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Abstract: Habitat loss is one of the major drivers of the reduction in biological diversity worldwide. European dry grasslands are particularly endangered. However, the persistence of populations can temporarily mitigate species loss - a process referred to as 'extinction debt'. We test this hypothesis using historical and present day habitat maps and current plant biodiversity data collected in the forest-steppe zone of Europe. In 16 5×5 km study sites, representing the landscape heterogeneity of the Kiskunság region (Hungary), 86 20×20 m vegetation plots were made in open and closed calcareous sand grasslands. Grassland diversity was measured as the number of specialist species, defined by statistical fidelity measures using primary and secondary grassland plots. Landscape context was quantified using the areal extent of semi-natural forest-steppe vegetation in a 300 m neighbourhood of the plots, based on recent and historical maps (1783, 1860, 1950s, 1987-89 and 2005). The number of specialist species was estimated with Poisson generalized linear models using the present landscape context, climatic conditions, and a proxy of soil type as covariates. To test for the effect of historical legacies, Pearson residuals from the present models were tested for significant relationships between the residuals and the historical landscape contexts using linear models.
We found that the present landscape context had no significant relationship with the specialist species richness of the primary grassland fragments. However, we found a significant relationship between the historical landscape context of the 19th century and the residuals of the present model. Even though the extent of natural vegetation in the 20th century showed more drastic changes, the landscape context in 1950s and 1987-1989 exhibited no significant statistical relationship with the residuals. This delay of species loss is consistent with the extinction debt hypothesis.

- Effect of present and past landscape context examined on sand grassland biodiversity.
- Primary grassland specialist species defined by statistical fidelity measures.
- Present landscape had no significant relationship with specialist species richness.
- Landscape context of 19^{th} century affects significantly the present biodiversity.
- Long term delay of species loss is consistent with the extinction debt hypothesis.

Weak evidence of long-term extinction debt in Pannonian dry sand grasslands.

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Abstract

Habitat loss is one of the major drivers of the reduction in biological diversity worldwide. European dry grasslands are particularly endangered. However, the persistence of populations can temporarily mitigate species loss – a process referred to as 'extinction debt'. We test this hypothesis using historical and present day habitat maps and current plant biodiversity data collected in the forest-steppe zone of Europe. In 16 5×5 km study sites, representing the landscape heterogeneity of the Kiskunság region (Hungary), 86 20×20 m vegetation plots were made in open and closed calcareous sand grasslands. Grassland diversity was measured as the number of specialist species, defined by statistical fidelity measures using primary and secondary grassland plots. Landscape context was quantified using the areal extent of semi-natural forest-steppe vegetation in a 300 m neighbourhood of the plots, based on recent and historical maps (1783, 1856, 1950s, 1987-89 and 2005). The number of specialist species was estimated with Poisson generalized linear models using the present landscape context, climatic conditions, and a proxy of soil type as covariates. To test for the effect of historical legacies, Pearson residuals from the present models were tested for significant relationships between the residuals and the historical landscape contexts using linear models.

We found that the present landscape context had no significant relationship with the specialist species richness of the primary grassland fragments. However, we found a significant relationship between the historical landscape context of the 19th century and the residuals of the present model. Even though the extent of natural vegetation in the 20th century showed more drastic changes, the landscape context in 1950s and 1987-1989 exhibited no significant statistical relationship with the residuals. This delay of species loss is consistent with the extinction debt hypothesis.

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Nomenclature: Simon (2000) for vascular plants.

1 Introduction

Loss and fragmentation of natural and semi-natural habitats are among the main reasons for the erosion of biological diversity experienced worldwide (Foley et al., 2005). In Europe, dry grasslands are particularly endangered by habitat loss and fragmentation; therefore, they are a major focus of nature conservation. Large areas of dry grasslands were ploughed prior to the 20th century (Drobnik et al., 2011; Török et al., 2011, Molnár et al., 2012), and the loss of dry grasslands continues to the present day due to afforestation and urbanization. The residual fragments are often degraded by inappropriate management (e.g. over- or undergrazing, lack of mowing). However, these remnants maintain significant plant biodiversity (Ruprecht et al., 2009; Wilson et al., 2012). Long term habitat continuity of semi-natural grasslands increases the proportion of grazing dependent species without significantly changing total species richness (Johansson et al., 2008).

Habitat loss and fragmentation result in a decline of species diversity due to both increased extinction risk and reduced colonization rate (Cristofoli et al., 2010; Cousins and Vanhoenacker, 2011). Species diversity reduction can happen immediately following habitat destruction but usually occurs after a species specific time lag or 'relaxation time' (Diamond, 1972). The number of species extinctions expected to occur in the future is termed 'extinction debt' (Tilman et al., 1994), which is offset when the community reaches its new equilibrium species diversity corresponding to the altered landscape configuration (Jackson and Sax, 2010). Revealing the magnitude and time scale of this delay is important to estimate the conservation potential of a given habitat (Kuussaari et al., 2009).

