

Diversity of plant assemblages in isolated depressional wetlands from Central-Western Europe

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Abstract A closed depression is defined as a geomorphologic element where a sediment depository is encircled by hillslopes. Despite the fact that closed depressions are often the only stagnant water points in many European landscapes, few ecological researches on their plant assemblages have been done. The main goal of this study was to give first results of the environmental factors responsible for the vegetation composition, richness and rarity in the closed depressions of the Lorraine biogeographical district (Belgium, France and grand-duché de Luxembourg). We surveyed for plant presence 85 forest and 77 grassland closed depressions. For each site, wetland area, local environmental factors and regional connectivities registered. For each species, the Ellenberg values were compiled. To investigate the main source of variation in species composition and in species richness (including richness in rare species), Non-metric Multidimensional Scaling analyses and Generalized Linear Models were respectively used. Species pools in forest (forest and preforest species) and in grassland (bog plants, pioneers, helophytes) were quite different. In both landscapes, a gradient from plants typical of basic high-productive soils to plants typical of acid low-productive soils reflects a shared successional gradient. The accumulation of organic matter allowed the establishment of *Sphagnum* spp., which slowly acidified the soil and thus acted as ecosystem engineers for the arrival of bog plants. Moreover, the species composition was additionally driven by the plant light tolerance in forests and by the plant water requirements in grasslands. Mechanisms of species accumulation (increase in species richness) were different in forests and in grasslands: respectively related to the plant light tolerance and to the wetland area. At the regional level, the averaged soil productivity was

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negatively related to the richness in rare species. Indeed, perennial highly-competitive plants such as *Glyceria* spp., *Iris pseudacorus* or *Urtica dioica* impeded the establishment of smaller and rarer species. At the habitat level, isolated closed depressions (due to either low connectivity or low grazing pressure) have more habitat rare species, giving evidences of dispersal limitation in plant assemblages of closed depressions.

Keywords Closed depressions · Connectivity · Fens · Forest · Grassland · Habitat area · Landscape matrix

Introduction

A geographically isolated wetland is defined as a wetland that is completely surrounded by upland (Tiner 2003). Among isolated wetlands, small closed depressions encompass all landscape elements where a sediment depository is encircled by hillslopes (Gillijns et al. 2005). The latter are eroded by rainfall waters and sediments are then trapped in the system (Norton 1986). The geomorphologic processes involved in the formation of closed depressions are still under research (Gillijns et al. 2005). Some closed depressions could 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). Moreover, anthropogenic origins may be possible in some singular cases: former small quarries, collapsing of ancient mines, bomb craters or excavated ponds. As a result, most of the so-called temperate closed depressions originate in several geomorphologic processes even if anthropogenic origins occur in some cases (Gillijns et al. 2005).

In several parts of the temperate Europe, a lot of closed depressions can be found throughout certain landscapes. Studying some closed depressions from the Lorraine biogeographical region (see Dufrière and Legendre 1991), Slotboom (1963) and Couteaux (1969) concluded that they had natural origins. Indeed, these closed depressions occur exclusively on certain geological horizons (Jurassic: Dogger and Liassic; Triassic: Keuper, Muschelkalk and Buntsandstein). In the east of the area, closed depressions are often found over gypsiferous marls. One hypothesis of their origins could therefore be the leaching out of the gypsum from the subsoil (Slotboom 1963). However, the occurrence of closed depressions is not exclusively linked with gypsiferous marls, so that the origin of the closed depressions in the west of the area must better be related to the local solution of CaCO_3 in marls from Jurassic and Triassic (Couteaux 1969). Whatever the origin, the evolution of the closed depressions seems convergent. Indeed, once formed, the clayey colluvium slowly 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 (Couteaux 1969; Slotboom 1963).

Closed depressions are often the only stagnant water points in many landscapes and their density may sometimes reach several hundreds of squares kilometer. Closed depressions are thus aquatic islands in a terrestrial landscape and can be considered, from a landscape ecological viewpoint, as a type of insular system (Cox and Moore 1993). Plant assemblages on habitat islands can be related to three ecological processes: local, regional and area factors. Of course, plant assemblages are firstly dependent on the local environment. Plant assemblages in water-filled closed depressions will certainly differ greatly from plant assemblages on peat-filled closed depressions owing to differences in successional stages. Second, species accumulation on a given closed depression is also the result of the establishment, to counterbalance random local extinction, of new species by dispersal from other closed depressions or other stagnant water points (the regional factor). However,

while dispersal of seeds by water plays a significant role in riparian community structure (e.g., Johansson et al. 1996; Nilsson et al. 2002), hydrochory does not likely occur between isolated closed depressions owing to their upland location. As a consequence, plant assemblages in closed depressions derived from seeds dispersed by wind or animals and should partly be related to the distance from propagule sources, as shown in other fragmented depressions (e.g., Bossuyt et al. 2003). Finally, the number of species in a closed depression also depends on the wetland size (Rosenzweig 1995). With increasing habitat area, both the probability of survival of a given species and the habitat heterogeneity increase. This results in a higher pool of species for which local ecological conditions are suitable.

