Relative importance of isolation, area and habitat heterogeneity for vascular plant species richness of temporary wetlands in east-German farmland

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The purpose of this investigation was to explore the determinants of vascular plant species richness for temporary, isolated wetland habitats which are influenced by hydrologic gradients and characterized by variation in habitat area. The dependent variables, total plant species richness and the number of obligate wetland species were analyzed consecutively. In regression analyses habitat area explained between 11 and 15% of the variation in the dependent variables. Habitat area was correlated with the heterogeneity of the hydroperiods between the upper and lower parts of the hydrologic gradients. In multivariate regression analyses, habitat heterogeneity accounted for 70–77% of the variation in the dependent variables, and habitat area did not have a significant impact. The results are most consistent with the habitat heterogeneity hypothesis. I therefore concluded that area is a surrogate variable for habitat heterogeneity which directly enhances vascular plant species diversity. There was no significant impact of isolation on species richness. The data suggest that the expanses of agricultural fields are not an effective barrier to the dispersal of the studied plant species. Only 10 of 52 wetland species were negatively influenced by isolation. This group of species did not differ from the other wetland species with respect to dispersal strategies and longevity of seed banks. However, the longevity of the seed banks was generally high, and there was a dominance of species whose propagules are transported with the soil clinging to the feet of birds. The results are discussed in the context of accurate dispersal strategies and remnant populations, which may counteract the effects of isolation.

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The species-area relationship is one of the most widespread generalizations in ecology (reviews in Connor and McCoy 1979, Rosenzweig 1995, Holt et al. 1999). This relationship has been tested in three types of studies (Rosenzweig 1995, Holt et al. 1999). The present study will focus on Type 2 relationships of total species richness and total area of island habitats which differ in size. The theory of island biogeography, which originally focused on true islands, predicts that the number of species on islands increases with island size and decreases with the degree of isolation (MacArthur and Wilson 1967). Subsequently, the theory has been successfully applied to many types of island-like habitats on the mainland (Møller and Rørdam 1985, Dzwonko and Loster 1989, Ouborg 1993).

Three explanations have been proposed for species-area relationships (Connor and McCoy 1979): colonization-extinction dynamics, habitat heterogeneity and passive sampling. In the dynamic equilibrium hypothesis, species richness depends on a balance between colonization and extinction (MacArthur and Wilson 1967). Colonization rates decrease with increasing isola-

tion and larger islands have lower extinction rates than smaller islands which typically have smaller populations more vulnerable to extinction as a result of stochastic events (area per se effect). The habitat heterogeneity hypothesis holds that habitat area is a surrogate variable of habitat heterogeneity, which directly influences species richness; a larger area typically corresponds to a wide range of habitats and their characteristic species (Williams 1964, Connor and McCoy 1979, Williamson 1981). Connor and McCoy (1979) suggested that the species-area relationship is largely a result of passive sampling. Larger islands may contain more individuals which are likely to belong to more species. The relative importance of these explanations for species-area relationships is still subject of considerable debate (Holt et al. 1999).

Subsequent studies have had varying results: while some outlined the importance of area per se (Simberloff 1976, Abbott 1978, Nilsson et al. 1988), others identified impacts of habitat heterogeneity (Reed 1981, Tangney et al. 1990, Kohn and Walsh 1994, Welter-Schultes and Williams 1999). Most of the studies were carried out on true islands (see above) or forest fragments (Ambuel and Temple 1983, Freemark and Merriam 1986), and it remains unclear the extent to which their conclusions are transferable to other habitat islands. However, in agricultural landscapes many habitats which may include potholes, temporary wetlands or small fallow sites, have characteristics similar to islands due to their isolated location in cultivated farmland.

