



# The relative importance of local, regional and historical factors determining the distribution of plants in fragmented riverine forests: an emergent group approach

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## ABSTRACT

**Aim** To investigate how local, regional and historical factors shape the herbaceous plant communities in fragmented riverine forests, and how the community composition and species richness of these fragments is related to the interplay between the environmental factors and specific plant life-trait combinations.

**Location** Riverine forest fragments in the Grand-duché de Luxembourg.

**Methods** Forest fragments were surveyed for their abundance in herbaceous plant species. All plant species were clustered into Emergent Groups (EG) by means of a formal classification based on 14 life-history traits. Within each EG, the local, regional and historical factors were related to the community composition using partial Canonical Correspondence Analyses (pCCA) and to the species richness using Generalized Linear Models (GLMs). The EG colonization ability was characterized by means of logistic regressions.

**Results** We defined and characterized seven EGs, among which three consisted of forest specialist species (barochorous perennials, short geophytes and zoochorous perennials), which exhibited specific life-trait combinations: large and short-lived seeds and/or vernal phenology. Differences in EG composition between forest fragments were mainly explained by local environmental factors such as soil productivity and pH. The richness of barochorous perennials and short geophytes was well predicted by the historical and regional factors. The colonization ability appeared very low for barochorous perennials and short geophytes.

**Main conclusions** Local environmental conditions appear to drive the differentiation of the riverine forest plant communities owing to the specific habitat requirements of many forest species. Spatial and temporal forest discontinuities affect the richness of forest specialist species, due to dispersal and/or recruitment limitations. The emergent group approach enhances the understanding of the relative influence of local, regional and historical factors by distinguishing between forest specialists from generalists or 'matrix' species, which have a masking effect.

## Keywords

Alluvial soils, colonization ability, forest connectivity, land-use history, life-history traits, Luxembourg, plant distribution, variation partitioning, western Europe.

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## INTRODUCTION

Community composition has long been considered to be the result of local environmental heterogeneity and local ecological processes such as predation and competition (Ricklefs, 1987). This is reflected, for example, in models of species coexistence, such as the intermediate biomass model (Grime, 1979) or the intermediate disturbance model (Connell, 1978; Huston, 1979); both models consider that the number of species is a function of local community interactions and also of local habitat characteristics. It is only in the last few decades that the influence of local processes has been complemented by an appreciation of other environmental factors that generate non-random patterns of community composition (Ricklefs & Schluter, 1993; Zobel, 1997).

Some of these factors, further referred to as regional factors, are related to the presence of neighbouring communities, which interact with the local community through species dispersal (e.g. Honnay *et al.*, 2001). This is especially true in temperate zones, where formerly continuous areas of forest habitat have been fragmented by humans (Wade *et al.*, 2003), and forest connectivity has been shown to influence the composition of local forest plant communities (e.g. Dzwonko & Loster, 1992; Grashof-Bokdam, 1997; Butaye *et al.*, 2001). Obviously, the plant community composition of a forest fragment not only depends on the species' ability to persist, but also to disperse to and establish in other fragments to counterbalance local extinctions (Hanski, 1999).

Besides local and regional factors, the history of the site also affects the composition of the forest plant community. Historical studies of temperate forests have highlighted that some species are confined to ancient forests (e.g. Hermy *et al.*, 1999). Ancient forests are defined as forests that have existed continuously since a known date, which is often close to 1800 in Europe (e.g. Hermy *et al.*, 1999). The absence of these 'ancient forest species' in recently established forests has been explained by their very slow colonization abilities (e.g. Brunet & Von Oheimb, 1998; Bossuyt *et al.*, 1999), especially in landscapes characterized by a high temporal turnover rate of forest fragments. It has been shown that the fragment occupancy of a species depends upon its ability to colonize newly emerging forests (Johst *et al.*, 2002; Jacquemyn *et al.*, 2003). Consequently, historical discontinuity of the forest land use yields an important loss of species diversity (Vellend, 2004).

Although our understanding of the role of local, regional and historical factors in shaping forest plant communities is growing, our knowledge of the relative importance of each of these factors remains in its infancy. The only relevant studies concluded that the relative influence of regional factors, on forest fragment occupancy patterns, was far less important than that of local habitat characteristics (Dupré & Ehrlén, 2002; Kolb & Diekmann, 2004). However, this relative contribution can be expected to vary both with the forest community descriptors (Graae *et al.*, 2004), i.e. composition and/or richness, and with the species life-traits considered

(Dupré & Ehrlén, 2002). First, Graae *et al.* (2004) found that species richness was unaffected by regional variables, while they accounted for a significant part of variation in community composition. Secondly, forest specialist life-traits, such as low seed production and ability for clonal growth, were negatively affected by the forest isolation (Dupré & Ehrlén, 2002). Moreover, historical continuity promotes the presence of species having life-traits characteristics of the 'ancient forest species' such as barochorous heavy seeds and transient seedbanks (Graae & Sunde, 2000). It therefore seems relevant to investigate simultaneously the response of the two commonly-used community descriptors (species richness and composition) and of the species life-traits in order to delineate better the relative influence of local, regional and historical factors shaping the herbaceous plant communities in fragmented riverine forests.

