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Does land-use continuity matter? The impact of almost two centuries of land-use history on temperate grasslands

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Abstract: Humans have been transforming and managing the landscape of central Europe for thousands of years. Traditional farming practices enabled the spread of many grassland species and supported the exceptional diversity of species-rich grasslands. However, profound changes in land use and management, initiated in the late 19th century and culminating in the mid-20th century, have led to widespread decline and extinction of many grassland species. Using historical land-use maps covering the entire Czech Republic from the mid-19th to the early 21st century, we examined the fine-scale landscape changes around the remaining grassland fragments. Using 7,367 grassland vegetation plots, we quantified long-term continuity (i.e. grassland stability) and connectivity. We showed that the extent of arable land within formerly open grassland landscapes peaked between the late 19th and mid-20th century, depending on grassland type. During this period, grasslands in most regions reached their minimum extent, but in many lowland landscapes disappeared entirely. Their spatial connectivity also dramatically decreased. Subsequent management cessation in many grasslands led to the encroachment of shrubs and trees, which has affected these habitats at both local and landscape scales (except in pioneer vegetation). We further evaluated how these historical patterns relate to present-day species richness and the occurrence of endangered (Red List) species. The effect of grassland continuity on conservation indicators was more pronounced for endangered species than for overall species richness, suggesting that the number of endangered species is a better indicator of conservation value. Although grasslands with long-term continuity are particularly valuable for biodiversity conservation, spatial connectivity also plays a crucial role in the persistence of endangered species. Conservation strategies should therefore focus not only on protecting isolated remnants of species-rich grasslands but also on creating a functional network of interconnected habitats.

Keywords: Czech Republic, dispersal ability, endangered species, grassland continuity, habitat stability, land-use changes, spatial connectivity, traditional management cessation

Introduction

Habitat loss and fragmentation are among the most important drivers of recent decline in biodiversity worldwide (Newbold et al. 2016, Fardila et al. 2017, IPBES 2019, de Souza Leite et al. 2022, Klinkovská et al. 2024, Yuan et al. 2024). Several studies have found

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that the numbers of specialized and rare species have recently declined across habitats, including European grasslands (Klinkovská et al. 2024, Horka et al. 2025). In central Europe, grassland vegetation has been continuously present throughout the Holocene, although the post-glacial climatic changes favoured the expansion of closed forests (Firbas 1949, Kuneš et al. 2015, Pokorný et al. 2015). In lowland areas, open patches in the landscape were maintained by large herbivores (Vera 2000), hunter-gatherers (Kuneš et al. 2008), and later by early farmers and livestock grazing (Kuneš et al. 2015). At higher elevations, the extent of alpine and subalpine grasslands was mainly limited by the position of the treeline, which was controlled by more or less stable climatic and abiotic factors (such as anemo-orographic systems or soil depth; Treml et al. 2008). In addition, human management of these grasslands has been documented for at least the last seven centuries in mid-elevations (Szabó et al. 2025) and even for thousands of years in high mountains, e.g. transhumance in the Alps since the Iron Age (Gilck & Poschlod 2021). All these factors and activities resulted in a fine landscape mosaic with many open patches that was preserved at all elevations until approximately the first half of the 20th century (Hájková et al. 2011, Pokorný et al. 2015). This was despite the fact that, in the second half of the 19th century, the landscape began to be affected by the Industrial Revolution, including changes in agricultural practices such as the introduction of new crops and increased fertilizer use. The widespread use of synthetic nitrogen fertilizers in the early 20th century following the development of industrial nitrogen fixation substantially increased agricultural productivity and further promoted the conversion and intensification of traditionally managed landscapes. After the Second World War, the growing human population across Europe led to more substantial changes in land use. Overexploitation of fertile regions was accelerated by the intensification of conventional agriculture. Together with collectivization, urban expansion and the development of transport infrastructure, these processes led to the abandonment of traditional grassland management in less favourable mountainous regions (Munteanu et al. 2014, Szabó et al. 2025).

The long-term continuity (temporal stability) of grasslands is one of the factors supporting their high species richness and the occurrence of rare plants, as demonstrated for central-European dry grasslands (Hájková et al. 2011, Pokorný et al. 2015, Willner et al. 2021, Novák et al. 2024) and for alpine and subalpine vegetation in various European mountain ranges (Ralska-Jasiewiczowa et al. 2006, Treml et al. 2008, Dudová et al. 2018). However, the long-term continuity of individual grassland patches is difficult to estimate. Pollen analyses can provide valuable insight into the deep Holocene history of vegetation (Divíšek et al. 2020); however, they suffer from limitations in taxonomy and low spatial resolution (Shaw & Whyte 2020). In contrast, historical geographical maps created after the establishment of geodetic foundations capture a shorter period of history, but usually with greater spatial accuracy, mainly since the 19th century. Examples include military topographic maps of Austria (Munteanu et al. 2014), Italy (Statuto et al. 2017), Germany (Wittig et al. 2010) and Denmark (Levin et al. 2025), topographic maps of Switzerland (Loran et al. 2018), or Ordnance Survey topographic maps from England (Gurnell & Hill 2022). Although these maps do not provide information on the plant species composition, they precisely delineate different types of land use (or land cover) and can be used to assess the continuity (stability) of grasslands. Historical maps typically reveal only a limited number of land-use or land-cover classes without any information on the quality of the patches to which the land-use classes were assigned. Nevertheless,

we might expect that grasslands captured on historical maps from the mid-20th century and earlier correspond predominantly to present-day habitats of high quality, as traditional management practices essential for maintaining most grasslands were widely used during that time (Hejcman et al. 2013, Straubinger et al. 2021, Szabó et al. 2025).

Such historical maps, some of them dating back even to the 18th century, have already been used for vegetation studies (Gustavsson et al. 2007, Johansson et al. 2008, Reitalu et al. 2012) despite their limitations. Land-use or habitat data derived from these maps may be biased due to the need to combine various cartographic sources (often accompanied by land censuses), their varying geometric quality and their limited regional extent (Johansson et al. 2008). At the same time, the different quality of 18th and 19th century maps, stemming from their age, storage conditions, etc., means that their (semi-)automatic processing is still quite difficult. Therefore, most studies using historical maps processed them manually and thus only covered areas up to the regional scale (Cousins & Eriksson 2008, Statuto et al. 2017, Loran et al. 2018). However, with the recent development of advanced machine learning techniques, (semi-)automatic approaches are becoming more effective and facilitate the use of these data to interpret spatial patterns of individual types of land cover (Gobbi et al. 2019), as well as habitats (Chýlová & Münzbergová 2008, Levin et al. 2025) and characteristic plant species at larger scales (Auffret et al. 2018, Raduła et al. 2020). Still, most of these historical land-use data are very coarse. For example, studies by Raduła et al. (2020) and Auffret et al. (2018) compared species richness or the distribution of target species with recent freely accessible data from CORINE Land Cover (Bossard et al. 2000), which has a minimum mapping unit of 25 hectares. This results in a highly generalized representation of community changes and under-represents fine-scale landscape heterogeneity.

