

Evaluation of the ecological restoration potential of plant communities in Norway spruce plantations using a life-trait based approach

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Summary

1. In Europe, intensively managed coniferous plantations rarely achieve similar nature conservation functions as deciduous woodlands. The ability to identify coniferous plantations that might be successfully converted to deciduous woodland is a key goal in forest management. The herbaceous plant community composition of mature plantations may be an accurate selection criterion for stands that are most suitable for initiating the conversion process to deciduous forest.

2. The herbaceous plant communities in Norway spruce plantations were analysed using a functional group approach. The analysis was conducted in three steps: (i) identification of emergent groups (EG) by multivariate classification; (ii) comparison of EG abundance between coniferous and deciduous stands (i.e. the target communities); (iii) partitioning the variation in EG abundance in coniferous plantations between forest management, local environmental and regional variables.

3. Seven EG were identified: two core forest groups (short geophytes and zoochoreous perennials), two groups from open habitats (annuals and helophytes) and three mixed groups (anemochoreous perennials, graminoids and short perennials).

4. Among the core forest groups, short geophytes were severely under-represented in plantations (because of their low dispersal abilities and specific habitat requirements) while zoochoreous perennials were slightly more abundant (because of their good dispersal and competitive abilities).

5. Regional variables largely influenced the abundance of core-forest EG. Restoration of communities rich in zoochoreous perennials is far easier than restoring short geophyte-rich communities because of the different colonization abilities of these EG.

6. Forest management variables were of secondary importance for the restoration potential of plantations. Because generalist EG were favoured by low stand densities, forest practitioners should avoid large thinning operations.

7. Local environmental variables played a minor role in determining EG abundance. However, short geophytes preferred rather high soil pH values and were therefore negatively affected by acidification caused by coniferous litter.

8. *Synthesis and applications.* The performance of short geophytes is the key to conversion success of Norway spruce plantations to deciduous forest. Stands located on base-rich soils and in landscapes with high forest connectivity are the most appropriate candidates for initiating the conversion process. For other types of stands, future work should explore the possibility of restoring other land-use types, such as annually mown meadows.

Key-words: alluvial soils, forest flora, functional groups, geophytes, *Picea abies*, variation partitioning

Journal of Applied Ecology (2005) **42**, 536–545
doi: 10.1111/j.1365-2664.2005.01048.x

Introduction

Ecological restoration of natural forests on sites formerly planted with non-indigenous tree species has become a primary aim of sustainable forestry (Ashton *et al.* 1997; Zerbe 2002). In temperate European forests, Norway spruce *Picea abies* (L.) Karst. has been widely planted for two centuries. Management of most of these plantations is based on rotational clear-fell plans that generally do not fulfil most of the currently expected forest functions, i.e. wood production but also nature conservation, recreation, groundwater supply and soil protection (FRA 1990). Therefore, conversion of these plantations is a great challenge for both forest managers and ecologists. To formulate restoration objectives, a reference or target system is essential (White & Walker 1997). This reference information consists, in the case of reconversion of Norway spruce stands, of mature deciduous forests established in similar abiotic conditions. The potential for successful restoration of coniferous plantations depends on the similarity between the plantation and the ecological reference in terms of herbaceous plant species composition.

Regional differences in species pools, as well as the need for results that are easily transposable to other areas, argue in favour of leaving the traditional species-centred approach (i.e. using indicator species) and focusing instead on functional groups defined by life-history traits. In this context, Lavorel *et al.* (1997) recommended the use of functional response groups that are context-specific, thus increasing the likelihood that functional groups of the same pool of organisms will differ greatly, depending on the type of disturbance studied (Gitay & Noble 1997). Insights into life-history traits of the species present may also lead to a better understanding of the ecological mechanisms behind the vegetation dynamics in coniferous stands, an understanding that, in turn, may allow better predictions of the future natural development of these plantations.

