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# Vegetation remains, specialist species fade: changes in Pannonian sand grasslands

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**Abstract:** Inland sand grasslands are highly threatened habitats in central Europe and the Pannonian biogeographical region. They harbour several specialized and threatened species adapted to the dry, nutrient-poor conditions of sandy soils. The area of these grasslands decreased dramatically in the 19th and 20th centuries. Many remaining patches have been included in protected areas, and their conversion to other land-use types has been limited in recent decades. However, changes in these plant communities may have occurred due to environmental changes and altered management practices. To assess temporal changes in plant diversity and species composition in sand grasslands in the Vienna Basin (Czech Republic, Slovakia and Austria), we resurveyed 86 vegetation plots in 2023–2024 that were first sampled between 1952 and 2010. We compared changes in species composition using principal coordinate analysis and distance-based redundancy analysis. We tested changes in species richness of vascular plants using a linear mixed-effect model, proportions of specialized, ruderal, threatened, alien and woody species using generalized estimating equation models, and ecological indicator values using permutation tests. We compared these changes among three main vegetation types of sand grasslands (pioneer, acidophilous and basiphilous). The results indicate that the main types of sand grasslands in the Vienna Basin have persisted over recent decades and have not been replaced by other vegetation types. However, specialized species of sand and dry grasslands, as well as species adapted to grazing, have declined. In contrast, species with higher nutrient and moisture requirements have increased. This indicates an effect of eutrophication and natural succession following the abandonment of previous management. The decline in sand specialists was most pronounced in the pioneer sand vegetation, where species with higher Ellenberg-type indicator values for temperature also decreased, indicating a transition to more closed sand grasslands. These results indicate that appropriate conservation management and future monitoring are needed to maintain the habitat quality of inland sand vegetation.

**Keywords:** abandonment, alien species, eutrophication, sand grassland, sand vegetation, vascular plants, vegetation change, vegetation resurvey

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## Introduction

Sandy soils provide a habitat for many specialized and threatened species adapted to dry, nutrient-poor conditions (Jentsch & Beyschlag 2003, Chytrý 2007, Schratt-Ehrendorfer et al. 2022). Since the Neolithic, inland sand grasslands have been maintained by human activities such as grazing or occasional mowing. These small-scale disturbances are necessary to maintain plant species diversity and the dynamic stability of sand grasslands (Jentsch & Beyschlag 2003, Eichberg et al. 2007, Warren 2014). However, since the 19th century, these habitats have undergone substantial changes in management. Formerly extensive pastures were afforested with pine or *Robinia pseudoacacia* plantations, and only small remnants of sand grasslands remained at managed sites, e.g. along railway lines or in military training areas (Biró et al. 2013, 2018, Vítková et al. 2017). As a result, pioneer sand vegetation and sand grasslands have become highly threatened habitats in Europe (Janssen et al. 2016, Chytrý et al. 2019). To preserve these communities, some sites have been declared protected areas in recent decades, and conservation management has been introduced to maintain habitat quality (Wiesbauer & Mazzucco 1997, Molnár 1998, Mackovčin et al. 2007). However, despite conservation efforts, the transition from traditional management may be accompanied by alterations or a lack of an appropriate disturbance regime, which can result in declining habitat quality (Jentsch et al. 2009).

In addition to land-use changes, sand grasslands are currently facing further challenges. Firstly, their specific, low-productive plant communities adapted to nutrient-poor soils are increasingly threatened by nutrient inputs from atmospheric nitrogen deposition and fertilizer spill-over from adjacent arable land (Bobbink et al. 1998, 2010, Jentsch et al. 2009). Eutrophication accelerates succession and favours the spread of strong competitors at the expense of stress-tolerant specialists (Süß et al. 2004). Secondly, climate changes, particularly rising temperatures and extreme climatic events, such as spring and summer droughts (Dai 2011, 2013, Spinoni et al. 2018), may also result in changes in species composition in dry habitats (Fischer et al. 2020, Orbán et al. 2023). Moreover, sandy habitats are highly threatened by the spread of alien species (Axmanová et al. 2021), which may also affect their species diversity (Hejda et al. 2009).

Several studies on temporal changes in central-European dry grasslands report a decline in dry grassland specialists associated with an increase in competitive mesophilous and nutrient-demanding species (e.g. Duprè et al. 2010, Hülber et al. 2017, Diekmann et al. 2019, Harásek et al. 2023, Klinkovská et al. 2024b). Inland sand habitats have been studied much less (but see e.g. Körmöczi 1991, Süss et al. 2010). However, given their vulnerability, analyses of temporal changes in these habitats are needed.

The Vienna Basin on the north-western border of the Carpathian (Pannonian) Basin is a unique model area with a historically large extent of sand grasslands (Krippelová & Krippel 1956, Šmarda 1961, Wiesbauer 2002). Due to different sediment origins, acidophilous sand vegetation has developed in the northern and eastern parts of the Vienna Basin, while basiphilous sand grasslands occur on base-rich soils in the western part (Valachovič et al. 1995, Chytrý 2007, Zuna-Kratky et al. 2009). Thus, it is possible to compare temporal trends in sand vegetation on different substrates.

In this study, we investigate changes in pioneer sand vegetation, closed acidophilous and ruderalized sand grasslands, and closed basiphilous sand grasslands in the Vienna Basin over the past decades. In 2023–2024, we resurveyed vegetation plots that were first sampled between 1952 and 2010. The aim was to determine: (i) How the diversity and species composition of sand vegetation have changed over time? (ii) Have these changes differed across vegetation types? (iii) Has there been a pronounced spread of alien species into sand vegetation?

## Materials and methods

### *Study area*

The study area is in the Vienna Basin in the borderland of Austria, Slovakia and the Czech Republic (48°12'–48°58'N, 16°39'–17°19'E; Fig. 1). The flat lowland landscape of the basin is formed by different Neogene and Quaternary sediments, including loess, alluvial sediments and aeolian sand (Baňacký et al. 1996, Fordinál et al. 2012, Czech Geological Survey 2024a, GeoSphere Austria 2024). Our sampling was conducted on sandy sediments at altitudes between 140 and 230 m a.s.l. in the northern and eastern part of the study area (Czechia and Slovakia). Acidic arenosols and arenic cambisols have developed on these sediments (Czech Geological Survey 2024b, Hraško et al. 2024). West of the Morava river in Austria, alkaline soils with a high base content have formed on calcareous sediments (Bundesforschungszentrum für Wald 2024). Climatically, this area belongs to the warmest and driest in central Europe. The mean annual temperature at the nearby weather station in Strážnice was 8.7 °C in 1961–1970, 9.5 °C in 1993–2002 and 10.5 °C in 2013–2022. The total annual precipitation at the Bzenec station was 587 mm in 1961–1970, 557 mm in 1993–2002 and 535 mm in 2013–2022. Changes in mean annual temperatures and total annual precipitation since the 1960s suggest a shift towards a warmer climate over the last six decades (Supplementary Fig. S1, Czech Hydrometeorological Institute 2024a, b).

