



Significant decline in habitat specialists in semi-dry grasslands over four decades

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Abstract

Semi-dry grasslands are among the most species-rich plant communities in the world, harbouring many specialised and threatened species. Most of these grasslands were traditionally maintained by grazing and hay-making. After traditional management ended, protected areas were established and conservation management was introduced to protect the most valuable grassland sites. However, recent changes in land use, eutrophication and climate warming are negatively impacting the biodiversity of these grasslands. In 2022, we resurveyed historical vegetation plots in the Central Moravian Carpathians (Czech Republic), first sampled in the 1980s, to test whether the plant species composition and richness of semi-dry grasslands are changing over time and, if so, whether the decline in habitat quality and plant diversity is absent or less severe in protected areas. We found significant changes in species composition. Species richness and the proportion of habitat specialists and Red-List species decreased, whereas competitively stronger species with higher moisture and nutrient requirements increased. These trends were more pronounced outside the protected areas but also occurred within protected areas. The main factor behind these changes appears to be the cessation of traditional management and natural succession supported by eutrophication.

Keywords Abandonment · *Cirsio-Brachypodium pinnati* · Conservation management · Succession · Vascular plants · Vegetation resurvey

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Introduction

Semi-dry grasslands belong to the most species-rich plant communities in Europe and globally (Merunková et al. 2012; Wilson et al. 2012; Roleček et al. 2014; Chytrý et al. 2015; Biurrun et al. 2021). They harbour many habitat specialists and threatened species and have high nature value (Veen et al. 2009). Most of these habitats are considered semi-natural because they replaced original forests cleared by prehistoric settlers and have been maintained by grazing and hay-making for many centuries. During the 20th century, the area of traditionally managed semi-dry grasslands decreased dramatically: most sites were abandoned because traditional grazing and hay-making were no longer economically profitable (Poschlod and WallisDeVries 2002; Dengler et al. 2014) and the habitat became more fragmented. Following the abandonment of traditional management, semi-dry grasslands often experienced successional changes and a shift towards more mesophilous communities associated with decreasing species richness and a decline in threatened species (Giarrizzo et al. 2017; Bohner et al. 2019; Rendeková et al. 2020). Habitat fragmentation has led to a decline in habitat connectivity and reduced fitness of populations of rare and specialised species (Butaye et al. 2005; Brückmann et al. 2010; Loos et al. 2021).

Due to their high nature value, semi-dry grasslands have been included in the EU Habitats Directive as Natural Habitat Types of Community Interest. To preserve them, protected areas have been established in many European countries, and conservation management, mainly by mowing, grazing and clearing encroaching woody plants, has been implemented (Mackovčín and Jatiová 2002; Mackovčín et al. 2007; Calaciura and Spinelli 2008; Barańska et al. 2013; Olmeda et al. 2019; Joint Nature Conservation Committee 2023).

However, new challenges have emerged for maintaining the biodiversity of natural habitats in recent decades. Increased nitrogen supply from the atmosphere and fertilisers applied to adjacent arable land may also influence the species richness and composition of semi-dry grasslands. According to several studies, eutrophication causes a shift in species composition toward mesophilous plant communities, while stronger competitors displace stress-tolerant species (Bobbink and Willems 1987; Bennie et al. 2006; Maskell et al. 2010; Newton et al. 2012; Ladouceur et al. 2022).

Another factor contributing to changes in species composition is climate warming, which may be associated with extreme climatic events such as summer and spring droughts, resulting in the spread of thermophilous and xerophilous species (Dai 2011; Dostálek and Frantík 2011; Napoleone et al. 2021). In contrast, some experimental studies simulating increasing temperature reported that higher temperatures extend the growing season, leading to larger biomass and faster successional processes (Hillier et al. 1994; Sternberg et al. 1999; Wu et al. 2011; Peringer et al. 2013).

Given these effects of various drivers of global change, it is still unclear whether the management of protected areas is sufficient, as some studies report relative stability of semi-dry grassland communities in protected areas (Hüllbusch et al. 2016), while others indicate a decline in species richness and habitat specialists despite conservation efforts (Fisher and Stöcklin 1997; Timmermann et al. 2015; Diekmann et al. 2019; Bauer and Albrecht 2020).

The effects of environmental change on habitat specialists are reflected in the biotic quality of habitats. In particular, declines in specialists and increases in generalist species and subsequent biotic homogenisation could alter ecosystem functioning (Clavel et al. 2011). In semi-dry grasslands, habitat specialists are mostly light-demanding and stress-tolerant spe-

cies that are bound to low-productive sites (Chytrý 2007; Fajmonová et al. 2013; Diekmann et al. 2014), which predisposes them to be the most threatened species group under changing environmental conditions (Sengl et al. 2016; Olsen et al. 2018).

