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RESEARCH ARTICLE

Colonization of central European abandoned fields by dry grassland species depends on the species richness of the source habitats: a new approach for measuring habitat isolation

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Abstract Abandoned fields are perceived as potential habitats for species of threatened semi-natural dry grasslands. However, information is lacking regarding how the spontaneous colonization of abandoned fields depends on the broader spatial context. We recorded the occurrence of 87 target species in 46 abandoned fields and 339 dry grasslands. We tested the effect of the isolation of abandoned fields from source grasslands on the number of dry grassland species occurring in abandoned fields either with or without habitat characteristics being used as covariates. The isolation of the fields was calculated using the distance and area (I_A) or distance and species richness (I_S) of source habitats. I_S always explained the number of grassland species in the abandoned fields better than I_A. The effect of isolation became smaller or even non-significant with the inclusion of covariates; it also changed with the method used for measuring distance (edge-to-edge or center-to-center), and it was lower when other abandoned fields were considered as additional source habitats. The different performance of the two isolation measures can be explained by the weak species–area relationship in the grasslands, indicating differences in their habitat quality. Species richness is a better proxy of habitat importance in terms of propagule source than habitat area, and the new isolation measure is therefore suitable for studying the effects of landscape structure on species richness in landscapes presenting a weak species–area relationship, such as areas exhibiting pronounced effects of land-use history. Inclusion of habitat characteristics as covariates may considerably alter conclusions regarding the effect of isolation, which might actually be overestimated when assessed separately.

Keywords Agricultural landscape · Connectivity · Czech Republic · Dispersal · Diversity · Fragmentation · *Festuco-Brometea* · Secondary succession

Introduction

The extent of species-rich semi-natural grasslands has been drastically declining throughout Europe over the past century. The remaining grasslands are fragmented

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and scattered within the landscape and the cessation of former management practices has led to overgrowth of many localities by shrubs and trees (Lipsky 1995; Poschlod and Bonn 1998; Eriksson et al. 2002; Luoto et al. 2003; Cousins 2009a). More recently, socio-economic changes and new technologies used in agriculture have brought about the abandonment of arable fields that were no longer profitable to maintain. This could be beneficial for grassland conservation, as the direct restoration of grasslands on ex-arable land is becoming a common practice (Pywell et al. 2002; Walker et al. 2004). Nevertheless, only a limited number of former fields can be intentionally converted into grasslands, and the question arises of whether fields can be successfully colonized by grassland species, even without conservation efforts (Ruprecht 2006; Oster et al. 2009a, b).

To assess the natural colonization of abandoned fields, the number of grassland species spontaneously growing in abandoned fields compared to the pool of species present in adjacent source grasslands must be known. However, the distribution of grassland plants in abandoned fields has only rarely been studied at a landscape scale (but see Ruprecht 2006; Cousins and Aggemyr 2008 for grazed ex-fields). Rather, studies addressing spatial patterns of species richness in abandoned fields usually only compare plots at different distances from an adjacent source habitat (Cook et al. 2005; Oster et al. 2009b).

The studies examining dispersal from a single source habitat focus on species' ability to disperse over relatively short distances, and dispersal from farther source habitats is overlooked. The broader spatial context of target fields can be quantified as the isolation of a field from source grasslands. Based on theory (Hanski 1999), the species richness of a particular habitat patch is expected to decrease with increasing isolation of this patch. However, many studies in grasslands have failed to demonstrate an effect of isolation on species richness (Lindborg and Eriksson 2004; Helm et al. 2006; Lobel et al. 2006; Oster et al. 2007). This may be caused by the very slow response of perennial plants to landscape changes (Helm et al. 2006; Cousins and Eriksson 2008; Cousins 2009b), indicating that species are in fact responding to landscape structure in the past and that their distribution is not in equilibrium with the current landscape (Lindborg and Eriksson 2004; Gustavsson et al. 2007). The ongoing process of colonization of recently abandoned fields by species from current grasslands provides an excellent opportunity to assess the effect of isolation on species richness without it being obscured by historical changes in landscape structure.