Another important factor influencing grassland species richness is landscape heterogeneity, which plays a key role in habitat connectivity. It is particularly essential in the context of current nature conservation efforts aimed at managing fragmented remnants of natural or semi-natural habitats (Plue et al. 2019). Specifically, there are two crucial spatial aspects that ensure the saturation of population and prevent genetic erosion (Helm et al. 2006, Cousins & Eriksson 2008): (i) The area of individual grassland patches and (ii) connectivity between them. Additionally, species richness is also influenced by (iii) a landscape matrix, which determines the regional species pool (Zobel 1992, Michalcová et al. 2014). A decline in any of these spatial aspects of grassland patches disrupts the spatial mass effects, leading to extinction debt (Helm et al. 2006, Hylander & Ehrlén 2013, Němec et al. 2022, Schüle et al. 2023) and a gradual decrease in species richness. Furthermore, the decline in grassland areas means that certain components of the landscape matrix, such as forest or built-up areas, increase, which can hinder the dispersal of seeds and pollen of grassland species (Auffret et al. 2018). However, all spatial aspects are interconnected and their interactions depend on the vegetation type (Janišová et al. 2014), as different habitats harbour species with different dispersal capacity (Guittar et al. 2020, Lososová et al. 2023), colonization potentials (Prach et al. 2017) and pollen dispersal mechanisms (O'Connell et al. 2007, Albrecht et al. 2009).

The current state of individual habitats in Europe is regularly monitored under the Natura 2000 network scheme, with the results available as fine-resolution habitat maps indicating habitat quality (Directive 2009/147/EC and Council Directive 92/43/EEC; European Union 1992, 2009), and land management initiatives such as the Land Parcel

Identification System (LPIS, Reumaux et al. 2023). Moreover, many grassland species have persisted in small patches of other habitats, such as field edges, road verges, forest edges, and within open forests (Cousins & Eriksson 2008, Jonason et al. 2014), as many of these habitats were historically managed in a manner similar to grasslands (Öllerer et al. 2019, Szabó et al. 2024). This enabled much higher connectivity than exists in the current landscape and leads us to expect that the continuity of historically interconnected grasslands may be highly important for explaining current diversity patterns.

In our study, we reconstructed the development of the fine-scale landscape mosaic surrounding a spatially stratified set of georeferenced vegetation plots (phytosociological relevés) using historical maps from the mid-19th century to the beginning of the 21st century, spanning 170 years, and covering the entire Czech Republic (78,871 km^2). Using these data, we investigated changes in land use in the surroundings of the plots and their effects on present-day plant species richness by addressing the following questions: (i) How has the landscape surrounding vegetation plots of different grassland types changed over this period? (ii) What proportion of grasslands and other land-use classes was stable (i.e. continuously present at a locality) across different grassland types? (iii) How does the extent of stable grasslands (continuously used as permanent grassland) influence the current species richness and the number of endangered (Red List) species? Furthermore, does the extent of stable forests affect current species richness, and could these relationships reflect species dispersal abilities? (iv) Does elevation modify the relationship between species richness or the number of endangered species and land-use stability?

Methods

Vegetation-plot data

We selected all georeferenced vegetation plots of grasslands from the Czech Vegetation Database (https://czechveg.github.io/) that were sampled after 1990, as precise geographic coordinates were required for further processing and data analyses. All these plots were classified into vegetation types using the CzechVeg-ESy expert system (Chytrý et al. 2020a), which is based on the presence of sociological species groups and the dominance of selected species (similar to the expert system for EUNIS Habitat Classification; Chytrý et al. 2020b; EUNIS-ESy). Subsequently, we only considered the plots classified by the CzechVeg-ESy (basic-v1-2020-01-12 and basic-v2-2020-01-19) into vegetation alliances or lower units. From these, we selected only plots assigned to six higher vegetation types: (i) mesic meadows and pastures (three alliances of the class *Molinio-Arrhenatheretea*: *Arrhenatherion elatioris*, *Polygono bistortae-Trisetion flavescentis* and *Cynosurion cristati*), (ii) intermittently wet and wet meadows (also three alliances of the class *Molinio-Arrhenatheretea*: *Molinion caeruleae*, *Deschampsion cespitosae* and *Calthion palustris*), (iii) *Nardus* grasslands (*Calluno-Ulicetea* without heathlands), (iv) pioneer vegetation of sandy and shallow soils (*Koelerio-Corynephoretea*), (v) narrow-leaved dry grasslands (four alliances of the class *Festuco-Brometea*: *Alysso-Festucion pallentis*, *Bromo pannonici-Festucion pallentis*, *Festucion valesiacae* and *Koelerio-Phleion phleoidis*) and (vi) broad-leaved dry grasslands (also four alliances of the class *Festuco-Brometea*: *Diantho lumnitzeri-Seslerion*, *Cirsio-Brachypodion pinnati*, *Bromion erecti* and *Geranion sanguinei*).

Due to highly uneven sampling intensity across the country (Knollová et al. 2005, Klímová et al. 2025), we applied a resampling procedure based on geographic distance and species similarity to our dataset to reduce the effect of local oversampling and obtain a more spatially balanced dataset (https://github.com/jdivisek/FilteringReleves; Divíšek & Chytrý 2018). This approach also helped to mitigate spatial autocorrelation in the residuals of our models. The final step in data preparation was to filter plots by plot size (sampled area of a plot), including only those that fell within the commonly used range of 16–25 m^2 (Otýpková & Chytrý 2006). The resulting dataset comprised 7,367 vegetation plots, belonging to the following six vegetation types: (i) mesic meadows and pastures – 2,497 plots; (ii) intermittently wet and wet meadows – 2,740 plots; (iii) *Nardus* grasslands – 346 plots; (iv) pioneer vegetation of sandy and shallow soils – 281 plots; (v) narrow-leaved dry grasslands – 370 plots and (vi) broad-leaved dry grasslands – 1,133 plots. The sufficient number of vegetation plots allowed us to divide each vegetation type into three or, in some cases, two elevation groups. We distinguished plots below 300 m a.s.l. as lowland, plots between 300 and 600 m a.s.l. as highland and plots above 600 m a.s.l. as mountain plots. For *Nardus* grasslands, we distinguished plots above 900 m a.s.l. as high-mountain plots.

Historical land use

We used the geographic coordinates of selected vegetation plots to extract land-use data from the TopoLandUse database for the Czech Republic (Sychrová et al. 2024). This database contains historical land-use data for five periods: 1836–1852 (hereafter the 1840s), 1876–1880 (1870s), 1952–1955 (1950s), 1988–1995 (1990s) and 2000–2006 (2006). These data are represented by vector polygon layers with a minimum patch size of 0.8 hectares (compared to the 25-hectare patch size of the CORINE database; Bossard et al. 2000) and were created by on-screen digitization of historical topographic and military maps (Skokanová et al. 2012). The land-use layers distinguish nine land-use categories: arable land, permanent grasslands, orchards, vineyards and hop fields, forests, water bodies, built-up areas, other areas (quarries or waste-disposal sites) and recreation areas. In our study, we used only eight categories, merging the recreation areas with built-up areas, as this category primarily included recreational facilities and their immediate surroundings, which correspond closely to the built-up area classification. For each plot, we applied a 1 km buffer to capture changes at the landscape scale (314 ha) and a 300 m buffer to assess land-use changes at the local scale (area of 28.3 ha; Fig. 1). By overlaying all land-use layers, we were able to identify plots with stable (unchanged) land use across all periods, which can serve as a measure of historical continuity of land use. We used the proportion (relative area) of each land-use category within each buffer around each plot for interpretation and further analyses.