From a methodological point of view, most previous studies have either focused on the fragment occupancy of individual species, hampering broad generalizations across regions and obscuring the underlying ecological mechanisms (Dupré & Ehrlén, 2002; Kolb & Diekmann, 2004), or they have analysed the life-traits one by one (e.g. Graae & Sunde, 2000). The consideration of life-traits in isolation, however, presents a rather abstract view. Obviously, in the real world, local, regional and historical factors, which act as ecological and evolutionary constraints, do not apply directly to each life-trait separately but to the species as a whole, which is a unique combination of life-traits. For a given species, life-traits can interact (synergistically, antagonistically or in many different interplays) in determining the species response to spatial and historical forest discontinuity. For instance, a large-seeded species is often viewed as a poor disperser (Mabry, 2004). However, when this trait is associated with a zoochorous dispersal, the species can possess very good dispersal abilities (Hérault *et al.*, 2005). In this way, it is likely that a combination of different life-traits is functionally more determinant for a species distribution than any individual trait considered separately. This argues for an approach based on emergent groups (*sensu* Lavorel *et al.*, 1997), which allows the consideration of a species as a functional unit of life-traits throughout the analysis. An emergent group (EG) is thus defined as a set of species that have similar morphological, physiological and phenological life-trait combinations (Lavorel *et al.*, 1997) and, therefore, have convergent ecological strategies.

In the present paper, we first aimed to identify EGs of functionally-similar herbaceous plants among the forest flora of fragmented deciduous riverine forests in the Grand-duché de Luxembourg. We then tested the hypothesis (H1) that the relative importance of local, regional and historical factors determining the composition of the EGs will differ according to the EG identity. Next, we put forward the hypothesis (H2) that the relative importance of local, regional and historical factors determining the richness of the EGs will also differ according to the EG identity. In other words, we expect that EG richness and composition

are associated with local factors in some groups, and regional and historic factors in others. Finally, we hypothesize (H3) that the differential responses of the EGs to spatial and temporal forest discontinuity are mainly explained by their differing colonization abilities, in turn a function of specific life-trait combinations.

## MATERIALS AND METHODS

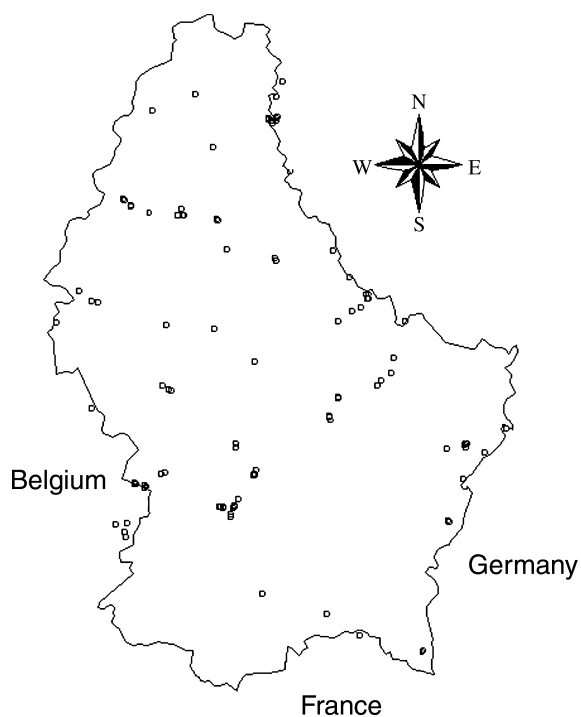
### Study area

The investigated forests were situated throughout the Grand-duché de Luxembourg (GDL) in Central-Western Europe (49°26′–50°10′ N, 5°42′–6°32′ E). The climate is sub-continental with an oceanic influence; the mean annual temperature is 9 °C. Annual rainfall ranges between 700 and 1000 mm (EFOR, 2002). The north of the sampling area consists of Lower Devonian geological layers, shales and gritty shales with low calcium and phosphorous contents whereas the south has more recent geological layers of sandy and calcareous rocks, from the Triassic and Jurassic periods. This sampling region encompassed a wide range of soil conditions, from poor-acidic soils to rich-basic ones; the land cover ranges from highly isolated stands to heavily forested areas. The four main rivers of GDL are the Alzette, the Clerve, the Sûre and the Our; all belonging to the Rhine watershed. Detailed flooding statistics are not available but overflows are quite regular. From our observations, overflows occur on average five days a year during autumn and winter.

### Data collection

We surveyed 153 deciduous forest fragments throughout the GDL (Fig. 1). These fragments were selected if they met two criteria: (1) sites on alluvial soils located in the river floodplain, in order to ensure we sampled similar forest communities; and (2) fragments having no obvious sign of a former plantation or of any current management activities. Poplar plantations were thus excluded. The sampling unit was the entire forest fragment. Sampling areas ranged from 500 to 12,190 m<sup>2</sup> and were estimated using digitized land-use maps. The fieldwork was carried out during the growing period (March–September) 2002 and 2003. All stands were completely surveyed twice a year: during spring and during summer/autumn and all herbaceous species were recorded. Each species received a crude cover value (1 : < 10% cover, 5: from 10% to 50% and 10: from 50% to 100%) to avoid any inaccuracies due to the large inventoried areas. Plant nomenclature follows Lambinon *et al.* (2004).

Three types of environmental characteristics were registered: local environmental, regional and historical variables (see Table 1 for details). The recorded variables were selected according to their successful use in studies regarding riverine forest ecology (Ruffinoni *et al.*, 2003), forest fragmentation (Kolb & Diekmann, 2005) and forest land-use history (Verheyen *et al.*, 1999).