Although extinction debt may be common in many natural communities worldwide (Kuussaari et al., 2009), our knowledge on the occurrence and magnitude of this phenomenon across ecosystems and taxa is highly incomplete (Krauss et al., 2010). Several studies found evidence of plant species extinction debt in semi-natural grasslands in north-western Europe (Lindborg and Eriksson, 2004; Helm et al., 2006; Piessens and Hermy, 2006; Ellis and Coppins, 2007; Cousins, 2009; Cousins and Vanhoenacker, 2011). Other studies did not detect the presence of extinction debt (Adriaens et al., 2006, Cousins et al., 2007).

However, knowledge of the presence of extinction debt in grasslands of the Eastern European forest steppe zone is lacking, and there is a clear need for more studies from different parts of the world (Cousins, 2009; Kuussaari et al., 2009).

Plant species differ significantly in their likelihood of showing an extinction debt (Vellend et al., 2006; Kuussaari et al., 2009; Piqueray et al., 2011a). When populations come close to their extinction threshold, time delay to their extinction can last for particularly long periods (Kareiva and Wennegren, 1995; Hanski and Ovaskainen, 2002). Relaxation time can be long in cases of long-lived species (Helm et al., 2006), species with persistent seed bank (Piessens and Hermy, 2006; Cristofoli et al., 2010), species showing long-distance dispersal potential by wind and animals (Purschke et al., 2012), and species able to spread clonally (Purschke et al., 2012). Species with a high degree of habitat specialization are expected to exhibit greater sensitivity to habitat changes than generalist species (Kuussaari et al., 2009); therefore, they are expected to have a smaller extinction debt than generalists (Cousins and Vanhoenacker, 2011). Despite this trend, several studies demonstrated extinction debt of habitat specialists (Ellis and Coppins, 2007; Cristofoli et al., 2010; Cousins and Vanhoenacker, 2011). As the effects of habitat change can be masked with the arrival of new species, the number of habitat specialists can be a better indicator of extinction debt than total species richness (Kuussaari et al., 2009). In the study by Helm et al. (2006), habitat specialists showed an extinction debt in Estonian alvar grasslands after 70 years, while past landscape structure did not have any significant effect on total species richness.

Kuussaari et al. (2009) describes several approaches to evaluate extinction debt. As long-term data on species occurrences are rarely available, most studies assess extinction debt by comparing current species richness in currently stable and unstable fragmented landscapes (Hanski and Ovaskainen, 2002; Helm et al., 2006; Piqueray et al., 2011a; Piqueray et al., 2011b) or by assessing if current species richness can be better interpreted by past rather than present landscape variables (Adriaens et al., 2006; Ellis and Coppins, 2007; Sang et al., 2010). Piqueray et al. (2011a) compared these two methods in calcareous grasslands in Belgium and found that the two methods resulted in the same conclusions. As the determination of stable and unstable fragmented landscapes is rather arbitrary, we use the second approach in our study.

In this paper, we address the following questions:

1. What is the magnitude of natural habitat loss in the surroundings of the Pannonian primary sand grasslands?
2. Is the number of specialists in primary grasslands related to either the current or historical extent of adjacent semi-natural forest steppe habitats?
3. Can extinction debt be observed in the vascular flora of primary sand grasslands in the European forest steppe zone?

2 Materials and methods

2.1 Study area

Our study area, the Kiskunság, is an inland sand dune area in the centre of the Pannonian biogeographic region with an extent of 7500 km^2. The climate of the region is continental with submediterranean influence. The mean annual temperature is 10 ^{o}C with monthly means ranging from –1 ^{o}C in January to 22 ^{o}C in July. Mean annual precipitation is 500–550 mm, with a peak in June, and a second, minor peak in November with a gradual decrease from

North to South and from West to East. (Borhidi, 1993; Kovács-Láng et al., 2000). The dominant substrate is calcareous sand, on which various sand soil types developed with high sand (over 90%) and low humus content (below 3%) (AGROTOPO, 1994; Csecserits et al., 2011). The elevation is between 110 and 160 m a.s.l. in the entire region. The natural vegetation mosaic consists of sand forest steppe with wetlands in lower elevation areas (Zólyomi, 1974). The major components of the forest-steppe complex have continuously persisted in a significant extent during the Holocene (Zólyomi and Fekete, 1994; Fekete et al., 2010; Magyari et al., 2010). Most of the endemic plant species in the region are dry grassland specialists (e.g. *Festuca vaginata, Festuca x wagneri, Colchicum arenarium, Dianthus diutinus, Dianthus serotinus, Iris arenaria*), which is also indirect evidence for the long-term persistence of dry grasslands in the region (Zólyomi and Fekete, 1994; Magyari et al., 2010). The species pool of sand forest steppe gets impoverished by loosing several elements of Central-European grasslands with decreasing precipitation eastwards and southwards in the Kiskunság region (Kovács-Láng et al., 2000; Fekete et al., 2010).