While closed depressions are very singular ecological systems in the landscape, in Europe (in North America see the reviews of Leibowitz 2003; Leibowitz and Nadeau 2003), few ecological studies on their plant assemblages have been done to our knowledge. Moreover, how wetland plant assemblages respond to different degree of isolation has received very little attention (but see Lopez et al. 2001). And Leibowitz and Nadeau (2003) stated in their review that “one major question is the role that isolation plays in the function of geographically isolated wetlands”. The main goal of this study is thus to give first results on the determinants of the plant assemblages’ diversity (at the species composition, richness and rarity levels) in closed depressions from Central-Western Europe. To achieve this, we studied closed depressions located in two contrasting landscapes, *i.e.* forest and grassland landscapes. The following hypotheses are tested:

1. Owing to strong differences in their neighboring environment, the vegetation composition in forest and grassland closed depressions should be different (H1). In other words, we expected that the species pools colonizing the 2 depression types are significantly divergent. Indeed, aquatic and semi-aquatic plant assemblages in isolated closed depressions receive water and nutrient inputs from the surrounding landscape and are thus likely to integrate the effects of the immediate environment.
2. Next, we put forward the hypothesis that the relative importance of habitat areas, local environmental factors, and regional factors (connectivity) determining the composition of the plant assemblages will differ according to the immediate environment (H2). Especially, we expected that plant assemblages in forest closed depressions were strongly related to the regional connectivity owing to the lower seed rain under the forest canopy.
3. Finally, we hypothesized that the species richness, the number of regionally rare and habitat rare species are strongly related to the closed depression connectivity owing to dispersal limitation (H3). In other words, we expected that some rare species had a limited distribution due to their inability to disperse and establish in the most isolated wetlands.

Methods

Sampling methods

The investigated closed depressions were situated throughout the Lorraine region (Belgium, France and grand-duché de Luxembourg) in Central-Western Europe. The climate is sub-continental with an oceanic influence. The mean annual temperature is 9°C; annual rainfall ranges between 700 mm and 1000 mm. The sampling area encompasses geological layers from the Triassic (Keuper) and Jurassic periods (Sinémurien and Hettangien) characterized by sandy and calcareous rocks (mainly marls and sometimes sandstones).

Table 1 Overview of the measured environmental variables

Variables	Details
Distance from forest edge ^a	As the crow flies (m), from wetland edge to forest edge
Grazing pressure ^b	0/1/2 (Without/localized/with grazing pressure)
Connectivity	Number of closed depressions within a 1000 m radius
Wetland area	Estimated in the field (m ²)
Water conductivity	Measured in spring/summer ($\mu\text{S}\cdot\text{cm}^{-1}$)
Water permanency	0/1/2 (Without/temporary/permanent water during summer)

^a Only measured in forest landscapes

^b Only measured in grassland landscapes

Following a field visit of a group of randomly selected closed depressions, the studied ones were chosen according to two criteria: (i) no strong human management activities and (ii) no evidence of excavation. In total, 85 forest closed depressions, ranging from 15 to 3140 m², and 77 grassland closed depressions, ranging from 16 to 4000 m², were surveyed. The fieldwork was carried out between 1991 and 2003. All closed depressions were completely surveyed for plant presence at least once during the period. Plant nomenclature follows Lambinon et al. (2004).

Five environmental variables were recorded (see Table 1). Distances from the closed depression edge to the nearest forest edge were only recorded for forest closed depressions while grazing pressures only were for grassland closed depressions.

Data analyses

Prior to analysis, all continuous environmental variables were tested for normality. In the forest dataset, the wetland area, the water conductivity and the distance from forest edge were log-transformed while the closed depression connectivity was squared-root transformed to meet normality assumptions. In the grassland dataset, the wetland area was log-transformed while the water conductivity was squared-root transformed.

