

Opportunities and constraints of using understorey plants to set forest restoration and conservation priorities

OLIVIER HONNAY, BRUNO HÉRAULT
AND BEATRIJS BOSSUYT

INTRODUCTION

Ecological restoration of natural forests on former agricultural land or on sites formerly planted with non-indigenous tree species has become a central component of sustainable forest management in many parts of the world (Angelstam *et al.* 2004; Hérault *et al.* 2005). To become operational at the stand or the landscape level, the principles of sustainable forest management need to be broken down into objectives and indicators to monitor.

To define the ecological objectives of restoration efforts, a reference or target system is essential. This information generally consists of contemporary ecological data from a reference site (Bakker *et al.* 2000). In the case of forest restoration, the reference may consist of ancient forests (Honnay *et al.* 2002). Ancient forest sites are commonly defined as sites that have been continuously wooded since a reference date in the past, and it is generally accepted that this continuity has not been broken by forest management practices such as coppicing but only by an alternative land-use such as cultivation or pasture (Peterken 1996). The reference date varies between regions and countries and, very pragmatically, reflects the availability of the first detailed land-use maps (e.g. 1600, Peterken (1974); 1700, Rackham (1980); 1789, Lawesson *et al.* (1998); 1850, Grashof-Bokdam (1997)).

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After setting the objectives, indicators can be measured repeatedly to examine whether they directionally change towards the objectives and to evaluate to what extent the objectives have been reached. Herbaceous plant species can be expected to be well suited as indicators to infer the restoration status of a forest. They are rather easy to identify in the field and it has extensively been demonstrated that some species only colonize newly established forests after a long time period, whereas others are able to recolonize relatively quickly (e.g. Matlack 1994; Wulf 1997; Bossuyt *et al.* 1999). This results in slow recovery rates of the understorey during the restoration process, so that its species composition can be considered to be a valuable indicator of the restoration status. Moreover, species-specific plant life-history traits such as those related to dispersal capacity may provide the necessary insights into the site-specific bottlenecks hampering forest restoration (Verheyen *et al.* 2003).

Broadly speaking, two types of bottleneck may hamper the recolonisation of recently restored forests by herbaceous plant species. The first relates to the inability of a species' diaspores to disperse to a restored forest stand. This is referred to as dispersal limitation. Logically, the importance of dispersal limitation increases as forests become more isolated within the landscape (Jacquemyn *et al.* 2001). The second bottleneck relates to the inability of successfully dispersed diaspores to germinate and grow into mature, reproductive plants. This is generally referred to as recruitment limitation. Especially in forests restored on former arable land, the latter may be an important colonization constraint because most forest plants lack the ability to compete successfully with species that grow fast on nutrient-rich soils (Verheyen *et al.* 2003).

The restoration status or conservation value of a forest stand can be assumed to increase asymptotically as a function of time since re-establishment (Jacquemyn *et al.* 2001) although considerable variance for a certain age class is expected, owing to site-specific constraints related to the two types of colonization bottleneck. The variability in restoration status between forests can be expected to be low just after re-establishment (no forest species present), to increase for intermediate age classes when differences in recruitment and dispersal limitation between sites are fully playing, and to decrease again finally when even the poor colonizers persist in all forest sites (Fig. 11.1).

In this chapter, we explore the opportunities and constraints of using understorey species to evaluate the degree to which forest restoration sites have developed towards their ecological reference, and hence to evaluate their conservation value. We distinguish between three approaches, each

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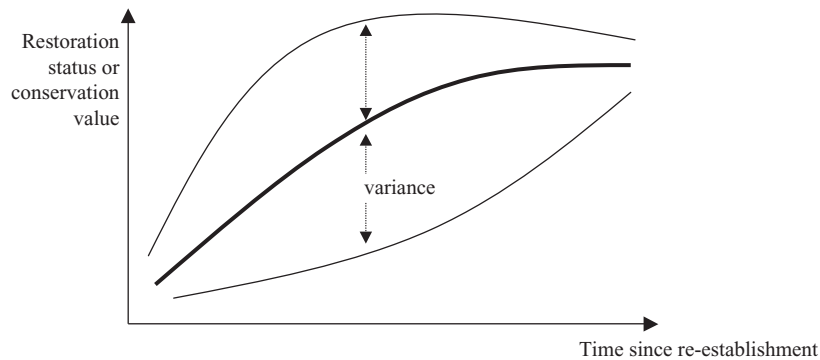