**Figure 1** Location of the 153 riverine fragmented forests in the studied area.

Local variables were chosen to assess the suitability of the forest fragments for the riverine forest plants. The depth of the reductive layer, which reflects the upper limit of the water table, was measured by means of an auger. The litter thickness was determined in the field during summer. To measure the soil pH, three soil samples were collected from each site. These sub-samples were mixed and pH was measured following the ISO 10390 protocol (amount of water addition equal to five times the dried soil weight, pH measured after 2 h at room temperature). No detailed soil chemical analyses were performed due to the large number of sites used. *N* Ellenberg values were used to assess the soil productivity. Ellenberg *et al.* (1992) assigned scores, along an arbitrary nine-point scale, to European plants according to their nitrogen requirements. These scores are now interpreted as a general measure of soil productivity rather than the strict nitrogen availability, given that *N* Ellenberg values are generally more correlated with measured biomass than with soil nutrient levels (Schaffers & Sýkora, 2000). For each stand, the soil productivity value was calculated using the optimal weighting function of Käfer & Witte (2004):

$$Wi = 0.5 + 0.5 \left( \frac{Ci - C_{\min}}{C_{\max} - C_{\min}} \right),$$

where *Wi* is the calculated plant cover weight, *C<sub>i</sub>* is the initial plant cover value, *C<sub>min</sub>* is the minimum plant cover value possible and *C<sub>max</sub>* is the maximum plant cover value possible. The soil productivity value for a given stand was then obtained by calculating a weighted mean using *Wi* as the cover weighting factors of the species Ellenberg values.

**Table 1** Overview of the environmental variables selected to explain the vegetation composition and richness in riverine forest fragments. FM, field measurement; LM, laboratory measurement; CI, computed index, see text for details

Variable name	Acquisition	Type	Details and range
<i>Historical</i>			
Forest age	LM	Ordinal	0/1/2/3/4 (< 48, 48, 97, 171, 225 years of forest presence)
<i>Local environmental</i>			
Depth of the reductive layer	FM	Ordinal	Upper limit of the alluvial water table in soil; 1/2/3/4/5 (< 25, < 50, < 100, < 150, > 150 cm in depth)
Litter thickness	FM	Continuous	Recorded in summer; from 0 to 10 cm
Soil productivity	CI	Continuous	From 5.53 to 7.32 ( <i>N</i> Ellenberg values)
Sampling unit area	LM	Continuous	Measured from digitized maps; from 500 to 12,194 m <sup>2</sup>
Soil pH	LM	Continuous	Measured from three mixed soil samples; ISO 10,390 norm; from 4.29 to 8.63 pH unit
<i>Regional</i>			
Forest connectivity	CI	Continuous	From 8 to 2621 (no unit, computed index)
Riverine forest connectivity	CI	Continuous	From 0 to 261 (no unit, computed index)

Regional variables encompassed two connectivity measures, which were computed using the incidence function model of Hanski (1994):

$$I_i = \sum_{j \neq i} \exp(-\alpha d_{ij}) A_j^b,$$

where  $I$  is the connectivity index,  $i$  is the stand in question,  $j$  each of the other forest fragments,  $d_{ij}$  is the distance from  $i$  to  $j$ ,  $1/\alpha$  is the average distance from  $i$  to  $j$ , and  $A$  the area of the fragment  $j$ . A value of 0.5 was used for the exponent  $b$  following the recommendation of Moilanen & Nieminen (2002). The *forest connectivity index* was calculated by taking into account all forest types within a radius of 1 km; whereas the *riverine forest connectivity index* only took into account the forests on alluvial soils, which constitute the rarer but most similar plant communities, situated within 2 km upstream or downstream along the river. The 1 km and 2 km distances were chosen to obtain a realistic value of  $\alpha$ , which scales the effect of distance to dispersal. In similar studies, values from 0.001 to 0.01 m<sup>-1</sup> have been used (Bastin & Thomas, 1999; Verheyen *et al.*, 2004). Our chosen distances produce  $\alpha = 0.007$  and 0.002 m<sup>-1</sup> for the *forest connectivity index* and the *riverine forest connectivity index*, respectively, which seems in agreement with the literature. Hydrochorous dispersal, which may occur over very long distances (Andersson *et al.*, 2000), was not taken into account.

The stand histories were reconstructed from 1777 onwards, consulting four historical maps (Ferraris *et al.*, 1777; Vandermaelen, 1831–32; Hansen, 1905; ACT, 1954) and the current map (ACT, 2002). Fifteen percent of all forests (23 forest fragments) were continuously covered with forest, at least since 1777. These forests will be referred to as ‘ancient forests’ and the others will be referred to as ‘new forests’ for the rest of this paper. The sampling unit areas differed slightly in relation to the forest history, the 171–224 years old forest fragments tending to be the largest (see Table 2).

**Table 2** Distribution of the riverine forest fragment areas among the classes of forest age

Forest age (years of forest presence)	<i>n</i>	Mean fragment area (m <sup>2</sup> )
< 48	55	2648 ± 1651
48–96	46	3662 ± 2723
97–170	22	3417 ± 2317
171–224	7	6000 ± 2268
> 224	23	2938 ± 2216

### Life-trait selection

Fourteen life-traits were selected for EG definition (Table 3). The 14 traits were chosen to reflect key events in the plant community assembly processes in fragmented forests, i.e. dispersal, establishment and persistence (Weiher *et al.*, 1999). Due to the high number of recorded species ( $n = 237$ ), trait information was compiled from the existing literature (mainly Harley & Harley, 1987; Grime *et al.*, 1988; Hodgson *et al.*, 1995; Kleyer, 1995; Julve, 1998), and completed by reference to monographs from the Biological Flora of the British Isles and by some data from the Nouvelle Flore de Belgique (Lambinon *et al.*, 2004). To assess seed longevity, the index of Thompson *et al.* (1998) was used when at least five records were present in the database from Thompson *et al.* (1997). To assess the seed shape, the ratio of the seed length to the seed breadth was used (Grime *et al.*, 1988). On average, 23% of trait information was lacking. This was mainly due to under-studied rare species, while life-trait values for common species were well known. Since the following statistical analyses are based on species abundance and richness (both measures being driven by common species), we consider that the results are unlikely to be influenced by this lack of information.

