

# Using life-history traits to achieve a functional classification of habitats

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## Abstract

**Question:** To establish a habitat classification based on functional group co-occurrence that may help the drawing up of conservation plans.

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

**Methods:** Forest fragments were surveyed for their abundance of vascular plants. These were clustered into emergent groups according to 14 life-traits related to plant dispersal, establishment and persistence. Forest fragments were classified according to similar distribution of the identified emergent groups. Environmental factors were related to the emergent group richness in each forest type using generalized linear models.

**Results:** Contrary to former species centred classifications, only two groups of forests, each with clearly different emergent group composition and conservation requirements, were detected: (1) swamp forests characterized by anemogamous perennials, annuals and hydrochorous perennials and (2) moist forests characterized by barochorous perennials, small geophytes and zoochorous phanerophytes. From a conservation point of view, priority should be given to large swamp forest with intact flooding regimes. This is in accordance with the high wind and water dispersal capacities of their typical emergent groups. For the moist forests, conservation priorities should be high forest connectivity and historical continuity since dispersal and establishment of their characteristic emergent groups are highly limited.

**Conclusions:** The described methodology, situated at an intermediate integration level between the individual species and whole community descriptors, takes advantage of both conservation plans built for single species and the synthetic power of broad ecological measures.

**Keywords:** Forest connectivity; Functional group; Habitat typology; Land-use history; Riverine forest; Species functional unity.

**Abbreviations:** EG = Emergent group; EU = European Union; GLM = Generalized Linear Model.

**Nomenclature:** Lambinon et al. (2004).

## Introduction

Classifying habitats with a similar species composition into vegetation types has a long history among ecologists (Mueller-Dombois & Ellenberg 1974). Among species-centred approaches, the European phytosociological classification consists of a hierarchy of vegetation units, strongly mimicking the rules of the Linnaean system of plant taxonomy (Braun-Blanquet 1928). In these classification systems the concept of differential species allows distinction of different communities. Classifying habitats according to plant composition has largely inspired the European conservation policies. EU Directive 92/43 on the conservation of natural habitats, for instance, is based on a phytosociological classification (Anon. 1992). Owing to a long practice of gathering species occurrence data and hence the availability of large datasets (Ewald 2003), species-centred approaches have played a crucial role in the designation of protected areas in Europe (Mucina et al. 1993).

The need to predict the effects of disturbance on biodiversity and to understand the role of biodiversity in ecosystem functioning has recently increased the interest in studying plant assemblages using a functional view (McIntyre et al. 1995, 1999; Mucina 1997; Smith et al. 1997). Classifying species by their shared morphological, physiological and phenological characteristics rather than by their strict phylogeny is the central theme of this approach. We see two arguments advocating complementary species centred approaches with a functional analysis.

1. Species-centred classifications of habitats of a biogeographical region cannot easily be used to classify habitats of another region having a different species pool. A functional classification based on life traits allows comparison of results between continents (Verheyen et al. 2003).

2. A common goal for nature managers is to provide conservation guidelines for many species simultaneously. As Functional Groups encompass species having simi-

lar biological attributes (Duckworth et al. 2000), their response to management can be expected to be similar (Gitay & Noble 1997; Héroult et al. 2005). For example, most of the species of conservation value from temperate riverine forests can be found in only two functional groups for which conservation guidelines can be easily derived (Héroult 2005).

Although the use of plant life traits in species classifications has become more and more frequent in literature (Héroult & Honnay 2005), habitat classification has received less attention. In fact, the proposed functional classifications are often based on a [Habitat × Life trait] matrix which is obtained by multiplying the [Habitat × Species] data by the [Species × Life trait] data (Lamb & Mallik 2003; Mallik et al. 2001). However, classifying habitats by life trait abundance seems rather unrealistic as such procedures consider habitats as free assemblages of a life trait pool. Life traits have not been clustering randomly throughout the evolutionary history and, therefore, life traits are not randomly distributed among species (Díaz & Cabido 1997; Grime et al. 1997). There are always associations between traits not only because of evolutionary trade-offs (e.g. between seed size and seed longevity), but also just because of common ancestry between species.