Figure 11.1. Expected evolution of the restoration status or conservation value of recently established forest stands as a function of time. Variance in the restoration status or conservation value is the result of site specific bottlenecks related to dispersal and recruitment limitation and is expected to be highest at intermediate age classes.

reflecting a certain component of the understorey species composition: (i) using ancient-forest indicator species, (ii) comparing species richness and community measures between sites, and (iii) using functional groups based on plant life-history traits. We tested the general performance of these three approaches on a dataset of 153 riverine deciduous forests located throughout the Grand-duché de Luxembourg in Central-Western Europe (details in Hérault and Honnay 2005). The selected forests were established on former fields or open grazed lands and showed no evidence of former plantation events or forestry management practices. Forest stands were grouped into four age classes, pragmatically defined by the available historical maps and reflecting the time since re-establishment (<50 years ($n = 55$), 51–100 years ($n = 46$), 101–225 years ($n = 29$), and >225 years ($n = 23$)). The oldest age class is regarded as the ecological restoration objective. Species abundance in each stand was surveyed in three cover classes: <10%, 10%–50% and >50%. Reliable indicators for the restoration status of a forest stand should fulfill at least two requirements (Fig. 11.1): (i) their values should covary with time since forest re-establishment, and (ii) although variation of the indicator value within a certain age class can be expected owing to site-specific colonization bottlenecks, variance should be low enough to discriminate statistically between different stand age classes. Additionally, the indicators should ideally offer insights into the ecological processes behind the ecological restoration. This means that when the time since re-establishment of the stands to restore is known, differences

in indicator values among stands of similar age can be explained in terms of the colonization bottlenecks. The latter may allow forest managers to lift colonization constraints (e.g. by introducing seeds or removing competitive species such as *Rubus* sp.), or to adapt conservation priorities.

INDICATOR SPECIES

An indicator species has been defined as an organism whose characteristics (presence or absence, population density, dispersal or reproductive success) are used as an index of attributes too difficult, inconvenient, or expensive to measure for other species or environmental conditions of interest (Landres *et al.* 1988). Indicator species have, for example, been used as short cuts to detect environmental pollution, to assess biodiversity, and also to infer forest continuity (e.g. Peterken 1974, Wulf 1997). In the latter case, the presence or absence of a suite of indicator species (generally referred to as “ancient-forest species”) in recently established forest stands allows the assessment of the age of the forest land use, which is often difficult to infer from ancient land use maps. This approach has been criticized for many different reasons, mainly because it is based on correlative assumptions and because ancient forest indicators have been identified without knowing why they are found only (or primarily) in the oldest stands (Rolstad *et al.* 2002; Norden and Appelqvist 2001). Forest stands established hundreds of years ago may, for example, lack certain indicator species simply because they are too isolated from species sources, hampering their colonization.

Here, we are aiming at assessing not forest continuity but rather the ecological status of the restored site in relation to the reference community. The idea is that the abundance of species with a significant affinity for ancient stands can be used as an indicator to infer the restoration status of a forest. Indicator species for ancient forest can be identified by using simple measures of categorical association such as the χ^2 test, or using more complex methods, for example combining a species' relative abundance with its relative frequency in various forest age classes (Dufrêne and Legendre 1997). Many lists of ancient-forest plant species have been derived (e.g. Peterken 1974; Wulf 1997; Hermy *et al.* 1999). Here we used the one compiled for Western and Central Belgium by Honnay *et al.* (1998) (based on a χ^2 test), and we calculated the average number of ancient forest indicator species in each of the four forest age classes.

