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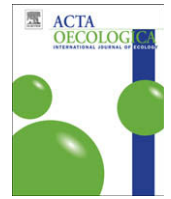
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Original article

How habitat area, local and regional factors shape plant assemblages in isolated closed depressions

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ABSTRACT

Classifying species by shared life-history traits is important if common ecological response groups are to be identified among different species. We investigated how habitat area, local and regional factors shape plant communities in small isolated closed depressions, and how the species richness is related to the interplay between environmental factors and specific life-history trait combinations. In Central-Western Europe, 169 closed depressions were completely surveyed for plant presence in two highly contrasted landscapes (forested and open landscapes). All species were clustered into 9 Emergent Groups based on 10 life-history traits related to plant dispersal, establishment and persistence. Habitat areas were related to species presence using logistic regressions. Most Emergent Groups were more area-dependent in open than in forested landscapes, owing to heterogeneous light levels in forest weakening the species–area relationship. In open landscapes, Floating Hydrophytes were severely underrepresented in very small depressions, owing to the absence of waterfowl population. Local environmental and regional factors were related to species richness using Generalized Linear Models. In open landscapes, local environmental factors such as water conductivity or soil productivity are respectively the main predictors. In forested landscapes, the abundance of most Emergent Groups was better predicted by regional factors, i.e., habitat connectivity and distance to the forest edge. Forested landscapes strongly impeded the closed depressions' colonization by the less mobile Emergent Groups such as Large-seeded Perennials.

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1. Introduction

A closed depression can be considered as an aquatic island in a terrestrial landscapes, a sort of insular system. Plant assemblages in these habitat islands are related to habitat area, local environmental and regional ecological processes. Firstly, the number of plants present in the system is obviously a function of the system area. All else being equal, a larger closed depression will contain a greater number of species because larger habitats have, on one hand, more habitats and, on the other, more individuals. More individuals decrease the probability of species extinction due to genetic drift, to random local extinctions or to unpredictable disturbances (Rosenzweig, 1995). Secondly, plant assemblages are dependent on biotic and abiotic conditions characterizing a closed depression (Kirkman et al., 2000), i.e., the local factors. For example, plant composition of young water-filled closed depressions differs greatly from plant assemblages of old peat-filled closed depressions (Klinger, 1996; Frankl and Schmeidl, 2000; Tiner, 2003; Héroult and

Thoen, 2008). Lastly, species accumulation in a given closed depression is the result of successive establishment of species dispersed from other closed depressions, i.e., the regional factor (Leibowitz, 2003). While hydrochory may play a crucial role in the structure of plant assemblages in river (Andersson et al., 2000) or in lowland wetlands (Middleton, 2003), seed dispersal by running water is impossible between upland closed depressions. Moreover, dispersal limitation greatly varies with the nature of the surrounding matrix (Murphy and Lovett-Doust, 2004). And it may be expected that a closed depression surrounded by forests may be less colonized by aquatic plants owing to the lower frequentation of these closed depressions by waterfowls (Green et al., 2002).

Processes of plant assemblages in upland closed depressions from European landscapes have not attracted many ecological researches. In particular, one issue that has received very little attention is how plant assemblages respond to spatial isolation (Leibowitz, 2003). Studies from other fragmented ecological systems (e.g., Médail et al., 1998; Dupré and Ehrlén, 2002; Héroult and Honnay, 2005) have concluded that the species specific response to area, local and regional factors is closely linked to syndromes of species life-history traits, i.e., Emergent Groups. An Emergent Group is defined as a set of species having similar

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combinations of morphological, physiological and phenological life-history traits (Lavorel et al., 1997; Hérault, 2007) so that convergent ecological and evolutionary strategies can be expected between members of a given Emergent Group (Holt, 2006; Scheffer and van Nes, 2006). Which plant life-history traits are needed to counterbalance random local extinctions in a fragmented habitat? Plants have to disperse to new closed depressions, they have to become established, and once established they have to persist as long as possible (Weiher et al., 1999). Dispersal occurs in two dimensions: a temporal and a spatial one. Dispersal in time depends on seed longevity (HilleRisLambers et al., 2005) while dispersal in space depends on a several seed key-properties (mass and dispersal mode, see Hewitt and Kellman, 2002). Establishment is firstly linked to germination requirements (chilling, drying, scarification, ..., see Baskin and Baskin, 2001). But the seed size is also critical for establishment, as larger seeds often result in larger and more competitive seedlings (Moles and Westoby, 2004). Additionally, the plant ability to vegetatively reproduce is crucial when few individuals initially colonize a closed depression (Hooftman and Diemer, 2002). And finally, persistence is correlated with many life-history traits (Weiher et al., 1999). The most successfully used are related to the mode of life (life-form, pollination vector, root anchorage for aquatic plants), to the competitive ability (plant height, seed mass) and to the strategy of resource acquisition (e.g., onset of flowering). The latter could be crucial in forested landscapes where vernal plants have evolved to capture resources before canopy closure in late spring (Lapointe, 2001).

