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Long-term changes in dry grasslands on rock outcrops in the Dyje/Thaya river valley, Czech Republic/Austria

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Abstract: Dry grasslands on rock outcrops in deep river valleys of the Bohemian Massif are typically small and difficult to access, forming isolated open patches surrounded by forests. Although probably partly maintained by historical low-intensity land use, these habitats have often been regarded as near-natural due to their extreme environmental conditions and long-term continuity. However, it remains unclear how strongly these habitats have responded to rapidly changing environmental conditions over recent decades. In 2020–2024, we repeated vegetation sampling conducted in the 1990s (42 semipermanent plots) to analyse long-term vegetation changes in dry grasslands in the Dyje/Thaya river valley. We revealed a decline in rare and xerophilous species, the expansion of ruderal and nutrient-demanding species, and the increased cover of dwarf shrubs and tree seedlings. These changes differed between areas located within the Podyjí/Thayatal National Park and those in less protected parts of the valley, reflecting differences in the surroundings, namely the proportion of woody vegetation, degree of anthropogenic disturbance, game management, and conservation interventions. This suggests that the state of grassland vegetation is strongly linked to the surrounding landscape conditions and the effects of conservation management. Our research provides evidence that even these environmentally extreme habitats are undergoing significant long-term vegetation changes. Shifts toward ruderalized vegetation were more pronounced at sites outside of national parks, whereas sites in national parks exhibited slower and less extensive vegetation change, likely reflecting both the establishment of strict protection and historically lower anthropogenic pressure.

Keywords: Austria, Czech Republic, dry grassland, functional groups, non-forest vegetation, outcrops, plant communities, temporal species turnover, vegetation change

Introduction

South-facing rocky slopes in deep river valleys in the Bohemian Massif host species-rich dry grassland vegetation with isolated populations of many rare thermophilous and endangered species (Kučera & Mannová 1998). Shallow soils and extreme microclimatic conditions make these habitats floristically distinct from the surrounding forest vegetation. These extreme conditions may also reduce the susceptibility of their species composition

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to successional changes (Ložek 2007). The occurrence of some dry grassland species has been interpreted as indicating long-term continuity of open habitats within otherwise forested landscapes (Černý et al. 2006, Hejcman et al. 2013, Pokorný et al. 2015). The long-term persistence of thermophilous species within a dynamic vegetation mosaic of open forests and grasslands on steep slopes of river valleys was probably also supported by human activities, particularly historical grazing (Auffret & Plue 2014). Open dry grasslands on rocky river-valley slopes are currently considered of high conservation value and are therefore frequently included within larger protected areas, such as the Podyjí National Park, the Křivoklátsko, Bohemian Karst, and Moravian Karst Protected Landscape Areas, and other nature reserves across the Czech Republic.

Along its middle course, the Dyje/Thaya River, together with its tributaries, has formed a long V-shaped valley at altitudes of 300–500 m a.s.l. containing numerous open rock outcrops, whose diversity has been further enhanced by a wide range of geological substrates. These habitats host many notable thermophilous and light-demanding plants, including the local endemic *Dianthus moravicus* and several other species occurring in isolated populations near the margins of their distribution ranges, such as *Allium flavum*, *Carex michelii*, *Dictamnus albus*, *Inula hirta*, *Oxytropis pilosa*, *Pulsatilla pratensis*, *Stipa capillata*, *Stipa pulcherrima*, and *Thalictrum minus* (e.g. Suza 1933, Kovanda 1990, Tichý et al. 1997, Chytrý et al. 2021).

It is well documented that the current landscape and various seminatural plant communities at low and middle altitudes in central Europe, which originated and have been historically maintained by traditional land use (e.g. grazing or mowing), are undergoing significant successional changes and species turnover (Jandt et al. 2022). Such changes have been confirmed for seminatural dry grasslands (Klinkovská et al. 2025), as well as for other habitats, including deciduous oak and oak-hornbeam forests (Hédl et al. 2010, Vild et al. 2024) and lowland alluvial forests (Petrášová et al. 2013). The changes described in the cited studies are typically characterized by the decline of endangered species and habitat specialists, increased presence of woody species and competitive grasses, higher biomass production, invasions of neophytes, and the spread of nutrient-demanding species. From the conservation perspective, these trends can be regarded as habitat degradation, marked by a chronic decline in species adapted to nutrient-poor conditions (Stevens et al. 2004).