The advantages of the indicator species approach are obvious. Starting from an existing indicator species list, only a survey of the presence or absence of the listed species at the restoration sites is required. In our case

Table 11.1. Average values of the different variables used to assess the restoration status of 153 deciduous forest stands of four age classes.

Different letters indicate a significant difference at the 0.05 level according to Tukey pairwise comparisons. *F*-values are from a one way ANOVA with four age classes. Symbols: *** $p < 0.001$; ** $0.001 < p < 0.01$; * $0.01 < p < 0.05$.

	< 50 yr (<i>n</i> = 55)	51–100 yr (<i>n</i> = 46)	101–225 yr (<i>n</i> = 29)	> 225 yr (<i>n</i> = 23)	<i>F</i> -statistic
Indicator species	9.6a	12.6b	13.9b	14.0b	11.5***
Species richness	34.0a	39.6b	38.5ab	40.8b	5.6**
Species diversity	3.26a	3.41b	3.39ab	3.48b	6.5***
Species evenness	0.929a	0.936ab	0.935ab	0.941b	2.9*
DCA axis 1	1.53a	1.92b	2.31c	2.32c	22.6***
DCA axis 2	1.50a	1.61ab	1.69ab	1.92b	4.6**
Barochoreous perennials	5.4a	7.3b	9.1c	9.1c	21.1***
Small geophytes	4.1a	5.6b	5.6b	7.6c	15.2***

study, however, the approach only allowed us to distinguish between the youngest and the three other age classes (Table 11.1). The variability in the number of indicator species, whereas each age class is very high, and even very recently restored forest patches may contain up to 16 indicator species, whereas at least one ancient forest only contains 8 (see Fig. 11.2). The main reason for the low resolution of ancient forest indicator species is related to problems regarding the generalization of these lists across regions. The composition of the species pools between regions is often different. Moreover, the species' ecological behavior may vary between biogeographical regions and between forest types (Rolstad *et al.* 2002). For example, *Mercurialis perennis*, often mentioned as an ancient forest indicator, colonizes new forest stands more easily on calcareous than on acidic soils (Peterken and Game 1981). Moreover, it is very problematic to infer why certain ancient forest plant species are present in a specific restoration site but absent from others of the same age. Indeed, the indicator species approach fails to offer any insight into the site-specific constraints related to species dispersal or recruitment limitation locally hampering the restoration process. For all these reasons, indicator species lists can be expected to perform poorly in comparing the status of restoration sites.

SPECIES DIVERSITY AND COMMUNITY MEASURES

Species richness or alpha diversity is the simplest way to describe community diversity (Gotelli and Colwell 2001) and has been used as an indicator

