



Policy analysis

Different extinction debts among plants and arthropods after loss of grassland amount and connectivity



Balázs Deák^{a,b,*}, Ádám Bede^a, Zoltán Rádai^a, Béla Tóthmérész^c, Péter Török^{d,e},
Dávid Nagy D.^c, Attila Torma^{b,f}, Gábor Lőrinczi^f, Antal Nagy^g, Szabolcs Mizser^c,
András Kelemen^{a,f}, Orsolya Valkó^a

^a Lendület Seed Ecology Research Group, Institute of Ecology and Botany, Centre for Ecological Research, Vácrátót, Hungary

^b 'Lendület' Landscape and Conservation Ecology, Centre for Ecological Research, Institute of Ecology and Botany, Vácrátót, Hungary

^c MTA-DE Biodiversity and Ecosystem Services Research Group, Debrecen, Hungary

^d MTA-DE Lendület Functional and Restoration Ecology Research Group, Debrecen, Hungary

^e Polish Academy of Sciences, Botanical Garden - Center for Biological Diversity Conservation in Powsin, Warsaw, Poland

^f University of Szeged, Department of Ecology, Szeged, Hungary

^g University of Debrecen, Institute of Plant Protection, Faculty of Agricultural and Food Sciences and Environmental Management, Debrecen, Hungary

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ABSTRACT

A decrease in habitat amount and connectivity causes immediate or delayed species extinctions in transformed landscapes due to reduced functional connections among populations and altered environmental conditions. We assessed the effects of present and historical grassland amount and connectivity as well as local habitat factors typical of the present landscape on the current species richness of grassland specialist and generalist plants and arthropods in grassland fragments. We surveyed herbaceous plants, ants, orthopterans, true bugs and rove beetles in 60 dry grassland fragments in Hungary. We recorded the area of the focal grassland, the slope and the cover of woody vegetation. By using habitat maps of the present and historical landscape, we calculated grassland amount and connectivity for four time periods covering 158 years (1858–2016). We found evidence for an unpaid extinction debt in specialist plants, suggesting that they have not come to equilibrium with the grassland amount and connectivity of the present landscape yet. This localised and typically long-lived group responded slowly to the landscape changes. Specialist arthropod taxa with short generation times responded much faster to habitat loss than plants and did not show an extinction debt. Generalist plants and animals adapted to a wide range of habitats were affected by the landscape-scale decline of grassland habitats. Despite decreased habitat connectivity, grassland fragments with dry environmental conditions and high environmental heterogeneity can sustain specialist plants in transformed landscapes. Unpaid extinction debt should be considered an early warning signal: Restoration of grassland connectivity is necessary to halt ongoing extinction processes.

1. Introduction

Loss and fragmentation of natural and semi-natural habitats pose a major threat for biodiversity worldwide (Bagaria et al., 2015). Habitat loss reduces the amount of available space that can be occupied by habitat specialist species, while fragmentation decreases the functional connectivity between the remaining habitat patches resulting in a restricted flow of individuals and genes at the metapopulation level

(Kuussaari et al., 2009; Figueiredo et al., 2019). Habitat loss and fragmentation are often coupled with additional effects that lead to the degradation of the habitat, which on the one hand threatens the survival and reproduction of habitat specialist species and on the other hand supports the establishment of generalists (Clavel et al., 2011). Such effects include altered abiotic conditions (Kuussaari et al., 2009), cessation of traditional management (Krauss et al., 2010), increased edge effects (Kuussaari et al., 2009; Bagaria et al., 2015) and propagule

* Corresponding author at: Lendület Seed Ecology Research Group, Institute of Ecology and Botany, Centre for Ecological Research, 2-4 Alkotmány street, H-2163 Vácrátót, Hungary.

E-mail address: debalazs@gmail.com (B. Deák).

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pressure of generalist and invasive species that are abundant in the surrounding landscape matrix (Figueiredo et al., 2019). As a result of habitat loss, fragmentation and degradation, specialists may show a considerable decrease in population size and fitness, which can finally lead to the local extinction of area- and disturbance-sensitive species (Figueiredo et al., 2019). The replacement of habitat specialists by generalists not only leads to the disappearance of species of conservation interest, but can also negatively affect ecosystem functioning by causing functional homogenisation (Clavel et al., 2011). Losing functional diversity due to the extinction of species specialised to a certain ecosystem can considerably decrease the community level resistance and resilience and thus further aggravate habitat degradation processes (Clavel et al., 2011).

Although populations of specialist species in small, fragmented and degraded habitats are often compromised, a decrease in habitat connectivity and an increase of ecosystem perturbation or degradation do not necessarily lead to their immediate extinction, but rather to a delayed extinction of a certain set of species by destabilising co-existence and enabling competitive exclusion (Tilman et al., 1994; Kuussaari et al., 2009; Figueiredo et al., 2019). Time-delayed extinctions, known as extinction debt, are typical of recently fragmented landscapes in which the area and/or the spatial configuration of the habitat fragments are just below the extinction threshold for certain species (Krauss et al., 2010; Löffler et al., 2020). Existence of extinction debt can be assumed when the characteristics of the past landscape explain current species richness better than the characteristics of the present landscape (Krauss et al., 2010). The time lag until the equilibrium between current habitat conditions and existing populations is reached is called relaxation time (Diamond, 1972). Although the signs are not obvious at first sight, extinction debt poses a huge challenge for biodiversity conservation, affecting a wide range of taxa and numerous ecosystems (Kuussaari et al., 2009; Figueiredo et al., 2019). In present-day transformed landscapes, many species may become extinct in the forthcoming decades even without any substantial future habitat loss (Krauss et al., 2010; Löffler et al., 2020).

The magnitude of extinction debt and the length of the relaxation time highly depend on the temporal dynamics of landscape changes, the spatial configuration of the habitats and the abiotic and biotic attributes of the focal habitat patch (Kuussaari et al., 2009; Lampinen et al., 2018). Former studies revealed large taxon-specific variations of the relaxation time from a few years to as much as one thousand years (Figueiredo et al., 2019). The sensitivity of taxa to extinction debt is considerably influenced by their ecological requirements, mobility and life-history traits (Adriaens et al., 2006; Sang et al., 2010; Piqueray et al., 2011). Species specialised to a certain habitat are generally more sensitive to changes in area, connectivity and quality of their habitat than generalist species, which can establish and persist in a wide range of habitats (Kuussaari et al., 2009; Auffret et al., 2015). It has been suggested that long-lived and less mobile taxa, such as vascular plants, have a longer relaxation time (Helm et al., 2006) compared to various arthropod taxa with short generation time, high turnover rate and high mobility (Sang et al., 2010; Bommarco et al., 2014; Lampinen et al., 2018). Besides a long life cycle, several other attributes typical of certain plant species such as the ability of clonal reproduction or self-pollination or to form persistent seed banks make them resistant to some extent against the negative effects of habitat losses (Piqueray et al., 2011).