In the early Holocene, sand grassland vegetation in this area likely occurred in a mosaic of sparse forests dominated by pine (*Pinus sylvestris*) and birch (*Betula pendula*) (Kuneš et al. 2015). *Quercus robur,* documented in the study area as early as the last glacial period (Hošek et al. 2024), gradually increased during the Holocene, forming denser forests that were not suitable for all grassland specialists. However, some open pine forests persisted on sandy soils (Kuneš et al. 2015), supporting the continuity of open patches. Since the Neolithic, the area has been settled, and open areas and sparse forests were grazed (Kuneš et al. 2015). From the 14th to the late 18th century, open forests were maintained by grazing, coppicing and hay-cutting (Jamrichová et al. 2013). The vegetation of open sand areas reached its greatest extent in the late 18th and early 19th centuries, when the sandy areas were mostly deforested and only covered with sparse trees and shrubs. Since the 19th century, pastures and woodlands have become separated (Jamrichová et al. 2013). At the same time, gradual afforestation with pine trees and the conversion of pastures to arable fields took place (Krippelová & Krippel 1956, Krippel & Ružička 1959, Šmarda 1961, Wiesbauer 2002). Currently, only remnants of open sand grasslands remain, which are threatened by encroaching grasses and woody plants (Mackovčin et al. 2007, Zuna-Kratky et al. 2009).

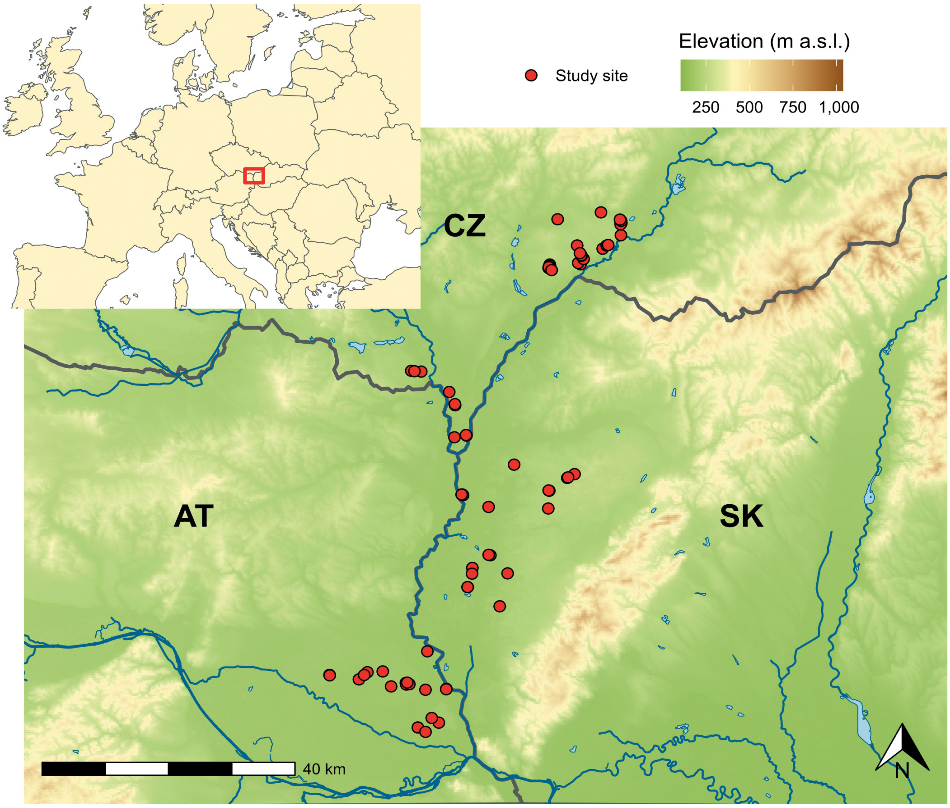

**Fig. 1.** Sites of the resurveyed vegetation plots.

### *Data acquisition*

To assess changes in sand vegetation over time, we resurveyed 86 historical vegetation plot records from multiple sources (Supplementary Table S1). The historical vegetation plots were first sampled between 1952 and 2010, with most of them sampled in 1994–1997 (n = 30) and 2001–2006 (n = 42). The resurvey was carried out in 2023–2024. We aimed to resample the vegetation plots at approximately the same phenological phase as originally recorded, but for some historical plots, information about the exact sampling date was unavailable. Therefore, we conducted the repeated sampling early in the season, which is the optimal phenological phase for surveying sand vegetation. During the second sampling, we attempted to relocate the historical plots as accurately as possible using geographical coordinates where available, original locality descriptions, and information on slope, aspect and altitude. Because the historical plots were not precisely georeferenced, we applied a conservative approach common in many resurvey studies, using species lists with abundance information from the first survey to select similar vegetation for resurvey. Of the 86 resurveyed plots, 45 were in the Czech Republic, 20 in Slovakia and 21 in Austria. We measured the geographical coordinates of each plot using GPS with a location uncertainty of 2–5 m. In 2024, most plots were also located using a GPS with an accuracy of approximately 5 cm (Topcon HiPer SR or Topcon HiPer HR) at each corner of the plot. In this way, we established a network of permanent plots for vegetation monitoring. The size and shape of the plots varied among the different sources of historical vegetation plots. Most plots were squares of 16 $m^2$ in the Czech Republic, 25 $m^2$ in Slovakia and 100 $m^2$ in Austria. During the resurvey, we always used the same plot size as in the first sampling. The percentage cover of each vascular plant species was estimated. The method of estimating cover differed depending on the source. The cover was either estimated using a cover scale, typically the seven-grade or nine-grade Braun-Blanquet scale (Westhoff & van der Maarel 1978), or in percentages.

### *Data analysis*

Vegetation-plot records from all sources were digitized using the Turboveg 2 program (Hennekens & Schaminée 2001). We standardized the taxonomic concepts and nomenclature according to the Czech excursion flora (Kaplan et al. 2019), and for taxa not occurring in the Czech Republic, we followed the Euro+Med PlantBase (Euro+Med 2025). We merged some species into aggregates to minimize false differences in species composition (pseudo turnover) caused by the different taxonomic concepts used in different sources (Supplementary Table S2). Prior to the analysis, we transformed the different cover scales into the seven-grade Braun-Blanquet scale, which uses fewest cover classes. Then, we converted the cover classes to percentages as the mean value of each cover class interval and square-rooted the percentage values (Tichý et al. 2020). Bryophytes and lichens were excluded from the analysis because of inconsistent sampling in different historical vegetation plots. Covers of woody species occurring in multiple layers were merged. To account for possible phenological differences due to sampling at different times of the vegetation season in the first and second surveys, we excluded from the analysis all annuals and vernal geophytes that might not be visible later in the season (Supplementary Table S3). This resulted in the exclusion of 60 species in the pioneer sand vegetation (36% of the species pool of this vegetation type, 38% of individual species records), 66 species (24%, 23%) in the closed acidophilous sand grasslands and ruderalized sand grasslands and 48 species (23%, 14%) in the basiphilous sand grasslands. In accordance with common practice in resurvey studies (Knollová et al. 2024), we hereafter refer to the pairs of vegetation-plot records from different time periods as a “plot” and the individual plot records as “observations”.