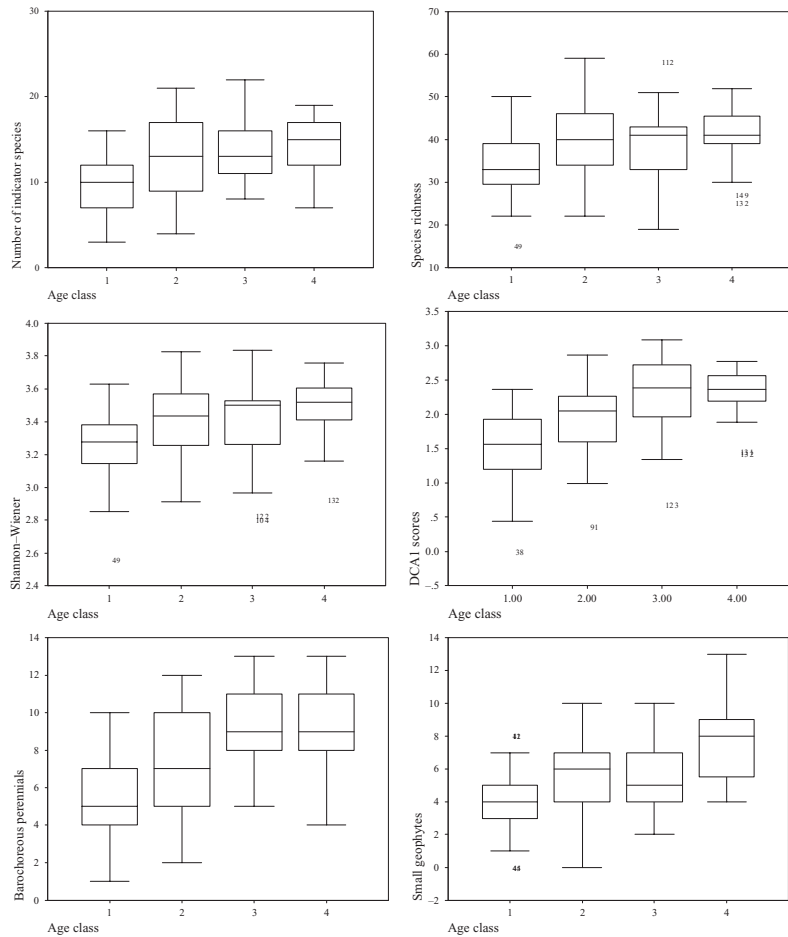


Figure 11.2. Box plots reflecting the median, range, and quartiles of the different variables used to assess the restoration status of 153 deciduous forest stands of four age classes: 1, <50 years ($n = 55$); 2, 51–100 years ($n = 46$); 3, 101–225 years ($n = 29$); 4, >225 years ($n = 23$).

for the restoration status of forest stands before (Pitkänen 1998). The number of plant species in the understorey has also been proven to increase with decreasing level of forest disturbance (Aubert *et al.* 2003; Onaindia *et al.* 2004) or with increasing level of forest continuity (Dumortier *et al.* 2002; Graae *et al.* 2003). Other studies, however, have not been able to demonstrate a univocal relationship between the level of forest disturbance or forest continuity on the one hand and species richness on the other (Graae and

Heskjaer 1997; Bossuyt and Hermy 2000; Verheyen *et al.* 2003). Species richness may be more related to habitat diversity within the stand (Dzwonko and Loster 1992; Honnay *et al.* 1999; Dumortier *et al.* 2002) than to the restoration status of the forest. Moreover, several non-specific forest species may be present in the understorey layer of recently established forest owing to high soil nutrient and light penetration levels, inflating the species numbers in these stands (Bossuyt and Hermy 2000).

In contrast to species number, species diversity and evenness measures also incorporate patterns of species abundance (Washington 1984; Pitkänen 1998). High evenness indicates that the occurring species are of equal abundance and suggests the absence of dominant species. Evenness is known to increase with succession (McCook 1994) and with decreasing disturbance (Onaindia *et al.* 2004). Evenness can be expected to be higher in restoration sites that are more similar to the reference forest since there is less dominance by competitive species, owing to lower soil nutrient contents and light penetration levels, increasing the competitive advantage of stress-tolerant forest species (Honnay *et al.* 1999; Graae *et al.* 2003).

Species richness and diversity and evenness measures, however, have also been shown to vary with the type of data, the level of observation, and the spatial resolution, resulting in a high intrinsic variability (Huston 1994; Keeley and Fotheringham 2005). Moreover, a given species richness or diversity may result from different ecological mechanisms of species coexistence (Nakashizuka 2001). Therefore, indicators based on species diversity may not be very useful for conservation purposes as they do not provide clues to the mechanisms of species coexistence (Aubert *et al.* 2003).

The reliability of community-based indicators may be improved by using indicators based on the similarity in species composition between the site being evaluated and the reference site, because they take also the identity of the occurring species into account (Onaindia *et al.* 2004). To simplify the similarity matrix, multivariate techniques such as Detrended Correspondence Analysis (DCA) (Hill and Gauch 1980) or non-linear multidimensional scaling (Clarke 1993), ordering vegetation survey plots in a multidimensional space, can be used to describe the main sources of variation in species composition. Plot scores on the axes reflect the species composition in the survey plots, and comparison of plot scores on the multivariate axes allows determining the (dis)similarity in species composition between the plots (e.g. Strandberg *et al.* 2005; Uotila and Kouki 2005).