Recent work has shown that plant species richness varies in response to topography-related habitat characteristics, such as site-specific solar radiation and slope (Pykala et al. 2005; Bennie et al. 2006). The species richness of grassland plants is also related to soil conditions (Janssens et al. 1998). However, studies on the effect of isolation on the species richness of grassland plants usually do not include habitat characteristics as explanatory variables in models explaining species richness (e.g., Lindborg and Eriksson 2004; Oster et al. 2007; Bruckmann et al. 2010). Therefore, the resulting effect of habitat isolation on species richness might be in fact overestimated due to spatial correlation of habitat characteristics and isolation. We aim to compare the effect of isolation of abandoned fields from source grasslands with and without inclusion of habitat characteristics.

To describe habitat isolation, different studies use very different measures (Moilanen and Nieminen 2002; Kindlmann and Burel 2008; Prugh 2009). However, all measures that have been used thus far to study the effect of habitat isolation on species richness are based on the distance from possible sources and/or the size of the source habitat and do not consider the species richness at the sources. The use of area in assessing isolation is based on the assumption that larger patches exhibit higher species richness and host larger populations and, thus, may provide more possible colonizers for the target patch (Hanski 1999; Kiviniemi 2008). In fragmented grasslands, however, a number of studies have failed to reveal a positive relationship between patch area and species richness (Eriksson et al. 1995; Kiviniemi and Eriksson 1999; Partel and Zobel 1999) or patch area and population size (Eriksson and Ehrlen 2001; Bruun 2005). This may be caused by different habitat conditions of the source patches resulting from factors such as different land-use histories at these patches (e.g., Cousins 2001; Lindborg et al. 2005; Chylova and Munzbergova 2008). We therefore hypothesize that using the species richness of surrounding source habitats instead of area may provide more meaningful results than when calculating isolation based on area.

Our study area in northern Bohemia, Czech Republic is situated in a landscape associated with a long tradition of agriculture and contains both grassland fragments and abandoned fields. This provides an excellent opportunity to examine and separate factors limiting the richness of grassland plants in abandoned fields. In this study, we performed an extensive field survey asking the following questions:

(i) How many dry grassland species were able to colonize arable fields abandoned in last two decades?
(ii) What is the effect of isolation of an abandoned field from source dry grasslands on number of grassland species colonizing the field?
(iii) How does the detected effect of isolation change with the method used for its calculation?
(iv) How does the detected effect of isolation change when habitat characteristics are included as covariates?

To answer these questions, we recorded the occurrence of 87 dry grassland plant species in 339 source dry grasslands and 46 target abandoned fields. For each abandoned field, we assessed a number of habitat characteristics that could be used as covariates. Finally, two different measures of the isolation of each field were calculated based either on area and distance or on species richness and the distance of surrounding source grasslands.

Methods

Study area and target species

The study area (8.5 by 8.5 km) is situated in the northern part of the Czech Republic (boundaries: 50°33′19.3″N, 14°14′25.1″E–50°33′47.4″N, 14°21′36.2″E; 50°28′46.3″N, 14°15′5.2″E–50°29′47.2″N, 14°21′40.9″E) at 200–270 m a.s.l. The long-term average temperature in the region is 7.7°C, and the long-term normal precipitation is 612 mm (Web 1). The prevailing bedrocks consist of sediments of different ages and origins, mainly sandstones and loess loams. The area is associated with a long tradition of agriculture with a prevalence crop production, accompanied by vineyards on steeper southern slopes and hop fields in alluvial areas. At present, agricultural land covers more than 70% of the study area (see map in Appendix 1 in Electronic supplementary material). Natural vegetation is represented by remnants of oak-hornbeam and thermophilous oak forests (alliance *Carpinion* and *Quercion petrae*, Ellenberg 1988), with total cover of approximately 10% within the study area. Calcareous dry grasslands (alliance *Bromion erecti*, Ellenberg 1988) occur in small fragments totaling 4% of the study area, and they host a vast small-scale diversity of vascular plants (Munzbergova 2004, Chylova and Munzbergova 2008), including a number of threatened species. At present, most of the grasslands in the region are not managed, and occasionally, some of them are completely destroyed by human activities (e.g., plowing or development of solar power plants). A previous study in the same region demonstrated some portions of the current area of dry grasslands were arable fields in the 1950s or even in 1980s (Chylova and Munzbergova 2008), suggesting that grassland species have been able to spread into novel habitats. In the past, fields, orchards, pastures, vineyards and grasslands formed a small-grain heterogeneous mosaic. Therefore, a mixture of different land use histories can be found containing both continuous grasslands and relatively recently (e.g., in the 1980s) abandoned fields within a single current grassland (Chylova and Munzbergova 2008). However, due to changes in agriculture, the fields in the current landscape are much larger and farther from the source grasslands than they were in the past. Moreover, increased application of fertilizers and the use of deep cultivation in the last decades might have considerably altered soil conditions. We therefore assume that species' colonization of currently abandoned fields will be limited both by habitat suitability and species' dispersal ability. Fields abandoned in last 20 years are already overgrown with grasses and ruderal herbaceous vegetation, e.g., *Arrhenatherum elatius*, *Dactylis glomerata*, *Cirsium arvense*, *Melilotus albus* and *M. officinalis*, and they make up approximately 1% of the study area.

