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Effect of habitat area and isolation on plant trait distribution in European forests and grasslands

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A number of studies show contrasting results in how plant species with specific life-history strategies respond to fragmentation, but a general analysis on whether traits affect plant species occurrences in relation to habitat area and isolation has not been performed. We used published data from forests and grasslands in north-central Europe to analyse if there are general patterns of sensitivity to isolation and dependency of area for species using three traits: life-span, clonality, and seed weight. We show that a larger share of all forest species was affected by habitat isolation and area as compared to grassland species. Persistence-related traits, life-span and clonality, were associated to habitat area and the dispersal and recruitment related trait, seed weight, to isolation in both forest and grassland patches. Occurrence of clonal plant species decreased with habitat area, opposite to non-clonal plant species, and long-lived plant species decreased with grassland area. The directions of these responses partly challenge some earlier views, suggesting that further decrease in habitat area will lead to a change in plant species community composition, towards relatively fewer clonal and long-lived plants with large seeds in small forest patches and fewer clonal plants with small seeds in small grassland patches. It is likely that this altered community has been reached in many fragmented European landscapes consisting of small and isolated natural and semi-natural patches, where many non-clonal and short-lived species have already disappeared. Our study based on a large-scale dataset reveals general and useful insights concerning area and isolation effects on plant species composition that can improve the outcome of conservation and restoration efforts of plant communities in rural landscapes.

Habitat fragmentation, i.e. shrinking and isolation of habitat patches, is hypothesized to reduce population size of species and to decrease colonization rate (MacArthur and Wilson 1967, Fahrig 2002). However, the impacts of these processes on plant populations and species richness vary. Some studies show diminishing plant populations and richness with decreasing habitat size and increasing isolation (Fischer and Stöcklin 1997, McIntyre and Hobbs 1999, de Blois et al. 2002, Dupré and Ehrlén 2002). Especially, fragmentation of forests has caused declines for many forest species (Grashof-Bokdam 1997, Petit et al. 2004), becoming restricted to small woodlots and few larger forest remnants (Kolb 2005). Results from grasslands have been less clear, where grassland habitat area, but not connectivity, has been found to be positively related to total species richness (Cousins et al. 2007), whereas other studies have found no effects on plant species richness of current grassland area or isolation (Lindborg and Eriksson 2004, Helm et al. 2006). An aggravating circumstance when studying fragmentation in real landscapes is that effects of isolation and area often are confounded with effect of land use and habitat quality, hence difficult to separate (Roschewitz et al. 2005).

A possible explanation for these disparate results is that species do not respond equally to habitat loss and isolation (Fahrig 2002). Small habitats can reduce species richness simply due to the well established species–area relationship, hence acting on population size and extinction processes, while isolation is expected to affect dispersal and colonization processes. To analyse these underlying mechanisms, the species richness measure built on presence and absence data is often too crude to capture shifts in plant community composition due to land use conversion. Instead, changes in abundance and extinction risk in local plant populations may be related to species specific life-history strategies (Verheyen et al. 2003, Kolb and Diekmann 2004, Herault and Honnay 2005, Lososová et al. 2008). Categorizing species based on their life-history traits or functional groups (Lavorel et al. 1997, Díaz and Cabido 2001) can improve the predictability of species extinction risks and simultaneously provide a deeper understanding of the ecological processes that govern the response and composition of communities in isolated habitat patches (Herault and Honnay 2005, Bommarco et al. 2010).

Dispersal capacity is one of the key ecological traits for plant species in a fragmented landscape (Tackenberg et al. 2003, Ozinga et al. 2004, 2009). The ability to move between and colonize remnant or new habitats can help to ensure regional persistence and to reduce risk of local extinctions (MacArthur and Wilson 1967, Venable and Brown 1988, Tilman 1994, Hanski 1999). In fragmented landscapes, a large number of habitats suitable for a given species may stay unoccupied because plant species are limited in their capacity to disperse and establish (Ackerman et al. 1996, Eriksson 1996, Ehrlén and Eriksson 2000, Tremlova and Münzbergová 2007). Among animals, positive relationships between species occurrence, patch area and connectivity are expected to be detected more often for species with poor dispersal capacity (Roland and Taylor 1997, Öckinger et al. 2010). However, results from corresponding plant studies have not been thoroughly summarized.