To test for differences in temporal changes among vegetation types, we classified the old plot observations using the Isopam algorithm (Schmidtlein et al. 2010) into three vegetation types interpreted as alliances of the national vegetation classifications (Mucina et al. 1993, Valachovič et al. 1995, Chytrý 2007) (Fig. 2): (i) pioneer sand vegetation with *Corynephorus canescens* (*Corynephorion canescentis*, n = 29), (ii) closed acidophilous sand grasslands and ruderalized sand grasslands (*Armerion elongatae,* n = 40), and (iii) closed basiphilous sand grasslands (*Festucion valesiacae*, n = 17).

To visualize changes in species composition, we calculated a principal coordinate analysis (PCoA) of all (both old and new) plot observations using square root-transformed Bray-Curtis dissimilarities. To test the significance of changes in species composition over time, we performed distance-based redundancy analysis (db-RDA) with the same dissimilarity measure as used in the PCoA. We used time (number of years since the

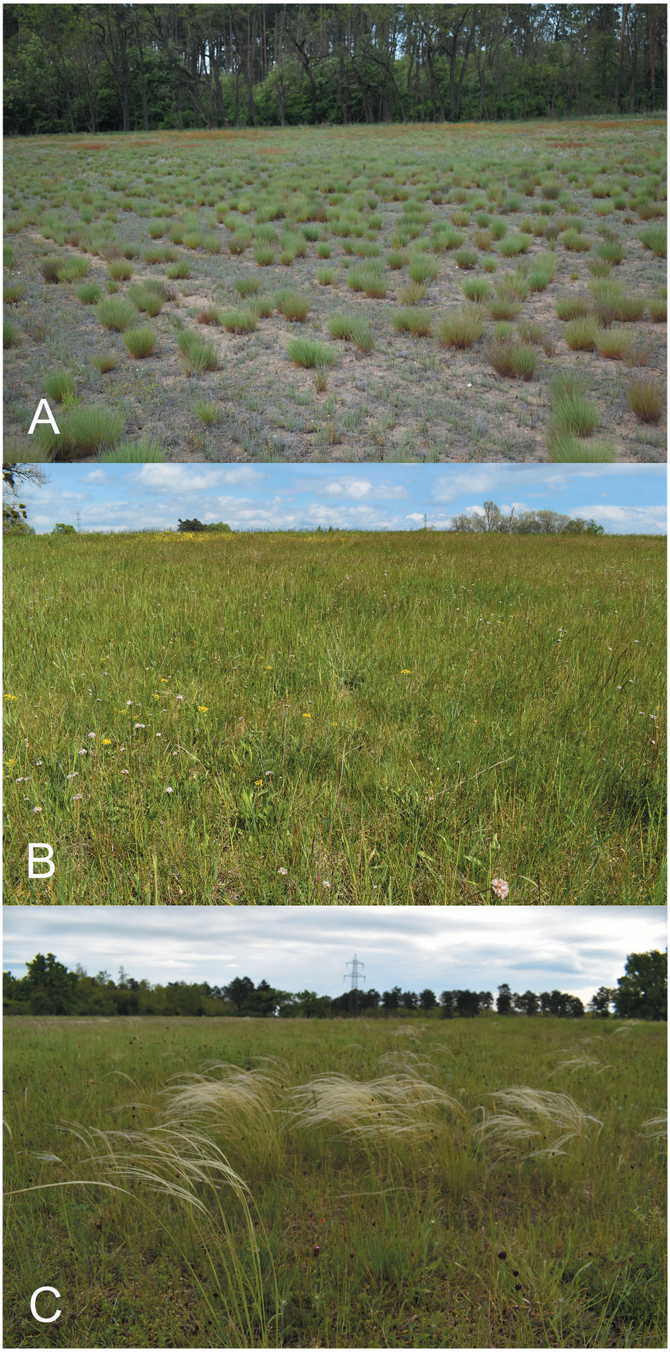

**Fig. 2.** Vegetation types studied: (A) pioneer sand vegetation (*Corynephorion canescentis*) dominated by *Corynephorus canescens* on an abandoned field near Lakšárska Nová Ves, SK, (B) closed acidophilous and ruderalized sand grasslands (*Armerion elongatae*) in the Nature Reserve Písečný rybník near Milotice, CZ, and (C) closed basiphilous sand grasslands (*Festucion valesiacae*) with *Stipa pennata* in the Nature Reserve Weikendorfer Remise, AT.

first survey of each plot) as the constraining (explanatory) variable, and plot identity as a covariate. We tested the significance of changes in species composition between old and new plot observations using a permutation test with 999 permutations of observations within blocks defined by plot identity. We determined significantly increasing and decreasing species by testing the significance of the relationship of individual species to the time-constrained axis of the db-RDA, using a permutation test with 999 permutations within blocks defined by plot identity. All ordination analyses were performed for the whole dataset and for each vegetation type separately.

To account for the different plot sizes when comparing species richness per plot, we fitted species-area curves in log-log space and used the estimated number of species per 25 $m^2$ as a measure of species richness. We tested for differences in species richness between the old and new observations using a linear mixed-effect model with time as a predictor and plot identity as a random effect, coded as an intercept term.

In addition, we tested changes in the proportion of different species groups using a generalized estimating equations model, assuming a binomial error distribution, with time, vegetation type and their interaction as predictor variables. If the interaction was not significant, the model was fitted with only time and vegetation type as predictors. Sand specialists were defined as species diagnostic for the phytosociological classes *Koelerio-Corynephoretea* and *Festucetea vaginatae* and their subordinate units according to national vegetation classifications (Mucina et al. 1993, Valachovič et al. 1995, Chytrý 2007) and the corresponding habitat types according to Chytrý et al. (2010) and Šuvada (2023). Dry grassland specialists were defined as species diagnostic for the phytosociological alliances *Koelerio-Phleion phleoidis* and *Festucion valesiacae* and their subordinate units according to the same sources. Species diagnostic for the phytosociological classes *Polygono arenastri-Poëtea annuae*, *Bidentetea tripartiti*, *Stellarietea mediae*, *Artemisietea vulgaris*, *Galio-Urticetea* and *Epilobietea angustifolii* and their subordinate units were considered ruderal species. Threatened species were defined as those assigned to the categories CR (Critically Endangered), EN (Endangered), VU (Vulnerable) and G (Threatened) according to national Red List assessments (Eliáš et al. 2015, Grulich 2017, Schratt-Ehrendorfer et al. 2022). As alien species, we considered those classified as alien (both archaeophytes and neophytes) in the national checklists of alien plants (Medvecká et al. 2012, Pyšek et al. 2022, Glaser et al. 2025). For threatened and alien species, the checklist for the respective country was used for each plot. Woody species were defined as those classified as trees or shrubs according to Dřevojan (2020).