For wetlands, Keddy (1991) emphasized that flooding creates strong gradients in resource availability. These hydrologic gradients result in different hydroperiods at lower and higher ends which may affect abiotic soil conditions; the germination abilities of plants and biotic interactions, especially competition, among species (Austin 1990, Coops and Van der Velde 1995, Lenssen et al. 1999). The heterogeneity of the hydroperiods is generally considered to be one of the most important variables influencing species richness along flooding gradients (Vivian-Smith 1997, Pollock et al. 1998).

According to the dynamic equilibrium hypothesis, the isolation of habitat islands plays a crucial role in the process of colonization (MacArthur and Wilson 1967). While the impact of isolation on species richness has been included in many species-area studies, the tested parameters of isolation usually explain only a minor percentage of the total variation. However, it was shown that isolation influences immigration rates of individual species and gene flows between populations, which may cause genetic erosion in isolated populations (Brown and Kodric-Brown 1977, Frankel and Soulé 1981). Accordingly, isolation might cause species-specific responses which have been explained by differences in dispersal abilities and longevity of seed banks

(Williamson 1981, Hermanutz et al. 1989, Primack and Miao 1992, Eriksson 1996).

The temporary wetlands in the eastern German agricultural landscape are influenced by hydrologic gradients and characterized by variation in area and isolation typical of island habitats. In this study, the extent to which vascular plant species richness of these habitats depends on habitat area, degree of isolation and heterogeneity of the hydroperiods is investigated. The hypothesis of passive sampling is considered as a null model as suggested by Connor and McCoy (1979). The correlations are tested separately for total species richness and for species richness of obligate wetland species. Furthermore, the impact of isolation will be tested for the individual wetland species. In particular, I will examine, if differences in the species response to isolation follow from distinctions in dispersal strategies or the longevity of seed banks.

Materials and methods

Location and description of the study sites

The study was carried out in the agricultural landscape of north-eastern Germany (between 53°22′N, 13°34′E and 52°22′N, 14°15′E). This younger Pleistocene landscape contains numerous types of potholes and temporary wetlands. These temporary wetlands are cultivated and typically produce crops in the driest years. During years of average or above-average precipitation, temporary wetlands retain water until spring or summer. While the highest elevated edges of the sites dry out in March, the lowest parts are inundated for the maximum extent of the hydroperiod, which depends on the substratum, the microtopography of the sites, the watershed area and the annual precipitation (Schmidt 1996). Therefore, wetlands in deeper hollows dry up slower than wetlands on more level surfaces. Infiltration is enhanced for sandy soils in comparison to loamy soils.

According to Klafs et al. (1973) temporary wetlands were continually distributed across north Germany. Because these wetlands seriously reduce the agricultural crop yield, in many cases they were drained, and consequently, wetlands disappeared from many, predominantly west Germany, landscapes. Different land use systems in east Germany meant that this practice occurred on some highly productive agricultural areas, while in other regions, e.g. the study sites, the present abundance of temporary wetlands still accurately reflects the historical distribution.

The selection of study sites was done by means of aerial photographs and field visits. They were grouped into eight study areas within the above-mentioned region. All study sites were inundated in March 1998 and 1999, but they showed substantial variation in their

maximum hydroperiod. Some of the 1998 wetlands disappeared in 1999 due to intensified amelioration of the farmland. Other new temporary wetlands emerged in 1999. Wetlands which did not appear in both years were excluded from the investigation leaving a total of 58 sampling sites.

Sampling design and estimation of parameters

The vegetation data were obtained in the course of a systematic transect search covering all sections of the hydrologic gradients for each temporary wetland. The data were compiled five times per year: once a month from March to July in 1998 and 1999. Transect searches were performed on each study site until no additional vascular plant species were found. Therefore, the more diverse sites were investigated more intensively until the collector's curve indicated saturation. Site species richness was estimated by combining the results of the transect searches.