### Identifying emergent groups

The EG delineation closely adhered to the methodology applied by Verheyen *et al.* (2003), and was based on a

**Table 3** List of the 14 plant life-traits selected due to their implication in ecological processes occurring in fragmented riverine forests: dispersal, establishment and persistence of herbaceous plants

Plant traits	Description	Missing values (%)	Variable type
Age at first flowering	1: < 3 months; 2: 3 months–1 year; 3: 1–2 years; 4: 2–3 years; 5: 3–6 years; 6: 6–15 years	59	Ordinal
Clonal propagation	0: no; 1: yes	25	Qualitative
Dispersal type*	1: barochory, myrmecochory; 2: anemochory; 3: hydrochory; 4: endo- & exo-zoochory	0	Qualitative
Germination requirement	1: immediate; 2: chilling or drying or light or scarification; 3: combinations of the latter	30	Ordinal
Life-forms†	1: chamaephyte; 2: geophyte; 3: hemicryptophyte; 4: therophyte	0	Qualitative
Onset of flowering	1: Period > 4 months; 2: spring (3–5); 3: summer (6–7); 4: autumn (8–9)	3	Qualitative
Mean shoot height	1: < 0.1 m; 2: 0.1–0.29 m; 3: 0.30–0.59 m; 4: 0.60–0.99 m; 5: 1.0–3.0 m	0	Ordinal
Pollination vector	1: autogamy; 2: anemogamy; 3: entomogamy	8	Qualitative
Potential mycorrhiza	0: 25% or less of records report infection with VA mycorrhiza; 1: 75% or more records report infection; 2: 26–74% of records report infection	10	Qualitative
Seed longevity	Index of Thompson <i>et al.</i> (1998); values range from 0 to 1	33	Quantitative
Seed weight	Six classes: 1: too small to be measured; 2: < 0.2 mg; 3: 0.21–0.50 mg; 4: 0.51–1.00 mg; 5: 1.01–2.00 mg; 6: 2.01–10.00 mg; 7: > 10.00 mg	25	Ordinal
Seed production per ramet	1: 1–1000; 2: 1001–10,000; 3: > 10,000	59	Ordinal
Seed shape	1: length/breadth ratio < 1.5; 2: ratio 1.5–2.5; 3: ratio > 2.5	24	Ordinal
Seed size	Average (length + breadth)	50	Quantitative

\*Barochory: no obvious dispersal mechanism; myrmecochory: dispersal by ants; anemochory: dispersal by wind; hydrochory: dispersal by running water, endozoochory: dispersal by animals throughout ingestion; exozoochory: dispersal by animals throughout adhesion.

†Chamaephyte: Low woody or herbaceous plant with perennating tissue within 25 cm of soil surface; geophyte: herbaceous plant with perennating tissue (bulbs, corms, rhizomes, stem tubers, root tubers) below the soil surface; hemicryptophyte: herbaceous perennial plant with perennating tissue at the soil surface; therophyte: plant with perennating tissue contained in seed (annual plant).

similarity matrix between individual species using Clustan-graphics (Clustan Ltd, 2001). To calculate the matrix, the Gower's similarity coefficient (Gower, 1971) was applied as this coefficient can deal with missing values as well as with mixed data, i.e. qualitative, ordinal and quantitative (Legendre & Legendre, 1998). The resulting Gower's similarity matrix was then imported under Statistica (Statsoft Inc., 2003) and used to cluster the species into EGs using Ward's method. The cut-level for EG end groups was determined graphically from visual screening of the dendrogram, with the goal of defining a small number of EGs which contained a similar number of species. To determine which traits defined the EGs, the relationships between individual traits and EGs were investigated by means of Pearson  $\chi^2$  tests (when the trait was qualitative) and a Kruskal–Wallis statistic (when the trait was quantitative or ordinal). For the latter, *post hoc* comparisons of mean ranks of all pairs of EGs were computed using the formula of Siegel & Castellan (1988).

### Composition of the emergent groups and environmental variables

Our aim was to determine the relative influence of the historical, local and regional factors on the composition of the EGs in each forest fragment. The original species-by-sites dataset was divided into sub-tables, each one corresponding to the species-by-sites data for each EG. Partial Canonical Correspondence Analyses (pCCA) were then used to deter-

mine the relative influence of the three groups of explanatory variables on the variability of the composition of the EGs (ter Braak, 1988; Borcard *et al.*, 1992). This technique considered all present plant species together and thus is an appropriate method by which to study variation in species composition. For each sub-table, forward selection of variables was performed to include in the CCA models only the environmental variables explaining a significant amount of variation, commencing with the best single variable. The procedure was iteratively repeated until the addition of one environmental variable in the model was not significant, at the 0.05 level. The significant variables of a specific group (local, regional, historical or group combinations) were then used as constraining variables while the significant variables of all other groups were assigned as covariables. The pCCA was performed and the unique fraction of variance explained by this specific group of variables was obtained (Økland, 2003). Finally, variation due to each group of variables and also the variation due to each group of combinations was calculated for each EG.

### Richness of the emergent groups and environmental variables

Our aim was to determine the influence of the historical, local and regional factors on the species richness of the EGs in each forest fragment. All continuous environmental variables were log-transformed. This led to zero skewness

and thus allowed the use of parametric statistical techniques (Graae *et al.*, 2004). The product of the presence/absence matrix (site by species), with the binary coded matrix of EG memberships (species by emergent groups), provided the species richness of each EG for each forest fragment. Prior to analysis, the EG species richness was corrected for the effect of the fragment area. To achieve this, the EG species richness was regressed against the logarithm of the fragment area. The residuals were then analysed with respect to the explanatory variables using generalized linear models (GLMs). The stepwise procedure (Legendre & Legendre, 1998) was applied to select the significant variables. The stepwise procedure alternated between forward selection and backward elimination. The first variable included in the GLM model was the most significant. Then the most significant of the remaining variables was added and the significance of the GLM model was tested. At this step, non-significant variables, if present in the GLM model, were excluded. This procedure was repeated until the GLM model was stable. This allowed us to eliminate variables included during the first steps but contributing little after incorporation of other variables (Legendre & Legendre, 1998). Finally, the stable GLM model was selected and the significance of the variables was tested using the Wald statistic (Statsoft Inc., 2003). To assess the relative importance of the explanatory variables, they were ordered in decreasing predictive power.

