits between emergent groups (Kruskal-Wallis non-parametric ANOVA, χ^2-values, $df = 2$ for all tests). If appropriate, *post-hoc* pairwise comparisons were executed and letters indicate which groups differ significantly ('a' being attributed to the group(s) with the highest median value and 'c' to the group with the lowest median value).

Traits	n	χ^2	Group 1	Group 2	Group 3
Canopy height	111	32.23***	a	b	b
Leaf size	52	2.45			
Lateral spread	97	18.58***	a	b	b
Life span	133	2.46			
Age at first flowering	34	6.02*	a	c	b
LDD potential	131	12.19**	a	b	b
Start of flowering period	133	3.83			
End of flowering period	133	6.32*	b	a	a

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

1 flower later in the season than those of groups 2 and 3; they also have a higher potential for dispersal over long distances. As for the association between nominal plant traits and group membership (Table 3), it appears that group 1 is dominated by competitive stress-tolerant plants, whereas group 2 mainly consists of competitive plants. Group 3 is a combination of competitive and competitive stress-tolerant plants. Life form also significantly differs between the groups: phanerophytes form the bulk of group 1, while groups 2 and 3 have relatively more
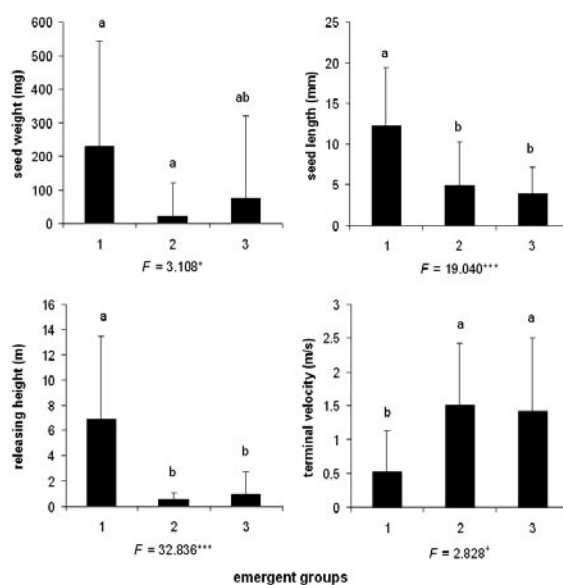

Fig. 1. Comparison (means + SD) of numerical plant traits that differ significantly among the three 'emergent' groups: group 1 ($n = 19$); group 2 ($n = 31$); group 3 ($n = 87$). *F*-values for all ANOVAs are given ([+] $P < 0.1$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$).

Table 3. Comparison of nominal traits between the 'emergent' groups (Pearson χ^2 statistic).

Traits	n	df	χ^2
Established strategy	97	12	36.00***
Life form	97	10	55.81***
Reproduction type	133	6	10.75
Seed shedding period	51	6	8.22
Season of seedling emergence	32	4	10.54*

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; for leaf distribution, shoot growth form, woodiness and branching the test statistic was not available due to lack of trait data.

chamaephytes, with many hemicryptophytes in group 3. For other nominal traits, data are inadequate to assess the differences among groups. Ancient forest plant species are only marginally significantly over- or underrepresented in any group (Pearson's $\chi^2 = 5.66$; $df = 2$; $P = 0.059$); group 3 includes more ancient forest species than expected.

These comparisons, along with inspection of floristic composition, suggest the following general description of the groups:

Group 1 ($n = 19$): shrubs and trees or climbers with fleshy or wind dispersed fruits (e.g. *Sambucus nigra, Rubus fruticosus, Betula pendula*);

Group 2 ($n = 31$): small, mainly vegetatively reproducing herbs (e.g. *Anemone nemorosa, Ajuga reptans, Ranunculus ficaria*);

Group 3 ($n = 87$): spring flowering herbs with large seeds, mainly unassisted dispersal (e.g. *Primula elatior, Mercurialis perennis, Paris quadrifolia).*

However, the groups are not entirely homogeneous. For example, *Frangula alnus* is found in group 3, which also contains a number of species not restricted to the forest interior but unable to survive in the agricultural matrix (e.g. *Filipendula ulmaria, Caltha palustris, Molinia caerulea*).