Because the time intervals between the first survey and the resurvey varied, we tested the relationship between interval length and the magnitude of change. This was done only for pioneer sand vegetation, where interval lengths ranged from 14 to 72 years. In contrast, acidophilous and ruderalized sand grasslands were resampled after 17–30 years, and all basiphilous grasslands were resampled after 27–28 years, limiting the effect of different time intervals. We tested the effect of interval length on the magnitude of changes in species composition using a linear model, with Bray-Curtis dissimilarity between the old and new observations of the same plot as the response variable, and the number of years between the first survey and the resurvey as the predictor. The effect of the interval length on changes in species richness was tested using a linear model with the difference in the estimated number of species per 25 $m^2$ between the old and new plot observations as the response variable and interval length as the predictor. Similarly, we fitted linear models with the difference in the proportion of sand specialists, dry grassland specialists, ruderal, threatened, alien and woody species as response variables and interval length as the predictor to test the effect of interval length on these variables.

We tested differences in unweighted mean Ellenberg-type indicator values (Tichý et al. 2023) and disturbance indicator values for European plant species (Midolo et al. 2023) between old and new plot observations using repeated measures ANOVA. Row-based (randomization of observations within plots) and column-based (randomization of indicator values for species before calculating plot observation means) tests were calculated using 999 permutations. The higher P-value of the two tests was considered (max test). The tests were calculated for the whole dataset and for each vegetation type separately.

Data analysis was performed in R (R Core Team 2023) with the packages isopam (Schmidtlein et al. 2010), vegan (Oksanen et al. 2022), lmerTest (Kuznetsova et al. 2017), geepack (Yan 2002, Yan & Fine 2004, Højsgaard et al. 2006) and weimea (Zelený 2021). For data handling, we used the tidyverse collection of packages (Wickham et al. 2019), readxl (Wickham & Bryan 2023), broom (Robinson et al. 2023) and janitor package (Firke 2023). Figures were created using functions from the tidyverse package ggplot2 (Wickham 2009) and patchwork package (Pedersen 2024).

The data and R code used for the analysis are available in the GitHub repository (https://github.com/klaraklink/Pannonian_sand_veg_change), which is preserved at Zenodo (https://doi.org/10.5281/zenodo.16258179). The data are also stored in the ReSurvey-Europe database (CZ_0039, Knollová et al. 2024; https://euroveg.org/resurvey/).

## Results

Temporal changes in the species composition of the sand vegetation are shown in Fig. 3. The strongest gradient in species composition (1st axis) reflects the differences between open pioneer sand grasslands and closed sand grasslands. Many plots initially assigned to pioneer sand vegetation shifted in species composition towards closed acidophilous and ruderalized sand grasslands, while a few plots changed in the opposite direction. Some acidophilous sand grasslands shifted towards vegetation with a higher abundance of competitive *Calamagrostis epigejos*. However, overall changes in species composition of both acidophilous and ruderalized sand grasslands and basiphilous sand grasslands were less pronounced and followed different directions (Supplementary Fig. S2). We found a significant change in species composition at the plot level when tested for the whole dataset and for each vegetation type separately (db-RDA, $P < 0.001$). Several specialized species of sand and dry grassland vegetation (e.g. *Cynodon dactylon*, *Jasione montana*, *Pimpinella saxifraga*, *Seseli annuum*, *Thymus serpyllum*) decreased significantly in abundance over time (Table 1). In contrast, neophytes (e.g. *Erigeron annuus*) and graminoids (e.g. *Agrostis vinealis*, *Anthoxanthum odoratum*, *Calamagrostis epigejos*, *Carex liparocarpos*, and *Poa pratensis* agg.) were among the species that increased most. We identified a significant increase in overall species richness over time, which was most pronounced in the basiphilous sand grasslands (Table 2, Fig. 4). The proportion of sand and dry grassland specialists per plot decreased over time in the whole dataset, and the decline of sand specialists was most pronounced in the pioneer sand vegetation. There were no significant changes in the proportion of ruderal and threatened species.