This paper examines temporal changes in dry grassland vegetation on rock outcrops along the Dyje/Thaya River at the south-eastern edge of the Bohemian Massif over 30 years. It focuses on two areas: the middle Dyje/Thaya river valley within a managed cultural landscape shaped by contemporary land-use practices, and the valley of the same river within the national parks of Podyjí (Czech Republic) and Thayatal (Austria), where natural and seminatural vegetation remains well-preserved. The two study areas differ not only in protection status but also in their broader landscape context, management regime, and historical land-use intensity. Outside the national parks, rock outcrops are more frequently located within areas with high proportions of commercially managed forests, conifer plantations, forest clearings, or agricultural land, which may increase nutrient input, disturbance intensity, and propagule pressure of ruderal, alien and expansive species. In contrast, sites within national parks are typically surrounded by seminatural forests with lower management intensity and regulated ungulate populations. In this context, we hypothesize that (i) dry grassland vegetation on rock outcrops within the national parks has undergone only limited changes in species composition and vegetation structure over the past 30 years due to conservation measures, and (ii) areas outside the national parks have experienced a decline in habitat quality reflected by the increase of ruderal, nutrient-demanding, disturbance-related and alien species.

Material and methods

Study sites

Our study focused on patches of dry grasslands located on the tops of rock outcrops in two distinct areas at the south-eastern edge of the Bohemian Massif (Fig. 1):

(i) Middle Dyje/Thaya valley: This dataset covers a section of the Dyje/Thaya River valley extending for approximately 50 km along the river course, between the village of Eibenstein, Austria (48.85°N, 15.58°E), and the town of Vranov nad Dyjí, Czech Republic (48.90°N, 15.82°E). The non-forest vegetation patches on rock outcrops in this area are typically small, often limited to a few tens of square meters.

(ii) National Parks: This dataset includes areas within the Podyjí and Thayatal National Parks, covering approximately 40 km of the Dyje/Thaya River valley along the river course, and the adjacent valleys of the Fugnitz and Kaja streams, between the towns of Vranov nad Dyjí (48.89°N, 15.82°E) and Znojmo (48.85°N, 16.04°E). In this section, the non-forest vegetation patches on these rock outcrops are typically larger and form a denser mosaic than those in the upper part of the valley, reflecting the greater depth and steepness of the valley slopes.

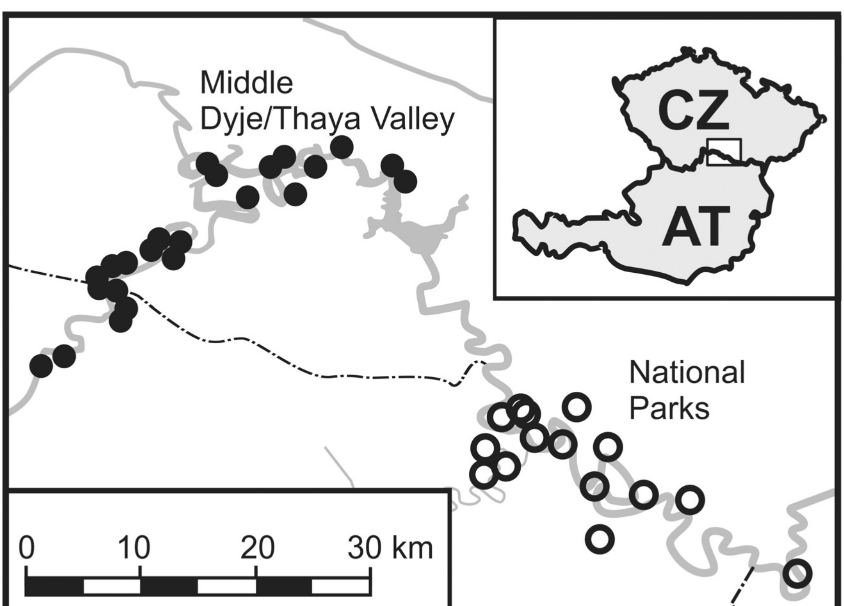

Fig. 1. Map of the study area showing the location of sampling sites for both datasets (27 and 15 semipermanent plots).

In the whole region, the Dyje/Thaya River follows a generally west-to-east course, meandering to create large areas of steep, mostly forested slopes that transition into a relatively flat surrounding plateau at approximately 450–550 m a.s.l. The elevation difference between the upper edges of the valley and its bottom reaches 100–200 m, and the valley slopes contain numerous rock outcrops rising above the surrounding forests. These rock outcrops (Figs 2–5) are characterized by shallow soils that support dry grassland vegetation. The bedrock in the study area includes acidic granitoids, gneisses, and mica schists, as well as base-rich amphibolites, crystalline limestones and other rocks (Czech Geological Survey 2025).