Data analyses

To assess land-use development in the surroundings of grassland plots, we performed a principal coordinates analysis (PCoA). Since the distribution of land-use proportions was right-skewed, we calculated Hellinger distance (Legendre & Legendre 2012) between each pair of plots in each period (Fig. 2). In addition, for each vegetation type, we analysed the temporal development of dominant land-use categories (arable land, permanent

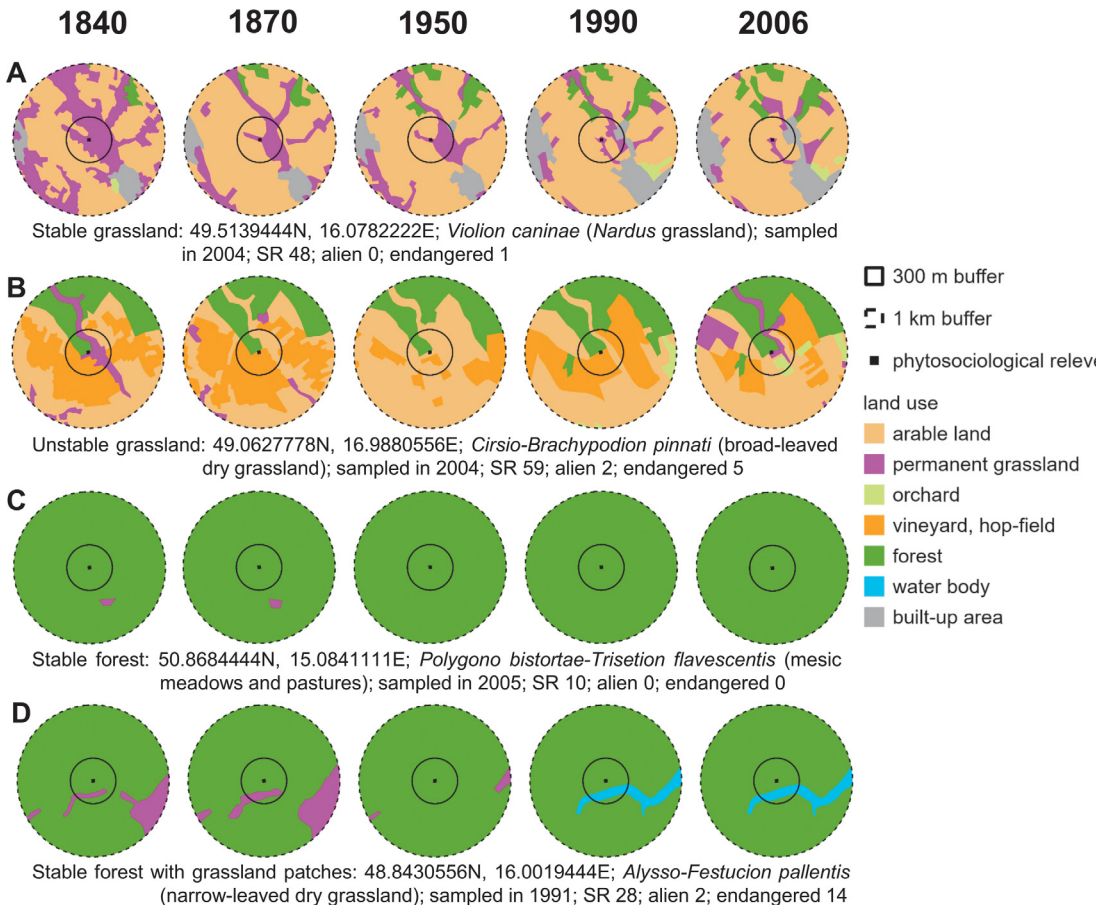

Fig. 1. Land-use changes in the surroundings of four different grassland vegetation plots across five historical periods. (A) represents a stable grassland (continuously used as permanent grassland) throughout the whole observation period (1840s–2006), while (B) shows an unstable grassland, (C) is a small grassland patch beyond our detection capabilities surrounded by a stable forest, and (D) represents a vegetation plot surrounded by a mosaic of continuous forest and small grassland patches on a steep slope (C and D show the limitation of our TopoLandUse database with a minimum patch size of 0.8 hectares). SR – species richness (number of all species in the plot); alien – number of all alien species in the plot (Pyšek et al. 2022); endangered – number of all endangered (Red List) species (Grulich 2017).

grassland, forest and built-up area) across five periods (1840s–2006) using boxplots. Differences in land-use proportions were tested using the Friedman test ($P < 0.001$), followed by post-hoc pairwise Wilcoxon signed-rank tests with Benjamini-Hochberg correction to control for multiple comparisons (results in Supplementary Figs S1–S6).

To explore differences in the proportion of the total area of all stable land-use types (i.e. land with unchanged use in the five periods from 1840 to 2006; irrespective of land-use categories) in the surroundings of grassland plots, we used boxplots and the non-parametric Kruskal–Wallis test, followed by a post-hoc Dunn's test with Benjamini-Hochberg correction (significance level was set to $\alpha = 0.001$; Supplementary Fig. S7).