The first aim of this study is to delineate plant Emergent Groups having similar life-history trait combinations implied in dispersal, establishment and persistence in temperate closed depressions. Next, the following hypotheses will be tested: (H1) the probability of species presence in a given closed depression increases with the closed depression area, (H2) plant assemblages in closed depressions from forested landscapes are more linked to habitat connectivity than in open ones, e.g., plant dispersal is easier in open than forested landscapes and (H3) the highlighted patterns in H1 and H2 strongly depend on the plant colonization ability, estimated by a combination of dispersal, establishment and persistence life-history traits.

2. Materials and methods

The 169 investigated closed depressions were situated throughout the Lorraine region in Central-Western Europe (49°26'–50°10'N, 5°42'–6°32'E). The climate is sub-continental with an Atlantic influence; the mean annual temperature is 9 °C.

Annual rainfall ranges between 700 and 1000 mm. Among isolated wetlands, small closed depressions encompass all landscape elements where a sediment depository is encircled by hillslopes (Gilljins et al., 2005). It has been hypothesized that some closed depressions derive from deflation hollows (French and Demitroff, 2001), karstic sinkholes (Drew and Jones, 2000), morainic kettle holes (Otto and Hofle, 1994) or pingos (De Gans, 1982). In the area east of the studied area, Slotboom (1963) hypothesized that they derived from the leaching out of the gypsum from the subsoil. In the west of the area, Couteaux (1969) suggested that the origin of the closed depressions must better be related to the local solution of CaCO₃ in marls from Jurassic and Triass. Finally, an anthropogenic origin, linked to ancient human settlement, may also be possible. Whatever the origin, the evolution of the closed depressions seems convergent. Indeed, once formed, the clayey colluvium makes the ground of the closed depression impermeable, so that the water is completely retained in the system that in turn allows the slow formation of peat in the stagnant water (Frankl and Schmeidl, 2000).

A field visit of a group of randomly-selected closed depressions allowed us to select the studied closed depressions according to three criteria: (i) no obvious management activities, (ii) no evidence of excavation and (iii) located in forested (closed depression located in forest) or open (closed depression located in grassland or meadow) upland landscapes. Closed depression located on a boundary (partly in forested and partly in open landscape) was not sampled. Areas were measured in the field and ranged from 16 to 4000 m² in open ($n = 77$) and from 15 to 3140 m² in forested ($n = 92$) landscapes. All closed depressions were completely and intensively surveyed for plant presence. Plant nomenclature follows Lambinon et al. (2004).

Nine environmental variables were registered (Table 1). The distance to the nearest forest edge was recorded in forested landscapes only while grazing pressure was for open landscapes only. Soil productivity and pH were estimated from the averaged Ellenberg values (1992) of the species present in a given closed depression. These values are now recognized as highly reliable to replace field measurements (Diekmann, 2003). To assess the habitat connectivity, the number of closed depressions present within a 0.1, 1 and 10 km radius was extracted from digitized maps in order to investigate different colonization-limitation patterns. This measure of habitat connectivity did not take into account variation in closed depression areas because numbers of closed depressions sometimes reached several hundred by km² and habitat area was completely undetectable on digitized maps and/or aerial photographs.

Table 1
Overview of the local environmental and regional variables.