This study uses a unique historical dataset of vegetation plots from semi-dry grasslands in an area with a relatively homogeneous environment. Some of the sampled sites are in currently protected areas and others are in non-protected areas. We resurveyed the same sites almost 40 years after the original survey. This allowed us to test whether vegetation is changing and if so, whether declines in habitat quality and plant diversity are absent or less severe in protected areas. We hypothesised that (1) plant diversity of all semi-dry grasslands is changing due to climate warming and eutrophication, (2) plant diversity of semi-dry grasslands outside of protected areas is also changing due to lack of management and succession, (3) habitat specialists of semi-dry grasslands are more affected by these changes than other species groups.

Materials and methods

Study area

The study area is in the Central Moravian Carpathians (Czech Republic, 49°06′04″–49°13′31″N, 16°56′58″–17°20′47″E; Fig. 1). Uplands with elevation ranging between 220 and 400 m a. s. l. are formed of Tertiary and Quaternary sediments, mainly Carpathian flysch composed of sandstone and claystone layers covered with loess in some places (Czech Geological Survey 2022a). Calcareous soils prevail, including black soils, brown soils, pararendzinas, and cambisols (Czech Geological Survey 2022b). Soil pH measured

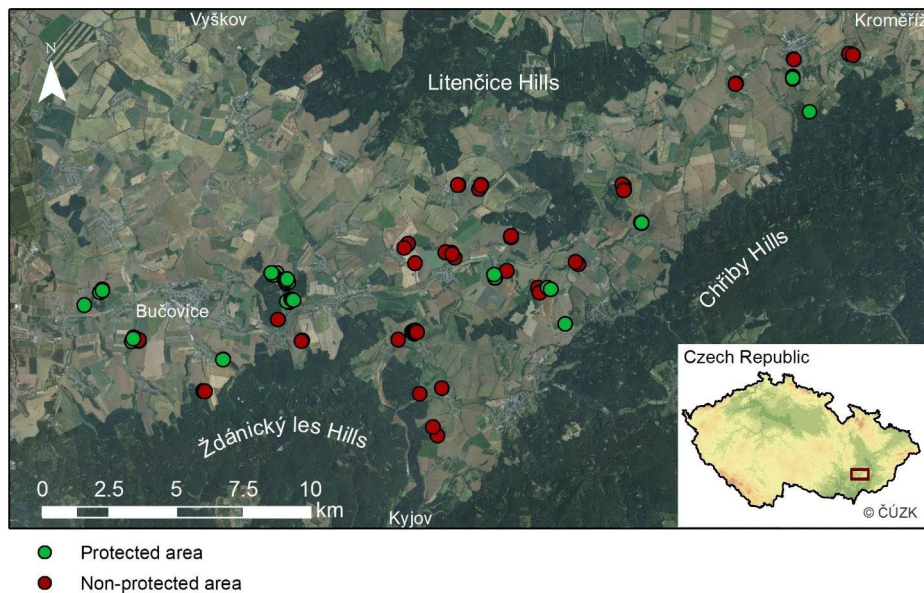


Fig. 1 Localities of resurveyed plots in the Central Moravian Carpathians. Background orthophoto source: Geoportal (2021)

in vegetation plots in 2022 ranged from 6.4 to 8.1. At the Brno-Tuřany station (241 m a. s. l., 18 km W of the study area), the mean annual temperature was 8.7 °C in 1965–1984 and 10.3 °C in 2002–2021, suggesting a temperature increase over the past 60 years (Appendix S1). The mean total annual precipitation in the study area (Bučovice station, 239 m a. s. l.) was 521 and 602 mm in 1965–1984 and 2002–2021, respectively, with a maximum in June (Czech Hydrometeorological Institute 2022).

Without human influence, the study area on the edge of the Pannonian forest-steppe would be largely covered with oak and hornbeam forests (Neuhäuslová et al. 1997). Due to continuous human occupation since the Neolithic, the landscape has been largely deforested, and dry grasslands on the slopes unsuitable for arable land were used for grazing and hay-making. Nowadays, the landscape is dominated by arable land, with small towns and villages. Remnants of dry grassland vegetation are found on steep slopes, which are usually surrounded by arable fields (Culek et al. 2013). In the past, such sites were used as extensive pastures or orchards. These steppe patches harbour species-rich dry grassland communities of the *Festucion valesiaca*, *Cirsio-Brachypodium pinnati* and *Bromion erecti* alliances with many threatened species, which are of high value for biodiversity conservation. Several small-scale protected areas (National Nature Reserves, Nature Reserves, National Nature Monuments, Nature Monuments) have been established to preserve the most valuable sites. Some areas became protected already in the 1950s, while others were established only in the 1980s, 1990s and 2000s. Since the main threat to these communities is the spread of shrubs and competitive grasses (e.g. *Arrhenatherum elatius*, *Calamagrostis epigejos*), conservation management, mainly in the form of mowing and removal of woody species, has been introduced in protected areas (Mackovčín and Jatiová 2002; Mackovčín et al. 2007). Some of the non-protected areas are also mown, but not for conservation purposes.