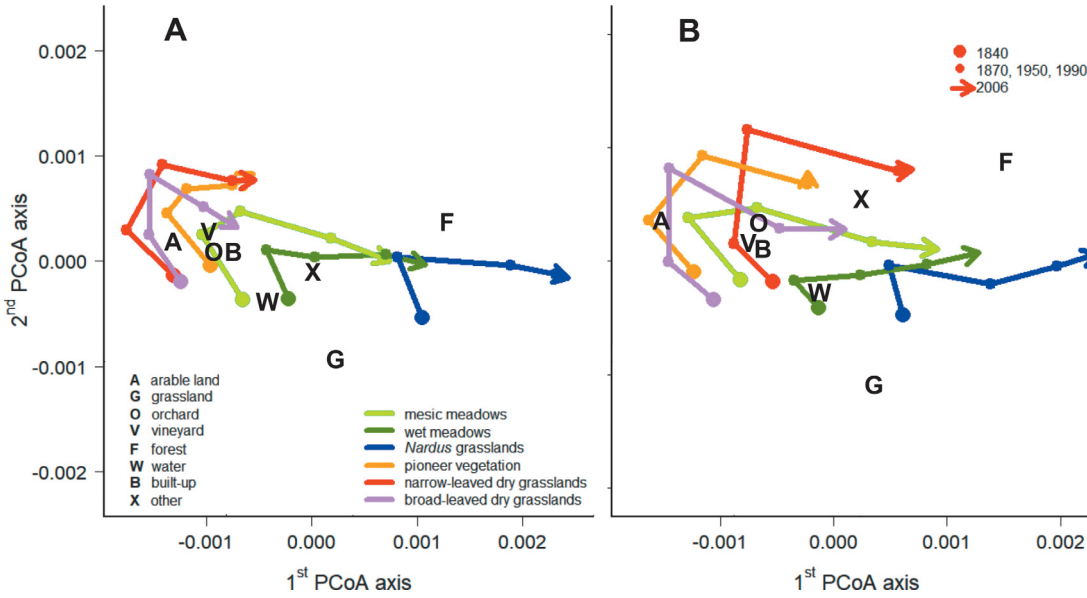

Fig. 2. Land-use development within (A) 1 km and (B) 300 m of grassland vegetation plots. The principal coordinates analysis (PCoA) used a pairwise Hellinger distance matrix calculated from area proportions of eight land-use categories detected in five historical maps (1840s, 1870s, 1950s, 1990s and 2006). Arrows represent shifts in the group centroids of vegetation plots of each grassland type from the 1840s (filled dot) to 2006 (arrow tip). Positions of individual land-use types are in the centre of the corresponding text label.

The same approach was also applied in the evaluation of seed dispersal and the index of colonization potential. Prior to these analyses, we calculated community-weighted means (CWMs) for each vegetation plot based on species composition (Zelený 2021) for species dispersal-distance classes according to Lososová et al. (2023) and the species colonization potential index according to Prach et al. (2017; Supplementary Fig. S8). To illustrate the general pattern of stable land-use types surrounding the grassland plots, we visualized the representation of all stable land-use types for each analysed grassland type using median values in pie charts (Figs 3 and 4).

We used generalized linear models (GLMs) to examine how species richness and the number of endangered species were related to the area of stable grassland or forest at both landscape (1 km buffer) and local scales (300 m buffer). Species richness was defined as the total number of species per plot, while the number of endangered species was determined based on the Red List of Vascular Plants of the Czech Republic (Grulich 2017). Since both dependent variables were count data, we initially used a Poisson distribution in the GLM. However, due to substantial overdispersion in the models, we used a quasi-Poisson distribution (with log link function) in the final models to correct for this issue.

All analyses were performed using ArcGIS (ESRI 2015; version 10.3.1) and the R program (R Core Team 2023; version 4.3.2) with the packages: ape (Paradis & Schliep 2019), FSA (Ogle et al. 2026), rsq (Zhang 2024), rstatix (Kassambara 2025), spdep (Bivand & Wong 2018), vegan (Oksanen et al. 2025) and weimea (Zelený 2021).

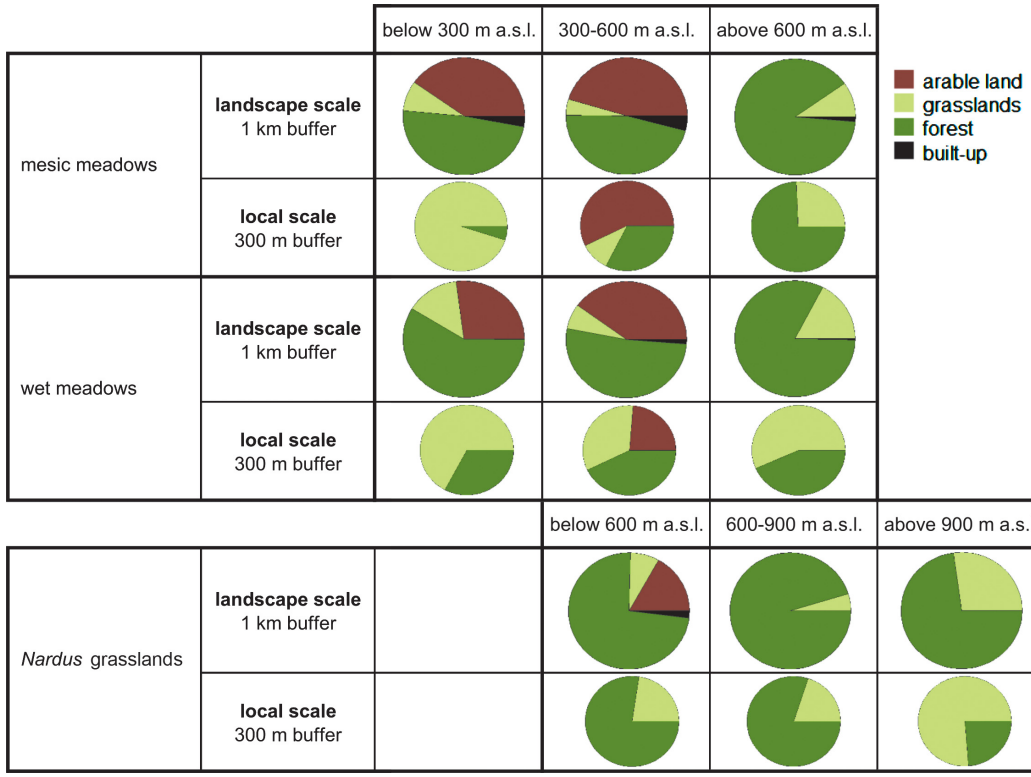

Fig. 3. Proportion of individual categories of stable land use (unchanged during 1840–2006; medians illustrating the common situation) in the surroundings of vegetation plots (landscape scale and local scale) of mesic and wet meadows and *Nardus* grasslands.

Results

Overall land-use changes in grassland plot surroundings

Ordination analysis (Fig. 2) of land-use types revealed that the landscape surrounding grassland plots changed dramatically during the observation period (1840s–2006) across all studied vegetation types. The extent of arable land at the landscape scale peaked in the 1870s in the surroundings of mesic and wet meadows, *Nardus* grasslands and pioneer vegetation across all altitudes (Fig. 2 and Supplementary Figs S1–S4). However, in the surroundings of both narrow- and broad-leaved dry grasslands, the conversion of fertile grassland soils to arable land continued until the mid-20th century, when arable land reached its greatest extent in both the lowlands and the highlands (Fig. 2 and Supplementary Figs S5–S6). At the same time, the grassland area decreased for all grassland types at both landscape (1 km buffer) and local scales (300 m buffer), with the exception of *Nardus* grasslands. By the mid-20th century, many grasslands had reached their smallest extent or had disappeared completely, a trend that is also reflected in the stable grassland area (Figs 3 and 4). In particular, only very small grassland patches of pioneer vegetation remained, while most of the lowland dry grasslands disappeared completely (Fig. 2 and Supplementary Figs S4–S6). Both the built-up area (except in the *Nardus* grasslands)