Among the temperate ecosystems, natural and semi-natural dry grasslands are among the ones that are most affected by anthropogenic land transformation activities. As a consequence, their remaining stands have become highly fragmented and are generally embedded in a matrix of hostile habitats (Cousins et al., 2007; Löffler et al., 2019; Löffler et al., 2020). Dry grassland ecosystems located in transformed landscapes are well suited for extinction debt studies because (i) they are well separated from other habitat types in the landscape due to their special habitat conditions, (ii) their former continuous stands have been severely fragmented in many regions and (iii) they often still harbour a high

biodiversity of specialist plant and animal communities (Piqueray et al., 2011). The dry grasslands of the Eurasian forest-steppe biome suffered from the most considerable habitat loss (Wesche et al., 2016). Many stands of these species-rich dry grasslands, such as the loess grasslands of the Pannonian Biogeographical region, have been converted into cropland (Biró et al., 2018). Due to their productive chernozem soils, these grasslands have been primary targets of land transformation from the Neolithic until the present days. Since the 18th century their area has been reduced by 98% in Hungary (Biró et al., 2018).

In transformed landscapes remnant dry grassland habitats are often represented by small-scale landscape features such as road verges, field margins, midfield islets, rocky outcrops, dolines and ravines, which are not suitable for arable farming due to their physical properties and/or special functions (Fekete et al., 2019; Batori et al., 2021; Dembicz et al., 2020; Deák et al., 2021a). In the continental parts of Eurasia, ancient burial mounds called 'kurgans', which date back to the Copper, Bronze and Iron Ages, are one of the most widespread anthropogenic landmarks that provide safe havens for dry grassland habitats in transformed landscapes (Deák et al., 2016a; Dembicz et al., 2020; Kuli-Révész et al., 2021). Because of their hill shape, which makes ploughing challenging, and their relatively undisturbed status due to the respect for their historical values, these mounds often harbour millennia-old dry grassland fragments, which have survived centuries of large-scale landscape transformations (Deák et al., 2016b; Dembicz et al., 2020). The fine-scale environmental heterogeneity with respect to heat load, microclimate and soil properties provided by slopes of different aspects make mounds safe havens for a large number of grassland specialist species (Lisetskii et al., 2014; Deák et al., 2021b). Despite their small size, the high number and high density of mounds (there are approximately 600,000 mounds in the forest-steppe and steppe biomes) make them essential elements of the dry grassland network in the landscape (Deák et al., 2020; Dembicz et al., 2020).

In the past, when their surroundings were characterised by natural open habitats, the dry grasslands on the mounds were generally grazed by livestock (Deák et al., 2017). This can still be observed on mounds situated in the few protected grasslands areas in Central and Eastern Europe (Deák et al., 2020; Dembicz et al., 2020) or in the vast virgin steppes of Central Asia (Deák et al., 2017). Due to the land use transformations in the past centuries, many of the Central and Eastern European mounds became isolated and surrounded by croplands, woody plantations and urban areas (Dembicz et al., 2020). The replacement of the original management regime by the establishment of croplands around the mounds caused a considerable isolation effect for many grassland species (Deák et al., 2021a). Due to the reduced size of the remaining grassland area in the landscape and the difficult accessibility of the grasslands on the mounds, grazing as a management tool has become unfeasible on them. As shown by previous studies, abandonment can cause a considerable decrease in the conservation value of dry grassland ecosystems due to the encroachment of woody species, the increasing dominance of a few competitor species and the increased level of litter accumulation (Gazol et al., 2012). The negative effects of abandonment are partly mitigated by the dry habitat conditions on mounds, which suppress woody and herbaceous competitor species and keep biomass production low (see also Deák et al., 2021b for mounds and Lindborg et al., 2014 for midfield islands).

In our study we aimed to explore the temporal dimensions of mechanisms related to extinction debt across plant and arthropod taxa (ants, orthopterans, true bugs and rove beetles) in a transformed agricultural landscape. For this, we related the species richness of habitat specialist and generalist species to the current and past landscape metrics referring to the total grassland area and patch connectivity in the surroundings of the focal patch. We used data from 60 dry grassland fragments covering a period of 158 years including important periods of socio-economic changes, which considerably affected land use regimes. We studied the present-day landscape, the period of collectivisation (1956–1975), the ages of technological developments in

agriculture (1881–1884) and the landscape before the large river regulation campaigns (1858–1864) (Table 1). We assumed that the relaxation time related to extinction debt is affected by (i) the habitat specificity of the studied taxa, (ii) landscape factors, i.e. the spatial and temporal changes in habitat amount and connectivity, and (iii) habitat factors, including the area of the focal patch, the environmental heterogeneity of the focal habitat and the level of woody encroachment. We hypothesised that (i) historical landscape factors explain the current species richness of habitat specialists more than that of generalists, (ii) habitat connectivity has a larger effect on specialist species than habitat amount and (iii) area and environmental heterogeneity of the focal grassland patch increase the relaxation time of specialists whereas encroachment of woody species decreases it.

2. Material and methods

2.1. Study area

Our study area covers approximately 50,000 km² of the Great Hungarian Plain (East Hungary). It is characterised by continental climate with an annual precipitation of 538 mm and a mean annual temperature of 10.4 °C (Fick and Hijmans, 2017). In historical times the study area was mainly covered by forest-steppe vegetation composed of mosaics of forest patches and dry grasslands such as loess steppe grasslands, alkali grasslands and sandy grasslands. In the lower lying areas and near to rivers, wetlands and gallery forests were typical. The transformation of dry grasslands into ploughlands began in the Neolithic and was accelerated after the landscape-scale river regulation projects in the 18th century. The loss of grassland area was the largest in loess grasslands since their chernozem soil is highly suitable for arable farming (Bíró et al., 2018). In present days remaining extensive stands of loess grasslands can only be found within the few protected areas present in the region. However, many small loess grassland fragments are scattered across the landscape, mostly preserved by burial mounds and road verges (Deák et al., 2021a).

Table 1

Time periods and sources used for mapping dry grassland habitats around the focal habitat patches.