Vegetation data

Middle Dyje/Thaya valley dataset: This dataset comprises 27 vegetation plots originally sampled in 1993–1994 by L. Tichý (Tichý et al. 1997) on south-facing rock outcrops in the Dyje/Thaya valley outside the national parks. The plots were not permanently marked but were relocated by the original author (L. Tichý) during the resurveys (semipermanent plots; corresponding to the category of quasipermanent plots in the terminology of Kapfer et al. 2017). The plots were resurveyed in 2020–2021 and again in 2024 to evaluate the consistency of detected vegetation trends and the potential effect of interannual climatic variability. This resulted in three records for each plot and a total of 81 vegetation-plot records (observations). Plot sizes ranged from 15 to 25 m^2, according to the availability of the same vegetation type.

National Parks dataset: This dataset includes 15 vegetation plots originally sampled in 1991–1992 (Chytrý & Vicherek 2003) within the Dyje/Thaya River valley and its right-bank tributaries, the Fugnitz and Kaja streams. Plots were also not permanently marked but were identified in the field by one of the original authors (M. Chytrý) and resurveyed in 2022 by him, most of them jointly with I. Axmanová, resulting in a total of 30 vegetation-plot records. Plot sizes ranged from 8 to 25 m^2 according to the availability of the same vegetation type.

In both datasets, the seven-grade Braun-Blanquet cover-abundance scale (Westhoff & van der Maarel 1978) was used and subsequently digitized as percentage values, calculated as midpoints of cover ranges, using the TURBOVEG program (Hennekens & Schaminée 2001). The total covers of the herb layer and the moss layer were estimated visually in the field.

Data analysis

All records of juvenile shrubs and trees were excluded from the analyses of species composition. However, their total cover was calculated and used as an explanatory variable. To identify species that increased or decreased over time within the vegetation of rock outcrops, we used paired Wilcoxon signed-rank tests to evaluate directional changes in species cover between baseline and resurveyed plot records. P-values were then adjusted for multiple testing using the false discovery rate correction method (Benjamini & Hochberg 1995). We conducted Principal Coordinates Analysis (PCoA) based on Bray-Curtis distances to illustrate directional changes in community composition between the two sampling events for each dataset separately. The significance of the effect of time on species composition was tested using paired permutational ANOVA (PERMANOVA; Anderson

Fig. 2. Bílý kříž Nature Reserve (Middle Dyje/Thaya valley dataset). The productivity of vegetation is limited by shallow soils (limestone and amphibolite bedrock). Photo L. Tichý 2020.

Fig. 3. Růžový vrch Nature Reserve (Middle Dyje/Thaya valley dataset) with small patches of rock outcrops on a mosaic of acidic, neutral and slightly basic soils (granite and amphibolite bedrock). Photo L. Tichý 2020.

Fig. 4. Hardeggské skály (National Parks dataset), a large complex of rock outcrops and open habitats on south-facing slopes, hosting numerous endangered thermophilous species outside their continuous range (a mosaic of acidic and basic bedrock). Photo M. Chytrý 2013.

Fig. 5. Vraní skála (National Parks dataset), steep, south-facing rocky slopes with many thermophilous plants, including several endangered species (a mosaic of acidic and basic bedrock). Photo P. Lazárek 2012.

2001, 2006). To identify the factors driving vegetation changes, species in each dataset were classified into functional groups based on species characteristics from the Pladias database (Chytrý et al. 2021), and changes in the number of species and their combined cover (Fischer 2015) within each group were tested using the paired Wilcoxon signed-rank test. The following species groups were used to characterize vegetation changes:

Graminoids: fundamental structural component of dry grasslands. – Legumes: nitrogen fixers, contributors to soil fertility. – Annual species: species adapted to disturbance. – Perennial non-clonal species: long-lived species contributing to the temporal continuity of dry grassland communities. – Dwarf shrubs: contributing to dry grassland structure. – Clump-forming clonal species: long-lived species with low spatial turnover. – Vegetatively spreading clonal species: species contributing to grassland homogenization through spreading stolons or rhizomes. – Species with ruderal tendency: species adapted to recurrent disturbance and habitat instability. Species were classified as ruderal if at least 10% of their occurrences within the vegetation database of the Czech Republic were recorded in ruderal vegetation defined by Chytrý (2009). – Frequent species from the 1990s: species present in at least one-third of the plots in the baseline survey period. Their increase would indicate further spread or increasing dominance of species that were already common in the 1990s. Conversely, a decline would suggest a retreat or reduced abundance of formerly frequent species. This approach allows tracking the persistence and shifts in the prevalence of initially frequent or dominant species over time. – Light-demanding species: species with Ellenberg-type indicator value for light (Chytrý et al. 2018) > 6, requiring high levels of sunlight. – Thermophilous species: species with Ellenberg-type indicator value for temperature > 6, requiring warm environments. – Drought-tolerant species: species with Ellenberg-type indicator value for moisture < 4, adapted to dry conditions. – Nutrient-demanding species: species with Ellenberg-type indicator value for nutrients > 4, favouring a nutrient-rich environment. – Rare species: species occurring in fewer than 300 quadrants of Central European Floristic Mapping grid in the Czech Republic (each 3' in latitude × 5' in longitude, according to the Pladias database; Wild et al. 2019), many of them of conservation concern. – Species of severely disturbed sites: species with disturbance severity indicator values for the herb layer > 0.3 (Herben et al. 2016). – Species of frequently disturbed sites: species with disturbance frequency indicator values for herb layer > –0.3 (Herben et al. 2016). – Ecological specialists: species with a specialization index > 5, calculated for Czech non-forest vegetation, indicating adaptation to specific ecological conditions (Zelený & Chytrý 2019). – Species of successionally young vegetation: species with index of colonization success > 6 (Prach et al. 2017). – Invasive and expansive species: non-woody species listed as invasive in Pyšek et al. (2022) or expansive in Axmanová et al. (2024). – Shrubs: woody species with a height from 1 m recorded within the shrub layer. – Juveniles: young trees and shrubs with a height of less than 1 m recorded within the herb layer.