First, we wanted to test the hypothesis of strong differences in plant composition and richness between forest and grassland closed depressions (H1). Because studies of isolated wetlands using ecological groups have provided successful results (Lopez et al. 2001), data were first split in 7 sub-datasets according to the ecological groups defined for the Belgian flora by Stieperaere and Franssen (1982): Bog plants, Forest edge plants, Forest plants, Grassland plants, Helophytes (freshwater plants with perennating tissue in soil beneath the water), Hydrophytes (aquatic plants) and Pioneers (Table 2). To test for differences in ecological group composition, Multi-Response Permutation Procedures (MRPP see Mielke et al. 1976) were used. MRPP has the advantage of not requiring multivariate normality and homogeneity of variances. To test for differences in ecological group richness between forest and grassland closed depressions, the Mann Whitney *U*-test was used. Next, the method proposed by Dufrêne and Legendre (1997) was used to detect the association of a species with a given landscape (forest or grassland). The statistical significance of the association is evaluated using a randomization procedure performed with 99,999 permutations. Analyses were performed using the computer program package Pc-ORD (McCune and Mefford 1999).

To investigate the main ecological gradients within the forest and grassland datasets (H2), two Non-metric Multidimensional Scaling (NMS) were performed, one each for

Table 2 Commonest species by ecological groups: their Ellenberg values, their relative frequencies in grassland (G) and in forest (F) closed depressions, their regional rarities and their indicator values

	Ellenberg values ^a				Relative frequencies (%)		Regional rarities ^c	Indicator value ^d
	L	F	R	N	G ^b	F ^b		
Bog plants								
<i>Galium palustre</i>	6	9		4	77	24	C	G ***
<i>Ranunculus flammula</i>	7	9	3	2	36	4	R	G***
<i>Carex canescens</i>	7	9	4	2	5	26	RRR	F**
<i>Carex nigra</i>	8	8	3	2	26	4	C	G**
<i>Veronica scutellata</i>	8	9	3	3	27	1	RR	G***
<i>Epilobium palustre</i>	7	9	3	2	17	4	RR	G**
<i>Carex rostrata</i>	9	10	3	3	16	1	C	G**
<i>Juncus acutiflorus</i>	9	8	5	3	14	1	R	G**
<i>Stellaria palustris</i>	5	9	4	2	10	1	RRR	G*
<i>Sphagnum spp.</i>					1	10	C	
Forest edge plants								
<i>Urtica dioica</i>		6	7	9	19	16	C	
<i>Galium aparine</i>	7		6	8	10	1	C	G*
<i>Prunus spinosa</i>	7	4	7		9	2	C	
Forest plants								
<i>Carex remota</i>	3	8			0	51	C	F***
<i>Dryopteris carthusiana</i>	5		4	3	0	45	C	F***
<i>Circaea lutetiana</i>	4	6	7	7	0	34	C	F***
<i>Carex elongata</i>	4	9	7	6	1	27	RR	F***
<i>Salix cinerea</i>	7	9	5	4	8	19	C	
<i>Salix aurita</i>	7	8	4	3	21	4	R	G**
<i>Athyrium filix-femina</i>	3	7		6	0	24	C	F***
<i>Alnus glutinosa</i>	5	9	6		0	22	C	F***
<i>Fraxinus excelsior</i>	4		7	7	1	16	C	F**
<i>Viburnum opulus</i>	6		7	6	0	13	C	F***
<i>Salix caprea</i>	7	6	7	7	5	6	C	
Grassland plants								
<i>Carex disticha</i>	8				47	2	C	G***
<i>Filipendula ulmaria</i>	7	8		5	25	16	C	
<i>Lysimachia vulgaris</i>	6	8			13	21	C	
<i>Myosotis scorpioides</i>	7	8		5	27	2	C	G***
<i>Scirpus sylvaticus</i>	6	8	4	4	14	13	C	
<i>Lychnis flos-cuculi</i>		7			25	0	C	G***
<i>Cardamine pratensis</i>	4	6			22	2	C	G**
<i>Cirsium palustre</i>	7	8	4	3	16	6	C	
<i>Alopecurus pratensis</i>	6	6	6	7	21	0	C	G***
<i>Valeriana repens</i>	7	8	6	6	9	9	C	
<i>Holcus lanatus</i>	7	6		5	16	0	C	G***
<i>Lathyrus pratensis</i>	7	6	7	6	16	0	C	G***
<i>Caltha palustris</i>	7	9		6	9	4	C	
Helophytes								
<i>Glyceria fluitans</i>	7	9		7	66	66	C	
<i>Carex vesicaria</i>	7	9	6	5	58	22	RR	G***
<i>Alisma plantago-aquatica</i>	7	10		8	53	7	C	G***
<i>Iris pseudoacorus</i>	7	9		7	29	24	C	
<i>Eleocharis palustris</i>	8	10			45	2	C	G***
<i>Solanum dulcamara</i>	7	8		8	16	31	C	F*
<i>Sparganium erectum</i>	7	10	7	7	27	0	C	G***
<i>Lythrum salicaria</i>	7	8	6		17	9	C	
<i>Epilobium hirsutum</i>	7	8	8	8	19	5	C	G**