Data collection

Field data collection

Based on studies performed within the same region (Munzbergova 2004; Tremlova and Munzbergova 2007; Chylova and Munzbergova 2008), we selected 87 target species as species restricted to dry grassland fragments (Table 1).

In 2009, using GPS, we located all fields abandoned in the last 15 years and all source grasslands within the

Table 1 List of target dry grassland species

Target species	Percentage occupied		Target species	Percentage occupied	
	Abandoned fields	Dry grasslands		Abandoned fields	Dry grasslands
Agrimonia eupatoria	96	92	*Koeleria pyramidata*	7	19
Coronilla varia	93	89	*Tanacetum corymbosum*	7	17
Fragaria viridis	89	81	*Asperula cynanchica*	7	15
Origanum vulgare	78	49	*Dianthus carthusianorum*	7	14
Inula salicina	76	67	*Veronica austriaca* subsp. *teucrium*	4	13
Festuca rupicola	74	75	*Aster amellus*	4	9
Knautia arvensis	72	88	*Melampyrum arvense*	4	9
Centaurea jacea	72	70	*Inula hirta*	4	3
Astragalus glycyphyllos	72	59	*Artemisia campestris*	4	2
Euphorbia cyparissias	67	81	*Centaurea rhenana*	4	2
Galium verum	67	73	*Thymus praecox*	2	27
Bupleurum falcatum	65	65	*Anthyllis vulneraria*	2	22
Brachypodium pinnatum	59	84	*Peucedanum cervaria*	2	16
Lotus corniculatus	57	78	*Genista tinctoria*	2	12
Salvia verticillata	54	50	*Potentilla arenaria*	2	11
Astragalus cicer	52	35	*Teucrium chamaedrys*	0	23
Centaurea scabiosa	48	65	*Helianthemum nummularium* subsp. *grandiflorum*	0	20
Trifolium medium	48	65	*Trifolium montanum*	0	18
Scabiosa ochroleuca	48	54	*Carex humilis*	0	17
Stachys recta	41	36	*Anemone sylvestris*	0	15
Plantago media	39	65	*Polygala vulgaris*	0	15
Linum catharticum	37	66	*Geranium sanguineum*	0	10
Sanguisorba minor	30	71	*Asperula tinctoria*	0	9
Carlina vulgaris	28	25	*Anthericum ramosum*	0	8
Eryngium campestre	26	46	*Melampyrum nemorosum*	0	7
Bromus erectus	22	40	*Sesleria albicans*	0	7
Gentiana cruciata	22	17	*Aster linosyris*	0	5
Cirsium eriophorum	22	9	*Filipendula vulgaris*	0	5
Hieracium pilosella	20	25	*Globularia elongata*	0	5
Pimpinella saxifraga	17	48	*Linum tenuifolium*	0	5
Medicago falcata	11	37	*Campanula rotundifolia*	0	4
Primula veris	11	31	*Listera ovata*	0	4
Ononis spinosa	11	22	*Linum flavum*	0	3
Euphrasia rostkoviana	11	3	*Onobrychis viciifolia*	0	3
Leontodon hispidus	9	46	*Scorzonera hispanica*	0	2
Briza media	9	44	*Seseli hippomarathrum*	0	2
Potentilla heptaphylla	9	42	*Thesium linophyllon*	0	2
Carex flacca	9	40	*Campanula glomerata*	0	1
Carex tomentosa	9	22	*Coronilla vaginalis*	0	1
Salvia nemorosa	9	13	*Gymnadenia conopsea*	0	1
Salvia pratensis	7	68	*Laserpitium latifolium*	0	1

