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Response of forest plant species to land-use change: a life-history trait-based approach

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Summary

1 Classifying species by shared functional characteristics is important if common functional response groups are to be identified among different taxa.

2 We investigated plant traits that determine the response of forest plant species to land use changes using literature data. Sources from eight European countries and four North-eastern American states, comprising 20 field studies yielded information on 216 forest plant species. For these species, data on 13 life history traits were collected.

3 Trait correlation structure was similar in the European and American data-sets and corresponded well to those described in the literature. The European and American herbs and the European graminoids were clustered into distinct emergent groups based on their plant traits. The profiles of the European and American emergent groups were similar.

4 Herb species belonging to emergent groups characterized by low dispersability (i.e. large seeds, low fecundity, unassisted dispersal) were relatively slow colonizers. Dispersability (and not recruitment) seems to be a key factor limiting the colonization of some forest plant species. The relationship between dispersability and colonizing capacity was less clear for graminoids.

5 A life history trait-based approach offers good opportunities to gain insight into the mechanisms behind species response to land-use change.

Key-words: secondary succession, disturbance, response groups, life-history traits, forest herbs

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Introduction

Classifying species by shared biological characteristics that relate to function, rather than by phylogeny, is increasingly recognized as a tool in identifying common functional response groups amongst differing taxa (Grime *et al*. 1988; Lavorel *et al*. 1997; Diaz & Cabido 2001). These classifications may be grouped into different categories in order of increasing specificity of objective (Lavorel *et al*. 1997): (i) emergent groups (e.g. Leishman *et al*. 1995), (ii) strategies (e.g. Grime 1977 and Grime *et al*. 1988), (iii) functional types (e.g. Thompson *et al*. 1996) and (iv) specific response groups (e.g. Noy-Meir *et al*. 1989; McIntyre & Lavorel 2001). Emergent groups are groups of species exhibiting correlations between a set of plant traits. Plant strategies and functional types, respectively, group species that are similar in resource use and in their role in ecosystem functioning. However, both Noble & Gitay (1996) and Lavorel *et al*. (1997) stressed that such classifications are unlikely to be feasible due to their generality and lack of relation with function. They advocated focusing on the identification of more specific response groups, which are context-specific functional classifications determined by a particular response to disturbance such as grazing or land use change.

We attempted to define trait-based groups of forest plant species related to their response to land use changes. Such species are evolutionarily adapted to stable environments, and the highly dynamic urban and agricultural landscapes of Europe and N-America therefore pose a major conservation problem (e.g. Hermy *et al*. 1999; Honnay *et al*. 2002). Deeper insight into the traits determining their responses may also allow prediction of vegetation changes in response to future changes in land use.

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We studied secondary colonization following a period of agricultural land-use. This approach offers good opportunities to determine how common life history traits among diverse species control the response to land-use change due to (i) the presence of a well-defined disturbance event (i.e. the complete removal of forest species during agricultural use), (ii) the ability to observe the response of the forest species by monitoring recolonization, and (iii) the empirical observation of widely varying colonizing capacities between species. Thus, it may take tens to hundreds of years for some species to recolonize secondary forests while others colonize within a few years (e.g. Hermy & Stieperaere 1981; Peterken & Game 1984; Whitney & Foster 1988; Motzkin *et al.* 1996). Previous observational studies (e.g. Matlack 1994; Brunet & von Oheimb 1998; Bossuyt *et al.* 1999; Butaye *et al.* 2001; Singleton *et al.* 2001; Verheyen & Hermy 2001) suggest that seed availability and recruitment ability are major bottlenecks during recolonization. This was partly confirmed by experimental studies in Sweden (Eriksson & Ehrlén 1992; Ehrlén & Eriksson 2000), but it is impossible to screen large sets of species within a reasonable time interval. The potentially more powerful trait-based approach has previously been largely unexplored (but see Graae & Sunde 2000). However, the availability of similar data-sets in North-eastern America and North-western Europe allows us to compile two independent data-sets and thus to generalize across temperate forest regions.

Different methodologies to delineate response groups are possible (McIntyre & Lavorel 2001). Our methodology consists of (i) the identification of slow and fast colonizing forest plant species (i.e. the response groups) based on an extensive literature review, (ii) the identification of emergent groups (*sensu* Lavorel *et al.* 1997) based on plant trait correlations, (iii) investigation of the relation between plant traits and emergent groups on the one hand and plant response to land-use change on the other.

Methods

THE SPECIES SETS

We compiled the available literature comparing the vegetation of ancient and recent forests for the cool temperate regions of North-eastern America (the area covered by Gleason & Cronquist 1991) and North-western Europe. Forests situated on land that was once cleared for agriculture, pasture or habitation, are defined as recent. In North-western Europe, forest that has existed continuously since the date of the oldest available historical site information, typically 150–400 years before present (cf. Hermy *et al.* 1999), is defined as ancient. However, given the prolonged and intensive human impact on the European landscape, one cannot assume that these forests had previously been continuously forested. In North-eastern America, ancient forests are those that have never been cleared since European settlement (~350 BP). It should however, be noted that most ancient forests on both continents have been managed and are therefore rarely virgin or old-growth forests.

We searched a large variety of data sources, including peer-reviewed journal papers, unpublished theses and reports, but only those studies that met the following criteria were used for further analyses: (i) the sampled forests are situated on mesic soils in lowlands or lower montane areas; (ii) a clear description of the land-use history is given; (iii) frequency data are available for herbaceous vascular plants in both forest types and (iv) in recent forests canopy closure had already taken place.

For North-western Europe, 12 studies from eight countries were used (data for 273 herbaceous plant species), whilst for North-eastern America, eight studies sampled similar communities (112 species) (Table 1). The American studies are clustered in a rather restricted area covering Massachusetts, New York, New Jersey and Delaware. Other studies were excluded because of limited sample sizes or the lack of clear land-use history descriptions (Bard 1952; Nyland *et al.* 1986; Vankat & Snyder 1991; De Mars & Runkle 1992; Halbach 1997). Three potentially suitable studies on xeric sand plains (Motzkin *et al.* 1996; Motzkin *et al.* 1999; Eberhardt 2001) were omitted to assure comparability.

Species nomenclature was standardized according to Gleason & Cronquist (1991) and Wisskirchen & Haeupler (1998) for the American and European species, respectively.

COLONIZING CAPACITY

For each species that was cited at least twice (i.e. 139 herbs + 33 graminoids = 172 European species and 44 herbs + 0 graminoids = 44 American species), a 'Colonizing Capacity Index' (CCI) was calculated using a similar index to that employed by Bekker *et al.* (1998) to assess the longevity of seeds in soil.

$$\mathrm{CCI} = [((1.5 \times A^* + A) - (1.5 \times R^* + R))/(A^* + A + R^* + R)] \times 100/1.5,$$

where A^* represents the number of studies in which species X is significantly more frequent in ancient forest; A the number of studies in which species X is more frequent, but not statistically significant, in ancient forest; R the number of studies in which species X is equally frequent or tends to be more frequent in recent forest and R^* the number of studies in which species X is significantly more frequent in recent forest. For studies lacking statistical analyses of species affinity with ancient forest, we calculated Pearson Chi^2 association measures (Table 1). The index ranges from –100 (strongly associated with recent forest) to +100 (strongly associated with ancient forest). An overview of the species and their CCI-values is provided in Appendix 1 (Supplementary Material).