At present, this region is dominated by agricultural fields, including both annual and perennial crops, as well as vast timber plantations consisting of native and non-native tree species. Nevertheless, the remnants of sand forest steppe vegetation also constitute a substantial component of the present land cover. Sand forest steppe vegetation is a fine scale mosaic of dry and semi-dry grasslands, *Juniperus communis-Populus alba* shrublands and open steppic *Quercus robur-Quercus pubescens* forests with small extents of closed *Quercus robur* and *Populus x canescens* forests at the lowest elevations. The ratio of grasslands to woodlands varies with the climatic gradient (Kovács-Láng et al., 2000). This ratio has also changed over centuries because of drastic alterations in land use and fire regime. Most of the grassland specialist plant species can also colonize and survive in the forested parts of the landscape, which means that the whole landscape is permeable for these species. According to archive maps, most of the grasslands were never ploughed. Hereafter, we refer to this never ploughed grassland components of the natural forest steppe vegetation complex as ’primary grasslands’. Until the 18th century, extensive grazing was the dominant land-use in the region. In the 19th century, a significant increase in human population and agricultural activities led to fragmentation of semi-natural vegetation. The maximum of agricultural activity in the region occurred after the Second World War in the 1950’s. This was followed by a process of land abandonment due to socio-economic changes, as well as a significant decrease in the groundwater table (Biró, 2003, Biró et al., 2008, Molnár et al., 2012). Former studies have found that the dry grassland vegetation of this region has a relatively good regeneration potential on abandoned agricultural fields (Csecserits & Rédei 2001, Csecserits et al., 2011). Henceforth, we refer to the regenerating grasslands of former agricultural areas as ’secondary grasslands’. Land abandonment, which still continues to impact this region today, was partly compensated by an increase of forestry activities. Large plantations of non-native trees, such as *Robinia pseudoacacia*, *Pinus nigra*, *Pinus silvestris* and *Populus x euramericana*, and the native trees, including *Populus alba* and *Populus x canescens*, were established on abandoned fields and also on primary grasslands (Biró et al., 2013)

2.2 Vegetation data

The vegetation sampling was done in June–August 2007 within the field site network of the Kiskun Long-Term Ecological Research program, which consists of 16 5×5 km sites representing the entire Kiskunság region (Figure 1.), with all major land cover types (agricultural, abandoned agricultural, forest plantation and semi-natural vegetation) in varying proportions (Rédei et al., 2008, Csecserits et al., 2011).

Plot selection for the sampling was based on a series of habitat maps starting from the first military survey (1783), and was verified in the field by observing the fine scale relief of the site to confirm the unploughed status of the plots. We recorded a total of 86 20×20 m plots in primary grasslands within the field sites. We sampled the following two types of primary grasslands: open perennial sand grassland with total canopy cover of vascular plants less than 50%, dominated by *Festuca vaginata* and *Stipa borysthenica* (n = 40) and closed perennial sand grasslands with total canopy cover more than 80%, dominated by *Festuca x wagneri*, *Stipa capillata, Poa angustifolia* and *Bothriochloa ischaemum* (n = 46). These two grassland types dominate the grassland component of the forest-steppe vegetation in the Kiskunság region, with open stands occupying coarse and poor sandy soils mainly on the top of the dunes and closed stands on humus rich sandy soils at lower elevations.

In addition to primary grassland data, we sampled 161 20x20 m plots in secondary grasslands on former cropland and vineyards abandoned after 1950 according to historical aerial photographs. The data from these secondary grasslands were used to determine the specialist species of primary grassland areas. Replicates of a given habitat were taken from separate grassland patches from different parts of each site (spatially stratified sampling). In each plot, the estimated percentage aboveground cover of each vascular plant species was recorded.

2.3 The number of specialist species

During our analysis, we used the richness of primary grassland specialist plant species (N_p) as a response variable. To define this species group, we used the data from all primary and secondary grassland plots. The fidelity of species to primary grasslands was determined by Fisher's exact test (Chytrý et al., 2002) with the Juice program (Tichý, 2002). Species faithful to open, closed or both primary grasslands types, at α = 0.01 level of significance, were regarded as specialist species of primary grasslands. Fidelity was tested in each case against the rest of grassland data in the table. Data of shrubs and trees were removed from the species list, because they were avoided during the field sampling of the grasslands and were present in the plots as rare accessory elements.