Vegetation survey and resurvey

To analyse vegetation change through time, 90 vegetation plots, originally surveyed in 1985 and 1986 by Bohumil Trávníček (Trávníček 1987), were resurveyed in 2022 by Klára Klinkovská. Of these, 40 were within protected areas and 50 were outside. To locate the historical plots as accurately as possible, a description of the location of each plot was used along with information on slope, aspect, elevation, and dominant species. In 2022, the geographical coordinates of each plot were measured using GPS with a location uncertainty of 3–5 m. All plots, both in the original survey and resurvey, were squares of 16 m². The total percentage covers of vascular plants and bryophytes were recorded in each plot, and the cover of each vascular plant species was estimated using the seven-grade Braun-Blanquet scale in the 1980s and the nine-grade Braun-Blanquet scale in 2022 (Westhoff and van der Maarel 1978). The nine-grade scale divides grade 2 of the seven-grade scale into three grades, while the scales remain compatible. In 2022, soil samples were collected from four places approximately in the middle of each quarter of the plot, below the litter layer at a depth of 5–10 cm. Mixed samples from each vegetation plot were dried at room temperature and sieved. A suspension with distilled water (weight ratio 1:2.5) was shaken in the Biosan PSU-10i orbital shaker for 5 min at 280 rpm and, after 5 h, soil pH was measured using the HACH HQ40D digital multimeter.

Data analysis

Vegetation-plot records from both the 1980s and 2022 were digitised using the Turboveg 2 program (Hennekens and Schaminée 2001). Taxonomic concepts and nomenclature were standardised in the Juice 7.1 program (Tichý 2002) according to Danihelka et al. (2012). The different cover-abundance scales were unified into a seven-grade Braun-Blanquet scale, and species covers were converted to percentages. Bryophytes (recorded only during the 1980s survey) were excluded from analyses, and woody species occurring in multiple layers were merged.

The vegetation-plot records were classified into vegetation types using a classification expert system for the national vegetation classification system of the Czech Republic (Chytrý 2007; Chytrý et al. 2020). Transitions between vegetation types observed during the initial survey and resurvey in the same plot were visualised in an alluvial plot drawn with the ggalluvial package in R (Brunson and Read 2020; R Core Team 2021).

To investigate whether observed trends differed by protection status, we identified plots located within and outside protected areas. To account for possible different trends caused by factors other than protection status (Joppa and Pfaff 2009), we tested for differences in elevation, slope, aspect, and soil pH between plots located within and outside protected areas using the Wilcoxon test. As none of the tests were significant (Appendix S2), we used protection status as the only predictor in the analyses.

We analysed the changes in species composition using ordination. A principal coordinate analysis (PCoA) with square-root transformation of species percentage covers and square-root of Bray-Curtis dissimilarity was performed to visualise the directions of changes in species composition between the 1980s and 2022 using the vegan package in R (Oksanen et al. 2022). To test for the significance of changes in species composition, constrained ordination (distance-based redundancy analysis, db-RDA) was used with the same cover transformation and dissimilarity measure as in PCoA. Time was used as a constraining (explanatory) variable and plot identity as a covariate. The significance of changes in species composition between the 1980s and 2022 was tested using a permutation test with 999 permutations of observations within plots.

To test whether observed changes in species composition differed by protection status, we ran a db-RDA with the interaction of time and protection status included as a constraining variable. The significance of differences was tested using a permutation test with 999 permutations within plots.

We determined which species significantly decreased or increased between the 1980s and 2022 by testing the significance of the relationship of individual species to the constrained axis of db-RDA (time as the constraining variable and plot identity as a covariate) using a permutation test with 999 permutations within blocks defined by plot identity. Increasing and decreasing species were also determined separately for the protected and non-protected areas.

For each plot, we calculated two temporal beta diversity indices: the Jaccard dissimilarity index for presence-absence data and the Ružička dissimilarity index for species abundances. Then we decomposed the two indices into the loss and gain components to see which predominated in determining the change in species composition, and tested the differences between species gains and losses using permutation tests with 999 permutations (Legendre 2019).

Differences in species richness (number of species per plot) were tested using a generalised least squares model with a correlation between observations from the same plot. We used a compound symmetry correlation structure because there were only two observations per plot. Time, protection status and their interaction were used as predictors. The model was fitted using the nlme R package (Pinheiro et al. 2023).

Changes in the proportion of threatened species (i.e. the IUCN categories CR – critically endangered, EN – endangered and VU – vulnerable according to the national Red List; Grulich 2017) were tested using a generalised estimating equations model with binomial distribution. An exchangeable correlation structure was specified between observations of the same plot. Time, protection status and their interaction were used as predictor variables. The geepack R package was used to fit the model (Yan 2002; Yan and Fine 2004; Hojsgaard et al. 2006). The same type of model was used to test changes in the proportion of semi-dry grassland specialists, defined as species diagnostic for the alliances *Cirsio-Brachypodium pinnati* or *Bromion erecti* according to the national vegetation classification (Chytrý 2007). Only plots classified into one of these alliances or subordinate associations in the 1980s (77 plots) were included in this model. The proportion of alien species (according to Pyšek et al. 2022) was also tested using the same model. In case of a non-significant interaction, the models were fitted with only two predictors – time and protection status.

