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IMPORTANCE OF SPECIES TRAITS FOR SPECIES DISTRIBUTION IN FRAGMENTED LANDSCAPES

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Abstract. Knowledge of the relationship between species traits and species distribution in fragmented landscapes is important for understanding current distribution patterns and as background information for predictive models of the effect of future landscape changes. The existing studies on the topic suffer from several drawbacks. First, they usually consider only traits related to dispersal ability and not growth. Furthermore, they do not apply phylogenetic corrections, and we thus do not know how considerations of phylogenetic relationships can alter the conclusions. Finally, they usually apply only one technique to calculate habitat isolation, and we do not know how other isolation measures would change the results.

We studied the issues using 30 species forming congeneric pairs occurring in fragmented dry grasslands. We measured traits related to dispersal, survival, and growth in the species and recorded distribution of the species in 215 grassland fragments.

We show many strong relationships between species traits related to both dispersal and growth and species distribution in the landscape, such as the positive relationship between habitat occupancy and anemochory and negative relationships between habitat occupancy and seed dormancy. The directions of these relationships, however, often change after application of phylogenetic correction. For example, more isolated habitats host species with smaller seeds. After phylogenetic correction, however, they turn out to host species with larger seeds.

The conclusions also partly change depending on how we calculate habitat isolation. Specifically, habitat isolation calculated from occupied habitats only has the highest predictive power. This indicates slow dynamics of the species.

All the results support the expectation that species traits have a high potential to explain patterns of species distribution in the landscape and that they can be used to build predictive models of species distribution. The specific conclusions are, however, dependent on the technique used, and we should carefully consider this when comparing among different studies. Since different techniques answer slightly different questions, we should attempt to use analyses both with and without phylogenetic correction and explore different isolation measures whenever possible and compare the results.

Key words: endozoochory; exozoochory; growth rate; habitat occupancy; habitat suitability; life history; metapopulation; phylogenetic contrast; seed bank; seed dispersal; seed size; terminal velocity.

INTRODUCTION

Habitat fragmentation is considered to be one of the major threats to biodiversity (Eriksson and Ehrlén 2001, Oostermeijer et al. 2003). Recent studies on patterns of distribution in fragmented landscapes have shown that a large number of habitats suitable for a given species stay unoccupied by this species (e.g., Eriksson and Ehrlén 1992, van der Meijden et al. 1992, Ackerman et al. 1996, Eriksson 1996, Ehrlén and Eriksson 2000, Münzbergová 2004). These results imply that distribution of species in such landscapes is largely limited by species ability to spread among localities and successfully establish.

This phenomenon of absence of species from suitable habitats has stimulated studies in which species traits (mainly related to dispersal ability) are related to the patterns of distribution of species in fragmented landscapes (Matlack 2005). Knowledge of such traits can help understanding current distribution patterns. It can also serve as background information for predictive models allowing quantification of the effect of future landscape changes on species distributions (e.g., Higgins et al. 2003, Münzbergová et al. 2005, Trakhtenbrot et al. 2005). The relationship between species traits, landscape attributes (distribution and sizes of localities) and species distribution has thus been a topic of many recent studies (e.g., Bastin and Thomas 1999, Dupré and Ehrlén 2002, Maurer et al. 2003, Kolb and Diekmann 2005). The existing studies on these relationships, however, suffer from several drawbacks.

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PLATE 1. Dry grasslands represent the most species-rich communities in the region. Photo credit: David Püschel.

First, most of the studies do not take into account phylogenetic relationships between species (e.g., Ouborg 1993, Quintana-Ascentio and Menges 1996, Hanski 1999, Kolb and Diekmann 2005; but see Maurer et al. 2003). While such analyses are useful and provide valuable insights into general traits determining species distribution in a landscape, without phylogenetic control, we cannot be sure whether presence of a species at a locality is related to the trait under study or to other traits correlated with these that are characteristic for the whole clade to which the species belongs (Westoby et al. 1995*a*, *b*).

Distinguishing between the traits that are really responsible for a pattern and traits correlated with these within larger species groups can be achieved by comparing results of analyses with and without phylogenetic correction. The necessity of such phylogenetic correction has been a highly debated issue (e.g., Harvey et al. 1995, Westoby et al. 1995*a*, *b*, Silvertown and Dodd 1996, Freckleton et al. 2002, Pocock et al. 2006) and many authors have suggested that the phylogenetical and ecological explanations for species distribution in a landscape are not mutually exclusive (see also Grime and Hodgson 1987). Separating the different causes for species distribution is thus relatively difficult. Still it is generally recognized that both of these types of analyses should be considered when trying to explain the effect of species traits on species distribution (e.g., Eriksson and Jakobsson 1998, Freckleton et al. 2002, Reich et al. 2003).

The second issue is related to our perception of the landscape and to ways of calculating isolation of the localities. While a lot of discussion has been devoted to the algorithms of measuring habitat isolation/connectivity (Tischendorf and Fahring 2000), much less effort has been devoted to consideration of what localities to include in the measure. There are two principal ways to calculate isolation: (1) only from occupied localities and (2) from all localities of the given type (subjectively or by external criteria classified as suitable). Bastin and Thomas (1999) demonstrated that these different ways of calculating habitat isolation might affect conclusions on effects of isolation. These different ways to estimate isolation correspond to different perceptions of the landscape. Using only occupied localities to define isolation is based on a perception of the landscape as static, and assumes that distribution of the species has not changed much in the past. In the other approach, landscapes are viewed as more dynamic, where potential distribution is more important than current distribution, which is likely to change over time.

The last issue we address in this paper is related to the species traits considered. It is relatively common to consider traits related to species dispersal such as seed mass, terminal velocity, seed production or seed bank (e.g., Jackel and Poschlod 2000, Soons and Heil 2002), or simple growth-related traits such as plant height, flowering time, or life history strategy (e.g., Dupré and Ehrlén 2002, Maurer et al. 2003). The effect of traits related to plant growth is, however, largely unknown. In spite of this, traits related to plant growth may be very important for species ability to spread in newly occupied localities and survive there since establishment and survival are important parts of colonization process (Eriksson and Jakobsson 1998).