Table 1 continued

Target species	Percentage occupied		Target species	Percentage occupied	
	Abandoned fields	Dry grasslands		Abandoned fields	Dry grasslands
Prunella vulgaris	7	32	*Melampyrum cristatum*	0	1
Cirsium acaule	7	29	*Scabiosa canescens*	0	1
Prunella grandiflora	7	29			

For each species, the percentages of occupied abandoned fields (from total 46) and dry grasslands (from total 339) are shown. The nomenclature follows Tutin et al. (1964–1983)

study area. A total of 46 abandoned fields ranging in size from 815 to 50,222 m^2 and 339 dry grasslands ranging in size from 6 to 274,800 m^2 were included. We defined a dry grassland as a site with visually homogenous vegetation separated from other localities by an unsuitable area and hosting at least one of the target dry grassland species. 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.

In all of the abandoned fields and dry grasslands, we recorded the occurrence of each of 87 target species. During the field survey, we recorded only adult, usually flowering, individuals because small juvenile plants and seedlings are almost impossible to detect in the dense vegetation of abandoned fields. For the purpose of our study, the species found in the abandoned fields are referred to as *generalists*. Species only found in the dry grasslands are referred to as *specialists*. We use these terms for simplicity, mainly to separate the two groups of species, which could be also classified as *early* and *late colonizers* or *good* and *poor colonizers*.

Data on habitat characteristics

For each abandoned field, we determined several types of habitat characteristics (Table 2). Information on the time since the abandonment of each field (further referred to as “Age”) was obtained through personal communication with landowners. As this information was only approximate, we divided the fields into three age categories: up to 7, 10 or 15 years. Several fields were also seeded with a commercial seed mixture in the last year before abandonment. The commercial seed mixture consisted of a few productive grasses and legumes (*Dactylis glomerata*, *Festuca pratensis*, *Lolium perenne*, *Lolium multiflorum* and *Trifolium pratense*) and did not contain any of the target species. Information related to seeding is important because it may influence the establishment success of the target species at the study sites.

We used ArcGIS 9.2 (ESRI 2006) to obtain mean values for the TWI (topographic wetness index), Slope and potential direct solar irradiation (PDSI) from December to June for each abandoned field. Based on digital geological data, we also assessed the percentage cover of eight bedrock types in each abandoned field (further referred to as Geology, Table 2). See Appendix 2 in Electronic supplementary material for technical details of the GIS analyses and an extended description of habitat characteristics.

Isolation of abandoned fields

The majority of studies assessing the effect of isolation on plant species richness in grasslands use the isolation measure originating from the Incidence Function Model of metapopulation dynamics (Hanski 1994). To incorporate different distances of source patches, this measure uses a negative exponential dispersal kernel (the probability density function of the dispersal distance for an individual or population), with parameter α scaling the effect of distance to migration. However, parameter α is species specific and is difficult to accurately estimate in studies on multiple species. We therefore decided to use a simpler quadratic rational dispersal kernel (e.g., Tremlova and Munzbergova 2007).

First, we calculated the isolation of each abandoned field (I_A) as the mass of the surrounding source dry

Table 2 List of parameters collected for each abandoned field ($N = 46$) and their effect on the species richness of the abandoned fields

Parameter	df	Type		R^2
Coordinates				0.15
x	**1**	**Continual**		
y	**1**	**Continual**		
x*y	**1**	**Continual**		
Habitat characteristics				0.48
Age	1	Continual		
Seeding	**1**	**Binomial**	**−**	**0.05**
Area	**1**	**Log(continual)**	**+**	**0.05**
TWI	1	Continual		
Slope	**1**	**Continual**	**+**	**0.12**
PDSI_December	1	Continual		
PDSI_January	1	Continual		
PDSI_February	1	Continual		
PDSI_March	**1**	**Continual**	**−**	**<0.01**
PDSI_April	1	Continual		
PDSI_May	**1**	**Continual**	**+**	**0.01**
PDSI_June	**1**	**Continual**	**−**	**0.17**
Geology	**7**	**Factorial**		**0.08**

TWI topographic wetness index; *PDSI* potential direct solar irradiation

Parameters in bold were selected by step-wise regression and, thus, were included in the final model. The sign ± indicates a positive/negative relationship of the parameters in the model

grasslands weighted by their distance to the target abandoned field following Eq. 1.

$$I_{Aj} = -\log \sum_{k=1}^{n} \left[\left(A_k / d_{jk}^2 \right) \right], \quad j \neq k, \tag{1}$$

where I_j is the isolation of abandoned field j; k represents all of the surrounding grasslands within a 0.5 km distance of abandoned field j; A_k is the area of grassland k; and d_{jk} is the distance between abandoned field j and grassland k.