Table 2 continued

	Ellenberg values ^a				Relative frequencies (%)		Regional rarities ^c	Indicator value ^d
	L	F	R	N	G ^b	F ^b		
<i>Typha latifolia</i>	8	10	7	8	19	4	C	G**
<i>Sparganium emersum</i>	7	10	6	7	8	12	RR	
<i>Scutellaria galericulata</i>	7	9	7	6	1	16	C	F**
<i>Lycopus europaeus</i>	7	9	7	7	14	2	C	G**
<i>Carex acuta</i>	7	9	6	4	10	5	R	
<i>Oenanthe aquatica</i>	7	10	7	6	12	2	RR	G*
<i>Angelica sylvestris</i>	7	8		4	10	1	C	G*
Hydrophytes								
<i>Lemna minor</i>	7	11		6	48	54	C	
<i>Ranunculus peltatus</i>	6	12	5	6	21	0	C	G***
<i>Potamogeton natans</i>	6	11	7	5	14	5	C	
<i>Lemna trisulca</i>	7	12	7	5	12	0	RR	G**
Pioneers								
<i>Juncus effusus</i>	8	7	3	4	83	44	C	G***
<i>Ranunculus repens</i>	6	7		7	69	28	C	G***
<i>Juncus inflexus</i>	8	7	8	4	53	0	C	G***
<i>Potentilla anserina</i>	7	6		7	36	0	C	G***
<i>Lysimachia nummularia</i>	4	6			30	5	C	G***
<i>Deschampsia cespitosa</i>	6	7		3	3	31	C	F**
<i>Carex hirta</i>	7	6		5	32	0	C	G***
<i>Poa trivialis</i>	6	7		7	22	4	C	G***
<i>Alopecurus geniculatus</i>	9	8	7	7	26	0	C	G***
<i>Rumex crispus</i>	7	7		6	22	0	C	G***
<i>Myosotis laxa</i>	7	9	4	7	19	0	R	G***
<i>Equisetum palustre</i>	7	8		3	14	2	C	G**
<i>Rumex obtusifolius</i>	7	6		9	5	8	C	
<i>Trifolium repens</i>	8	5	6	6	13	0	C	G***
<i>Carex cuprina</i>	6	8	7	6	5	7	C	

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

^a Ellenberg values for L (from low to high light incidences, from 1 to 9), F (from low to high water availability, from 1 to 12), R (from acid to basic pH, from 1 to 9) and N (from low to high soil productivity, from 1 to 9)

^b Percentage of closed depressions in which the plant was found in forests (F) and in grasslands (G)

^c Index of regional rarity (C: common, R: rather rare, RR: rare, RRR: very rare) according to Lambinon et al. (2004)

^d Indicator values calculated with method of Dufrière and Legendre (1997). Letters G or F refer, respectively, to a greater frequency in Grassland or Forest closed depressions

forest and grassland settings. NMS is a direct gradient analysis that is well suited for data that are non-normal (McCune and Mefford 1999). First, the number of axes to investigate was determined following a Monte Carlo test of significance. Then, simultaneous plotting of closed depressions and species in the ordination space was performed. Next, relationships between the scores of the closed depressions and the field-measured environmental variables were investigated using Spearman rank correlations. In the same way, relationships between the species scores and the Ellenberg values were searched (see for example Bennie et al. 2006). What are the Ellenberg values? Ellenberg et al. (1992) attributed scores, along an arbitrary scale, to European plants according to their light, soil pH, soil nitrogen and water requirements. These values are now recognized as highly reliable to replace field measurements (Diekmann 2003). However, the nitrogen Ellenberg value

should be better interpreted as a general measure of soil productivity rather than of the strict nitrogen availability (Hill and Carey 1997). Finally, the mean position of each ecological group on each axis was calculated.

Next, the aim was to determine the influence of the environmental variables and of the Ellenberg values on the species richness and on the richness in rare species (H3). For each closed depression, four synthetic Ellenberg values (light, nitrogen, pH and water) were calculated averaging the values for all present species (see for instance Hérault and Honnay 2005, 2007; Hérault et al. 2005). Two rarity indexes were distinguished. Firstly, the species which were regionally classified as rather rare, rare and very rare for the Lorraine biogeographical area in Lambinon et al. (2004) received respectively a coefficient of 1, 2 and 3. Coefficients were added up for each closed depression, giving us a regionally rarity index (species rare at the regional level, see Table 2). Secondly, species recorded in less than 5% in one dataset (either the forest or the grassland one) were counted in order to provide a habitat rarity index (species rare at the habitat level). The variations in species richness and in rarity indexes were analyzed by means of Generalized Linear Models using environmental variables and averaged Ellenberg values as input variables. Logarithmic link functions and Poisson distribution of errors were used as the response variables were discrete (species counts or rarity indexes). The stepwise procedure (forward selection and backward elimination alternately) was applied to select the significant explanatory variables (Legendre and Legendre 1998).

