

Landscape and habitat filters jointly drive richness and abundance of specialist plants in terrestrial habitat islands

Balázs Deák · Orsolya Valkó  · Péter Török · András Kelemen ·
Ádám Bede · András István Csathó · Béla Tóthmérész

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Abstract

Context Landscape and habitat filters are major drivers of biodiversity of small habitat islands by influencing dispersal and extinction events in plant metapopulations.

Objectives We assessed the effects of landscape and habitat filters on the species richness, abundance and trait composition of grassland specialist and generalist plants in small habitat islands. We studied traits related to functional spatial connectivity (dispersal ability by wind and animals) and temporal

connectivity (clonality and seed bank persistence) using model selection.

Methods We sampled herbaceous plants, landscape (local and regional isolation) and habitat filters (inclination, woody encroachment and disturbance) in 82 grassland islands in Hungary.

Results Isolation decreased the abundance of good disperser specialist plants due to the lack of directional vectors transferring seeds between suitable habitat patches. Clonality was an effective strategy, but persistent seed bank did not support the survival of specialist plants in isolated habitats. Generalist plants were unaffected by landscape filters due to their wide habitat breadth and high propagule availability. Clonal specialist plants could cope with increasing woody

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B. Deák · O. Valkó (✉) · B. Tóthmérész
MTA-DE Biodiversity and Ecosystem Services Research
Group, Egyetem tér 1, Debrecen 4032, Hungary
e-mail: valkoorsi@gmail.com

A. Kelemen · B. Tóthmérész
Department of Ecology, University of Debrecen, Egyetem
tér 1, Debrecen 4032, Hungary

P. Török
MTA-DE Lendület Functional and Restoration Ecology
Research Group, Egyetem tér 1, Debrecen 4032, Hungary

A. Kelemen
MTA's Postdoctoral Research Programme, MTA TKI,
Nádor utca 7, Budapest 1051, Hungary

Á. Bede
Department of Geology and Paleontology, University of
Szeged, Egyetem utca 2-6, Szeged 6722, Hungary

A. I. Csathó
Körös-Maros National Park Directorate, Anna-liget 1,
Szarvas 5540, Hungary

encroachment due to their high resistance against environmental changes; however, they could not cope with intensive disturbance. Steep slopes providing environmental heterogeneity had an overall positive effect on species richness.

Conclusions Specialist plants were influenced by the interplay of landscape filters influencing their abundance and habitat filters affecting species richness. Landscape filtering by isolation influenced the abundance of specialist plants by regulating seed dispersal. Habitat filters sorted species that could establish and persist at a site by influencing microsite availability and quality.

Keywords Biotic interactions · Dispersal filter · Historical landscape · Kurgan · Landscape composition · Spatial connectivity · Temporal connectivity

Introduction

Habitat loss and land use changes have led to a considerable degradation of European rural landscapes over the past centuries (Fahrig 2003; Lindborg et al. 2014). Because of the increasing needs of the expanding human population, grasslands on fertile soils were especially affected by conversion into arable land (Deák et al. 2016a). In intensively used agricultural landscapes, small remnant grasslands, which act as refuges for several grassland specialist species, are generally located in areas unsuitable for arable farming (Auffret et al. 2015; Deák et al. 2016b; Lindgren and Cousins 2017). These habitat islands are functional elements of the semi-natural grassland network maintaining metapopulations of specialist plants (Lindborg et al. 2014). According to the metapopulation theory, in fragmented landscapes the regional existence of a certain species is driven by dynamic colonisation and extinction processes (Hanski 2011). Both landscape filters (i.e. the amount of proper habitats in the landscape and the connectivity between habitat patches) and habitat filters (i.e. the local environmental conditions) can considerably influence metapopulation dynamics in habitat fragments (Gazol et al. 2012; Janečková et al. 2017). Landscape and habitat filters progressively drive local species assemblages by sorting species from the

regional species pool that are able to disperse to a certain habitat patch and to establish and persist there (de Bello et al. 2013). Studies on plant traits contribute to the understanding of species distribution patterns in fragmented landscapes by providing a deeper insight into the mechanisms driven by abiotic and biotic filters, revealing the effects of abiotic and biotic factors (Janečková et al. 2017).

Local and regional habitat isolation influences species composition of grassland fragments by affecting both spatial and temporal habitat connectivity (Auffret et al. 2015; Janečková et al. 2017). Spatial habitat connectivity is regarded as a realised movement of genetic material in space, which in case of plant means seed or pollen dispersal between populations (Auffret et al. 2015). Limited spatial connectivity caused by habitat loss often leads to genetic isolation and extinction of local populations by impeding recolonisation due to dispersal limitation (Ozinga et al. 2004; Brückmann et al. 2010). However, there are contrasting opinions regarding the usefulness of enhanced dispersal abilities for the survival of species in isolated habitats. On the one hand, plant species with good dispersal ability are expected to cope better with isolation compared to poor dispersers because the latter cannot bridge large distances between suitable grassland patches, which leads to reduced or disrupted metapopulation dynamics and a lowered chance for a locally extinct species to recolonise (Ozinga et al. 2004; Auffret et al. 2015). On the other hand, effective, but random dispersal might, according to Darwin's wind hypothesis, result in a high seed mortality in highly fragmented landscapes because seeds have a high chance of being dispersed into an unsuitable environment (Nathan et al. 2002; Riba et al. 2009). Unlike wind dispersal, zoochory is known as a directional dispersal type, which can considerably increase the chance for propagules to reach suitable habitats (Poschlod et al. 1998).

Temporal connectivity allows populations to persist in a certain location and to cope with the effects of habitat loss and degradation and to some extent even with disrupted metapopulation connections (Kuussaari et al. 2009; Auffret et al. 2015). Life-history traits such as clonality and seed longevity can considerably support long-term persistence (Honnay and Bossuyt 2005; Marini et al. 2012). Clonal species tend to cope well with the effects of isolation as they are not

dependent on sexual reproduction and less affected by genetic constraints, pollen limitation and the lack of proper microsites for seedling establishment (Honnay and Bossuyt 2005; Heinken and Weber 2013). Persistent seed banks allow species to bridge unfavourable periods (Valkó et al. 2014; Kiss et al. 2016) and delay their extinction from isolated grasslands (Ozinga et al. 2004).

Clonal spreading and seed longevity can also increase the likeliness of species survival by buffering the unfavourable effects of habitat transformation (Honnay and Bossuyt 2005; Bossuyt and Honnay 2008). Habitat filters such as woody encroachment and human disturbances have a considerable impact on the species pool of grassland islands (Nathan et al. 2002; Gazol et al. 2012). Woody encroachment, which is one of the most typical results of grassland abandonment, can suppress specialist plants by increased shading and by transforming soil properties (Poschlod et al. 1998; Cierjacks et al. 2013). Human disturbances such as ploughing, building activity or the application of chemicals considerably alter the abiotic environmental conditions (e.g. soil pH, light conditions and availability of open surfaces), which has a considerable effect on the species composition by altering biotic interactions such as inter- and intraspecific competition (MacDougall et al. 2013). Species persistence might also be influenced by the topography of the habitat islands, e.g. variations in slope inclination. Steep slopes provide drier habitat conditions compared to adjacent flat areas and thus favour drought-tolerant grassland specialist plants (Sudnik-Wójcikowska and Moysiyanenko 2014; Deák et al. 2016b).