Table 5. Univariate GLM analyses for **a**. alluvial forests; **b**. *Quercion* forests, to compare relative occurrences (Rel. occ.) for each group (1: $n = 19$; 2: $n = 31$; 3: $n = 87$) in forest patches of different age and size, having a different isolation status (no ancient forest within 1000 m of the edge of the focal patch or at least one other ancient forest patch in this buffer area).

	Rel. occ.	F (all. for.)	F (*Quercion*)
Forest area	group 1	8.014**	2.855+
(log)	group 2	33.231***	32.725***
	group 3	43.211***	54.367***
Isolation	group 1	12.096**	1.279
	group 2	12.411**	0.192
	group 3	13.065***	2.832+
Forest age	group 1	4.470*	0.069
	group 2	5.388*	0.024
	group 3	12.575**	0.769

+ $P < 0.1$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Table 4. Results of multivariate GLM analyses for **a**. all forests; **b**. alluvial forests and **c**. *Quercion* forests to compare relative occurrences of different emergent groups (group 1: $n = 19$; group 2: $n = 31$; group 3: $n = 87$) in forest patches of different age and size, sustaining different forest types (only for **a.**; alluvial vs. *Quercion*), and having a different isolation status (no ancient forest within 1000 m of the edge of the focal patch or at least one other ancient forest patch in this buffer area).

	Phillai's trace value	Error df	F
(a) all forests			
forest type	0.338	231	39.268***
log(forest area)	0.312	231	34.875***
forest type × isolation	0.096	231	8.148***
isolation	0.057	231	4.695**
forest age	0.041	231	3.314**
(b) alluvial forests			
log(forest area)	0.264	132	15.817***
isolation	0.115	132	5.701**
forest age	0.086	132	4.153**
(c) Quercion forests			
log(forest area)	0.386	95	19.799***
isolation	0.040	95	1.312
forest age	0.011	95	0.356

Hypothesis $df = 3$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Comparison of relative occurrence of the groups in different forest patches

Throughout the study area, species of group 1 are relatively more common than species of group 3, while the relative occurrence of species in group 2 does not differ from the other groups (ANOVA; $F_{2,134} = 13.099$; $P < 0.001$). Multivariate GLM analyses show that forest age, area, isolation and forest type (as well as their interaction) all contribute to the explanation of relative occurrences of the groups among forest patches (Table 4a). Separate analyses for alluvial and *Quercion* forests (Table 4b, c) indicate that, while relative occurrences of the groups are mainly governed by forest area in *Quercion* forests, isolation and forest age also significantly affect these occurrences in alluvial forests (Fig. 2). Univariate tests for each of the groups (Table 5) for both forest types, show that: (a) effects of isolation, forest age and area are stronger for the group 3 and (b) forest age has only marginally significant impact on the relative occurrence of species in groups 1 and 2. However, relative occurrences for all the groups are higher in forest patches having ancient forest within 1000 m compared to isolated patches (Fig. 2).
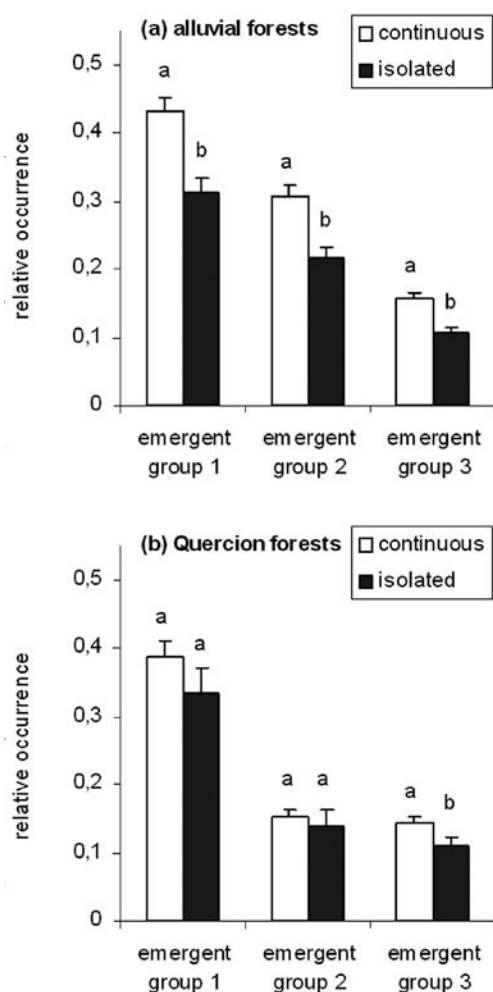
Fig. 2. Comparison of relative occurrence (means + SE) of each emergent group for isolated (no ancient forest within 1000 m of the edge of the focal patch) vs. more continuous (presence of ancient forest patches within 1000 m of the edge of the focal patch) alluvial **(a)** and *Quercion* **(b)** forests. Letters indicate whether relative occurrences differ significantly ($\alpha = 0.05$, with Bonferroni correction for multiple tests) between isolated and more continuous forests for each emergent group.