Results

Based on the results of the Multi-Response Permutation Procedures (Table 3), we clearly rejected the null hypothesis of no differences in ecological group composition between the forest and the grassland closed depressions. The Mann Whitney U tests revealed no differences in species richness for the Forest edge plants and for the Hydrophytes. In forest closed depressions, the forest plants were more abundant while in grassland closed depressions, bog plants, grassland plants, helophytes and pioneers were favored (see Tables 2 and 3).

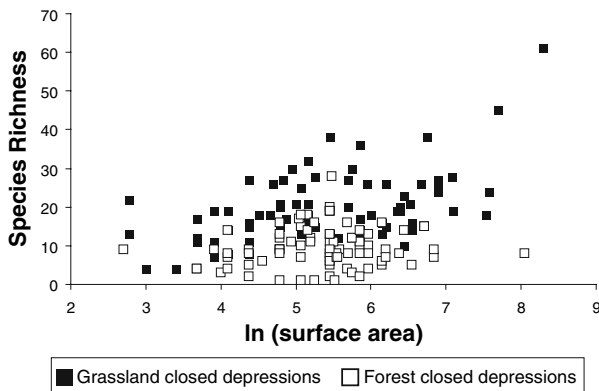


Fig. 1 Relationships between species richness and wetland areas within forest and grassland landscapes

Table 3 Comparison of the ecological group composition and richness between the forest and the grassland closed depressions

	Species composition MRPP		Species richness Mann Whitney <i>U</i> -test		
	A	<i>P</i>	Forest (median)	Grassland (median)	<i>P</i>
Bog plants	0.13	***	0	2	***
Forest plants	0.06	***	3	0	***
Forest edge plants	0.10	***	0	0	ns
Grassland plants	0.09	***	0	3	***
Helophytes	0.05	***	2	5	***
Hydrophytes	0.10	***	1	1	ns
Pioneers	0.09	***	1	5	***

MRPP: Multi response Permutation Procedures

A = 1 – (observed delta/expected delta)

Observed delta = the average within-group (forest or grassland) distance

Expected delta = the mean delta for all possible partitions of datas

A max = 1 when all species are identical within closed depression groups

A = 0 when heterogeneity within groups of closed depressions equals expectation by chance

ns non significant, ****P* < 0.001

Forest closed depressions

The species richness in forest closed depressions varied from 1 to 28 with a median of 9 species (Fig. 1).

The 1st and 2nd axes of the forest NMS were significant (*P* < 0.05). The first axis revealed a gradient from closed depressions characterized by high water permanency to closed depressions with low water permanency. On this axis, plant assemblages were distributed from species having high soil pH/productivity Ellenberg values to species having low soil pH/productivity Ellenberg values (Table 4). The latter consisted of bog plants (Table 5) such as *Sphagnum* spp., *Carex canescens* and *Galium palustre* (Table 2). On the second axis of variation, plant distribution was highly related to their light Ellenberg values (Table 4). This axis clearly separated hydrophytes (e.g. *Lemna* spp.), helophytes (e.g., *Glyceria* spp.), grassland (e.g., *Filipendula ulmaria* and *Lysimachia vulgaris*) and bog plants from the forest and forest edge species (e.g., *Carex remota*, *Dryopteris carthusiana*, see Table 5 and 2).

The averaged light Ellenberg value was a recurrent predictor sorted out by the stepwise selection procedure of the GLM models. The species richness, the habitat rarity index and the regional rarity index (Table 6) increased with the degree of light availability. The water permanency led to an increase in species richness and in the presence of species rare at the habitat level whereas the averaged plant water requirement decreased the species richness and the habitat rarity index. The averaged soil productivity decreased the presence of rare species at both the habitat and regional levels. And the greater the connectivity between closed depressions was, the less likely to find species rare at the habitat level.

Grassland closed depressions

The species richness in grassland closed depressions varied from 4 to 61 with a median of 18 species (Fig. 1).