The composition of the herbaceous plant communities in coniferous stands is determined by (i) the persistence of the herbaceous plants (either seeds or individuals) after the plantation event; (ii) their dispersal capacity from neighbouring deciduous source stands; and (iii) their establishment success in abiotic conditions that are slightly different from those of deciduous forests. The dispersal, establishment as well as persistence success for a plant depends on a wide range of environmental factors, including not only local variables, such as habitat quality and stand management types, but also regional variables, such as forest connectivity (Grashof-Bokdam & Geertsema 1998). For deciduous forests, it has been shown that the relative importance of these variables may vary between study areas (Graae *et al.* 2004) and between soil types (Dzwonko 1993). In addition, it is likely that the relative importance of habitat quality, forest management and forest connectivity varies with the life-history traits considered. For example, it has been shown that

traits specifically associated with forest species are more sensitive to habitat configuration than traits from generalist species (Dupré & Ehrlén 2002; Kolb & Diekmann 2004). Therefore, it seems relevant to combine a functional group approach with variation partitioning of the environmental variables in order to evaluate the potential for ecological restoration of Norway spruce stands.

The general aims of this study were to: (i) gain insight into the plant-specific trait combinations responsible for the persistence, dispersal and establishment of herbaceous species in conifer plantations; and (ii) determine the relative effects of forest management, local environmental conditions and regional variables on the restoration potential. We therefore conducted a three-step analysis: (i) identification of emergent groups (EG) (*sensu* Lavorel *et al.* 1997) from the local flora, based on a multivariate classification of species life traits; (ii) comparison of abundance of the identified EG between coniferous stands and target communities (i.e. deciduous forests growing in comparable ecological conditions); and (iii) determination of the relative importance of forest management, local environmental and regional variables that have driven the abundance of the different EG under *P. abies*.

Materials and methods

DATA COLLECTION

All investigated forest stands were situated throughout the Grand-duché de Luxembourg and neighbouring areas (49°26'–50°10'N, 5°42'–6°32'E). The climate is subcontinental with an oceanic influence, the mean annual temperature is 9 °C and the annual rainfall ranges between 700 and 1000 mm. The north of the sampling area consisted of lower Devonian geological layers, shales and gritty shales with low calcium and phosphorous contents, whereas the south had more recent geological layers of sandy and calcareous rocks from the Triassic and Jurassic periods. The region encompassed a wide range of soil conditions, from poor-acidic to rich-basic soils, and land cover from highly isolated stands to heavily forested areas (see map 2 in Groot Bruinderink *et al.* 2003). All stands were situated on alluvial soils. Norway spruce stands were ±45 years old, which is close to the exploitation time in the area, and were planted on former alluvial meadows. The deciduous stands belonged to the Alno-Padion phytosociological alliance and were selected to show no obvious sign of former plantation or of current management activity. Their age varied between 50 and 220 years.

Eighty-five Norway spruce plantations, ranging from 840 to 14 570 m², and 155 deciduous stands, ranging from 500 to 12 190 m², were surveyed twice a year (spring and summer–autumn) during the growing periods 2002 and 2003. Stand areas were estimated using digitized maps. All herbaceous species were recorded. Forest

margins were omitted to avoid edge effects. Each species received a cover coefficient coded as 1 (< 10% cover), 5 (10–50%) and 10 (50–100%). Species nomenclature follows Lambinon, Delvosalle & Duvigneaud (2004).

For the 85 Norway spruce plantations, three groups of environmental variables were estimated. (i) Forest management variables comprised basal surface estimated with the Bitterlich relascop, tree density extrapolated from a 20 × 20-m subplot, maximum tree height determined with a clinometer, and area of the management unit. (ii) Local environmental variables comprised depth of the oxydo/reduction layer in the soil (upper limit of the alluvial water table), litter thickness and soil pH (ISO 10390 norm). (iii) Regional variables comprised forest connectivity and riverine forest connectivity. The two connectivity measures were computed using the incidence function model of Hanski (1994). This takes into account distance as well as area of all forest fragments (forest connectivity) or of forest fragments on alluvial soils (riverine forest connectivity) as follows:

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

where I is the connectivity index, i is the stand in question, j is each of the other patches in turn, d_{ij} is the distance from i to j , $1/\alpha$ 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). For each stand, the forest connectivity index was calculated within a radius of 1 km, whereas the riverine forest connectivity index only took into account the forests situated on alluvial soils within 2 km upstream and downstream from the studied stand.

