

The age of island-like habitats impacts habitat specialist species richness

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Abstract. While the effects of contemporaneous local environment on species richness have been repeatedly documented, much less is known about historical effects, especially over large temporal scales. Using fen sites in the Western Carpathian Mountains with known radiocarbon-dated ages spanning Late Glacial to modern times (16 975–270 cal years before 2008), we have compiled richness data from the same plots for three groups of taxa with contrasting dispersal modes: (1) vascular plants, which have macroscopic propagules possessing variable, but rather low, dispersal abilities; (2) bryophytes, which have microscopic propagules that are readily transported long distances by air; and (3) terrestrial and freshwater mollusks, which have macroscopic individuals with slow active migration rates, but which also often possess high passive dispersal abilities. Using path analysis we tested the relationships between species richness and habitat age, area, isolation, and altitude for these groups. When only matrix-derived taxa were considered, no significant positive relation was noted between species richness and habitat size or age. When only calcareous-fen specialists were considered, however, habitat age was found to significantly affect vascular plant richness and, marginally, also bryophyte richness, whereas mollusk richness was significantly affected by habitat area. These results suggest that in inland insular systems only habitat specialist (i.e., interpatch disperser and/or relict species) richness is influenced by habitat age and/or area, with habitat age becoming more important as species dispersal ability decreases.

Key words: bryophytes; dispersal abilities; habitat age; habitat specialist; isolated fen habitats; path analysis; species richness; terrestrial and freshwater mollusks; vascular plants.

INTRODUCTION

While the effects of contemporaneous local environmental conditions on species richness have been repeatedly documented in many systems, investigations on the role of habitat age has been mainly limited to oceanic archipelagos across evolutionary time scales (e.g., Badano et al. 2005, Fattorini 2010, Zobel et al. 2011). Few previous studies have investigated patchy inland systems, and these have been generally limited to short time scales. For instance, over a 100-year period, Rejmánek and Rejmánková (2002) analyzed changes of vascular flora species richness of artificial fishpond-islands, and Krauss et al. (2009) found no effect of habitat age on wild bee species richness at limestone quarries. Across longer time scales, habitat age has been only roughly investigated. Pärtel and Zobel (1999) estimated community age by measuring habitat height above sea level, and Frey et al. (2007) estimated potential age of subalpine coniferous forest patches in

the American Southwest through climate models. The reason for the lack of objective analysis of habitat age on community richness is relatively simple: in most cases this variable is difficult, if not impossible, to measure (Nekola 1999, Frey et al. 2007).

Additionally, most works that study the relationship between island age, area, and species richness have only considered total species richness (but see Zobel et al. 2011, which limited analysis to a given habitat's species pool). In such studies it is difficult to distinguish between habitat island effects per se vs. processes involving the surrounding habitat matrix (landscape matrix of habitat patches) (Cook et al. 2002). While oceanic islands are isolated for all terrestrial species, generalist species in island-like habitats can colonize from adjacent matrix habitats (Wiser and Buxton 2008). In contrast, habitat specialists will experience a much higher degree of isolation, as they are incapable of establishing populations between habitat patches. Whittaker (1998) termed generalist species originating from the surrounding matrix as “matrix-derived” species, and habitat specialists as “interpatch dispersers.”

In this study we investigate the impact of habitat age on the number of matrix-derived and specialized species

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from a community in which formation times can be documented. The community consists of treeless calcareous-spring fens in the Western Carpathians, which can have their ages exactly determined via radiocarbon dating of basal organic sediments. We have limited analyses to ecologically uniform calcareous-spring fens in order to at least partially control for known influence of groundwater chemistry on species occurrence (see Hájek et al. 2006 for more references). In plots of uniform size we analyzed species richness for three organism size groups (vascular plants, bryophytes, and mollusks; see Plate 1). These groups were chosen because they differ sharply in their dispersal modes, and may thus experience variable species richness vs. habitat age relationships. Vascular plants have macroscopic seeds with generally low but variable passive dispersal abilities due to substantial recruitment limitation and small population sizes (Stammel et al. 2006, Hájek et al. 2011b). In contrast, bryophytes are highly adapted to long-distance passive dispersal through their microscopic wind-dispersed spores (e.g., Frahm 2008). Mollusks represent an intermediate case. On one hand, they are poor active dispersers that often move no more than 1–10 m over a lifetime (e.g., Baur 1988), and show similar spatial effects within fens as vascular plants when their compositional changes along a variable set of fen habitats were analyzed (Hájek et al. 2011b). On the other hand, small species (see Plate 1), such as those that greatly predominate in calcareous fens (Schamp et al. 2010), are among the most efficient known passive dispersers in the animal kingdom (Gittenberger et al. 2006, Cameron et al. 2010). As a result, small land snails commonly possess ranges of continental extent and often saturate available habitats within their range (Nekola 2009). Thus, we expect higher dispersal abilities for mollusks than for vascular plants in calcareous fens.