Our aim was to identify the mechanisms shaping the species composition of specialist plants on grassland islands and to test whether they respond differently to landscape and habitat filters than generalists. Due to their often reduced dispersal ability and their demand for special habitat conditions, specialist species are often restricted to a narrow set of remnant proper habitats and persist as metapopulations in fragmented landscapes. Thus, they are good indicators of isolation and changes in local habitat conditions (Brückmann et al. 2010; Lindborg et al. 2014). Furthermore, specialist plants are in the focus of nature conservation and restoration activities. Generalist plants are generally less sensitive or even supported by unfavourable landscape or habitat changes because of their wide habitat breadth and

their disturbance tolerance (Brückmann et al. 2010; Lindgren and Cousins 2017). We tested the following hypotheses: (i) Species richness and abundance of specialist plants with improved spatial dispersal (good wind and/or animal dispersal ability) decrease in isolated habitat patches due to the higher chance of seed mortality related to random wind dispersal and the lack of livestock dispersal vectors (Heinken and Weber 2013). (ii) Species richness and abundance of specialist plants with improved establishment traits (good clonal spreading ability, persistent seed banks) increase with increasing isolation as these species can bridge unfavourable periods in isolated habitats and buffer stochastic disturbances of a hostile matrix (Auffret et al. 2015). (iii) Increased woody encroachment and human disturbance increase the species richness and abundance of specialists with good clonal spreading ability and with persistent seed banks as these traits can support species survival in suboptimal habitats (Poschlod et al. 1998; MacDougall et al. 2013). (iv) Steep slopes provide a proper habitat for the establishment of specialist plants (Deák et al. 2016b); thus, in kurgans with steeper slopes we expect a higher abundance and species richness of specialist plants regardless of their dispersal and persistence traits.

Material and methods

Study area

The study area is in the Great Hungarian Plain and covers approximately 38,000 km². The region is characterised by a continental climate with a mean annual precipitation of 550 mm and a mean annual temperature of 9.5 °C (Deák et al. 2016b). Due to the agricultural intensification and urbanisation of the past centuries, the landscape has been greatly transformed by human activities. Steppe grasslands with fertile humus-rich chernozemic soils have suffered a dramatic habitat loss of approximately 97% over the past millennia (Molnár et al. 2008a). In most cases only small fragments of their original stands were preserved in places unsuitable for arable farming (i.e. kurgans and roadside verges; Deák et al. 2016b). In spite of their small area, steppe grassland fragments still harbour several protected and/or rare species such as *Agropyron cristatum*, *Anchusa barrelieri*, *Inula*

germanica, *Phlomis tuberosa*, *Ranunculus illyricus*, *Sisymbrium polymorphum* and *Stipa capillata*; thus, they sustain biodiversity in intensively used agricultural landscapes and are therefore of high conservation importance.

For our research we selected grasslands located on ancient burial mounds (so-called ‘kurgans’). Kurgans are iconic elements of Eurasian steppes and forest steppes; their total number is estimated to be between 400,000 and 600,000 (Deák et al. 2016a). Kurgans are characterised by a peculiar hill-like shape and specific abiotic conditions (humus-rich topsoil and dry microclimate). They can be considered as habitat islands characterised by vegetation that is distinctly different from the adjacent areas (Deák et al. 2016a). Even though the original vegetation of many kurgans has been degraded or even destroyed by intensive agriculture and urbanisation in the western countries of the steppe and forest steppe zone, several kurgans still harbour dry grassland vegetation with many grassland specialist plants (Sudnik-Wójcikowska and Moyseyenko 2014, Bede et al. 2015; Deák et al. 2016a, b) (Fig. 1). The biodiversity conservation potential of kurgans has a strong positive correlation with the steepness of their slopes. Steep slopes have prevented ploughing in the past and also act as a habitat filter as they provide dry environmental conditions due to enhanced water runoff (Deák et al. 2016b). Grassland habitats on kurgans are characterised by different levels of isolation and show a high variability regarding abiotic and biotic habitat filters; thus, they are proper objects for simultaneously studying the effects of landscape and habitat filters on grassland biodiversity.

Vegetation sampling

For the study we selected 82 kurgans covered by loess steppe grasslands from our own database (for further details see Deák et al. 2016b). In each locality we surveyed the vegetation of the whole kurgan between May and June 2016 following a standardised protocol: Three surveyors spent 10 minutes per 0.1 ha for recording species lists and percentage covers of vascular plants. One kurgan was considered as one sample unit.

Selection of habitat and landscape filters

We focused on filters that can directly influence the dispersal and persistence of specialist plants on habitat and landscape level. Following Deák et al. (2016a, b), encroachment of woody vegetation, level of human disturbance and steepness of slope were considered as the most significant habitat filters. Even though habitat area is known to be an important driver of species richness in habitat islands (Brückmann et al. 2010), we did not include it in our model, because all surveyed kurgans had approximately the same size (mean area \pm SE = 2529.1 \pm 165.4 ha) so that we did not expect the habitat area to have a significant effect (see also Deák et al. 2016b). Woody encroachment was expressed by the percentage cover of woody vegetation on the kurgans. For estimating the level of human disturbance, we adapted the survey methodology and list of disturbance factors from the Hungarian Natura 2000 assessment protocol (for further details see Deák et al. 2016b). We registered the following disturbances on the kurgans: soil extraction, ploughing, building activities, burning, trampling, presence of dirt tracks, disturbance by animals (e.g. fox and badger holes) and garbage deposition. A disturbance factor was considered as relevant when it affected at least 10% of the kurgan’s surface. For the final score, we summed up the number of relevant disturbance factors for each kurgan. Inclination was expressed as the mean inclination of northern, southern, eastern and western slopes.