LIFE-TRAIT SELECTION

Fourteen easy-to-measure plant traits were selected for EG definition (Table 1). The 14 traits were chosen to reflect key events in vegetation development processes in coniferous plantations, i.e. six traits related to dispersal, five to establishment and six to plant persistence (Weiher *et al.* 1999). These traits have already been successfully used for delineating response groups related to forest perturbation (Skov 2000; Verheyen *et al.* 2003; Decocq *et al.* 2004). Because of the high number of recorded species (264), trait information was compiled from the existing literature (mainly Grime, Hodgson & Hunt 1988; Harley & Harley 1987; Hodgson *et al.* 1995; Kleyer 1995; Julve 1998) completed by monographs from the Biological Flora of the British Isles (Table 1). 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, Bakker & Bekker (1997). On average, 23% of trait information was lacking. For 223 out of 262 species, information was available for 50% or more of the traits.

IDENTIFYING EMERGENT GROUPS

Classifying species into EG (*sensu* Lavorel *et al.* 1997) by life-history traits offers two main advantages: (i) simplifying the data matrices by reducing the numerous species inventoried to a few relevant groups (Friedel, Bastin & Griffin 1988) and (ii) keeping the correspondence between traits at the species level in all steps of the data analysis. In other words, throughout the analysis each species is considered as a functional unit of life traits (Kleyer 1999; Verheyen *et al.* 2003). Indeed, in the real world, the local, regional and forest management variables do not apply to each life trait separately but to the whole plant.

The methodology for EG delineation adhered closely to the framework used by Verheyen *et al.* (2003). Identification of EG was first done by calculating the Gower similarity coefficient (Gower 1971) between individual species under Clustangraphics (Clustan Ltd 2001), giving equal weight to all traits considered. This coefficient can deal both with missing values and mixed data (Legendre & Legendre 1998). The resulting similarity matrix was clustered using the Ward method. The cutting level for EG definition was determined graphically from visual screening of the dendrogram. The relationships between individual traits and EG were investigated by means of the Pearson χ^2 test and Kruskal–Wallis statistic. For the latter, post-hoc comparisons of mean ranks of all pairs of EG were computed.

ASSESSING DIFFERENCES BETWEEN DECIDUOUS AND CONIFEROUS STANDS

A matrix of EG abundance (EG × stand) was calculated as the matrix product of the matrix of species abundance (stand × species) with the binary matrix of EG memberships (emergent group × species). To standardize for differences in the number of species per stand, a matrix of EG relative abundance was obtained by calculating the total abundance of all EG for each stand, and dividing the abundance of each EG by this total abundance. Differences in EG relative abundance between stand type (either deciduous or coniferous) were analysed using the Mann–Whitney U -test.

RELATING EG ABUNDANCE IN CONIFEROUS STANDS TO MANAGEMENT, LOCAL AND REGIONAL FACTORS

Variations in EG abundance with respect to environmental variables were analysed using multiple regression models. Management unit area, stand density and litter thickness were square-rooted to meet normality assumptions. The backward selection procedure (Legendre & Legendre 1998) was then applied to determine the variables that best explained the distribution of EG abundance. Groundwater level, tree basal surface and tree maximum height were removed from the final multiple regression models because of non-significance.