Our main hypothesis is that the number of specialized species will be significantly related to habitat age, while matrix-derived species will demonstrate no positive relationships. Further, the positive response of specialized species richness to habitat age should be inversely related to dispersal ability, being most pronounced in poorly dispersing groups that take considerable time to colonize all suitable sites. Because species richness can be influenced by several factors that may correlate with habitat age in this system, we assume the following potential interrelationships to exist (Fig. 1). First, species richness should positively correlate with fen area. This pattern is also indirectly generated because larger sites tend to be older (Hájek et al. 2011a) and better buffered against short-term negative environmental change. Second, we expect the impact of altitude to vary with taxon group. While for bryophytes and vascular plants, colder high-altitude sites may actually have increased richness due to the presence of several late-Pleistocene relicts (Rybníček 1966, Hájek et al. 2011a), a negative correlation is expected for mollusks, as only two such relicts are known from the study area

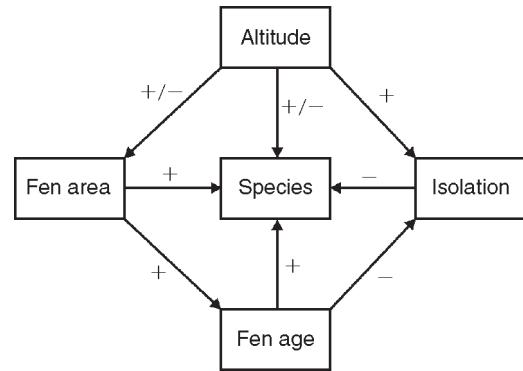


FIG. 1. A priori path model representing hypothesized relationships among the variables species richness (Species), Altitude, Fen area, Fen age, and Isolation. The expected sign of these relationships is shown near the arrows; +/- means that different signs are plausible depending on the taxonomic group considered (i.e., between altitude and species richness) or because of lack of specific knowledge (i.e., between altitude and area). The rationale behind the model is explained in full in the *Introduction*.

(Horsák and Cernohorsky 2008), and many land snail species apparently do not have cryoprotective chemicals (Riddle 1983). Third, we hypothesize that altitude may potentially influence habitat area and isolation through at least two opposing mechanisms: on the one hand, large fens are more likely to occur in broad lowland vs. steep and narrow high-altitude mountain valleys. On the other hand, low-altitude sites are also more likely to have been destroyed or reduced in size by agricultural or forestry-related drainage. Therefore, we are unsure about the form that potential area vs. altitude relationships may take. Lowland sites, however, are expected to be indirectly less isolated because of the absence of topographic barriers and the increased frequency of fen sites due to impeded drainage. Fourth, as time increases, a greater likelihood exists for successful interpatch dispersal colonization. However, species with high dispersal ability (i.e., bryophytes) will demonstrate a weaker impact of age on isolation because they should be able to rapidly colonize even the most isolated sites. Additionally, because colonization success is time dependent, we expect that perceived habitat isolation will positively correlate with low dispersal ability while negatively correlating with increasing habitat age.