Table 4 Ecological significance of the axes of the Non-metric Multidimensional Scaling Analyses performed on the vegetation data from forest and grassland closed depressions

	Forest closed depressions				Grassland closed depressions			
	Axis 1		Axis 2		Axis 1		Axis 2	
	R	P	R	P	R	P	R	P
Measured environmental variables ^a								
Distance from forest edge			-0.21	*				
Connectivity					0.36	**		
Wetland area			-0.22	*	0.35	**		
Water permanency	-0.45	***						
Ellenberg values ^b								
Light incidence			0.39	***				
Soil pH	-0.24	*			-0.21	*		
Soil productivity	-0.29	**			-0.21	**	0.16	*
Water availability			0.32	**	0.19	*	0.31	***

^a Spearman rank correlations (R) between the site coordinates and the site environmental variables

^b Spearman rank correlations (R) between the species coordinates and the species Ellenberg values

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

Table 5 Mean positions of the ecological groups on the axes of the Non-metric Multidimensional Scaling Analyses performed on the vegetation data from forest and grassland closed depressions

	Forest closed depressions		Grassland closed depressions	
	Axis 1	Axis 2	Axis 1	Axis 2
Bog plants	0.43 ± 0.10	0.35 ± 0.11	0.23 ± 0.07	-0.16 ± 0.05
Forest edge plants	-0.01 ± 0.12	-0.03 ± 0.12	-0.16 ± 0.07	-0.07 ± 0.06
Forest plants	0.07 ± 0.06	-0.08 ± 0.07	-0.09 ± 0.07	0.09 ± 0.07
Grassland plants	0.03 ± 0.11	0.30 ± 0.11	0.17 ± 0.04	-0.14 ± 0.04
Helophytes	0.01 ± 0.08	0.39 ± 0.08	0.11 ± 0.04	0.06 ± 0.04
Hydrophytes	-0.25 ± 0.17	0.31 ± 0.17	0.08 ± 0.07	0.10 ± 0.07
Pioneers	-0.09 ± 0.13	0.12 ± 0.14	0.09 ± 0.04	-0.05 ± 0.04

The 1st and 2nd axes of the grassland NMS were highly significant ($P < 0.01$). The first axis revealed a gradient from small highly-isolated closed depressions to large weakly-isolated closed depressions. On this axis, plant assemblages were distributed from species having high soil pH/productivity Ellenberg values to species having low soil pH/productivity Ellenberg values (Table 4). The latter consisted of Bog plants such as *Cirsium palustre*, *Menyanthes trifoliata* and *Dactylorhiza majalis*. On the second axis, plant distribution was highly related to their water Ellenberg values (see Table 4). The most characteristic species from closed depression with high water availabilities were hydrophytes such as *Lemna* spp., *Potamogeton* spp. and *Callitriche* spp. (Table 5 and Table 2). On the other hand, low water availabilities strongly favored the development of species from grasslands (e.g., *Carex disticha*) and bogs (e.g., *Galium palustre*, *Ranunculus flammula*, see Table 2).

The wetland area was by far the main predictor sorted out by the GLM stepwise selection procedure, as wetland area always ranked first with high Wald statistics (Table 7). Increasing areas therefore increased species richness (see Fig. 1), habitat rarity index as well as regional rarity index. The averaged water availability was another strong predictor.

Table 6 Influence of environmental variables on the species richness, on the habitat rarity index and on the regional rarity index in forest closed depressions (Generalized Linear Models with Logarithmic link function and Poisson distribution of errors)

	Wald statistic ^a	<i>P</i>	Regression coefficient
Species richness			
Water permanency	11.64	***	0.61
Averaged water availability	7.83	**	−1.41
Averaged light incidence	4.61	*	0.78
Habitat rarity index ^b			
Connectivity	60.15	***	−2.49
Averaged light incidence	19.99	***	3.08
Averaged water availability	13.70	***	−3.24
Averaged soil productivity	9.78	**	−2.83
Water permanency	4.24	*	0.82
Regional rarity index ^c			
Averaged soil productivity	12.79	***	−1.53
Averaged light incidence	8.02	**	1.09

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

^a The Wald statistic is a test of significance of the regression coefficient; it is based on the asymptotic normality property of maximum likelihood estimates

^b Number of species having a frequency $< 5\%$ in the dataset

^c Index based on the number of species classified as rather rare, rare and very rare in Lambinon et al. (2004)

Table 7 Influence of environmental variables on the species richness, on the habitat rarity index and on the regional rarity index in grassland closed depressions (Generalized Linear Models with Logarithmic link function and Poisson distribution of errors)

	Wald statistic ^a	<i>P</i>	Regression coefficient
Species richness			
Wetland area	57.83	***	1.39
Averaged soil productivity	15.99	***	−0.88
Habitat rarity index ^b			
Wetland area	42.62	***	2.52
Grazing pressure	12.09	***	−0.94
Averaged water availability	6.67	**	−1.03
Regional rarity index ^c			
Wetland area	71.31	***	2.27
Averaged soil productivity	26.86	***	−2.01
Averaged water availability	9.14	**	0.98

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

^a The Wald statistic is a test of significance of the regression coefficient; it is based on the asymptotic normality property of maximum likelihood estimates

^b Number of species having a frequency $< 5\%$ in the dataset

^c Index based on the number of species classified as rather rare, rare and very rare in Lambinon et al. (2004)

However, when habitat rarity indexes were negatively related to the averaged water availability, regional rarity index was positively. The averaged soil productivity was another good predictor since it was negatively related with both the species richness and the regional rarity index. Increasing the grazing pressure decreased the habitat rarity index.