Moreover, life traits can interact (synergistically, antagonistically or in many different ways) so that a combination of different life traits may be functionally more determinant for a species' distribution than the arithmetic sum of the behaviour associated with each life trait separately (Lavorel et al. 1999). This urges to adopt a statistical approach based on emergent groups (EGs) (Lavorel et al. 1997) that allows the consideration of each species as a functional unit of life traits throughout the analyses. To illustrate how EGs can be used to define habitat types, we present a case study using the occurrence of vascular plant species in riverine forest fragments.

## Materials and Methods

### Data collection

The 153 investigated riverine forest fragments were situated throughout the Grand-duché de Luxembourg in central-western Europe. The climate is sub-continental; the mean annual temperature is 9 °C and annual rainfall ranges between 700 and 1000 mm. The north of the sampling area consists of shales with low calcium and phosphorous contents whereas the south consists of sandy and calcareous rocks. Flooding statistics are unavailable but overflows are quite regular (5-10 days per year during autumn).

The forest fragments were selected only if no signs of former plantation and of current management activities was obvious. Areas ranged from 500-12190 m<sup>2</sup>. Forest fragments were completely surveyed twice a year: during spring and during summer/autumn 2002 and 2003. Each species was given a crude cover value (1: < 10% cover, 5: 10 - 50% and 10: 50 - 100%) to counterbalance inaccuracies due to the fragment size.

Nine environmental variables were registered (Table 1). The Ellenberg values for nitrogen (Ellenberg et al. 1992) were used to assess the soil productivity which was calculated, for each fragment, using the optimal weighting function of Käfer & Witte (2004) on the herbaceous data only (long-lived trees may have experienced environmental changes). The soil texture (relative % of clay, silt and sand) was estimated in the field. On these estimations we conducted a PCA (Principal Component Analysis using Pc-Ord 4, see McCune & Mefford 1999).

Along the first axis (56% of variation) forest fragments were well distributed from clayey soils (negative co-ordinates) to silty soils (co-ordinates around 0) and to sandy soils (positive co-ordinates). Fragment co-ordinates along this axis were used as a single variable.

Two forest connectivity measures were computed using Hanski's (1994) incidence function model. The

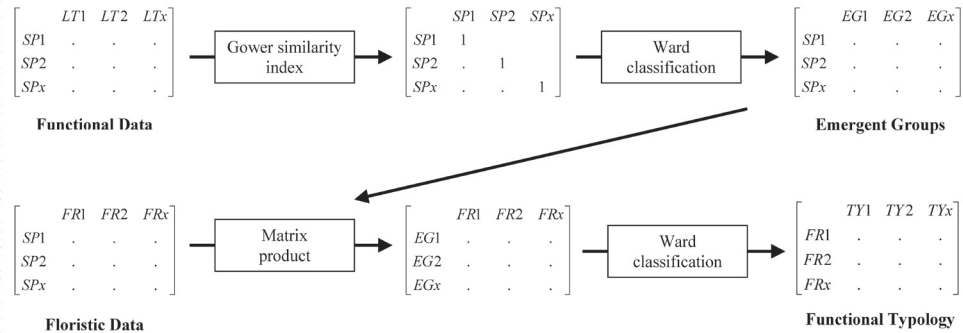
**Table 1.** Overview of the measured environmental variables.

Variable name	Acquisition <sup>1</sup>	Type <sup>2</sup>	Details and range
Area of the forest fragment	LM	C	Measured from digitized maps; from 500 to 12194 m <sup>2</sup>
Connectivity of the forest	CI	C	From low (min = 8) to high (max = 2622) forest connectivity
Connectivity of the riverine forest	CI	C	From low (min = 0) to high (max = 293) riverine connectivity
Depth of the soil reductive layer	FM	O	Upper limit of the alluvial water table in soil; 1/2/3/4/5 (<25, < 50, < 100, < 150, > 150 cm in depth)
Historical continuity	LM	O	0/1/2/3/4 (< 48, 48, 97, 171, 225 years of forest presence)
Litter thickness	FM	C	Recorded in summer; from 0 to 10 cm
Soil productivity	CI	C	From 5.54 to 7.40
Soil pH	LM	C	Measured from 3 mixed soil samples; ISO 10390 norm; from 4.29 to 8.63 pH unit
Soil texture	CI	C	From clayey (-2.24) to sandy (1.90) soils

<sup>1</sup> FM = Field measurement, LM = Laboratory measurement, CI = Computed index (see text for details).