Table 1 Overview of the publications used for the analyses

Publication	Country/ State	Forest type	Data collection unit	Sample size in ancient forest	Sample size in recent forest	Place in work
North-western Europe						
1 Brunet (1994)*	S	Broadleaf	Plots	290	49	Table 1
2 Dzwonko & Gawronski (1994)*	PO	Broadleaf	Plots	37	30	Table 4
3 Dzwonko & Loster (1989)	PO	Broadleaf	Patch	63	6	Table 2
4 Hermy & Stieperaere (1981)	B	Broadleaf	Plots	28	36	Table 2
5 Hermy (1985)	B	Broadleaf	Plots	315	230	Tables 3, 12
6 Honnay *et al.* (1998)	B	Broadleaf	Patch	58	46	Table 1 and unpubl.
7 Kubikova (1987)*	CZ	Broadleaf	Patch	11	7	Tables 2, 3 and 4
8 Peterken & Game (1984)*	GB	Broadleaf	Patch	89	273	Tables 7, 8
9 Petersen (1994)*	DK	Broadleaf	Plots	9	16	Tables 1, 5–10
10 Sciama (2000)*	FR	Broadleaf	Plots	65	62	App. 2
11 Wulf (1997)	GE	Broadleaf	Patch	285	30	Table 1
12 Zacharias (1994)*	GE	Broadleaf	Patch	11	11	Table 3
North-eastern North America						
1 Bellemare (2001)	MA	Broadleaf	Plot	18	11	Table 3
2 Gerhardt (1993)	MA	Mixed	Plot	24	32	Tables 11 and 18
3 Glitzenstein *et al.* (1990)*	NY	Mixed	Plot	42	34	Table 3
4 Matlack (1994)	NJ & DE	Broadleaf	Plot	17	26	Table 5
5 Nash (1994)	MA	Broadleaf	Plot & transect	15	15	Tables 4 and 6
6 Singleton (1998)	NY	Broadleaf	Plot	25	25	Fig. 1.4
7 Sobey (1995)	Prince Edward Island (CA)	Mixed	Plot	930	270	Tables 1-1, 1-2 and 1-4
8a & b Whitney & Foster (1988)	MA & NH	Broadleaf (a) & conifer (b)	Plot	33 (a) & 59 (b)	52 (a) & 46 (b)	Table 3

*, Statistical analysis (Pearson Chi^2) performed by us. B, Belgium; CZ, Czech Republic; DK, Denmark; FR, France; GB, Great Britain; GE, Germany; PL, Poland; S, Sweden; CA, Canada; DE, Delaware; MA, Massachusetts; NH, New Hampshire; NJ, New Jersey; NY, New York.

SPECIES TRAITS

For the same 172 European and 44 American species, data on 13 traits were compiled based on a list of core traits suggested by Weiher *et al.* (1999) supplemented with traits believed to affect plant species colonization (e.g. dispersule production, age of first reproduction; Table 2). Compilations of autecological information of European species (The Biological Flora of the British Isles; Ellenberg *et al.* 1992; Hodgson *et al.* 1995; Kleyer 1995; Thompson *et al.* 1997; Bouman *et al.* 2000) and American species (Montgomery 1977; Gleason & Cronquist 1991; Cullina 2000; Mabry *et al.* 2000; Kern unpubl.) were used in addition to species descriptions found in the ecological literature (a full list of references is available from the authors). As we are not aware of any suitable American seed bank compilation, this variable was omitted from the American data-set. On average, trait data were lacking for 30% of the European herb species, 27% of the European graminoids and 16% of the American herbs (Table 2).

DATA ANALYSIS

Separate statistical analyses were performed for the European and American data-sets as well as for the different growth forms (graminoids and herbs; cf. McIntyre & Lavorel 2001), although no American graminoids were included in the data-set. Except where mentioned, all analyses were performed with SPSS 10.0 (SPPS 1999).

In an exploratory phase, correlations between the traits were examined using Spearman rank correlation coefficients calculated between the ordinal and ratio scaled traits. The relationships between ordinal and nominal traits were assessed by means of a Kruskal–Wallis test and the association between nominal traits was determined with the Pearson Chi^2 test-statistic (Siegel & Castellan 1988). A Mantel test using PopTools 2.1 (Hood 2001) was used to determine whether a similar correlation structure was found between the traits in Europe vs. North America. For this analysis, proximity matrices based on Spearman rank correlations were used (eight traits) and 999 random permutations were calculated. The intercontinental congruence of the relationships between nominal traits was assessed using the average rank of the ordinal and continuous traits in the nominal trait classes (these ranks are generated by the Kruskal–Wallis test; see above). We then counted the number of traits with a similar ranking of nominal trait classes in Europe and America. Next, emergent groups based on plant trait correlations were identified. This was done by calculating Gower's Similarity Coefficients (GSC; Gower 1971) among a subset of species for which information was available on more than 50% of the studied traits (102 and 44 European and American herbs and 25 European graminoids). GSC is a general measure of proximity that can cope with mixed data-types (nominal, ordinal, interval and ratio) as well as with missing values. The calculated Gower proximity matrices were then used to (i) ordinate the species by non-metric multidimensional scaling (NMDS) and (ii) cluster the species into emergent groups using Ward's method (Clustangraphics 5.08; Clustan Ltd. 2001). The optimal cluster number was determined through visual inspection of the cluster dendrogram and the ordered proximity matrices. NMDS-ordination plots were made to visualize the relationships between the groups. NMDS-ordinations were performed with the ALSCAL algorithm implemented in SPSS 10.0 (SPSS 1999).

Finally, the relationship between the species' colonization capacity, the individual traits, and the emergent groups was quantified by means of Spearman rank correlation coefficients and Kruskal–Wallis tests (Siegel & Castellan 1988). Using the same methods, the relationships between the CCI and the traits within the emergent groups of European herb species was assessed. Due to sample size limitations, these analyses could not be performed for the American herbs or the European graminoids.

Results

SPECIES RESPONSE TO LAND-USE CHANGE

On both continents, the CCI spans the whole range between −100 and +100 but the index scores for most species are intermediate (see Appendix 1). Species with extreme CCI scores exhibit a consistent response across the studies, while species with intermediate scores often exhibit divergent responses in different studies.

RELATIONSHIPS AMONG THE TRAITS AND DELINEATION OF THE EMERGENT GROUPS

Many of the traits investigated are significantly correlated for both European and American herb species (Tables 3 & 4, respectively). Mantel analysis for the ordinal and continuous traits ($r_M = 0.64$; $P = 0.002$) and similar rankings of dispersal and flowering phenology classes for four out of eight traits indicate that the correlation structures of both data-sets are similar. Note that all of the American species are perennials and therefore, 'life cycle' was not included as a variable in the analyses. Fewer significant intertrait correlations were found for the European graminoids, all of which were perennials (Table 5). This is at least partly a result of the small sample size.

The optimal cluster numbers for the emergent groups were four (European herbs), three (American herbs) and three (European graminoids). The most characteristic traits were used to label the groups (Table 6). Most groups separated out well in the ordination space (Fig. 1), although some overlap exists with the European herbs.