Discussion

Although forest and grassland closed depressions derived from similar geomorphological processes, floristic composition of their plant assemblages differed greatly (Table 3). One could expect that these differences result from changes in relative abundance of the same pool of species. However, the MRPP procedure (based on species composition and not on relative abundance) clearly led us to reject this hypothesis. In other words, the species pools in forest and in grassland closed depressions were quite different. This validates H1. For example, in forest closed depressions, one of the most frequent (51%) plants was the herbaceous *Carex remota*. In grassland closed depressions, the latter was not observed in any site (Table 2). One common grassland closed depression species, *Carex disticha*, was only recorded in 2 out of 85 forest closed depressions, while it was observed in 47% of the grassland closed depressions (Table 2). The ecological group richness also differed (Table 3). Forest plant richness was obviously highest in forest closed depression. On the other hand, bog plants, grassland plants, helophytes and pioneers are typical ecological groups associated with open habitats. The low levels of light in forest closed depressions seem thus the main cause of their discrepancy in forests.

Vegetation composition

The first axes of the two Non-metric Multidimensional Scaling (NMS) analyses highlighted an environmental gradient shared between forest and grassland closed depressions: from closed depressions having plant assemblages with high soil pH and nitrogen Ellenberg values to closed depressions having plant assemblages with low pH and nitrogen Ellenberg values (Table 5). This invalidates H2. This gradient was not related to differences in the underlying geological layers because the investigated closed depressions were randomly located on similar geological layers, i.e., mainly marls from Keuper and Sinémurien. This gradient should better reflect a successional gradient, as it was suggested earlier by local ecologists (Coureaux 1969; Overall 1997; Slotboom 1963) and as the negative correlation between water permanency and the first forest axis could indicate (Table 4). Indeed, once the water percolation stopped due to the plugging by clay elements (high water permanency), organic matter from the surroundings started to accumulate up to the water surface level. Once the accumulation of organic matter reached the water surface (low water permanency), plants adapted to marsh environments like *Sphagnum* spp. arrived and slowly acidified the closed depressions (Klinger 1996) that, in turn, strongly favored species from peat bog habitats (Table 5). The arrival of *Sphagnum* species thus contributed to change the abiotic conditions allowing bog plants to establish in the system. In other words, the *Sphagnum* species acted as ecosystem engineers (Frankl and Schmeidl 2000). This suggests some important facilitation processes during plant succession in closed depressions (Bruno et al. 2002). However, the axis 1 was also correlated with the connectivity and wetland area in grassland closed depressions (Table 4). Plants from peat bogs (e.g., *Carex rostrata* or *Stellaria palustris*, see Table 2) thus appear colonization-limited. In other words, bog plants hardly colonized small and isolated grassland closed depressions: either bog plants are dispersal-limited (i.e., they cannot reach very isolated depressions) or they are establishment-limited (i.e., there is a critical surface for a viable population). Seed sowing studies (Turnbull et al. 2000) should elucidate this question.

The second axis of the forest NMS clearly put forward a light gradient, from closed depressions located near the forest edge to those located deeper inside the forest (Table 4). Unsurprisingly, helophytes such as *Glyceria fluitans* or *Iris pseudoacorus* dominated the

former location as these species require full light for optimal development (Wetzel and van der Valk 1998). Therefore, reducing the light availability lowered the frequency of these highly competitive helophytes. Typical forest species (e.g., *Carex remota*), which are often smaller than Helophytes, took advantage of this lower competition (Table 5). The second axis of the grassland NMS separated plants according to their water Ellenberg values (Table 4). Unsurprisingly, water availability has a considerable influence on the community composition since deep waters allowed the establishment of hydrophytes species (Table 5), mainly *Lemna minor* (Table 2), which had full light in grasslands for a rapid growing.

Species richness and rarity indexes

First, the averaged light Ellenberg value was recurrently sorted out by the forest GLM models (Table 6). Indeed, some sites were so covered by the forest canopy that just a few shade-tolerant species (i.e., *Athyrium filix-femina*) had been able to grow. Moreover, not many shade-tolerant species (forest or forest edge species) were regionally rare (Table 2). Therefore, increasing the light incidence boosted the number of species that in turn increased the number of rare shade-intolerant species both at the habitat and at the regional level (Table 6).