Table 1. List of the 14 plant traits compiled from the literature

Plant traits	Description	Implication*	Missing values	Variable type	Main sources
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; 7, > 15 years	P	59%	Ordinal	Kleyer (1995)
Clonal propagation	0, no; 1, yes	D	25%	Qualitative	Hodgson <i>et al.</i> (1995); Kleyer (1995)
Dispersal type	1, barochory, myrmecochory; 2, anemochory; 3, hydrochory; 4, endo- and exozoochory	D	0%	Qualitative	Hodgson <i>et al.</i> (1995); Julve (1998); Kleyer (1995)
Germination requirement	1, immediate; 2, chilling or drying or light or scarification; 3, combinations of the latter	E	31%	Ordinal	Grime, Hodgson & Hunt (1988); Hodgson <i>et al.</i> (1995); Kleyer (1995)
Life forms	1, chamaephyte; 2, geophyte; 3, hemicryptophyte; 4, therophyte	P	0%	Qualitative	Hodgson <i>et al.</i> (1995); Julve (1998)
Onset of flowering	1, period > 4 months; 2, spring (3–5); 3, summer (6–7); 4, autumn (8–9)	P	3%	Qualitative	Julve (1998); Kleyer (1995)
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	P	0%	Ordinal	Hodgson <i>et al.</i> (1995); Kleyer (1995); Lambinon, Delvosalle & Duvigneaud (2004)
Pollination vector	1, autogamy; 2, anemogamy; 3, entomogamy	P	8%	Qualitative	Julve (1998); Kleyer (1995)
Potential mycorrhiza	0, 25% or less of records report mycorrhiza; 1, 75% or more records report infection with VA mycorrhiza; 2, 26–74% of records report infection with VA mycorrhiza	E, P	12%	Qualitative	Harley & Harley (1987)
Seed longevity	Index of Thompson <i>et al.</i> (1998); values range from 0 to 1	E	33%	Quantitative	Thompson, Bakker & Bekker (1997)
Seed weight	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	D, E	25%	Ordinal	Hodgson <i>et al.</i> (1995); Kleyer (1995)
Seed production per ramet	1, 1–1000; 2, 1001–10 000; 3, > 10 000	D, E	58%	Ordinal	Kleyer (1995)
Seed shape	1, length/breadth ratio < 1.5; 2, ratio 1.5–2.5; 3, ratio > 2.5	D	25%	Ordinal	Hodgson <i>et al.</i> (1995); Kleyer (1995)
Seed size	Average (length + breadth)	D, E	51%	Quantitative	Grime, Hodgson & Hunt (1988)

*Implication of plant traits in vegetation development processes (Weiher *et al.* 1999): plant dispersal (D), establishment (E) and persistence (P).

The magnitude of the beta coefficient allowed comparison of the relative contribution of each independent variable to EG abundance. To assess the relative importance of forest management (tree density and management unit area), habitat quality (litter thickness and soil pH) and habitat configuration (forest connectivity and riverine forest connectivity) on EG abundance, variation partitioning was performed by means of partial linear regression (Legendre & Legendre 1998).

Results

The most characteristic traits that drove the clustering were chosen to denominate the EG (Table 2 and see the Appendix). (i) Anemochoreous perennials are tall, produce numerous light diaspores that are dispersed by wind, germinate easily and have a persistent seed bank. (ii) Annuals flower in the first year, die at the end of the growing season, and possess a persistent seed bank. (iii) Graminoids (i.e. Cyperaceae, Poaceae and Juncaceae) are wind-pollinated. (iv) Helophytes are tall and non-mycorrhizic. (v) Short perennials are barochoreous, entomogameous and are able to propagate clonally. (vi) Short geophytes are spring ephemerals characterized by large and heavy seeds (except orchids), with specific germination requirements. (vii) Zoochoreous perennials are tall, have few heavy zoochoreous seeds, and transient seed banks.

Comparing EG abundance between Norway spruce and deciduous forests yielded contrasting differences among EG. Short perennials were more or less equally abundant under coniferous and deciduous stands, but the six other EG showed very different relative abundance (Table 3). Three EG (annuals, anemochoreous perennials and zoochoreous perennials) were enhanced under conifers, whereas three others (graminoids, helophytes and short geophytes) were disadvantaged. Differences between the two forest types were highest for short geophytes (Table 3).