Variable name	Details	Forested landscapes ^a	Open landscapes ^a
Surface area		235 [120; 350]	190 [105; 565]
<i>Local environmental variables</i>			
Soil pH	Based on Ellenberg values	5.58 [5.00; 6.00]	5.57 [5.33; 6.00]
Soil productivity	Based on Ellenberg values	5.65 [4.97; 6.00]	5.32 [5.08; 5.78]
Water conductivity	Measured in spring/summer (μS cm ⁻¹)	146 [111; 227]	351 [230; 515]
Water permanency	0/1/2 (without/temporary/permanent water)	2 [1; 2]	2 [1; 2]
<i>Regional variables</i>			
Distance to forest edge ^b	From closed depression edge to forest edge (m)	95 [40; 181]	–
Connectivity 100	Number of closed depressions within a 100 m radius	1 [0; 2]	1 [0; 2]
Connectivity 1000	Number of closed depressions within a 1000 m radius	6 [3; 8]	5 [3; 7]
Connectivity 10000	Number of closed depressions within a 10,000 m radius	112 [49; 149]	73 [52; 158]
Grazing pressure ^c	0/1/2 (without/localized/with grazing)	–	1 [0; 2]

^a Values are medians and quartiles.

^b Only measured in forested landscapes.

^c Only estimated in open landscapes.

2.1. Identifying Emergent Groups

Ten traits were chosen according to their implication in dispersal, establishment and persistence (see Appendix 2). Trait information was compiled from the existing literature (mainly Grime et al., 1988; Hodgson et al., 1995; Kleyer, 1995; Julve, 1998; Klimeš and Klimešová, 1999). On average, 8% of trait information was lacking.

Bog Mosses were regarded as a full Emergent Group owing to the low number of species (5). For the other plants, the classification methodology adhered to the concept of Emergent Group applied in several recent studies (among others, see Verheyen et al., 2003). As classification procedures perform better in a hierarchical manner within growth forms (Lavorel et al., 1997), the following procedure largely detailed in Hérault and Honnay (2007) was applied three times: once for the aquatic plants, once for the herbaceous and once again for trees. First, a similarity matrix between species was calculated based on the life-traits 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 and Legendre, 1998). The resulting matrix was used to cluster the species into Emergent Groups using Ward's method. The cutting-level for Emergent Group individualization was determined graphically from visual screening of the dendrogram with the goal of obtaining ecologically meaningful Emergent Groups. To find which life-history trait combination characterized each Emergent Group, Pearson χ^2 tests (when the trait was qualitative) and Mann–Whitney U Tests or Kruskal–Wallis statistics (when the trait was quantitative or ordinal) were respectively used (see Appendices 3–5).

2.2. Colonization limitation and habitat areas

Logistic models were used to relate the presence of a given species to the logarithm of the habitat area (H1). The parameter estimates of the logistic models were retained as an 'index of area limitation'. In other words, a positive estimate meant that this species was less frequent in small closed depressions and was thus strongly area-dependent. Estimates were sometimes negative, i.e., species more frequent in small than in large closed depressions. Comparisons of the index values between landscapes were done using t tests. Comparisons of the index values between Emergent Groups in a given landscape were done using Tukey HSD statistics.

2.3. Species richness, local and regional factors

The second aim was to quantify the relative influence of local environmental and regional factors on species richness of each Emergent Group in two contrasted landscapes (H2 and H3). To obtain well-behaved model residuals, distance to the forest edge, water conductivity and densities on a 1 km scale were squared-root transformed. The influence of local and regional factors on species richnesses within Emergent Groups was analyzed using Generalized Linear Models. The logarithm of the closed depression area was introduced as a covariable into each Emergent Group model in order to correct for differential species richness due to differences in area. Logarithmic link functions and Poisson distribution of errors used as the response variables were discrete (species counts). Finally, variation partitioning among local and regional factors was done by means of partial linear regression (Legendre and Legendre, 1998).

3. Results

Nine Emergent Groups were delineated using our classification procedure: 2 aquatic, 4 herbaceous, 2 woody and the Bog Mosses. Details on their characteristic syndromes of life-history traits are available in Table 2 and statistics are given in detail in Appendices 3–5.

3.1. Species presence and habitat area

Between landscapes, comparing the area limitation indexes revealed that species presence in most Emergent Groups was more area-dependent in open than in forested landscapes (Table 3). These differences were highly significant for Animal-dispersed Trees, Annuals, Floating Hydrophytes and Graminoids.