2.4 Landscape context

We created 6×6 km habitat maps for each study site (containing the 5×5 km site plus a buffer of 500 m) for the current day (2005) and four historical timelines. Habitat maps were based on the first and second military maps of the Austrian Empire (from 1783 and the 1850s, respectively), as well as on aerial photos from the 1950s and from 1987-89.

The first military map (originally prepared without projection) was georeferenced by identifiable objects and landscape context, with an accuracy usually not better than 100 m. The second military map (originally prepared in Cassini projection, geodetic datum is Zach-Oriani ellipsoid) were georeferenced by projection transformation, with an accuracy mostly better than 100 m. Old aerial photos were orthorectified, and a polynomial fitting was performed based on a digital terrain model and old military maps. Local polynomial fitting improved all old maps and photos to an accuracy of better than 30 m. Recent aerial photos were also orthorectified and fitted to the terrain model and recent geographical maps, with an accuracy of about 1 m.

We distinguished the following habitat types on the habitat maps: semi-natural grasslands, semi-natural forests, forest plantations, secondary grasslands of abandoned fields, wetlands, agricultural lands and other man-made objects (e.g. buildings, roads). The habitat categories and the classification protocol used are documented in Rédei et al., 2008. The landscape context of the plots was characterized by using the total percentage cover of semi-natural forest steppe habitats (dry and semi-dry grasslands, shrublands, and semi-natural forests combined) in the 100, 300 and 500 m radius zone around the plots in each habitat map with the help of the GIS software ArcGIS 9.2 (ESRI, 2006).

2.5 Other environmental predictors

In order to fit sensible models for the species richness of the studied grasslands, we considered several basic environmental factors in the models in addition to landscape context. We used two climatic variables (annual precipitation and mean annual temperature) as a minimum set of environmental variables. Annual precipitation was derived from interpolated climatic data from 1961-1990 from the Hungarian Meteorological Service (HMS 2001), whereas temperature data come from the WORLDCLIM database (Hijmans et al., 2005). Furthermore, even though we did not possess any soil data for our plots, habitat type (open and closed sand grasslands) can be regarded as a proxy of soil fertility in case of sand steppe grasslands. Accordingly, our minimum set includes two climatic predictors and a proxy for soil type.

2.6 Data analysis

To test for the presence of extinction debt in the Kiskunság landscape, we applied the following strategy. As a preliminary step, we performed an extensive data validation check following the recommendations of Zuur et al. (2010). During this step, we found that our response variables match a Poisson distribution with no significant overdispersion, landscape and environmental predictors are only minimally correlated, and that the residuals of the overfitted Poisson generalized linear models (GLM) (see later) for specialist species are free from spatial autocorrelation. All calculations were performed in the R statistical environment ver. 2.15.0 (R Development Core Team, 2012), and several add on packages were used, including *pscl::odTest* to test for overdispersion (Jackman, 2009), *car::vif* to check for collinearity, *ncf::correlog* (Bjornstad, 2009) to test for spatial autocorrelation, and the *reshape* package for data conversion (Wickham, 2007).

We compared three potential buffer sizes (100, 300 and 500 m) to quantify the amount of semi-natural vegetation in the surrounding landscape around the plots (landscape context) based on the most recent (2005) aerial photographs. To this end, we fitted Poisson GLM at the number of primary grassland species (N_p), using climate, habitat type and landscape context as predictors for each buffer size. We quantified the AIC values characterizing model fit to compare the models with the different buffer sizes. The buffer size which yielded the most informative (best fitting) landscape context predictor was selected, and used as ’the best buffer‘ size during all subsequent analyses.

As a next step, we fitted GLM with Poisson error distribution to N_p in the plot data. Grassland type, annual precipitation, annual mean temperature and the most recent (2005) landscape context as well as their second order interactions were used as predictors. We derived the Pearson residuals from the GLM. Using all of these predictors and their binary interactions results in an overfitted model, but this does not lead to any problem as far as only the residuals are used for testing further predictors.

To study the long-term impacts of the historical landscape contexts (i.e. extinction debt), we fitted linear models between landscape contexts (one by one for each historical timeline) and the residuals. The different timelines were compared using the residual sum of squares as a goodness of fit measure, which is in a strictly monotonous relationship with likelihood and thus AIC over this limited set of models with the same number of parameters. The historical landscape context (timeline) with the highest fit was thereafter selected and tested for significance compared to a constant null model for the residuals from the GLM with specialist species. A significant relationship between any of the residuals and a historical landscape context can be interpreted as an evidence of long-term effects of landscape changes, which can shed insight on the existence of extinction debt in primary grasslands of the Kiskunság landscape.