Period	Time interval	Relevance	Sources
I	1858–1864	Landscape typical before the regulation of large rivers	Second Military Survey of the Hungarian Empire, 1:28,000 (Institute and Museum of Military History, Budapest)
II	1881–1884	Technological developments in agriculture after the river regulation campaigns	Third Military Survey of the Hungarian Empire, 1:25,000 (Institute and Museum of Military History, Budapest)
III	1956–1975	Collectivisation during the communist era	Military Survey of the Hungarian People's Republic, 1:10,000 (Institute and Museum of Military History, Budapest) Aerial photographs (source: www.fentrol.hu)
IV	2014–2016	Present day landscape	Unified National Projection System, 1:10,000 topographic map of Hungary (Institute and Museum of Military History, Budapest) Satellite images (Google Maps) Field survey

2.2. Study design

As focal grassland habitats we selected 60 mounds that were embedded in agricultural landscapes, but still held loess grassland vegetation. They had not been affected by soil excavations or building activities in the past. The mean area of the mounds was 2329.6 m² (SE = 158.8), and the mean slope inclination was 15.6° (SE = 0.5). The mean distance between the focal grassland habitats and other dry grassland habitats within the 500 m buffer around the focal habitat patches was 199.6 m (SE = 14.0) in the 21st century, 207.8 m (SE = 13.9) in the middle of the 20th century, 189.8 (SE = 11.7) at the end of the 19th century and 155.8 (SE = 13.4) in the middle of the 18th century. Based on preliminary fieldwork and the available current and historical maps, aerial photos and satellite data, we selected the mounds for this study to cover a wide range of local environmental factors (i.e. habitat heterogeneity expressed by various slope aspects and the level of woody encroachment) and landscape change situations (i.e. changes in current and historical grassland area and connectivity in the surroundings of the focal habitats) (Appendix 1). We selected only unmanaged mounds (no mowing or grazing present). Although most of the mounds in the region used to be grazed in the past, the majority became abandoned in the 20th century. Only a small proportion of mounds situated in protected sites remained to be grazed, and a few mounds are mown. Mowing is generally typical to mounds harbouring churches, graveyards or crosses still maintained by local citizens (Deák et al., 2020). Since abandonment is typical of Central and Eastern European mounds embedded in transformed landscapes (Deák et al., 2021a; Dembicz et al., 2020) and also poses a serious threat to other fragmented dry grasslands across Europe (Cousins, 2006), we decided to focus only on abandoned mounds.

Grasslands preserved on the mounds served as focal habitats in our study. We considered changes in current and historical grassland amount and connectivity in a 500-metre buffer around all focal habitat patches. We digitised the location and area of dry grassland habitat patches within the buffer zones taking into account four time periods covering 158 years (Fig. 1). The studied time periods reflect the main socio-economy related landscape-scale changes affecting the amount and connectivity of grasslands in lowland areas of Central and Eastern Europe (Table 1). The main sources were georeferenced military and topographic maps, aerial photos and satellite images (Table 1). In the case of historical sources from the 19th century, we improved the spatial accuracy of the maps by adding georeferenced points (such as cross-roads, churches and bridges) using QGIS 3.1 (QGIS.org, 2021) before mapping the grassland habitats.

The studied focal grasslands were situated on mounds, which are positive landforms in an otherwise plain landscape. Being unique landmarks, mounds served as important orientation points for military mapping and were also often used as natural markers of administrative borders (Deák et al., 2016a). Consequently, their positions and sizes were precisely indicated even in maps from the 19th century and could be further fine-tuned by current topographic maps. For mapping dry grassland patches in the present landscape, we firstly prepared a preliminary map deriving information from the land cover categories in the 1:10,000 topographic maps of Hungary (Unified National Projection System; UNPS) and from Google Maps satellite images. We validated and if necessary corrected this map during the field survey by visiting all grassland patches. For mapping dry grasslands in the past landscape, we used land cover data derived from historical maps. Historical land cover data were checked and if necessary corrected, taking into account the geomorphological position, elevation above sea level (derived from the UNPS maps) and current distribution of dry grasslands. As a result we could compile a spatially and thematically improved map of dry grasslands in the studied areas. For fine-tuning maps from the third period (1956–1975), we used archive aerial photographs. For comparability reasons we eliminated very small grassland patches (<0.1 ha) from the present day maps since they were not delineated in the historical maps. We used QGIS 3.1 to georeference archive maps and aerial photographs

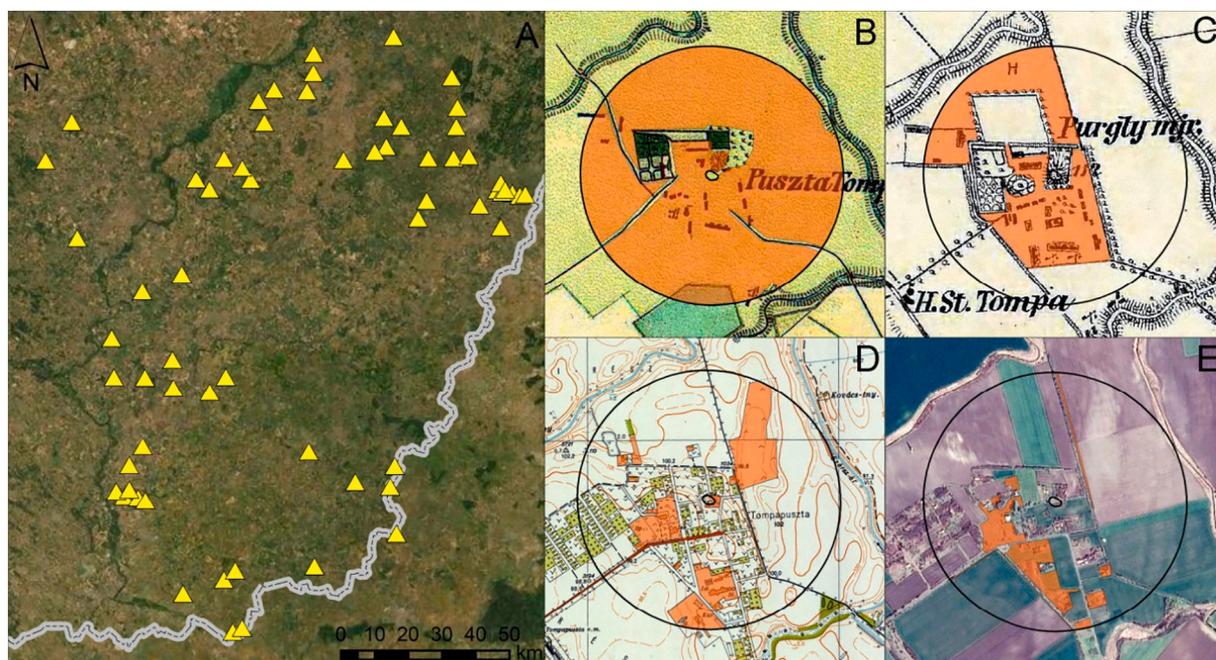


Fig. 1. A – Map of the surveyed grassland fragments in the Hungarian Great Plain ($n = 60$). B–E: Changes in the grassland cover around one of the studied focal habitat patches over time: B – Period I (1858–1864), C – Period II (1881–1884), D – Period III (1956–1975), E – Period IV (2014–2016).

and to digitise grassland habitat patches and calculate their area.