### Assessing the colonization ability

As most of the forest specialist species do not form persistent seed banks (Bossuyt & Hermy, 2001), the presence of such species in new forests is very likely related to a colonization event. This pool of data (132 new forests, i.e. with historical discontinuity) was used to assess the colonization ability of the identified EGs. A new forest connectivity index was calculated, as described above, but only taking into account the ancient forests (source of diaspores) present within a 1-km distance ( $\alpha = 0.006 \text{ m}^{-1}$ , see above). For each species with a frequency higher than 5%, logistic regressions were used to relate the presence/absence data with the forest connectivity index. The significance (*P*-value) of the regression relationship was retained as a colonization ability index. Positive significant relationships meant that the species was less frequent in isolated forests and thus had strong colonization limitations. If non-significant or negative relationships were found, the species was equally or more frequent in isolated forests than in connected forests, implying high colonization ability. When the relationship was negative, the index was arbitrary set to one, as one is the highest possible *P*-value. A colonization index was thus assigned to each species. This index was compared among EGs using the Kruskal–Wallis test statistics and post-hoc comparisons of median ranks were computed (Siegel & Castellan, 1988).

All statistical analyses were conducted using Statistica 6.1 (Statsoft Inc., 2003).

## RESULTS

### Emergent group identification

Life-form, dispersal mode and mean shoot height were the main life-traits driving the clustering, as species were often gathered according to these three traits (not shown). These traits were therefore chosen to denominate the EGs. Seven EGs were derived and characterized (see Tables 3 & 4 for definitions): (1) *annuals* consist of therophytes, which formed persistent seed banks; (2) *barochorous perennials*, which are hemicryptophytes with short-lived seeds; (3) *graminoids*, mainly encompassing some Cyperaceae, Poaceae and Juncaceae, which are wind-pollinated; (4) *helophytes*, which are non-mycorrhizic; (5) *Short geophytes*, which are spring ephemerals with large, hardly-germinating seeds; (6) *anemochorous perennials*, which produce a lot of light diaspores that germinate easily and persist for a long time; and (7) *zoochorous perennials*, which mainly produce exo-zoochorous seeds in small numbers.

### Factors influencing the composition of the emergent groups

The pCCA results revealed that little variation in the relative importance of the environmental variable groups was detected with respect to EG identity, i.e. local variables were followed by regional factors and then by site history (Table 5). Local environmental variables mainly explained differences in species composition of the EGs, between different forests (Table 5). Local factors accounted for more than 50% of the observed variation in six out of seven cases. Soil productivity was the first retained variable in five out of seven cases. Site history influenced the composition of barochorous perennials, helophytes and short geophytes EGs, while forest connectivity (both forest and riverine forest) appeared only important for the composition of annuals and anemochorous perennials. Regional variables were not retained by the selection procedure in two cases (helophytes and short geophytes), whereas site history was not retained for the composition of the zoochorous perennials. Given the relatively low amount of variation shared, the relative effects of the different explanatory variable groups were well defined.

### Factors influencing the species richness of the emergent groups

The GLMs were not significant for helophytes and zoochorous perennials. Overall, the connectivity indexes (either forest or riverine forest) were strongly associated with the EG species richness. Indeed, except for anemochorous perennials, these predictors ranked first in the stepwise selection procedure (Table 6). The relationship between forest connectivity and richness was often positive, except for annuals. Among the local environmental factors, the soil productivity was inversely

**Table 4** Comparison of the life-trait values between the seven emergent groups defined in the herbaceous flora of fragmented riverine forests