Within landscapes, values of the index of area limitation were very different between Emergent Groups (Table 3). Values ranged from -1.04 (Annuals) to 0.069 (Large-seeded Perennials) in forested landscapes and from -0.006 (Animal-dispersed Trees) to 0.084 (Floating Hydrophytes) in open landscapes.

3.2. Determinants of the Emergent Groups' richness

In forested landscapes, Emergent Groups' species richness was mostly linked to regional factors (Table 4): (i) positively correlated with connectivity values (except Wind-dispersed Trees) and (ii) negatively linked with distances to the forest edge. Generalized Linear Models were not significant for three Emergent Groups: Animal-dispersed Trees, Bog Mosses and Fixed Hydrophytes.

Table 2

Life-history traits related to dispersal, establishment and persistence of the aquatic, herbaceous and woody identified Emergent Groups and commonest species.

	n	Dispersal	Establishment	Persistence	Commonest species
<i>Aquatic</i>					
Fixed Hydrophytes	16	Fixed, clonal multiplication		Tall, summer flowering, entomogameous	<i>Callitriche</i> spp., <i>Potamogeton</i> spp., <i>Ranunculus</i> gr. <i>Batrachium</i>
Floating Hydrophytes	5	Floating, clonal multiplication		Small, spring flowering, hydrogameous	<i>Lemna</i> spp., <i>Utricularia</i> spp.
<i>Herbaceous</i>					
Annuals	18	High seed longevity	No clonal multiplication	Annual	<i>Bidens</i> spp., <i>Galium aparine</i> , <i>Persicaria</i> spp.
Graminoids	52	Hydrochorous, low seed longevity	Clonal multiplication	Anemogameous, geophytes, summer flowering	<i>Carex</i> spp., <i>Glyceria</i> spp., <i>Juncus</i> spp.
Small-seeded Perennials	60	Wind- and animal-dispersed, low seed longevity	Clonal multiplication, no germination requirement, light seeds	Hemicryptophytes	<i>Alisma plantago-aquatica</i> , <i>Ranunculus repens</i> , <i>Solanum dulcamara</i>
Large-seeded Perennials	41	No dispersal adaptation, low seed longevity	Heavy seeds	Entomogameous	<i>Galium palustre</i> , <i>Iris pseudacorus</i> , <i>Lysimachia</i> spp.
<i>Trees</i>					
Wind-dispersed Trees	16	Wind-dispersed	No germination requirement, light seeds	Anemogameous	<i>Alnus glutinosa</i> , <i>Fraxinus excelsior</i> , <i>Salix</i> spp.
Animal-dispersed Trees	17	Animal-dispersed	A lot of germination requirements, heavy seeds	Entomogameous	<i>Crataegus</i> spp., <i>Prunus</i> spp., <i>Viburnum opulus</i>

Table 3

Comparisons of the indexes of area limitation between forested and open landscapes (in lines, *t* tests, values are means ± standard deviation) and between Emergent Groups in each landscape (in columns, Tukey HSD tests, different letters indicated significantly different indexes at the 0.05 level within a given landscape). Indexes are based on the parameters' estimates from the logistic models linking the presence/absence data of a given species and the logarithm of the wetland area.

	Forested landscapes	Open landscapes	<i>t</i>	<i>P</i>
Animal-dispersed Trees	-0.199 ± 0.279 ^b	-0.006 ± 0.089 ^b	4.71	***
Annuals	-1.04 ± 0.001 ^e	0.047 ± 0.095 ^{ca}	75.32	***
Fixed Hydrophytes	-0.011 ± 0.001 ^{abcd}	0.015 ± 0.081 ^{bc}	-0.50	ns
Floating Hydrophytes	0.004 ± 0.001 ^{acd}	0.084 ± 0.028 ^a	20.1	***
Graminoids	-0.053 ± 0.115 ^d	0.030 ± 0.058 ^{bc}	10.9	***
Large-seeded Perennials	0.069 ± 0.131 ^c	0.062 ± 0.071 ^a	-0.59	ns
Small-seeded Perennials	0.013 ± 0.012 ^a	0.035 ± 0.058 ^c	3.05	**
Wind-dispersed Trees	-0.024 ± 0.154 ^{ad}	0.011 ± 0.065 ^{bc}	1.77	ns

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

In open landscapes, Emergent Groups' species richness was mostly linked to local environmental factors. Hydrophytes were negatively associated with water conductivity and positively with water permanency (Table 4). Soil productivity favored Annuals but strongly decreased the richness in Large-seeded Perennials and in Graminoids. The soil pH was negatively related to Annuals but positively to Animal-dispersed Trees. Generalized Linear Models were not significant for two Emergent Groups: Small-seeded Perennials and Wind-dispersed Trees.