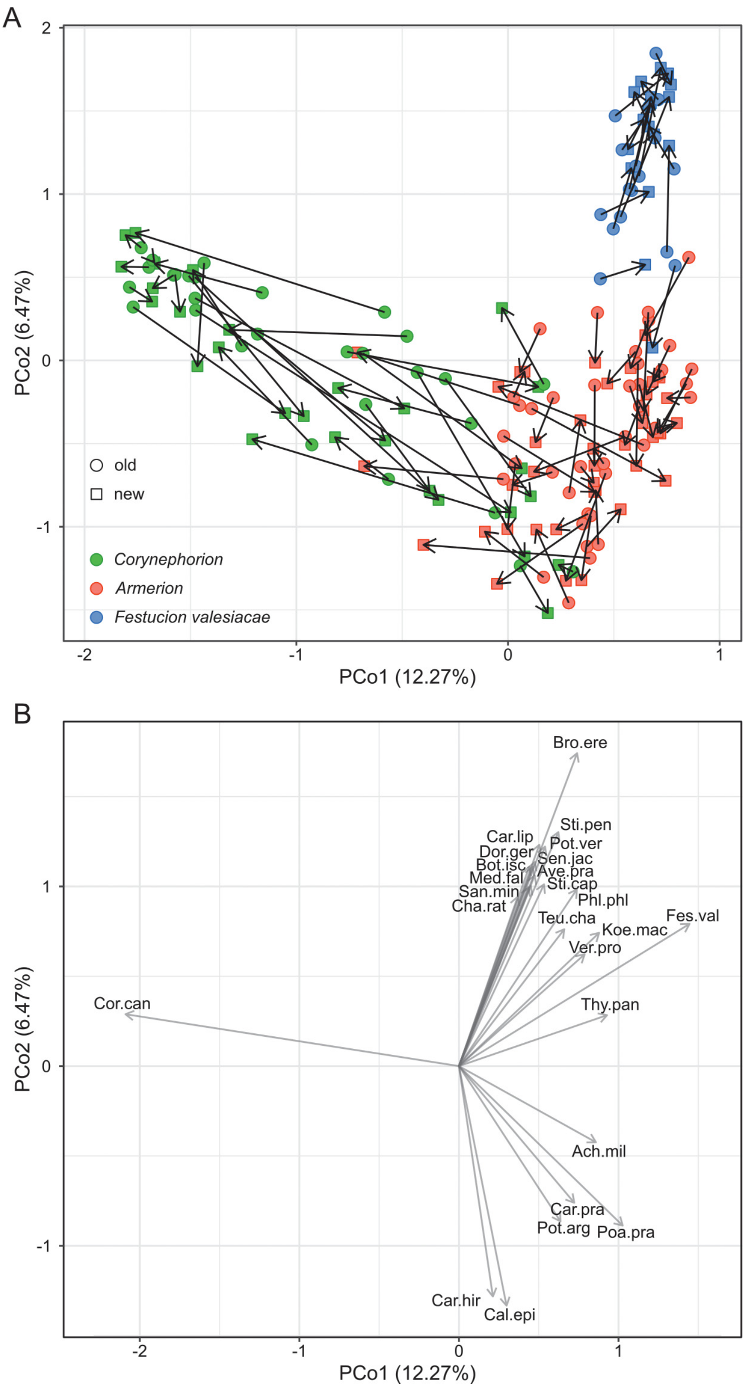

**Fig. 3.** Principal coordinate analysis (PCoA) for the whole dataset with scores for (A) sites and (B) correlations of species with ordination axes. Species names are abbreviated to the first three letters of the genus name and species epithet (see Supplementary Fig. S2 for full names). Only the 25 best-fitting species are shown.

**Table 1.** Species that significantly increased or decreased over time according to the db-RDA analysis, with time as a constraining variable and plot identity as a covariate. Species are sorted from the strongest to the weakest trend; *** P < 0.001, ** P < 0.01, * P < 0.05. Abbreviations indicate species groups: sand specialists (s), dry grassland specialists (d), ruderal species (r), alien species (Ar – archaeophyte, Neo – neophyte) and Red List species (CR, EN, VU); if the species is not classified into a given category in all three countries, the two-letter code of the country for which the classification applies follows the category assignment (AT – Austria, CZ – Czech Republic, SK – Slovakia). Frequencies of individual species in the old and new plots are listed in Supplementary Table S4.

| Whole dataset | | Pioneer sand vegetation (*Corynephorion*) | |
|---|---|---|---|
| Increasing | Decreasing | Increasing | Decreasing |
| *Calamagrostis epigejos**** (r) | *Seseli annuum*** (d, VU - AT) | *Poa pratensis* agg.*** (s, d, r) | *Cynodon dactylon*** (s, d, r, Ar) |
| *Anthoxanthum odoratum**** (d, r) | *Cynodon dactylon*** (s, d, r, Ar) | *Rumex acetosella** (s, d, r) | *Thymus serpyllum*** (s, r) |
| *Securigera varia**** (s, r) | *Thymus serpyllum** (s, r) | *Hypochaeris radicata** (s, d) | *Eryngium campestre** (s, d, r) |
| *Carex liparocarpos**** (s, VU - AT) | *Pimpinella saxifraga** (d) | | *Jasione montana** (s, d) |
| *Plantago lanceolata*** (s, d, r) | *Jasione montana** (s, d) | | |
| *Senecio jacobaea*** | *Asperula cynanchica** (d) | | |
| *Erigeron annuus*** (r, Neo) | | | |
| *Hypochaeris radicata*** (s, d) | | | |
| *Rumex acetosella*** (s, d, r) | | | |
| *Agrostis vinealis*** (s, d) | | | |
| *Tragopogon dubius** (r, Ar) | | | |
| *Stipa borysthenica** (s, EN - CZ, CR - AT) | | | |
| *Avenula pubescens** | | | |
| *Fragaria viridis** (d) | | | |
| *Elymus hispidus** | | | |
| *Dorycnium germanicum** (d) | | | |
| *Filipendula vulgaris** (VU - AT) | | | |
| *Cruciata laevipes** (r) | | | |
| *Convolvulus arvensis** (d, r, Ar - CZ) | | | |
| *Rumex thyrsiflorus** (s, r, Neo) | | | |

| Acidophilous sand grasslands (*Armerion*) | | Basiphilous sand grasslands (*Festucion valesiacae*) | |
|---|---|---|---|
| Increasing | Decreasing | Increasing | Decreasing |
| *Erigeron annuus*** (r, Neo) | *Potentilla verna* agg.* (d) | *Galium verum*** (s, r) | *Poa pratensis* agg.* (s, d, r) |
| *Calamagrostis epigejos*** (r) | *Festuca valesiaca* s. l.* (d) | *Carex liparocarpos*** (s, VU - AT) | |
| *Anthoxanthum odoratum*** (d, r) | *Phleum phleoides** (d) | *Koeleria macrantha*** (s, d, VU - AT)* | |
| *Plantago lanceolata*** (s, d, r) | *Pimpinella saxifraga** (d) | *Senecio jacobaea*** | |
| *Corynephorus canescens** (s, r) | | *Securigera varia** (s, r) | |
| *Agrostis vinealis** (s, d) | | *Silene otites** (s, d, VU - AT) | |
| *Rumex acetosella** (s, d, r) | | *Dorycnium germanicum** (d) | |
| *Tragopogon dubius** (r, Ar) | | *Fragaria viridis** (d) | |
| | | *Eryngium campestre** (s, d, r, NT - AT) | |
| | | *Medicago falcata** (d, r) | |