A trade-off that may affect plant species ability to persist in small habitat patches has been suggested, where long-lived plants are inferior colonizers and vice versa (Venable and Brown 1988, Tilman 1994, Ehrlén and van Groenendael 1998). Some studies suggest that small seeded species are better dispersers (Kiviniemi and Eriksson 1999) and species with large seeds are better recruiters (Geritz 1995), but empirical evidence for many trade-offs remain scarce and contradictory (Kneitel and Chase 2004, Moles and Westoby 2004, 2006). Contrasting results concerning the sensitivity of plants to area loss or isolation depending on specific life-history traits have also been presented. For example, short-lived and non-clonal plants are proposed to be more sensitive to area and/or habitat loss than long-lived and clonal plants (Bruun 2000, Eriksson and Ehrlén 2001, Lindborg 2007, Liira et al. 2008). In contrast, case study observations confirm that clonal plants may be neutral (Sutton and Morgan 2009) or even more sensitive to small habitat area than non-clonal species (Kolb and Diekmann 2004). The suggested underlying mechanism is that although clonal plant species often have good persistence abilities, substantial loss of habitat area, especially when it hits the populations of clonal species, can still lead to local extinction (Honnay and Bossuyt 2005). Isolation may also have negative effect on long-lived clonal plants (Holt et al. 1995, Collins et al. 2009) because of dispersal limitation between patches (Holt 1992). With respect to seed size, plants with large seeds have been suggested to be more sensitive to isolation than small seeded plants (Soons et al. 2005, Römermann et al. 2008). Although studies on effects of habitat area and isolation on plant species with contrasting life-history strategies are amassing, a general analysis on whether life-history traits modify plant species occurrences in relation to habitat loss has not been performed.

The baseline assumption for our study is that plant species responses to area and increased isolation are related to species traits. We hypothesize that species persistence-related traits are more associated to habitat area and dispersal-related traits more to isolation. To examine this we assembled published data from studies on plant species in grassland and woodland patches across Europe. From these we drew estimates for the relationships of individual plant species sensitivity to local extinction, as indicated by their occupancy patterns, with habitat area and with habitat isolation. Information on three core traits representing contrasting plant strategies that reflect persistence, dispersal and recruitment (life-span, clonality and seed weight) were added to each species. With this we examined general patterns for how the three species traits modified species sensitivity to habitat isolation and area, in remnant forest or grassland habitats, and with and without phylogenetic correction (Westoby et al. 1995a, b, Freckelton 2009).

Material and methods

Literature search

We searched ISI-Web of science for the words; plant AND area AND (isolation OR connectivity), and found 480 studies in total. We included only studies carried out in Europe, and kept only studies including species specific information on the relationship between occurrence and/or abundance, and habitat area and/or isolation measured as connectivity. In all studies, the connectivity was measured as distance between patches using variants of incidence function models (cf. Moilanen and Hanski 2006), calculating the smallest distance between the focal patch and any other patch within the study buffer. All single species studies were excluded due to risk of biased sampling, where only results that support the investigated hypothesis may be published (Rosenthal 1979, Kotiaho and Tomkins 2002). All selected studies were conducted at a relatively large landscape to regional scale. Based on these criteria we were able to gather information from 19 datasets from across north-central Europe (Fig. 1) with 11 studies from forests (mixed deciduous forests) and 8 studies from grasslands (dry-mesic semi-natural grasslands) (Supplementary material Appendix 1). Although the methods used to assess species specific habitat quality among studies varied (e.g. soil, Ellenberg index, species composition) they all fit within the above definition of forests and grasslands. Some of the studies in the data set are rather studies on land use

Figure 1. Location of the European studies (n = 19) included in the dataset.

history and colonization of new patches than of fragmentation per se, and could hence not be viewed as remnants in a fragmented landscape. However, since it is difficult to separate spatial and temporal effects of fragmentation and habitat quality in any study of real landscapes, we consider these studies equally relevant for this analysis as those focusing explicitly on fragmentation effect.