Second, we replaced the area of the surrounding grasslands with the number of target species occurring in each grassland and calculated isolation (I_S) following Eq. 2.

$$I_{Sj} = -\log \sum_{k=1}^{n} \left[\left(S_k / d_{jk}^2 \right) \right], \quad j \neq k, \tag{2}$$

where I_j is the isolation of abandoned field j; k represents all of the surrounding grasslands within a 0.5 km distance of abandoned field j; S_k is the number of target species in grassland k; and d_{jk} is the distance between abandoned field j and grassland k. We measured d_{jk} either as the center-to-center or edge-to-edge (shortest) distance.

The other surrounding fields could theoretically also serve as propagule sources for target species. Therefore, we considered surrounding abandoned fields as additional source habitats when calculating isolation and compared the results obtained from the models when abandoned fields were not considered.

The mean edge-to-edge distances between the source and target habitats were 253 and 226.4 m (range 1–500 m) when source habitats were represented either by grasslands or both grasslands and abandoned fields, respectively. The mean center-to-center distances were 288.9 and 271.5 m (range 20–500 m), respectively.

The resulting isolation value was higher for more isolated sites, i.e., abandoned fields that were farther from source grasslands and/or when the source grasslands were smaller (I_A) or hosted fewer target species (I_S). For the most isolated abandoned fields, $I_A = 1.88$, and $I_S = 3.83$. For the least isolated abandoned fields, $I_A = -5.12$, and $I_S = -2.01$.

Data analysis

To asses differences in the number of target species occurring in individual grasslands and abandoned fields, differences in the areas of the two habitat types must be taken into account. In a linear regression, the number of target species was employed as a dependent variable, and habitat type (grassland/field) and the logarithm of area and their interaction were used as independent variables. The relationship between the number of target species and the logarithm of habitat area was also analyzed separately for the two habitat types using linear regression. In grasslands, it was further tested separately for specialist and generalist species. Because some of the grasslands were either larger than the largest abandoned field or smaller than the smallest abandoned field, we also tested the species–area relationship using only grasslands within the same span of areas as the abandoned fields.

To identify factors determining the number of species occurring in the abandoned fields, we used linear regression. First, we corrected for possible spatial gradients within the study area (such as related to climate). We used the x and y coordinates of the centers of abandoned fields and their interaction (x*y) as independent variables (Table 2) and tested their effects on the number of target species in the abandoned fields. The significant coordinates were thus used as covariates in selecting habitat characteristics. Some habitat characteristics were strongly correlated with each other (Appendix 2 in Electronic supplementary material). Therefore, we selected only the most important ones by bi-directional step-wise selection based on the AIC (Akaike Information Criterion, a form of penalized log-likelihood analysis, Crawley 2002).

Finally, we tested the overall effect of isolation of the abandoned fields, I_A (i.e., calculated based on the area of surrounding grasslands) or I_S (i.e., calculated based on the species richness of surrounding grasslands), on the number of target species occurring in the abandoned fields. To test the pure effect of isolation, pre-selected coordinates and habitat characteristics were used as covariates.

All of the analyses were performed in S-Plus 2000 (MathSoft 1999).

Results

We found 59 out of the 87 (i.e., 68%) target dry grassland species in the abandoned fields. Twenty-eight species were not found in the abandoned fields and were therefore considered to be grassland specialists (Table 1).

The number of target species in each abandoned field varied from 3 to 34 (mean 18), whereas the number of target species in the dry grasslands varied from 5 to 63 (mean 26). When considering only generalists (species occurring in at least one abandoned field), the number of target species occurring in the dry grasslands varied from 3 to 47 (mean 24). Grasslands harbored significantly more target species than abandoned fields when considering both generalists and specialists ($F_{1,382} = 55.88$, $P < 0.001$, $R^2 = 0.12$) or generalists alone ($F_{1,382} = 47.66$, $P < 0.001$, $R^2 = 0.10$; Fig. 1).