3 Results

3.1 Landscape changes

Figure 2. shows changes in distribution of the proportion of semi-natural habitats in 300 m buffers around the sampling plots during the last 230 years. At the time of the first Military Survey (1783), nearly the entire landscape was covered by semi-natural forest steppe vegetation. Land use intensification began locally in the second half of the 19th century (Second Military Survey, 1850's). From the middle of the 20th century, when arable farming reached its maximum extent, we found variable levels of land use intensity in the region. The proportion of semi-natural vegetation decreased further in the second half of the 20th century through to the end of the communist period in Hungary (1989). In the 20 years following the intensification of land-use decreased.

3.2 Specialist species of primary grasslands

The complete set of 247 plots in primary and secondary grasslands contained 365 vascular plant species. Altogether 249 species occurred in the 86 20x20 m primary grassland plots, 141 and 233 species in the open and closed types, respectively. The average species richness of open perennial sand grasslands (N=40) were 29.98 (standard deviation 6.27), while it was 36.17 (standard deviation 7.99) for the closed grasslands (N=46).

We found 54 native species faithful to primary grasslands according to fidelity values. Additional 7 and 15 species were faithful exclusively to open or closed grasslands, respectively. *Tragus racemosus*, a neophyte species, was faithful to open primary grasslands, but was excluded from further analyses because of its local history completely different from that of indigenous specialists. Accordingly, we involved altogether 76 species as specialists of primary grasslands in the further analyses. The average number of specialist species was 21.44 (standard deviation 4.17) in open grasslands, and 25.3 (standard deviation 5.9) in closed grasslands.

3.3 The effect of landscape on grassland species richness

We found that the landscape context of a medium size (i.e. 300 m) provides more information on the number of primary grassland species than either larger (500 m) or smaller (100 m) buffer sizes.

The goodness of fit of the linear models between the present day residuals and the historical landscape contexts from the studied time horizons are shown in Figure 3. The relationship between the residuals and all of the past landscape contexts were tested and the landscape context in 1856 (second Austrian military mapping) was found significant at the a=.05 level (Table 1.). To further understand the nature of this relationship, we created a series of diagnostic plots (Figure 4.). These plots reveal that human landscape transformation was a gradual process, and even though there were relatively few sites which had been transformed early during the 18th century, these sites can be associated with strong negative anomalies in present species numbers, which can explain the significant relationship observed.

4 Discussion

The time series of the landscape data of our sampling sites shows continuous habitat loss of the sand forest steppe vegetation since the second half of the 18th century. Similarly, Biró et al. (2008) showed that between 1783 and 2005 93-94% of the forest steppe vegetation was destroyed in the whole Kiskunság region.

We found 76 habitat specialist species faithful to primary grasslands by using statistical fidelity measures (Chytrý et al., 2002). Although sand grasslands of the region are generally assumed to have significant regeneration potential in abandoned arable fields (Csecserits and Rédei 2001, Halassy 2004, Csecserits et al. 2011), there are several specialist species (e.g. *Astragalus varius, Onosma arenaria, Silene borysthenica*) of limited colonisation potential which are therefore particularly sensitive to the loss of primary habitats. Consequently, the remaining primary grassland fragments are the most important refuges of these species in the region. The relatively high number of primary grassland specialists (76 of 249 species) confirms that habitat continuity is a determining factor in forming grassland biodiversity patterns in the examined region. According to former studies, the extent of semi-natural habitats in the surrounding landscape can be an important predictor of species richness in semi-natural habitat fragments (e.g. Johansson et al., 2008; Aavik and Liira, 2009). Semi-natural habitat fragments with nearby semi-natural habitats can maintain higher species richness with larger and more persistent populations (Andrén 1994; Krauss et al., 2004; Adriaens et al., 2006, Reitalu et al., 2012) due to increased survival and decreased extinction rates (Hanski and Ovaskainen, 2002; Bennie et al., 2006). In our study, however, the current extent of semi-natural habitats in circles with a 300 m radius had no significant effect on dry grassland specialist species richness, while the extent of the semi-natural habitats in the same circles in 1856 showed a weak significant effect. The extent of semi-natural habitats in 1783 was nearly significant in a statistical sense (p=0.094), even though this relationship was based only on two plots with entirely fragmented natural neighborhood. The later periods (i.e. 1950, 1989) did not show a pattern of delayed impact. The habitat losses that occurred in these time periods did not convey any information independent from the present extent of semi-natural habitats.