2.3. Survey of plant and arthropod species

Each focal grassland habitat ($n = 60$) was surveyed at one sampling occasion between May and June 2014–2016. Botanical and zoological surveys were done simultaneously. During the field survey we recorded the list of all herbaceous vascular plant species considering one mound as one sample unit. Ants (Hymenoptera: Formicidae), orthopterans (Orthoptera), true bugs (Heteroptera) and rove beetles (Coleoptera: Staphylinidae) were collected by sweep netting and D-vac sampling in transects along the four cardinal directions from the bottom to the top of the mounds. Along each transect we made 50 sweeps with a 40 cm diameter sweep net and took 15 D-vac samples. We used a collecting bag attached to a 12 cm diameter sampling cone, which was held in position slightly above the soil surface for 5 s per sample. Samples collected by the sweep net and the D-vac were stored in labelled plastic bags. Individuals of the selected taxa were extracted from the samples in the laboratory and preserved in 70% ethanol. Each specimen was identified to species level using standard keys (Harz, 1957; Harz, 1960; Lohse, 1974; Vásárhelyi, 1978; Vásárhelyi, 1983; Seifert, 2018; Király, 2009; Assing and Schülke, 2011; Czechowski et al., 2012). When evaluating the results of the survey it should be taken into account that due to the applied sampling methodology (each mound was surveyed only once), thus a certain proportion of species might not have been detected. This is especially true for groups with many species characterised by very different phenology (such as true bugs and orthopterans). For the statistical analyses we used the pooled species lists of the four transects originating from the same mound.

2.4. Assignment of taxa to specialist and generalist groups

Based on their habitat requirements, we classified all species as dry grassland specialists or generalists. We considered a species to be a grassland specialist if in the studied region it is confined exclusively to dry grassland habitats and characterised by specific habitat requirements (i.e. preference for short grasslands with warm and dry habitat conditions). For these species both non-grassland natural

habitats (e.g. wetlands, open water surfaces, closed forests) and man-made habitats (e.g. woody plantations, ploughlands) act as hostile matrices, which are inadequate for their establishment and form dispersal barriers. For assigning plants to the specialist group, we used habitat preferences according to by Borhidi (1995) and Király (2009). For assigning arthropods to the grassland specialist group, we considered also their dietary and overwintering plant preferences (i.e. predominant use of plants that only occur in dry grasslands). For ants we used the habitat preference descriptions provided by Czechowski et al. (2012), for orthopterans the categories given by Rácz (1998). Data on habitat and host plant requirements of true bug species were based on Wachmann et al. (2004, 2006, 2007, 2008). For assigning rove beetles to the specialist group we used Koch (1989) and Ádám (2004). All non-grassland specialist plant and arthropod species were considered generalists.

2.5. Environmental variables

As a proxy of environmental heterogeneity, we measured the inclination of the north-, east-, south- and west-facing slopes on each mound with an inclinometer. For the models we used mean slope inclination calculated by averaging the inclination of north-, east-, south-, and west-facing slopes. We also recorded the total cover of woody vegetation, which is considered an important threat factor for grassland specialist species. The total cover of woody species was visually estimated in the field. The area of the focal habitat patch was calculated from present day habitat maps and present day and historical topographic data. The focal habitat area was constant across the studied timescale, as we studied dry grasslands situated on mounds that have a fixed size. The grassland amount in the neighbouring landscape was expressed by the percentage cover of grasslands around the focal habitat patch. We estimated the habitat connectivity of dry grassland habitat patches within the 500 m buffer using the connectivity index by Hanski et al. (2000):

$$CI_i = \sum \exp(-\alpha d_{ij}) A_j^{\beta}$$

where A_j is the area of the neighbouring grassland, d_{ij} the distance from the focal grassland patch to the neighbouring grassland, α a species-

specific parameter related to its dispersal ability and β a parameter describing the scaling of immigration. As we applied the habitat connectivity index to entire communities, we set both parameters to 0.5.

2.6. Data analyses

All data handling and statistical data analyses were carried out in R (v. 4.0.5, R Core Team). For testing differences in habitat amount and connectivity among the four time periods, we used Conover-Iman tests with Bonferroni's P-value adjustment for multiple pairwise comparisons.

Subsequently we carried out an analysis assessing the effect of historical and present grassland amount and connectivity on the species richness of specialist and generalist species. We used hierarchical partitioning (with the R-package "hier.part"; Nally and Walsh, 2004) and separate modelling to identify both statistical significance and explanatory power of the used variables. As of the latter we fitted generalised linear regression models (GLMs) separately for each response-predictor combination (response variables were the species richness of specialist and generalist plants, ants, orthopterans, true bugs and rove beetles; predictors were grassland amount and connectivity scores from the four studied periods). For species richness data we used negative binomial linear models. For each response variable we selected the landscape variable that best explained the variation in the given response variable (based on its Nagelkerke's R^2 ; from R-package "performance" by Lüdecke et al., 2021), and used this variable in the subsequent analyses. Notably, such a selection procedure for environmental explanatory variables was necessary because the eight landscape variables (four grassland amount and four connectivity values) were correlated (precluding their simultaneous usage in linear regression models due to multicollinearity) and we aimed at identifying the environmental variable and time period with the strongest ecologically relevant effect on current species richness.

Finally, we fitted GLMs on the species richness scores. In these models the most relevant landscape variable for the given response was used as predictor, along with the area of the focal grassland, the mean slope inclination and the total percentage cover of woody species. Negative binomial linear models were used for fitting species richness data. Initially we used site ID as a random factor to control for non-independence in our repeated sample data, but random effect variances were near zero (causing model convergence warnings), indicating negligible between-site variation in the responses; therefore, we excluded random effects from the final models.