Vascular plant species were separated according to habitat preference into non wetland and wetland species, with the latter indicated by "F-values" between 7 and 12 (Ellenberg et al. 1992). Furthermore, the wetland species were classified with respect to their dispersal strategies. The classification was based on Grime et al. (1988); species not mentioned were included according to Frank and Klotz (1990). The classes of anemochorous, endo-, epizoochorous, water-dispersed and unspecialized species were differentiated. A new class was introduced for the wetland species which propagules are transported in the mud clinging to the feet of waterbirds (Bonn and Poschlod 1998). This strategy will hereafter be referred to as "bird dispersal". Most of these species were previously classified as dispersed by water, which is very unlikely for species inhabiting small wetland islands not connected by riverine systems.

The database of Thompson et al. (1997) summarizes soil seed bank studies. They classified the longevity of seeds for individual species into three categories: transient (<1 yr), short-term persistent (1–4 yr) and long-term persistent (>4 yr). Most of the species were recorded in several categories. In the present study, I

calculated a longevity index of the seed banks for each of the wetland species according to a method of Bekker et al. (1998), which expresses the proportion of persistent (short-term and long-term persistent) records for the species seed banks. The longevity index varies between 0 (no persistent seed banks recorded) and 1 (all seed banks were recorded as persistent). The appendix provides a list of the vascular plant species of the temporary wetlands and their classification. Nomenclature follows Rothmaler (1994).

The area of the sites was measured in the middle of March. The water edge at this time was used as a boundary of the biotopes towards the rest of the field. For each temporary wetland, the maximum hydroperiod was recorded as the month when it completely dried out. The minimum hydroperiod was defined as the middle of March. The heterogeneity of the hydroperiod was coded as the number of months between the maximum and the minimum hydroperiod. The heterogeneity of the hydroperiod will hereafter be referred to as habitat heterogeneity.

I included nine indices of isolation in the study, which were determined from digitalized 1:10000 maps in ArcView GIS 3.0 (Table 1). I calculated the distance to the next pothole (distpot) and to the next temporary wetland (disttemp) because wetland species inhabit both habitat types. Accordingly, apart from the habitat specialists, there are species occurring in potholes as well as in temporary wetlands. For these species, both distance measures partially define the isolation of the habitats. The temporary wetlands, which included the most diverse community of vascular plant species in each of the eight study areas, were defined as the source communities. The distance from each temporary wetland to this source community was included as an index of isolation (distsource). According to Ouborg (1993), distance measures provide only a part of the information about the isolation of habitats. Some of the isolation effects are altered by the density of the habitats, which are important for metapopulation structures. Therefore, I included four density measures of the temporary wetlands in the study (see Table 1). The combined group of the distance and the density measures will subsequently be called indices of isolation.

Table 1. Indices of isolation and their description. SD = standard deviation.

Indices	Description	Mean ± SD	Range
disttemp	distance to the next temporary wetland	149 ± 223	15 m/1200 m
distpot	distance to the next pothole	109 ± 111	5 m/370 m
distwet	distance to next wetland (temporary wetland or pothole)	65 ± 79	5 m/300 m
distsource	distance to the source community	956 ± 1631	0 m/5400 m
distfield	distance to the edge of the field	119 ± 100	5 m/400 m
density 1	density of temporary wetlands within 1 km^2	5 ± 2	0/9
density 2	density of temporary wetlands within 1.5 km^2	6 ± 3	0/18
density 3	density of temporary wetlands within 2 km^2	8 ± 4	0/23
density 4	density of temporary wetlands within 5 km^2	12 ± 7	1/25

Data analysis

All variables were checked for normality and linearity. The variables site area, disttemp, distsource, distpot, and distwet (see Table 1) required natural logarithmic transformation to meet these assumptions. The internal correlation structure of the independent variables was checked with Pearson's product-moment correlation. This analysis was performed to determine, first, if site area and habitat heterogeneity were correlated, and secondly, if the indices of isolation were independent.

I entered the correlated indices of isolation in a PCA with a varimax rotation (Hair et al. 1995). Principal components (PC) with an eigenvalue bigger than one were extracted. The scores of the PCs were used as independent variables of isolation in all further analyses. They were used as substitutes for the correlated indices of isolation.