Next, the water permanency strongly increased the species richness in forests (Table 6). The presence of permanent water allowed the establishment of floating hydrophytes (which died if the water was not permanent) such as *Lemna* spp. or *Potamogeton natans*. However, the averaged Ellenberg value of water availability was negatively related both to the species richness and to the habitat rarity index not only in forest but also in grassland closed depressions (Table 6 and 7). This looks contradictory but high water availabilities reflected young closed depressions with high depths of water and with steep slopes (commonly up to 45°). Therefore, the vegetation zonation (Blom and Voeselek 1996), which is source of plant diversity (van der Valk and Pederson 2003), is less detectable in these young closed depressions than in older depressions where the slopes were often gentle (commonly less than 20°). This led to the simplification of the concentric rings of plant communities that, in turn, strongly decreased the species richness in forest closed depressions (Table 6) and the habitat rarity index in all closed depressions (Table 6 and 7).

On the whole, the averaged Ellenberg value of soil productivity was negatively related to the two rarity indexes and to the species richness in forests or in grasslands (Table 6 and 7). On highly productive soils, perennial highly-competitive plants such as *Glyceria* spp., *Iris pseudoacorus* or *Urtica dioica* dominated the plant assemblages so that the establishment of smaller and rarer species was impeded. Therefore, human eutrophication (e.g. fertilization of adjacent grasslands) threatens the integrity of the remaining closed depressions, especially those having evolved in fens, because low availability of nutrients controls some of their distinctive characteristics (Bedford and Godwin 2003), in turn involved in the presence of rare species (Table 7).

The wetland area was by far the main predictor of richness and rarity in grassland closed depressions (Table 7). For example, for a 300 m² closed depression the habitat index averaged 10 and the regional index averaged 6 while for a 3000 m² closed depressions the habitat index averaged 22 and the regional index averaged 12. This relation was not observed in forest closed depressions (despite similar range of wetland areas, see Fig. 1) because light was the first limiting factor (Table 6). Light was not limiting in grassland (Table 7) so that a typical species-area relationship was highlighted (Rosenzweig 1995). In a nutshell, mechanisms of species accumulation were very different in the two kinds of closed

depressions: mainly dependent from the light availability in forest closed depressions (Table 6) while plant diversity of grassland closed depressions was area-dependent (Table 7).

Finally, the regional factor (number of closed depressions within a 1000 m radius) had no influence on the species richness (Table 6 and 7). This invalidates H3 and confirms the results of Lopez et al. (2001) who found that the species richness was poorly related to regional variables. However, the grazing pressure was negatively related to the habitat rarity index; i.e., grazed sites had less habitat-rare species than ungrazed sites. This suggests a homogenizing effect of grazing. Indeed, diaspores (fruits, seeds and spores) from many species could disperse from one closed depression to another via cows as either exo-dispersal (by seeds attaching to the animal's coat, Couvreur et al. 2004) or endo-dispersal vectors (by seeds passing through the animal's digestive system, Cosyns et al. 2005). Next, the negative correlation between the forest closed depression connectivity and the habitat rarity index is very interesting (Table 6). The underlying ecological mechanism is certainly the effect of isolation on the colonization process. The more a closed depression is isolated, the more likely its chance of being colonized by singular plant assemblages and in turn, the more the habitat diversity index will increase. In other words, in forested landscapes where closed depressions be isolated from each other, the plant assemblages are likely to be less similar (owing to divergent successions) than where closed depressions are in close proximity (Nekola and White 1999). This support the hypothesis that the predictability of local species composition from environmental conditions is partly influenced by dispersal-limitation in many terrestrial systems (Ozinga et al. 2005).

Conclusions

First, the inferences made in the discussion remain hypothetical and we recommend that further experimental studies are carried out for a better understanding of the ecological processes at work within isolated closed depressions. But, this study has demonstrated that the vegetation composition in isolated closed depressions is strongly influenced by the surrounding landscapes, i.e., forests or grasslands. This emphasizes the importance of the landscape matrix on the plant assemblages colonizing fragmented habitats (Kupfer et al. 2006). Indeed, the species richness, habitat and regional rarity indexes were light-limited in the former while they were area-limited in the latter. On the other hand, both types of closed depressions shared similar ecological processes. Indeed, some of the ecological mechanisms at work (e.g., accumulation of organic mater, colonization by *Sphagnum* spp., facilitation processes for bog plant establishment) in the two landscapes tend to be similar. Therefore, shared as well as landscape-influenced ecological processes should be taken into account by nature managers when they build their conservation plans at the landscape level.

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