Univariate multiple regression models were highly significant for five out of seven EG (Table 4). Variation partitioning was performed only when the multiple regression model was highly significant, i.e. in five cases (Fig. 1). The model was poor for helophytes, while it led to a weak significance for annuals. The soil pH and litter thickness were determinant for the latter EG, both variables being negatively correlated with the abundance of annuals. Denser stands strongly reduced graminoid abundance. This was also the case for short perennials, but connectivity indexes as well as soil pH were positively correlated with the abundance of this EG. Therefore, variation partitioning revealed the effects of both forest management and regional factors, and also of their interaction (Fig. 1). Forest connectivity strongly enhanced the zoochoreous perennials (Table 4). The multiple regression model was highly significant for anemochoreous perennials ($R^2 = 0.45$). Increasing stand density, riverine forest connectivity and soil pH diminished their abundance. On the other hand, anemo-

choreous perennials benefited from a large management unit area. Finally, increasing riverine forest connectivity as well as soil pH resulted in a high gain in abundance of short geophytes. Consequently, local plus regional factors accounted for nearly 90% of the variation of short geophyte abundance (Fig. 1).

Discussion

McIntyre, Lavorel & Tremont (1995) have shown that life forms correlate with numerous plant traits. This is supported by the present study (eight significant correlations out of 13 possible; data not shown), where EG delineation was primarily driven by life forms. Among the seven EG identified, only two groups consisted of typical forest species. Short geophytes and zoochoreous perennials exhibited specific life-trait combinations (large seeds associated with vernal phenology or zoochoreous dispersal) that reflected their successful adaptation to the forest environment (Bierzuchudek 1982). Short geophytes have the highest conservation value in temperate forests (Keddy & Drummond 1996; Hermy *et al.* 1999). Three other groups encompassed a mixture of forest and generalist species (anemochoreous perennials, graminoids and short perennials) while the remaining groups were composed of species often associated with open habitats (annuals and helophytes). Because a common restoration goal for forest managers is to obtain rich forest-specialist communities, the following discussion mainly focuses on the forest plant EG.

Traditionally, forest restoration frameworks have focused on local and management variables (Holl & Crone 2004). However, one of the main results of this study is that the abundance of forest plant EG is largely influenced by forest connectivity (Table 4). This may be partly the result of the choice of connectivity measures. Moilanen & Nieminen (2002) have already demonstrated the superiority of the indices used in this study compared with buffer and nearest-distance measures. Moreover, the Norway spruce stands were planted on former meadows, and the majority of forest plant species do not form a persistent seed bank (Table 2; Bossuyt & Hermy 2001). Therefore, it can be assumed that the target EG for restoration have colonized the plantation from outside (Middleton 2003). Because of the combination of large seeds and unspecialized dispersal (Table 2), most short geophytes have extremely low dispersal rates (Brunet & Von Oheimb 1998; Bossuyt, Hermy & Deckers 1999; Dzwonko 2001). Some of these species (e.g. *Anemone ranunculoides*, *Corydalis solida* and *Gagea lutea*) were confined to the alluvial plain, where the forest connectivity was often low as a result of a high demand for other land uses. Therefore the colonization of coniferous plantations by short geophytes is strongly impeded (Table 3). The abundance of zoochoreous perennials also showed a relationship with forest connectivity. Zoochoreous perennials possess large seeds that are dispersed by large forest herbivores (red deer, roe deer and wild boar in the study area;