I used stepwise regression analyses to determine the relationships between the independent variables (site area, habitat heterogeneity, indices of isolation) and the dependent variables (species richness and the number of wetland species). I used a significance level of 0.05 for entering a variable into the stepwise regression model and a significance of 0.1 to retain the variable.

Univariate regression analyses were performed with site area as independent variable to determine its importance independent of the side effects of habitat heterogeneity. For these analyses, the dependent variables were transformed to ln(x). Afterwards, the statistical results were summarized as power laws $S = cA^z$, where S represents the number of species, A the area, z the slope of the relationship and c is a constant.

The isolation effects were analyzed for the individual wetland species. Presence-absence data for the wetland species and the principal components of the isolation indices were entered in Spearman's rank-order correlation tests. I separated the group of wetland species with significant correlations from the other wetland species. For these two groups of species, I was looking for differences concerning their dispersal strategies and the longevity indices of their seed banks. The frequencies of the dispersal strategies in the two groups were compared with the χ^2 test. I entered the longevity indices of the species in an analysis of variance (ANOVA) with type III sums of squares in a saturated model.

Results

Independent variables, correlation analysis and PCA

The smallest site covered an area of 79 m^2 and the largest an area of 2827 m^2 with an average size of 636 m^2 (arithmetic mean). The habitat heterogeneity of the investigated sites ranged between 1 (central parts inun-
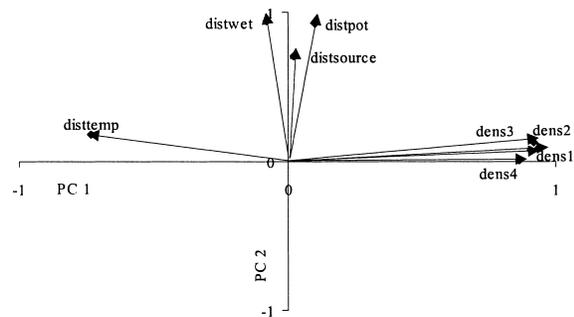

Fig. 1. PCA diagram of the indices of isolation. The total variance explained by the two principal components was 77%. PC = principal component, dens = density. Abbreviations according to Table 1.

dated until the middle of April) and 4 (central parts inundated until the middle of July). A positive correlation between site area and habitat heterogeneity was small but significant (r = 0.41, p < 0.01, n = 58).

The values of the indices of isolation are summarized in Table 1. Their internal correlation structure revealed that distfield was the only independent parameter. The other indices of isolation were highly correlated and were entered in a PCA. The first two principal components (PC) with eigenvalues of 3.84 and 2.29 explained 77% of the total variance. The four indices which express the density of temporary wetlands had a highly positive correlation. The distance to the next temporary wetland showed a strong negative correlation with these indices. These five indices were substituted by the first PC (Fig. 1). The second PC represented the indices distpot, distwet and distsource.

Species-area relationships

The total number of vascular plant species found was 115. The species richness of the sites ranged between 6 and 38 species with an average of 20 (arithmetic mean). There were between 1 and 24 wetland species (average = 9).

The species area relationships were tested using univariate regression analyses (Table 2). The area of the sites explained between 11 and 15% of the variation in the dependent variables. In general, area was positively correlated with species richness (Fig. 2). None of the larger sites had low species richness. However, the

Table 2. Results of univariate regression analyses of the natural-log transformed dependent variables (total species richness, number of wetland species) on the natural-log of area. r^2 is the coefficient of determination.