Table 2 Overview of the plant traits incorporated in the database

Traits	Description	Measurement scale	Percent missing values EH $n = 139$	EG $n = 33$	AH $n = 44$
Reproductive traits					
1. Seed mass (mg)*	Eight classes modified from Hodgson *et al.* (1995): 0: too small to be measured; 1: < 0.20 mg; 2: 0.21–0.50 mg; 3: 0.51–1.00 mg; 4: 1.01–2.00 mg; 5: 2.01–10.00 mg; 6: 10.01–100 mg; 7: 100.01–1000 mg	Ordinal	29	24	50
2. Seed size (mm)	Average of seed length, width and thickness.	Ratio	81	85	20
3. Seed shape*	Three classes according to Hodgson *et al.* (1995): 1: length/width ratio < 1.5; 2: ratio 1.5–2.5; 3: ratio > 2.5.	Ordinal	32	24	20
4. Seed production per plant†	Five classes modified from Mabry *et al.* (2000): 1: < 25; 2: 26–100; 3: 101–1000; 4: 1001–10000; 5: > 10 000	Ordinal	55	70	7
5. Dispersal type*	Three types according to van der Pijl (1982): 1: anemochory 2: endozoochory & exozoochory; 3: ballistochory; myrmecochory; unassisted.	Nominal	3	3	7
6. Seed bank (only Europe)†	Seed bank longevity index proposed by Bekker *et al.* (1998). Values range from 0 (strictly transient) to 1 (strictly persistent).	Ratio	45	24	/
7. Germination requirements	Three types modified from Hodgson *et al.* (1995) and Cullina (2000) and ranked according to increasing specificity: 1: Immediate; 2: Dry, Chilling, Scarification, Light; 3: Orchid; Difficult, Warm + Chill, Chill + Warm + Chill, Chill + Wash.	Ordinal	39	33	25
8. Age of first reproduction (year)	Six classes according to Kleyer (1995): 1: < 0.25 year; 2: 0.25–1 year: 3: 1–2 year; 4: 2–3 year; 5: 3–6 year; 6: 6–15 year.	Ordinal	56	55	55
Vegetative traits					
9. Growth form	Two classes: Graminoids and Herbs	Nominal	0	0	0
10. Life cycle*	Annual; Biennial and Perennial	Nominal	8	0	0
11. Vegetative spread†	Three classes: Absent, Intermediate and Strong	Ordinal	28	21	7
12. Max. height (m)*	Five classes modified from Hodgson *et al.* (1995): 1: < 0.1 m; 2: 0.11–0.29 m; 3: 0.30–0.59 m; 4: 0.60–0.99 m; 5: 1.0–3.0 m	Ordinal	8	3	2
Phenological traits					
13. Flowering phenology*	Five classes according to Mabry *et al.* (2000): 1: spring flowering; 2: mid summer flowering; 3: spring-mid summer flowering; 4: fall flowering; 5: mid-summer-fall flowering.	Nominal	8	3	0

*, Easy (to measure) core trait; †, hard (to measure) core trait according to Weiher *et al.* (1999). EH, European herbs; EG, European graminoids; AH, American herbs.

Table 3 Relationships among traits and with the CCI for European herb species. Values are Spearman rank correlations, Kruskall Wallis test statistics (italic) and Pearson Chi^2-measures of association (underlined)

	Seed mass	Seed size	Seed shape	No. seeds plant^{-1}	Max. height	Veg. spread	Germin. requir.	Age first reprod.	Seed bank	Dispersal type	Life cycle	Flowering phenology
Seed size	0.79*** _n_ = 27											
Seed shape	−0.30** _n_ = 94	0.07 NS _n_ = 27										
No. seeds plant^{-1}	−0.76*** _n_ = 58	−0.38(*) _n_ = 23	−0.40** _n_ = 56									
Max. height	0.00 NS _n_ = 98	0.30 NS _n_ = 27	0.23* _n_ = 95	0.31* _n_ = 62								
Veg. spread	0.07 NS _n_ = 95	0.06 NS _n_ = 26	−0.13 NS _n_ = 93	−0.06 NS _n_ = 61	−0.13 NS _n_ = 100							
Germin. requir.	0.03 NS _n_ = 84	0.37(*) _n_ = 25	0.09 NS _n_ = 83	0.00 NS _n_ = 48	−0.20(*) _n_ = 85	0.06 NS _n_ = 83						
Age first reprod.	−0.13 NS _n_ = 60	0.24 NS _n_ = 21	0.06 NS _n_ = 58	0.02 NS _n_ = 47	0.00 NS _n_ = 61	0.38** _n_ = 60	0.37** _n_ = 53					
Seed bank	−0.55*** _n_ = 66	−0.46* _n_ = 21	0.00 NS _n_ = 65	0.69*** _n_ = 41	0.07 NS _n_ = 75	−0.16 NS _n_ = 69	−0.22(*) _n_ = 61	−0.47*** _n_ = 44				
Dispersal type	_43.4***_ _n = 94_	_4.8(*)_ _n = 27_	_12.2**_ _n = 91_	_29.0***_ _n = 62_	_14.4***_ _n = 121_	_6.5*_ _n = 96_	_0.1 NS_ _n = 82_	_2.9 NS_ _n = 59_	_3.9 NS_ _n = 73_			
Life cycle	_1.5 NS_ _n = 97_	_0.3 NS_ _n = 27_	_1.2 NS_ _n = 94_	_0.5 NS_ _n = 61_	_5.5(*)_ _n = 127_	_41.0***_ _n = 100_	_0.8 NS_ _n = 84_	_24.3***_ _n = 60_	_4.9(*)_ _n = 75_	4.5 NS _n_ = 120		
Flowering phenology	_10.7*_ _n = 98_	_4.1 NS_ _n = 27_	_6.7(*)_ _n = 95_	_12.9**_ _n = 62_	_45.1***_ _n = 127_	_6.1 NS_ _n = 100_	_7.0(*)_ _n = 61_	_17.1***_ _n = 61_	_17.8***_ _n = 75_	26.1*** _n_ = 120	14.7(*) _n_ = 126	
CCI	0.04 NS _n_ = 98	0.18 NS _n_ = 27	−0.07 NS _n_ = 95	−0.28* _n_ = 62	−0.05 NS _n_ = 128	0.31** _n_ = 100	0.20(*) _n_ = 85	0.41*** _n_ = 61	−0.24* _n_ = 76	_0.1 NS_ _n = 132_	_9.9**_ _n = 127_	_14.7**_ _n = 127_

***$P \leq 0.001$; **$P \leq 0.01$; *$P \leq 0.05$; (*) $P \leq 0.1$; NS, not significant.

Table 4 Relationships among traits and with the CCI for American herb species. Values are Spearman rank correlations, Kruskall Wallis test statistics (italic) and Pearson Chi^2-measures of association (underlined)

	Seed mass	Seed size	Seed shape	No. seeds plant^{-1}	Max. height	Veg. spread	Germin. requir.	Age first reprod.	Dispersal type	Flowering phenology
Seed size	0.93*** *n* = 22									
Seed shape	−0.25 *n* = 22	−0.49** *n* = 35								
No. seeds plant^{-1}	−0.27 NS *n* = 21	−0.49** *n* = 35	0.53*** *n* = 34							
Max. height	0.45* *n* = 22	0.42* *n* = 27	−0.14 NS *n* = 35	0.22 NS *n* = 18						
Veg. spread	0.10 NS *n* = 21	0.04 NS *n* = 35	0.14 NS *n* = 33	−0.07 NS *n* = 38	−0.03 NS *n* = 41					
Germin. requir.	0.44(*) *n* = 19	0.47** *n* = 29	−0.14 NS *n* = 29	−0.31(*) *n* = 32	−0.09 NS *n* = 33	−0.08 NS *n* = 32				
Age first reprod.	0.27 NS *n* = 17	0.24 NS *n* = 18	−0.18 NS *n* = 18	0.11 NS *n* = 20	−0.01 NS *n* = 20	−0.20 NS *n* = 19	0.40 NS *n* = 18			
Dispersal type	*11.3**** *n = 20*	*17.4**** *n = 31*	*17.9**** *n = 31*	*24.8**** *n = 38*	*5.6(*)* *n = 39*	*1.3 NS* *n = 38*	*6.1** *n = 31*	*2.3 NS* *n = 19*		
Flowering phenology	*11.2** *n = 22*	*18.7**** *n = 34*	*14.8*** *n = 34*	*17.4**** *n = 40*	*2.6 NS* *n = 42*	*3.6 NS* *n = 41*	*6.9(*)* *n = 33*	*2.7 NS* *n = 20*	33.2*** *n* = 40	
CCI	0.25 NS *n* = 22	0.25 NS *n* = 35	−0.01 NS *n* = 35	−0.25 NS *n* = 41	0.01 NS *n* = 43	−0.05 NS *n* = 41	0.46** *n* = 33	0.34 NS *n* = 20	*5.2(*)* *n = 40*	*2.8 NS* *n = 43*