METHODS

Selection of study sites

On the basis of our extensive surveys of Western Carpathian fen plant and animal communities (e.g., Horsák and Cernohorsky 2008), we identified a target list of 139 extant calcareous sites (representing the *Caricion davallianae* alliance with water conductivity >260 $\mu\text{S}/\text{cm}$, Ca + Mg concentration more than ~ 100 mg/L; Fig. 2) across the Czech Republic, Slovakia, and Poland. The geologic and climatic conditions of the study area are described in Horsák (2006). Within this

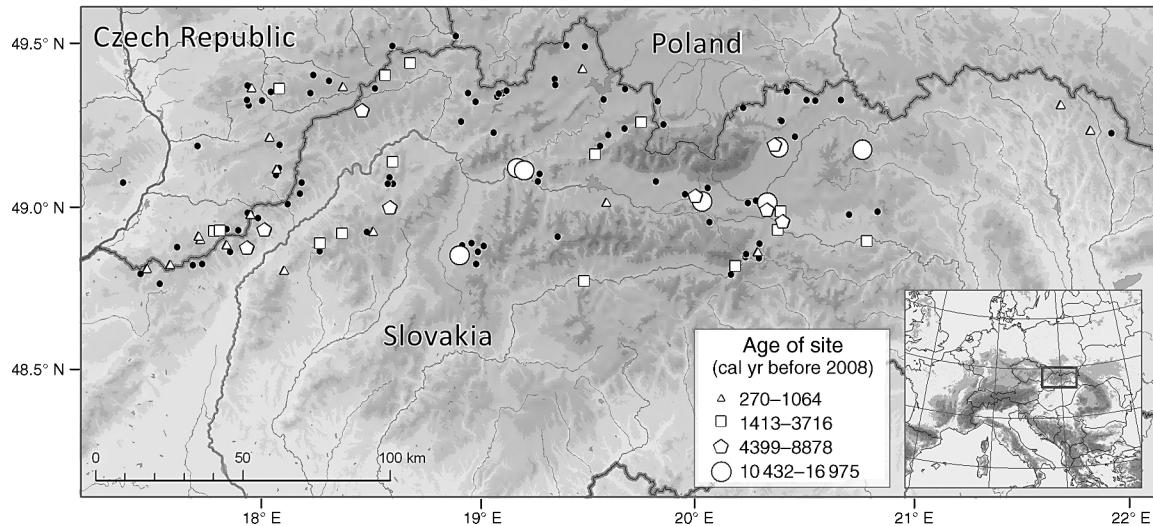


FIG. 2. Location of study area and position of all 139 calcareous-fen sites used in calculation of isolation. White symbols show the positions of 47 sites, classified based on their absolute age, used in species richness calculation and modeling.

region we selected a subset of 47 sites that represent high-quality fens lacking drainage channels, possessing low-productivity sedge–moss vegetation, and that have experienced no substantial reduction in habitat size over the last 50 years (Fig. 2). Target sites were stratified mainly with respect to their location within two adjacent Western Carpathian subregions: the Inner (eastern part) or Outer (western part). While the Inner subregion contains fen sites of Pleistocene/Holocene age, in the Outer subregion most sites originated during Late Middle Ages deforestation related to Wallachian colonization (Hájek et al. 2011a). Within each subregion we selected an approximately equal number of sites (24 in the former and 23 in the latter) that maximize spread across both community composition and geography. There are no significant differences in environmental factors (including water pH and conductivity) and habitat isolation ($P \gg 0.05$, Mann-Whitney U test) between these subregions. While a marginally significant difference in altitude was noted ($P = 0.045$, Mann-Whitney U test), the absolute range of sites in both subregions greatly overlapped.

Determining species composition and defining fen specialists

All sites were sampled at the end of May during 2008 and 2009. Samples were collected from standard 4×4 m plots representing homogeneous vegetation composition and structure in the central part of each site. Within this plot we recorded the presence of all vascular plant, bryophyte, and mollusk species occurring in the area. While species-level vascular plant identifications were largely conducted in the field, bryophyte determinations were made in the laboratory using collected material. Mollusks were documented via a 12-L organic detritus sample taken from the uppermost part of the soil profile. Previous studies have revealed that this volume is

sufficient for estimating the entire species pool for a given site (Cernohorsky et al. 2010). Mollusks were extracted by carefully washing each sample over a bowl-shaped 0.5-mm mesh sieve (see Horsák 2006). Shells were brought back to the laboratory where they were sorted, identified, and counted using a stereo microscope. Species noted from empty shells only were excluded from analyses.