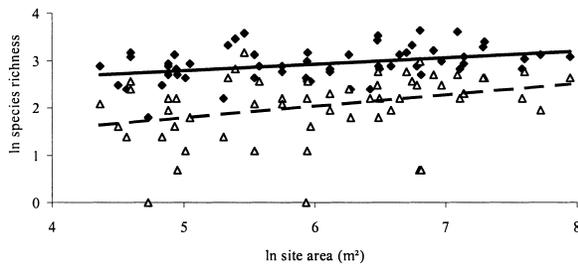| Dependent variable	Power law	r^2	p	n
all species	$S = 7.84\ A^{0.15}$	0.15	**	58
wetland species	$S = 1.76\ A^{0.24}$	0.11	*	58

Fig. 2. Univariate regression analyses of total species richness (—) ($r^2 = 0.15$, $p < 0.01$, $n = 58$) and number of obligate wetland species (– –) ($r^2 = 0.11$, $p < 0.05$, $n = 58$) on site area. All variables have been transformed to natural-log.

model did not apply to the small sites at which low as well as high species richness was observed.

Species richness, site area, habitat heterogeneity and isolation

Stepwise regression analyses revealed that habitat heterogeneity is the most important independent variable for the dependent variables (Table 3). It accounted for 77% of the variation in total species richness and 70% of the variation in the number of wetland species (Fig. 3). While habitat heterogeneity was highly correlated with species richness, site area was excluded in all analyses. Furthermore, there was no significant impact of PC1, PC2 and distfield on the dependent variables.

Impact of isolation on the wetland species

Only 11 of 52 wetland species were significantly correlated with PC1 or PC2. With one exception, all of these species were correlated with PC2. Due to the fact that PC1 expresses the density of temporary wetlands, a negative correlation with this variable does not indicate an impact of isolation. Therefore, only the species with negative correlations with PC2 were combined in a group of species which are negatively influenced by isolation (Group 1). The second group consisted of the remaining wetland species (Group 2).

The hypothesis was tested, that the different impacts of isolation on these two groups of species were mediated by differences in the means of dispersal in space or in the longevity of the species seed banks. Both groups were dominated by species which are specialized for

bird dispersal (Fig. 4). Forty-two and 34% of the species, respectively, were assigned to this dispersal strategy. Apart from the unspecialized species, which accounted for 25 and 26% of the species, the proportions of species with other dispersal strategies were < 20%. None of the groups of species differed according to their means of seed dispersal ($\chi^2 = 5.63$, $DF = 6$, $p = 0.466$). The mean longevity index of the seed banks was 0.68 ± 0.34 (arithmetic mean $\pm$ SD) in Group 1 and 0.65 ± 0.27 in Group 2 (Fig. 5). Univariate analysis of variance revealed no differences in the longevity of the seed banks between the two groups ($F_{1,19} = 0.042$, $p = 0.84$).

Discussion

In this paper, the impact of biogeographical parameters and habitat heterogeneity was compared with respect to two dependent variables: total vascular plant species richness and number of wetland species. In particular, focus was directed to the parameters area per se, isolation and heterogeneity of the hydroperiods.

The effects of site area on the dependent variables were small but significant if area was tested as single predictor variable. However, the proportion of variation in species richness explained by site area was lower than in other studies of habitat islands on the mainland, which are generally > 20% (Gilbert 1980, Ambuel and Temple 1983, Møller and Rørdam 1985, Boecklen 1986, Dzwonko and Loster 1989, Ouborg 1993). This indicates that the species-area relationship on temporary wetlands is relatively weak.

In this study, site area was correlated with habitat heterogeneity and did not show a significant impact on the dependent variables if both independent variables were analyzed simultaneously. Habitat heterogeneity was by far the most reliable variable for predicting species richness. These results are most consistent with the habitat heterogeneity hypothesis (Williams 1964, Connor and McCoy 1979, Williamson 1981). The dynamic equilibrium hypothesis and the passive sampling hypothesis require an independent impact of site area on species richness. However, the residuals of the species richness-habitat heterogeneity regressions were not correlated with site area. As it has been pointed out by Connor and McCoy (1979), correlation studies of habitat heterogeneity and species richness cannot be used to

Table 3. Results of stepwise multiple regression analyses with total species richness and number of wetland species as dependent variables and habitat heterogeneity, natural-log of area, PC 1, PC 2 and distfield as independent variables. SE = standard error. r^2 is the coefficient of determination. Abbreviations according to Table 1.