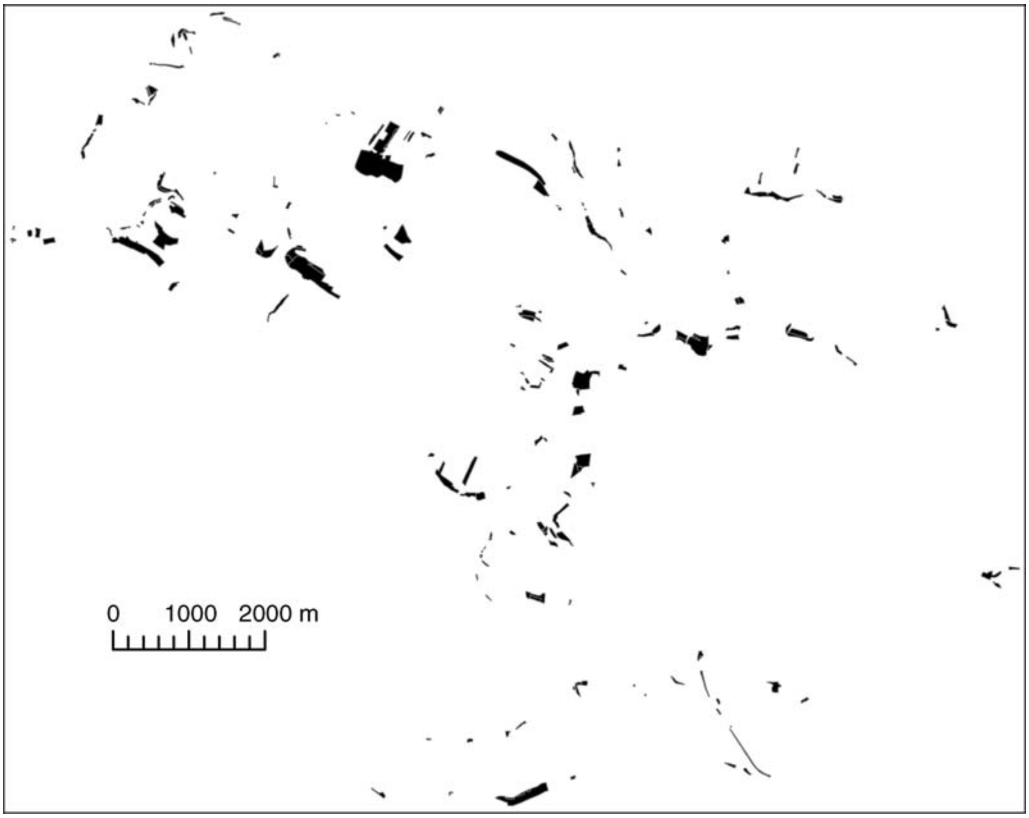

FIG. 1. Distribution of the studied dry grasslands in the landscape.

In this study, we take into account all the abovementioned issues and ask the following questions: (1) What is the effect of dispersal and growth related traits for current species distribution in a landscape? (2) How do the conclusions of the study change when applying phylogenetic correction? (3) How do the conclusions depend on the way of defining habitat isolation?

To address these questions, we selected 30 species forming pairs of congeneric species occurring in fragmented dry grasslands, a habitat not usually considered in studies of this type. We measured traits related to dispersal, individual survival and growth in the species and recorded distribution of the species in 215 grassland fragments.

METHODS

Study area and species

This study was carried out in northern Bohemia, Czech Republic. The study area is delimited by the Labe River on the south and by the villages of Štětí, Křešice u Litoměřic, and Tuhaň a Úštěk. In this region, calcareous dry grasslands form distinct localities surrounded mainly by agricultural fields (see Plate 1). A total of 215 dry grasslands were mapped representing all dry grassland localities within a region of approximately 40 km^2 (Fig. 1). A locality is defined as a continuous grassland with visually homogenous vegetation separated from other localities by an unsuitable area. In cases of abrupt vegetation change within continuous grassland, the parts with different vegetation were treated as different localities. These cases were not common; in all of them there was a visual topographic barrier between the localities such as a small ditch or change of slope from very steep to flat.

We selected 30 native perennial herbs that were restricted to dry calcareous grasslands in the study region and that are neither very rare nor extremely common in these localities. The species were also selected to form 15 pairs of closely related species (Table 1). While most pairs consisted of species of the same genus, in four cases, the pairs consisted of relatively closely related species from the same family (Table 1). To explore the effect of these four more distantly related species pairs on the conclusions, we carried all analyses both with and without them.

Species traits

We measured two types of traits: traits related to species dispersal ability and traits related to species survival and growth. They were terminal velocity, plant height, ability to attach to sheep fur (exozoochory), seed mass, seed production, seed germination, proportion of viable seeds, seed dormancy, ability to flower in the first year (early flowering), production of aboveground and belowground biomass within one field season, and survival in the seed bank.

Terminal velocity was estimated by measuring the flight time of a seed from a predefined height (3 m; Münzbergová 2004). Ten seeds from each of three different populations of each species were measured. The type of propagule used for the measurements corresponded to the propagule leaving the plant. Mean dispersal distance (D, referred to as anemochory) was expressed as

$$D = (w \times h)/t \tag{1}$$

where w is the wind speed, h is the plant height, and t is the terminal velocity. The wind speed used for the calculation was a maximum daily mean wind speed detected at a nearby meteorological station (Doksany) between 1993 and 2003 (13.7 m/s). This value was selected just to illustrate the possible consequences of the terminal velocity and plant height for seed dispersal. Since wind speed is a constant in the calculation, using other values would not affect the results. Plant height was estimated by measuring the height of 10 randomly selected flowering plants per locality at each of three selected localities.

We are aware that our dispersal model is very simplified. Nevertheless, it has been successfully used in other studies to characterize mean dispersal distance of seeds (e.g., Soons and Heil 2002, Münzbergová et al. 2005, Herben et al. 2006) and is the easiest way to combine the three key parameters affecting dispersal. We thus suggest that it is a useful proxy of potential wind dispersal distances for comparison among the species.

Ability to disperse via exozoochory was assessed by gently placing a piece of sheep fur over a tray containing 100 seeds, removing it and counting the number of attached seeds (Münzbergová 2004).

Seed mass was estimated by weighing five groups of 10 seeds from three source populations. It is generally recognized that seed mass can serve as proxy of seed dispersal ability and germination as well as competitive ability of the species.

Seed production was estimated as number of flowering plants per square meter counted in 10 quadrats in each of three populations of the species. The quadrats were intentionally selected in areas with the highest density of the species that could be found in the different populations. This number was multiplied by seed production per plant estimated in these populations. This value was then multiplied by the proportion of viable seeds to estimate number of viable seeds produced per area per year. This value provides information on maximum seed production by a stand of a given species. It thus provides an estimate of the potential supply of seeds ready to colonize other localities.

Traits related to plant growth were estimated in a common garden experiment. In late summer (August to September) 2003, 50 seeds of a single species were sown in 19 × 19 × 19 cm pots in a common garden in a 1:2 mixture of sand and garden substrate. For each species, seeds originating from three different localities were used. Seeds from one locality were placed into one pot; there were three replicates per locality and species thus yielding nine pots per species.

In November 2003, we recorded the number of germinated seedlings per pot. Since the species either germinated at a high rate in the autumn or did not germinate at all, we coded this information as a binary variable (dormancy; yes or no). The ability to germinate early indicates that the seeds do not posses any type of dormancy. For determining seed dormancy, it is important that the seeds be sown shortly after being harvested. This information provides an indication of the germination dynamics of the species and thus about the potential performance of the seedlings at the localities.

The number of plants in the pot was also recorded in May 2004 for all species to have the same recording date for species with and without seed dormancy. For the early germinating species, the May germination was the number of germinated plants in autumn reduced by winter mortality. This number served as an estimate of germination fraction (germination in Petri dishes was used only to estimate production of viable seeds per area).

Table 1. List of species used in the study.

Pair no.	Species	Abbreviation	Family
1	*Agrimonia eupatoria*	Agr eup	Rosaceae
	Sanguisorba minor	San min	Rosaceae
2	*Asperula cynanchica*	Asp cyn	Rubiaceae
	Asperula tinctoria	Asp tin	Rubiaceae
3	*Astragalus cicer*	Ast cic	Leguminosae
	Astragalus glycyphyllos	Ast gly	Leguminosae
4	*Brachypodium pinnatum*	Bra pin	Gramineae
	Bromus erectus	Bro ere	Gramineae
5	*Campanula glomerata*	Cam glo	Campanulaceae
	Campanula rotundifolia	Cam rot	Campanulaceae
6	*Carex tomentosa*	Car tom	Cyperaceae
	Carex flacca	Car fla	Cyperaceae
7	*Centaurea jacea*	Cen jac	Compositae
	Centaurea scabiosa	Cen sca	Compositae
8	*Cirsium acaule*	Cir aca	Compositae
	Cirsium pannonicum	Cir pan	Compositae
9	*Coronilla vaginalis*	Cor vag	Leguminosae
	Coronilla varia	Cor var	Leguminosae
10	*Inula hirta*	Inu hir	Compositae
	Inula salicina	Inu sal	Compositae
11	*Laserpitium latifolium*	Las lat	Umbelliferae
	Peucedanum cervaria	Peu cer	Umbelliferae
12	*Linum flavum*	Lin fla	Linaceae
	Linum tenuifolium	Lin ten	Linaceae
13	*Lotus corniculatus*	Lot cor	Leguminosae
	Medicago falcata	Med fal	Leguminosae
14	*Salvia pratensis*	Sal pra	Labiatae
	Salvia verticillata	Sal ver	Labiatae
15	*Trifolium medium*	Tri med	Leguminosae
	Trifolium montanum	Tri mon	Leguminosae

Note: The nomenclature follows Tutin et al. (1964–1983).