Vascular plant and bryophyte species were identified as calcareous-fen specialists (Appendix A) through analysis of 60 454 geographically stratified vegetation plots stored in Czech and Slovak phytosociological databases (Schaminée et al. 2009). We used the COCKTAIL method which defines the groups of species tending to occur within similar habitats (Kočí et al. 2003). We initiated analysis using two European calcareous-fen specialists: *Primula farinosa* (group 1) and *Triglochin maritimum* (group 2). We merged these resulting lists with additional species that were either insufficiently covered by the databases or that possessed unclear nomenclature (for details see Appendix A and Hájek et al. 2011a). The calcareous-fen specialists identified through this process are not able to survive elsewhere in the landscape. Because similar data for mollusks are not available, we created a list of mollusk specialists based on published species autecology (Ložek 1964, Kerney et al. 1983) in combination with our own field experience. In total we recorded 31 fen specialist vascular plant species (out of 193), 7 specialist bryophyte species (out of 36), and 9 specialist mollusk species (out of 59), with all of the mollusks representing terrestrial gastropods (Appendix A).

Explanatory variables

To determine habitat age, we sampled the bottom ~3 cm of sediment (mostly pieces of wood and plant tissue)

from the area of thickest peat accumulation within each site. This material was then radiocarbon dated with data being calibrated using the IntCal09 curve in the OxCal4 software (see Hájek et al. 2011a). We used elapsed age from the middle value of the calibrated age 1δ range (68% confidence interval) up to 2008 (the year of survey). All calibrated site ages along with additional details on sediment sampling, radiocarbon dating, and individual site ages are presented in Hájek et al. (2011b).

An additional three environmental variables, known or expected to control species richness in this system, were also measured: (1) Habitat area was determined in the field for sites ranging up to ~ 0.25 ha. For larger sites, area was measured with ArcGIS 8.3 (ESRI 2003) using recent orthophoto maps. Patches of shrubs and trees within a fen site were excluded from area measurements. (2) Altitude was determined from 1:50 000 topographic maps in conjunction with site coordinates as determined from GPS. Altitude strongly correlates with mean January temperature in our study system (see Horsák and Cernohorsky 2008), and is here used as a proxy for climatic variation. (3) Isolation was expressed as the mean distance between a given calcium-rich fen and its two nearest neighbors (Fig. 2). This metric is highly correlated with the distance to five nearest neighbors ($r_S = 0.89$) out of the universe of 139 sites outlined above. We recognize that this metric is overly simplistic, as it disregards prior landscape configurations: for instance, a site that may have been well connected in the past may today be quite isolated. However, alternative approaches are not practicable, because we do not possess ages for all fens, and because there is no way to know the location of all fen sites back to 17 000 years before the present.

Water chemistry, which generally influences mire species distribution (Hájek et al. 2006), was not used for two reasons. First, we attempted to control for this effect by selecting only extremely rich fens with calcium carbonate precipitation. Second, water pH in these sites is rather uniform (Horsák 2006). Although water conductivity was found to vary between 261 and 1500 $\mu\text{S}/\text{cm}$ in our study sites (Horsák 2006), we found no significant correlation with species richness except for a slightly negative correlation with matrix-derived bryophytes ($r_S = -0.33$, $P = 0.02$). Because of this and the fact that no relationship between conductivity and habitat age is expected, this variable was not included in our path model.

Statistical analyses

Species richness relationships across the three taxa groups were first analyzed using Spearman rank correlations. Path analysis was then employed to determine if causal inferences were consistent with the observed data (Bollen 1989). We did not use multiple regression, as this approach possesses a limited range of causal structures and can suggest an incorrect model under cases of complex causality (Shipley 2000).

The following five variables were used in the path model: (1) matrix and specialized species richness, (2) altitude, (3) habitat area, (4) habitat age, and (5) habitat isolation. The model assesses both direct and indirect effects of these explanatory variables (i.e., altitude, area, age, and isolation) on species richness (Fig. 1). Because our preliminary analyses have documented nonlinear relationships between variables, the following transformations were applied. Area and isolation were log-transformed, while age was transformed using the Box-Cox algorithm. Maximum likelihood was used to evaluate the model, using chi-square distribution (χ^2) to test for the congruence between observed and expected covariance. We also evaluated the accuracy of the model using the GFI (goodness-of-fit index; conventionally GFI should be ≥ 0.9 in order for the model to be accepted) and RMSEA (root mean square error of approximation). Conventionally a good model is accurate when RMSEA is ≤ 0.05 . More details are found in Bollen (1989). Path analysis was computed using R (R Development Core Team 2010) with the package SEM.