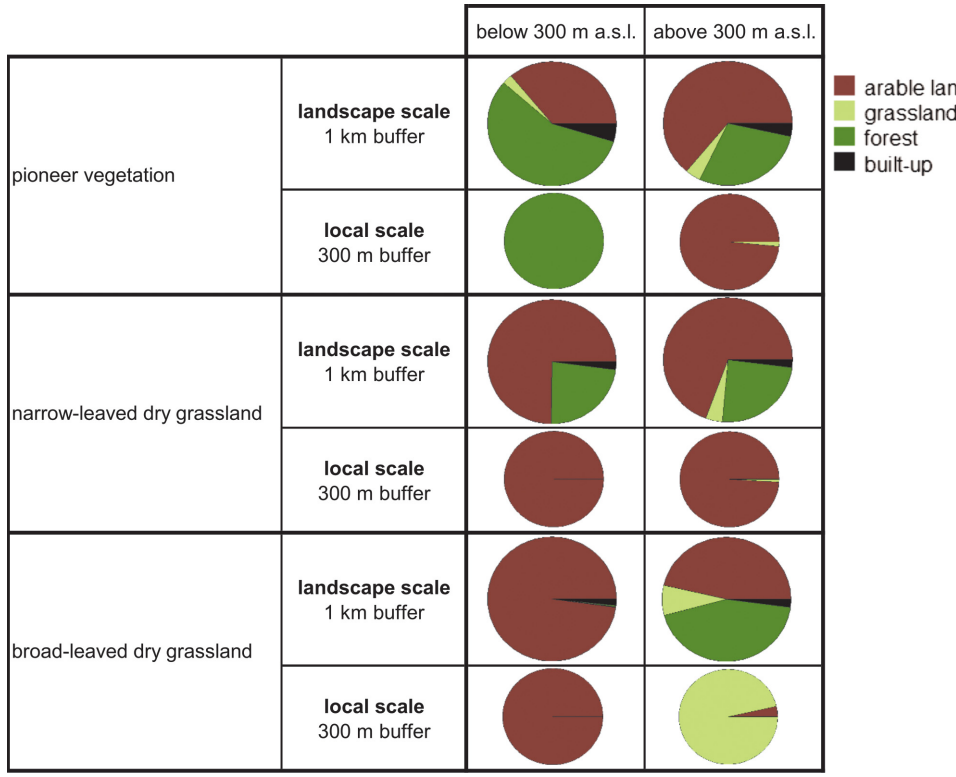

Fig. 4. Proportion of individual categories of stable land use (unchanged during 1840–2006; medians illustrating the common situation) in the surroundings of vegetation plots (landscape scale and local scale) of pioneer vegetation, narrow-leaved and broad-leaved dry grasslands.

and, more notably, the forest area, expanded in the surroundings of all plots across the studied vegetation types (with the exception of pioneer vegetation) and have continued to increase until 2006. More recently, some grasslands have been sown on former arable land and water bodies have been restored. At the local scale, the patterns were largely similar, although the direct overgrowth of grasslands by woody vegetation has been more pronounced since the mid-20th century and continues to the early 21st century.

Land-use stability in grassland plot surroundings

The total area of all stable land-use types varied only among some vegetation types at both landscape and local scales (Supplementary Fig. S7). However, the stability of individual land-use categories showed distinct patterns across elevations and spatial scales (Figs 3 and 4). When looking at individual vegetation types, we found the following patterns:

(i) The extent of stable land use in the surroundings of mesic meadows and pastures was similar in lowlands and mid-elevations. At the local scale, a higher proportion of preserved stable grasslands was found in lowlands, whereas only small, fragmented stable patches remained in mid-elevations. In contrast, stable forests dominated among the

unchanged land-use categories in the surroundings of mesic meadows and pastures at higher elevations at both the landscape and local scales.

(ii) Wet meadows followed a pattern similar to mesic meadows, but with larger stable grassland areas at both mid- and high-elevations. This is in contrast to the lowland wet meadows, where the stable grassland area was smaller than in mesic meadows and pastures.

(iii) *Nardus* grasslands occurred in landscapes dominated by stable forests, with only small patches of stable grasslands. However, larger stable grassland patches have been preserved in the surroundings of the plots in high mountain regions (above 900 m a.s.l.). A similar pattern was observed at the local scale, where extensive stable grassland areas were characteristic of high-elevation plots.

(iv) Pioneer vegetation and vegetation of shallow soils occurred in landscapes with only very small stable grassland patches, but with extensive stable forests in the lowlands and extensive areas of stable arable land in mid-elevations. In lowland areas, current plots were located in patches with no larger stable grasslands around, and forests represented the only land-use category with historical stability. In contrast, at mid-elevations, approximately half of the buffer area was covered by stable arable land, while land uses within the second half changed with little or no stable grasslands at all.

(v) Narrow-leaved dry grasslands were primarily found in areas dominated by stable arable land. We found no stable grasslands in the lowlands, and only small patches of stable grasslands in mid-elevations at both landscape and local scales.

(vi) Broad-leaved dry grasslands in the lowlands occurred in landscapes dominated by stable arable land and some stable settlements, but with no stable grasslands, a pattern that was consistent at both scales. However, we detected some stable grasslands in the mid-elevation buffers at the landscape scale, and even larger stable grassland areas at the local scale.

Effect of stable grassland and stable forest area on the current species richness

A significant positive relationship between the extent of stable grasslands and the number of endangered (Red List) species was found in almost all studied vegetation types in the Czech Republic at both the landscape and local scales (Table 1). The only exceptions were pioneer vegetation at both scales and narrow-leaved dry grasslands at the landscape scale, where no significant relationship was found. A positive relationship between the extent of stable grassland in the surroundings and current species richness was observed for mesic meadows, wet meadows, and broad-leaved dry grasslands. In contrast, a negative relationship was found between the extent of stable forest and the species richness of *Nardus* grasslands and pioneer vegetation at both scales, which corresponds to their shorter seed-dispersal distances compared with other grassland types (Supplementary Fig. S8). However, for wet meadows and broad-leaved dry grasslands we found a positive relationship between the extent of stable forest and species richness at the landscape scale.

Looking at finer units of grassland vegetation, a positive relationship between the extent of stable grassland and the number of endangered species was identified in lowland to submontane mesic meadows (*Arrhenatherion elatioris*) and in all three alliances of intermittently wet to wet meadows, which are distributed across the whole Czech Republic (Table 2). A positive relationship between the extent of stable grasslands and species richness was also detected in lowland to submontane mesic meadows (*Arrhenatherion*

Table 1. The relationship between the species richness of all and endangered species and the area of stable grassland and forest (during 1840–2006) in the closer (300 m buffer; local scale) or broader (1 km buffer; landscape scale) surroundings. Results are shown separately for six broad vegetation types across the whole Czech Republic. Arrows indicate a positive or negative relationship ($P < 0.001$), while their width shows two levels of the effect size: thin arrow for $R^2 < 0.1$ and thick arrow for $R^2 > 0.1$; n.s. = not significant.