TABLE 2. List of traits used in the study.

Parameter	Units
Seed mass†	mg
Terminal velocity	m/s
Anemochory†	mean dispersal distance (m)
Seed production†	viable seeds/m^2
Seed bank†	100 − (percentage decline in germination ability after 1 yr)
Exozoochory†	seeds attached to sheep fur (%)
Germination fraction‡	plants after 1 yr from sown seeds (%)
Dormancy†,‡	0/1 (germination in autumn/spring)
Early flowering†,‡	1/0 (flowering in the first year)
Aboveground biomass†,‡	g (for one plant after 1 yr)

† These parameters were used in the test presented in this study.

‡ These parameters come from the common garden experiment.

In autumn (September–November) 2004, we recorded the presence of flowering plants in the pots to assess the ability of the species to flower in the first year (early flowering; yes or no). In November 2004, the plants were harvested. Each harvested plant was divided into above- and belowground biomass, dried to constant mass, and weighed. We used the mass of the largest plant per species as an estimate of growth ability of the species; in all cases there were one to three large plants in the pot and sometimes also many small ones. We suggest that the size of the largest plant provides a relatively good estimate of what a plant can do in natural conditions within one year. This indicates that the flowering can also be interpreted as the ability of the species to do so, since at least some plants did not suffer from high competition. The division of the species into early and late flowering categories, and biomass production of the plant, correspond well with our personal observations on performance of the plants in the field. We thus suggest these data can provide insights into growth dynamics of the plants in the field.

To estimate the ability to survive in the seed bank, three nylon bags per species, each containing 50 seeds, were buried at each of two different localities in November 2003 and excavated in October 2004. The excavated seeds were tested for viability. The seeds were regularly watered with distilled water on the Petri dishes and kept in a growth chamber under a fluctuating regime (12 hours light at 20°C, 12 hours dark at 10°C). Germinated seeds were regularly removed. The seeds of species that did not germinate were stimulated by adding giberelic acid and abraded by sandpaper. The seeds that still did not germinate and did not decay were then tested for viability using the tetrazolium test. All seeds identified as viable by any of the methods were summed. The same procedure was used to estimate the viability of fresh seeds (proportion of viable seeds) to provide a baseline from which to estimate the decline in germination over time. The ability to form a seed bank indicates that the seed can survive given that it does not have suitable conditions for germination. It, however, does not imply it has any intrinsic dormancy.

All measured traits are listed in Table 2 and values of these traits for each species are in Appendix A. In all cases, we were working with average values for each species.

Habitat suitability

To calculate habitat occupancy and isolation of a habitat, we had to define suitable localities. Suitable localities were defined using a Beals index (Beals 1984, Münzbergová and Herben 2004). This index calculates the probability of encountering a species at a locality using data on the presence of other species at that locality and on patterns of co-occurrence of the target species with other species. To estimate the species co-occurrence patterns, we used 2984 relevés on species composition of dry calcareous grasslands in the Czech Republic from the Czech national phytosociological database (Chytrý and Rafajová 2003). Unoccupied localities with a Beals index reaching at least the 5% quantile of the Beals index of occupied localities were considered suitable. Using 1% or 10% quantiles did not significantly affect the conclusions.

We also used data on abiotic conditions of the localities (geology, potential direct solar radiation, and slope of the target localities) to assess habitat suitability. These gave very similar results to the Beals index, so we use only the former in the study.

Habitat isolation

We used three different approaches to calculate habitat isolation in this study. First, we calculated isolation of a locality using its distance from all dry grasslands, subjectively assumed to be suitable for all the species, in the study region. In this case, habitat isolation of a given locality was the same for all the species. Second, we calculated isolation only from all occupied localities. In this and in the following case, habitat isolation of a single locality differed among species. Finally, we calculated isolation from all localities classified as suitable for the species using the Beals index. See *Introduction* for the rationale behind calculating isolation from unoccupied localities and Eq. 2 for the exact way to do this.

Calculation of habitat isolation was based on centroids of the localities, derived from a digital map of the localities provided by T. Chýlová. Isolation of a locality was expressed as a mass of surrounding localities weighted by its distance to the target locality. Isolation of a locality was expressed as follows:

$$I_{ij} = \sum_{k=1}^{n}\left[\left(P_k/d_{jk}^2\right) \times O_k\right], j \neq k \qquad (2)$$

where I_{ij} is isolation of locality j for species i, k are all the surrounding localities within 1.8 km distance from the target locality, P_k is a size of locality k in square kilometers, d_{jk} is distance between localities j and k in

TABLE 3. Correlations among single traits used in the study.

Parameter	Seed mass	Anemochory	Seed production	Dormancy	Early flowering	Aboveground biomass	Seed bank	Exozoochory
Without phylogenetic correction								
Seed mass		−0.135	−0.127	−0.073	−0.066	0.233	0.118	0.104
Anemochory	−0.135		−0.050	0.193	−0.181	−0.273	−0.106	**0.475**
Seed production	−0.127	−0.050		0.254	−0.091	−0.091	0.266	−0.312
Germination fraction	0.153	−0.147	0.216	−0.117	0.177	−0.215	−0.180	0.079
Dormancy	−0.073	0.193	0.254		**−0.391**	−0.258	−0.103	0.248
Early flowering	−0.066	−0.181	−0.091	**−0.391**		**0.498**	0.122	−0.129
Aboveground biomass	0.233	−0.273	−0.091	−0.258	**0.498**		**0.653**	**−0.375**
Seed bank	0.118	−0.106	0.266	−0.103	0.122	**0.653**		**−0.500**
Exozoochory	0.104	**0.475**	−0.312	0.248	−0.129	**−0.375**	**−0.500**	
With phylogenetic correction								
Seed mass		−0.069	−0.052	0.342	−0.125	−0.326	−0.293	**0.488**
Anemochory	−0.069		0.066	−0.174	−0.056	0.050	0.205	0.199
Seed production	−0.052	0.066		−0.317	0.142	0.257	**0.413**	−0.057
Germination fraction	−0.312	−0.144	0.133	**−0.428**	**0.405**	−0.068	−0.149	0.134
Dormancy	0.342	−0.174	−0.317		**−0.589**	−0.186	0.100	0.081
Early flowering	−0.125	−0.056	0.142	**−0.589**		−0.286	−0.159	0.006
Aboveground biomass	−0.326	0.050	0.257	−0.186	−0.286		**0.390**	**−0.571**
Seed bank	−0.293	0.205	**0.413**	0.100	−0.159	**0.390**		−0.278
Exozoochory	**0.488**	0.199	−0.057	0.081	0.006	**−0.571**	−0.278	

Notes: Significant correlations ($P < 0.05$) are in boldface. No correction for multiple testing was used here.

kilometers, and O_k is a binary (0,1) variable coding occupancy or suitability of a locality. When calculating isolation from all localities, O_k is always 1.