3. Results

3.1. Temporal changes in area and connectivity of grasslands

We observed significant changes in both amount ($X^2 = 22.4$; $P < 0.001$) and connectivity ($X^2 = 11.7$; $P = 0.01$) of grasslands in the four studied periods (Fig. 2). The amount of grasslands around the focal patches was the highest in the middle of the 19th century (Period I), and it constantly decreased by time. Grassland connectivity was constant in the first three periods, but it significantly decreased during the last period.

3.2. Species richness

We recorded 106 specialist and 224 generalist plant, 21 specialist and 11 generalist ant, 16 specialist and 2 generalist orthopteran, 68 specialist and 96 generalist true bug and 10 specialist and 66 generalist rove beetle species in the studied focal grasslands. For a detailed list of grassland specialist and generalist species, see Appendices 2–6. Means and standard errors and minimum and maximum values of the species richness of grassland specialist and generalist plants and arthropods are listed in Appendix 7.

3.3. Effect of present and historical landscape

Both present and historical (Period III; second half of the 20th century) grassland amount and connectivity had a positive effect on the species richness of specialist plants (Fig. 3). According to the derived model, present richness of specialist plants was best explained by landscape connectivity measured in the second half of the 20th century (Period III; $R^2 = 0.23$). The studied landscape factors did not significantly explain the species richness of generalist plants. Neither present nor past habitat amount and connectivity affected the species richness of arthropod specialist and generalist species. For all results see Appendix 8.

3.4. Effect of environmental factors

The final GLMs revealed that species richness of specialist plants was higher on mounds with steeper slopes (Fig. 4, Appendix 9). There were less specialist true bugs and more generalist ant species on mounds with high woody cover. Other environmental factors had no significant effect on any of the studied specialist or generalist groups.

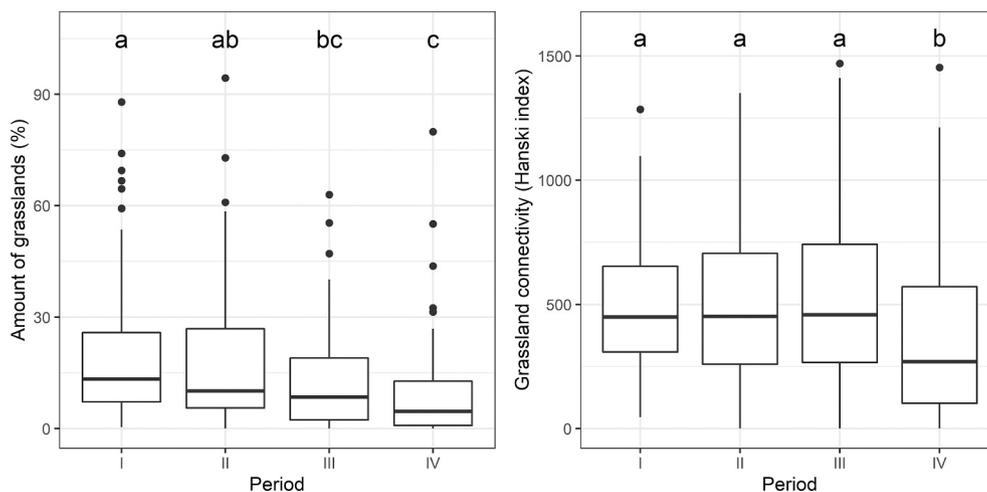


Fig. 2. Changes in habitat area (a) and connectivity (b) of dry grasslands around the focal patches ($n = 60$). Different letters denote significant differences between groups according to the Conover-Iman test with Bonferroni correction. Periods refer to the time intervals defined in Table 1 (Period I: 1858–1864, Period II: 1881–1884, Period III: 1956–1975, Period IV: 2014–2016).

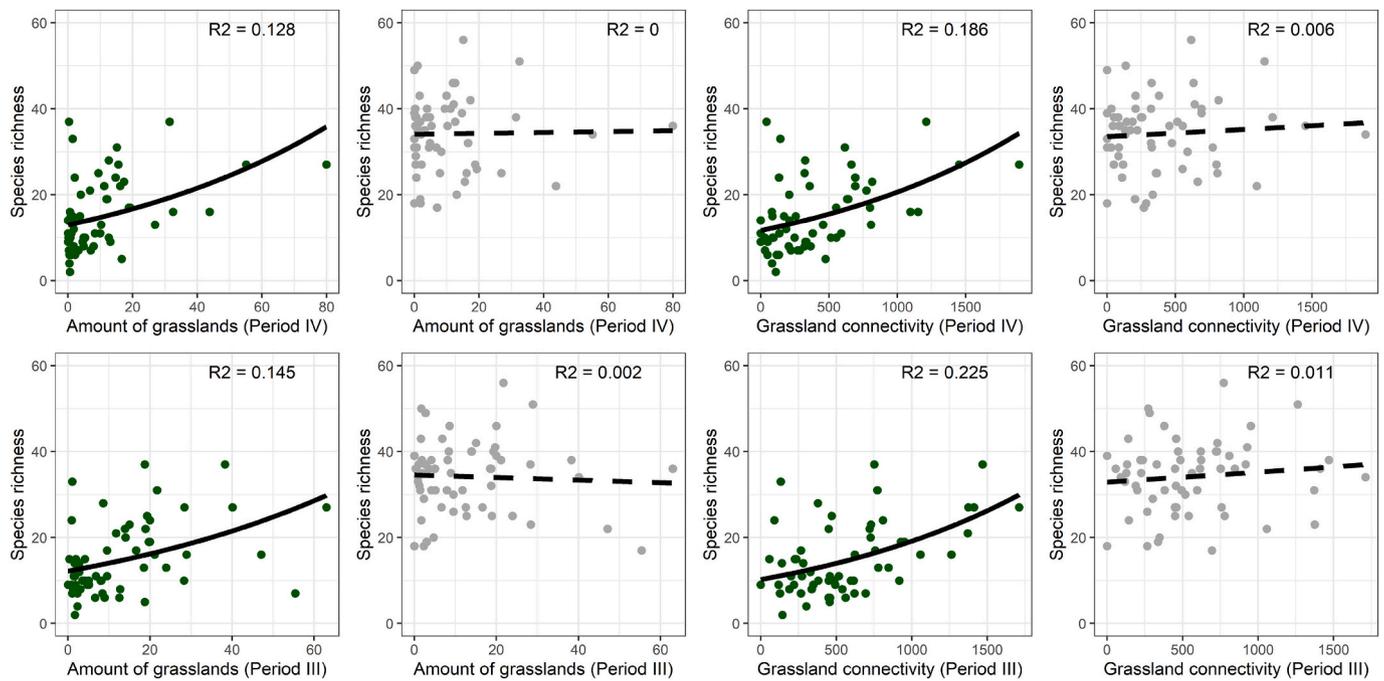


Fig. 3. Effect of grassland amount and connectivity on the species richness of specialist (green dots) and generalist (grey dots) plant species in Periods III–IV. Solid lines represent significant, dashed lines non-significant relationships. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