*** $P \leq 0.001$; ** $P \leq 0.01$; * $P \leq 0.05$; (*) $P \leq 0.1$; NS, not significant.

Table 5 Relationships among traits and with the CCI for European graminoids. Values are Spearman rank correlations, Kruskall Wallis test statistics (italic) and Pearson Chi^2-measures of association (underlined)

	Seed mass	Seed size	Seed shape	No. seeds plant^{-1}	Max. height	Veg. spread	Germin. requir.	Age first reprod.	Seed bank	Dispersal type	Flowering phenology
Seed size	0.55 NS *n* = 5										
Seed shape	0.09 NS *n* = 25	0.18 NS *n* = 5									
No. seeds plant^{-1}	−0.34 NS *n* = 10	/ *n* = 2	0.40 NS *n* = 10								
Max. height	0.05 NS *n* = 25	0.15 NS *n* = 5	0.37(*) *n* = 25	0.55(*) *n* = 10							
Veg. spread	−0.30 NS *n* = 25	0.15 NS *n* = 5	−0.02 NS *n* = 25	0.17 NS *n* = 10	−0.14 NS *n* = 26						
Germin. requir.	0.45* *n* = 22	/ *n* = 4	−0.05 NS *n* = 22	−0.17 NS *n* = 8	0.36 NS *n* = 22	−0.25 *n* = 22					
Age first reprod.	0.02 NS *n* = 15	/ *n* = 3	−0.18 NS *n* = 15	0.32 NS *n* = 8	0.05 NS *n* = 15	0.12 NS *n* = 15	0.07 *n* = 13				
Seed bank	−0.22 NS *n* = 20	−0.82(*) *n* = 5	−0.56** *n* = 20	−0.06 NS *n* = 8	−0.20 s *n* = 24	−0.39(*) *n* = 69	−0.05 *n* = 19	0.00 *n* = 13			
Dispersal type	*0.2 NS* *n = 23*	*0.4 NS* *n = 5*	*5.8** *n = 23*	*0.7 NS* *n = 10*	*4.0 NS* *n = 30*	*2.9 NS* *n = 24*	*0.13 NS* *n = 20*	*4.5** *n = 15*	*3.3 NS* *n = 23*		
Flowering phenology	*0.4 NS* *n = 25*	*0.8 NS* *n = 5*	*9.6*** *n = 25*	*0.5 NS* *n = 10*	*1.0 NS* *n = 32*	*2.2 NS* *n = 26*	*0.4 NS* *n = 22*	*2.0 NS* *n = 15*	*6.6** *n = 24*	5.5 NS *n* = 30	
CCI	0.34(*) *n* = 25	0.67 NS *n* = 5	−0.29 NS *n* = 25	−0.07 NS *n* = 10	−0.15 NS *n* = 32	0.05 NS *n* = 26	0.50* *n* = 22	0.30 NS *n* = 15	0.18 NS *n* = 25	*3.2 NS* *n = 30*	*5.2(*)* *n = 32*

**$P \leq 0.01$; *$P \leq 0.05$; (*) $P \leq 0.1$; NS, not significant.

Table 6 Overview of the traits associated with the emergent groups. (a) European herbs; (b) American herbs; (c) European graminoids

(a) European herbs			Short lived herbs	Tall perennials with light seeds	Tall perennials with heavy seeds	Small perennials with heavy seeds
		n	*16*	*24*	*17*	*45*
Seed mass†	***	*97*	3.94a	1.00b	3.93a	3.81a
Seed size†	NS	*27*	2.01a	1.40a	1.57a	2.22a
Seed shape†	***	*95*	1.88ab	2.41a	1.60ab	1.43b
No. seeds plant^{-1}†	***	*62*	2.60a	4.53b	2.78a	2.13a
Max. height†	***	*102*	3.12a	3.33a	3.94a	2.36b
Veg. spread†	***	*100*	1.00a	1.91b	2.59c	2.41c
Germin. requir.†	NS	*84*	1.87a	2.00a	1.79a	1.94a
Age first reprod.†	***	*61*	2.00a	4.13b	4.50b	3.85b
Seed bank†	***	*69*	40.45ab	62.85b	18.14a	20.06a
Dispersal type (1, 2, 3)‡	***	*98*	−2.2/2.8/−0.5	16.2/−6.4/−9.8	−2.9/2/0.9	−11.0/1.6/9.4
Life cycle (1, 2, 3)‡	***	*101*	8.2/3.7/−12.1	−2.3/0.2/2.1	−1.7/−1.3/3.0	−4.5/−2.6/7.0
Flowering phenology (1, 2, 3, 5)‡	***	*102*	−4.1/0.1/2.1/1.9	−6.6/1.1/0.2/5.3	−6.5/8.8/−2.0/−0.3	17.1/−10.0/−0.3/−6.8
CCI†	***	*102*	−35a	−3ab	0ab	23b

(b) American herbs			Perennials with light seeds	Perennials with heavy seeds that are animal dispersed	Perennials with heavy seeds that are passively dispersed
		n	*16*	*12*	*16*
Seed mass†	***	*22*	2.17a	5.88b	4.88ab
Seed size†	***	*35*	1.08a	3.25b	2.19b
Seed shape†	**	*35*	2.29a	1.2b	1.36b
No. seeds plant^{-1}†	***	*41*	2.67a	1.64ab	1.27b
Max. Height†	*	*43*	2.75a	3.73a	2.69a
Veg. spread†	NS	*41*	2.73a	2.60a	2.38a
Germin. requir.†	**	*33*	2.38a	3.00b	2.83ab
Age first reprod.†	NS	*20*	3.25a	3.83a	3.30a
Dispersal type (1, 2, 3)‡	***	*41*	6.8/−2.4/−4.4	−2.9/7.9/−5.0	−3.9/−5.5/9.4
Flowering phenology (1, 2, 3, 5)‡	***	*43*	−7.7/−1.4/5.2/3.9	3.0/0.9/−2.2/−1.7	4.7/0.5/−3.0/−2.2
CCI†	*	*44*	−9a	13ab	51b

(c) European graminoids			Small, summer flowering vegetatively spreading graminoids	Large, summer flowering graminoids	Early flowering graminoids
		n	*6*	*6*	*13*
Seed mass†	NS	*25*	2.33a	3.83a	3.23a
Seed shape†	**	*25*	1.75a	2.00ab	2.20b
No. seeds plant^{-1}†	NS	*10*	2.50a	2.83a	1.85a
Max. height†	*	*25*	2.33a	3.50b	2.92ab
Veg. Spread†	***	*25*	3.00a	1.83b	2.31ab
Germin. Requir.†	**	*22*	1.00a	2.00b	1.67ab
Age first reprod.†	NS	*15*	2.80a	2.83a	2.50a
Seed bank†	*	*20*	24.67a	13.25a	57.00a
Dispersal type (2, 3)‡	(*)	*23*	0.1/−0.1	2.1/−2.1	−2.3/2.3
Flowering phenology (1, 2, 3)‡	***	*25*	−2.9/2.6/0.3	−2.9/1.6/1.3	5.8/−4.2/−1.6
CCI†	(*)	*25*	−27a	0a	28a

†, Kruskall–Wallis test. Values are group averages and groups that are significantly different are indicated with different letters (a, b, c). A Bonferroni correction with alfa = 0.05 was performed for the multiple comparisons between the groups (Siegel & Castellan 1988: 213). ‡, Pearson Chi^2 association test. Values are the differences between the observed and expected values for the different classes (see Table 2). ***$P \leq 0.001$; **$P \leq 0.01$; *$P \leq 0.05$; (*) $P \leq 0.1$; NS, not significant.