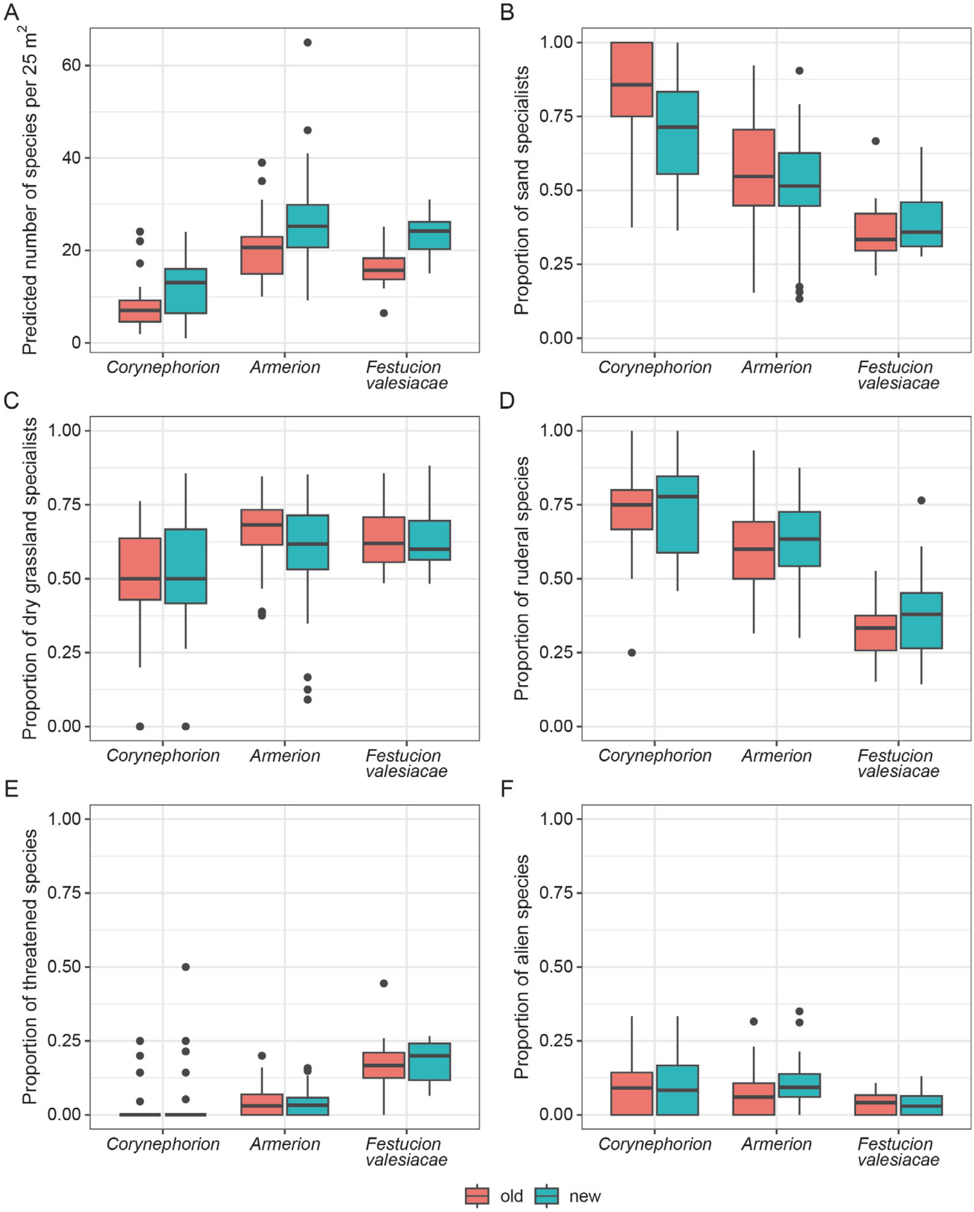

**Fig. 4.** Comparison of (A) predicted numbers of species per 25 m$^2$; (B) proportions of sand specialists; (C) proportions of dry grassland specialists; (D) proportions of ruderal species; (E) proportions of threatened species; (F) proportions of alien species between the first survey (old) and the resurvey (new).

**Table 2.** Results of the linear mixed effect model (species richness) and generalized estimating equations models with binomial distribution (sand and dry grassland specialists, ruderal, threatened, alien, and woody species). The regression coefficients and the significances of the effects are shown. The intercept represents the historical plot observations of *Corynephorion*. *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, n.s. (non-significant) $\geq 0.05$.

| | Intercept | Time | Time: *Armerion* | Time:*Festucion valesiacae* |
|---|---|---|---|---|
| Species richness | 7.912*** | 3.795** | 1.437 n.s. | 4.079* |
| Proportion of sand specialists (logit scale) | 1.358*** | –0.774*** | 0.584** | 0.953*** |
| Proportion of dry grassland specialists (logit scale) | 0.360** | –0.194** | – | – |
| Proportion of ruderal species (logit scale) | 0.761*** | 0.094 n.s. | – | – |
| Proportion of threatened species (logit scale) | –1.748*** | –0.005 n.s. | – | – |
| Proportion of alien species (logit scale) | –1.830*** | 0.00002 n.s. | – | – |
| Proportion of woody species (logit scale) | –1.566*** | –0.158 n.s. | | |

The proportion of alien species (both archaeophytes and neophytes) per plot was very low and did not change significantly over time. However, the summed frequency of alien species increased from 91 occurrences in the old plot observations to 147 in the new plot observations. There were also more plots with the alien species recorded in the resurvey: at least one was present in 55 old plot observations and 68 new plot observations. *Ailanthus altissima*, *Crepis foetida*, *Medicago ×varia*, *Onobrychis viciifolia*, *Saponaria officinalis* and *Syringa vulgaris* were recorded only in old plot observations, whereas *Acer negundo*, *Aristolochia clematitis*, *Asclepias syriaca*, *Asparagus officinalis*, *Chelidonium majus*, *Cirsium arvense*, *Erodium cicutarium*, *Oxalis* sp., *Prunus cerasifera*, *Reseda lutea*, *Tragopogon dubius,* and *Viola odorata* were recorded only in the new plot observations. The frequency of *Arrhenatherum elatius* increased from 15 occurrences in the old plot observations to 21 in the new plot observations. *Erigeron annuus* increased from 2 to 15 occurrences, while *Silene latifolia* subsp. *alba* increased from 7 to 20 occurrences. The frequency of other alien species remained similar in both time periods.

The length of the period between the first survey and the resurvey did not have a significant effect on the magnitude of changes in species composition in pioneer sand grasslands ($P = 0.17$, not tested for other vegetation types). The magnitude of changes in species richness and the proportions of individual species groups also did not differ significantly with the length of the interval between the first survey and the resurvey (species richness: $P = 0.94$, sand specialists: $P = 0.10$, dry grassland specialists: $P = 0.92$, ruderal species: $P = 0.59$, threatened species: $P = 0.36$, alien species: $P = 0.30$, woody species: $P = 0.10$).

We identified several changes in mean ecological indicator values per plot. Across the whole dataset, moisture and nutrient indicator values increased significantly, while indicator values for grazing pressure decreased (Table 3). A decrease in indicator values for temperature was only marginally significant for the whole dataset, but it was significant in pioneer sand vegetation. In acidophilous and ruderalized sand grasslands, there was a marginally significant increase in indicator values for moisture, nutrients and disturbance severity, while indicator values for grazing pressure decreased significantly. There were no significant changes in indicator values in basiphilous sand grasslands except for a marginally significant increase in indicator values for soil disturbance.