Isolation of a locality was calculated only for 187 localities out of 215. The other localities were excluded because there were unanalyzed localities within 1.8 km of these localities. The 1.8-km zone was selected as a distance over which habitat isolation was measured; this was the maximum distance that we were able to reliably cover by the field survey. Not all marginal localities had to be excluded, however, since large areas of arable fields surrounded some of the localities. Only the 187 localities were used in all the subsequent analyses.

Data analysis

To reduce the high dimensionality of the trait-by-species matrix, we selected only a subset of traits that were expected to be most informative and not too closely correlated with other traits (Table 2). Correlation of the remaining species traits was studied using simple correlation analysis. The traits that changed values over several orders of magnitude (seed mass, seed production, aboveground biomass) were logarithmically transformed before the analysis. This analysis was then repeated after subtracting the mean trait value for each species pair from the trait value of each species in that pair; this was done to explore correlation among traits after phylogenetic correction.

Some traits used in the analysis were significantly correlated (Table 3), but we did not want to exclude those since they carry different biologically meaningful information. In all the subsequent analyses, we were thus using multiple partly correlated traits. This could theoretically bias our conclusions. To explore this, we in all cases compared a test with all the variables included with results of stepwise analysis.

To visualize similarity between the different species in their traits we used principal component analysis (PCA). The data on single species traits were treated as "species," and data on each species represented "samples." The analysis was centered and standardized by "species"; in this way all the traits were expressed in the same, relative, units. For this as well as for subsequent analyses, we used only traits marked in Table 2.

Percentage of occupancy of the localities was expressed as the portion of all occupied localities either from all localities, or from all suitable localities. To estimate the effect of plant traits on overall habitat occupancy, we used generalized linear models (GLM), assuming binomial distribution of the dependent variable. Numbers of occupied and all available localities were used as bind dependent variables (the variables were combined into one variable using command cbind in S-PLUS 2000 (MathSoft, Needham, Massachusetts, USA), the resulting variable carries information on frequency of an event), and all species traits were used as independent variables. The same analysis was then repeated with pair code as another independent variable.

To estimate the effect of species traits and landscape properties on species occurrence at a locality, we used logistic regression. Presence of each species in each locality was used as the dependent variable, and size and isolation of a locality, all species traits, and the interaction of all species traits with habitat size and isolation were used as independent variables. In the text, however, we present only the results for the interaction terms of habitat isolation/size and species traits. The results of the main effects would actually be a more

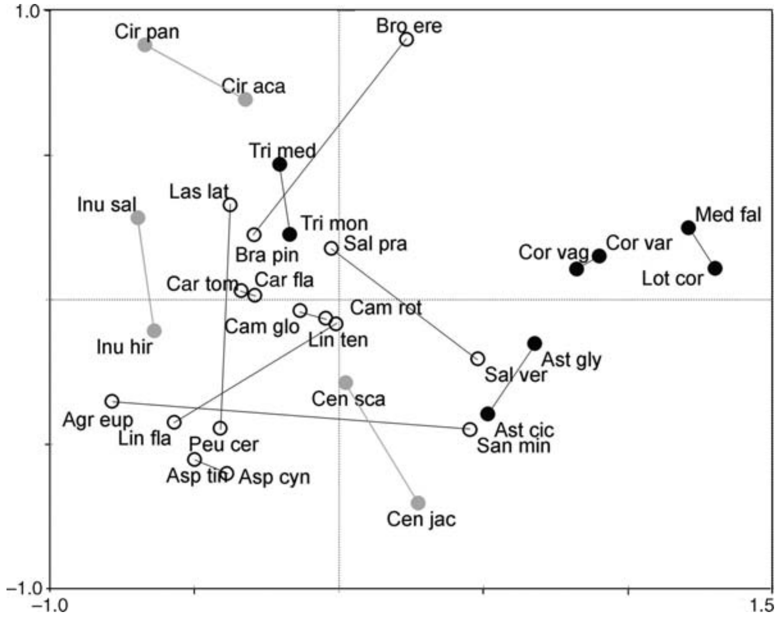

FIG. 2. Relationship between individual species determined by principal component analysis (PCA) using trait data as dependent variables. Species with solid black symbols are from the family Leguminosae, species with solid gray symbols are from the family Compositae, and species with open symbols are from the other families (each of these pairs is from a different family). Species abbreviations are provided in Table 1.

complicated approach to study the effect of traits on habitat occupancy mentioned above.

Analyses calculating isolation from all dry grasslands in the region and from only occupied localities were based on all the studied localities. In the analyses with isolation calculated from all suitable localities, we use data only from suitable localities for each species.

To visualize interactions of traits and landscape properties in a graphic form, we plotted the traits for species occurring in localities with a given property against the property. The species missing at each locality were not visualized in these graphs. To visualize the results after phylogenetic correction, we used species traits after subtracting the mean of the trait value for each species pair from the trait value.

All the above analyses are based on traits across all 30 species and do not allow easy interpretation of the distribution of the single species. To show how single species respond to habitat size and isolation, we performed a multivariate canonical correspondence analysis (CCA) using presence of all the species at the locality (species composition based on the 30 species) as the dependent variable and habitat size or isolation as independent variables. To separate the effect of habitat size and isolation, we also performed analyses with habitat size as an independent variable and isolation as covariate and the other way round. The analyses were done only for isolation from all localities, i.e., the type of isolation that is the same for all the species.

All the univariate analyses were done using S-PLUS 2000; all the multivariate analyses were done using CANOCO (ter Braak and Šmilauer 1998). All the univariate analyses were done with type III sum of squares, so the effect of each independent variable was estimated after removing the effect of all the other independent variables.

RESULTS

Correlation of the different traits shows a positive relationship between anemochory and exozoochory. There is also a positive relationship between aboveground biomass of a plant in the first year and its ability to flower in the first year and to produce a seed bank. Plants with high aboveground biomass tend to have low ability to disperse via exozoochory. There is also a negative relationship between ability to create seed bank and exozoochory and between seed dormancy and ability to flower early (Table 3).

Only three of these relationships stay significant after phylogenetic correction (between aboveground biomass and seed bank and exozoochory and between early flowering and dormancy). There is also a significant positive relationship between seed mass and exozoochory and seed production and seed bank (Table 3). The correlations partly change after removing the four noncongeneric pairs (see Appendix B).

Comparison of traits of species within the pairs indicates that many species within a pair are rather dissimilar (Fig. 2). Nevertheless, species pair explains 78% of the total variation in the dataset as identified using PCA with species pair as a covariate.

Tests exploring the effect of species traits on habitat occupancy indicate many significant patterns (Table 4). When working with all localities and without phyloge-

TABLE 4. Effect of species traits on habitat occupancy estimated using general linear models assuming binomial distribution of the dependent variable.

	All habitats				Suitable habitats			
	Without PC		With PC		Without PC		With PC	
Parameters	P	R^2	P	R^2	P	R^2	P	R^2
Seed bank	0.681		0.152		0.002	0.012 (+)	0.749	
Anemochory	0.016	0.005 (+)	0.207		<0.001	0.043 (+)	0.195	
Seed mass	0.138		0.837		0.090		0.945	
Early flowering	0.007	0.006 (−)	<0.001	0.035 (+)	0.001	0.015 (−)	<0.001	0.042 (+)
Dormancy	<0.001	0.08 (−)	<0.001	0.066 (+)	<0.001	0.075 (−)	<0.001	0.079 (+)
Aboveground biomass	<0.001	0.151 (+)	<0.001	0.013 (−)	<0.001	0.131 (+)	<0.001	0.024 (−)
Exozoochory	<0.001	0.107 (+)	<0.001	0.016 (−)	<0.001	0.131 (+)	<0.001	0.027 (−)
Seed production	<0.001	0.038 (+)	<0.001	0.02 (+)	0.182		<0.001	0.03 (+)

Notes: For analysis without phylogenetic correction (PC), error df = 21; for analysis with phylogenetic correction, error df = 7. The sign of the relationship is provided in significant results.

netic correction, species with higher habitat occupancy have a significantly better ability to disperse by wind, higher seed production, lower dormancy, flower later, have higher aboveground biomass, and disperse better by exozoochory (Table 4).