Table 2. Characteristic plant traits of the identified emergent groups

	<i>P</i>	Anemochoreous perennials	Annuals	Graminoids	Helophytes	Short perennials	Short geophytes	Zoochoreous perennials
<i>n</i>		34	33	40	28	76	30	23
Age at first flowering†	***	3 ^{ab}	2 ^b	2 ^{ab}	3 ^a	3 ^a	4 ^a	4 ^a
Clonal propagation‡	***	3·4/–3·4	18·9/–18·9	–4·4/4·4	–4·9/4·9	–17·5/17·5	–0·1/0·1	4·5/–4·5
Dispersal type‡	***	–14·2/24·2/–2/–8	4·2/–0·5/–2·9/–0·8	5·7/–7·1/0·6/0·8	–9·7/7·8/7·6/–5·6	14·2/–15·7/1·4/0·1	1·5/–2·8/–2·6/3·9	–1·6/–5·9/–2/9·6
Germination requirements†	***	1 ^a	2 ^b	1–2 ^{ab}	2 ^{abc}	2 ^{ab}	3 ^{bc}	2 ^{abc}
Life forms‡	***	–1·3/–6·4/12·4/–4·6	–1·3/–6·3/–20/27·5	–1·5/–5·6/12·5/–5·5	–0·1/8·7/–5·8/–2·8	6·1/–11·4/13·6/–8·4	–1·1/24·3/–19·1/–4·1	–0·9/–3·4/6·4/–2·1
Mean shoot height†	***	4 ^c	4 ^b	3 ^{ab}	4 ^c	2 ^a	2 ^a	4 ^c
Onset of flowering‡	***	6·8/–6·5/–3·1/2·9	7·8/–6·5/–4·1/2·9	2·9/–6·9/7·9/–3·8	–3·6/1·3/–4·0/6·3	3·9/11·8/–10·4/–5·3	–9·0/11·1/–0·3/–1·8	–8·7/–4·3/14/–1·1
Pollination vector‡	***	4·7/–4·6/0	9·0/–4·9/–4	–4·9/29·8/–24·9	–0·5/–0·8/1·3	–0·3/–13·5/13·8	–4·6/–6·3/10·9	–3·3/0·4/3·0
Potential mycorrhiza‡	***	–7·8/5·2/2·5	3·7/–4·6/0·9	2·9/–7·5/4·6	10/–6·1/–3·9	–4·2/0·9/3·3	–4·0/8·2/–4·2	–0·7/3·9/–3·3
Seed longevity†	***	0·73 ^{ac}	0·80 ^c	0·37 ^{ab}	0·26 ^{abd}	0·29 ^{abd}	0 ^d	0 ^{bd}
Seed weight†	***	2 ^b	5 ^{ac}	4 ^{ac}	3 ^{bc}	4 ^{ac}	4 ^{abc}	6 ^a
Seed production†	*	2 ^a	1 ^a	1 ^a	2 ^a	1 ^a	1 ^a	1 ^a
Seed shape†	***	2 ^{ab}	1 ^{bc}	2 ^{ab}	2 ^{abc}	1 ^c	3 ^{abc}	3 ^a
Seed size†	***	0·8 ^a	1·8 ^{abc}	1·6 ^{abc}	1·2 ^{ab}	1·7 ^{bc}	2·9 ^c	2·3 ^{abc}

†Kruskal–Wallis test, values are medians. Numbers with different letters are significantly different at the 0·05 level.

‡Pearson χ^2 test, values are differences between the observed and expected frequencies from the contingency tables for the different categories defined in Table 1.

*** $P \leq 0\cdot001$; ** $P \leq 0\cdot01$; * $P \leq 0\cdot05$.

Table 3. Relative abundance of emergent groups according to forest types, Mann–Whitney *U*-test, values are percentage medians

	<i>P</i>	<i>Picea</i> plantations (%)	Deciduous forests (%)
<i>n</i>		85	155
Anemochoreous perennials	***	15.3	10.0
Annuals	*	10.4	9.3
Graminoids	***	14.3	15.9
Helophytes	***	7.5	9.3
Short perennials	NS	32.1	30.8
Short geophytes	***	9.7	14.6
Zoochoreous perennials	**	10.4	9.1

****P* ≤ 0.001; ***P* ≤ 0.01; **P* ≤ 0.05; NS, not significant.

Table 2), increasing the chance a plantation will be reached by diaspores (Grashof-Bokdam & Geertsema 1998; Matlack 1994). In addition, the large seeds of this EG are characteristic of plants adapted to shady environments (Hodkinson *et al.* 1998) and have higher survival rates under natural conditions (Moles & Westoby 2004). Moreover, mature plants of this EG have good competitive abilities because of their height (Weiher *et al.* 1999). Once established, zoochoreous perennials would benefit from the lower abundance of dispersal-limited plants, which would increase their own relative abundance (Table 3). Therefore the restoration of rich zoochoreous perennial communities seems a relatively easy target for forest managers.