Changes in species' indicator values (Ellenberg-type indicator values for Czech flora; Chytrý et al. 2018; indicator values for disturbance for Czech flora; Herben et al. 2016) were tested using the Spearman correlations between species scores along the constrained axis in db-RDA and their indicator values. Time and the interaction between time and protection status were used as constraining variables in the db-RDA to test for changes between the 1980s and 2022 and for different trends in protected and non-protected areas, respectively.

Results

Vegetation types and transitions between them

The expert system classified most of the historical plots as the broad-leaved semi-dry grasslands of the alliance *Cirsio-Brachypodium pinnati* or its subordinate associations *Scabioso ochroleucae-Brachypodietum pinnati* and *Polygalo majoris-Brachypodietum pinnati*. Some plots were assigned to the alliance *Bromion erecti*, which is very similar in species composition to the previous alliance. A few plots were classified as mesic grasslands (*Arrhenatherion elatioris*), narrow-leaved dry grasslands (*Festucion valesiacae*) and thermophilous fringe and tall-herb vegetation (*Geranion sanguinei*).

Although most plots were assigned to the same vegetation type in 2022 as in the 1980s, some transitions between vegetation types occurred (Fig. 2). Mainly in non-protected areas, some dry grasslands changed to more mesophilous vegetation types: narrow-leaved dry grasslands (*Festucion valesiacae*) became broad-leaved semi-dry grasslands (*Cirsio-Brachypodium pinnati*) and broad-leaved dry grasslands (*Cirsio-Brachypodium pinnati* and *Bromion erecti*) became mesic grasslands (*Arrhenatherion elatioris*). In addition, some types of xerophilous ruderal vegetation (*Dauco carotae-Melilotion* and *Convolvulo arvensis-Elytrigion repentis*) that were not recorded in the 1980s appeared in the non-protected areas.

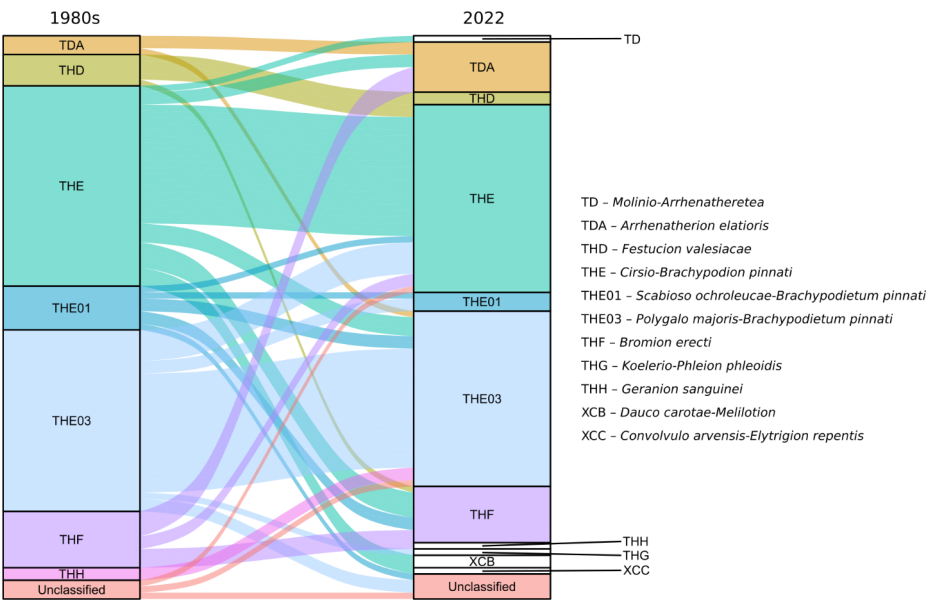


Fig. 2 Transitions between vegetation types

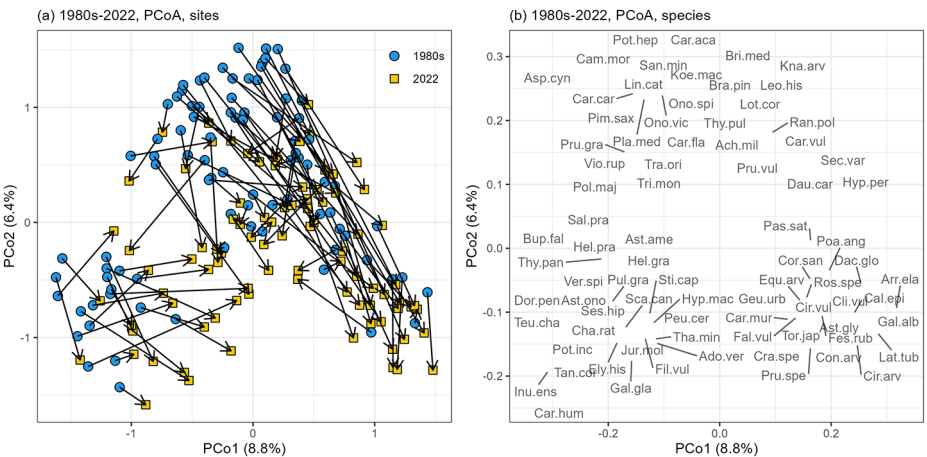


Fig. 3 Unconstrained ordination (PCoA) with positions of sites (a) and species (b). Eigenvalues for the first and second ordination axes are 5.378 and 3.896, respectively. Species names are abbreviated to the first three letters of the genus name and species epithet (see Appendix S3 for full names). Only the 80 best-fitting species were displayed