Several of these results change with phylogenetic correction. Specifically, there was no significant effect of anemochory on habitat occupancy. The effect of dormancy and early flowering changed from negative to positive and the effect of aboveground biomass and exozoochory changed from positive to negative (Table 4). The species pair explained 67.8% of the total variation in habitat occupancy.

Several patterns also changed when analyzing habitat occupancy using suitable localities only. In none of the cases, however, did the sign of the relationship switch (Table 4). The relationships also changed relatively little when using stepwise analyses. Specifically, a few traits that were nonsignificant when all traits were included were dropped from the model, but the direction of the relationships stayed the same indicating that the patterns identified are not dependent on the exact formulation of the model (not shown). When performing the analyses without the four non-congeneric pairs, the signs of the relationships stayed the same, although fewer patterns were significant, probably due to smaller sample size (not shown).

All traits except for seed production and exozoochory significantly interact with landscape properties at least in some cases (Table 5), although the R^2 of these relationships are quite weak. This is likely due to the fact that main effects of the variables account for large part of the variation, so the variation left unexplained is relatively low. A higher number of significant interactions was observed for habitat isolation than for habitat size. The highest number of significant results was observed when calculating isolation from occupied localities only. Phylogenetic correction resulted in similar significance values; the sign of the relationship, however, reversed in several cases (Table 5). Species pair explains 18.6% of species presence at a locality.

When working with isolation from occupied localities only and without phylogenetic correction there was a significant negative interaction between habitat size and early flowering. With phylogenetic correction there was a significant positive interaction between habitat size and seed bank, indicating that plants occurring on smaller localities are those that survive less in the seed bank (Table 5).

There were multiple interactions with habitat isolation in the analysis without phylogenetic correction when isolation from occupied localities was used. Specifically, plants that occur more frequently in more isolated localities had seeds with lower ability to disperse by wind (Fig. 3A), smaller seeds (Fig. 3B), higher dormancy, higher aboveground biomass, tend to flower in the first year, and have higher ability to survive in the seed bank (Table 5). Phylogenetic correction changed the pattern in several cases. Specifically, species that occur in more isolated localities actually have larger seeds (Fig. 3C) and lower aboveground biomass. The effect of dormancy and early flowering became nonsignificant (Table 5). As above, the signs of the relationships stayed the same when selecting variables using stepwise regression. Also there were very few changes when removing the four non-congeneric pairs, although, again, fewer significant results probably due to smaller sample size.

Contrary to the frequent reversal of the sign of the relationship in analyses with and without phylogenetic correction, the sign of the relationship never reversed in analyses with different definitions of habitat isolation. The number of significant relationships was, however, much lower when habitat isolation was calculated from all localities or suitable localities compared to cases when isolation was calculated only from occupied localities (Table 5).

Habitat isolation, but not size, significantly affected species composition at the localities ($P = 0.006$; it explained 9.02% of the variation that could be explained by one ordination axis). The effect of habitat size was only marginally significant ($P = 0.07$, it explained 6.01% of variation that could be explained by one ordination axis). Analyses with habitat size or isolation as a

TABLE 5. Effects of interactions between habitat size/isolation and species traits on species occurrence at a locality estimated using logistic regression.

	Without PC				With PC			
	Habitat size		Isolation		Habitat size		Isolation	
Parameters	*P*	R^2	*P*	R^2	*P*	R^2	*P*	R^2
Occupied localities								
Seed mass	0.895		**0.05**	0.005 (−)	0.384		**0.01**	0.002 (+)
Anemochory	0.622		**<0.001**	0.006 (−)	0.584		**<0.001**	0.006 (−)
Seed production	0.32		0.178		0.666		0.749	
Dormancy	0.337		**0.001**	0.002 (+)	0.524		0.236	
Early flowering	**0.049**	0.001 (−)	**<0.001**	0.003 (+)	0.401		0.13	
Aboveground biomass	0.441		**0.004**	0.002 (+)	0.978		**<0.001**	0.002 (−)
Seed bank	0.281		**0.024**	0.001 (+)	**<0.001**	0.003 (+)	**0.022**	0.002 (+)
Exozoochory	0.736		0.56		0.384		0.35	
All localities								
Seed mass	0.424		0.941		**0.049**	0.001 (+)	0.854	
Anemochory	0.437		0.107		0.344		**0.078**	0.001 (−)
Seed production	0.286		0.509		0.682		0.789	
Dormancy	0.228		0.456		0.405		0.601	
Early flowering	**0.05**	0.001 (−)	0.733		0.445		0.558	
Aboveground biomass	0.341		0.117		0.995		0.114	
Seed bank	0.251		0.14		**0.086**	0.001 (+)	**0.065**	0.001 (+)
Exozoochory	0.707		0.522		0.381		0.578	
Suitable localities								
Seed mass	0.446		0.776		**0.049**	0.001 (+)	0.46	
Anemochory	0.244		**0.001**	0.002 (+)	0.396		**0.003**	0.002 (−)
Seed production	0.238		0.3		0.525		0.434	
Dormancy	0.829		0.508		0.71		0.796	
Early flowering	0.239		0.381		0.693		0.488	
Aboveground biomass	0.535		0.152		0.977		0.234	
Seed bank	0.228		0.092		0.086		**0.047**	0.001 (+)
Exozoochory	0.809		0.3		0.383		0.193	

Notes: The sign of the relationship is provided for significant results. Error df = 3707 and 3692 for analyses using isolation from all or occupied localities without and with phylogenetic correction (PC), respectively; error df = 3274 and 3259 for analyses using isolation from all suitable localities without and with phylogenetic correction, respectively.

covariate did not change these results very much and thus are not shown. In more isolated localities, species such as *Inula hirta*, *Campanula rotundifolia*, *Cirsium acaule*, *Salvia pratensis*, and *Astragalus glycyphyllos* are more common. On the other hand, species such as *Linum flavum*, *Laserpitium latifolium*, *Cirsium pannonicum*, *Coronilla vaginalisi*, and *Campanula glomerata* are more common in less isolated localities (see Table 6 for full list of species). Smaller localities host species such as *Campanula glomerata*, *Laserpitium latifolium*, *Bromus erectus*, and *Cirsium pannonicum*, while in larger localities *Inula hirta*, *Linum tenuifolium*, *Campanula rotundifolia*, and *Asperula tinctoria* are more common (see Table 5 for a full list of species). These relationships did not change much after removing the non-congeneric pairs. The main difference was a lower percentage of variation explain by habitat size and isolation (not shown).

DISCUSSION

Results of this study show a strong relationship between species traits and species distribution in the landscape. This is true both when looking at percentage of habitat occupancy and when looking at species response to habitat size and isolation. However, the specific nature of the relationships often changes after phylogenetic correction or with different definitions of habitat isolation.

Exploration of species traits studied in this paper indicates many significant relationships between these. For example, we have demonstrated significant relationship between the ability to disperse by anemochory and exozoochory (see also Fischer et al. 1996). Our results, however, also indicate that this pattern disappears when performing phylogenetic correction. Similarly, we found a negative relationship between seed dispersal ability (exozoochory) and survival in the seed bank (see also Ehrlén and Groenendael 1998). Again, this relationship disappeared after phylogenetic correction. The reversal of the relationships between species traits after phylogenetic correction is in agreement with previous studies (e.g., Silvertown and Dodd 1996) and suggests that we should expect different conclusions in the subsequent analyses with and without phylogenetic correction.