**Table 3.** Results of the row-based and column-based permutation tests for changes in ecological indicator values. The higher P-value of the two tests was considered (max test); ↓ decreasing, ↑ increasing, *** P < 0.001, ** P < 0.01, * P < 0.05, + P < 0.1, n.s. (non-significant) P ≥ 0.1.

| | Whole dataset | *Corynephorion* | *Armerion* | *Festucion valesiacae* |
|---|---|---|---|---|
| Light | n.s. | n.s. | n.s. | n.s. |
| Temperature | ↓ + | ↓ * | n.s. | n.s. |
| Moisture | ↑ * | n.s. | ↑ + | n.s. |
| Reaction | n.s. | n.s. | n.s. | n.s. |
| Nutrients | ↑ * | n.s. | ↑ + | n.s. |
| Disturbance severity | n.s. | n.s. | ↑ + | n.s. |
| Disturbance frequency | n.s. | n.s. | n.s. | n.s. |
| Mowing frequency | n.s. | n.s. | n.s. | n.s. |
| Grazing pressure | ↓ * | ↓ + | ↓ * | n.s. |
| Soil disturbance | n.s. | n.s. | n.s. | ↑ + |

## Discussion

### *Changes in species composition*

The main vegetation types of sand grasslands in the Vienna Basin have remained relatively stable in many characteristics over the last few decades. However, there have been significant changes in species composition in all vegetation types: pioneer sand grasslands, acidophilous and ruderalized sand grasslands and basiphilous sand grasslands. The pioneer sand vegetation showed consistent, unidirectional changes towards more closed acidophilous sand grasslands. In contrast, changes in the acidophilous and ruderalized sand grasslands and basiphilous sand grasslands followed multiple directions, possibly due to the greater stability of these more successionally developed communities. The larger species pool of closed sand grasslands might also contribute to the varied directions of change in species composition. Across the whole dataset, specialists of both sand vegetation (e.g. *Cynodon dactylon*, *Jasione montana*, *Thymus serpyllum*) and dry grasslands (e.g. *Asperula cynanchica*, *Pimpinella saxifraga*, *Seseli annuum*) declined over time, with the decline most pronounced in pioneer sand vegetation. Sand specialists are adapted to very dry, nutrient-poor conditions and are supported by disturbances such as sheep grazing or topsoil removal (Jentsch et al. 2009, Faust et al. 2011, Henriksson et al. 2019, Řehounková et al. 2021). Their decline is also well documented in sand vegetation and dry grasslands in other European countries and is often attributed to eutrophication and natural succession following the abandonment of traditional management (Bahr et al. 2012, Harásek et al. 2023). The possible effects of these factors in the current study were also indicated by changes in ecological indicator values. We observed an increase in species associated with higher indicator values for nutrients and moisture and a decline in species adapted to higher grazing pressure. An increase in moisture indicator values in our dataset may also indicate eutrophication and natural succession towards more closed grasslands. Species of closed vegetation are less drought-adapted than sand specialists occurring in pioneer sand vegetation, and in our dataset, indicator values for moisture are positively correlated with those for nutrients (Supplementary Fig. S3). In addition, a significant decline in Ellenberg-type indicator values for temperature was observed in pioneer sand vegetation. The decline in thermophilous species does not correspond with the increase in mean annual temperature. However, it may also be interpreted as a result of natural succession, as species in open pioneer sand grasslands are the most thermophilous, and a shift towards closed grasslands is associated with an increase in species with lower indicator values for temperature. Closed acidophilous sand grasslands have undergone a significant decline in species adapted to higher grazing pressure, which may also indicate the effects of abandoning traditional management. Basiphilous sand grasslands appear to be the most stable, as no significant changes in ecological indicator values were detected.

The increase in nutrient availability favours succession and may lead to the decline of stress-tolerant specialists due to overgrowth by stronger competitors (Storm & Süss 2008, Mårtensson & Olsson 2010, Faust et al. 2012). Additionally, these shifts may also be supported by changes in the disturbance regime. Since the abandonment of pastures and the beginning of afforestation in the study area, sand dunes have been stabilized, and there has been a considerable reduction in disturbances from grazing animals and wind erosion (Vicherek 1975, Wiesbauer 2002, Zuna-Kratky et al. 2009). Although conservation management has been established in the protected areas to support the natural dynamics of the sand ecosystems (Mackovčin et al. 2007), natural succession may occur at sites with lower disturbance. It is difficult to separate the effects of eutrophication and natural succession in a reduced disturbance regime, as both processes may jointly lead to an increase in competitively stronger species and the competitive exclusion of stress-tolerant specialists, contributing to changes in vegetation composition. However, a successional shift towards more closed vegetation after the abandonment of traditional management appears to be a stronger driver, given that we identified not only an increase in nutrient indicator values, but also an increase in mesophilous species, in contrast to a decline in thermophilous species and species adapted to higher grazing pressure. In acidophilous and ruderalized sand grasslands, the decline in species adapted to higher grazing pressure was even stronger than the increase in indicator values for nutrients.

One of the species that increased most in this dataset was *Calamagrostis epigejos*, a competitive grass spreading in various habitat types (Hršak 2004, Süss et al. 2010, Klinkovská et al. 2024b) and considered an expansive species in the Czech Republic (Axmanová et al. 2024). The spread of *Calamagrostis epigejos* is favoured by nutrient-rich conditions and reduced disturbance. In such conditions, it often forms monodominant stands and outcompetes species from the original community, including habitat specialists (Fiala et al. 2003, Somodi et al. 2008). Frequently recorded species also included *Bromus erectus* and *Carex hirta*, which, like *Calamagrostis epigejos*, are considered expansive in central Europe (Axmanová et al. 2024, Fartmann et al. 2025), but whose spread we did not observe in our dataset.

### *Changes in species richness*

Several studies on vegetation change in central-European sand grasslands report trends in species richness over time, including increases (Körmöczi 1991, Bahr et al. 2012), no change (Csecserits & Rédei 2001, Matus et al. 2005) and decreases (Süss et al. 2010).

Our results indicate an increase in species richness over time, particularly in pioneer sand vegetation with *Corynephorus canescens*, which may be associated with successional development of the communities and a shift towards more closed sand grasslands. This is also suggested by the significant decline in indicator values for temperature, as closed sand grasslands include fewer thermophilous species than pioneer sand vegetation. However, changes in species richness in resurvey studies should be interpreted with caution, as sampling effort may have an effect. To match the location of the historical plot as precisely as possible, we used the lists of species present in the historical plot. We adopted this conservative approach to minimize pseudo turnover due to a relocation error. However, this may have resulted in detecting more species than the authors of the historical plots, as we had information on which species previously occurred in the plot and might have been overlooked during ongoing sampling. The historical plots originated from multiple sources, including master's theses by possibly less experienced botanists, which might also contribute to differences in the number of species detected. Moreover, a positive trend in species richness is expected in resurvey studies because under changing environmental conditions, colonizations are likely to be detected earlier than extinctions (Kuczynski et al. 2023). There is also a risk of overestimating changes in species richness in resurvey studies due to different weather conditions in the year of the resurvey.