4. Discussion

4.1. Habitat area limits plant colonization

The theory of island biogeography, originally written for terrestrial islands in an inhospitable sea, predicts that, all else being equal, the probability of presence of a given species increases with the island size (MacArthur and Wilson, 1967). Our results fall short of these expectations in open landscapes (H1 only validated in open landscapes). Indeed, values of the area limitation index are highly differentiated between Emergent Groups in forested landscapes (Table 3).

In open landscapes, two Emergent Groups were highly area-dependent: Floating Hydrophytes and Large-seeded Perennials. Two types of bottleneck may have occurred. First, propagules may be not

able to reach the smallest closed depressions. This is very likely for Large-seeded Perennials, because of their unassisted dispersal (Table 2). Secondly, small closed depressions could be too small to maintain viable plant populations in the long term. This looks also plausible for Perennials but not for Hydrophytes, which are well-known to efficiently propagate using asexual multiplications (Table 2). Their discrepancy in small closed depressions is likely related to the absence of waterfowl populations. Indeed, very small closed depressions are not large enough to attract and maintain breeding waterfowl couples (Horn et al., 2005), which are well-known to be the main propagules' dispersers (Green et al., 2002).

Among the highly-debated explanations proposed to explain the species–area relationships (Rosenzweig, 1995), the habitat heterogeneity hypothesis holds that habitat area is a surrogate of habitat heterogeneity, which directly modifies the probability of species presence (Brose, 2001). We believe that the significant decreases of the index of area limitation for most Emergent Groups (Table 3) in forested landscape are essentially due to more heterogeneous habitats and especially to more heterogeneous light-incidence levels in forested landscapes. Indeed, in closed depressions located in forested landscapes, the degree of light incidence is highly variable (some parts of the closed depression are deeply shaded, others receive full sunlight) depending on the degree of canopy closure. This leads to the coexistence of very heterogeneous habitats in a restricted area that strongly weakens the species presence–area relationships (e.g., Honnay et al., 1999; Brose, 2001).

4.2. Local factors structure plant assemblages in open landscapes

Our results indicated that local environmental variables are more important in open than in forested landscapes (Fig. 1, H2 validated).

Unsurprisingly, the water permanency and conductivity were strongly linked to the occurrence of Hydrophytes and Bog Mosses (Table 4). High water conductivities clearly reduced the diversity in Hydrophytes towards a shift to duckweed (*Lemna* spp., Floating Hydrophytes) dominance (Scheffer et al., 2003). Mats of duckweeds reduce light penetration and gaseous exchanges between water and atmosphere, avoiding in turn the growth of most Fixed Hydrophytes (Boedeltje et al., 2005). While water conductivity was closely linked to the aquatic Emergent Groups, the soil productivity was obviously

Table 4
How local environmental and regional factors drive the Emergent Groups' richness in two contrasted landscapes (Generalized Linear Models with logarithmic link function).

	Local environmental factors				Regional factors				GLM model
	N	R	WC	WP	C100	C1000	C10000	DFE	
<i>Forested landscapes</i>									
Annuals								(-)*	*
Floating Hydrophytes				(+)					**
Graminoids	(-)*		(-)*		(+)**			(-)*	**
Large-seeded Perennials					(+)*		(+)*	(-)	***
Small-seeded Perennials					(+)*			(-)**	**
Wind-dispersed Trees						(-)**			*
<i>Open landscapes</i>									
								GP	
Animal-dispersed Trees		(+)*				(-)*			*
Annuals	(+)**	(-)*					(+)*		**
Bog Mosses			(-)*						*
Fixed Hydrophytes			(-)*					(+)*	**
Floating Hydrophytes			(-)*	(+)**					***
Graminoids	(-)						(+)*		***
Large-seeded Perennials	(-)							(-)*	***

N: soil productivity, R: soil pH, WC: water conductivity, WP: water permanency, C100: connectivity 100, C1000: connectivity 1000, C10000: Connectivity 10000, DFE: distance to forest edge, GP: grazing pressure.