Dependent variable	Independent	Coefficient + SE	r^2	p	n
species richness	heterogeneity	5.76 + 0.43	0.77	***	58
wetland species	heterogeneity	3.81 + 0.34	0.70	***	58
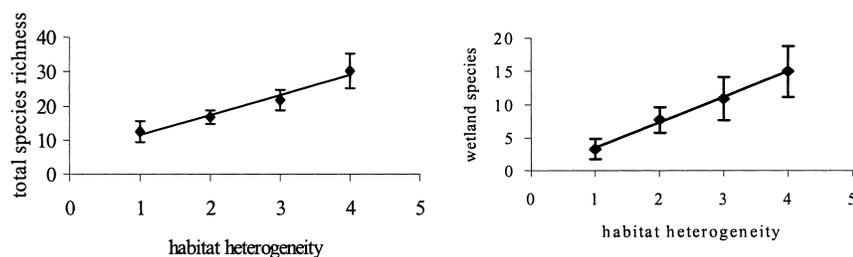
demonstrate the lack of any relationship between extinction probabilities and site area. Furthermore, it cannot be concluded that there is no relationship between colonization and distance to some source community. However, the results suggest that area and isolation are not the crucial factors determining vascular plant species richness of the temporary wetlands.

The correlation of species richness and spatial heterogeneity is consistent with theories of facilitated coexistence of species in heterogeneous environments (Tilman 1982, Tilman and Pacala 1993). Pollock et al. (1998) have demonstrated the strong correlation between vascular plant species richness in riparian wetlands and the heterogeneity in the frequency of floodings. Such correlations have been explained by a greater variety of available germination microsites (Vivian-Smith 1997), the heterogeneity of disturbances (Pollock et al. 1998) and by a shift between abiotic and biotic controlled vegetation dynamics on flooding gradients (Lenssen et al. 1999).

There was no significant impact of isolation on species richness. Considering the fact that total species richness includes transient species, it is not surprising that there is no isolation effect. However, even the number of obligate wetland species seems not to be influenced by isolation. The results are in accordance with an overall pattern: while most studies which were carried out on true islands reveal a significant impact of isolation on species richness, the opposite is true for mainland studies (Ouborg 1993, Rosenzweig 1995). The distances in the present study (mean values between 65 and 956 m) are much less than between islands and mainlands. In their study of actual islands within 4 km off the mainland, Nilsson et al. (1988) documented that there was no depressing effect of isolation on species richness. Accordingly, the shorter distances rather than the effect of surrounding water account for the differences between the present study and most island studies.

Only 10 of 52 wetland plant species were negatively influenced by isolation. Furthermore, the correlations were relatively weak. Overall, it does not seem that isolation plays an important role in the dispersal of the temporary wetland species which were investigated because most of the species did not show a response. In addition, the response of the remaining species, while

significant, was small. These species did not differ from the other wetland species according to means of dispersal or in the longevity of their seed banks. This might be due to the fact that most of the species are well-adapted to survival under the changing conditions of a frequently disturbed agricultural ecosystem. With respect to dispersal strategies, the species specialized on bird dispersal dominated the communities. Due to the fact that water birds frequently move from one temporary wetland to another while gathering food, the propagules of these plant species should accurately be dispersed. This might be one reason for the lack of a relationship between isolation and plant species richness.