Changes in species composition and richness

The changes in species composition of individual plots are shown in Fig. 3. The constrained ordination revealed a significant change in species composition between the 1980s and 2022 ($p=0.001$, eigenvalue of the constrained axis=1.793, proportion of explained varia-

tion=2.9%) and significantly differing trends of changes in protected and non-protected areas ($p=0.001$, eigenvalue of constrained axis=0.439, proportion of explained variation=0.7%). Significantly decreasing and increasing species are listed in Table 1 and, with separation between protected and non-protected areas, in Appendix S4. Many dry-grassland specialists (e.g. *Bupleurum falcatum*, *Linum catharticum*, *Prunella grandiflora*), including some light-demanding species (e.g. *Asperula cynanchica*, *Carex caryophylla*, *C. humilis*, *Potentilla heptaphylla*) and Red-List species (Grulich 2017; e.g. *Campanula moravica*, *C. sibirica*, *Pulsatilla grandis*) declined. In contrast, there was an increase in woody species (e.g. *Cornus sanguinea*, *Crataegus* sp., *Prunus* sp., *Rosa* sp.), forest herbs (e.g. *Brachypodium sylvaticum*, *Clinopodium vulgare*, *Viola riviniana*) and species with a ruderal tendency (e.g. *Agrimonia eupatoria*, *Cirsium arvense*, *Geum urbanum*).

Temporal beta diversity indices indicated large shifts in species composition and the community dominance structure. The dissimilarity due to species losses prevailed over the dissimilarity due to species gains in 64% of the plots (Jaccard index, $p=0.001$). In contrast, more gains than losses in abundance occurred in 52% of the plots, but this difference was not significant (Ružička index, $p=0.329$).

Both species richness (Fig. 4a) and proportion of threatened species (Fig. 4b) decreased significantly over time in the dataset ($p<0.001$), with no significant difference between protected and non-protected areas. Instead, trends in the proportion of specialists were clearly different between protected and non-protected areas (Fig. 4c). While the proportion of specialists decreased in the entire dataset ($p<0.001$), a significantly greater decrease was observed in non-protected areas ($p=0.005$). The proportion of alien species (Fig. 4d) was significantly higher in non-protected areas ($p<0.001$) and significantly increased in the whole dataset ($p<0.001$) between the 1980s and 2022. Ten of the alien species present in the dataset are considered invasive according to Pyšek et al. (2022): *Arrhenatherum elatius*, *Bromus sterilis*, *Cirsium arvense*, *Conyza canadensis*, *Echinops sphaerocephalus*, *Erigeron annuus* agg., *Juglans regia*, *Lactuca serriola*, *Robinia pseudoacacia* and *Solidago canadensis*. *Arrhenatherum elatius* (archaeophyte) was the most common, with 39 occurrences in the 1980s and 55 in 2022. *Cirsium arvense* (archaeophyte) occurred in 5 plots in the 1980s and 16 plots in 2022, and *Erigeron annuus* agg. (neophyte) was present only in 7 plots in 2022. The other invasive species occurred in fewer than 5 plots.

Indicator values for light, temperature and disturbance frequency decreased significantly, while indicator values for moisture and nutrients increased (Table 2). There was no significant trend in indicator values for soil reaction and disturbance severity. The only different trend between protected and non-protected areas was a significantly higher increase in the indicator value for nutrients in non-protected areas.

Discussion

The vegetation of semi-dry grasslands in the Central Moravian Carpathians has undergone significant changes in species composition over the last four decades. The species richness and the proportion of semi-dry grassland specialists (typically xerophilous and light-demanding species) and Red-List species decreased. In contrast, competitively strong species with high demands for moisture and nutrients spread along with woody species,

causing a decline in habitat quality and a shift from semi-dry to mesic grasslands. The proportion of alien species also increased, with some invasive species becoming more frequent.

Effects of abandonment and lack of management

The main cause of the changes in species composition and species richness of the semi-dry grasslands studied appears to be the lack of management and ongoing succession, as indicated by the decrease in disturbance frequency indicator values. Similar changes in the species composition of semi-dry grasslands after abandonment of traditional management have been found in several studies across Europe (e.g. Jandt et al. 2011; Giarrizzo et al. 2017; Diekmann et al. 2014, 2019; Rendeková et al. 2020; Ridding et al. 2020; Meier et al. 2021). Changing habitat conditions after abandonment lead to increasing litter accumulation, retention of nutrients in the ecosystem and increasing biomass (Kanianska et al. 2017; Jernej et al. 2019; Bohner et al. 2019). The resulting higher amounts of nutrients and moisture in the soil and lower light availability in taller and denser vegetation support the spread of nutrient-demanding and mesophilous species over light-demanding and thermophilous habitat specialists (Jacquemyn et al. 2003; Kelemen et al. 2014; Jernej et al. 2019). Declines in species richness may also be related to the intermediate disturbance hypothesis (Huston 1979): infrequent disturbance leads to the spread of competitively stronger species, the exclusion of weaker competitors and a decrease in species richness (Dupré and Diekmann 2001; Jacquemyn 2003).