A significantly positive relationship between the number of target species in dry grasslands and the logarithm of grassland area was found only when analyzing the whole range of grasslands (Fig. 1; $F_{1,337} = 68.85$, $R^2 = 0.170$, $P < 0.001$ for all target species; $F_{1,337} = 70.320$, $R^2 = 0.173$, $P < 0.001$ for generalists; $F_{1,337} = 22.840$, $R^2 = 0.063$, $P < 0.001$ for specialists) However, the species–area relationships were relatively weak, indicating differences in habitat quality between individual grasslands. The weakest species–area relationship was found when it was calculated only for specialists. However, when we considered only grasslands within the same span of areas as the abandoned fields, the species–area relationship was not significant ($F_{1,206} = 3.12$, $P = 0.078$ for all species; $F_{1,206} = 3.53$, $P = 0.06$ for generalists; $F_{1,206} = 0.66$, $P = 0.419$ for specialists), nor was the relationship between the number of target species occurring in abandoned fields and field area ($F_{1,44} = 0.047$, $P = 0.829$).

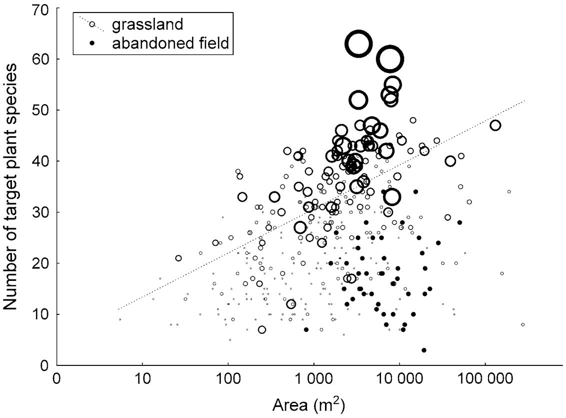

Fig. 1 Relationship between habitat area and the number of target species in grasslands and in abandoned fields. The size of the *open circles* denotes the number of grassland specialists (species not found in abandoned fields). Grasslands with no specialists are depicted as *small dots*. A *regression line* is shown for the full range of grasslands ($F_{1,337} = 68.85$, $R^2 = 0.170$, $P < 0.001$); the species–area relationship was not significant for abandoned fields ($F_{1,44} = 0.047$, $P = 0.829$) or for grasslands when using the same span of areas as for abandoned fields ($F_{1,206} = 3.12$, $P = 0.078$)

All of the three tested spatial coordinates (x, y and x*y) and seven out of 13 habitat characteristics were selected in a stepwise analysis in the most parsimonious model explaining the number of target species in abandoned fields (Table 2). We found a negative effect of seeding and PDSI in March and June and positive effects of area, slope and PDSI in May (Table 2). The topographic wetness index (TWI) and field age were not included in final model.

More target species always occurred in less isolated abandoned fields. When habitat characteristics were used as covariates, the number of target species in

Table 3 Variability explained by the two measures of isolation in different models

Habitat characteristics	Distance	Source habitats	I_A			I_S		
			R^2	F	P	R^2	F	P
Included	Edge-to-edge	Grasslands	**0.05**	**4.38**	**0.046**	**0.07**	**6.19**	**0.019**
		Grasslands + abandoned fields	–	0.47	0.500	–	1.24	0.275
	Center-to-center	Grasslands	–	0.56	0.460	–	2.55	0.122
		Grasslands + abandoned fields	–	0.19	0.663	–	0.12	0.732
Not included	Edge-to-edge	Grasslands	–	1.76	0.191	**0.10**	**4.82**	**0.033**
		Grasslands + abandoned fields	–	1.18	0.284	**0.10**	**4.95**	**0.031**
	Center-to-center	Grasslands	–	1.90	0.175	**0.16**	**8.54**	**0.005**
		Grasslands + abandoned fields	–	1.14	0.291	**0.12**	**6.16**	**0.017**

I_A was based on the area of source habitats, and I_S was based on the number of target species in the source habitats. Habitat characteristics were selected in step-wise regression (Table 2)

Values in bold are significant on $P < 0.05$

abandoned fields was significantly affected by I_A (calculated using the area of source habitats) and I_S (calculated using the species richness of target species on source habitats) only when edge-to-edge distance and grasslands alone as source habitats were used for the calculations (Table 3). Isolation I_S explained 34% more variability in the number of target species in abandoned fields than isolation I_A. In contrast, when habitat characteristics were not included, isolation I_S always had a significant effect on the number of target species in abandoned fields, and the effect of I_A was never significant (Table 3). The effect of isolation was generally more pronounced when only grasslands were used as source habitats. The explained variability also differed between models using different measures of distance (edge-to-edge and center-to-center; Table 3).