Furthermore, the longevity of the seed banks is high compared to other plant communities. Mean seed longevities > 0.6, as in the present study, have been recorded for arable weed communities and for pioneer communities of dune slacks (Bekker et al. 1998, 1999). In accordance with these findings, the plant communities of the temporary wetlands are characterized by a mixture of arable weed communities with pioneer species of wet sites. Although there is no differentiation between the two groups of wetland species by the longevity of the seed banks, the generally high longevity of the seeds might counteract the effects of isolation on the plant communities. This could be a second reason for the lack of isolation effects on species richness on the temporary wetlands. It may be concluded that although wetland species are not found in the surrounding fields, the temporary wetlands can not be considered as isolated island habitats. This phenomenon which also occurs in other habitats has generally been explained by altered colonization-extinction
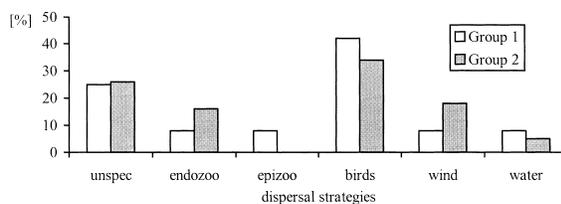

Fig. 4. Proportions of the dispersal strategies within the two groups of wetland species. Group 1 = negatively influenced by isolation, Group 2 = not negatively influenced by isolation, unspec = unspecialized.
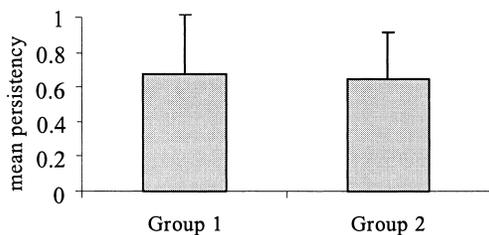
Fig. 5. Mean and SD of the seed bank longevity within the two groups of wetland species. Group 1 = negatively influenced by isolation, Group 2 = not negatively influenced by isolation.

dynamics and by enrichment via source-sink, remnant and metapopulation dynamics on the mainland (Holt 1993, Eriksson 1996). These explanations are in accordance with the present results of accurate dispersal by birds and the high longevity of the seeds which might lead to remnant populations.

This study has shown that the spatial heterogeneity of hydroperiods of temporary wetlands has a strong impact on vascular plant species richness while biogeographical parameters are relatively unimportant. However, the influence of source-sink, remnant and metapopulation dynamics on immigration and extinction rates remains open. The effects of the biogeographical parameters might be leveled out by accurate dispersal and by persistent seed banks of the species. Biogeographical studies of habitats in agricultural landscapes should take these factors into account. The results suggest that future research on vascular plant species of temporary wetlands should be directed towards the understanding of niche separation on the hydrologic gradient for generating models of the processes determining species richness.

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Appendix. List of vascular plant species found on temporary wetlands with classification. Dispersal (dispers) and longevity of seed banks (long) are only classified for wetland species (wet). Abbreviations: unspec. = unspecialized, birds = dispersal with the soil clinging to the feet of birds, epi = epizoochorous, endo = endozoochorous, wind = anemochorous.