	Whole area of the Czech Republic					
	Species richness		Endangered species		Species richness	
	Stable grassland area		Stable grassland area		Stable forest area	
	landscape	local	landscape	local	landscape	local
Mesic meadows and pastures	↗	↗	↗	↗	n.s.	n.s.
Intermittently wet to wet meadows	↗	↗	↗	↗	↗	n.s.
Nardus grasslands	n.s.	n.s.	↗	↗	↘	↘
Pioneer vegetation	n.s.	n.s.	n.s.	n.s.	↘	↘
Narrow-leaved dry grasslands	n.s.	n.s.	n.s.	↗	n.s.	n.s.
Broad-leaved dry grasslands	↗	↗	↗	↗	↗	n.s.

Table 2. The relationship between the species richness of all and endangered species and the area of stable grassland or forest (during 1840–2006) for six alliances of the class *Molinio-Arrhenatheretea* across the whole Czech Republic. For details, see Table 1.

	Whole area of the Czech Republic					
	Species richness		Endangered species		Species richness	
	Stable grassland area		Stable grassland area		Stable forest area	
	landscape	local	landscape	local	landscape	local
Arrhenatherion elatioris	↗	↗	↗	↗	n.s.	n.s.
Polygono bistortae-Trisetion flav.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Cynosurion cristati	↗	↗	n.s.	n.s.	n.s.	n.s.
Molinion caeruleae	↗	↗	↗	↗	n.s.	n.s.
Deschampsion cespitosae	n.s.	n.s.	↗	↗	↗	↗
Calthion palustris	↗	↗	↗	↗	n.s.	n.s.

elatioris), intermittently wet meadows (*Molinion caeruleae*), wet tall-herb meadows (*Calthion palustris*), and mesic pastures (*Cynosurion cristati*). Additionally, the species richness of lowland floodplain meadows (*Deschampsion cespitosae*) showed the only significant positive relationship with the extent of stable forests at both landscape and local scales.

Role of elevation in the relationship between species richness and land-use stability

Analysis along the elevation gradient in the Czech Republic revealed a positive relationship between the extent of stable grassland and the number of endangered species in (i) mesic and (ii) wet meadows at all elevations and at both landscape and local scales, while it was not significant for other grassland types (Table 3). A positive relationship between the extent of stable grasslands and species richness was only found at mid-elevations for both vegetation types, and at high elevations, only for wet meadows at the landscape scale. In contrast, the relationship between the extent of stable forests and species

Table 3. The relationship between the species richness of all and endangered species and the area of stable grassland or forest (during 1840–2006) for six broad vegetation types according to the elevation gradient. For details, see Table 1.

	Species richness		Endangered species		Species richness	
	Stable grassland area		Stable grassland area		Stable forest area	
	landscape	local	landscape	local	landscape	local
Mesic meadows and pastures						
Below 300 m a.s.l.	n.s.	n.s.	↗	↗	↗	↗
300–600 m a.s.l.	↗	↗	↗	↗	n.s.	↘
Above 600 m a.s.l.	n.s.	n.s.	↗	↗	↘	n.s.
Intermittently wet to wet meadows						
Below 300 m a.s.l.	n.s.	n.s.	↗	↗	↗	↗
300–600 m a.s.l.	↗	↗	↗	↗	n.s.	n.s.
Above 600 m a.s.l.	↗	n.s.	↗	↗	↘	↘
Nardus grasslands						
Below 600 m a.s.l.	↗	n.s.	↗	n.s.	n.s.	n.s.
600–900 m a.s.l.	n.s.	n.s.	n.s.	n.s.	↘	↘
Above 900 m a.s.l.	n.s.	n.s.	↗	↗	n.s.	n.s.
Pioneer vegetation						
Below 300 m a.s.l.	n.s.	n.s.	n.s.	n.s.	n.s.	↘
Above 300 m a.s.l.	n.s.	n.s.	n.s.	n.s.	↘	↘
Narrow-leaved dry grasslands						
Below 300 m a.s.l.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Above 300 m a.s.l.	n.s.	n.s.	n.s.	↗	n.s.	↗
Broad-leaved dry grasslands						
Below 300 m a.s.l.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Above 300 m a.s.l.	↗	↗	↗	↗	↗	n.s.

richness varied with elevation. In the lowlands, both mesic and wet meadows showed a positive relationship, whereas at mid-elevations, mesic meadows showed a negative relationship at the local scale. At higher elevations, both vegetation types showed a negative relationship with the extent of stable forest.

For *Nardus* grasslands, we found a positive relationship between the extent of stable grassland and the number of endangered species in high mountains (above 900 m a.s.l.) and at the landscape scale, also at mid-elevations (below 600 m a.s.l.; Table 3). A positive relationship between the extent of stable grasslands and species richness was also detected at mid-elevations at the landscape scale. In contrast, a negative relationship between the extent of stable forest and species richness was confirmed only at higher elevations.

For pioneer vegetation, we found no relationship between the extent of stable grassland and either the species richness or the number of endangered species. However, a significant negative relationship between the extent of stable forest and species richness was observed both in the lowlands and at mid-elevations at the landscape scale, but only in the lowlands at the local scale (Table 3).

For both narrow-leaved and broad-leaved dry grasslands, significant relationships were detected only at mid-elevations, but not in the lowlands (Table 3). Narrow-leaved dry grasslands showed two positive relationships at the local scale: between the extent of stable grassland and the number of endangered species and between the extent of stable forest and species richness. In contrast, almost all relationships tested for broad-leaved dry grasslands were significantly positive.

Discussion

Historical land-use development

For centuries, and in some places for millennia, humans have managed the cultural landscape as a mosaic of open grasslands, natural forests and fields, thereby maintaining species-rich grasslands (Hájková et al. 2011, Hejcman et al. 2013). However, the Industrial Revolution from the 18th through the 19th century triggered rapid and widespread transformations of the European landscape. In parts of central Europe, the extent of arable land peaked in the 1870s (Krausmann 2001, Ye et al. 2023, Sychrová et al. 2024), whereas in other regions, such as Romania, East Asia or Russia, the peak occurred between the 1940s and 1960s (Klein Goldewijk 2001, Munteanu et al. 2014). Our results reflect these historical trends (Fig. 2, Supplementary Figs S1–S6). In particular, we confirmed that the extent of arable land in the surroundings of the current grassland plots peaked in the 1870s for the landscapes with mesic and wet meadows, *Nardus* grasslands, and pioneer vegetation at all elevations (Fig. 2, Supplementary Figs S1–S4). In contrast, in landscapes with dry grasslands, especially on fertile soils, the peak in arable-land area occurred in the mid-20th century in both lowlands and highlands (Supplementary Figs S5–S6). During the 19th century and the early decades of the 20th century, farmyard manure was applied almost exclusively to arable fields, while most grasslands remained unfertilized except for some mountain regions (Hejcman & Schellberg 2009). This unequal distribution of nutrients likely contributed to the maintenance of nutrient-poor conditions in many semi-natural grasslands. The widespread use of synthetic nitrogen fertilizers developed only later and accelerated after the Second World War. The mid-20th-century peak of arable land in dry-grassland landscapes coincided with the introduction of modern agricultural technologies and tools, including tractors and other machinery, which enabled more intensive land use. These land-use changes were also influenced by differing legislative and socio-economic constraints. While transitions between arable land and grasslands were relatively unrestricted, conversions involving forests were subject to stricter regulation, which limited the reduction of forest cover beginning with the Forest Act of 1852 (Gingrich & Schmid 2026). In mountainous regions, post-war depopulation following the expulsion of Germans further accelerated land abandonment and substantially altered traditional landscape management (Sychrová et al. 2024). As a result, most grasslands reached their minimum extent during these periods, a trend that has also been documented across the Baltic region (Eriksson & Cousins 2014). The widespread loss of grasslands had profound effects on grassland stability (Figs 3 and 4) and the metapopulation dynamics of many species. We found that only small patches of stable grasslands persisted in pioneer vegetation, whereas in many lowland dry grasslands, stable grassland patches disappeared completely (Fig. 4). However, these findings may be partly influenced by the characteristics of the land-use maps we used, which did not capture patches smaller than 0.8 hectares (e.g. small forest canopy openings or small grasslands on rocky outcrops; Figs 1C and D). Despite this loss, it is likely that the species pools were preserved at the landscape scale, as many grassland species survived in small patches such as field edges, road verges, forest edges, or open woodlands (Cousins & Eriksson 2008, Jonason et al. 2014). Such habitats were historically managed in a similar way to grasslands (Öllerer et al. 2019, Szabó et al. 2024), which contributed to the high connectivity of such small grassland patches. Additionally,