Discussion

Habitat isolation is known to be an important factor reducing the species richness of dispersal-limited taxa in a wide range of habitats. For grassland plants, however, the effect of present habitat isolation on species richness is often thought to be obscured by land use history (Lindborg and Eriksson 2004; Helm et al. 2006; Gustavsson et al. 2007). Even highly isolated grasslands might be species rich due to the longevity and persistence of species from a time when the grassland was larger and/or more connected to other grasslands. Here, we studied the colonization patterns of grassland species in recently abandoned fields, and the distribution of dry grassland species in these habitats should only reflect the present landscape structure. We showed that the effect of isolation strongly depends on the inclusion of habitat characteristics in the model as well as on the parameters used when calculating isolation.

The new approach developed in the present study for measuring isolation based on the species richness of source habitats (I_S) always produced better results than a commonly used area-based measure (I_A). This confirmed our hypothesis that the area of surrounding grasslands may not fully reflect their importance as a source of propagules. The use of area-based isolation (I_A) is justified by the fact that larger habitats are generally richer in species and host larger populations. However, in many previous studies in grasslands (e.g., Eriksson and Ehrlen 2001; Lindborg and Eriksson 2004; Bruun 2005; Helm et al. 2006; Lobel et al. 2006), species-area or population size–area relationships were found to be weak or even non-existent. Similarly, our results revealed that the most species-rich grasslands were not the largest by far (Fig. 1), suggesting that factors other than area are more important for the species richness of the grasslands in our study system.

To deal with differences among propagule sources, Ruprecht (2006) weighted the areas of source grasslands according to their phytosociological classification. However, this type of approach relies on division of habitats into several categories and may not be optimal. We suggest that species richness might be a better proxy of habitat importance in terms of propagule sources than vegetation type, and our new measure of isolation based on the species richness of source habitats (I_S) can be more widely applied.

It is likely that isolation could be interconnected with important habitat characteristics. Where conditions are more suitable for grassland species, grasslands might be more abundant and clumped and therefore less isolated compare to areas with less suitable conditions. Indeed, when habitat characteristics were included, Lobel et al. (2006) did not demonstrate an effect of the isolation of grassland fragments on plant species richness, and Adriaens et al. (2006) found only a marginal effect of habitat isolation on a few functional of groups of plant species. Other studies demonstrating the effect of habitat isolation on the species richness in grasslands have not taken habitat characteristics into account (e.g., Reitalu et al. 2009; Bruckmann et al. 2010). Our results confirm that inclusion of habitat characteristics as covariates might considerably alter conclusions regarding the effect of isolation.

The relative importance of isolation also changed when different measurements of distance were applied. When calculating the isolation of individual abandoned fields, we considered all source habitats within a distance of less than 0.5 km. As a consequence, when using edge-to-edge distance, we included 3–4 more source habitats on average than when using center-to-center distance. Therefore, isolation calculated using edge-to-edge distance was systematically lower than isolation based on center-to-center distance. The greater amount of variability explained by isolation based on center-to-center than on edge-to-edge distance suggests that grassland plants are limited by dispersal at distances even shorter than 0.5 km. Nevertheless, the above-mentioned pattern only held when habitat characteristics were not included in the model. In contrast, isolation based on edge-to-edge distance was the only significant isolation measure when covariates were included. Edge-to-edge isolation measures isolation at a larger spatial scale, and it may therefore not be as strongly affected by the habitat conditions of the sites as is the center-to-center measure of isolation.