***: *P* ≤ 0.001; **: *P* ≤ 0.01; *: *P* ≤ 0.05; ns: non-significant; (+) positive relationship, (-) negative relationship.

Non-significant models are not reported.

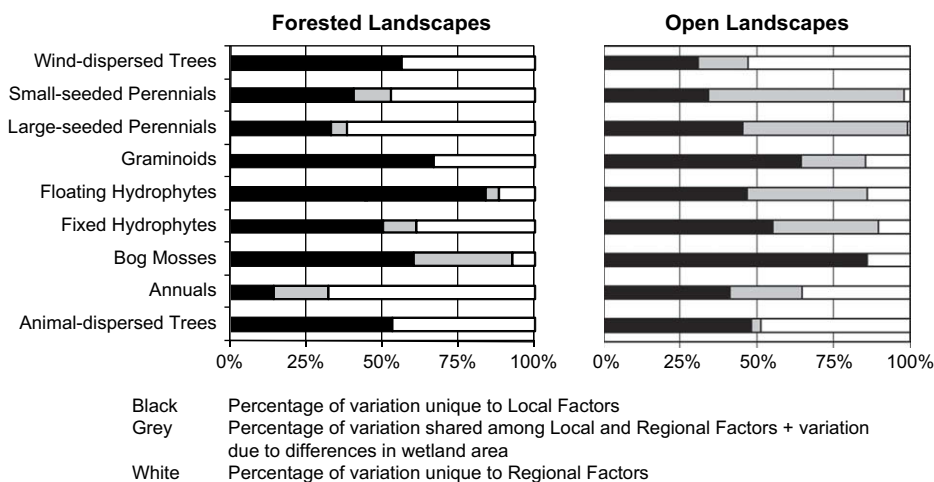


Fig. 1. Assessment of the relative influence of local environmental and regional factors on the Emergent Groups' richness in two contrasting landscapes using Multiple Regression partition of variation.

more related to terrestrial Emergent Groups. High soil productivity levels decrease the richness in Graminoids and in Large-seeded Perennials but increase the richness in Annuals (Table 4). Such a curious pattern was also observed in grasslands (Paschke et al., 2000) and woodlands (Prober et al., 2005) and could be related to different strategies of resource acquisition (Pastor and Durkee Walker, 2006). Annuals don't have perennial tissues that can store nutrients so that they cannot buffer the temporal variability in soil water saturation. Perennials store nutrients in rhizomes or bulbs (Graminoids, see Appendix 4) and roots (Large-seeded Perennials) so that they can mobilize these reserves to counterbalance environmental variations in low-nutrient environments.

4.3. Regional factors structure plant assemblages in forested landscapes

Our results indicated that colonization-limitation is more important in forested than in open landscapes (Table 4 and Fig. 1, H2 validated). Moreover, our results suggest that habitat connectivity affects species distribution at very small spatial scales in forested landscapes (most positive relationships were detected for a 100 m radius, Table 4) and that distance to forest edge is crucial.

Wetland plants are actively dispersed by waterfowl in open landscapes (Green et al., 2002; Charalambidou and Santamaria, 2005). Our results suggested that local waterfowl migrations less efficiently counterbalanced the effects of isolation in open than in forested landscapes. And it may be expected, that the level of waterfowl frequentation for forested closed depressions depends on the distance to the forest edge. In forests, plant colonization is also linked to seed dispersal by wind. Uplifts of seeds in forested landscapes occurred in low leaf area index conditions, i.e., in early spring (Nathan et al., 2002) and explain why seeds of most forest species fall in spring. But seeds of most wetland species do not fall in spring (Table 4). Consequently, only closed depression located near the forest edge received the seed rain from wetland plants during summer.

Regional factors were thus predominant in shaping herbaceous assemblages in forested landscapes. But each Emergent Group has a unique ecological behaviour: from lowly affected (Annuals) to highly-affected by isolation (Large-Seeded Perennials). On one hand, Annuals have very long-lived seeds that allow these plants to survive unsuitable conditions through their seed banks. For example, periodical populations of *Bidens tripartita* are sufficient to ensure its long-term persistence in very fragmented landscapes (Brandel, 2004). On the other hand, Large-seeded Perennials lack

any dispersal adaptations, possess heavy seeds and produce highly transient seed banks (Table 2). An efficient dispersal event is thus expected to be very rare.