<sup>2</sup> C = Continuous variable, O = Ordinal variable.

EG: Emergent Group  
 FR: Fragment name  
 LT: Life Trait  
 SP: Species  
 TY: Type of habitat



**Fig. 1.** A methodological framework for delineating Emergent Groups and setting up a functional typology of fragmented habitats

*forest connectivity index* was calculated 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 situated within 2 km upstream and downstream along the river. The 1 km and 2 km distances were chosen to obtain realistic distances of maximum dispersal (Butaye et al. 2001). The forest fragment histories were reconstructed from 1777 onwards, consulting four historical land-use maps (Anon. 1954, Ferraris et al. 1777; Hansen 1905; Vandermaelen 1831-1832).

*Identifying the emergent groups*

Persistence, dispersal and establishment are widely acknowledged to be three key events determining the survival of an organism in our fragmented landscapes (Maurer et al. 2003; Verheyen et al. 2003). Fourteen life traits were chosen to reflect these three key events in the plant community assembly process. Trait information was compiled from the existing literature (App. 1). The procedure described below (Fig. 1) was applied twice, once for herbaceous and once for woody species. First, a similarity matrix between species was calculated based on the life trait values and using Gower’s similarity coefficient. This coefficient can deal with missing values as well as with mixed data, i.e. qualitative, ordinal and quantitative (Legendre & Legendre 1998). The resulting matrix was used to cluster the species into EGs using Ward’s method. The cutting level for EG individualization was determined graphically from visual screening of the dendrogram with the goal of obtaining ecologically meaningful EGs. Relationships between individual traits and EGs were investigated by Pearson  $\chi^2$  tests when the trait was qualitative and Kruskal-Wallis statistics when the trait was quantitative or ordinal. We did not correct for phylogenetic relationships. If phylogenetically related

species share similar trait information, they also share similar functions in the system.

*Towards a functional classification*

The aim was to classify the fragmented riverine forests into groups having a similar EG distribution. The product of the abundance matrix [site  $\times$  species] with the binary coded matrix of EG memberships [species  $\times$  EGs] provided the absolute abundance of each EG in each fragment. Differences in the species number per fragment were standardized by dividing the EG absolute abundance by the total EG abundance in each fragment. The obtained matrix was clustered using Ward’s method. The cutting level for the site classification was determined graphically from visual screening of the dendrogram with the goal of obtaining a typology applicable by nature managers. Applying this criterion, two types were delineated. Differences in environmental variables and in EG relative abundances were investigated using Mann-Whitney *U* tests. The characteristic EGs for each forest type were highlighted.

The second aim was to determine the influence of the environmental factors on the EG richness to provide some accurate selection criteria for nature conservation. First, to provide a normally distributed data set, the area of the forest fragment and the connectivity of the riverine forest were squared-root transformed while litter thickness was log transformed. Next, variations in the richness of the characteristic EGs with respect to the environmental variables were analysed using Generalized Linear Models (GLMs). Logarithmic link functions and Poisson distribution of errors were used, as the response variables were discrete. The stepwise procedure (Legendre & Legendre 1998) was applied to select the significant variables, which were tested using Wald statistics. This procedure described above was applied twice, once for each forest type.

## Results

### *Emergent Group identity*

Because life forms and dispersal modes were associated with the first clustering divisions, they were chosen to name the EGs. Seven EGs were derived and characterized (Table 2 and App. 2). 1. Anemochorous perennials produced a lot of light diaspores, which germinated easily and persisted a long time in the soil. 2. Anemogamous perennials mainly encompassed *Cyperaceae*, *Poaceae* and *Juncaceae*, which are wind-pollinated. 3. Annuals consisted of therophytes, which form persistent seed

banks. 4. Barochorous perennials were hemicytrophites with short-lived seeds. 5. Hydrochorous perennials were non-mycorrhizic. 6. Small geophytes were spring ephemerals with large, infrequently germinating seeds. 7. Zoochorous perennials mainly produced exo-zoochorous seeds in small numbers.