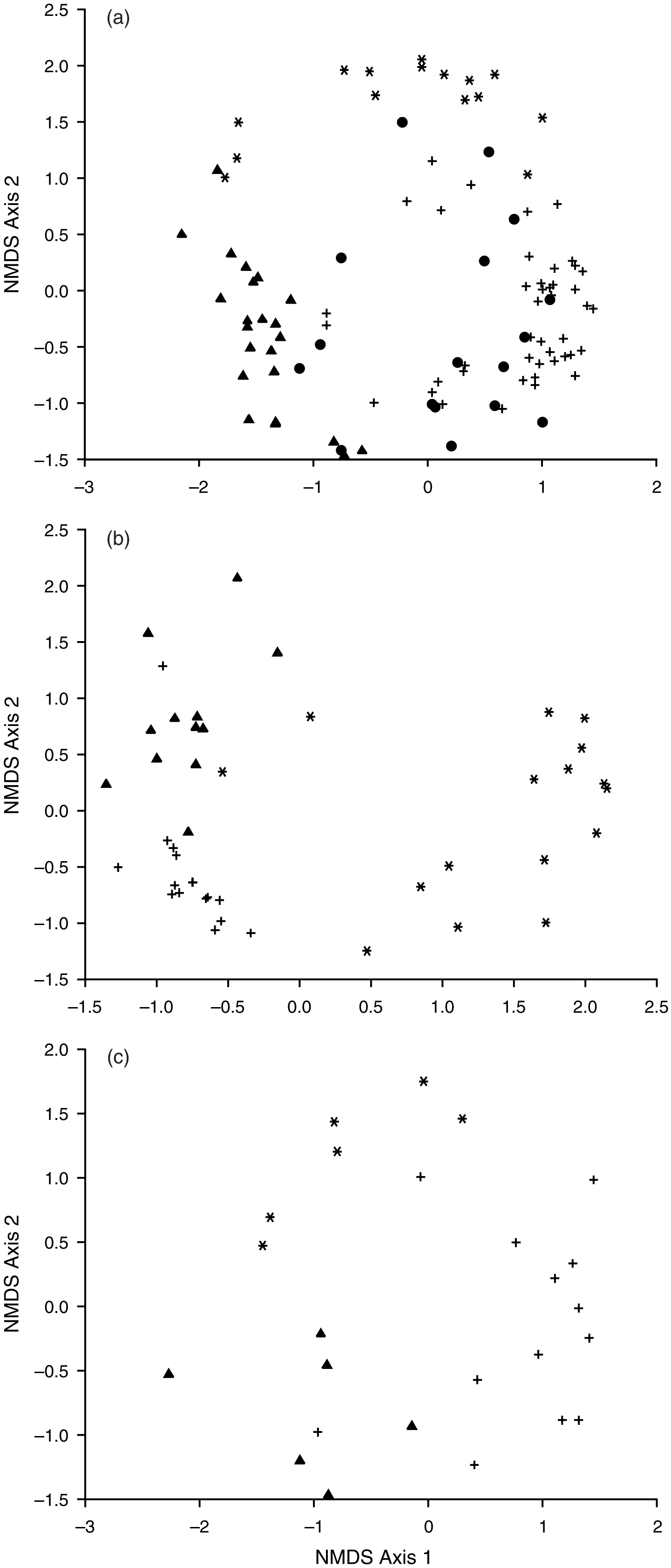

Fig. 1 Ordination of the species using Gower proximity coefficients and non-metric multidimensional scaling (NMDS). Symbols indicate the emergent groups derived from the clustering of the Gower similarity coefficients with Ward's method (see Table 6). (a) European herbs (n = 102), emergent groups: *, short-lived herbs; ▲, tall perennials with light seeds; ●, tall perennials with heavy seeds; +, small perennials with heavy seeds. (b) American herbs (n = 44), emergent groups: *, perennials with light seeds; ▲, perennials with heavy seeds that are animal dispersed; +, perennials with heavy seeds that are passively dispersed. (c) European graminoids (n = 25), emergent groups: *, small, summer flowering, vegetatively spreading graminoids;, large, summer flowering tussock forming graminoids; +, early flowering graminoids.

Not unexpectedly, the European s*hort lived herbs* (mostly annuals and biennials, e.g. *Melampyrum pratense*) differ from the other three emergent groups by their short generation time and limited vegetative spread (Table 6). The species belonging to this group do not flower early and produce relatively few but heavy seeds. No predominant dispersal strategy is present and the seed bank is relatively persistent. Species grouped as *tall perennials with light seeds* (e.g. *Solidago virgaurea*) also have a distinct profile (Table 6 and Fig. 1), producing many light seeds that are mostly wind dispersed and form a persistent seed bank. These species are typically late-flowering, have a long generation time and exhibit intermediate vegetative spread. There are relatively few differences between the two emergent groups characterized by heavy seeds (Table 6 and Fig. 1). Both groups contain species that produce relatively few heavy seeds that do not form a persistent seed bank and that exhibit strong vegetative spread. These two emergent groups differ by the size, flowering time and dispersal strategy of the species. The *tall perennials with heavy seeds* (e.g. *Stachys sylvatica*) primarily flower during mid-summer and have varying dispersal strategies. By contrast, the *small perennials with heavy seeds* (e.g. *Anemone nemorosa*) typically flower in the spring and are passively dispersed.

There are some striking similarities between the three groups that emerged from the American herb data-set and the three groups with European perennials (Table 6). The American *perennials with light seeds* – group contains species that produce many small wind-dispersed seeds and flower late (e.g. *Solidago caesia*), while the two other American groups contain species with heavy seeds. The latter groups are primarily discriminated by dispersal type (animal vs. unassisted). Exemplary species are, respectively, *Smilacina racemosa* and *Cardamine diphylla*.

The three emergent groups in the European graminoids exhibit different trait combinations compared to the herb species. The *small, summer flowering vegetatively spreading graminoids* (e.g. *Deschampsia flexuosa*) have relatively small, more spherical seeds that germinate easily and do not form a persistent seed bank. The *large, summer flowering graminoids* are generally taller and characterized by limited vegetative spread (e.g. *Festuca gigantea*). The seeds tend to be larger, more elongated and germinate less easily. Except for flowering time and dispersal and seed bank type, most traits of the *early flowering graminoids* have values intermediate between those of the two other groups. Species of the early flowering graminoids like *Milium effusum* tend to flower early, are more passively dispersed, and produce a persistent seed bank.

RELATIONSHIPS BETWEEN TRAITS, EMERGENT GROUPS AND SPECIES RESPONSE TO LAND-USE CHANGE

The strongest relationships between individual traits and the CCI were found for the European herb species (Table 3). The American herb species exhibit fewer significant correlations with the CCI (Table 4), although similar trends to the European species were observed (e.g. seed production, age of first reproduction). Slow colonizing European graminoids tend to be early flowering species, species with relatively heavy seeds, or species requiring specific germination conditions (Table 5).

The emergent groups are also closely related with the species response to land-use change (Table 6). The short-lived herbs and the small seeded perennial herbs tend to have good colonizing capacities, while large seeded perennials have relatively poor colonizing capacities. The colonizing capacity of the graminoids decreases from the *small, summer flowering vegetatively spreading* species to the *large, summer flowering* species to the *early flowering graminoids* (Table 6).

For European herbs, the varied responses to land-use change within emergent groups was due to differential responses to one or more traits (Table 7).