Decline in thermophilous species

Given the significant rise in temperature between the period before the initial survey and the period before the resurvey, we observed an unexpected decline in thermophilous species. This result does not support the first hypothesis that climate change contributes to changes in species diversity in semi-dry grasslands. However, this can be explained by the positive correlation of Ellenberg-type indicator values for temperature, light and disturbance frequency in our dataset (Appendix S5). Indicator values for temperature were also negatively correlated with values for moisture and nutrients. In the study area, species with higher Ellenberg-type indicator values for temperature are often xerophilous S-strategists. Their decline is related to the effects of abandonment and ongoing natural succession, which supports species with higher demands for moisture and nutrients against xerophilous, light-demanding and thermophilous species. Abandonment appears to be a stronger driver of changes in species composition than global warming (Diekmann 2019; Rendeková et al. 2020). Future studies should examine community response to global warming using microclimatic data, as microclimatic conditions may buffer macroclimatic changes (Lenoir 2013, 2017).

Effects of eutrophication

Increasing Ellenberg-type indicator values for nutrients may also indicate the effects of eutrophication caused by nutrient enrichment from the atmosphere and fertilisers applied to adjacent arable land. This supports the hypothesis that eutrophication contributes to the changes in semi-dry grasslands. Increased nitrogen supply has been identified as a major

Table 1 Increasing and decreasing species in the entire dataset determined by db-RDA with time as the constraining variable and plot identity as a covariate; Red List categories CR, EN, VU and NT (Grulich 2017) and alien species (Ar – archaeophyte, Neo – neophyte; Pyšek et al. 2022) are given in brackets after the species names; semi-dry grassland specialists (species diagnostic for the *Cirsio-Brachypodium pinnati* (THE) and *Bromion erecti* (THF) alliances; Chytrý 2007) are given in bold; species are sorted from the highest to the lowest strength of the trend (species with $p < 0.001$ are sorted alphabetically due to the limitation of the permutation test); *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$

Decreasing species	Increasing species
<i>Asperula cynanchica</i> ***	<i>Agrimonia eupatoria</i> ***
<i>Bupleurum falcatum</i> ***	<i>Allium oleraceum</i> ***
<i>Campanula moravica</i> (NT) ***	<i>Arrhenatherum elatius</i> (Ar) ***
<i>Campanula sibirica</i> (NT) ***	<i>Astragalus glycyphyllos</i> ***
<i>Carex caryophylla</i> ***	<i>Cirsium arvense</i> (Ar) ***
<i>Carlina acaulis</i> ***	<i>Clinopodium vulgare</i> ***
<i>Leontodon hispidus</i> ***	<i>Cornus sanguinea</i> ***
<i>Linum catharticum</i> ***	<i>Crataegus</i> sp. ***
<i>Ononis spinosa</i> ***	<i>Dactylis glomerata</i> ***
<i>Picris hieracioides</i> ***	<i>Fragaria viridis</i> ***
<i>Pilosella bauhini</i> ***	<i>Lathyrus tuberosus</i> (Ar) ***
<i>Pimpinella saxifraga</i> ***	<i>Ligustrum vulgare</i> ***
<i>Plantago media</i> ***	<i>Prunus</i> sp. ***
<i>Potentilla heptaphylla</i> ***	<i>Rosa</i> sp. ***
<i>Pulsatilla grandis</i> (VU) ***	<i>Trisetum flavescens</i> ***
<i>Seseli annuum</i> (NT) ***	<i>Veronica chamaedrys</i> agg. ***
<i>Veronica spicata</i> ***	<i>Geum urbanum</i> **
<i>Carex humilis</i> (NT) **	<i>Viola hirta</i> **
<i>Koeleria macrantha</i> K. <i>pyramidata</i> **	<i>Acer campestre</i> **
<i>Salvia pratensis</i> **	<i>Rhamnus cathartica</i> **
<i>Acinos arvensis</i> **	<i>Brachypodium sylvaticum</i> **
<i>Potentilla incana</i> (NT) **	<i>Tilia cordata</i> **
<i>Artemisia campestris</i> **	<i>Bromus erectus</i> **
<i>Seseli hippomarathrum</i> (NT) **	<i>Chamaecytisus ratisbonensis</i> (NT) *
<i>Prunella grandiflora</i> (NT) *	<i>Gentiana cruciata</i> (EN) *
<i>Sanguisorba minor</i> *	<i>Inula salicina</i> (NT) *