Among the forest management variables, stand density is directly related to forestry interventions, i.e. to the thinning frequency. This primarily influences the light availability in the understorey layers. Generalist EG are strongly favoured by high degrees of light penetration (Table 4; De Keersmaecker *et al.* 2004), therefore light is an indirect determinant of competition between forest and unspecialized species (Decocq *et al.* 2004). In practice, forest managers should thus avoid large thinning operations to prevent any increase in abundance of light-demanding species such as *Urtica dioica*. Management unit area only had a positive influence on the abundance of anemochoreous perennials

and graminoids (Table 4). A positive stand area–species richness relationship is often related to a positive stand area–habitat diversity correlation in temperate forests (Honnay, Hermy & Coppin 1999a,b). However, the former period of meadow exploitation in the study site and the plantation process itself (digging, surface leveling and draining) had certainly caused a loss in habitat diversity. As a result of this habitat diversity loss, the influence of the management unit area remained low (Table 4). Despite the fact that forest management factors are the easiest variables to control by restoration managers, these factors seem of secondary importance regarding restoration potential (Fig. 1).

On the whole, a small amount of variation in EG abundance was attributable to local environmental variables (Fig. 1). Only two variables (pH and litter thickness) showed a predictive power (Table 4). Detailed soil chemical analyses were not performed and thus additional soil measures could have increased the relative importance of local factors (Kolb & Diekmann 2004). In addition, it is likely that local habitat quality limitations occurred more at the individual species level than at the life-history trait level (Dupré & Ehrlén 2002). Indeed, the presence of a given species in a particular habitat depends in the first place on the ecological range of the species. The only exception is the short geophytes, which are highly dependent on local factors, especially pH values. Most of these species are high-pH demanding (Table 4; Lapointe 2001). This habitat limitation, occurring at the whole EG level, was probably enhanced by soil acidification as a result of Norway spruce litter (Augusto *et al.* 2002). Local variables are often seen as the main environmental variables by restoration practitioners (Holl & Crone 2004). Our results show that they are only partly responsible for the restoration success.

On the whole, our results show that the key to conversion success of Norway spruce plantations is the performance of short geophytes, the target group for nature conservation. The importance of both regional and local variables in determining their abundance suggests that Norway spruce stands, located both on base-rich soils and in a landscape with high riverine

Table 4. Univariate multiple regressions of emergent group abundance within the Norway spruce stand pool

	IFMf		IFMr		pH		LT		MUA		SD		Model
	β	<i>P</i>	β	<i>P</i>	β	<i>P</i>	β	<i>P</i>	β	<i>P</i>	β	<i>P</i>	
Anemochoreous perennials			−0.21	*	−0.31	**	−0.15	(*)	0.30	***	−0.44	***	***
Annuals					−0.32	**	−0.22	*					*
Graminoids			0.17	(*)					0.18	*	−0.46	***	***
Helophytes					−0.24	(*)							NS
Short perennials	0.28	**	0.19	*	0.28	**			0.17	(*)	−0.34	***	***
Short geophytes			0.39	***	0.35	**							***
Zoochoreous perennials	0.32	**			*0.20	(*)					−0.18	(*)	***

IFMf, forest connectivity; IFMr, riverine forest connectivity; pH, soil pH; LT, litter thickness; MUA, management unit area; SD, stand density.