RESULTS

Variation across species richness and all explanatory variables can be found in Appendix B. Among pairwise combinations of explanatory variables, we found that only habitat age and area significantly covary ($r_S = 0.48$, $P = 0.001$). Matrix vascular plant species richness was significantly correlated only with habitat age ($r_S = -0.55$) and area ($r_S = -0.37$), whereas specialized species richness was significantly correlated to habitat age ($r_S = 0.50$), area ($r_S = 0.53$), and altitude ($r_S = 0.48$) (Table 1 and Appendix C). Matrix bryophyte species richness was significantly correlated with habitat age ($r_S = -0.42$) and area ($r_S = -0.47$), but no significant relationships were observed for bryophyte specialists. Matrix mollusk species richness was significantly correlated with altitude ($r_S = -0.44$), while specialist mollusk species richness was significantly correlated with habitat age ($r_S = 0.38$) and area ($r_S = 0.42$; Table 1).

Via path analysis we observed a positive and significant relationship from area to age (0.56) and from altitude to area (0.28). Because these values are standardized they can be interpreted as partial regression coefficients. The hypothesized positive path from altitude to isolation, as well as the negative path from age to isolation, was not significant. The hypothesized path models were not significant ($\chi^2 = 0.86$, $\text{df} = 2$, $P = 0.65$), indicating that our model assumptions cannot be rejected. Models were all highly accurate, with GFI > 0.99 and RMSEA = 0.0. Examination of standardized residuals did not reveal substantial discrepancies. Standardized path coefficients are shown in Fig. 3, where solid arrows represent significant relationships ($P < 0.05$). The models for matrix-derived species explained less variation than those for specialized mollusk and vascular plant species, respectively (mollusks, $R^2 =$

TABLE 1. Spearman correlations between the study species and fen site parameters in the Western Carpathian Mountains across the Czech Republic, Slovakia, and Poland.

Groups	Age	Area	Altitude	Isolation
Matrix-derived vascular plant species	-0.55***	-0.37**	-0.17 NS	<0.01 NS
Vascular plant species specialists	0.52***	0.53***	0.48***	-0.10 NS
Matrix-derived bryophyte species	-0.42**	-0.47***	<0.01 NS	0.02 NS
Bryophyte species specialists	0.17 NS	<0.01 NS	0.17 NS	0.20 NS
Matrix-derived mollusk species	-0.22 NS	-0.32*	-0.44**	0.09 NS
Mollusk species specialists	0.38**	0.42**	0.12 NS	-0.02 NS

Notes: Spearman correlations between number of species (specialist and matrix) of vascular plants, bryophytes, and mollusks for a 16-m² plot in each of 47 isolated fen sites and maximum site age, current area (ha), altitude (m above sea level) and isolation (average distance to two nearest known fen sites in kilometers). Correlations that are significant after Bonferroni correction (at $P = 0.013$) are in boldface type. For scatterplots among these variables see Appendix C.

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; NS, not significant.

0.24 vs. 0.28; vascular plants, $R^2 = 0.31$ vs. 0.51). In contrast, the model of matrix-derived bryophyte species explained more variance than that for bryophyte specialists ($R^2 = 0.28$ vs. 0.17). The models also explained a substantial proportion of the total variance for age ($R^2 = 0.32$), but little for area ($R^2 = 0.08$) and isolation ($R^2 = 0.02$). Altitude positively and significantly affected specialized vascular plant (0.42) and bryophyte (0.28) species richness, with a significant negative relationship also being found for matrix-derived land snail species (-0.33).