The studied landscape filters were isolation indices on local and regional spatial scales: (i) The local isolation index was calculated as the summed-up percentage cover of all habitats excluding semi-natural dry grasslands around each kurgan. These habitats included human-transformed habitats such as croplands, urban areas, tree plantations, forests, roads, channels, orchards, intensively fertilised sown grasslands and weedy patches, semi-natural habitats such as wetlands, wet meadows and reedbeds and open water surface (Fahrig 2003). As most grassland specialist plants have a short effective spreading distance of usually less than 100 m (Novák and Konvička 2006), a distance of 200 m was chosen for testing the effects of local isolation (see also Deák et al. 2016b). For the calculations we used habitat maps created in the field. For habitat mapping we used the satellite images provided by the Open Layer plug-in of Quantum GIS

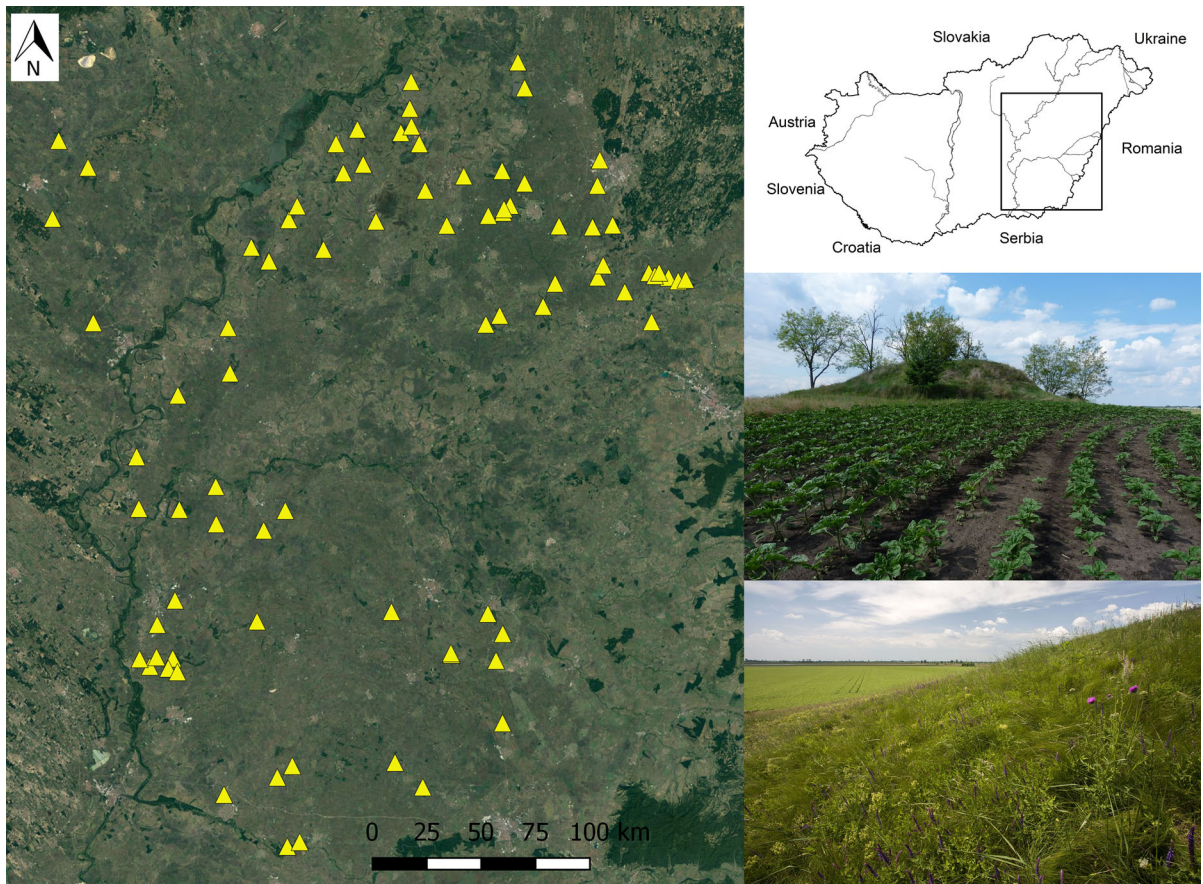


Fig. 1 Map of the study area. Yellow triangles denote the location of the studied kurgans. The photos on the right show two isolated kurgans harbouring loess grassland vegetation (photos by B. Deák). (Color figure online)

2.2. (ii) To measure the regional isolation index, we used the landscape cadastre of Hungary (Molnár et al. 2008b) and the Corine Land Cover (CLC) database (European Environment Agency 2010). Firstly landscape units comprising areas between 117 and 486 km² with similar geography and vegetation were delineated based on the landscape cadastre. Secondly the regional isolation index was calculated by summing up the percentage cover of the area of all habitat types located in a certain landscape unit excluding the categories ‘Natural grasslands’ (321) and ‘Pastures’ (231). The categories of the CLC are broader than semi-natural dry grasslands, but at the regional scale, they are good proxies for determining the proportion of grassland areas.

Data analyses

We considered species of dry grasslands, i.e. herbaceous species of the phytosociological class Festuco-Brometea, as specialist plants (Borhidi 1995; Deák et al. 2016b). All other spontaneously occurring herbaceous species were considered as generalists. We classified plants into the following functional groups: wind-dispersed, animal-dispersed (dispersal traits), clonal species and species with a persistent seed bank (persistence traits). For a detailed list of specialist and generalist plants and functional groups, see Table S1 and S2. For the dispersal assignment we used the anemochory and epizoochory ranking indices of the D³ database (Hintze et al. 2013). These ranking indices range from 0 to 100, where 0 indicates species with the lowest and 100 indicates species with the highest potential for the given dispersal type. Based on

the ranking indices, we classified plants with indices >50 into the corresponding dispersal group. For clonal spreading we used the CLO-PLA database (Klimešova et al. 2017). Species with a potential clonal spreading of $> 0.01 \text{ m a}^{-1}$ were considered as clonal species. For the classification of the seed bank persistence, the LEDA database (Kleyer et al. 2008) was used. Since for most species various seed bank types are given in the database, we classified a species as ‘persistent’ when the majority of records showed any kind of persistence.

The patch occupancy of specialist plants was represented by a histogram in which the number of specialist species found in a patch was plotted against the (classified) number of patches. We calculated the correlation between patch occupancy and mean abundance of species using Spearman correlation in SPSS 20.

The species richness of the four functional groups (wind-dispersed, animal-dispersed, clonal species and species with a persistent seed bank) of specialist and generalist plants were fitted with Generalised Linear Models (GLM) using a Poisson distribution with log link function. The percentage cover of specialist and generalist plants in each functional group was log-transformed to approximate a normal distribution and then analysed with GLMs using a Gaussian distribution with identity link function. Explanatory variables were the local and regional isolation index (landscape filters) and the percentage cover of woody species, the level of recent disturbance and the inclination of the slope (habitat filters). We calculated the variance inflation factors (VIF) between all explanatory variables to test for multicollinearity. As the VIF was lower than 1.3 (i.e. the rate of multicollinearity was negligible) in each case, we considered all explanatory variables as uncorrelated and used them for the statistical analyses. To calculate the VIFs, we used the ‘faraway’ package in R (Faraway 2014). Species richness and abundance of the studied functional groups from the GLMs were tested for spatial autocorrelation using Moran’s I with squared inverse Euclidean distances. Moran’s I index was calculated by the Spatial Autocorrelation tool in ArcMap 10.2.