the high seed dispersal ability of dry grassland species (Supplementary Fig. S8A; Lososová et al. 2023) combined with their strong colonization potential (Supplementary Fig. S8B; Prach et al. 2017), together with preserved habitat connectivity, may have prevented genetic erosion in many populations (Münzbergová et al. 2013). In accordance with these characteristics, Chýlová & Münzbergová (2008) identified broad-leaved dry grasslands as habitats with high variation in past land use, as illustrated in Fig. 1B.

The most critical period for grassland species was the second half of the 20th century, particularly during socialist collectivization. This process involved the merging of small fields into large land blocks and the removal of many linear and patchy landscape elements such as field margins and farm tracks. This process led to the loss of the fine-scale landscape mosaic that had maintained habitat connectivity and supported the persistence of a relatively large regional species pool. At the same time, agricultural intensification, including the widespread and frequently excessive use of synthetic fertilizers and pesticides together with large-scale mechanization, became particularly pronounced in lowland areas. The resulting high nutrient inputs caused widespread eutrophication of agricultural landscapes including grasslands (Prach et al. 2021), while traditional farming methods were largely abandoned in mountainous and less agriculturally favourable regions (Klinkovská et al. 2023, 2024, Sychrová et al. 2024, Szabó et al. 2025). Both trends contributed to the fragmentation and isolation of grasslands, leading to succession, extinction debt, and eventual overgrowth by woodlands, as also visible in our results (Fig. 2 and Supplementary Figs S1–S6). This shift was further supported by the non-intervention approach to nature conservation, which was also applied to some of the most valuable grasslands. In addition, increasing nitrogen inputs through atmospheric deposition, including long-range transport of reactive nitrogen compounds and emissions associated with intensive agriculture, industry and road traffic, contributed to widespread eutrophication of the landscape (Shibata et al. 2015, Gallego-Zamorano et al. 2022). This is reflected in an overall increase in nutrient-demanding species (Midolo et al. 2026). Together with the abandonment of traditional management, these processes accelerated woody encroachment in small and scattered habitat patches that had previously served as stepping stones for the dispersal of grassland species. Active grassland management was only gradually reintroduced in the Czech Republic after 1990. Despite these efforts, our data show a gradual expansion of forest cover across all grassland types at both the landscape and local scales until 2006 (except for pioneer vegetation; Fig. 2 and Supplementary Figs S1–S6). This trend can likely be explained by insufficient funding and labour shortages, challenges observed throughout Europe (Tokarczyk 2018). In addition, the encroachment of woody species into grassland areas is likely to be accelerated by climate change, contributing to a globally observed trend of shrub expansion (Eldridge et al. 2011).

Relationships of conservation values and land-use stability across elevation

Previous studies have highlighted the importance of both habitat continuity and connectivity for grassland biodiversity (Hájková et al. 2011, Scherreiks et al. 2022, Novák et al. 2024). Grasslands with long-term stability (continuity) are considered among the most valuable habitats for biodiversity conservation (Veldman et al. 2015), and connectivity has been shown to be even more important than the species mass effect in determining

grassland species richness (Reitalu et al. 2012). Our results extend these findings by showing that both historical continuity (temporal stability) and spatial connectivity vary substantially among grassland habitat types, a pattern that is consistent with previous research based on coarser CORINE land cover data (Janišová et al. 2014). We found a positive relationship between species richness and the area of stable grassland (1840–2006) only for mesic and wet meadows and broad-leaved dry grasslands across the whole Czech Republic (Table 1). This is in contrast to some studies that reported historical land use as a stronger predictor of both species richness and the number of grassland specialists than contemporary land use across all grassland habitats (Helm et al. 2006, Gustavsson et al. 2007, Auffret et al. 2018). For instance, Gustavsson et al. (2007) emphasized that land use in the 18th century was more important than land use in 1961. In contrast, Raduła et al. (2020) found that grassland continuity over 60 years only had a positive effect on the number of characteristic grassland species, but not on total species richness in Lower Silesian grasslands. Similarly, Cousins & Eriksson (2008) reported no effect on species richness in Swedish grazed and abandoned grasslands, which may be explained by species trait-based responses to habitat area and fragmentation (see Lindborg et al. 2012).

We also showed that elevation plays a significant role in shaping diversity–land-use patterns in central Europe. We found a significant relationship between species richness and stable grassland in mesic and wet meadows and broad-leaved dry grasslands only in the highlands (> 300 m a.s.l.; Table 3) but not at other elevations across the Czech Republic (except for mountainous wet meadows at the landscape scale; Table 3). Similarly, finer vegetation units, specifically alliances of the class *Molinio-Arrhenatheretea*, showed a positive relationship only when they were not predominantly found in lowlands or mountains (Table 2). These findings correspond with those of Cousins & Eriksson (2008), who found only a weak effect of historical land cover on present-day species richness in highly transformed agricultural landscapes. One possible explanation is that species richness does not always reflect the conservation value of vegetation (Janišová et al. 2014, Padullés Cubino et al. 2023). In particular, lowland areas are more susceptible to the spread of some alien species, nitrophytes, ruderal species, and expansive species (Janišová et al. 2014, Pyšek et al. 2022, Axmanová et al. 2024). This aligns with recent findings on the expansion of generalist species and shrubs across the Czech Republic (Klinkovská et al. 2024). In addition, the predominance of species-poorer grassland vegetation in mountain regions (Chytrý 2007, Klinkovská et al. 2023) and the slower succession rates in extensive abandoned grasslands probably explain the lack of a significant relationship for these grassland habitats (Tables 1–3).