Table 1 (continued)

Decreasing species	Increasing species
<i>Helianthemum grandiflorum</i> subsp. <i>obscurum</i> *	
<i>Euphrasia officinalis</i> var. <i>rozkoviana</i> *	<i>Erigeron annuus</i> agg. (Nco) *
<i>Viola rupestris</i> (NT) *	<i>Lithospermum officinale</i> (VU) *
<i>Campanula glomerata</i> *	<i>Rubus caesius</i> *
<i>Linum tenuifolium</i> (NT) *	<i>Viola riviniana</i> *
<i>Melilotus albus</i> (Ar) *	<i>Geranium pratense</i> *
<i>Tragopogon orientalis</i> *	
<i>Hypericum perforatum</i> *	
<i>Euphrasia stricta</i> subsp. <i>stricta</i> *	
<i>Centaurea scabiosa</i> *	
<i>Orchis militaris</i> (EN) *	
<i>Scabiosa canescens</i> (NT) *	
<i>Campanula rapunculoides</i> *	
<i>Leucanthemum vulgare</i> agg. *	
<i>Carlina vulgaris</i> agg. *	
<i>Veronica prostrata</i> *	
<i>Daucus carota</i> *	

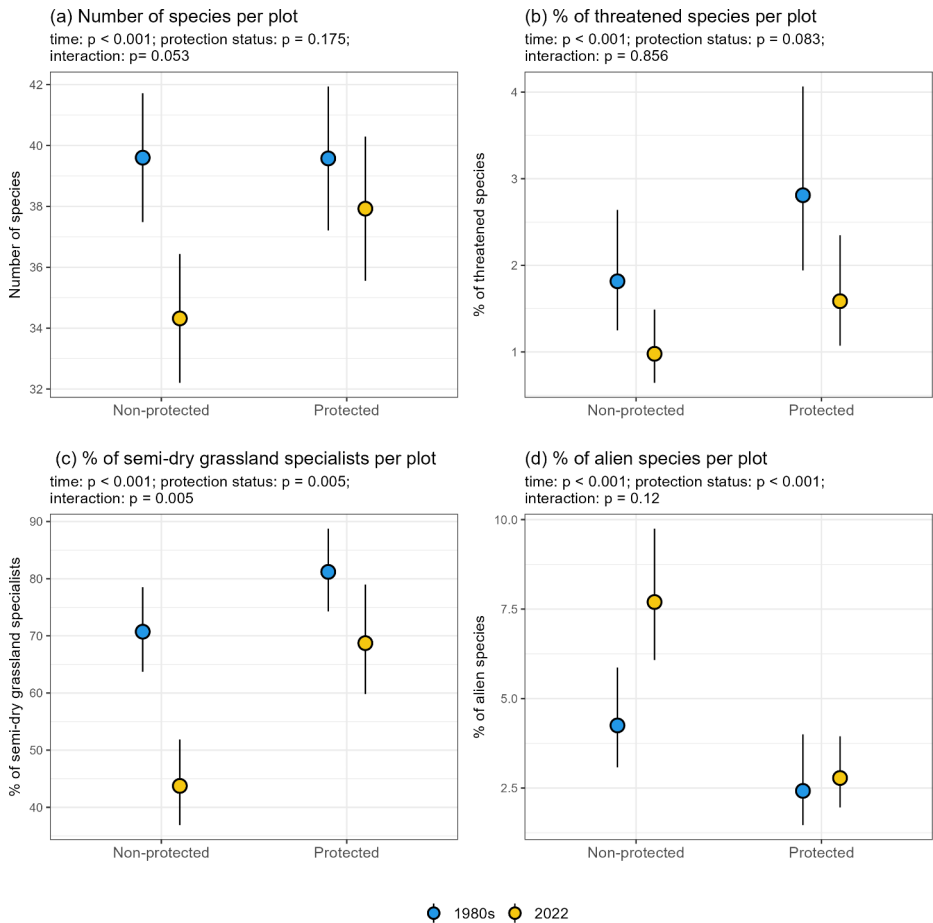


Fig. 4 Comparison of number of species and proportions of species groups between the 1980s and 2022 in protected and non-protected areas, points represent means and lines 95% confidence intervals. **(a)** Number of species ($n=90$); **(b)** Proportion of threatened species (IUCN categories CR, EN and VU (Grulich 2017); $n=90$); **(c)** Proportion of semi-dry grassland specialists (species diagnostic for the *Cirsio-Brachypodium pinnati* (THE) and *Bromion erecti* (THF) alliances (Chytrý 2007); $n=77$); **(d)** Proportion of alien species (Pyšek et al. 2022; $n=90$)

cause of a decrease in species richness and habitat specialists in European dry grasslands in several studies (e.g., Bobbink et al. 1998; Stevens et al. 2004; Diekmann et al. 2014). However, it is difficult to separate the effects of eutrophication and land-use change, as both factors support the increase of stronger competitors and competitive exclusion of grassland specialists and rare species (Huston 1979; Bobbink and Willems 1987; Jacquemyn et al. 2003). It is likely that both factors jointly contribute to changes in vegetation composition and reinforce each other's effects (Jacquemyn et al. 2003; Jandt et al. 2011; Diekmann et al. 2019; Ridding et al. 2020).