We used Akaike’s Information Criterion (AIC) and the information-theoretic approach to evaluate multiple regression models and to select those which explained the relationship between vegetation composition and habitat and landscape filters (Burnham

and Anderson 2002) best. To assess the effect of the explanatory variables on the species richness and the percentage cover of the studied functional groups, we fitted GLMs for all possible combinations of the studied explanatory variables. After fitting GLMs in the full model, we calculated the relative importance of the explanatory variables using model-comparison techniques applied in the information-theoretic framework (Burnham and Anderson 2002). We calculated the values of Akaike’s Information Criterion corrected for a small sample size (AICc) for each model. AICc provides an estimation of the information lost when a certain model is used, which allows the selection of the most relevant models and explanatory variables. Based on the suggestions of Burnham and Anderson (2002), we selected the best model ($\Delta \text{AICc} = 0$) and models with a substantial support ($\Delta \text{AICc} \leq 2$) for further calculations. We calculated the significance of explanatory variables from the supported models with Z statistics using the ‘MuMIn’ package (Barton 2011) in an R statistical environment (R Core Team 2018).

Results

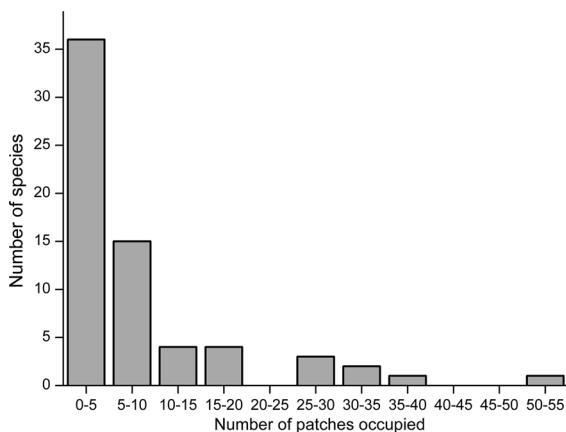
The attributes of the surveyed kurgans are summarised in Table 1. We detected no significant spatial autocorrelation among the response variables. The studied kurgans harboured 65 specialist and 281 generalist herbaceous plants (Tables S1, S2). Specialist plants included many protected species such as *Aster sedifolius*, *Anchusa barrelieri*, *Carduus hamulosus*, *Centaurea scabiosa* subsp. *sadleriana*, *Chamaecytisus rochelii*, *Inula germanica*, *Phlomis tuberosa*, *Ranunculus illyricus* and *Sisymbrium polymorphum* and characteristic species of loess grasslands, some of which (*Agropyron cristatum*, *Astragalus austriacus*, *Stipa capillata* and *Thalictrum minus*) have become regionally endangered due to marked habitat loss in the past centuries. Generalist species involved many widely distributed grassland species such as *Centaurea scabiosa*, *Galium verum*, *Poa angustifolia* and *Salvia nemorosa* and weedy species such as *Carduus acanthoides*, *Convolvulus arvensis* and *Elymus repens*. Woody species were mainly represented by invasive trees and shrubs such as *Robinia pseudoacacia*, *Lycium barbarum*, *Celtis occidentalis*, *Gleditsia triacanthos* and *Elaeagnus angustifolia*. These five

Table 1 Data of the surveyed kurgans (n = 82)

Explanatory variables	Minimum	Maximum	Mean \pm SE
Habitat filters			
Inclination (degree)	8	28	15.1 \pm 0.5
Cover of woody vegetation (percentage)	0	80	23.9 \pm 2.9
Level of recent disturbance	0	4	1.1 \pm 0.1
Landscape filters			
Local isolation index (radius of 200 m; percentage of hostile and unfavourable habitats)	4.8	100	83.9 \pm 2.8
Regional isolation index (regional level; percentage of all habitat types excluding 'Natural grasslands' and 'Pastures')	39.8	96.1	84.7 \pm 1.8

species represented approximately half of the total woody cover.

We detected a unimodal, L-shaped distribution in the patch occupancy of specialist plants (Fig. 2). There was a significant correlation between the patch occupancy and mean abundance of specialist species (Spearman's $\rho = 0.405$, $p = 0.001$). Increased local and regional isolation decreased the abundance of wind- and animal-dispersed specialist plants (Table 2; Fig. 3; Tables S3, S4). Increased local isolation increased the abundance of animal-dispersed generalist plants (Table 3; Fig. 4; Tables S5, S6). Isolation did not affect the species richness and abundance of clonal species. Species richness of specialist plants with a persistent seed bank was negatively affected by local isolation; their abundance increased with increasing regional isolation. An increased level of woody cover decreased the species richness of animal-dispersed specialist plants and of

**Fig. 2** Patch occupancy frequency distribution of specialist plants. Number of species 66; number of patches 82

specialist plants with a persistent seed bank (Table 2; Fig. 3) as well as the abundance of wind-dispersed and clonal generalist plants (Table 3; Fig. 4). An increased level of disturbance decreased the species richness of wind- and animal-dispersed and clonal specialist plants as well as the species richness of all studied functional groups of generalist plants. Disturbance decreased the abundance of wind- and animal-dispersed specialist plants. Steep inclinations enhanced the species richness of all studied functional groups of specialist and generalist plants.

Discussion

Landscape filters and dispersal traits

We found that effective spatial seed dispersal was a disadvantageous strategy for the populations of specialist plants in transformed landscapes with a low proportion of dry grasslands. Interestingly, landscape filters had a significant effect on the abundance of good disperser specialist plants, but not on their species richness. A possible and plausible explanation is that local habitat filters overrode the effects of landscape filters, i.e., they had a more important role in sorting the species that can cope with special habitat conditions provided by the kurgans. Compared to specialists, generalist plants were less affected by landscape filters.

In case of undirected dispersal such as wind dispersal, seeds generally arrive in the landscape in a random pattern, irrespective of the attributes of the habitat (Riba et al. 2009). Accordingly, in landscapes with a low proportion of suitable grassland habitats, a

Table 2 Supported models ($\Delta AICc \leq 2$) fitted on the species richness and abundance of the studied functional groups of specialist plants

Dependent variables	Explanatory variables	Species richness					Abundance				
		Imp ^a (%)	Estimate ^b	SE	z value	p	Imp ^a (%)	Estimate ^b	SE	z value	p
Wind-dispersed specialist species	Isolation (local)	100.0	− 0.004	0.003	1.500	n.s.	100.0	− 0.006	0.002	2.780	0.005
	Isolation (regional)	37.5	− 0.005	0.005	1.124	n.s.	100.0	− 0.009	0.003	2.503	0.012
	Woody cover	100.0	− 0.009	0.003	2.457	n.s.	NA	NA	NA	NA	NA
	Disturbance	49.8	− 0.259	0.096	2.666	0.008	60.4	− 0.153	0.063	2.384	0.017
	Inclination	100.0	0.040	0.015	2.572	0.010	100.0	0.021	0.012	1.717	n.s.
Animal-dispersed specialist species	Isolation (local)	100.0	− 0.004	0.003	1.500	n.s.	100.0	− 0.006	0.002	2.717	0.007
	Isolation (regional)	100.0	− 0.005	0.005	1.124	n.s.	100.0	− 0.008	0.003	2.559	0.011
	Woody cover	100.0	− 0.009	0.003	2.457	0.014	22.4	− 0.002	0.002	0.775	n.s.
	Disturbance	49.8	− 0.259	0.096	2.666	0.008	100.0	− 0.138	0.060	2.267	0.023
	Inclination	37.5	0.040	0.015	2.572	0.010	25.7	0.011	0.011	0.922	n.s.
Clonal specialist species	Isolation (local)	NA	NA	NA	NA	NA	17.5	− 0.002	0.003	0.624	n.s.
	Isolation (regional)	NA	NA	NA	NA	NA	77.4	0.008	0.004	1.792	n.s.
	Woody cover	27.3	− 0.002	0.002	0.491	n.s.	NA	NA	NA	NA	NA
	Disturbance	100.0	− 0.228	0.104	2.149	0.032	NA	NA	NA	NA	NA
	Inclination	100.0	0.039	0.017	2.305	0.021	17.1	0.009	0.015	0.592	n.s.
Specialist species with a persistent seed bank	Isolation (local)	100.0	− 0.006	0.003	2.400	0.016	100.0	− 0.004	0.003	1.469	n.s.
	Isolation (regional)	17.9	− 0.003	0.004	0.706	n.s.	42.6	0.009	0.004	2.186	0.029
	Woody cover	100.0	− 0.008	0.003	2.455	0.014	12.7	− 0.002	0.003	0.643	n.s.
	Disturbance	62.4	− 0.140	0.086	1.599	n.s.	14.0	− 0.059	0.074	0.780	n.s.
	Inclination	100.0	0.059	0.014	4.203	0.001	11.5	0.008	0.014	0.512	n.s.