The populations of target species found in abandoned fields typically consisted of a few individuals to tens of individuals, and their long-term prospects are therefore uncertain. Nevertheless, even transient populations might positively influence species persistence at the landscape scale (Loehle 2007). Our results thus confirm the importance of abandoned fields in the landscape dynamics of dry grassland species. Two-thirds of the target species were able to become established and could potentially spread farther in the landscape. However, when we used abandoned fields as additional source habitats for calculating isolation, the resulting effect of isolation was almost always less pronounced than when using only grasslands as source habitats. The importance of abandoned fields as sources of propagules of dry grassland species is therefore rather low in the study area.

There is increasing evidence that different processes control the species richness as well as the distributions of specialist and generalist species (Pandit et al. 2009) and that these two groups of species respond differently to landscape changes (With and Crist 1995). Bartha et al. (2003) showed that the influx of new colonizers was highest in the first 5–6 years after field abandonment, with much lower numbers of new species appearing later. The fields surveyed in our study were abandoned a maximum of 15 years ago and we can therefore expect that most of the species with the ability to colonize the abandoned fields would have already done so. Therefore, our definition of grassland specialists (species that were not able to colonize any of the abandoned fields in the time span of 15 years) to some degree reflects poor dispersal abilities of species together with narrow habitat requirements.

The difference in the strength of the species–area relationship between specialists and generalists confirms that there is an obvious difference between the landscape dynamics of the two groups and that our division is not arbitrary. Moreover, relaxed species–area relationship of specialists in grasslands implies that habitat quality is more important for their distribution than habitat area. Habitat quality might be associated with certain specific habitat conditions, either abiotic (such as pH or water holding capacity; Munzbergová 2004; Lobel et al. 2006) or biotic (such as character of soil biota, Hartnett and Wilson 1999; van der Heijden et al. 2008). Both biotic and abiotic conditions are likely to be influenced by the land-use history of a site (e.g., Karlik and Poschlod 2009; Oehl et al. 2010; Postma-Blaauw et al. 2010). We therefore suggest that similar to “ancient forest species” (Honnay et al. 1998; Hermy et al. 1999), our specialists are restricted to grasslands with long continuity of land use. However, this needs to be further tested. Our results nevertheless show that pure presence-absence surveys carried out in grasslands and fields may help to distinguish the most specialized species, which are likely to suffer most from the loss of their habitat.

In our extensive field survey, two-thirds of the target dry grassland species were found in fields abandoned in the last two decades. However, the number of target species in abandoned fields was still significantly lower than the number of target species found in grasslands. Moreover, the difference was not due to specialists missing in the abandoned fields, it holds also when compared only numbers of generalist species on fields and grasslands. This implies that even for those species that can reach abandoned fields, some limitations still exist.

The suitability of abandoned fields for dry grassland species may be decreased by numerous factors. Because the simple species–area relationship was not significant for the abandoned fields, we assume that grassland plants do not benefit from the greater heterogeneity of larger fields because they are only able to colonize a few, more open sites. The extent of these suitable sites within each field is influenced more by other habitat characteristics than by field area. We assume the strongest negative effect to be associated with vigorously growing grass and weedy species. Indeed, fewer target species were found in fields that were seeded with a commercial seed mixture prior abandonment resulting in the formation of dense vegetation cover. Similarly, in steeper fields, nutrients are washed away faster than in flat fields, and vegetation becomes less dense and more hospitable for new colonizers.

Conclusion

We revealed an unexpectedly high success of grassland species in the colonization of fields abandoned in the last two decades. These abandoned fields may thus play an important role in the landscape dynamics of many grassland species, but their dispersal is probably often limited to short distances (less than 0.5 km). The proximity of species-rich rather than large source habitats was shown to be important for field colonization. Our new isolation measure using the distance and species richness of surrounding habitats may be helpful in studying the effects of landscape structure on species richness in landscapes with pronounced effects of land-use history or other important factors reducing the species–area relationship.

Assessing the species richness of source habitats would appear to be much more time-consuming than just calculating their areas. However, in the majority of studies addressing habitat isolation, there is no distinction made between target and source habitats, and species richness is known for all habitats under study to be the main response variable. Therefore, there is no additional effort needed for this type of assessment (except for substitution into a formula), and our approach might be easily applied and further tested.

We have also shown that inclusion of habitat characteristics as covariates may considerably alter conclusions about the effects of isolation, which could actually be overestimated when assessed separately. We therefore highly recommend considering habitat characteristics when studying habitat isolation. Through comparison of results obtained with and without inclusion of habitat characteristics, we may gain novel insights into factors affecting species richness.

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