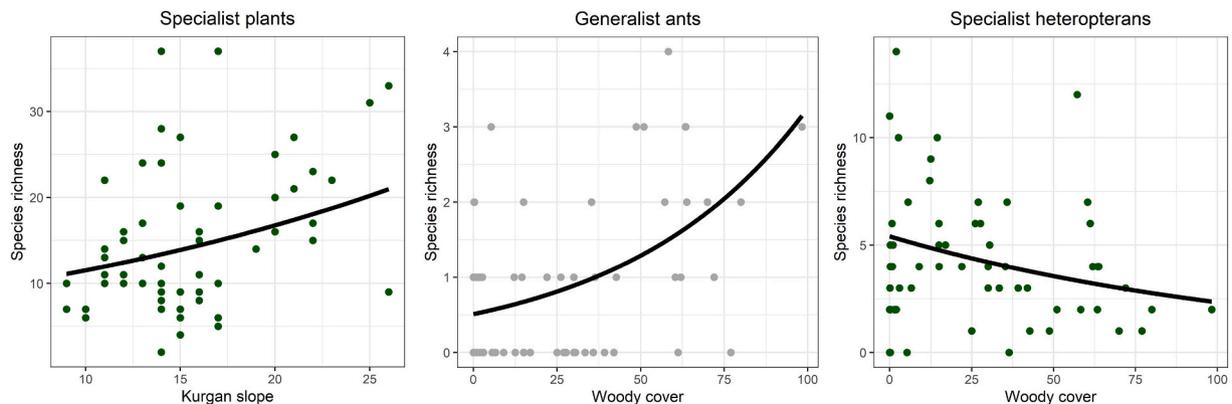


Fig. 4. Effect of environmental factors derived from the final generalised linear model on species richness scores of specialist (green dots) and generalist (grey dots) taxa. Only significant effects are plotted, for non-significant relationships see Appendix 9. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

4. Discussion

4.1. Landscape changes

We found that in the study area the amount of dry grasslands has been declining constantly from the 1850s until present days. As typical also of many fertile lowland areas of Central Europe, this decline was mainly due to the expansion of arable land at the expense of dry grasslands with fertile soil (Deák et al., 2020). Interestingly, the constant loss of habitats during the four studied periods did not result in a significant loss of habitat connectivity for an extended time interval during the first three periods (from 1858 to 1975). In the first two periods in the 19th century, the still existing and often interconnected large dry grassland patches considerably contributed to the preservation of grassland connectivity. Later, from the second half of the 20th century formerly extensive grasslands became fragmented due to the expansion of arable land. Despite the large efforts put into agricultural

intensification and collectivisation during the communist regime, a dense network of functioning small farming systems remained present in the landscape. The diverse land use systems related to each individual farm preserved many small dry grassland fragments, which were used as pastures for livestock, as agricultural parcels or to delineate homesteads. The existence of small but numerous grassland fragments across the whole landscape could compensate for the increasing loss of pristine grasslands and habitats and maintain grassland connectivity. In the later phase of the communist era and during the change of regime in the 1990s, the former typical network of small farms and the related dry grasslands disappeared, and the landscape was homogenised by the formation of large crop monocultures (Biró et al., 2018). Although the loss of grassland habitats has slowed down in many regions of Europe since the 1990s because of improved conservation measures (Carvalho et al., 2013), further losses could be observed in the post-communist countries, especially in lowland agricultural landscapes, due to the socio-economic changes following the change of regime (Biró

et al., 2018). As shown by the observed significant decline in grassland amount and connectivity, this process severely affected the dry grassland habitats in Period IV.

4.2. Extinction debt of specialist and generalist plants

Current species richness of specialist plants correlated stronger with grassland amount and connectivity typical to the landscape five to seven decades ago than with present landscape characteristics. We found that the effect of past grassland connectivity was larger on specialist plants than the effect of past grassland amount. The likely reason is that while the amount of grasslands has just slightly declined since the period of collectivisation, the disappearance of many small grassland stands has resulted in a considerable loss of functional connections between the remaining habitat patches on the landscape level. These results suggest that the populations of specialist plants in the focal habitat patches still have not come to equilibrium with the attributes of the present landscape. Thus, further extinctions can be expected especially in the case of specialist species sensitive to the loss of metapopulation connections (Krauss et al., 2010). The length of the time lag observed in our study is congruent with the results of previous studies (Helm et al., 2006; Bommarco et al., 2014), which documented an extinction debt of grassland specialist plants 40–100 years after a considerable loss in grassland amount and connectivity.

The reason for the long relaxation time is that in general, plants as sessile organisms react slowly to changes in the neighbouring landscapes and in local conditions (Krauss et al., 2010; Lampinen et al., 2018; Löffler et al., 2020). The strong positive effect of historical connectivity of grasslands on specialist plant richness is due to the life-history traits of plants, which support their long-term maintenance even under suboptimal conditions (Bagaria et al., 2015). The decline in grassland connectivity on the landscape level and the consequences of abandonment (such as litter accumulation) on the site level can be counterbalanced by the long life span and generation time of many plant species, which allows them to persist even though the neighbouring landscape or the local conditions become inadequate (Helm et al., 2006; Deák et al., 2021a). As theory predicts, dispersal-limited species, such as most of the dry grassland species, may persist for a long time before extinction at a certain habitat patch despite substantial changes in the neighbouring landscape (Bommarco et al., 2014; Löffler et al., 2020).

The fact that we observed a considerable extinction debt for specialist plants, but no effect of historical landscape on generalists suggests that specialists are more susceptible to extinction debt compared to generalists due to their narrow habitat preference and often limited dispersal (Kuussaari et al., 2009). Whereas the loss of amount and connectivity of grasslands results in a considerable reduction of proper habitats and decline in metapopulation connections for grassland specialist plants, these changes are not necessarily detrimental for generalists, which might also establish in transformed non-grassland habitats (Kuussaari et al., 2009; Lampinen et al., 2018).