Significant effects are marked with boldface. ^aImportance of a variable within the supported models ($\Delta AICc \leq 2$), ^bmodel-averaged parameter estimates. NA—factors not included in the supported models

high number of wind-dispersed propagules of specialist plants arrived in areas unsuitable for establishment such as arable land and urban areas and did thus not contribute to the maintenance of the local populations (Lindborg et al. 2014). In contrast to anemochory, zoochory is considered a directional dispersal mechanism (Auffret 2011). Over the last few centuries there has been a considerable change in the spectra of

dispersal vectors in human-modified landscapes, which especially affected plant species of grassland habitats (Auffret and Plue 2014). The number of extensively grazing domestic livestock has decreased considerably, and due to habitat fragmentation, a major part of the landscape is now inaccessible for livestock (Auffret 2011). This overall decrease in the number of primary dispersal vectors was an important

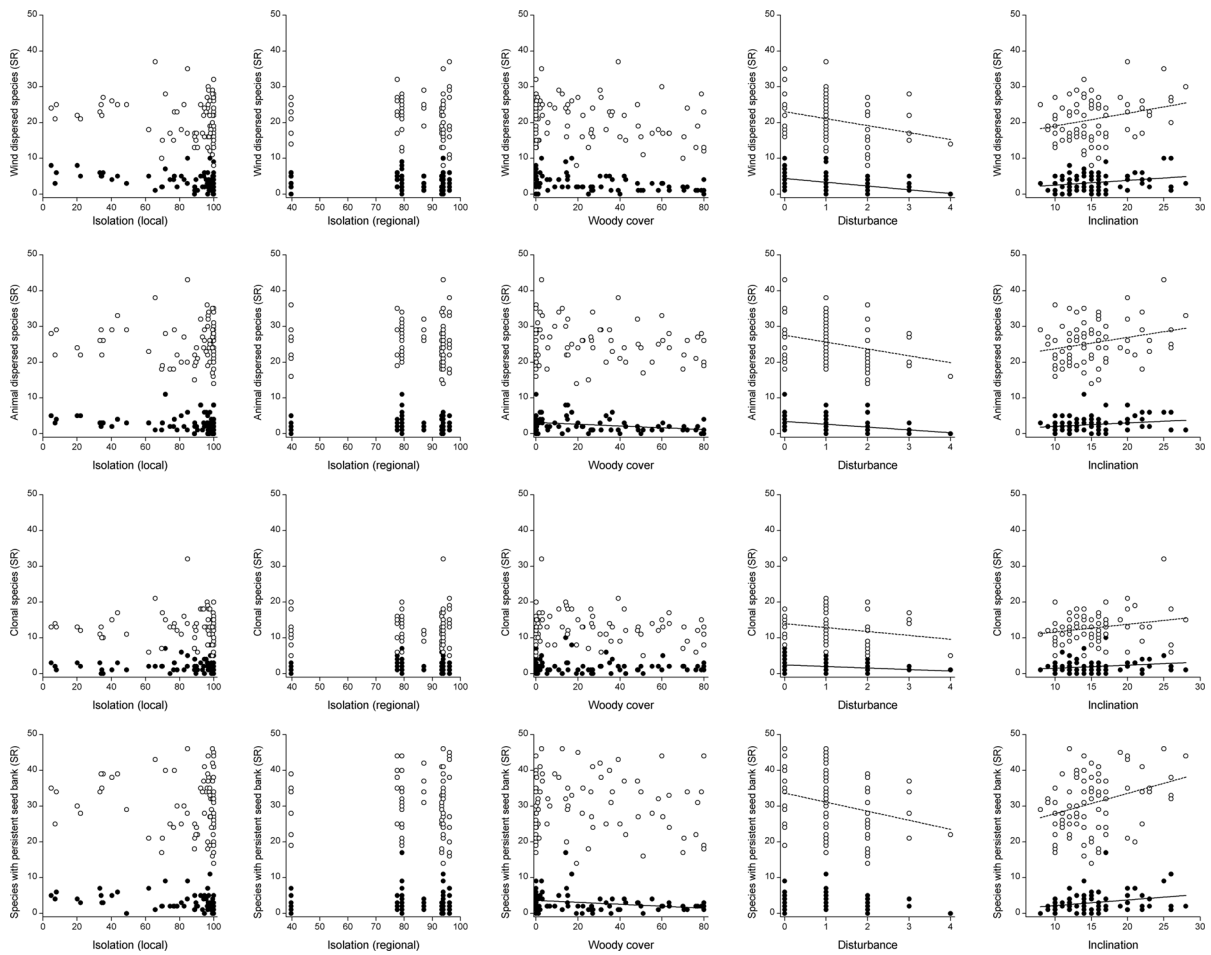


Fig. 3 Relationship between the species richness of specialist (filled symbols) and generalist plant (empty symbols) functional groups and landscape and habitat filters. Lines are fitted in case of a significant relationship revealed by the model selection

reason for the decline of zoochorous species in the studied isolated habitat islands (see also Lindborg et al. 2014). In many regions, including our study sites, game including red deer, wild boar and small mammals became the most important biotic seed dispersal vector (Poschlod et al. 1998; Auffret 2011). This change also induced a shift in the directionality of animal dispersal. Dispersal by livestock is a directional dispersal type because livestock almost exclusively use grassland habitats (Auffret et al. 2015). Seeds thus have a high chance of being dispersed to a suitable habitat, where they can contribute to the maintenance of metapopulation dynamics. Contrarily, game populations use several non-grassland habitats, especially arable land (Auffret and Plue 2014), so that seeds of specialist plants can be randomly dispersed to either suitable or unsuitable habitats, mainly

determined by landscape-scale habitat availability. In case of generalist plants, an increasing level of isolation did not have a severe effect on their species richness or abundance regardless of their seed dispersal types. In isolated habitats the proportion of animal-dispersed generalist species even increased, which means that these species could be effectively dispersed from the neighbouring habitats by game. The reason is that generalist species have a wider habitat breadth compared to specialists. While the specialist plants treated in our study are confined exclusively to dry grassland patches, generalist plants can occupy a wider set of habitats including meadows, agricultural areas or even forest patches (Lindgren and Cousins 2017). Thus, their existence in a patch is less dependent on dispersal processes as for them the