Discussion

Intertrait relationships

Intertrait correlations resulting from this study are consistent with those earlier reported in literature for forest species in particular (e.g. Bierzychudek 1982; Verheyen et al. 2003a) or for plant species in general (e.g. Grime et al. 1988). In particular, it appears that larger seeds have less persistent seed banks, which supports the conclusions of Thompson et al. (1993) and Bekker et al. (1998). However, consideration of a broad set of traits calls for extraction of general patterns between traits associated with persistence, longevity and dispersal functions. Ehrlén & van Groenendael (1998) postulated that a trade-off between resource allocation to longevity functions and dispersal mechanisms would influence colonization and extinction and act selectively in shaping the life histories of plants. However, the trade-off between dispersability and longevity, noted by Grime et al. (1988) in the British flora, is not detected in this study. Rather than a trade-off with dispersal *in space*, an inverse relationship is found between life span and dispersal *in time* (seed bank longevity; App. 2a). Moreover, consistent with the findings of Verheyen et al. (2003a) for European forest herb species, a negative correlation between seed bank longevity and age at first flowering is detected.

The pattern of plants with a delayed age of first flowering investing more in lateral spread also corresponds to the results of Verheyen et al. (2003a) and to significantly longer life spans for species displaying vegetative reproduction (App. 2b). Due to a lack of data we were not able to test for a negative correlation between seed number and life span, but together with an inverse relationship between life span and duration of flowering, all these intertrait relationships point towards an underlying trade-off between longevity and fecundity.

Determinants of relative occurrence of forest plant species groups

Relative occurrence of the three groups is significantly affected by forest age, patch area, isolation and forest type (Table 4). When traits of species composing the groups are considered, differences in trait combinations for species in ancient vs. recently established forest patches are consistent with those described by Graae & Sunde (2000) with regard to flowering phenology, Raunkiær life form, lateral spread and CSR (competitor, stress tolerator, ruderal) strategy according to Grime et al. (1988).