The woody species mainly segregated according to their dispersal mode (App. 3). 1. Anemochorous phanerophytes were tall, anemogamous and possessed medium sized seeds dispersed by wind and germinating easily. 2. Zoochorous phanerophytes were entomogamous and possessed large, heavy seeds.

**Table 2.** Morphologic, physiologic and phenologic life traits characteristic of dispersal, establishment and persistence for each of the nine emergent groups.

	<i>n</i>	Dispersal	Establishment	Persistence	Common species
<b>Woody species</b>					
Anemochorous phanerophytes	23	Anemochorous, Medium sized seeds	Easy germination	Tall size, Anemogamous	<i>Acer campestre</i> , <i>Acer pseudoplatanus</i> , <i>Alnus glutinosa</i> , <i>Carpinus betulus</i> , <i>Fraxinus excelsior</i>
Zoochorous phanerophytes	41	Zoochorous, Large seeds	Uneasy germination, Heavy seeds	Medium size, Entomogamous	<i>Corylus avellana</i> , <i>Crataegus monogyna</i> , <i>Hedera helix</i> , <i>Sambucus nigra</i> , <i>Viburnum opulus</i>
<b>Herbaceous species</b>					
Anemochorous perennials	23	Anemochorous, Numerous seeds, Small seeds	Easy germination, Persistent seed bank, Light seeds	Hemicytrophite, Tall size	<i>Athyrium filix-femina</i> , <i>Cirsium oleraceum</i> , <i>Dryopteris dilatata</i> , <i>Dryopteris filix-mas</i> , <i>Senecio ovatus</i>
Anemogamous perennials	39	Elongated seeds		Hemicytrophite, Anemogamous	<i>Alliaria petiolata</i> , <i>Brachypodium sylvaticum</i> , <i>Geum urbanum</i> , <i>Poa nemoralis</i> , <i>Urtica dioica</i>
Annuals	29	Compact seeds	Persistent seed bank	Therophyte, Autogamous, Early 1st flowering	<i>Chrysosplenium oppositifolium</i> , <i>Galeopsis tetrahit</i> , <i>Galium aparine</i> , <i>Geranium robertianum</i> , <i>Impatiens noli-tangere</i>
Barochorous perennials	29	Barochorous, Few seeds, large seeds	Transient seed bank, Heavy seeds	Hemicytrophite, Entomogamous, Late 1st flowering, Vernal phenology	<i>Aegopodium podagraria</i> , <i>Anthriscus sylvestris</i> , <i>Glechoma hederacea</i> , <i>Stellaria holostea</i> , <i>Stellaria nemorum</i>
Hydrochorous perennials	53	Anemochorous/ Hydrochorous	No mycorrhiza	Entomogamous	<i>Angelica sylvestris</i> , <i>Filipendula ulmaria</i> , <i>Heracleum sphondylium</i> , <i>Phalaris arundinacea</i> , <i>Silene dioica</i>
Small geophytes	29	Large seeds	Transient seed bank, Difficult germination	Geophyte, Entomogamous, Late 1st flowering, Small size, Vernal phenology	<i>Adoxa moschatellina</i> , <i>Anemone nemorosa</i> , <i>Arum maculatum</i> , <i>Gagea lutea</i> , <i>Ranunculus ficaria</i>
Zoochorous perennials	35	Zoochorous, Few seeds, large seeds			<i>Deschampsia cespitosa</i> , <i>Elymus caninus</i> , <i>Festuca gigantea</i> , <i>Ranunculus repens</i> , <i>Stachys sylvatica</i>

*Classification of the forest types*

We delineated two groups of forest fragments. The comparison of the environmental variables revealed that the *P* value was the lowest for the depth of the reductive layer (Table 3), which was used to name the two groups. On one hand, ‘swamp forests’ (characteristic EGs: anemogamous perennials, annuals, hydrochorous perennials) were mainly characterized by a water table with low depth, a low connectivity with the other riverine forests and a frequent historical discontinuity. On the other hand, ‘moist forests’ (characteristic EGs: zoochorous phanerophytes, barochorous perennials, small geophytes) showed a deep water table, a high connectivity with the riverine forests and long historical continuity.