Several studies have concluded that there are better measures of habitat conservation value than species richness, such as the number of endangered species (Padullés Cubino et al. 2023), proportion of target species (Janišová et al. 2014, Klinkovská et al. 2024) or characteristic species (Raduła et al. 2020). Therefore, we also analysed the relationship between the number of endangered (Red List) species and the area of stable grassland. A positive relationship was found for all grassland types across the Czech Republic, with the exception of pioneer vegetation at both scales and narrow-leaved dry grasslands at the landscape scale (Table 1). This aligns with previous findings that pioneer vegetation typically harbours fewer endangered species (Chytrý 2007, Grulich 2017), as do specific alliances of pastures (*Cynosurion cristati*) and montane mesic meadows (*Polygono bistortae-Trisetion flavescentis*; Table 2). In contrast, dry grasslands, which typically harbour a large number

of endangered species, have suffered significant losses, particularly in lowland areas, where many localities have been destroyed entirely. As a result, only very small or no patches of stable dry grasslands remain even at the landscape scale (Fig. 4). This fragmentation may also explain the weaker relationship between species richness and stable grassland area. Despite the high seed dispersal ability of many dry grassland species (long seed dispersal distances; Supplementary Fig. S8A), the loss of landscape connectivity has prevented the localities from being replenished from the regional species pool, as grassland cover has drastically decreased or disappeared at the landscape scale (Fig. 4). A similar pattern appears in pioneer vegetation, which also includes early successional stages that eventually become overgrown (Chytrý 2007). While species of pioneer vegetation have high colonization potential, they surprisingly have shorter seed dispersal distances (Supplementary Figs S8A and B). Thus the dominance of stable forest or arable land in the surrounding landscape creates a significant barrier to species dispersal, both at the landscape and local scales (Fig. 4 and Tables 1 and 3). We also confirmed such a barrier effect in mountainous regions, particularly in mesic and wet meadows and *Nardus* grasslands, where extensive spruce-dominated forests limit the dispersal of grassland species. However, in lowlands, mesic and wet meadows showed the opposite pattern (Table 3), likely because deciduous forests often harbour a portion of the grassland species pool (Janišová et al. 2014). Interestingly, we found a similar pattern in highland dry grasslands, which contradicts Janišová et al. (2014). This discrepancy may stem from differences in methodology. Their study used the present forest area, while we analysed only the area of stable forests (1840s–2006) at a much finer spatial scale. In highlands, dry grasslands are often found on slopes, where isolated patches of sparse forest and forest edges have provided refuge for some heliophilous species, potentially mitigating the loss of connectivity.

Conclusions

Our study confirmed that historical continuity plays a crucial role in the preservation of endangered species, even at the landscape scale (within a 1 km buffer around a given locality). Long-term connectivity between localities and habitat patches supports the persistence of species-rich grassland communities and viable populations. Nature conservation efforts should not only focus on protecting isolated remnants of grassland habitats harbouring valuable biodiversity, but also on creating a functional network of interconnected grasslands. While grasslands with long-term stability (continuity) are the most valuable for biodiversity conservation, often only small remnants of such habitats have survived. Therefore, the use of historical maps is essential to identify these sites and include them in conservation planning and prioritization. Additionally, continuity should not be overlooked in the implementation of the Nature Restoration Law, as it represents a unique opportunity for biodiversity conservation and habitat restoration. Even in already overgrown or degraded fragments of stable (continuous) grasslands, restoration ecology provides effective methods for selecting appropriate approaches to regeneration and recovery for rebuilding a connected grassland network that can sustain viable plant and animal populations. The legacy of stable grasslands often persists through soil seed banks, other diaspores of native species, and the preservation of soil structure and composition.

In the broader landscape context, grassland connectivity could also be enhanced by incorporating managed open-canopy tree stands, such as traditional orchards, as well as extensive agroforestry belts, which can serve as stepping stones between grassland patches while maintaining ecological value.

Supplementary materials

Fig. S1. Proportions of predominant land-use categories of mesic meadows and pastures.
Fig. S2. Proportions of predominant land-use categories of intermittently wet to wet meadows.
Fig. S3. Proportions of predominant land-use categories of *Nardus* grasslands.
Fig. S4. Proportions of predominant land-use categories of pioneer vegetation.
Fig. S5. Proportions of predominant land-use categories of narrow-leaved dry grasslands.
Fig. S6. Proportions of predominant land-use categories of broad-leaved dry grasslands.
Fig. S7. Proportions of the total area of all stable land uses in the surroundings of grassland plots.
Fig. S8. Seed dispersal and colonization-potential index for analysed grassland plots.

Supplementary materials are available at https://www.preslia.cz

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Záleží na kontinuitě využívání krajiny? Vliv téměř dvousetleté historie využívání krajiny na temperátní trávníky

Krajina střední Evropy je člověkem značně ovlivňována již tisíce let. Tradiční zemědělské hospodaření podpořilo výskyt mnoha světlomilných druhů travinných společenstev a přispělo tak k mimořádné druhové rozmanitosti těchto stanovišť. Až zásadní změny ve využívání krajiny a způsobech hospodaření, které nastaly přibližně v polovině 20. století, způsobily rychlý a rozsáhlý ústup a vymizení mnoha druhů travinných společenstev.

Pomocí historických map typů využití krajiny v České republice od poloviny 19. do počátku 21. století jsme analyzovali změny struktury jemné krajinné mozaiky v okolí dochovaných fragmentů trávníků. Současně jsme testovali, zda dlouhodobá kontinuita trávníků (tj. jejich stabilita) ovlivňuje současnou druhovou bohatost a výskyt ohrožených druhů (dle Červeného seznamu pro ČR). Analýzy 7367 fytocenologických snímků odhalily, že podíl orné půdy v okolí trávníků dosáhl maxima mezi koncem 19. a polovinou 20. století, v závislosti na vegetačním typu trávníku. V tomto období zároveň dosáhla rozloha většiny travních ploch svého kritického minima, přičemž v mnoha nížinných oblastech trávníky zcela zanikly. Následné ukončení hospodaření vedlo v řadě zbylých trávníků k zarůstání keři a stromy, což nepříznivě ovlivnilo jejich stav jak na lokální, tak na krajinné úrovni (s výjimkou pionýrské vegetace). Naše výsledky ukazují, že hodnocení dlouhodobé kontinuity závisí na typu trávníku. Vliv kontinuity na druhovou bohatost byl silnější u ohrožených druhů než u celkové druhové bohatosti, což naznačuje, že počet ohrožených druhů je vhodnějším ukazatelem ochranářských hodnot. Trávníky s dlouhodobou kontinuitou představují klíčová stanoviště pro ochranu biodiverzity, avšak prostorová konektivita hraje zásadní roli pro přežívání ohrožených druhů. Strategie ochrany a obnovy by se proto měly zaměřit nejen na izolované fragmenty druhově bohatých trávníků, ale také na vytváření funkční sítě vzájemně propojených stanovišť.

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