Discussion

Predicting the effects of land-use changes on plant community composition is a major challenge for ecologists. Using readily available data on relevant plant traits, the trait-based methodology enabled us to identify patterns of species response to land-use change, irrespective of factors such as local environmental conditions and region, and may be used to predict the response of species not included in this data-set.

THE CCI AND SPECIES RESPONSE TO LAND-USE CHANGE

The colonizing capacity index (CCI) proved to be a useful, synthetic measure to objectively combine species responses from different studies. The weighting given to studies in which species are significantly more frequently in either ancient or recent forest is debatable. However, changing this weight is unlikely to affect the results drastically.

Although not formally analysed, some closely related species (e.g. *Allium ursinum* vs. *A. tricoccum*; *Asarum europaeum* vs. *A. canadense*; *Paris quadrifolia* vs. *Trillium* spp.; *Polygonatum multiflorum* vs. *Polygonatum* spp.) exhibit similar responses on both continents. Similarly, Kornas (1972) noted an ecological correspondence between disjunct pairs of species in Eurasia and North America, a pattern that is striking given the fact that the disjunct patterns in temperate forests of the northern hemisphere had established by the Miocene and further diversification of species on one or both continents took place afterwards (e.g. Wen 1999). Some species or related taxa (e.g. *Arum maculatum* vs. *Arisaema triphyllum*; *Circaea lutetiana*; *Oxalis acetosella*) have different colonizing abilities in Europe vs. North-eastern America, perhaps as a result of differences in landscape characteristics. As convincingly shown by Vellend (2003), colonization success is

Table 7 Spearman rank correlations between the CCI and the traits within the emergent groups of the European herbs. Using the Kruskall–Wallis test, no significant differences were found for dispersal type and flowering phenology (results not presented). Life cycle was not included in these analyses since it was nearly constant within the groups

Traits	Short lived herbs	Tall perennials with light seeds	Tall perennials with heavy seeds	Small perennials with heavy seeds
Seed mass	−0.21 NS 16	0.04 NS 24	−0.26 NS 15	0.19 NS 42
Seed size	−0.11 NS 7	/	/	0.07 NS 12
Seed shape	0.27 NS 16	−0.08 NS 22	0.13 NS 15	−0.10 NS 42
No. seeds plant^{-1}	0.09 NS 10	0.33 NS 19	−0.84** 9	−0.40 NS 24
Max. height	0.28 NS 16	0.41* 24	−0.10 NS 17	−0.21 NS 45
Vegetative spread	/	0.60** 23	−0.35 NS 17	0.10 NS 44
Germin. requir.	−0.21 NS 16	0.13 NS 20	0.64* 14	0.26 NS 34
Age first reproduction	0.31 NS 12	0.00 NS 15	0.05 NS 8	0.45* 26
Seed bank	0.05 NS 11	0.41 NS 13	−0.53* 14	−0.23 NS 31

***, $P \leq 0.001$; **, $0.001 < P \leq 0.01$; *, $0.01 < P \leq 0.05$; (*), $0.05 < P \leq 0.1$; NS, not significant; /, less than 5 observations. No correlations calculated.

strongly dependant on the proportion of ancient forests in the landscape and on the overall degree of forest fragmentation. In general, far less ancient forest exists and actual forest cover is much lower in North-Western Europe than North-Eastern America.

RELATIONSHIPS AMONG THE TRAITS AND DELINEATION OF EMERGENT GROUPS

Our results are consistent with well-established correlation patterns among plant traits (e.g. Harper 1977; Grime *et al.* 1988) and, in particular, with the characterization of life-history attributes of temperate forest herbs by Bierzychudek (1982). A formal analysis of trade-offs, which is beyond the scope of this paper, should account for phylogenetic relationships and possibly confounding effects on some measures (e.g. size-related effects on fecundity; cf. Jakobsson & Eriksson 2000). Our results are, however, consistent with those previously reported. The negative correlation between seed number and seed size (e.g. Harper *et al.* 1970; Jakobsson & Eriksson 2000; Leishman 2001), the association between fecundity and dispersal type (e.g. Eriksson & Jakobsson 1999) and the association between flowering time on the one hand and seed size and germination requirements on the other (e.g. Grime *et al.* 1981; Primack 1987) are all known. In addition, it appears that larger seeds have less persistent seed banks (see also Thompson *et al.* 1993; Bekker *et al.* 1998). However, similar to Leishman & Westoby (1998), we did not find correlations between seed shape and seed bank persistence for forest herb species.

The emergent groups identified illustrate the different ways that understorey species have adapted to forest environments. The similarity between the three groups of perennial herbs on both continents suggests that the ecological correspondence extends beyond disjunct taxa (see above), but pertains to the entire forest flora. In that respect, it is likely that an analogue of the European group of short lived forest species also exists in North-Eastern America, but that it was not well-represented in our analyses due to the limited sample size. These observations also raise the question of whether the corresponding suites of species assemble into forest communities in similar ways on both continents.

RELATIONSHIPS BETWEEN TRAITS, EMERGENT GROUPS AND SPECIES RESPONSE TO LAND-USE CHANGE

Our results demonstrating correlations between life-history attributes and colonization capacity match closely the results of Rejmanek & Richardson (1996) who compared life-history traits of invasive vs. non-invasive pine species. In Danish forests, Graae & Sunde (2000) found that species with heavy seeds, transient seed banks, ant dispersed seeds, early and short flowering time, low stature and high extent of lateral spread were more common in ancient forests, while the proportion of species with small, long-lived seeds, epizoochorous dispersal, little lateral spread and longer flowering period was higher in recent forests. However, Graae & Sunde (2000) restricted their analyses to bivariate correlations between traits and the species response to land-use change and did not take the correlations among the traits explicitly into account. This limitation was resolved in this study by first delimiting emergent groups based on trait correlations and by then assessing the match between these emergent groups and the response to land use change (cf. McIntyre & Lavorel 2001).

The grouping of species with similar response to land-use change suggests that low dispersability (*sensu* Ehrlén & van Groenendael 1998) is the most important constraint for forest plant recovery after a period of agricultural land-use. This supports previous results from analyses of colonization patterns (e.g. Brunet & von Oheimb 1998; Bossuyt *et al.* 1999; and Verheyen & Hermy 2001) and from experimental introductions of forest species into empty patches (e.g. Eriksson & Ehrlén 1992; Ehrlén & Eriksson 2000).

Nevertheless, there is still considerable variation in response within the emergent groups (cf. Table 7). So, while the range of possible colonization capacities is strongly related to the group the species belongs to, trait-variation within the group determines species' variation in colonization capacity. On average, *small perennials with large seeds* species are relatively poor colonizers (CCI = 23, Table 6). However, colonization becomes even more problematic for species which have a delayed age of first reproduction (Table 7), confirming the need to analyse responses to land-use change (and disturbance in general) in a hierarchical way (Lavorel *et al.* 1997).

Recent attempts to incorporate such trait variation into mathematical models describing population spread (e.g. Clark *et al.* 2001; Higgins & Cain 2002) also indicate that colonization ability cannot be predicted from information on a single trait like disperal strategy or fecundity. Interactions among traits and with landscape characteristics (cf. Vellend 2003) greatly affect colonization rates and must therefore be explicitly taken into account.

Finally, it is noteworthy that some species that readily colonize mesic sites are much slower to colonize xeric sites (e.g. *Kalmia angustifolia*, *Vaccinium angustifolium*; Motzkin *et al.* 1999 and Eberhardt 2001). It seems that the production of large quantities of good dispersing seeds is no guarantee for the colonization of sites with more extreme environmental conditions. This may indicate that recruitment, and not dispersal, is the prime factor limiting colonization of some types of sites.