In fragmentation studies the main interest is on species that are either habitat specialists or species that are core species in the specific species pool for target habitat types (Kuussaari et al. 2009). In most of the selected studies, a relatively broad definition of habitat specialists was used. As habitat specialists tend to differ between regions (Krauss et al. 2010), we did not unify the specialists group, but used the definition of specialists presented in each study. The species recorded in the 19 studies were assigned into two separate non-overlapping lists for forest and grassland species respectively (Supplementary material Appendix 2). For each included species we described its relationship to habitat isolation and area as a binary response variable, where a species was assigned a 1 if its occurrence increased with increasing habitat area or connectivity, i.e. a significantly positive relationship, (species) and a 0 for a non-significant response. In very few cases, where the response was significantly negative the species was also assigned a 0. Species occurring in several studies were assigned a 1 if a positive relationship was found in at least one study.

Life-history traits

We collected information on three life-history traits for each species: life-span, clonality and seed weight. The following trait databases were used for this: BiolFlor (Kühn et al. 2004); Kew: <http://data.kew.org/sid/>, published literature Dupré and Ehrlén (2002), Grime et al. (2007), Lindborg (2007), as well as data from our own fieldwork. BiolFlor database was also followed if contradictory information occurred in different databases for a species.

The three traits were categorized as being related to either persistence (life-span and clonality) or dispersal/recruitment (seed weight). Clonality and seed weight are frequently debated whether they should be regarded as persistence or dispersal traits. Here we define seed weight mainly as a dispersal/recruitment trait (Eriksson 1996, Ehrlén and Eriksson 2000, Tremlova and Münzbergová 2007) whereas clonality is most related to persistence (Honnay and Bossuyt 2005, Cody 2006). For life-span, the species were classified as either short-lived (annuals and biennials) or long-lived (perennials). A species was categorized as clonal if it was vegetatively dispersed or vegetatively and seed dispersed, and as non-clonal if it was mainly dispersed by seeds or spores and dispersed vegetatively only on rare occasions. Clonal species often are limited in seed dispersal and are expected to have shorter dispersal kernels than non-clonal species (Zobel et al. 2010). As our main aim was to contrast two species groups rather than testing different clonal growth strategies, we did not use classifications including more detailed information of clonal growth organs (Klimešová and de Bello 2009). The seed weight of the dispersule for each species was added as a continuous variable. We examined correlations between pairs of traits across species in a Kendall Tau correlation matrix to assess the degree of collinearity among traits.

Phylogenetic information

To include phylogeny in the analysis, phylogenetic information was collected from the BiolFlor database on central European (Kühn et al. 2004, Gerhold et al. 2008, Knapp et al. 2008). Previous studies from Europe have shown that all three traits are moderately phylogenetically conserved, i.e. where variation of traits within lineages is smaller than between lineages as indicated by the retention index for each trait (Farris 1989). The retention index can vary between 0 and 100% and is minimal when a trait only changes between lineages and not within. Retention index for various traits in European flora varies between 10 and 65 (Prinzing et al. 2008). The retention index drawn from Prinzing et al. (2008) indicates that for European plant species, traits included in our study are evolutionarily conserved; 21.8 for life-span, 23.6 for clonality and 31.4 for seed size.

Statistical analysis

Relationship between area and isolation and species traits were analyzed separately for forest and grassland species. We analyzed the data both across species and by including phylogenetic relationships between species since we were both interested in whether some species in Europe with specific traits are associated with sensitivity to habitat loss and isolation, and whether there might be evolutionary ecological causal effects (Freckleton 2009).

For the analysis across species, every species from each study was marked as dependent on area size or not, and sensitive or not to isolation based on the information collected from literature. These relationships to area and isolation were used as a binary response variable (as described above) and related to the three traits across species in generalized linear models with binomial distribution (R package lme4, function lmer, R Development Core Team 2009).