We calculated average species richness, species diversity and evenness, and DCA scores for each of the four forest age classes (Table 11.1). The

DCA was performed with Canoco for Windows 4.5 (ter Braak and Šmilauer 2002). Because species abundance was surveyed in only three abundance classes, the species diversity and evenness metrics are relatively rough estimates and should be cautiously interpreted against the values of other age classes. Species number, species diversity, and evenness increased with increasing forest age (Table 11.1; Fig. 11.2). Based on these measures, however, only the youngest age class can be distinguished from the other three categories. Variance of the metrics within each age class is very high. Species richness, for example varies between 22 and 50 species within the most recently established forests, whereas it varies between 30 and 52 species in the reference community (Fig. 11.2). This implies that even recently established forests may be very rich in species. The plant species recorded, however, are generalist species, occurring under high light penetration levels on disturbed, nutrient-enriched soils (Hérault and Honnay 2005). The conservation value of these forests is relatively low. As with the indicator species, all metrics based on diversity have in common that they fail to provide a reliable estimation of the restoration status of the forest. Moreover, no insight into the underlying ecological mechanisms behind the variance within an age class is provided.

Compared to the other community based indicators, the DCA scores, and in particular those on the first DCA axis, best discriminate the stand age classes (Table 11.1). Additionally, multivariate techniques offer the opportunity to incorporate environmental variables in the analysis, so that the potential determining factors of the differences in species composition can be identified (Graae and Heskjaer 1997). This increases the insight in the underlying ecological processes. However, although multivariate techniques may relate site-specific abiotic conditions to differences in species composition, they do not offer insight into species-specific constraints related to dispersal or recruitment limitation hampering the restoration process. Therefore, indicators taking into account specific life-history traits of the occurring species may still perform much better.

FUNCTIONAL GROUPS

The concept of plant functional groups dates back to the beginning of the nineteenth century, when Von Humboldt (1806) drew up the first recognized classification of physiognomic plant types from South America. The first modern functional classification, however, was the life-form system of Raunkiaer (1934), which is still commonly used today. During the past decades, functional classifications of plants have received renewed attention

as a useful tool to predict the effects of human disturbance on biodiversity on the one hand (Pimm *et al.* 1995) and to understand the role of the species diversity on ecosystem functioning on the other (Hooper *et al.* 2005). Therefore, plant functional groups were commonly defined as indicators of response to various types of disturbance, such as fire (Keith and Bradstock 1994), grazing management (McIntyre *et al.* 1995) or global climate change (Johnson *et al.* 1993). More recently, the functional group concept has been applied to habitat fragmentation studies (e.g. Médail *et al.* 1998). In managed forest landscapes, influential works were the one of Metzger (2000) in the tropics and the one of Verheyen *et al.* (2003) in temperate areas. Both studies showed that the functional group approach provides valuable insights into the ecological processes underlying plant species assembly in restored fragmented forests. The use of functional groups as a selection criterion for forest restoration and/or conversion purposes (Gondard *et al.* 2003; Hérault *et al.* 2005) or as a tool for the evaluation of forest management practices (Gondard and Deconchat 2003), however, still remains in its infancy.

A functional group can be defined as a set of species that have similar morphological, physiological, and phenological life-history trait combinations (Lavorel *et al.* 1997). In other words, members of a plant functional group share similar life-history traits, with differences between members within one group being smaller than those among groups (Duckworth *et al.* 2000). It is thus expected that species from a functional group have convergent ecological and evolutionary strategies. However, a consensual definition of plant functional group is still lacking in the scientific community (Wilson 1999). Indeed, some researchers advocate functional groups based on plant response to disturbance (Gitay and Noble 1997) whereas others prefer a definition based on resource use (Hooper and Vitousek 1998). In an attempt at reconciling these views, Lavorel and Garnier (2002) argued that the nature of a functional group remains clearly dependent on the scientific aim of the study.