Conclusions

We conclude that the trait-based approach offers insight into the mechanisms responsible for variation in forest plant colonization. The results of this study suggest that the response of forest plant species to land-use coincides with a clustering of species based on a combination of (mostly regenerative) life-history traits and that slow colonizing species are typically characterized by traits that result in low dispersability. Hence, conservation measures should focus on the existing populations of slow colonizing species, many of which occur in ancient forests, and on forest expansion in the immediate vicinity of source populations. In highly fragmented agricultural and urban landscapes, introductions in potentially suitable but unoccupied sites may also be appropriate (cf. van Groenendael *et al.* 1998).

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Supplementary material

The following material is available from http://www.blackwellpublishing.com/products/journals/suppmat/JEC/JEC789/JEC789sm.htm

Appendix S1 Overview of the species cited in at least two studies.

References

Bard, G.E. (1952) Secondary succession on the piedmont of New Jersey. *Ecological Monographs*, **22**, 195–215.

Bekker, R.M., Bakker, J.P., Grandin, U., Kalamees, R., Milberg, P., Poschlod, P., Thompson, K. & Willems, J.H. (1998) Seed size, shape and vertical distribution in the soil: indicators of seed longevity. *Functional Ecology*, **12**, 834–843.

Bellemare, J. (2001) *Legacies of the agricultural past in the forested present: historical land-use effects in Northeastern Mesophytic Forests, USA*. Master in Forest Science Thesis, Harvard University, Cambridge, MA.

Bierzychudek, P. (1982) Life histories and demography of shade-tolerant temperate forest-herbs: a review. *New Phytologist*, **90**, 757–776.

Bossuyt, B., Hermy, M. & Deckers, J. (1999) Migration of herbaceous plant species across ancient-recent forest ecotones in central Belgium. *Journal of Ecology*, **87**, 628–638.

Bouman, F., Boesewinkel, D., Bregman, R., Devente, N. & Oostermeijer, G. (2000) *Verspreiding Van Zaden* (in Dutch). KNNV Uitgeverij, Utrecht.

Brunet, J. (1994) Der Einfluss von Waldnutzung und Waldgeschichte auf die Vegetation südschwedischer Laubwälder (in German). *Norddeutsche Naturschutzakademie-Berichte*, **3**, 96–101.

Brunet, J. & Von Oheimb, G. (1998) Migration of vascular plants to secondary woodlands in southern Sweden. *Journal of Ecology*, **86**, 429–438.

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.

Clark, J.S., Lewis, M. & Horvath, L. (2001) Invasion by extremes: population spread with variation in dispersal and reproduction. *American Naturalist*, **157**, 537–554.

Clustan Ltd (2001) *Clustangraphics 5.08*. Clustan Ltd, Edinburgh.

Cullina, W. (2000) *Guide to Growing and Propagating Wildflowers of the United States and Canada*. A Frances Tenenbaum Book, Boston.

De Mars, B.G. & Runkle, J.-R. (1992) Groundlayer vegetation ordination and site-factor analysis of the Wright State University woods (Greene County, Ohio). *Ohio Journal of Science*, **92**, 98–106.

Diaz, S. & Cabido, M. (2001) Vive la différence: plant funtional diversity matters to ecosystem processes. *Trends in Ecology and Evolution*, **16**, 646–655.

Dzwonko, Z. & Gawronski, S. (1994) The role of woodland fragments, soil types, and dominant species in secondary succession on the western Carpathian foothills. *Vegetatio*, **111**, 149–160.

Dzwonko, Z. & Loster, S. (1989) Distribution of vascular plant species in small woodlands on the Western-Carpathian foothills. *Oikos*, **56**, 77–86.

Eberhardt, R.W. (2001) *Implications of land-use legacies in the sand plain vegetation of Cape Cod National Seashore*. Master in Forest Science Thesis, Harvard University, Cambridge, MA.

Ehrlén, J. & Eriksson, O. (2000) Dispersal limitation and patch occupancy in forest herbs. *Ecology*, **81**, 1667–1674.

Ehrlén, J. & van Groenendael, J.M. (1998) The trade-off between dispersability and longevity. An important aspect of plant species diversity. *Applied Vegetation Science*, **1**, 29–36.

Ellenberg, H., Weber, H.E., Düll, R., Wirth, V., Werner, W. & Paulissen, D. (1992) *Zeigerwerte Von Pflanzen in Mitteleuropa*. Verlag Erich Goltze, Göttingen.

Eriksson, O. & Ehrlén, J. (1992) Seed and microsite limitation of recruitment in plant populations. *Oecologia*, **91**, 360–364.

Eriksson, O. & Jakobsson, A. (1999) Recruitment trade-offs and the evolution of dispersal mechanisms in plants. *Evolutionary Ecology*, **13**, 411–423.

Gerhardt, F. (1993) *Physiographic and historical influences on forest composition in Central New England, USA*. Master in Forest Science Thesis, Harvard University, Cambridge, MA.

Gleason, H.A. & Cronquist, A. (1991) *Manual of vascular plants of Northeastern United States and adjacent Canada*. New York Botanical Garden, NY.

Glitzenstein, J.S., Canham, C.D., McDonnel, M.J. & Streng, D.-R. (1990) Effects of environment and land-use history on upland forests of the Cary Arboretum, Hudson Valley, New York. *Bulletin of the Torrey Botanical Club*, **117**, 106–122.

Gower, J.C. (1971) A general coefficient of similarity and some of its properties. *Biometrics*, **27**, 857–874.

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.

Grime, J.P. (1977) Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *American Naturalist*, **111**, 1169–1194.

Grime, J.P., Hodgson, J.G. & Hunt, R. (1988) *Comparative plant ecology, a functional approach to common British species*. Unwin-Hyman Ltd, London.

Grime, J.P., Mason, G., Curtis, A.V., Rodman, J., Band, S.R., Mowforth, M.A.G., Neal, A.M. & Shaw, S. (1981) A comparative study of germination characteristics in a local flora. *Journal of Ecology*, **69**, 1017–1059.

van Groenendael, J.M., Ouborg, N.J. & Hendriks, R.J.J. (1998) Criteria for the introduction of plant species. *Acta Botanica Neerlandica*, **47**, 3–13.

Halbach, S.M. (1997) *The distribution of herbaceous species in primary and secondary woodlots in Williamstown*. Bachelor Thesis, Williams College, Williamstown, MA.

Harper, J.L. (1977) *Population Biology of Plants*. Academic Press, London.

Harper, J.L., Lovell, P.H. & Moore, K.G. (1970) The shapes and sizes of seeds. *Annual Review of Ecology and Systematics*, **1**, 327–356.

Hermy, M. (1985) *Ecologie en fytosociologie van oude en jonge bossen in Binnen-Vlaanderen* (in Dutch). PhD Thesis, University of Ghent, Ghent.

Hermy, M., Honnay, O., Firbank, L., Grashof-Bokdam, C.J. & Lawesson, J.E. (1999) An ecological comparison between ancient and other forest plant species of Europe, and the implications for forest conservation. *Biological Conservation*, **91**, 9–22.

Hermy, M. & Stieperaere, H. (1981) An indirect gradient analysis of the ecological relationships between ancient and recent riverine woodlands to the south of Bruges (Flanders, Belgium). *Vegetatio*, **44**, 43–49.

Higgins, S.I. & Cain, M.L. (2002) Spatially realistic plant metapopulation models and the colonization-competition trade-off. *Journal of Ecology*, **90**, 616–626.

Hodgson, J.G., Grime, J.P., Hunt, R. & Thompson, K. (1995) *The electronic comparative plant ecology*. Chapman & Hall, London.

Honnay, O., Degroote, B. & Hermy, M. (1998) Ancient-forest plants species in Western Belgium: a species list and possible ecological mechanisms. *Belgian Journal of Botany*, **130**, 139–154.