### *Alien species*

Because of frequent disturbances and the open character of the stands, sand vegetation belongs to the habitats most threatened by invasions of alien species (Chytrý et al. 2008, Axmanová et al. 2021). In our dataset, the proportion of alien species was generally very low and did not change significantly over time. However, the overall frequency of alien species and the number of plots in which they occurred increased over time, suggesting that the threat posed by alien species should not be neglected. The invasive neophyte *Erigeron annuus* was among the most strongly increasing species, which is in line with Klinkovská et al. (2024a) who report this species as one of the most strongly increasing in the Czech Republic since the 1960s. According to Axmanová et al. (2021), *Erigeron annuus* is one of the three most common invasive species in European grasslands. Some neophytes also colonized the plots, e.g. *Asclepias syriaca*, an invasive species spreading in recent decades, especially in warm lowland regions (Pyšek et al. 2012, Follak et al. 2021), and causing negative effects on the native communities (Kelemen et al. 2016, Pergl et al. 2016, Bakacsy 2019). The spread of alien species is likely to be favoured by climate change (Walther et al. 2009, Dullinger et al. 2017), therefore, future monitoring and conservation actions are needed to mitigate their effects on sand vegetation.

### *Relative stability of sand vegetation*

Our results indicate relatively small changes in sand vegetation over the study period. This may be because most study sites are in protected areas with appropriate conservation management. This aligns with studies reporting long-term stability of sand vegetation under appropriate disturbance regimes (Csecserits & Rédei 2001, Daniëls et al. 2008, Faust et al. 2011). However, this study mainly reports changes that occurred over the last two to three decades, during which sand vegetation in the study area had already been degraded to some degree. The fact that the length of the interval between the first and second survey had no significant effect on the magnitude of this trend indicates that major changes in vegetation did not occur within the period of this study. During the 19th and 20th centuries, large-scale afforestation in the region stabilized open sand dunes, resulting in the loss of open sandy habitats (Wiesbauer & Mazzucco 1997, Jamrichová et al. 2013). The first protected areas were established after the destruction of most sandy areas, e.g. the oldest Austrian nature reserve, Weikendorfer Remise, was established in 1927 (Šmarda 1961, Wiesbauer 1999, 2002). Consequently, it is likely that the largest land use changes occurred before the period covered by this study. For example, even five decades ago, Vicherek (1975) reported that sand vegetation in southern Moravia was already damaged by human activities.

Another aspect to consider is the methodology used for resampling historical plots. Using the conservative approach, we likely captured the remnants of representative sand vegetation even at sites that became considerably smaller or degraded in some parts. Sites that had changed completely, e.g. were transformed into arable land, built-up areas or afforested, which occurred at several sites, especially in Slovakia, were not resampled, thus, these major changes were not recorded. As a result, it is likely that the results underestimate the changes in sand vegetation. The establishment of permanent plots will ensure more precise monitoring in the future.

## Conclusions

This study indicates that the main types of sand grassland vegetation have persisted in the Vienna Basin over recent decades, but there have been significant changes in their species composition. Specialized species of sand vegetation and dry grasslands have declined over time, with the decline in sand specialists most pronounced in pioneer sand vegetation. The increase in species with high nutrient and moisture requirements, and the decline in those adapted to higher grazing pressure indicate the effects of eutrophication and natural succession following the abandonment of previous management. Pioneer sand vegetation witnessed a decline in Ellenberg-type indicator values for temperature, indicating a shift towards more closed sand grasslands. The decline in habitat specialists, combined with the increase in competitive species such as *Calamagrostis epigejos*, highlights the need for appropriate conservation management and monitoring to maintain the habitat quality of sand vegetation in the study area.

## Supplementary materials

**Fig. S1.** Time series of climatic data for the study area.
**Fig. S2.** Principal coordinate analysis (PCoA) for individual vegetation types.
**Fig. S3.** Correlation matrix of the indicator values of species in the dataset.
**Table S1.** Sources of historical vegetation-plot records.
**Table S2.** List of species names modified for the analysis.
**Table S3.** List of annual species and vernal geophytes excluded from the analysis.
**Table S4.** Numbers of plots in which particular species occurred in the old and new plots.

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

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## Vegetace přetrvává, specializované druhy ubývají – změny v panonských trávnících písčitých substrátů

Suché trávníky písčitých substrátů patří ve střední Evropě a její panonské biogeografické oblasti k silně ohroženým biotopům. Vyskytuje se v nich několik specializovaných a ohrožených druhů, které jsou přizpůsobeny růstu v suchých a živinami chudých půdách. Rozloha těchto biotopů se v 19. a 20. století dramaticky zmenšila. Pro velkou část zbývajících porostů byla zřízena územní ochrana, díky níž se v posledních desetiletích podařilo výrazně omezit další zmenšování jejich rozlohy. Rostlinná společenstva písečných trávníků se však mohou měnit kvůli změnám hospodaření i abiotického prostředí. Tato studie zkoumá změny diverzity a druhového složení rostlinných společenstev na píscích ve Vídeňské pánvi včetně její české (Dolnomoravský úval), slovenské (Záhorská nížina) a rakouské (Moravské pole) části. V letech 2023–2024 jsme zopakovali zápis 86 fytocenologických snímků, které byly poprvé zapsány v letech 1952 až 2010. Zkoumali jsme změny v druhové bohatosti cévnatých rostlin, podílu specializovaných, ruderálních, ohrožených a nepůvodních druhů a dřevin a ekologických indikačních hodnot. Porovnali jsme trendy v pionýrské vegetaci písků (svaz *Corynephorion canescentis*), acidofilních a ruderalizovaných psamofilních trávnících (*Armerion elongatae*) a bazifilních trávnících písčitých substrátů (*Festucion valesiacae*). Výsledky naznačují, že na píscích ve Vídeňské pánvi během posledních desetiletí zůstávají zachovány stále stejné typy vegetace, aniž by kterýkoli z nich byl nahrazen jiným vegetačním typem. Specializované druhy vegetace písků a suchých trávníků, stejně jako druhy přizpůsobené vyššímu pastevnímu tlaku, však zaznamenaly pokles. Naopak přibyly druhy s vyššími nároky na živiny a vlhkost. To naznačuje vliv eutrofizace a přirozené sukcese po zániku dřívějšího hospodaření. Ústup specializovaných druhů písků byl nejvýraznější v pionýrské vegetaci, kde zároveň ubyly druhy s vyššími ellenbergovskými indikačními hodnotami pro teplotu, což naznačuje přechod k zapojenějším písčitým trávníkům. Pro zachování kvality písečných biotopů je nezbytné nastavit vhodný ochranářský management a průběžně monitorovat jejich změny.

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