Based on our study, we can give a rough estimation for the local time scale of resilience. In our sampling areas, the richness of primary grassland species was reduced in areas where natural habitat loss in the surrounding landscape began prior to the 19th century. The weak but significant relationship found between the extent of natural habitat in 1856 and recent biodiversity can be seen as a delayed impact of long term intensive land use upon the local biodiversity.

One possible explanation is that richness of specialist species has not come to equilibrium with the current land use since 1856, i.e. there may be an extinction debt of specialist species of dry primary grasslands in the Kiskunság region. The presence of extinction debt is determined by the extinction threshold conditions of populations (Hanski and Ovaskainen, 2002): species capacity for developing remnant populations below an extinction threshold (Lindborg and Eriksson, 2004), magnitude of habitat loss, and time elapsed since habitat loss (Kuussaari et al., 2009). Although habitat specialist species are more sensitive to habitat changes and therefore generally face extinction earlier than generalists (Cousins and Vanhoenacker, 2011), inclusion of every species into the analyses may mask the potential presence of delayed extinction following semi-natural habitat loss if altered landscape elements can maintain generalist species populations (Kuussaari et al., 2009). Most studies consider extinction debt of grassland species following habitat loss 50-100 years ago (Sang et al., 2010; Cousins and Vanhoenacker, 2011; Piqueray et al., 2011); however, earlier timelines are rarely investigated (Gustavsson et al., 2007; Cristofoli et al., 2010; Purschke et al., 2012). The study of extinction debt for more than a century is severely constrained in many cases, as high-quality historical habitat data are often not available for evaluation (Kuussaari et al., 2009) or major habitat loss started only in the last century (Krauss et al., 2010).

The potential existence of extinction debt of dry grassland specialist species in the Kiskunság region for 150 years may indicate that these species possess traits allowing for long-term persistence in habitat fragments (Vellend et al 2006). These species may have either long life span and are therefore subjected to slower turnover rate (Lindborg and Eriksson, 2004; Helm et al., 2006), or may regenerate due to a persistent seed bank (Piessens and Hermy, 2006) or long-distance dispersal potential (Purschke et al., 2012). Furthermore, the high heterogeneity of the sand dune landscape complex results in the presence of small-scale landscape elements (e.g. small forest fringes, verges, embankments and sand pits) that may work as temporary refuges in the heavily transformed landscape and support the significant resistance of dry grassland specialists against habitat loss even at the time scale of centuries.

Undiscovered extinction debt may lead to incorrect evaluation of individual species sensitivity to habitat loss, consequent overestimation of long-term species richness and underestimation of habitat loss effects (Kuussaari et al., 2009; Sang et al., 2010). As long as species predicted to become extinct persist, there is an opportunity to reduce extinction debt by mitigating the effects of habitat loss (Kareiva and Wennegren 1995, Helm et al., 2006; Kuussaari et al., 2009).

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Figure captions

Figure 1. Map of the study area with the 16 sampling sites.

Figure 2. Changes in the distribution of the proportion of the seminatural forest steppe habitats during the last 230 years.

Plotted based on the 300 m radius buffers around the 86 sampling plots. Horizontal axis refers to the cumulative proportion of the plots with equal or less percentage extent of seminatural forest steppe habitats delineated on vertical axis.

Figure 3. RSS and AIC values of the linear models predicting present-day GLM residuals.

Based on historical landscape contexts (the percentage of natural habitats in a 300 m buffer of the plots) for the studied timelines. RSS values at 2005 equal the total sum of squares of the response variable.

Figure 4. Present day GLM residuals of specialist species number plotted against historical landscape context values for the studied timelines.

Landscape context was characterized by the percentage cover of natural habitats in a 300 m buffer of the plots. The trend line of the linear regression in 1856 indicates a significant relationship.

Table title and description

Table 1.: F test results describing the relationship between the 1856 landscape context (LC_{1856} – defined as the percentage cover of semi-natural forest steppe habitats in 1856 in a 300 m circle around each plot), and the residuals of the number of specialist plant species in 2008 after removing the influence of the present-day landscape context in the Kiskunság region of Hungary.

Table 1.