To test the effect of phylogeny, we examined whether residuals from the generalized linear models had a significant phylogenetic signal (Blomberg's K, calculated by R package picante, function phylosignal). We found no evidence of phylogenetic signal for any of the models ($p > 0.20$). Even if the phylogenetic correlation was not significant, it is surely present and might influence our results. Therefore we used additionally generalized estimating equations (GEE) with binomial distribution and logit link function where phylogenetic correlation structure was defined (R package ape, function compar.gee, Paradis 2006). GEE is a method of analyzing auto-correlated data that otherwise could be modeled by generalized linear models.

Results

In total, 351 species were included in the study; 177 of them were found in forests and 174 in grasslands (see Supplementary material Appendix 1 and 2 for references and species list). The species were distributed among trait groups as follows: for life-span 12% forest species and 16% grassland species were short-lived, and for clonality 33% of the forest and 60% of the grassland species were clonal plants. Seed weight was generally higher for forest species than for grassland species. In general, more forest species were sensitive to area and isolation as compared to grassland species (Fig. 2, 3). From the 351 included species, 121 species (89 from forests and 32 from grasslands) were dependent on habitat area, and 128 species (88 from forests and 40 from grasslands) were sensitive to isolation (Fig. 2).

Correlations between pairs of traits across species showed that all traits were weakly correlated with each other ($p < 0.05$) (Kendall Tau correlation matrix: life-span – clonality 0.11, life-span – seed weigh 0.21, and clonality – seed weight –0.13). As correlation coefficients ranged from 0.11 to 0.21, they were not high enough to exclude any trait due to collinearity.

Sensitivity to area

Clonality and life-span, the persistence related traits in this study, were related to habitat area, as expected. In contrast to some earlier studies, our results suggested that clonal species are more dependent on area size than non-clonal species, both in forests and grasslands (Table 1; Fig. 3). Long-lived grassland species, but not forest species, showed positive dependence on habitat area. Seed weight across all plants in either habitat type did not explain occupancy patterns in relation to habitat area (Table 1). The results were identical to the cross-species analysis where a phylogenetically informed analyses (phylogenetic generalized estimating equations (GEE)) was applied (Table 1).

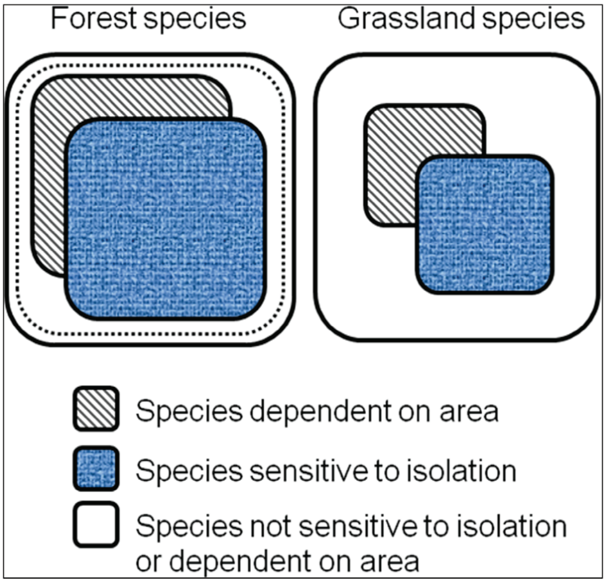

Figure 2. The proportion of vascular plant species dependent on area and sensitive to isolation in European forests and grasslands expressed as percentage visualized in Venn diagrams. Note: for forest species the larger frame indicates species considered in area and isolation studies (n = 184), and smaller frame with dashed line indicates the subset of studies considering habitat area only (n = 157).