Contrary to our hypothesized model, area showed both positive and negative effects on species richness, depending on the taxonomic group and whether matrix or specialist species were considered. Significant positive influence was found on specialized mollusk species (0.42) and negative influence on matrix-derived bryophyte species (-0.45). Similar complex results were obtained for habitat age (Fig. 3), with this factor significantly and positively affecting specialized vascular plant species richness (0.33), and marginally also specialized bryophyte species richness (0.30, $P = 0.07$). A significant and negative relationship was observed between age and matrix-derived vascular plant species richness (-0.50). Isolation did not affect species richness in any model. Finally, significant differences were noted in the ratio between the number of specialized species vs. the total species pool across all taxonomic groups (Kruskal-Wallis test, $H = 80.4$, $P \ll 0.001$). The highest ratio was found for bryophytes (median value = 0.50), the middle value for vascular plants (0.32), and the lowest for mollusks (0.10).

Habitat age and area were not randomly distributed across the study area, with smaller and younger sites being more frequent toward the west (Fig. 2). Because of this potential confounding variable, we also tested whether this spatial structure influenced results. To do this we re-ran the model on only the 24 sites located in the Inner subregion where sites covered the entire range of habitat ages (results not shown). Although we did not observe any significant equations in this subset due to low statistical power, the relative amounts of explained variation and the nature of relationships between the

variables (i.e., positive or negative) remained essentially identical. We furthermore believe that spatial autocorrelation has not influenced results because: (1) no significant differences in environmental characteristics were noted between subregions, and (2) none of the specialized species demonstrate local endemism, with all having ranges that extend across Europe and typically the Palaearctic as well.

DISCUSSION

Confirmed predictions

This study may represent the first time that the joint impact of habitat age (on the Holocene scale), size, isolation, and altitude/climate on species richness has been investigated for a set of inland insular habitats. Path analysis generally supports our hypothesis that habitat age has a greater influence on specialized species (i.e., interpatch dispersals and relicts) than on matrix-derived floras/faunas. This result is expected because matrix-derived species that are capable of surviving in multiple intervening habitats are usually not as dispersal limited and as such are able to colonize a given site much more rapidly. As a result, matrix-derived species tend to saturate potential habitats more rapidly and make habitat age a less important predictor of richness. This is evident in our analyses where no significant positive relation was noted between habitat age and matrix-derived species for any investigated group. We further confirmed the initial hypothesis that the relationship between habitat age and specialist richness is stronger for poorer dispersers.

We also found that habitat size significantly influences habitat age, with large sites being better able to survive Holocene climate change (Hájek et al. 2011a). Habitat area was also positively influenced by altitude, reflecting the increased risk of lowland sites destruction/alteration through human activities. Even though the Inner Western Carpathian lowlands were initially more environmentally suitable for development of large fens, in the last 60 years many sites were drained to create arable land (Stanová 2000). Additionally, low-altitude sites in the southwestern part of the study area are very small spring fens that originated through medieval deforesta-