****P* ≤ 0.001; ***P* ≤ 0.01; **P* ≤ 0.05; (*) *P* ≤ 0.1; NS, not significant.

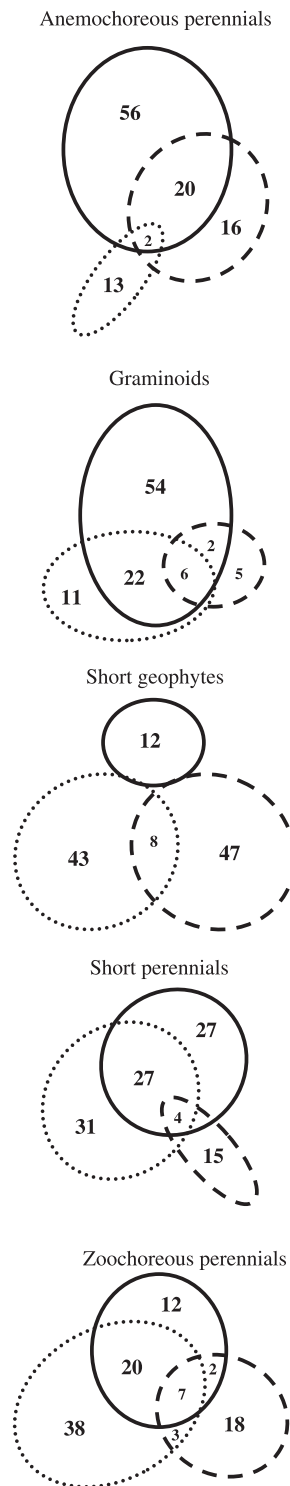


Fig. 1. Variation partitioning of forest management (solid line), local environmental (dashed line) and regional (dotted line) variables. Numbers explain the variation part for each variable group (negative and null numbers are not represented).

forest connectivity, have the highest conservation value and are the most relevant candidates for a conversion process. Fortunately these stands are also the most suitable for the spontaneous regeneration of riverine tree species (Hérault, Bouxin & Thoen 2004; Hérault, Thoen & Honnay 2004). The conversion process should be

implemented gradually, both to prevent excessive disturbance to the understorey (Gondard & Deconchat 2003) and to limit competition with light-demanding herbaceous species (De Keersmaecker *et al.* 2004; Decocq *et al.* 2004). Progressive selection cuttings that maintain similar light levels (for deciduous stands see Beaudet, Messier & Leduc 2004) should be very beneficial for the core forest species (Deconchat & Balent 2001), but there is a need for well-designed experiments to assess the ecological effects of progressive harvesting on the core forest species (Bennett & Adams 2004). For other kinds of stands, and especially for isolated stands established on very acidic soils, initiating a conversion process seems to be much less appropriate because of the low abundance of target EG. Exploring possible restoration for other land uses is therefore recommended. For example, in the study area, annually mown meadows, which represent the former land use, would be an alternative, given the fact that graminoids generally establish well under restoration (Pywell *et al.* 2003).

For decades, forest ecologists have tried to find indicator species for forest continuity and disturbance (Hermy *et al.* 1999). This approach has been criticized for several reasons (Nordén & Appelqvist 2001) and has hampered broad generalizations. The EG approach offers a methodology for comparing results across regions (Verheyen *et al.* 2003). Moreover, studying life traits offers insights into the ecological processes underlying species' distribution patterns. This methodological framework seems to be applicable to other forest taxonomical groups (e.g. mosses and land snails) and may contribute to the development of better integrated forest management and land-use plans.

Acknowledgements

B. Hérault was supported by a doctoral research grant (BFR01/060) from the Ministère de la Culture, de l'Enseignement Supérieur et de la Recherche (Luxembourg), and by the following institutions in Luxembourg: Administration des Eaux et Forêts, Musée national d'histoire naturelle. O. Honnay has a postdoctoral fellowship from the Flemish Fund for Scientific Research (FWO). Thanks to Jeff Schenck for improving the language.

Supplementary material

The following supplementary material is available for this article online.

Appendix S1. The most common members of the identified emergent groups and their relative frequencies in coniferous and deciduous stands.

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Received 10 September 2004; final copy received 16 February 2005
Editor: Phil Hulme