Honnay, O., Verheyen, K., Butaye, J., Jacquemyn, H., Bossuyt, B. & Hermy, M. (2002) Possible effects of climate change and habitat fragmentation on the range of forest plant species. *Ecology Letters*, **5**, 525–530.

Hood, G. (2001) *Poptools 2.1*. CSIRO, Canberra.

Jakobsson, A. & Eriksson, O. (2000) A comparitive study of seed number, seed size, seedling size and recruitment in grassland plants. *Oikos*, **88**, 494–502.

Kleyer, M. (1995) *Biological traits of vascular plants. A database*. Arbeitsberichte Institute für Landschaftsplannung und Ökologie, University Stuttgart.

Kornas, J. (1972) Corresponding taxa and their ecological background in the forests of temperate Eurasia and North America. *Taxonomy, Phytogeography and Evolution* (ed. D.H. Valentine), pp. 37–60. Academic Press, London.

Kubikova, J. (1987) Cultivated forest stands in Central Bohemia, their floristic composition and history. *Wissenschaftlige Beiträge (M. Luther University)*, **46**, 155–165.

Lavorel, S., McIntyere, S., Landsberg, J. & Forbes, T.D.A. (1997) Plant functional classifications: from general groups to specific groups based on response to disturbance. *Trends in Ecology and Evolution*, **12**, 474–478.

Leishman, M. (2001) Does the seed size/number trade-off model determine plant community structure? An assessment of the model mechanisms and their generality. *Oikos*, **93**, 294–302.

Leishman, M.R. & Westoby, M. (1998) Seed size and shape are not related to persistence in soil in Australia in the same way as in Britain. *Functional Ecology*, **12**, 480–485.

Leishman, M.R., Westoby, M. & Jurado, E. (1995) Correlates of seed size variation: a comparison among five temperate floras. *Journal of Ecology*, **83**, 517–530.

Mabry, C., Ackerly, D. & Gerhardt, F. (2000) Landscape and species-level distribution of morphological and life history traits in a temperate woodland flora. *Journal of Vegetation Science*, **11**, 213–224.

Matlack, G.R. (1994) Plant species migration in a mixed-history forest landscape in eastern North America. *Ecology*, **75**, 1491–1502.

McIntyre, S. & Lavorel, S. (2001) Livestock grazing in subtropical pastures: steps in the analysis of attribute response and plant functional types. *Journal of Ecology*, **89**, 209–226.

Montgomery, F.H. (1977) *Seeds and fruits of plants of eastern Canada and northeastern United States*. University of Toronto Press, Toronto.

Motzkin, G., Foster, D.R., 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.

Motzkin, G., Patterson,W.A. III & Foster, D.R. (1999) A historical perspective on pitch pine-scrub oak communities in the Connecticut Valley of Massachusetts. *Ecosystems*, **2**, 255–273.

Nash, K.M. (1994) *The role of dispersal mechanisms on the colonization of spring herbaceous flora in secondary woodlands*. Bachelors Thesis, Williams College, Williamstown, MA.

Noble, I.R. & Gitay, H. (1996) A functional classification for predicting the dynamics of landscapes. *Journal of Vegetation Science*, **7**, 329–336.

Noy-Meir, I., Gutman, M. & Kaplan, Y. (1989) Responses of Mediterranean grassland plants to grazing and protection. *Journal of Ecology*, **77**, 290–310.

Nyland, R.D., Zipperer, W.C. & Hill, D.B. (1986) The development of forest islands in exurban central New York State. *Landscape and Urban Planning*, **13**, 111–123.

Peterken, G.F. & Game, M. (1984) Historical factors affecting the number and distribution of vascular plant species in the woodlands of central Lincolnshire. *Journal of Ecology*, **72**, 155–182.

Petersen, P.M. (1994) Flora, vegetation, and soil in broadleaved ancient and planted woodland, and scrub on Rosnaes, Denmark. *Nordic Journal of Botany*, **14**, 693–709.

van der Pijl, L. (1982) *Principles of Dispersal in Higher Plants*. Springer-Verlag, Berlin.

Primack, R.B. (1987) Relationships among flowers, fruits, and seeds. *Annual Review of Ecology and Systematics*, **18**, 409–430.

Rejmanek, M. & Richardson, D.M. (1996) What attributes make some plant species more invasive? *Ecology*, **77**, 1655–1661.

Sciama, D. (2000) *Dynamique de la végetation forestière dans des terrains en deprise agricole en Petite Montagne Jurassienne* (in French). PhD Thesis, Ecole Nationale du Génie Rural, des Eaux en des Forêts, Nancy.

Siegel, S. & Castellan, J.N. (1988) *Nonparametric statistics for the behavioral sciences*. McGraw-Hill Co, New York.

Singleton, R.A. (1998) *Recovery of forest herb community in post-agricultural forests in central New York: pattern and process*. PhD Thesis, Cornell University, Ithaca, NY.

Singleton, R.A., Gardescu, S., Marks, P.L. & Geber, M.A. (2001) Forest herb colonization of post-agricultural forests in central New York, USA. *Journal of Ecology*, **89**, 325–338.

Sobey, D.G. (1995) *Analysis of the ground flora and other data collected during the 1991 Prince Edward Island Forest Inventory. III A comparison of the vegetation and environmental factors of pre-1935 and post-1935 forested sites*. The Institute of Island Studies, University of Prince Edward Island, Charlottetown, PEI.

SPSS (1999) *SPSS 10.0*. SPSS Inc, Chicago.

Thompson, K., Bakker, J. & Bekker, R.M. (1997) *The soil seed banks of North West Europe: methodology, density and longevity*. Cambridge University Press, Cambridge.

Thompson, K., Band, S.R. & Hodgson, J.G. (1993) Seed size and shape predict persistence in soil. *Functional Ecology*, **7**, 236–241.

Thompson, K., Hillier, S.H., Grime, J.P., Bossard, C.C. & Band, S.R. (1996) A functional analysis of a limestone grassland community. *Journal of Vegetation Science*, **7**, 371–380.

Vankat, J.L. & Snyder, G.W. (1991) Floristics of a chronosequence corresponding to old-field successions in southwestern Ohio. I. Undisturbed vegetation. *Bulletin of the Torrey Botanical Club*, **118**, 365–376.

Vellend, M. (2003) Habitat loss inhibits recovery of plant diversity as forests regrow. *Ecology*, in press.

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.

Weiher, E., van der Werf, A., Thompson, K., Roderick, M., Garnier, E. & Eriksson, O. (1999) Challenging Theophrastus: a common core list of plant traits for functional ecology. *Journal of Vegetation Science*, **10**, 609–620.

Wen, J. (1999) Evolution of Eastern Asian and Eastern North American disjunct distributions in flowering plants. *Annual Review of Ecology and Systematics*, **30**, 421–455.

Whitney, G.G. & Foster, D.R. (1988) Overstorey composition and age as determinants of the understorey flora of woods of Central New England. *Journal of Ecology*, **76**, 867–876.

Wisskirchen, R. & Haeupler, A. (1998) *Standardliste der Farn- und Blütenpflanzen Deutschlands*. Ulmer, Stuttgart.

Wulf, M. (1997) Plant species as indicators of ancient woodland in northwestern Germany. *Journal of Vegetation Science*, **8**, 635–642.

Zacharias, D. (1994) Bindung von Gefässpflanzen an Wälder alter Waldstandorte im nördlichen Harzvorland Niedersachsens – ein Beispiel für die Bedeuting des Alters von Biotopen für den Pflanzenartenschutz (in German). *Norddeutsche Naturschutzakademie-Berichte*, **3**, 76–88.

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