Percentage of habitat occupancy was significantly affected by both traits related to seed dispersal and traits related to plant growth. A high number of species traits explaining habitat occupancy is in agreement with previous studies exploring this relationship (e.g., Ouborg

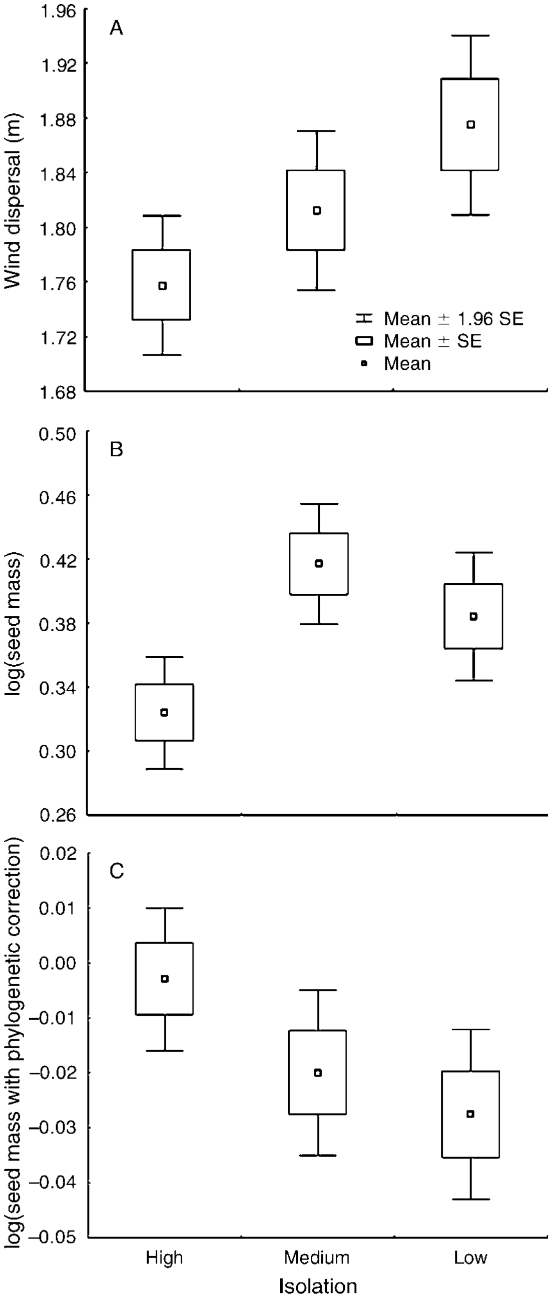

FIG. 3. Relationship between species traits and landscape properties: (A) anemochory and habitat isolation, (B) log(seed mass) and habitat isolation, and (C) log(seed mass) after phylogenetic correction and habitat isolation. For the purpose of the graph, habitat isolation was divided into three equidistant categories. In each case, only species occurring at the given locality are included. All the patterns are significant (Table 5).

1993, Eriksson and Jakobsson 1998, Maurer et al. 2003, Kolb and Diekmann 2005). In our study, more widely distributed species had better dispersal ability as well as faster growth. Kolb and Diekmann (2005) found a similar pattern for dispersal. On the other hand, Eriksson and Jakobsson (1998) and Maurer et al. (2003) have shown that habitat occupancy does not depend on traits related to dispersal.

Species traits also determine species response to habitat size and isolation; with more significant interactions with habitat isolation than with size. This is in agreement with conclusions of Piessens et al. (2004) and Kolb and Diekmann (2005), who showed higher effects of habitat isolation than size on species occurrence in forest fragments. In all comparisons, we have shown that species with higher anemochory are missing from isolated localities. This contrasts with conclusions of Piessens et al. (2005), who suggested that anemochory is the most important trait allowing species survival at isolated localities. The observed pattern clearly indicates that anemochory is not the main factor that can guarantee species occurrence in isolated localities. Also we did not find any significant effect of exozoochory. This may indicate that it is not dispersal but rather establishment that limits species distribution at isolated habitats. It is, however, also possible that other dispersal traits that were not measured in this study, such as endozoochory, are the most important dispersal types in the studied landscape (e.g., Bonn 2004). Isolated localities also host species with significantly smaller seeds suggesting that seed size might be better predictor of dispersal than our (assumed) more direct measures of dispersability (Ehrlén and Eriksson 2000).

In agreement with Piessens et al. (2004), we have shown that survival in the seed bank is important for species presence in isolated localities. This pattern is also in agreement with many other studies that indicate that survival in seed bank is crucial for population survival (e.g., Thompson et al. 1998, Turnbull et al. 2000).

The results also show that species occurring in smaller localities flower earlier than species in larger localities. This can be explained by the fact that small localities have a higher edge-to-area ratio and are thus more disturbed. Disturbed localities have also been shown to host early flowering species in previous studies (e.g., Thompson and Rabonowitz 1989, Thompson and Hodkinson 1998, Silvertown and Charlesworth 2001, Ehrlén and Lehtilä 2002).

An important conclusion from this study is that the effect of species traits on species response to habitat size and isolation can completely reverse when applying phylogenetic correction (reversals after phylogenetic correction were found also by Murray et al. [2002] and Pocock et al. [2006] but not, e.g., by Maurer et al. [2003] and De Bello et al. [2005]). For example, species were detected to have smaller seeds when occurring at more isolated localities, but this relationship reversed direction after phylogenetic correction (see also Eriksson and Jakobsson 1998). The contradiction between the two patterns is probably a consequence of the stability of seed size within species phylogenies (e.g., Mazer 1989, Kelly and Purvis 1993, Kelly 1995). The main effect of seed size was thus probably removed when performing

TABLE 6. Response of studied species to habitat isolation and size determined using canonical correspondence analysis (CCA).

Response to isolation		Response to habitat size	
Species	Position	Species	Position
Inula hirta	−0.402	*Campanula glomerata*	−0.6187
Campanula rotundifolia	−0.2091	*Laserpitium latifolium*	−0.6081
Cirsium acaule	−0.1722	*Bromus erectus*	−0.1377
Salvia pratensis	−0.1411	*Cirsium pannonicum*	−0.127
Astragalus glycyphyllos	−0.1187	*Linum flavum*	−0.0943
Bromus erectus	−0.1017	*Sanguisorba minor*	−0.0753
Carex tomentosa	−0.0655	*Brachypodium pinnatum*	−0.0681
Trifolium medium	−0.0629	*Salvia verticillata*	−0.0597
Asperula tinctoria	−0.0604	*Coronilla varia*	−0.0585
Lotus corniculatus	−0.0503	*Centaurea jacea*	−0.0429
Carex flacca	−0.0404	*Agrimonia eupatoria*	−0.0162
Agrimonia eupatoria	−0.0139	*Asperula cynanchica*	−0.0024
Centaurea scabiosa	0.0037	*Trifolium montanum*	0.0091
Coronilla varia	0.0111	*Lotus corniculatus*	0.0094
Brachypodium pinnatum	0.0215	*Cirsium acaule*	0.0142
Medicago falcata	0.0276	*Medicago falcata*	0.016
Sanguisorba minor	0.0384	*Carex flacca*	0.0305
Trifolium montanum	0.0457	*Trifolium medium*	0.0382
Centaurea jacea	0.0591	*Coronilla vaginalis*	0.0447
Salvia verticillata	0.0601	*Centaurea scabiosa*	0.0562
Linum tenuifolium	0.0664	*Salvia pratensis*	0.0612
Inula salicina	0.1001	*Inula salicina*	0.0694
Astragalus cicer	0.1112	*Carex tomentosa*	0.0737
Asperula cynanchica	0.1184	*Astragalus glycyphyllos*	0.1182
Peucedanum cervaria	0.3271	*Astragalus cicer*	0.1682
Campanula glomerata	0.3499	*Peucedanum cervaria*	0.1968
Coronilla vaginalis	0.363	*Asperula tinctoria*	0.2291
Cirsium pannonicum	0.7953	*Campanula rotundifolia*	0.2575
Laserpitium latifolium	0.8394	*Linum tenuifolium*	0.3596
Linum flavum	1.0103	*Inula hirta*	0.6533