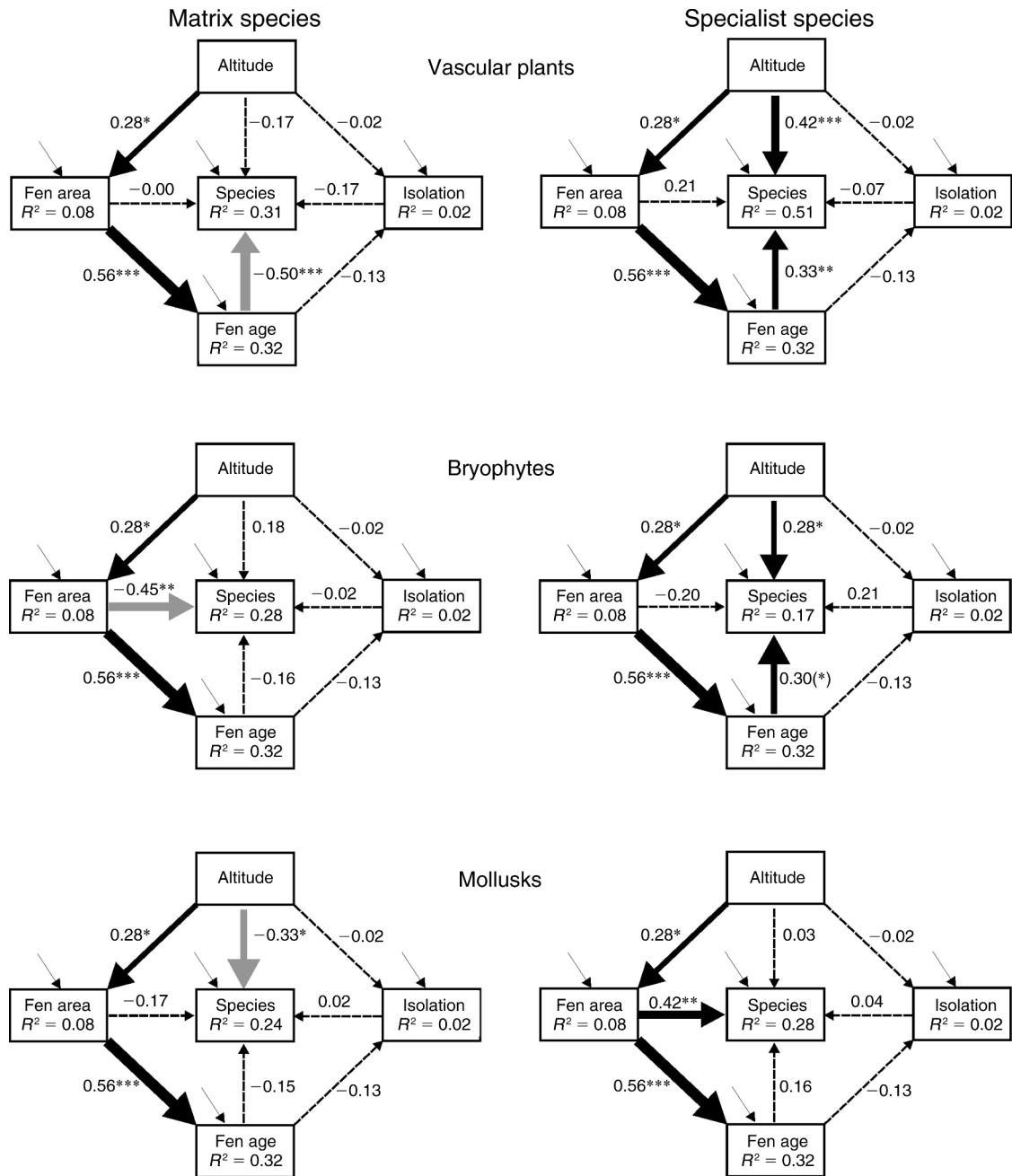


FIG. 3. Path models for species richness (Species), Altitude, Fen area, Fen age, and Isolation, for matrix-derived and specialist species in vascular plants, bryophytes, and mollusks. Continuous arrows are significant relationships (black positive; gray negative); dashed arrows are not significant (at $P < 0.05$). The width of the arrows is proportional to the strength of the path. Values on arrows represent completely standardized regression coefficients. A standardized path coefficient shows the mean response, in standard deviation units of the dependent variable, to one standard deviation of change in an explanatory variable, holding constant the other variables in the model. Short arrows indicate the existence of residual variance in endogenous variables.

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

tion (Hájek et al. 2011a). We found that such spatial autocorrelation in habitat age did not influence contemporaneous environmental characteristics between sites.

Group-specific response to altitude was also verified. The decrease of matrix-derived mollusk richness with increasing altitude is likely related to poorly evolved

cold-hardiness (Cameron and Greenwood 1991) in combination with the presence of only two glacial relicts in the system (Hájek et al. 2011b). In contrast, specialist vascular plant and bryophyte richness significantly increased with altitude. Some of the vascular plant species shaping this pattern (e.g., *Primula farinosa* and



PLATE 1. A view of one of the largest study sites, Demänová, a well-preserved calcareous fen in the Western Carpathian Mountains (central Slovakia). Representatives of the studied organisms and their propagules are depicted and ordered based on their dispersal abilities (from low to high). For each taxon a characteristic habitat specialist is shown: vascular plant, *Eriophorum latifolium*; mollusk, *Vertigo geyeri*; and bryophyte, *Philonotis calcarea* (see Appendix A). The numbers refer to the maximum dimension of the object, except for the vascular plant where it refers to fruit size only (the medium-gray oval object in lower left of the round vascular plant inset); propagule size including the pappus is about 20 mm. Photo credits: lower left vascular plant and lower right bryophyte, P. Hajkova; all others, M. Horsák.