In a restoration context, it is necessary first to define the specific key requirements for a given herbaceous plant species to survive in a typically fragmented forest landscape consisting of different-aged forest stands. This plant has to persist in the forest stands already colonized and disperse to and establish in the restoration sites. A functional classification of herbaceous plants therefore acknowledges life-history traits involved in persistence, dispersal, and establishment (see Table 11.2 and Weiher *et al.* 1999). Persistence is enhanced by many life-history traits, but the most common ones are related to life-span (e.g. life-form, age at first flowering),

Table 11.2. *Selected plant life-history traits for the functional group approach*

<i>Dispersal-related traits</i>
Clonal propagation
Dispersal type
Seed longevity
Seed production
Seed shape
Seed size
<i>Establishment-related traits</i>
Germination requirements
Relative Growth Rate
Seed mass
<i>Persistence-related traits</i>
Age at first flowering
Life-forms
Mean shoot height
Onset of flowering
Pollination vector
Potential mycorrhizas

competitive ability (e.g. seed mass, plant height) and to strategy of resource acquisition (e.g. onset of flowering). The latter is very important in temperate forests, where numerous spring ephemerals are specifically adapted to capture resources before canopy closure (Lapointe 2001). Dispersal has a spatial and a temporal dimension (Weiher *et al.* 1999). Dispersal in time can be assessed by measuring the seed longevity (Thompson *et al.* 1998). Dispersal in space is obviously associated with seed mass (i.e. wind-dispersed seeds are lighter, see Leishman *et al.* 1995) but also with seed dispersal mode (anemochory, zoochory, unassisted). Finally, establishment firstly depends on the germination requirements of the seeds. Indeed, some seeds have the ability to immediately germinate after falling, whereas others need chilling, drying, light, or even scarification (Baskin and Baskin 2001). Secondly, the seedling size is also commonly considered to be critical for successful establishment. Seedling size is often viewed as a combination of both seed size and relative growth rate (Weiher *et al.* 1999), life-history traits which are easier to measure.

The first step in the delineation of the functional groups is to compile the life-history trait information for the plant species of interest from the existing literature. In Europe, several databases are already available (e.g. Grime *et al.* 1988; Hodgson *et al.* 1995; Julve 1998; Kleyer 1995; Thompson

et al. 1997); other more ambitious ones should be available in the near future (Knevel *et al.* 2003). Next, a similarity matrix between plant species is calculated based on the life-history trait values of the individual species. At this stage, a similarity coefficient has to be chosen taking into account the specific properties of the data. Life-history trait data are often of mixed nature (qualitative, quantitative, and ordinal trait values) and incomplete. Few similarity coefficients can deal with such data properties (Legendre and Legendre 1998). The Gower coefficient (Gower 1971) is one of them and was used here. The resulting similarity matrix is then used to cluster the species into functional groups by applying a cluster method (here, we used Ward's method). The cutoff level for delineating the functional groups is determined graphically from visual screening of the obtained dendrogram. At this stage, common goals are both not to inflate the number of functional groups and to obtain ecologically meaningful functional groups. This emphasizes the subjective role of the expert's knowledge. Alternatively, an objective criterion such as the Bayesian information criterion can be used (Kolb and Diekmann 2005). To obtain the characteristic life-traits for each functional group, Pearson χ^2 tests (qualitative life-history traits) and Kruskal–Wallis statistics (ordinal and quantitative life-history traits) can be used *a posteriori* to compare the trait values between the identified functional groups (Héroult and Honnay 2005). Next, functional groups can be named according to the life-history traits that drove the clustering procedure.

Seven functional groups were delineated from the studied flora (details in Héroult and Honnay 2005). The product of the presence–absence matrix [site by species] with the binary coded matrix of functional group membership [species by functional group] provides the frequencies of each functional group in each forest stand. These frequencies were tested for their association with the forest age classes to identify which functional groups are good indicators of the restoration status. The abundance of two functional groups strongly increased with forest age and can be considered reliable indicators for the restoration status of the stands (Table 11.1): the barochoreous perennials and the small geophytes.