	<i>P</i>	Annuals	Barochorous perennials	Graminoids	Helophytes <sup>§</sup>	Short geophytes	Anemochorous perennials	Zoochorous perennials
<i>n</i>		29	29	39	53	29	23	35
Age at 1st flowering†	***	2 <sup>a</sup>	3.5 <sup>b</sup>	3 <sup>b</sup>	3 <sup>b</sup>	4 <sup>b</sup>	3 <sup>ab</sup>	3 <sup>b</sup>
Clonal propagation‡	***	16.2/-16.2	-3.5/3.5	-5.6/5.6	-6.3/6.3	-0.0/0.0	-0.0/0.0	-0.5/0.5
Dispersal type‡	***	6.8/-0.1/-2.8/-3.9	12.8/-7.1/-1.8/-3.9	7.5/-7.5/0.2/-0.2	-7.4/8.0/11.9/-12.5	1.8/-2.1/-2.8/3.2	-9.7/17.4/-2.2/-5.4	-11.8/-8.6/-2.4/22.7
Germination requirements†	***	2 <sup>a</sup>	2 <sup>ab</sup>	1 <sup>bc</sup>	1 <sup>bc</sup>	3 <sup>a</sup>	1 <sup>c</sup>	2 <sup>bc</sup>
Life-form‡	***	-0.1/-6.0/-17.0/23.1	0.9/-5.0/8.0/-3.9	-1.5/-6.1/12.8/-5.3	-2.0/4.0/4.1/-6.2	-1.1/23.0/-18.0/-3.9	-0.9/-44.8/8.7/-3.1	4.7/-5.2/1.3/-0.7
Mean shoot height†	***	3 <sup>abcd</sup>	3 <sup>abcd</sup>	3 <sup>bd</sup>	3 <sup>acd</sup>	2 <sup>b</sup>	4 <sup>ac</sup>	3 <sup>abcd</sup>
Onset of flowering‡	***	6.0/-4.3/-3.9/2.2	-8.6/8.9/1.3/-1.7	0.9/-3.5/5.3/-2.7	9.1/-5.5/-7.5/3.9	-8.6/10.9/-0.7/-1.7	4.3/-4.6/-0.8/1.0	-3.2/-2.0/6.2/-1.1
Pollination vector‡	***	11.6/-4.3/-7.4	-3.4/-6.3/9.6	-2.9/27.6/-24.7	-3.1/-7.1/10.3	-4.4/-6.3/10.6	5.0/-2.8/-2.2	-2.8/-0.9/3.7
Potential mycorrhiza‡	***	3.9/-5.2/1.3	-3.9/3.4/0.5	4.5/-8.2/3.7	9.5/-12.6/3.1	-3.8/7.6/-3.8	-5.8/8.6/-2.8	-4.4/6.3/-1.9
Seed longevity†	***	0.81 <sup>a</sup>	0.04 <sup>c</sup>	0.39 <sup>b</sup>	0.34 <sup>b</sup>	0.00 <sup>cd</sup>	0.66 <sup>ab</sup>	0.38 <sup>bd</sup>
Seed weight†	***	5 <sup>ac</sup>	5 <sup>c</sup>	4 <sup>ac</sup>	3 <sup>ba</sup>	4 <sup>bac</sup>	2 <sup>b</sup>	4.5 <sup>ac</sup>
Seed production†	**	1 <sup>ab</sup>	1 <sup>b</sup>	1 <sup>ab</sup>	2 <sup>ab</sup>	1 <sup>ab</sup>	2 <sup>a</sup>	1 <sup>b</sup>
Seed shape†	**	1 <sup>a</sup>	2 <sup>ab</sup>	2 <sup>b</sup>	2 <sup>ab</sup>	3 <sup>ab</sup>	2 <sup>ab</sup>	1 <sup>ab</sup>
Seed size†	***	1.60 <sup>ab</sup>	2.00 <sup>b</sup>	1.45 <sup>ab</sup>	1.45 <sup>ab</sup>	2.93 <sup>b</sup>	0.78 <sup>a</sup>	1.95 <sup>b</sup>
Common taxa		<i>Galeopsis tetralix</i> <i>Geranium robertianum</i> <i>Impatiens noli-tangere</i>	<i>Agropodium podagraria</i> <i>Glechoma hederacea</i> <i>Stellaria nemorum</i>	<i>Millium effusum</i> <i>Poa nemoralis</i> <i>Urtica dioica</i>	<i>Filipendula ulmaria</i> <i>Petasites hybridus</i> <i>Phalaris arundinacea</i>	<i>Adoxa moschatellina</i> <i>Arum maculatum</i> <i>Ranunculus ficaria</i>	<i>Cirsium oleraceum</i> <i>Dryopteris filix-mas</i> <i>Senecio ovatus</i>	<i>Aconitum lycoctonum</i> <i>Festuca gigantea</i> <i>Stachys sylvatica</i>

\**P* ≤ 0.05; \*\**P* ≤ 0.01; \*\*\**P* ≤ 0.001

†Kruskal–Wallis test, values are medians; numbers with different letters are significantly different at the 0.05 level.

‡Pearson  $\chi^2$  test, values are differences between observed and expected frequencies for the different categories defined in Table 3.

§Helophytes: Fresh water plants with perennating tissue in soil beneath the water.

**Table 5** Assessment of the relative influence of historical (*H*), local environmental (*L*) and regional (*R*) variables on the composition of plant emergent groups from riverine forest fragments ( $n = 153$ ) using Canonical Correspondence Analysis partition of variation (the significant variables of a given variable group were used as constraining variables while the other significant variables were assigned as covariables). Numbers refer to the part of the total variation in a given emergent group

	Sorting order*	$L (R \cup H)^a$ (%)	$R (L \cup H)^b$ (%)	$H (L \cup R)^c$ (%)	$(L \cap R) H^d$ (%)	$(L \cap H) R^e$ (%)	$(R \cap H) L^f$ (%)	$L \cap R \cap H^g$ (%)
Annuals	Ln, Rr, Rf, Lr, Lp, Ls, H	54	27	8	7	1	0	3
Barochorous perennials	H, Ln, Ll, Lp, Lr, Rf, Rr, Ls	56	13	7	4	2	11	7
Graminoids	Ln, Lr, Ll, Rr, H, Lp, Rf	62	16	9	4	4	1	3
Helophytes	Ln, H, Ll, Lp, Lr, Ls	78	/	16	/	6	/	/
Short geophytes	Ln, H, Lp	60	/	38	/	2	/	/
Anemochorous perennials	Rf, Lp, H, Ln	41	26	15	12	3	4	0
Zoochorous perennials	Ln, Lr, Rf, Ll, Lp	74	16	/	10	/	/	/

\*Following forward selection of variables, only selected variables appeared.

Abbreviations are: H, site history; L, local variables; Ll, litter thickness; Ln, soil productivity; Lp, soil pH; Lr, depth of the reductive layer; Ls, site area; R, regional variables; Rf, forest connectivity; Rr, riverine forest connectivity.

<sup>a</sup>Variation unique to local variables; <sup>b</sup>variation unique to regional variables; <sup>c</sup>variation unique to the site history; <sup>d</sup>variation shared among local and regional variables, not explained by the site history; <sup>e</sup>variation shared among local variables and the site history, not explained by regional variables; <sup>f</sup>variation shared among regional variables and the site history, not explained by local variables; <sup>g</sup>variation shared among local, regional variables and the site history.