*Environmental variables and richness of the characteristic Emergent Groups*

Species richness within the EG characteristic of the swamp forest fragments was well predicted by the area of the forest fragment (Table 4). However, the richness in annuals was negatively related to the connectivity of the riverine forest and positively to the soil productivity. The connectivity of the forest was the main predictor of the richness of the EG characteristic of the moist forest fragments (Table 4). However, the historical continuity sorted out first for the small geophytes.

**Table 3.** Comparison of the values of the environmental variables and of the emergent group relative abundances between the two identified forest types (Mann-Whitney *U* test, values are medians).

	<i>P</i>	Swamp forests ( <i>n</i> = 72)	Moist forests ( <i>n</i> = 81)
<i>Environmental variables<sup>a</sup></i>			
Area of the forest fragment	ns	2635	2886
Connectivity of the forest	*	1182	1474
Connectivity of the riverine forest	***	67	111
Depth of the soil reductive layer	***	2.5	5
Historical continuity	***	0	2
Litter thickness	*	0.5	0.2
Soil productivity	ns	6.6	6.5
Soil pH	**	6.0	6.8
Soil texture	**	-0.17	0.43
<i>Emergent Groups</i>			
Anemochorous phanerophytes	ns	9.8 %	8.8 %
Zoochorous phanerophytes	***	10.5 %	21.5 %
Anemochorous perennials	ns	5.0 %	4.9 %
Anemogamous perennials	***	14.6 %	13.1 %
Annuals	***	10.4 %	5.7 %
Barochorous perennials	***	14.5 %	18.4 %
Hydrochorous perennials	***	16.4 %	7.4 %
Small geophytes	***	9.7 %	15.0 %
Zoochorous perennials	ns	6.9 %	6.2 %

\*\*\* : *P* ≤ 0.001; \*\* : *P* ≤ 0.01; \* : *P* ≤ 0.05; ns : non-significant;  
<sup>a</sup> Values are defined in Table 1.

**Discussion**

The results of the clustering of a [species × life trait] matrix are obviously data dependent and this may question the general applicability of our results. As a whole, the delineated EGs fell short of an intuitive classification of the species present. For example, the commonly used subdivision of phanerophytes into anemochorous and zoochorous species (e.g. Clark et al. 2005) and the well known correlations between life forms and numerous life traits (Lavorel & Garnier 2002) give evidence that empirical classifications have strong mechanistic backgrounds. Moreover, there is increasing evidence that variations in life trait combinations are widely shared among biogeographical areas (Díaz et al. 2004). For example, anemochorous perennials were similarly delineated among European and American forest plants (the perennials with light seeds of Verheyen et al. 2003). It can therefore be expected that our results reflect more general laws underlying the functional organization of plant assemblages.

Species centred classifications of riverine hardwood forests traditionally reflect their location along the river course. In the same study area, Noirfalise (1984) distinguished the *Carici remotae-Fraxinetum* for streams,

**Table 4.** Influence of the environmental variables on the species richness of the emergent groups characteristic of swamp (*n* = 72) and moist (*n* = 81) forests, Generalized Linear Models with logarithmic link function

Response group / Predictor	Wald statistic	<i>P</i>	Regression coefficient
<b>Swamp forests</b>			
Anemogamous perennials			
Area of the forest fragment	16.8	***	0.64
Annuals			
Connectivity of the riverine forest	19.0	***	- 1.01
Soil productivity	10.3	**	0.88
Connectivity of the forest	9.1	**	0.59
Historical continuity	4.7	*	0.49
Area of the forest fragment	4.0	*	0.47
Hydrochorous perennials			
Area of the forest fragment	4.3	*	0.45
<b>Moist forests</b>			
Barochorous perennials			
Connectivity of the forest	26.1	***	0.56
Soil productivity	10.6	**	0.20
Area of the forest fragment	9.8	**	0.10
Depth of the reductive layer	6.7	**	0.08
Small geophytes			
Historical continuity	10.2	**	0.26
Connectivity of the forest	6.3	*	0.12
Zoochorous phanerophytes			
Connectivity of the forest	9.2	**	0.10
Litter thickness	8.4	**	0.33
Area of the forest fragment	6.6	*	0.23
Soil pH	5.6	*	0.29

\*\*\* : *P* ≤ 0.001; \*\* : *P* ≤ 0.01; \* : *P* ≤ 0.05; ns : non-significant.

the *Stellario-Alnetum* for small rivers and the *Ulmo-Fraxinetum* for large rivers. This classification reflects the widely known species replacement along river systems (Nilsson et al. 1989). Our results suggest that the EG relative abundance remains similar along the river course while the species composition of the forests changes. In other words, when an upstream species disappears downstream, it is replaced by a functionally redundant species from the same EG (Naeem 1998; Walker 1992).