Species	Habitat	Dispers	long	Species	Habitat	Dispers	long
Achillea millefolium	non wet			*Myosurus minimus*	wet	wind	–
Agropyron repens	non wet			*Oenanthe aquatica*	wet	unspec.	–
Agrostis stolonifera	wet	unspec.	0.38	*Papaver dubium*	non wet		
Alisma lanceolatum	wet	birds	–	*Peplis portula*	wet	birds	1
Alisma plantago-aquatica	wet	birds	1	*Petasites hybridus*	wet	wind	–
Alopecurus aequalis	wet	birds	1	*Phalaris arundinacea*	wet	water	0.2
Alopecurus geniculatus	wet	birds	0.73	*Phleum pratense*	non wet		
Alopecurus pratensis	non wet			*Plantago intermedia*	wet	unspec.	–
Anagallis arvensis	non wet			*Plantago lanceolata*	non wet		
Anchusa arvensis	non wet			*Plantago major*	non wet		
Apera spica-venti	non wet			*Poa annua*	non wet		
Arctium lappa	non wet			*Poa palustris*	wet	unspec.	–
Artemisia vulgaris	non wet			*Poa pratensis*	non wet		
Bidens tripartita	wet	epi	0.6	*Poa trivialis*	wet	unspec.	0.75
Butomus umbellatus	wet	–	–	*Polygonum amphibium*	wet	endo	–
Callitriche palustris	wet	birds	–	*Polygonum aviculare*	non wet		
Capsella bursa-pastoris	non wet			*Polygonum lapathifolium*	wet	unspec.	–
Centaurea cyanus	non wet			*Polygonum persicaria*	non wet		
Chamomilla recutita	non wet			*Ranunculus aquatilis*	wet	birds	–
Chenopodium album	non wet			*Ranunculus peltatus*	wet	birds	–
Chenopodium polyspermum	non wet			*Ranunculus repens*	wet	birds	0.68
Cichorium intybus	non wet			*Ranunculus sardous*	wet	unspec.	–
Cirsium arvense	non wet			*Ranunculus scelerathus*	wet	birds	0.89
Convolvulus arvensis	non wet			*Rorippa amphibia*	wet	birds	–
Conyza canadensis	non wet			*Rorippa palustris*	wet	birds	–
Echinochloa crus-galli	non wet			*Rumex crispus*	non wet		
Eleocharis palustris	wet	endo	0.38	*Rumex maritimus*	wet	unspec.	1
Epilobium adnatum	wet	wind	–	*Rumex obtusifolius*	non wet		
Epilobium hirsutum	wet	wind	0.66	*Rumex x pratensis*	non wet		
Equisetum arvense	non wet			*Rumex stenophyllus*	wet	unspec.	–
Euphorbia helioscopia	non wet			*Salix purpurea*	wet	wind	–
Fumaria officinalis	non wet			*Schoenoplectus tabernaemontani*	wet	endo	–
Galeopsis tetrahit	non wet			*Scirpus sylvaticus*	wet	unspec.	0.21
Glyceria fluitans	wet	birds	0.54	*Sonchus arvensis*	non wet		
Gnaphalium uliginosum	wet	wind	0.91	*Sonchus asper*	non wet		
Holcus lanatus	non wet			*Sparganium erectum*	wet		
Hypericum humifusum	wet	unspec.	–	*Spergularia rubra*	wet	unspec.	–
Juncus articulatus	wet	birds	0.88	*Stellaria media*	non wet		
Juncus bufonius	wet	birds	0.87	*Taraxacum officinale*	non wet		
Juncus spp.	wet	–	–	*Thlaspi arvense*	non wet		
Juncus tenagaeia	wet	birds	–	*Trifolium dubium*	non wet		
Lactuca serriola	non wet			*Trifolium hybridum*	non wet		
Lamium maculatum	non wet			*Trifolium repens*	non wet		
Lamium purpureum	non wet			*Urtica dioica*	non wet		

Appendix. (Continued).

Species	Habitat	Dispers	long	Species	Habitat	Dispers	long
Limosella aquatica	wet	birds	–	*Veronica anagallis-aquatica*	wet	wind	–
Lolium multiflorum	non wet			*Veronica arvensis*	non wet		
Lycopus europaeus	wet	birds	–	*Veronica catenata*	wet	unspec.	–
Lythrum hyssopifolia	wet	birds	–	*Veronica polita*	non wet		
Lythrum salicaria	wet	birds	0.24	*Vicia angustifolia segetalis*	non wet		
Matricaria maritima inodora	non wet			*Vicia hirsuta*	non wet		
Medicago lupulina	non wet			*Vicia lathyroides*	non wet		
Mentha aquatica	wet	water	0.39	*Vicia sativa*	non wet		
Mentha arvensis	wet	water	0.44	*Vicia sepium*	non wet		
Myosotis arvensis	non wet			*Vicia tenuissima*	non wet		
Myosotis laxiflora	wet	birds	–	*Vicia tetrasperma*	non wet		
Myosotis stricta	non wet			*Vicia villosa*	non wet		
Myosoton aquaticum	wet	wind	–	*Viola arvensis*	non wet		