	Df	Sum Sq	Mean Sq	F value	Pr(>F)	
LC_{1860}	1	5.244	5.2442	5.5848	0.02	*
Residuals	84	78.878	0.939			

Figure
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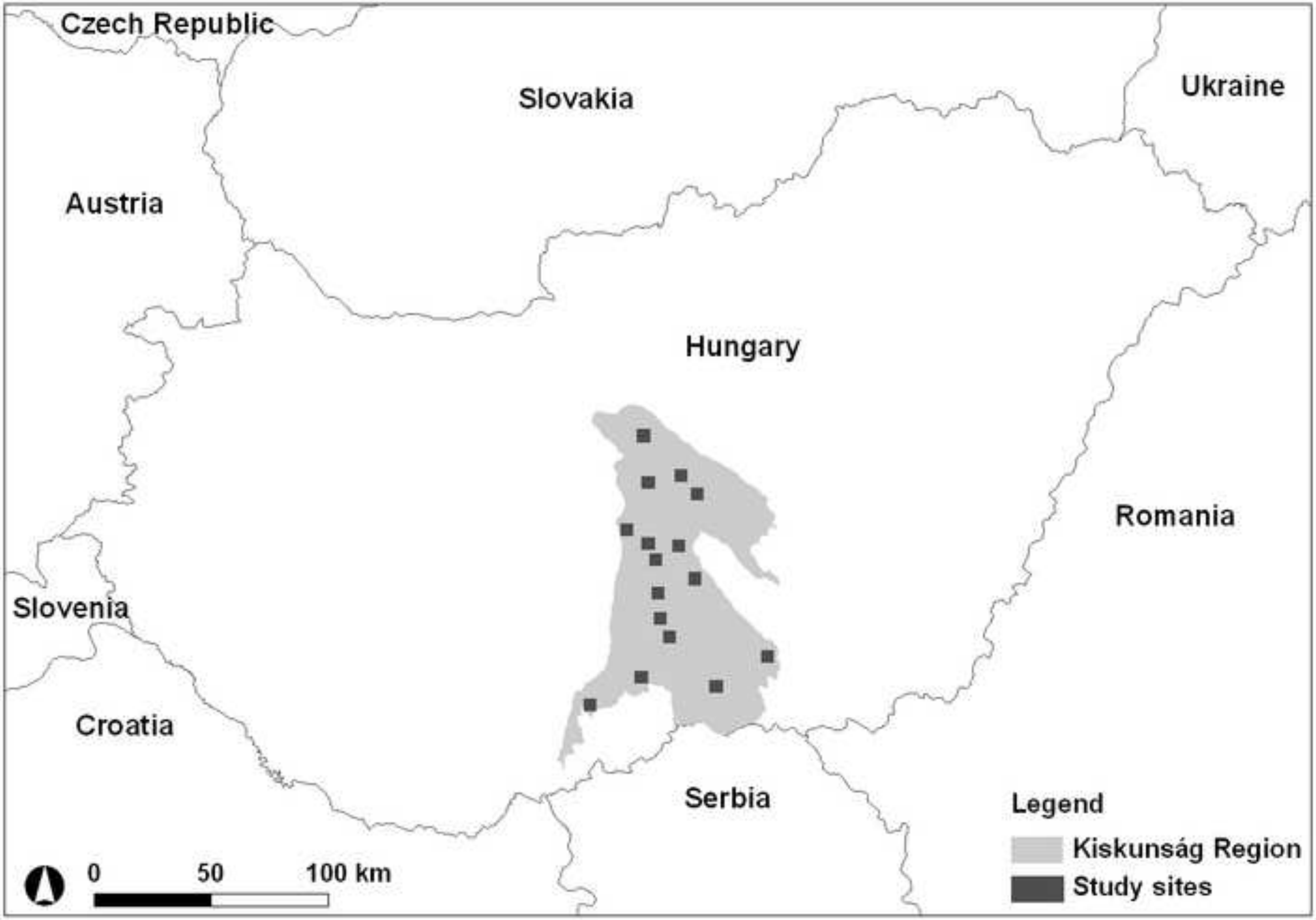