Table 3 Supported models ($\Delta\text{AICc} \leq 2$) fitted on the species richness and abundance of the studied functional groups of generalist plants

Dependent variables	Explanatory variables	Species richness					Abundance				
		Imp ^a (%)	Estimate ^b	SE	z value	p	Imp ^a (%)	Estimate ^b	SE	z value	p
Wind-dispersed generalist species	Isolation (local)	51.7	− 0.002	0.001	1.470	n.s.	78.8	0.002	0.001	1.892	n.s.
	Isolation (regional)	58.2	− 0.003	0.002	1.593	n.s.	34.8	0.002	0.002	1.097	n.s.
	Woody cover	100	− 0.002	0.001	1.614	n.s.	100	− 0.002	0.001	2.224	0.026
	Disturbance	56.4	− 0.079	0.031	2.480	0.013	68.4	0.047	0.028	1.653	n.s.
	Inclination	100	0.018	0.005	3.227	0.001	9.9	0.004	0.005	0.749	n.s.
Animal-dispersed generalist species	Isolation (local)	NA	NA	NA	NA	NA	100	0.002	0.001	2.335	0.020
	Isolation (regional)	33.6	− 0.002	0.001	1.229	n.s.	NA	NA	NA	NA	NA
	Woody cover	19.3	− 0.001	0.001	0.639	n.s.	NA	NA	NA	NA	NA
	Disturbance	100	− 0.073	0.027	2.676	0.007	28.2	0.014	0.025	0.564	n.s.
	Inclination	100	0.012	0.005	2.364	0.018	NA	NA	NA	NA	NA
Clonal generalist species	Isolation (local)	NA	NA	NA	NA	NA	59.0	0.002	0.001	1.670	n.s.
	Isolation (regional)	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
	Woody cover	33.1	− 0.001	0.001	0.882	n.s.	100	− 0.003	0.001	2.112	0.035
	Disturbance	100	− 0.080	0.038	2.060	0.039	19.1	0.026	0.037	0.705	n.s.
	Inclination	100	0.015	0.007	2.263	0.024	36.3	− 0.009	0.007	1.303	n.s.
Generalist species with a persistent seed bank	Isolation (local)	21.1	0.000	0.001	0.546	n.s.	14.7	0.001	0.001	0.791	n.s.
	Isolation (regional)	100	− 0.003	0.001	1.92	n.s.	13.7	0.001	0.001	0.701	n.s.
	Woody cover	NA	NA	NA	NA	NA	11.5	0.000	0.001	0.408	n.s.
	Disturbance	77.3	− 0.079	0.025	3.181	0.001	16.5	0.025	0.027	0.923	n.s.
	Inclination	100	0.018	0.005	4.006	0.001	12.6	− 0.003	0.005	0.576	n.s.

Significant effects are marked with boldface. ^aImportance of a variable within the supported models ($\Delta\text{AICc} \leq 2$), ^bmodel-averaged parameter estimates. NA—factors not included in the supported models

availability of proper habitats and the permeability of the landscape is higher than for specialist plants.

Landscape filtering by isolation affected the abundance of effectively dispersed specialist plants by reducing the vitality of their populations. First, reduced vitality could be caused by the trade-off between dispersal and persistence strategies, i.e., species with an effective dispersal strategy can

generally allocate less resources to persistence; however, increased persistence ability would be more beneficial in isolated small habitat islands (see also Marini et al. 2012). Secondly, effectively dispersed seeds are generally transported further from the mother plant. In case of small habitat islands, this often means that seeds are transported away from the limited suitable habitat. The consequence is that

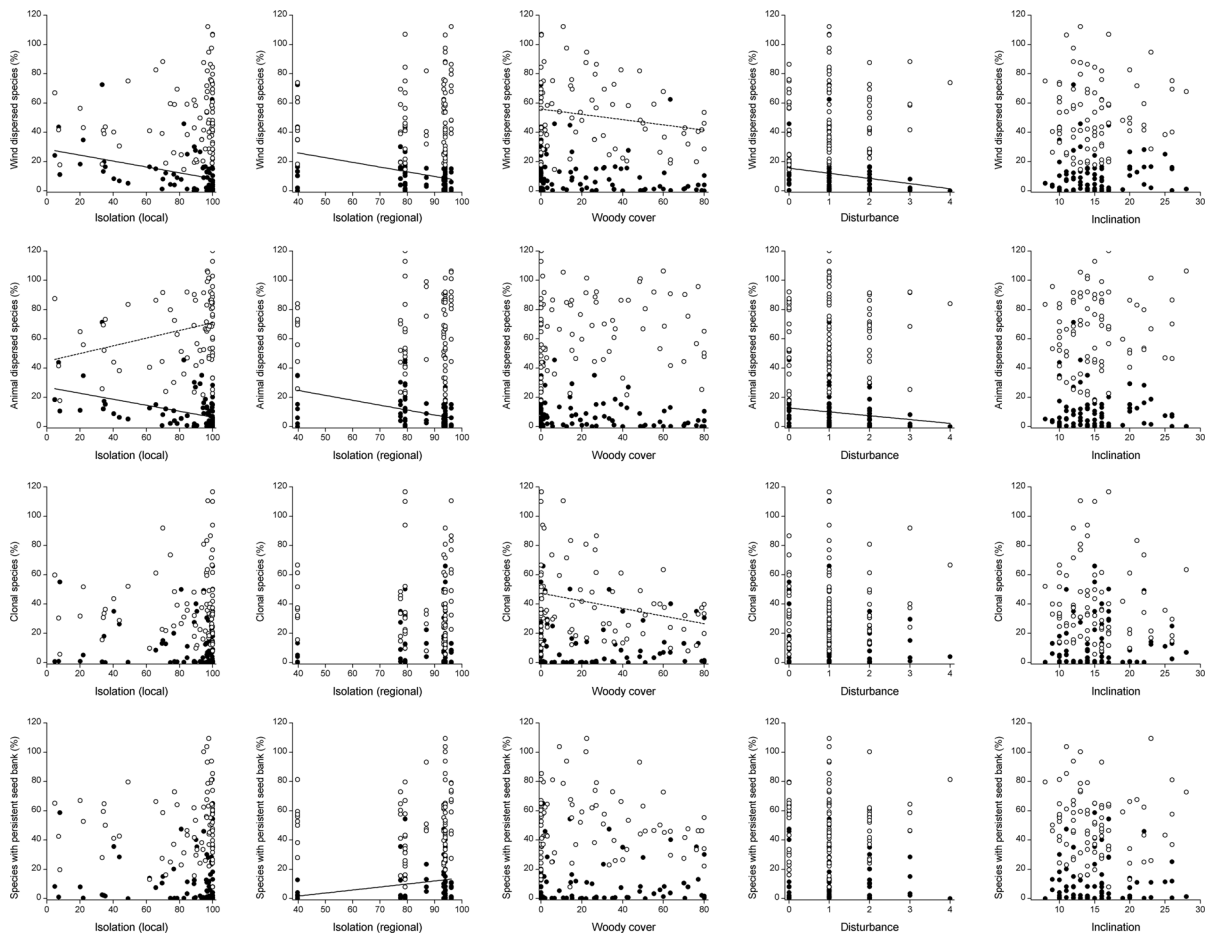


Fig. 4 Relationship between the abundance of specialist (filled symbols) and generalist plant (empty symbols) functional groups and landscape and habitat filters. Lines are fitted in case of a significant relationship revealed by the model selection