### Swamp Forests

The main characteristics of the swamp forests, differentiating them from the moist forest, are their (1) high water table, (2) historical discontinuity and (3) low connectivity with other forests (Table 3). The EG composition of these forests (high abundance of anemogamous perennials, annuals and hydrochorous perennials) can easily be understood in terms of these characteristics.

Anemogamous perennials encompass generalist species such as *Urtica dioica*, *Alliaria petiolata* and *Geum urbanum*, which also occur in the landscape matrix. Even given the historical discontinuity and the low connectivity, these species have always been able to quickly colonize newly emerging forest fragments. Annuals are typical pioneer species with a persistent seed bank, compact seeds and a very short time until first flowering (Table 2). They successfully establish on bare soils after flooding events. Finally, the hydrochorous perennials encompassed many helophyte species, which were able to grow even when the water table permanently reaches the soil surface. Most hydrochorous perennials are hydrochorous and sometimes anemochorous, allowing them to disperse easily even when forest connectivity is low (Dzwonko & Loster 1992; Nilsson et al. 1991).

The most important variable explaining the frequency of the characteristic EGs was fragment area, yielding a typical species-area relationship (Rosenzweig 1995). This is probably due to the correlation between fragment area and habitat diversity as has previously been demonstrated in temperate forests (Honnay et al. 1999). In riverine areas, habitat diversity is highly dependent on the maintenance of a natural flooding regime (Amoros 2001). For instance, annuals require recurrent overflows to maintain on bare soils (Henry et al. 1996). Therefore, as well as focusing on the forest fragment area, nature managers should also conceive their conservation plans emphasizing the preservation of the hydrological processes. Finally, since patch area and hydrology, rather than connectivity and historical continuity, affect the EG richness, it is relatively feasible to recreate new, species rich, forest fragments.

### Moist forests

Three EGs were strongly associated with moist Forests. First, the zoochorous phanerophytes possess large and heavy seeds, which do not germinate easily (Table 2). These seeds are adapted for dispersal through animal movement. Seeds of *Crataegus* spp. and *Sambucus nigra*, for example, easily disperse between fragments through ingestion by birds (Debussche & Isenmann 1994) while nuts from *Corylus avellana* are actively dispersed by rodent activities (Vander Wall 2001). Because animal movements are linked to habitat connectivity (Debinski & Holt 2000; Saab 1999), zoochorous phanerophytes are more abundant in moist forests (Table 3). The same is true for barochorous perennials, which are lacking any seed adaptation for long distance dispersal and are therefore confined to forests with the highest connectivity and historical continuity. Small geophytes encompass many plants flowering before the apparition of tree leaves (Table 2) and are specifically adapted to capture resources before the canopy closure (McKenna & Houle 2000). Due to their low stature and their vernal phenology, small geophytes do not endure prolonged spring overflows, which are less frequent in moist forests owing to the lower water table (Table 3).

On the whole, the GLM showed that forest connectivity is the best predictor of the EG richness in moist forests. Species characteristic of moist forests are unable to colonize new fragments either because of their limited dispersal abilities (barochorous perennials) or owing to their low establishment success associated with a long generation time (small geophytes). Plant populations of these two EGs are often restricted to ancient connected forests and can persist a very long time through prolonged clonal growth (Honnay & Bossuyt 2005; Honnay et al. 2005). Conservation plans for moist forests should give priority to fragments having both highest forest connectivity and historical continuity.

### Conclusions

A common goal among nature managers is to conserve or protect all vegetation types in a given area. The procedure proposed in this study cannot deal with such a conservation goal but it can identify different types of functional group assemblages independent of their species composition. This can help nature managers as it is expected that different functional types will respond similarly to management in its broadest sense. In our case study, our results provide clear guidelines (selecting swamp forests according to patch area and hydrological processes and moist forests according to their connectivity and land-use history), which cannot be inferred using

a classical, species centred classification. Therefore, we recommend using these two classification procedures complementary and conducting studies in other temperate regions to test the relevance of our classification.