Barochoreous perennials (e.g. *Stellaria nemorum*, *Glechoma hederacea*, and *Aegopodium podagraria*) encompass plants with unassisted dispersal, unlike all the other groups. They are often hemicryptophytes. Small geophytes (e.g. *Adoxa moschatellina*, *Arum maculatum*, and *Ranunculus ficaria*), on the other hand, are herbaceous plants with perennating tissue (bulbs, corms, rhizomes, stem or root tubers) below the soil surface. They are also characterized by their low stature (<30 cm). Both functional groups flower

after one or two years, and preferentially in spring. Both groups also have big and heavy seeds, which are produced in very small numbers. These seeds typically persist less than one year in the topsoil. Moreover, barochoreous perennials and small geophytes exhibit specific life-history traits, such as their vernal phenology, which reflects their successful adaptation to and their restricted distribution in forest habitats (Bierzychudek 1982). Owing to these particular properties, the conservation of populations of barochoreous perennials and small geophytes is of high relevance in temperate forests (Hermý *et al.* 1999; Keddy and Drummond 1996).

Why do these two functional groups fail to quickly colonize recently restored forest stands? First, the newly established forest stands were predominantly located on former meadows or arable land. Both barochoreous perennials and small geophytes do not form a persistent seed bank. Therefore, it can be assumed that these functional groups have colonized the plantation from the surroundings whereas plants from other functional groups could have survived deforestation periods through their seed banks. Secondly, most barochoreous perennials have extremely low seed dispersal rates (Bossuyt *et al.* 1999; Brunet and Von Oheimb 1998; Dzwonko 2001) because of the combination of large and rare seeds and the lack of dispersal adaptations. Therefore, the strong decrease of barochoreous perennials in newly established forests is very likely dispersal-dependent. Thirdly, small geophytes were under-represented in all restored forests (Table 11.1, Fig. 11.1). Unlike the barochoreous perennials, seeds of small geophytes encompass all dispersal types. Their typical life-history traits are recalcitrant germination and their extremely low stature. Both traits may reflect establishment-limitation. Indeed, low germination rates and low stature may result in a strong competitive disadvantage in nutrient-rich, recently restored forests.

In a nutshell, our results suggest that the distribution and abundance of the two derived functional groups are good indicators to infer the restoration status of a forest stand, as shown by the high *F*-statistics (Table 11.1). Although variance within each age class remains relatively high (Fig. 11.1), their combined use allows to discriminate all age classes. Moreover, the abundance of both of the functional groups in a certain age class provides valuable insights into the ecological mechanisms driving the restoration. Barochoreous perennials will more rapidly colonize a recently established forest located close to an ancient stand than an isolated forest. The absence of small geophytes rather reflects recruitment limitation due to high soil nutrient levels or low canopy closure. These results may provide useful management guidelines for foresters.

Table 11.3. Comparison of the three different methods used to assess the restoration status of a forest stand

	Indicator species	Community measures	Functional groups
Reliability	low	medium	high
Time/cost efficiency	high	medium	medium
Required statistical skills	low	medium	medium/High
Insights in ecological process	low	low	high
Extrapolation potential to other regions	low	low	high
Applicability by forest managers	high	medium	medium

The disadvantages of the approach presented mainly relate to the rather complicated statistical analyses, at least when deriving functional groups from scratch. A strong background in functional ecology is required and this may hamper the application by field practitioners in everyday work. On the other hand, the advantages of using the functional groups when defining and monitoring the restoration status are clear. First of all, studying life-history traits offers valuable insights into the ecological processes underlying the species' distribution patterns, which in turn can support management decisions. At a site scale, this allows the forest managers to understand the biological mechanisms locally hampering or speeding up the restoration process. Additionally, transgressing the species concept substantially increases the predictive and applied power of the obtained results. Although species-centered approaches have led to locally interesting findings and have largely inspired conservation policies, conclusions cannot easily be extrapolated to other biogeographical regions. This seems permitted when using functional groups and allows forest managers to discuss with colleagues from other regions using a common language despite different species pools.

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