neither the immigration by incoming seed rain nor the subsistence by local propagule sources contribute to the maintenance of the local populations (Riba et al. 2009). Thus, in such a situation, specialist plants with an effective seed dispersal are especially exposed to extinction processes. Loss of functional spatial connectivity with the metapopulations hinders the gene flow of specialist plants by limited dispersal of pollen and seeds between population units. In the long term it likely results in a genetic drift and inbreeding (Young et al. 1996; Heinken and Weber 2013). As was pointed out by Jacquemyn et al. (2010), loss of genetic variability and expression of deleterious alleles can affect species persistence by lowering their individual vitality, and in the long run it can decrease their ability to respond to changing environmental conditions. Kuussaari et al. (2009) found that this effect is more

severe in populations restricted to small grassland patches (such as our studied grasslands) because due to their small size, such habitats often maintain populations close to extinction thresholds, with limited genetic variability. Based on our results, isolation due to habitat loss can eventually lead to a decreased abundance or even the extinction of good wind- and animal-disperser specialist plants (Riba et al. 2009; Lindborg et al. 2012).

Landscape filters and persistence traits

We hypothesised that persistence traits support species survival in human-modified landscapes. We found that whilst clonal specialist plants could successfully cope with habitat isolation, a persistent seed bank did not support the survival of specialist plants. In case of

generalist plant species, persistence traits did not show any correlation with isolation. Persistence by clonal reproduction was proven to be an essential trait in sustaining remnant populations of specialist plants in grassland islands since it can mitigate the consequences of genetic isolation even for an extended period (see also Lindborg et al. 2014; Auffret et al. 2015). Previous studies suggested that clonality alone, without other persistence traits such as a persistent seed bank, is an almost certain route to local extinction (Honnay and Bossuyt 2005). However, we found that in human-modified landscapes, clonal spreading could support the persistence of several specialist plants that predominantly have a transient seed bank. Specialist plants with a persistent seed bank declined with increasing local isolation. The likely reason for the different adaptive value of the studied persistence traits is that unlike the realised advantages of clonality, seed persistence offers a potential for future establishment for specialist plants (Thompson et al. 1997). This advantage might be realised in the future; however, this potential is strongly influenced by habitat filters. Interestingly, we found that regional-level isolation increased the abundance of specialist plants with a persistent seed bank. In heavily transformed landscapes it is likely that species with a persistent seed bank have a higher chance for recolonisation even after their extinction from the aboveground vegetation (Marini et al. 2012). Generalist species were unaffected by landscape filters regardless of their persistence traits. This is probably due to the high availability of proper non dry-grassland habitats in the vicinity of the studied grassland islands. Increased habitat availability decreased the importance of persistence abilities since the high overall habitat availability could sustain large and stable populations of generalists and supported an increased level of immigration from neighbouring habitat patches.

Habitat filters

Our findings confirmed that the fate of specialist plants in terrestrial habitat islands is highly affected by habitat filters. We found that habitat filters mainly determined the local persistence or extinction of specialist plants and thus generally had a more robust effect on their richness than on their abundance. The likely reason for this phenomenon is that even if

diaspores of a certain species have the potential to reach a grassland habitat, it might be filtered out by specific habitat properties, which hinder plant establishment and persistence (see also Janečková et al. 2017). Generalist plants were less sensitive for habitat filters due to their wider tolerance against unfavourable environmental changes (Lindgren and Cousins 2017).

Whilst woody encroachment had a negative effect on the species richness of animal-dispersed specialist plants, it did not affect the species richness of wind-dispersed ones. The likely reason for this is that the dispersal vectors might avoid woody areas so that zoochorous seed dispersal is hindered there. The lack of a negative effect of woody encroachment on specialist plants dispersed by wind might be due to the seed trap effect of woody vegetation (Cadenasso and Pickett 2001). Even though wind-dispersed species can hardly get into the woody patches, the edge of the high and dense vegetation, acting as an obstacle, can trap propagules arriving by wind. Thus, wind-dispersed plants can establish effectively at the edge of woody patches. Increased woody cover can change habitat properties by increased shading and a milder and more balanced temperature due to the dense canopy cover (Gazol et al. 2012). Nitrogen enrichment of the soil, mainly caused by the high abundance of the nitrogen-fixing *Robinia pseudoacacia* (present on 47% of the kurgans with a mean cover of 24.8%), could also change the habitat conditions. Altered environmental conditions can also lead to a considerable decrease in the availability of proper microsites, which may act as an establishment filter for most of the specialist and even for generalist plants (Gazol et al. 2012). Specialist plants with different persistence traits responded differently to increased woody cover. Clonal species, due to their resistance against unfavourable environmental conditions, were not affected by increased woody cover (see also Janečková et al. 2017). In contrast, specialist plants with a persistent seed bank were suppressed by it. The reason is that even though species with a persistent seed bank have a high potential for re-establishment after unfavourable periods, this strategy is not effective in a site permanently covered by woody species since here the number of proper microsites is permanently limited. According to our results, clonality could support persistence of specialists in such environments as clonal specialists—given their long

lifespan and reduced dependency on sexual reproduction and microsite availability—could cope with changing or unfavourable environmental conditions for an extended period (Heinken and Weber 2013). Local populations of clonal specialist plants could bridge long unfavourable phases and survive even in degraded grassland habitats characterised by a high cover of woody species (Honnay and Bossuyt 2005). The species richness of generalist species with good clonal spreading ability was not affected by the cover of woody species, but their cover decreased with an increasing level of woody encroachment, probably due to the shading effect and lower availability of establishment microsites.