Response group	Predictor	Wald statistic	<i>P</i>	Regression coefficient
Annuals	Forest connectivity	6.86	**	4.31
	Soil productivity	4.82	*	7.11
	Riverine forest connectivity	4.47	*	-9.78
	Soil pH	3.95	*	4.58
Barochorous perennials	Forest connectivity	7.81	**	2.76
	Forest age	4.49	*	1.61
Graminoids	Riverine forest connectivity	7.10	**	8.47
	Soil productivity	3.86	*	-5.21
Helophytes				
Short geophytes	Riverine forest connectivity	4.02	*	8.06
Anemochorous perennials	Soil productivity	5.89	*	-9.92
Zoochorous perennials				
Total richness	Riverine forest connectivity	4.27	*	9.04

\* $P \leq 0.05$ ; \*\* $P \leq 0.01$ ; \*\*\* $P \leq 0.001$

related to the richness in anemochorous perennials and graminoids but also positively linked to the richness in annuals. We found that soil pH was positively related to the richness in annuals and that forest age could be used as a predictor of the richness of one EG: the barochorous perennials.

### Colonization ability of emergent groups

The identified EGs could be divided into three groups (Table 7): poor colonizers (colonization index close to zero: barochorous perennials and short geophytes); good colonizers (colonization indexes equal to one: graminoids and helophytes); and intermediates (annuals, anemochorous perennials and zoochorous perennials).

**Table 6** Assessment of the relative influence of historical, local environmental and regional variables on the species richness of plant emergent groups from riverine forest fragments ( $n = 153$ ) using generalized linear models with a logarithmic link function

## DISCUSSION

The emergent group delineation was primarily driven by life-form. Indeed, it is well-known that life-form correlates with numerous morphological and physiological traits (McIntyre *et al.*, 1995; Lavorel *et al.*, 1997). Among the seven identified EGs, plants from four groups exhibited life-trait combinations associated with generalist species (small seeds, anemochorous seed dispersal and/or long-lived seed bank), whereas the remaining three groups possessed singular life-trait combinations that reflected their strong adaptation to the forest environment (Bierzychudek, 1982). Barochorous perennials and short geophytes encompass spring ephemerals specifically adapted to capture resources before the closure of the canopy (Lapointe, 2001). Seeds of zoochorous perennials are dispersed

**Table 7** Comparison of the colonization index (CI) between plant emergent groups from the flora of riverine forest fragments (Kruskall–Wallis test, values are medians, numbers with different letters are significantly different at the 0.05 level). CI is based on the *P*-value of a logistic regression between the presence/absence data of a given species and an historical forest connectivity index

	<i>n</i>	CI
Annuals	12	0.88 <sup>abc</sup>
Barochorous perennials	18	0.05 <sup>c</sup>
Graminoids	24	1.00 <sup>ab</sup>
Helophytes	33	1.00 <sup>a</sup>
Short geophytes	17	0.11 <sup>bc</sup>
Anemochorous perennials	13	0.54 <sup>abc</sup>
Zoochorous perennials	20	0.66 <sup>abc</sup>

by large forest herbivores (Red deer, Roe deer and Wild boar in the study area). Furthermore, plants from these three EGs possess large heavy seeds which have a low longevity, properties generally considered to be indicators that a species is restricted to shady forest environments (Hodkinson *et al.*, 1998; Bossuyt & Hermy, 2001; Mabry, 2004). Due to their particular habitat requirements, these three EGs are a high conservation value in temperate forests (Keddy & Drummond, 1996; Hermy *et al.*, 1999).

### Community composition is mainly related to local factors

Many significant predictors of the community composition were sorted by the selection procedures (Table 5). The relative constancy of the importance of local, regional and historical factors on the EG composition, independently of the EG identity (Table 5), invalidates H1. On the other hand, predictors of EG richness were less frequent and varied more with the EG of interest (Table 6). This tends to validate H2. Local factors, and especially soil productivity, were the best predictors for community composition of the different EGs (Table 5), whilst regional factors were the main predictors of the species richness (Table 6). However, historical plus regional factors still explained 16–41% of the variation in species composition (Table 5). Local and historical variables still appeared, even if in a secondary position, in the species richness models (Table 6).

In general our results suggest that the ecological range of a given species is primarily driven by its habitat requirements (e.g. soil fertility and pH) when species exhibiting similar life-trait combinations (and thus belonging to the same EG), may be encountered at distinct sites due to divergent habitat preferences. For example, *Anemone nemorosa* and *Anemone ranunculoides* are two closely related species which have most of their life-traits in common and consequently are members of the same EG: the short geophytes. This indicates that the two *Anemone* species have similar ecological niches and ecosystem functions. Their

regional distribution shows no geographical segregation in the studied area, and occasionally both species were registered in the same stand. We found that the comparison of values of the environmental variables between the two groups of sites where the species occurred (omitting shared stands) shows no significant differences for regional and historical factors but shows a significant difference in soil productivity and pH values (Student's *t*-test:  $P < 0.001$ ;  $t = 3.35$  and  $P < 0.05$ ;  $t = 2.47$ , respectively). We also observed that the comparison of sites where at least one species occurred, with sites where neither species was present, leads to a high significance of the forest connectivity index (Student's *t*-test:  $P < 0.001$ ;  $t = 3.64$ ). Such distribution patterns greatly contributed to the preponderance of the local variables in the pCCA variation partitioning and of the regional factors in forest specialist richness analyses. In other words, this means that studies which focus on community composition (pCCA or similar multivariate analyses) or on each species independently (Dupré & Ehrlén, 2002) will often place the emphasis on local environmental properties, but if the study focuses on the richness in forest specialist EGs then regional factors will be highlighted (Graae *et al.*, 2004).