4.3. Extinction debt of specialist and generalist arthropods

In contrast to specialist plants, the species richness of the studied specialist and generalist animal taxa (ants, orthopterans, true bugs and rove beetles) was not related to grassland amount or connectivity; thus, they were either unaffected by landscape changes or have already paid their extinction debt induced by landscape transformations in the past. Whereas plant dispersal is limited and passive so that plants have to cope with altered local and landscape conditions in fragmented landscapes, animals can actively disperse and leave habitats that have become unsuitable due to unfavourable changes (Krauss et al., 2010). However, when animals are not able to relocate to another suitable habitat patch, local extinction processes might be much faster for them compared to plants (Kuussaari et al., 2009). This applies especially to animal species that depend on metapopulation networks and have a short lifespan and a

fast generation turnover (Krauss et al., 2010).

Even though ants and orthopterans can in general cover certain distances among patches, the species present in the study area are characterised by a reduced mobility (Harz, 1960; Poniatowski and Fartmann, 2010; Seifert, 2018); thus, it is likely that they could not cope with the drastic reduction in grassland connectivity. Ants and orthopterans can persist for a long time even in small and isolated populations (Poniatowski and Fartmann, 2010) so that an extinction debt can be expected for these taxa (Löffler et al., 2020). Still we did not observe such pattern, probably due to the small area of the studied focal habitat patches (mean area = 0.23 ha). We assume that marked changes in the landscape composition and connectivity together with the small focal grassland area resulted in the fast extinction of area-sensitive specialists with low mobility. In contrast to ants and orthopterans with a limited mobility, rove beetles with a larger movement radius (Tóthmérész et al., 2014) were likely not severely affected by the changes in landscape factors since they can quickly react to changes in habitat availability. As it was found for butterflies (Lampinen et al., 2018; Brückmann et al., 2010), true bugs and rove beetles can also cross unsuitable habitats in the neighbouring matrix and thus leave an unfavourable focal habitat patch easily.

In the long run the short relaxation time of specialist arthropods might affect the relaxation time of specialist plants as well. Arthropod species are essential elements of dry grassland ecosystems and contribute to their preservation as a whole: Orthopterans reduce litter accumulation by foraging living plant biomass and function as prey for other taxa (Samways, 2005), ants improve soil conditions by increasing soil porosity and nutrient content (Folgarait, 1998), and rove beetles accelerate decay of dead biomass (Tschamtko et al., 2005) and predate herbivorous arthropods (Perdikis et al., 2011). The reduction of these services can negatively affect the ecosystem functions in grassland ecosystems and thus shorten the relaxation time of specialist plants.

Although our rapid biodiversity survey (i.e., each grassland patch was surveyed only once) allowed us to detect a large part of the species pool for multiple taxa across a large number of sampled sites, it might have affected the number of the detected species of certain groups. Application of a rapid survey likely did not considerably influence the list of plant species present. Plant species of loess grasslands can be detected at any time during our sampling period and early-spring annuals were still visible due to the lack of management. However, the rapid sampling might have caused some bias in case of certain arthropod species groups, such as true bugs or orthopterans, that are characterised by high within-group differences in phenology. As each grassland was surveyed only once, it is possible that despite we detected a large part of the species pool, some species could have been missed (e.g., those present only as eggs, larvae, or pupae) during the survey. Despite this limitation, we believe that our results provide a good approximation of the species pools of specialist and generalist species in the focal grasslands. For the taxon-specific investigation of the general patterns revealed by the present study, further surveys with multiple sampling dates focusing on the phenology of a particular species group are needed.

4.4. Effect of habitat amount and connectivity

We found that the present and historical grassland connectivity was a better predictor of the richness of grassland specialist plants than the grassland amount. The reason for this may be that in transformed landscapes the existence of a well-connected dry grassland network consisting of small but connected habitat patches can more effectively support the conservation of local populations than a few large but isolated habitat patches (Batáry et al., 2020). In this sense it can be assumed that populations have a high probability to persist even in small habitat patches if these are well-connected (Helm et al., 2006). Functioning metapopulation connections can support the stability of communities by maintaining the equilibrium between extinction and establishment

processes (Auffret et al., 2015). As suggested by previous studies, extinction debt is typical in recently fragmented landscapes, where despite a recent habitat loss, large and connected fragments still exist and thus metapopulation connections are not completely lost (Krauss et al., 2010; Löffler et al., 2020). Our results confirm the findings of previous studies suggesting that extinction debt is typical when after habitat losses at least 10% of the original habitat remains in the landscape (Adriaens et al., 2006; Cousins, 2009; Piqueray et al., 2011) as in our study system the proportion of the remaining dry grasslands is approximately 9.7%.

In general, extinction debt studies do not consider landscape changes that occurred more than one century ago, partly because of the lack of high-quality historical maps (Kuussaari et al., 2009). However, a few published studies (Cousins and Vanhoenacker, 2011; Rédei et al., 2014; Lampinen et al., 2018) that included extended time frames found that in the case of grassland specialist plants, the relaxation time might even be longer than one century. In our study area we did not observe such a long-lasting effect of historical grassland connectivity. The probable reason might be that the studied landscapes were already considerably transformed in the middle of the 19th century, which suggests that major losses in grassland amount and connectivity had occurred even earlier. Thus, even at that time a considerable amount of fragmentation-sensitive plant species might already have gone extinct or been near to their extinction thresholds.

4.5. Effect of local habitat factors

Although drastic loss of grassland connectivity occurred in the studied landscape even before the first studied period (middle of the 19th century), we detected a considerable extinction debt in the case of specialist plants, which is likely due to the dry soil conditions and the high level of environmental heterogeneity typical to the focal grassland habitats. High slope inclination, which had a significant positive effect on the species richness of specialist plants in the final generalised linear model, was a proper proxy for both dry environmental conditions and high environmental heterogeneity. Mounds as positive landforms provide drier habitat conditions than the neighbouring plain areas due to the increased distance from the groundwater and the enhanced water runoff on their slopes (Lisetskii et al., 2014; Deák et al., 2021b). Steep slopes increase the distance between the roots and the moist deeper soil layers and the proportion of precipitation running off on the surface without infiltrating into the soil. Thus, high slope steepness is correlated to dry habitat conditions. As was suggested by previous studies (Cousins et al., 2007; Janišová et al., 2014; Deák et al., 2020), dry grasslands are more resistant to fragmentation compared to wet grasslands and can harbour specialist plants even without management. Cousins (2006) also found that dry grassland specialist plants showed slow extinction rates in small habitat fragments characterised by dry environmental conditions. The reason is that dry environmental conditions favour stress-tolerant dry grassland species and hinder the establishment of competitive generalist species (Janišová et al., 2014).