Finally, results from the GLM analyses suggested a negative association between regional factors and species richness in Wind-dispersed Trees (Table 4). This reveals a complex pattern behind our data, i.e., the interplays between common and rare trees (Héroult and Thoen, 2008). Wind-dispersed Trees mainly comprised Willow species: one common *Salix aurita* and the others rare in this habitat. The commonest willow formed monospecific assemblages in low-nutrient closed depressions, which are not isolated. In very-isolated closed depressions, this common willow was replaced by a multi-specific assemblage of the other rare willows such as *Salix alba*, *Salix cinerea* or *Salix purpurea*. In other words, when the common willow is absent due to closed depression isolation, it is replaced by two or more functionally equivalent trees (Héroult, 2007) that enhanced Wind-dispersed Tree richness.

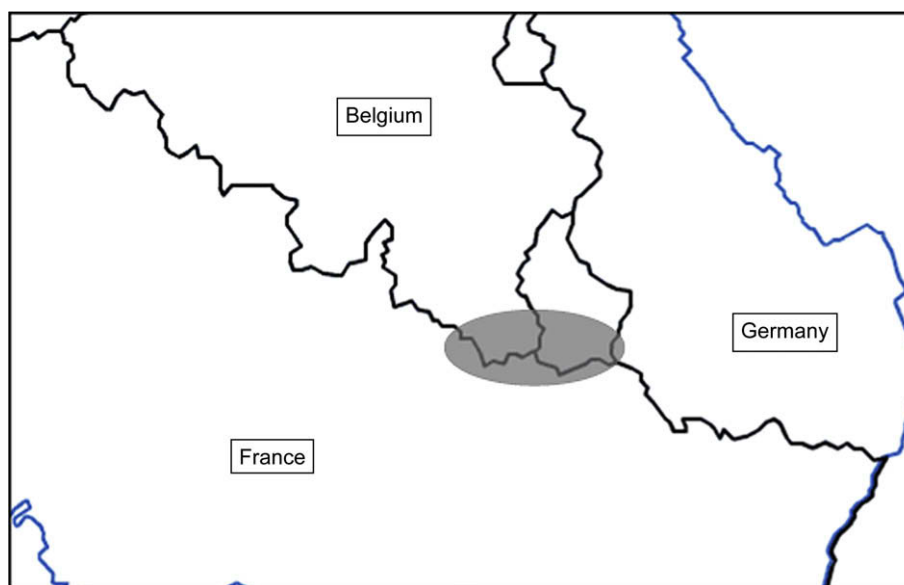
5. Conclusion

We have shown that plant assemblages in isolated closed depressions are influenced by the surrounding landscape: plant assemblages are severely colonization-limited in forests while local environmental variables and habitat area are the main sources of variability in open landscapes (Fig. 1). Moreover, the relative importance of local versus regional factors shaping the plant assemblages clearly depends on the Emergent Group of interest. Indeed, plants from different Emergent Groups respond in different ways to isolation. The ecological behaviors emphasized here at the Emergent Group levels are often hidden at the whole community level (Lopez et al., 2001) and are less detectable at the species level (Héroult, 2007). As Emergent Groups encompass species having similar biological attributes, their response to nature management and landscape planning in its broadest sense can be expected to be similar (Duckworth et al., 2000). Nature managers should thus take into account not only the local environmental factors but also the landscape context when they aim to conserve, restore or create closed depressions.

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Appendix 1. Map of the studied area (in grey) in the Lorraine Region of central-western Europe



Appendix 2. List of the 10 life-history traits compiled from the literature

Life-history traits	Coding and description	Variable type ^c	Missing values (%)
Clonal propagation	0: No clonal propagation; 1: clonal propagation	Q	0
Dispersal type	1: Barochory or myrmecochory; 2: anemochory; 3: hydrochory; 4: endo- and exo-zoochory	Q	1
Germination requirement	1: Immediate; 2: chilling or drying or light or scarification; 3: combinations of the latter	O	26
Life-forms ^a	1: Chamaephyte; 2: geophyte; 3: hemicryptophyte; 4: therophyte	Q	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)	Q	2
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	O	2
Pollination vector ^d	1: Autogamy; 2: anemogamy; 3: entomogamy; 4: hydrogamy	Q	4
Seed longevity	Index of Thompson (1998); values range from 0 to 1	C	25
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	O	20
Soil fixing ^b	0: Fixing; 1: floating	Q	0

^a Only recorded for herbaceous plants.