Sensitivity to isolation

Seed weight, defined as a dispersal and recruitment related trait, was related to habitat isolation both in forest and grassland species, but in different directions. Forest species with large seeds and grasslands species with small seeds showed susceptibility to increasing isolation. In addition, we found

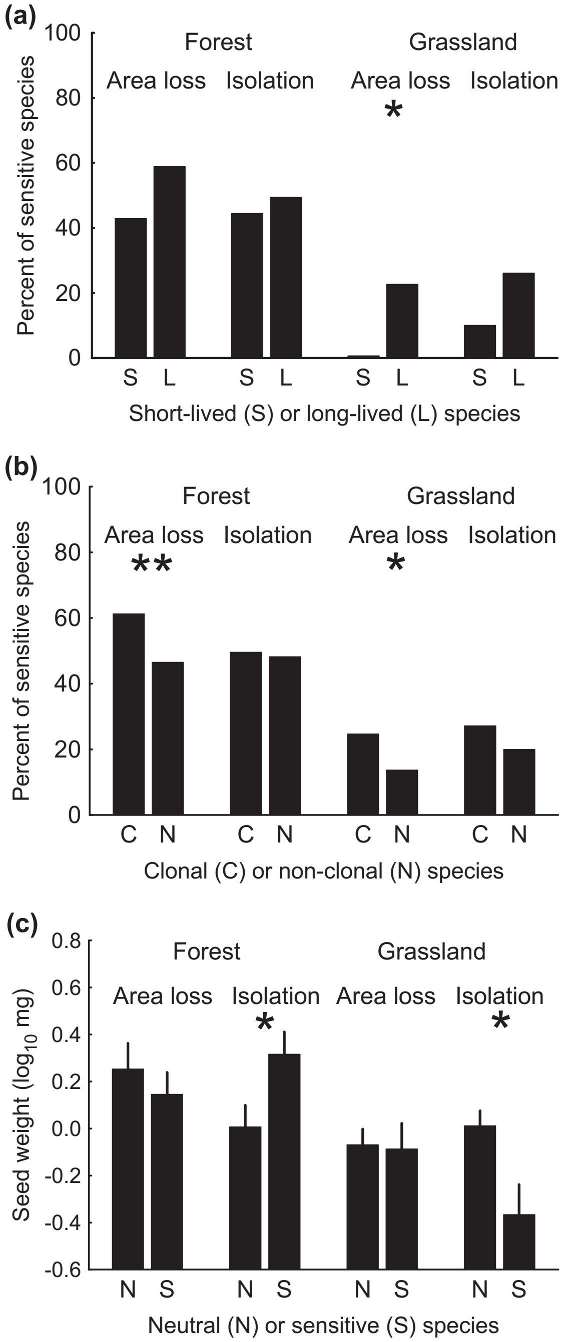

Figure 3. Proportions of vascular plant species with shared life history traits (life-span, clonality and seed weight) that are dependent on area and sensitive to isolation in forests and grasslands. The mean and standard errors are presented in the lower graph for seed weight. Significant differences between sensitive and neutral species are shown by asterisks above the bars (*$p < 0.05$, **$p < 0.01$, ***$p < 0.001$) Actual p-values for each statistical test are presented in Table 1.

Table 1. The relationship between three trait (life-span, clonality and seed weight), and area and isolation for plants occurring in grasslands and forest habitats. The analyses are made with and without phylogenetic correction, using GEE and GLM, respectively.

	Area				Isolation			
	GLM		GEE		GLM		GEE	
Life-history traits	Estimates	p-value	Estimates	p-value	Estimates	p-value	Estimates	p-value
Life-span								
Forest	+0.109	0.745	+0,395	0.250	+0.218	0.516	+0.279	0.416
Grassland	+**1.137**	**0.034**	+**1.463**	**0.009**	+0.910	0.059	+0.613	0.217
Clonality								
Forest	+**0.972**	**0.006**	+**1.066**	**0.005**	+0.188	0.578	+0.039	0.908
Grassland	+**0.878**	**0.045**	+**0.941**	**0.041**	+0.480	0.224	+0.041	0.917
Seed weight								
Forest	−0.014	0.877	−0.018	0.841	+**0.221**	**0.023**	+0.158	0.119
Grassland	−0.036	0.776	+0.111	0.391	−**0.276**	**0.023**	−0.127	0.309

a non-significant trend that long-lived grassland species were more sensitive to isolation than short-lived (Table 1, Fig. 3). Clonality was not related to isolation. In contrast to the phylogenetically uninformed analysis (GLM), no relationship between species sensitivity to isolation and seed weight could be detected with phylogenetic GEE analyses (even if GLM residuals showed no phylogenetic structure).