### The influence of regional factors

The graminoids and the helophytes possessed good colonizing abilities (Table 7). The colonization rate of graminoids was high given their barochorous dispersal (Table 4). However, this EG encompassed some species from the adjacent alluvial meadows, which are widespread habitats in the studied area. These species likely transgressed to the riverine forests and thus were met in the graminoid EG. Helophytes were mainly characterized by hydrochorous dispersal (Table 4), which may occur over long distances (Andersson *et al.*, 2000). Moreover, helophytes were typical generalists also occurring in the landscape matrix. The combination of high dispersal abilities and widespread distribution led to strong colonization capacities (Table 7).

Annuals, anemochorous perennials and zoochorous perennials possessed intermediate colonizing abilities (Table 7). A common life-trait of the first two EGs was their high seed longevity (Table 4). In this context, it cannot be excluded that some species survived the deforestation period through their seeds. Anemochorous perennials wind-dispersed seeds far from the forest sources whilst annuals often acted as pioneers in riverine areas, colonizing soils of newly emerging forest fragments. The early successional role of the annuals may explain why increasing riverine forest connectivity decreased the richness in annuals (Table 6). Indeed, it can be expected that the pioneer communities survived for longer when the forest was isolated from other riverine forests, due to the extended colonization time of specialist riverine forest species (Table 7). However, the positive association between richness of annuals and forest connectivity still remains odd. The zoochorous perennial richness showed no relationship to

forest connectivity (Table 6). Zoochorous perennials possessed large seeds which were dispersed by large forest herbivores, increasing the chance for seeds to reach a new forest (Grashof-Bokdam & Geertsema, 1998). Moreover, the studied area is characterized by high densities of large herbivores (Groot Bruinderink *et al.*, 2003). In this context, the migration of zoochorous perennials was not impeded (Table 6).

Among the poor colonizers (Table 7), the barochorous perennials lacked any dispersal adaptations, whereas diaspores of short geophytes were encountered among all dispersal types (Table 4). Consequently, colonization limitations were higher for barochorous perennials than for short geophytes as was shown in both the EG richness models (positive relationships between forest connectivity and species richness in Table 6) and the colonization indexes (Table 7). Furthermore, both EGs produced highly transient seed banks (Table 4). Thus, in new forests, low dispersal ability appears to be the major constraint for the recovery of the richness in both barochorous perennials and short geophytes (see also Verheyen *et al.*, 2003).

Overall, these results validate H3, i.e. differential colonization ability as a function of EG life-trait combinations.

### Historical continuity promotes barochorous perennials

Forest age or historical continuity affects herbaceous communities in two different ways. First, there is an effect of the continuity *per se*. Barochorous perennials failed to colonize new forests, consistent with their low colonization index (Table 7), they remained restricted to ancient forests (Table 6). Plant populations of these species are referred to as remnant populations. They are able to survive many years under sub-optimal ecological conditions because they exhibit very long generation times and prolonged clonal growth (Ehrlén & Lehtilä, 2002; Honnay & Bossuyt, 2005).

Secondly, it has been shown that historical discontinuities of the forest cover may have profound and long-term effects on forest soil properties (Verheyen *et al.*, 1999; Dupouey *et al.*, 2002). Soils of forests newly established on former arable land contain significantly higher amounts of nutrients, especially of phosphorus (Koerner *et al.*, 1997; Honnay *et al.*, 1999). The comparison of the soil productivity index between the youngest forests (i.e. < 97 years;  $n = 55$ ) and others ( $n = 98$ ) confirms these findings (Student's *t*-test;  $P < 0.05$ ;  $t = 2.04$ ). It is well-known that this soil enrichment stimulated highly competitive herbaceous perennials, such as *Urtica dioica* (De Keersmaecker *et al.*, 2004), which likely hampered the establishment of rich forest specialist communities. However, other ecological processes occurring in new forests (such as greater seed predation or lower germination rate) cannot be excluded *a priori*.

Consequently, due to intrinsic species properties, historical discontinuity isolated barochorous perennials to older forests. However due to habitat changes, historical discontinuity

promoted forest generalists (Table 5) through the creation of favourable habitats in newer forests. The relative contribution of dispersal limitation vs. recruitment limitation (probably through nutrient enrichment) remains unclear and can only be resolved through seed sowing experiments (Ehrlén & Eriksson, 2000).

### The emergent group approach

During the last decade, forest ecologists have attempted to produce lists of indicator species for historical continuity (e.g. Wulf, 1997; Hermy *et al.*, 1999). However, the regional variations in species pools, as well as the specific habitat requirements of many forest specialists, have hampered broad spatial extrapolations. Such generalizations across geographical regions seem permitted with the emergent group approach (see Verheyen *et al.*, 2003) although this concept, and especially the life-trait selection, remains clearly dependent on the scientific aims of the study (Lavorel *et al.*, 1997). The emergent group approach also led to a better understanding of the combination of life-traits driving the response to forest fragmentation whilst adhering to the functional unit of the species throughout the statistical analyses. This enabled us to define several ecological profiles (or emergent groups) among the forest flora and thus may offer an opportunity to predict and model their distinctive responses to spatial and temporal discontinuities (Matlack & Monde, 2004; Verheyen *et al.*, 2004).

Our results also highlight the dangers of relying solely on broad community measures instead of using a detailed ecological group investigation (Robinson *et al.*, 1992). For instance, when focusing only on the species richness one might conclude that it is hardly affected by the historical discontinuity (Table 6) or by the degree of forest fragmentation (Graae *et al.*, 2004; Holl & Crone, 2004; Vellend, 2004). However, species from different EGs responded in different ways to forest fragmentation and historical discontinuity. Effects seen at the emergent group level can be hidden at the whole community level. The EG approach is therefore useful to distinguish statistically (and not empirically) forest specialist and generalist species. This enabled us to analyse independently forest specialist EGs that in turn allowed us to test accurately the influence of spatial and historical discontinuities by omitting generalist species which have a masking effect (Cook *et al.*, 2002).

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