^b Only recorded for aquatic plants.

^c C: Continuous variable, O: ordinal variable, Q: qualitative variable.

^d Autogamy: self-fertilization, Anemogamy: wind-fertilization, entomogamy: insect-fertilization, hydrogamy: water-fertilization.

Appendix 3. Comparison of the life-history trait values between the two aquatic Emergent Groups

	P	Fixed Hydrophytes	Floating Hydrophytes
Clonal propagation ^b	ns	1.4/–1.4	–1.4/1.4
Dispersal type ^b	ns	0.5/0.0/–0.5/0.0	–0.5/0.0/0.5/0.0
Germination requirements ^a		2	No data available
Mean shoot height ^a	***	4	1
Onset of flowering ^b	***	0.3/–2.0/1.8/0.0	–0.3/2.0/–1.8/0.0
Pollination vector ^b	*	0.0/0.5/0.9/–1.3	0.0/–0.5/–0.9/1.3
Seed longevity ^a	ns	0	0
Seed mass ^a		4	No data available
Soil fixing ^b	***	–3.8/3.8	3.8/–3.8

^a Mann–Whitney U test, values are medians.

^b Pearson Chi² test, values are differences between observed and expected frequencies for the different categories defined in Appendix 2.

Appendix 4. Comparison of the life-history trait values between the 4 herbaceous Emergent Groups

	<i>P</i>	Annuals	Graminoids	Small-seeded Perennials	Large-seeded Perennials
Clonal propagation ^b	***	15.4/–15.4	–5.6/5.6	–6.8/6.8	–3.0/3.0
Dispersal type ^b	***	2.2/–1.9/–2.1/1.8	–5.7/–5.3/8.1/2.8	–6.3/13.0/–9.7/3.0	9.8/–5.9/3.6/–7.6
Germination requirements ^a	**	2a	2ab	1b	2ab
Life-form ^b	***	–0.5/–4.0/–11.6/16.1	–1.5/10.4/–3.5/–5.5	0.2/–5.3/11.4/–6.3	1.8/–1.1/3.6/–4.3
Mean shoot height ^a	ns	4a	4a	3a	3a
Onset of flowering ^b	***	1.1/–0.8/–5.2/4.9	–16.1/–0.2/22.4/–6.1	25.2/–4.0/–20.2/–1.1	–9.5/4.9/2.4/2.2
Pollination vector ^b	***	3.9/–3.2/–0.7/0.0	–3.9/27.7/–23.7/0.0	4.8/–8.1/3.3/0.0	–4.8/–16.3/21.1/0.0
Seed longevity ^a	***	0.88a	0.28bc	0.38b	0.17c
Seed mass ^a	**	5.5ab	4ab	3a	5b

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

^a Kruskal–Wallis test, values are medians. Numbers with different letters are significantly different at the 0.05 level.

^b Pearson Chi² test, values are differences between observed and expected frequencies for the different categories defined in Appendix 2.

Appendix 5. Comparison of the life-history trait values between the two woody Emergent Groups

	<i>P</i>	Wind-dispersed Trees	Animal-dispersed Trees
Clonal propagation ^b	ns	0.5/–0.5	–0.5/0.5
Dispersal type ^b	***	0.0/7.7/0.0/–7.7/0.0	0.0/–7.7/0.0/7.7/0.0
Germination requirements ^a	**	1	2
Mean shoot height ^a	ns	7	6
Onset of flowering ^b	*	–0.5/3.5/–2.5/–0.5/0.0	0.5/–3.5/2.5/0.5/0.0
Pollination vector ^b	***	0.0/5.2/–5.2/0.0	0.0/–5.2/5.2/0.0
Seed longevity ^a	ns	0.05	0.00
Seed mass ^a	***	2	7

^a Mann–Whitney *U* test, values are medians.

^b Pearson Chi² test, values are differences between observed and expected frequencies for the different categories defined in Appendix 2.

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