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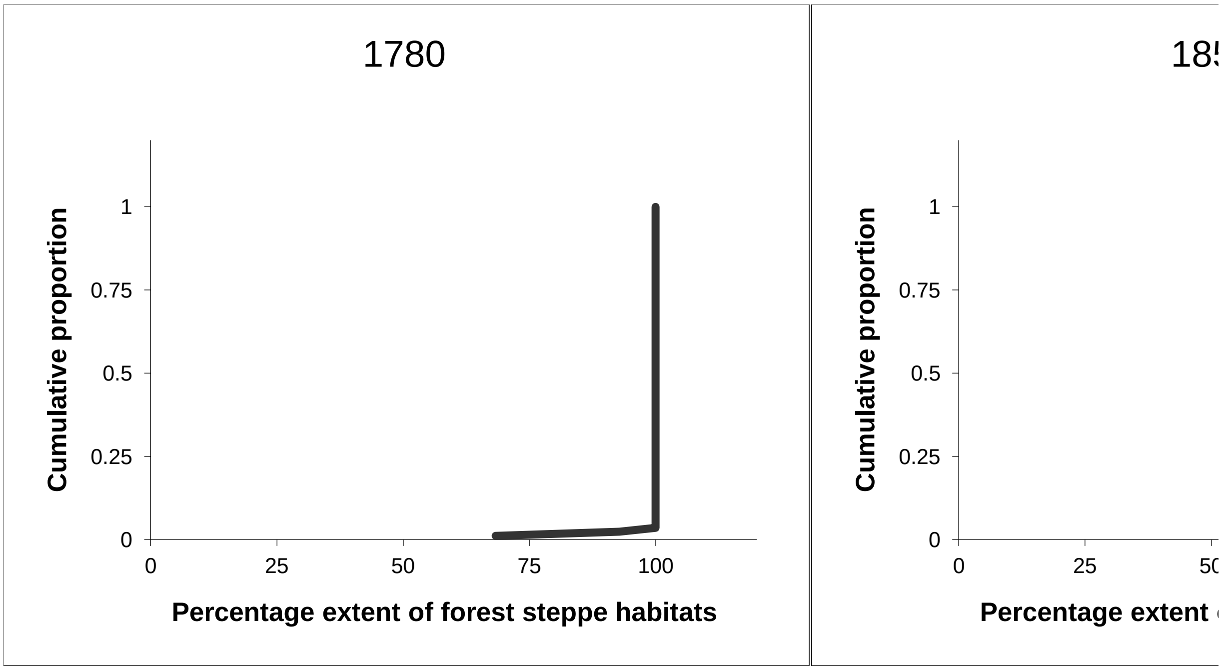

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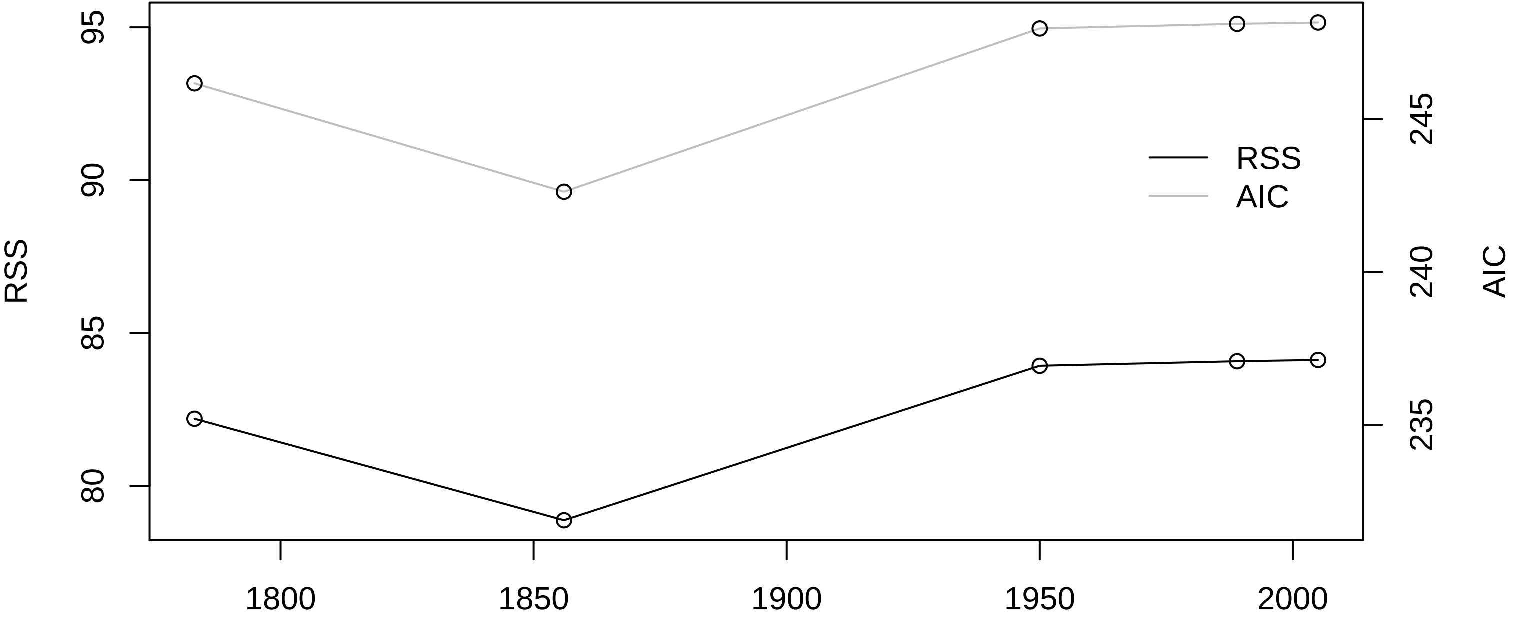

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