While dispersal, establishment and persistence are influenced by a range of local environmental factors and regional variables such as forest connectivity (Matlack 1994; Grashof-Bokdam & Geertsema 1998), the weight of these variables may vary between study areas (Graae et al. 2004), soil types (Dzwonko 1993) or forest types (Hérault et al. 2005). Here, relative importance of factors predicting group occurrences varies between forest types and among species groups (Table 5) In particular, our results, especially for alluvial forests, add to the growing evidence that species with unassisted dispersal and large seeds (i.e. group 3, mainly spring flowering herbs) are severely limited in their potential to colonize recent forests

(e.g. van Ruremonde & Kalkhoven 1991; Dzwonko & Loster 1992; Matlack 1994; Grashof-Bokdam & Geertsema 1998; Brunet & von Oheimb 1998a, b; Butaye et al. 2001). Not surprisingly, ancient forest plant species are overrepresented in this group. However, group 3 also contains a relatively large number of species that do not absolutely rely on forest habitat. While these do not persist in the current agricultural landscape, they may already have been present at the time of afforestation, blurring the effects of forest age and isolation, especially in *Quercion* forests. In their study on differential environmental response of plant functional types in hedgerow habitats, Deckers et al. (2004) also concluded that for herbaceous species, historical variables had a relatively strong impact on species with woodland preference in comparison with other species groups.

Even if forest age and proximity of ancient forests are significant determinants of their relative occurrence, species of group 2 (small, mainly vegetatively reproducing herbs), seem to be less affected by these factors than species of group 1. Possibly their high persistence capacity (through vegetative reproduction, lateral spread, relatively persistent seed bank) allows local survival through (short) breaks in forest continuity. Indeed, after clearing, relic woody elements such as hedgerows (Corbit et al. 1999; Endels et al. 2004a) or other small landscape elements (Endels et al. 2004b) may hold viable populations of these forest species during prolonged periods and some forest species may survive in pastures or hayfields (e.g. *Primula vulgaris* in more humid regions in England; Rackham 1980). This local persistence may have been important in recolonization of new forest patches in the past, but is unlikely to be significant now due to intensification of agricultural practices and destruction of hedgerows in recent decades. Some authors (e.g. Myers et al. 2004; Vellend et al. 2003) hypothesized that epi- or endozoochory (even for species whose seeds have no specific adaptations) may account for long distance dispersal to recent forest patches. It may also be that forest continuity (through forest age) and isolation have a relatively lower impact on group 1, which mainly consists of species with relatively high dispersal capacity. While for this group, patterns also differ between forest types, forest area mainly determines their occurrence in forest patches.

While the observed differences between forest types may be partly blurred by their different spatial distributions in the landscape (alluvial forests are slightly more connected over longer distances compared to upland forests in the study area), the patterns generally correspond to those of Graae (2000b) for Danish deciduous forests. Next to an overrepresentation of species adapted to long-distance dispersal in recent forests, she also found forest continuity and proximity to ancient forests to be better predictors for plant species composition of forests on rich, moist soils compared to those on sandy soils. Similarly, in their study of herbaceous plant community structure of ancient and recent forests in *Alno-Padion* and *Quercion* forest types, Verheyen et al. (2003b) found that community recovery appeared to be slower in unproductive *Quercion* forests. While they attributed the persistent differences in both communities to the strong dispersal limitation of many of the involved species, in their view recovery of the *Quercion* forests is probably also severely hampered by establishment limitation.

In conclusion, we stress the importance of both forest continuity (age of patches) and connectivity for most of the forest species of alluvial forests in the study area, regardless of group membership. However, for highly persistent species (group 2) or species more or less adapted to long-distance dispersal (group 1), forest patch area (probably as a surrogate for habitat diversity; see earlier studies of Honnay et al. (1999, 2000) in northern Belgium) appears to limit occurrence. Recently, by re-analysing several datasets (including the one of our study area), Vellend et al. (2006) were able to demonstrate an extinction debt. This would imply that effects of forest age or isolation are possibly underestimated in our study. Given the importance of forest patch area and age it is of utmost importance to preserve the actual forest area including the spatial setting, and to enhance dispersal through restoration of hedgerow networks within the landscape before thinking about restoring actual forest connectivity, which is inherently a long-term process.

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For App. 1-2, see also JVS/AVS Electronic Archives;