Steep slopes are also a proxy for increased environmental heterogeneity. Due to their hill shape, mounds are characterised by a diverse topography, which leads to a high environmental heterogeneity within a small area. As was validated by Deák et al. (2021b), topographic heterogeneity induces heterogeneity in other environmental components such as microclimate and soil properties. Consequently, mounds hold several microsites characterised by a unique combination of microclimatic and soil conditions. High environmental heterogeneity can also increase the chance for the long-term persistence of plants within the focal grassland patch since even short distance disperser plant species can achieve short shifts within the focal habitat to establish in the microsite that is edaphically and climatically most favourable for them (Deák et al., 2021b). The positive effect of environmental heterogeneity on the richness of specialist plants was substantiated by their high species numbers on mounds with steep slopes. It was shown by the final

generalised linear model that a high woody cover suppressed the species richness of specialist true bugs, probably due to the altered light conditions (i.e. shading) and microclimate (increase in cool and humid microsites) and also by decreasing the availability (abundance) of food plants typical to grasslands (Torma and Gallé, 2011). A high cover of woody species favoured generalist ant species richness by providing proper habitat for forest-related generalist ants, which benefited from the enhanced structural complexity and humidity and the increased availability of nesting and foraging sites (Lanan, 2014). Interestingly, the level of woody encroachment did not have any significant effect on the species richness of specialist plants in the studied focal habitats. A possible reason is that even though woody cover was high in some of the studied mounds, it never reached 100%. Thus, in the focal habitat there was always an open dry grassland patch, which provided feasible habitat conditions for dry grassland plants. Although there are some dry grassland species (such as *Agropyron cristatum* and *Phlomis tuberosa*) that can persist for a long period under the dense canopy cover of wooded mounds (see also Deák et al., 2016b), the vast majority of the dry grassland plants were present in the openings. The low area-sensitivity of specialist plants suggests that long-term maintenance of their populations is rather influenced by the existence of functioning metapopulation connections than by the locally available habitat amount.

4.6. Conservation implications

As shown by our results, dry grassland specialist plants can exist for an extended time after a drastic decline in the amount and connectivity of grasslands in the landscape. Despite the reduced spatial and functional connections between the remaining grasslands, dry environmental conditions and high environmental heterogeneity typical of the studied mounds supported the long-term existence of specialist plants. However, the fact that dry grassland specialist plants showed a partially paid extinction debt suggests that their observed current species richness is not in equilibrium with the composition and configuration of the present landscape yet. This can be considered an early warning signal suggesting that even if grassland loss will be reduced in the landscape, further extinctions may be expected, which reduce the biodiversity of the focal habitat fragment and also the biodiversity of specialist plants on a landscape level. Mitigating these negative processes should be considered a conservation priority as in heavily fragmented lowland agricultural landscapes, a considerable amount of grassland-specific species is only maintained by small habitat islands (Gazol et al., 2012; Deák et al., 2020). We found that grassland specialist arthropod taxa, which are more mobile and have shorter generation times compared to plants, responded much faster to habitat loss. Therefore, extinctions of such taxa have most likely already taken place in the studied ecosystem due to the historical loss of grassland amount and connectivity.

Extinction debt is an actual, but often unnoticed risk typical of transformed landscapes. Considering only current patch occupancy patterns might overestimate the biodiversity potential of the landscape (i.e. the number of specialist species that the present habitat patches can support in the long term), leading to an underestimation of the threats that may negatively affect the species richness of specialists (Sang et al., 2010; Piqueray et al., 2011). Thus, we suggest that the rate of extinction debt should be seriously considered in conceptual landscape-scale conservation planning. Passive conservation of the current status quo is unlikely to be sufficient for halting the further time-delayed extinction of dry grassland specialist plant species. Active management and restoration measures have to be taken with the aim of improving local habitat conditions and increasing grassland area and connectivity between remaining grassland patches.

Dry habitat conditions typical of dry grassland islands can mitigate the negative consequences of abandonment such as litter accumulation and the encroachment of generalist herbaceous and woody species (Gazol et al., 2012). Although management of small grassland patches embedded in anthropogenic habitats is often challenging and costly, as

was shown by the study of Otsu et al. (2017), increasing the quality of a focal habitat patch by ensuring proper management measures can effectively compensate the losses in its area. By providing open microsites suitable for the colonisation by specialists, suppressing the inter-specific competition by generalists and halting the encroachment of woody species, proper management can increase the survival chances of grassland specialists, decrease the rate of extinctions and thus considerably elongate their relaxation time (Otsu et al., 2017). Proper management of the remaining natural (such as verges, field margins, midfield islets and mounds) or suitable novel habitat patches (such as clearings under electric wires, grasslands on dams) can also increase grassland amount and connectivity at the landscape level (Lampinen et al., 2018; Fekete et al., 2019; Bátorfi et al., 2020). Although, as shown by our results, dry grassland plant species can survive even in small grassland islands without any management, gradual changes in habitat properties due to abandonment such as litter accumulation or woody encroachment might pose a serious threat for their existence in the long run.

Establishment of novel grassland habitats in sites such as arable fields, highway embankments or urban areas can further improve grassland connectivity in transformed landscapes and thus mitigate extinctions, especially if the newly established grasslands are situated at strategic points in the networks of semi-natural habitats supporting metapopulation connectivity (Lampinen et al., 2018). The EU Biodiversity Strategy (European Commission, 2020) aims to bring back at least 10% of the current agricultural area under high-diversity landscape features. This offers a great opportunity for strategic restoration planning with the aim of creating a network of functionally connected habitats in agricultural landscapes and mitigating extinction of grassland specialist species.

CRedit authorship contribution statement

The concept of the paper was developed by BD and OV. BD, OV, BT, PT and DND contributed to the study design. Field data collection and data preparation were performed by BD, OV, PT, DND, AK, GL, AT, AN and SM. Present habitat maps were prepared by BD, historical habitat maps were prepared by ÁB. Data analyses were performed by ZR. The first draft of the manuscript was written by BD and OV and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

Declaration of competing interest

The authors declare no conflict of interest.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2021.109372>.

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