Discussion

Using representative European datasets, we were able to confirm the general assumption that species persistence-related traits are more associated to habitat area and dispersal-related traits more to isolation. However, the directions of the responses expose interesting trends that partly challenge some previously posed hypotheses for species trait distribution in fragmented landscapes. Clonal plants in both grassland and forest, and long-lived plants in grasslands, were more affected by habitat area loss and were less often found in small habitat patches, as compared to non-clonal plants (Table 1). These findings contradict some previous results indicating that clonal plants cope comparably well with habitat loss and increasing isolation (Bruun 2000, Lindborg 2007, Liira et al. 2008). Our results are, however, congruent with experimental studies where the abundance of clonal plants, but not non-clonal, varied systematically with patch size (Robinson et al. 1992) and where clonal perennial species persisted longer in large compared to small patches (Collins et al. 2009). Since most of these European forests and grasslands have been subjected to substantial loss during the last decades (Pykälä 2000, Kolb and Diekmann 2004, Krauss et al. 2010) clonal plants may be more prone to go extinct as a result of area loss as they are more limited to escape to nearby remaining suitable patches. The findings that occurrences of clonal species vary with patch size are relevant for explaining the plant community structure, not only in studies focusing directly on fragmentation and habitat decline, but also in studies of isolation and re-colonisation of patches (Jacquemyn et al. 2001). Due to low frequency of seed dispersal, species-area relationships are predicted to be steeper for clonal species than non-clonal species as they probably have more limited capacity to spread in new habitat patches or to respond to changing environmental conditions (Zobel et al. 2010). This could more often result in local extinctions for clonal than non-clonal species (Buckley and Freckleton 2010).

Our result may also be explained in the context of the historical land use of European grassland and forest. More specifically, slow intrinsic dynamics of many populations might delay local extinctions following habitat loss (Jackson and Sax 2009). This phenomenon is often detected amongst long-lived organisms (e.g. perennial plants) but more rarely found amongst short-lived and more mobile taxa such as arthropods (Kuussaari et al. 2009, Krauss et al. 2010). In contrast to our result, some studies on the susceptibility of plants to habitat loss and increasing isolation show that the species that first go extinct in a fragmented landscape are short-lived and non-clonal (Bruun 2000, Lindborg 2007, Liira et al. 2008). These species also have better dispersal but lower competitive abilities, hence responding quickly to unsuitable conditions like declining habitat area and changed habitat quality. Rather, clonal species may persist longer in isolated patches, but when they eventually go extinct they have limited re-colonization ability. Time since the most extensive period of habitat loss, deterioration of habitat quality and isolation can thereby influence the trait distribution in current habitats. Forests in high productive agricultural areas have probably suffered loss much earlier than grassland fragments have (Cousins 2009), and land use change has occurred at different pace and historical periods in different parts of Europe. For instance, rural landscapes in Sweden have shown historical legacies on plant communities in previous studies (Lindborg and Eriksson 2004, Krauss et al. 2010). No differences in the results appeared, however, when excluding the Swedish studies from the analysis, and shifts in plant species community composition that we see in the current analysis could be a result of a relaxation time or extinction debt already paid in a majority of the collected case studied.

Another explanation to the occurrence of short-lived and non-clonal species found in the sites is that several of them are 'matrix species', with a shorter turn-over time, that are more dependent on local habitat characteristics rather than habitat size or isolation, making them less dependent on one specific habitat type. In the few cases where effects of fragmentation and habitat quality have been studied simultaneously, habitat quality is found to be the most important variable affecting plant species richness and distribution (Adriaens et al. 2006, Liira et al. 2008, Marini et al. 2008, Baeten et al. 2009). The variation in definitions and measures of isolation and habitat quality among our selected case studies could be a potential methodological problem affecting the results. However, the studies are located within the same broader region in north-central Europe, and are fitting the broader definition of grasslands and forests.