Notes: Habitat isolation explained 9.02% of the variation in species composition that could be explained by one ordination axis; the effect is significant. Habitat size explained 6.01% of the variation in species composition that could be explained by one ordination axis; the effect is marginally significant. The table shows position on the first ordination axis; negative values indicate species prevailing at isolated and small localities, respectively.

the analysis of phylogenetically contrasting pairs. The residual variation in seed size may describe differences in species ability to establish at these localities (reserve effect [Westoby et al. 1996]) given that they disperse there.

The potential reversal of conclusions after application of phylogenetic correction indicates that interpretation of the results of previous studies on this topic (e.g., Ouborg 1993, Quintana-Ascentio and Menges 1996) in terms of factors responsible for species distribution in the landscape is partly problematic. Since these studies usually do not perform the phylogenetic correction, it is not clear which patterns are really the effects of the given trait and which are just due to other correlated properties of the whole genus. On the other hand, even results with phylogenetic correction have to be interpreted with caution since we may miss patterns that are characteristic for the whole species group. Both types of relationship should thus be explored to understand species-traits–landscape-structure relationships.

The results also show strong differences in conclusions when working with different isolation measures. The highest number of significant relationships was found when working with isolation calculated from occupied localities only; this model thus has the best predictive ability for species distribution. This is a measure that has been previously used by others (e.g., Quintana-Ascentio and Menges 1996, Johansson and Ehrlén 2003, Hanski et al. 2004). Its significance suggests that it is current landscape occupancy, and not distribution of suitable localities in the landscape, that determines the probability of species occurrence on single localities. While both conclusions would be compatible with the predictions of metapopulation theory (e.g., Hanski 1999), we suggest that higher predictive power of a model measuring isolation from occupied localities indicates relatively slow dynamics of the species.

The analysis of effect of habitat size and isolation on species composition of the locality confirms that habitat isolation is more important than habitat size. The group of species restricted to non-isolated localities includes many endangered species such as *Linum flavum, Cirsium pannonicum*, and *Coronilla vaginalis*. This indicates that habitat fragmentation constitutes a serious threat to dry grassland species in the region.

In this paper, we have explored the effect of species traits on species distribution in the current landscape as described by current habitat size and isolation. It has, however, been repeatedly shown that species distribution may depend not only on current landscape structure, but also on landscape structure in the past (Jacquemyn et al. 2001, Johansson and Ehrlén 2003, Lindborg et al. 2005, Herben et al. 2006). However, exploring the effect of past landscape structure was beyond the scope of the current study.

Conclusions

We have shown many significant relationships between species traits related to both dispersal and growth and species distribution in the landscape. The directions of these relationships, however, often change after application of phylogenetic correction. The conclusions also partly change depending on whether isolation is calculated from all potential localities or occupied localities. All this indicates that species traits have a high potential to explain the pattern of species distribution in the landscape. To build predictive models of species distribution, however, we have to carefully consider the technique used. We suggest that the results without phylogenetic correction can be better used for predicting patterns of distribution for large species groups. The phylogenetically corrected results might be more suitable for predicting selection pressures on changes of life history traits within smaller species groups. It has to be, however, kept in mind that the results are complementary and both of these should be carefully considered when trying to understand species distributions.

All the results suggest also that when comparing relationships between species traits and species distribution among published studies we have to carefully consider the technique used in each particular case. In the future we should thus attempt to use analysis both with and without phylogenetic correction and explore different isolation measures whenever possible and try to identify the differences in conclusions between these.

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LITERATURE CITED

Ackerman, J. D., A. Sabat, and J. K. Zimmerman. 1996. Seedling establishment in an epiphytic orchid: an experimental study of seed limitation. Oecologia 106:192–198.

Bastin, L., and C. D. Thomas. 1999. The distribution of plant species in urban vegetation fragments. Landscape Ecology 14:493–507.

Beals, E. W. 1984. Bray-Curtis ordination: an effective strategy for analysis of multivariate ecological data. Advances in Ecological Research 14:1–55.

Bonn, S. 2004. Dispersal of plants in the Central European landscape: dispersal processes and assessment of dispersal potential exemplified for endozoochory. Dissertation zur Erlangung des Doktorgrades der Naturwissenschaften, Universität Regensburg, Germany.

Chytrý, M., and M. Rafajová. 2003. Czech national phytosociological database: basic statistics of the available vegetation-plot data. Preslia 75:1–15.

De Bello, F., J. Lepš, and M. T. Sebastia. 2005. Predictive value of plant traits to grazing along a climatic gradient in the Mediterranean. Journal of Applied Ecology 42:824–833.

Dupré, C., and J. Ehrlén. 2002. Habitat configuration, species traits and plant distributions. Journal of Ecology 90:796–805.

Ehrlén, J., and O. Eriksson. 2000. Dispersal limitation and patch occupancy in forest herbs. Ecology 81:1667–1674.

Ehrlén, J., and K. Lehtilä. 2002. How perennial are perennial plants? Oikos 98:308–322.

Ehrlén, J., and J. M. van Groenendael. 1998. The trade-off between dipersability and longevity: an important aspect of plant species diversity. Applied Vegetation Science 1:29–36.

Eriksson, O. 1996. Regional dynamics of plants: a review of evidence for remnant, source–sink and metapopulations. Oikos 77:248–258.

Eriksson, O., and J. Ehrlén. 1992. Seed and microsite limitation of recruitment in plant populations. Oecologia 91:360–364.

Eriksson, O., and J. Ehrlén. 2001. Landscape fragmentation and the viability of plant populations. Pages 157–175 *in* J. Silvertown and J. Antonovics, editors. Integrating ecology and evolution in a spatial context. Blackwell, Oxford, UK.

Eriksson, O., and A. Jakobsson. 1998. Abundance, distribution and life histories of grassland plants: a comparative study of 81 species. Journal of Ecology 86:922–933.

Fischer, S. F., P. Poschlod, and B. Beinlich. 1996. Experimental studies on the dispersal of plants and animals on sheep in calcareous grasslands. Journal of Applied Ecology 33:1206–1222.

Freckleton, R. P., P. H. Harvey, and M. Pagel. 2002. Phylogenetic analysis and comparative data: a test and review of evidence. American Naturalist 160:712–726.

Grashof-Bokdam, C. 1997. Forest species in an agricultural landscape in the Netherlands: effects of habitat fragmentation. Journal of Vegetation Science 8:21–28.

Grime, J. P., and J. G. Hodgson. 1987. Botanical contributions to contemporary ecological theory. New Phytologist 106: 283–295.

Hanski, I. 1999. Metapopulation ecology. Oxford University Press, New York, New York, USA.

Hanski, I., C. Eralahti, M. Kankare, O. Ovaskainen, and H. Siren. 2004. Variation in migration propensity among individuals maintained by landscape structure. Ecology Letters 7:958–966.