Table 2 Changes in species indicator values between the 1980s and 2022 and differences in trends between protected and non-protected areas; significant results are in bold

Indicator value	Change between the 1980s and 2022				Different trends in protected (Pr) and non-protected (NPr) areas			
	Trend	Correlation coefficient (Rho)	Test statistic (S)	p-value	Trend	Correlation coefficient (Rho)	Test statistic (S)	p-value
Light	↓	-0.335	8,070,831	<0.001		0.072	5,445,275	0.265
Temperature	↓	-0.165	7,042,680	0.003		-0.024	6,186,353	0.670
Moisture	↑	0.357	3,889,184	<0.001		-0.079	6,522,960	0.150
Soil Reaction		-0.082	6,541,746	0.135		0.080	5,562,928	0.148
Nutrients	↑	0.413	3,546,248	<0.001	Pr<NPr	-0.167	7,053,386	0.002
Disturbance frequency	↓	-0.249	5,076,868	<0.001		0.114	3,602,524	0.053
Disturbance severity		0.049	3,865,063	0.404		-0.055	4,289,800	0.348

Less pronounced changes in protected areas

As the environment in the study area is relatively homogeneous, more pronounced changes in vegetation composition outside of protected areas suggest a stronger effect of land abandonment than landscape eutrophication. This supports our second hypothesis, but it is worrying that habitat specialists and threatened species are also declining in protected areas, where conservation management has been introduced to maintain semi-dry grassland diversity. Similar trends were observed in resurvey studies of dry grasslands in other European countries (e.g., Timmermann et al. 2015; Boch et al. 2019; Diekmann et al. 2019; Bauer and Albrecht 2020; Rendeková et al. 2020). The reason can be that management practices in protected areas are insufficient or inappropriate. Unlike mowing, extensive grazing helps maintain the diversity of semi-dry grasslands not only by biomass reduction but also by selective defoliation, trampling, creating gaps suitable for seed germination and transport of seeds (Rook et al. 2004; Metera et al. 2010). Widespread shift from traditional grazing to mowing, the environmental homogenisation resulting from cutting the whole area at the same time by machine mowers and less frequent interventions (as suggested by lower indicator values for disturbance frequency) likely cause losses of some species. In addition, eutrophication may have worsened the trend so that management intensity is no longer sufficient to slow succession or control the spread of nutrient-demanding species (Jacquemyn et al. 2003; Diekmann et al. 2019).

As hypothesised, many habitat specialists appeared among the declining species. Their decline, as well as the decline of threatened species, may result from an extinction debt, suggesting that species with low competitive ability may become extinct with a time lag even in the absence of current habitat destruction or deterioration (Tilman et al. 1994; Mitchell et al. 2017; Löffler et al. 2020). In the past, semi-dry grasslands occupied much larger areas in the Central Moravian Carpathians (Skokanová et al. 2009; Mackovčín 2011). Large areas probably supported functioning metapopulations of specialist species, although semi-dry grasslands were fragmented. The decline in habitat area of semi-dry grasslands may have caused some metapopulations to become dysfunctional and, consequently, specialist species are slowly going extinct at individual sites, although grasslands in protected areas are well

managed in most cases. If this is true, conservation measures and subsidised management can slow but not stop the decline of these specialists and threatened species. To sustain the plant diversity of semi-dry grasslands and the functioning of metapopulations of specialised species, restoration of semi-dry grassland patches at suitable sites and an increase of connectivity of fragmented grasslands may be needed.

Conclusion

The species composition of semi-dry grasslands in the Central Moravian Carpathians has changed significantly over the last four decades. The species richness of the communities has decreased, and the habitats have also lost a significant proportion of semi-dry grassland specialists (typically xerophilous and light-demanding species) and/or threatened species (Grulich 2017). On the other hand, competitively stronger species with higher nutrient and moisture requirements spread along with juvenile shrubs, causing a shift toward more mesophilous communities. These changes in species composition were more pronounced in non-protected areas, suggesting that the primary driver of these changes is natural succession in the absence of appropriate conservation management, likely supported by eutrophication. This suggests that appropriate conservation measures are needed to maintain the plant species richness and habitat quality of semi-dry grassland communities.

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Author contributions BT conducted the field survey in the 1980s and KK conducted the resurvey in 2022, KK analysed the data under the supervision of MC and MGS and prepared the first draft of the manuscript, all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Data Availability The data and R code used for the analysis are available in the GitHub repository (https://github.com/klaralink/SMor_semi-dry_grass_change.git) preserved at Zenodo (<https://doi.org/10.5281/zenodo.10060598>). The data are also stored in the ReSurveyEurope database (<http://euroveg.org/eva-database-re-survey-europe>).

Declarations

Competing interests The authors declare no competing interests.

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