Finally, our results also highlighted the dangers of relying on broad community measures. Indeed, nature managers have often based their action either on the conservation value of a single species (Lindenmayer et al. 2000) or on synthetic ecological indicators such as species richness or diversity (Holl & Crone 2004). The EG concept is located at an intermediate level between individual species approach and whole community measures. This concept thus takes advantage of the specificity of conservation plans built for a singular species and of the synthetic power of broad ecological measures.

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For App. 1-3, see *JVS/AVS Electronic Archives*;

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**App. 1.** Coding, description and missing values of the 14 life-traits compiled from literature.

Life-traits	Coding and description	Missing values
Age at first flowering	1: less than 3 months ; 2: from 3 months to 1 year ; 3: from 1 to 2 years ; 4: from 2 to 3 years; 5: from 3 to 6 years ; 6: from 6 to 15 years	59%
Clonal propagation	0: no clonal propagation ; 1: clonal propagation	28%
Dispersal type	1: barochory or myrmecochory ; 2: anemochory ; 3: hydrochory ; 4: endo- and exo-zoochory	0%
Germination requirement	1: immediate; 2: chilling or drying or light or scarification; 3: combinations of the latter	32%
Life-forms	1: chamaephyte ; 2: geophyte ; 3: hemicryptophyte ; 4: therophyte	0%
Onset of flowering	1: during a period superior to 4 months ; 2: during spring (March - June); 3: during summer (July - August); 4: during autumn (September - October)	3%
Mean shoot height	1: less than 0.1 m ; 2: from 0.1 to 0.29 m ; 3: from 0.30 to 0.59 m ; 4: from 0.60 to 0.99 m ; 5: from 1.0 to 2.99 m ; 6: from 3.0 to 5.99 m ; 7: from 6.0 to 14.99 m ; 8: more than 15.0 m	0%
Pollination vector	1: autogamy ; 2: anemogamy ; 3: entomogamy	7%
Potential mycorrhiza	0: 25% or less of records report infection with Vesicular-Arbuscular mycorrhiza ; 1: 75% or more records report infection with Vesicular-Arbuscular mycorrhiza ; 2: 26-74% of records report infection with Vesicular-arbuscular mycorrhiza	18%
Seed longevity	Index of Thompson (1998) ; values range from 0 to 1	43%
Seed mass	1: too small to be measured ; 2: less than 0.2 mg ; 3: from 0.21 to 0.50 mg ; 4: from 0.51 to 1.00 mg ; 5: from 1.01 to 2.00 mg ; 6: from 2.01 to 10.00 mg ; 7: more than 10.00 mg	25%
Seed production per ramet	1: from 1 to 1000 seeds ; 2: from 1001 to 10000 seeds ; 3: more than 10000 seeds	56%
Seed shape	1: length/breadth ratio lower than 1.5 ; 2: ratio from 1.5 to 2.5 ; 3: ratio higher than 2.5	23%
Seed size	Average (length + breadth)	53%

**App. 1-3.** Internet supplement to: Hérault, B. & Honnay, O. 2007. Using life-history traits to achieve a functional classification of habitats. *Appl. Veg. Sci.* 10: 73-80.