We found that disturbance had an overall negative effect on the species richness of all studied specialist and generalist groups by causing the direct damage or mortality of individuals and loss of grassland area. The reason for this overall negative effect might be that disturbance is the only filter that can lead to a considerable level of mortality, i.e. immediate loss of genetic variance; thus, it can significantly decrease the fitness of the population. The negative effect of disturbances is further aggravated by isolation as the re-establishment of specialists is limited due to their low dispersal ability if there are no available seed sources in the adjacent areas (Jacquemyn et al. 2010). The only exception was the species richness of specialist plants with a persistent seed bank, which was unaffected by disturbance. Furthermore, disturbance was the only habitat filter that significantly affected the abundance scores of wind- and animal-dispersed specialist plants; however, it did not affect good disperser generalist plants. This difference is probably caused by the mass effect: As generalist species are more abundant in the different habitat patches of the landscape, they can recolonise the disturbed habitats more effectively than the specialist species. Even though clonality was proven to be an effective persistence trait, disturbances had a detrimental effect on clonal specialist species. Although the species of this group can cope with stochastic environmental changes, the lack of sexual reproduction reduces their ability for re-establishment if their populations are fundamentally damaged (Lindborg et al. 2012). We found that specialist plants with a persistent seed bank were not significantly affected by disturbances. The likely reason is that they could re-establish from the seed banks after the disturbances

and sometimes even profit from the open soil created by the disturbance factors.

Steep inclinations significantly increased the species number of established specialist and generalist plants regardless of their dispersal and persistence traits. Slopes with different inclinations harbour specific microhabitats characterised by different soil moisture, microclimate and level of solar radiation (Lisetskii et al. 2016; Deák et al. 2017). By enhancing topographic heterogeneity, an increase in steepness also results in an increase in the contrast between the attributes of microhabitats (Sudnik-Wójcikowska and Moysiyeenko 2014). The general increase in the species richness of specialists can be explained by the niche theory, which assumes that there is a positive diversity-environmental heterogeneity relationship, i.e., a greater variation in microhabitats results in an increased species richness (Tamme et al. 2010). The effective niche separation due to several available microhabitats led to the co-existence of species with different environmental requirements even on a small scale (Gazol et al. 2012; Deák et al. 2015; Lindgren and Cousins 2017).

Patch occupancy of specialist plants

We found that the patch occupancy of specialist species showed a unimodal pattern with an overrepresentation of rare species (Fig. 2). This pattern confirmed the results of former empirical studies, which predicted that assemblages with a high proportion of species with low dispersal ability harbour only a few core species (McGeoch and Gaston 2002). The most abundant core species were mostly good disperser grasses (such as *Agropyron cristatum*, *Festuca* spp., *Bromus inermis* and *Koeleria cristata*) with an enhanced clonal spread or tussock forming and with a good competitive ability. These species are best adapted to the specific habitat conditions in dry grasslands and constitute the community matrix, reflected by the high abundance of core grasses on the kurgans. We also detected a high number of less abundant satellite species. Their wide geographical distribution is probably hampered by dispersal and niche limitations and by low competitive abilities (Bossuyt et al. 2004). These species are most threatened by the negative consequences of environmental changes, as—given their low dispersal ability and

sparse distribution—there is a very low chance for re-colonisation after a drastic disturbance event.

Conclusions and conservation remarks

We propose a model exploring the effects of habitat and landscape filters on grassland specialist plants occurring in habitat islands (Fig. 5). Our findings demonstrated that by influencing the colonisation and extinction processes, the interplay of landscape and habitat filters drives the abundance patterns and species richness of specialist plants in terrestrial habitat islands. Landscape filtering by habitat isolation determines the overall vitality of specialist plants (by affecting their abundance). Habitat filters have a great importance in sorting specialist plants that can or cannot persist in the case of severe habitat loss (by affecting their species richness). Our findings revealed that decreased vitality caused by unfavourable landscape composition and thus limited metapopulation connections could be counterbalanced by favourable local environmental conditions or even further

aggravated by anthropogenic disturbances and the negative effects of woody encroachment. We emphasise that it is important to consider the concurrent mechanisms driven by habitat and landscape filters for an understanding of the complex assembly rules in habitat islands.

In small and isolated semi-natural habitat islands, populations of specialist plants are especially threatened by the lack of spatial connectivity with metapopulations and also by the often stochastic and unfavourable environmental changes. Unfavourable changes on landscape and habitat level can enhance species extinction and reduce the rate of species immigration into grassland habitat islands. Habitat specialist plants are especially vulnerable because of their limited dispersal ability and specific habitat requirements. For sustaining their populations in small habitat islands it is important to enhance the spatial connectivity between the habitats and also to increase the quality of the remnant semi-natural habitat patches by active conservation measures. These aims can be fulfilled by newly created habitat patches, which increase the permeability of the landscape, even for

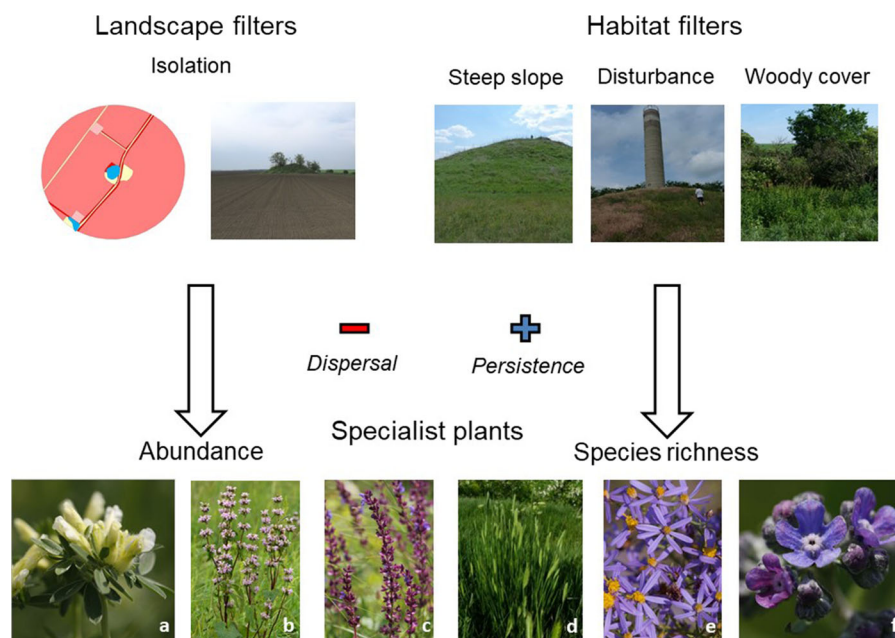


Fig. 5 Model of the effect of habitat and landscape filters on grassland specialist plant species. Description of the filters: isolation—summed percentage cover of non dry grassland habitats around the kurgan; steep slopes—high mean inclination; disturbance—high level of human or natural disturbances affecting at least 10% of the kurgan’s surface; woody cover—

high level of woody cover. Grassland specialist plants (herbaceous species of the phytosociological class Festuco-Brometea) were considered as “specialist plants”. Species names: **a**—*Chamaecytisus rochelii*; **b**—*Phlomis tuberosa*; **c**—*Salvia nemorosa*; **d**—*Agropyron cristatum*; **e**—*Aster sedifolius*; **f**—*Anchusa barrelieri* (photos by B. Deák)

specialist plants with a low dispersal ability. Providing a proper management in the existing habitats by the reintroduction of grazing animals, suppressing woody encroachment and reducing the level of human and natural disturbances is also crucial.

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