Carex dioica) represent putative glacial relicts (Hájek et al. 2011a) that become more common with decreasing temperature. The same is true for bryophytes, where some species with a boreal distribution (e.g., *Drepanocladus cossonii* and *Calliergon giganteum*) are more common at higher altitudes.

Differences from our initial predictions

Three important differences between our initial predictions and the final results were noted. First, we hypothesized that habitat age would impact richness of all specialist organisms. While vascular plant specialist richness was positively affected by habitat age, no significant effects were noted for bryophyte and mollusk specialists. In bryophytes, this is likely due to their excellent dispersal abilities (Nekola 1999, Frahm 2008). Thus, like highly mobile bees (Krauss et al. 2009), both generalist and specialist bryophytes appear to not experience significant dispersal limitation within this landscape after only ~100 years following habitat formation. It is possible that a significant relationship between specialist bryophyte richness and habitat age may have been noted if the data set had been expanded to include intermediate-rich fens that are known to support the highest bryophyte species richness within

mire habitats in the region (e.g., Hájek et al. 2006). For instance, a number of glacial-relict mosses occur on moderately acid but still calcium-rich sites (Rybníček 1966). In mollusks, the lack of effect of habitat age on specialist richness is likely due not only to the high passive dispersal ability of minute species (e.g., Cameron et al. 2010), but also potentially to their shorter life spans. The terrestrial gastropods dominating this system are mostly short lived (with a life span of only 1–3 years), with most individuals dying in the year following hatching (Myzyk 2010). This may create a higher extinction risk through lowered relaxation time (Kuussaari et al. 2009, Krauss et al. 2010) and lessened ability to survive environmental fluctuations as compared to longer-lived and propagule-bank-creating wetland vascular plants (Sosnová et al. 2010, Hájek et al. 2011a).

Second, while vascular plant specialist richness was significantly and positively affected by habitat age, a significant negative relation occurred when only matrix-derived species were considered. This incongruity is rooted in the history of the study sites: most of the young fens analyzed originated during the Middle Ages when human-induced deforestation increased the area of open habitats, increasing rates of rainwater infiltration, decreasing evapotranspiration, and ultimately resulting

in greater groundwater discharge (Hájek et al. 2011a). Because the vast majority of fen vascular plants are long-lived clones (Sosnová et al. 2010), matrix-derived vascular plant species in these sites are likely enriched due to the persistence of shade-demanding species that grew in preceding alder carrs (damp alder forests). Extended persistence (e.g., >100 years) of clonal plants in unfavorable habitats has been noted in a number of grassland and forest studies (Helm et al. 2006, Lindborg 2007, Johansson et al. 2011) and can explain the presence of forest species in these young treeless fens.

Conservation implications

Our results suggest that dispersal limitation will have long-lasting impacts on habitat specialist richness, especially for long-lived organisms with poor dispersal abilities such as vascular plants. Because of this, older habitats will more likely possess richer floras/faunas through both long-term relict-species persistence as well as the longer time required for interpatch dispersers with poor dispersal abilities to effectively saturate potential habitats within a landscape. Ancient and large habitat fragments therefore deserve priority in conservation. Nevertheless, the lack of occurrence of certain species from a given isolated habitat does not necessarily indicate that the site is not environmentally appropriate and should not be protected. Rather, the site may simply not have been in existence long enough to guarantee successful recruitment of appropriate colonists (Nekola 1999, Cristofoli et al. 2010). Such sites may be expected to accumulate species over time. Conservation planners should therefore consider not only current levels of diversity when selecting potential reserves, but also the potential of sites to harbor additional biodiversity and to augment rates of interpatch dispersal.

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SUPPLEMENTAL MATERIAL

Appendix A

The list of vascular plant, bryophyte, and mollusk species identified as calcareous-fen specialists (*Ecological Archives* E093-095-A1).

Appendix B

Descriptive statistics for variables used in the analysis (*Ecological Archives* E093-095-A2).

Appendix C

Scatter plots between four predictors (habitat age, habitat area, altitude, and isolation) used in path analysis to explain variation of individual species richness categories (*Ecological Archives* E093-095-A3).