**App. 2.** Comparison of the life-trait values between the 7 herbaceous Emergent Groups.

<i>P</i>	Anemochorous perennials	Annuals	Barochorous perennials	Graminoids	Hydrochorous Perennials	Small geophytes	Zoochorous perennials
Age at 1st flowering <sup>1</sup>	3 <sup>ab</sup>	2 <sup>a</sup>	3,5 <sup>b</sup>	3 <sup>b</sup>	3 <sup>b</sup>	4 <sup>b</sup>	3 <sup>b</sup>
Clonal propagation <sup>2</sup>	-0.0 / 0.0	16.2 / -16.2	-3.5 / 3.5	-5.6 / 5.6	-6.3 / 6.3	-0.0 / 0.0	-0.5 / 0.5
Dispersal type <sup>2</sup>	-9.7 / 17.4 / -2.2 / -5.4	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	-11.8 / -8.6 / -2.4 / 22.7
Germination requirements <sup>1</sup>	1 <sup>c</sup>	2 <sup>a</sup>	2 <sup>ab</sup>	1 <sup>bc</sup>	1 <sup>bc</sup>	3 <sup>a</sup>	2 <sup>bc</sup>
Life form <sup>2</sup>	-0.9 / -4.8 / 8.7 / -3.1	-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	4.7 / -5.2 / 1.3 / -0.7
Mean shoot height <sup>1</sup>	4 <sup>ac</sup>	3 <sup>abd</sup>	3 <sup>abcd</sup>	3 <sup>bd</sup>	3 <sup>acd</sup>	2 <sup>b</sup>	3 <sup>abcd</sup>
Onset of flowering <sup>2</sup>	4.3 / -4.6 / -0.8 / 1.0	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	-3.2 / -2.0 / 6.2 / -1.1
Pollination vector <sup>2</sup>	5.0 / -2.8 / -2.2	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	-2.8 / -0.9 / 3.7
Potential mycorrhiza <sup>2</sup>	-5.8 / 8.6 / -2.8	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	-4.4 / 6.3 / -1.9
Seed longevity <sup>1</sup>	0.66 <sup>ab</sup>	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>	0.38 <sup>bd</sup>
Seed mass <sup>1</sup>	2 <sup>b</sup>	5 <sup>ac</sup>	5 <sup>c</sup>	4 <sup>ac</sup>	3 <sup>ba</sup>	4 <sup>bac</sup>	4,5 <sup>ac</sup>
Seed production <sup>1</sup>	2 <sup>a</sup>	1 <sup>ab</sup>	1 <sup>b</sup>	1 <sup>ab</sup>	2 <sup>ab</sup>	1 <sup>ab</sup>	1 <sup>b</sup>
Seed shape <sup>1</sup>	2 <sup>ab</sup>	1 <sup>a</sup>	2 <sup>ab</sup>	2 <sup>b</sup>	2 <sup>ab</sup>	3 <sup>ab</sup>	1 <sup>ab</sup>
Seed size <sup>1</sup>	0.78 <sup>a</sup>	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>	1.95 <sup>b</sup>

<sup>1</sup> Kruskal-Wallis test, values are medians. Numbers with different letters are significantly different at the 0.05 level

<sup>2</sup> Pearson  $\chi^2$  test, values are differences between observed and expected frequencies for the different categories defined in App. 1  
 \*\*\*:  $P \leq 0.001$ ; \*\*:  $P \leq 0.01$

**App. 3.** Comparison of the life-trait values between the two woody Emergent Groups.

	<i>P</i>	Anemochorous phanerophytes	Zoochorous phanerophytes
Age at first flowering <sup>1</sup>	ns	7	6
Clonal propagation <sup>2</sup>	ns	-1.1/1.1	1.1/-1.1
Dispersal type <sup>2</sup>	***	-0.4/14.0/0.0/-13.7	0.4/-14.0/0.0/13.7
Germination requirements <sup>1</sup>	***	1	2
Mean shoot height <sup>1</sup>	***	8	6
Onset of flowering <sup>2</sup>	**	-0.4/6.4/-5.7/-0.4	0.4/-6.4/5.7/0.4
Pollination vector <sup>2</sup>	***	-0.7/10.7/-10.0	0.7/-10.7/10.0
Potential mycorrhiza <sup>2</sup>	ns	0.0/-0.4/0.4	0.0/0.4/-0.4
Seed longevity <sup>1</sup>	ns	0	0
Seed mass <sup>1</sup>	**	3	7
Seed production <sup>1</sup>	**	2	1.5
Seed shape <sup>1</sup>	*	2	1
Seed size <sup>1</sup>	*	0.9	3.95

<sup>1</sup> Mann-Whitney U test, values are medians;

<sup>2</sup> Pearson  $\chi^2$  test, values are differences between observed and expected frequencies for the different categories defined in App. 1;

\*\*\* :  $P \leq 0.001$  ; \*\* :  $P \leq 0.01$  ; \* :  $P \leq 0.05$  ; ns : non significant.