Harvey, P. H., A. F. Read, and S. Nee. 1995. Why ecologists need to be phylogenetically challenged. Journal of Ecology 83:535–536.

Herben, T., Z. Münzbergová, M. Mildén, J. Ehrlén, S. O. A. Cousins, and O. Eriksson. 2006. Long-term spatial dynamics of *Succisa pratensis* in a changing rural landscape: linking dynamical modeling with historical maps. Journal of Ecology 94:131–143.

Higgins, S. I., J. S. Clark, R. Nathan, T. Hovestadt, F. Schurr, J. M. V. Fragoso, M. R. Aguiar, E. Ribbens, and S. Lavorel. 2003. Forecasting plant migration rates: managing uncertainty for risk assessment. Journal of Ecology 91:341–347.

Jackel, A. K., and P. Poschlod. 2000. Persistence or dispersal: Which factors determine the distribution of plant species? Zeitschrift für Ökologie und Naturschutz 9:99–107.

Jacquenym, H., J. Butaye, and M. Hermy. 2001. Forest plant species richness in small fragmented mixed deciduous forest patches: the role of area, time and dispersal limitation. Journal of Biogeography 28:801–812.

Johansson, P., and J. Ehrlén. 2003. Influence of habitat quantity, quality and isolation on the distribution and abundance of two epiphytic lichens. Journal of Ecology 91: 213–221.

Kelly, C. K. 1995. Seed size in tropical trees: a comparative study of factors affecting seed size in Peruvian angiosperms. Oecologia 102:377–388.

Kelly, C. K., and A. Purvis. 1993. Seed size and establishment conditions in tropical trees: on the use of taxonomic relatedness in determining ecological patterns. Oecologia 94:356–360.

Kolb, A., and M. Diekmann. 2005. Effects of life-history traits on responses of plant species to forest fragmentation. Conservation Biology 19:929–938.

Lindborg, R., S. A. O. Cousins, and O. Eriksson. 2005. Plant species response to land-use change: *Campanula rotundifolia*, *Primula veris* and *Rhinanthus minor*. Ecography 28:29–36.

Matlack, G. R. 2005. Slow plants in a fast forest: local dispersal as a predictor of species frequencies in a dynamic landscape. Journal of Ecology 93:50–59.

Maurer, K., W. Durka, and J. Stöcklin. 2003. Frequency of plant species in remnants of calcareous grassland and their dispersal and persistence characteristics. Basic and Applied Ecology 4:307–316.

Mazer, S. J. 1989. Ecological, taxonomic, and life-history correlates of seed mass among Indiana dune angiosperms. Ecological Monographs 59:153–175.

Münzbergová, Z. 2004. Effects of spatial scale on factors limiting species distributions in dry grassland fragments. Journal of Ecology 92:854–867.

Münzbergová, Z., and T. Herben. 2004. Identification of suitable unoccupied habitats in metapopulation studies using co-occurrence of species. Oikos 105:408–414.

Münzbergová, Z., M. Mildén, J. Ehrlén, and T. Herben. 2005. Population viability and reintroduction strategies: a spatially explicit landscape-level approach. Ecological Applications 15:1377–1786.

Murray, B. R., P. H. Thrall, and B. J. Lepschi. 2002. Relating species rarity to life history in plants of eastern Australia. Evolutionary Ecology Research 4:937–950.

Oostermeijer, J. G. B., S. H. Luijten, and J. C. M. den Nijs. 2003. Integrating demographic and genetic approaches in plant conservation. Biological Conservation 113:389–398.

Ouborg, N. J. 1993. Isolation, population size and extinction: the classical and metapopulation approaches applied to vascular plants along the Dutch Rhine system. Oikos 66: 298–308.

Piessens, K., O. Honnay, and M. Hermy. 2005. The role of fragment area and isolation in the conservation of heathland species. Biological Conservation 122:61–69.

Piessens, K., O. Honnay, K. Nackaerts, and M. Hermy. 2004. Plant species richness and composition of heathland relics in northwestern Belgium: Evidence for a rescue effect? Journal of Biogeography 31:1683–1692.

Pocock, M. J. O., S. Hartley, M. G. Telfer, C. D. Preston, and W. E. Kunin. 2006. Ecological correlates of range structure in rare and scarce British plants. Journal of Ecology 94:581–596.

Quintana-Ascencio, P. F., and E. S. Menges. 1996. Inferring metapopulation dynamics from patch-level incidence of Florida scrub plants. Conservation Biology 10:1210–1219.

Reich, P. B., I. J. Wright, J. Cavender-Bares, J. M. Craine, J. Oleksyn, M. Westoby, and M. B. Walters. 2003. The evolution of plant functional variation: traits, spectra, and strategies. International Journal of Plant Sciences 164:143–164.

Silvertown, J. W., and D. Charlesworth. 2001. Introduction to plant population biology. Osney Mead, Oxford, UK.

Silvertown, J., and M. Dodd. 1996. Comparing plants and connecting traits. Philosophical Transactions of the Royal Society of London, B 351:1233–1239.

Soons, M. B., and G. W. Heil. 2002. Reduced colonization capacity in fragmented populations of wind-dispersed grassland forbs. Journal of Ecology 90:1033–1043.

ter Braak, C. J. F., and P. Šmilauer. 1998. CANOCO reference manual and user's guide to Canoco for Windows: software for canonical community ordination, version 4.5. Microcomputer Power, Ithaca, New York, USA.

Thompson, K., J. P. Bakker, R. M. Bekker, and J. G. Hodgson. 1998. Ecological correlates of seed persistence in soil in the north-west European flora. Journal of Ecology 86:163–169.

Thompson, K., and D. J. Hodkinson. 1998. Seed mass, habitat and life history: a re-analysis of Salisbury 1942, 1974. New Phytologist 138:163–167.

Thompson, K., and D. Rabinowitz. 1989. Do big plants have big seeds? American Naturalist 133:722–728.

Tischendorf, L., and L. Fahring. 2000. On the usage and measurement of landscape connectivity. Oikos 90:7–19.

Trakhtenbrot, A., R. Nathan, G. Perry, and D. M. Richardson. 2005. The importance of long-distance dispersal in biodiversity conservation. Diversity and Distributions 11:173–181.

Turnbull, L. A., M. J. Crawley, and M. Rees. 2000. Are plant populations seed-limited? A review of seed sowing experiments. Oikos 88:225–238.

Tutin, T. G., V. H. Heywood, N. A. Burges, D. H. Valentine, S. M. Walters, and D. A. Webb, editors. 1964–1983. Flora Europaea. Cambridge University Press, New York, New York, USA.

van der Meijden, E., P. G. L. Klinkhamer, T. J. De Jong, and C. A. M. Van Wijk. 1992. Meta-population dynamics of biennial plants: how to exploit temporary habitats. Acta Botanica Neerlandica 41:249–270.

Westoby, M., M. R. Leishman, and J. M. Lord. 1995*a*. Further remarks on phylogenetic correction. Journal of Ecology 83: 727–729.

Westoby, M., M. R. Leishman, and J. M. Lord. 1995*b*. On misinterpreting the phylogenetic correction. Journal of Ecology 83:531–534.

Westoby, M., M. R. Leishman, and J. M. Lord. 1996. Comparative ecology of seed size and dispersal. Philosophical Transactions of the Royal Society of London, B 351: 1309–1317.

APPENDIX A

Values of all the traits for all the studied species (*Ecological Archives* E088-060-A1).

APPENDIX B

Correlation among single traits used in the study after removing the four non-congeneric species pairs (*Ecological Archives* E088-060-A2).