A larger proportion of forest species were affected by habitat isolation and area, as compared to grassland species (Fig. 2). Forest habitats are highly fragmented in the European agricultural landscapes (Kolb and Diekmann 2004), where parts of this ancient forest help to colonize new post-agricultural forests (Jacquemyn et al. 2001, Verheyen and Hermy 2001). These patches are possibly more isolated than grasslands that often form part of networks of small marginal habitats such as road verges, shading trees, mid-field islets, and set asides (Kleijn and Báldi 2005, Tscharntke et al. 2005). These marginal habitats may function as stepping stones or sources of dispersal (Dorrough et al. 2007, Cousins and Lindborg 2008), and hence contribute to species dispersal among fragments enhancing colonization and mitigating local extinctions (Fischer and Stöcklin 1997).

In agreement with previous results, seed weight was sensitive to isolation of patches when phylogeny was not considered. The current information about importance of seed weight in changing landscapes is contradictory as both light and heavy seeds have been found to react strongly to isolation, possibly depending on the habitat type in question (Kolb and Diekmann 2004, Adriaens et al. 2006, Lindborg 2007, Tremlova and Münzbergová 2007). In our study, isolation sensitive forest species had heavier seeds than isolation neutral species. By contrast, in grasslands, species sensitive to isolation had smaller seeds than isolation neutral species. In forest patches, this may be related to dispersal in time through seed bank, as small-seeded species more often a have persistent seed bank (Bekker et al. 1998), and large seeds could have a competitive advantage (Geritz 1995). In grasslands, however, only approximately half of all plant species contribute seeds to the seed bank (Bakker and Berendse 2001). Large seeds are in general poorer dispersers in space, and often dispersed by animals (Westoby et al. 1996). Since more forest than grassland plants are dispersed by animals, isolation is likely to more strongly affect large seeded forest plants than grassland plants, but see Johst et al. (2002), Purves et al. (2007). If, however, the area is very small, dispersal might not be the key factor for survival and then the small seeds are outcompeted. Small seeded species are often wind dispersed, self-dispersers (Westoby et al. 1996) or transported long distances in the fur of animals (Kiviniemi and Eriksson 1999). Especially in grasslands, self-dispersers cannot colonize other habitat patches whereas wind dispersed species might reach isolated patches. Unfortunately, our data set did not allow us to test for dispersal vectors or attributes as too many species were categorized as having unspecific dispersal attribute or vector.

The phylogenetically informed analysis did not differ in its results from the cross-species analysis except for the seed weight, where the significant relationship in both grassland and forest disappeared when including phylogeny. We could not link this lack of relationship to occurrence of specific plant families. Instead, it indicates that seed weight is related through phylogeny to other traits which actually causes the ecological adaptation. For instance, seed size is negatively related to seed number reflecting a trade-off between many small seeds or few large seeds (Jakobsson and Eriksson 2000). Species with few large seeds showed more dependence on isolation in forests. However, the persistent seed bank of small seeds (Bekker et al. 1998) could mask the actual relationship to the habitat spatial structure.

All included studies related occurrence of habitat specialist species to current patterns of habitat area and isolation in the landscape. Habitat loss in most of the studied regions has been vast, especially for grasslands. The studies that reported the velocity of habitat loss showed that only 0.4–11% of original grassland area has remained and landscapes have been fragmented already for a long time. Landscapes with such long-term decreases of habitat quantity and quality may suffer from loss of sexual heterogeneity and dominance of monoclonal populations causing a decrease in population viability (Holt 1992). Based on the overall observation where long-lived and clonal plants, but not short-lived and non-clonal plants, showed relationship with habitat area and isolation, we suggest that further decrease in habitat area or a continued small patch area will lead to an irreversible change in plant community composition. It is likely that this alteration has been reached in many European landscapes that have been fragmented for a long time and where many non-clonal and short-lived species have already to a large extent disappeared. With this study we show that by using a large-scale dataset, built on solid case studies, it is possible to reveal more general patterns concerning fragmentation effects on European grasslands and forests, information that would have been difficult to detect in single local to regional scale case studies.

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Supplementary material (Appendix E7286 at <www.oikosoffice.lu.se/appendix>). Appendix 1–2.