Vegetation data were archived and prepared for analyses using Turboveg (Hennekens & Schaminée 2001) and JUICE (Tichý 2002) software. We performed all statistical analyses in R (R Core Team 2025). Multivariate analyses were conducted using the vegan package (Oksanen et al. 2025), and Wilcoxon signed-rank tests were performed using standard R functions. Taxonomy and nomenclature follow the Key to the Flora of the Czech Republic (Kaplan et al. 2019) for vascular plants.

Results

While the Middle Dyje/Thaya valley dataset showed an increase in both the total number of recorded species and the average number of species per plot, the total number of recorded species in the National Parks dataset decreased, and the average number of species per plot did not change significantly (Table 1). The average covers of the herb and moss layers decreased in both datasets. Although individual sites varied in the magnitude and direction of changes, an overall significant change in species composition was detected in both datasets (paired PERMANOVA: Middle Dyje/Thaya valley, $P < 0.001$; National Parks, $P < 0.01$). The test of homogeneity of dispersion was not significant when analyzed separately for each dataset. The PCoA ordination (Fig. 6) further illustrated these directional changes in species composition. Although both datasets exhibited a compositional shift, the direction of change differed between them. Both resurveys of the Middle Dyje/Thaya valley confirmed the same trend.

Table 1. Summary of the basic characteristics of the two datasets analyzed in this study. Total numbers of species illustrate temporal changes in species composition within each dataset, whereas mean comparisons between datasets are based on mean values per plot. Values in brackets indicate statistical significance of the paired Wilcoxon signed-rank tests comparing the baseline survey with the period represented by the respective column (n.s. $P \geq 0.1$; . $P < 0.1$; * $P < 0.05$; ** $P < 0.01$).

	Middle Dyje/Thaya valley			National Parks	
	1993–1994	2020–2021	2022–2024	1991–1992	2022
No. of plots	27	27	27	15	15
Time interval	–	26–27 yrs	29–31 yrs	–	30–31 yrs
No. of vascular plant species (without juveniles)	138	152	171	177	140
Disappeared species	–	30	21	–	58
Newly found species	–	44	54	–	31
No. of juvenile species	7	10	18	4	15
Mean no. of vascular plant species per plot	24.5	27.6 (**)	29.0 (**)	30.5	29.6 (n.s.)
Mean cover of the shrub layer (%)	1.9	0.4 (*)	3.0 (n.s.)	0.0	0.1 (n.s.)
Mean cover of the herb layer (%)	73.7	72.0 (n.s.)	66.1 (**)	84.0	71.0 (**)
Mean cover of the moss layer (%)	8.4	2.9 (*)	4.7 (n.s.)	17.7	10.9 (.)

Groups of species categorized by different characteristics (Table 2) indicated that in the Middle Dyje/Thaya valley dataset, there were increases in both the number and cover of ruderal and nutrient-demanding species, tree seedlings, and species adapted to severe disturbances. The cover of dwarf shrubs also increased significantly. Conversely, there was a decline in rare and xerophilous species, and a decrease in the overall occurrence of frequent species present in the 1990s dataset (Table 2). Differences between the first and second resurvey were non-significant, although some variables showed minor shifts in significance without affecting the trends. The only exception was the group of annuals, which showed a weak non-significant trend in the opposite direction.

In contrast, the National Parks dataset showed a significant decrease in annuals, ruderal species, and species associated with frequent and severe disturbances. However, similar to the first dataset, both the number and cover of rare species decreased, while dwarf shrubs increased.

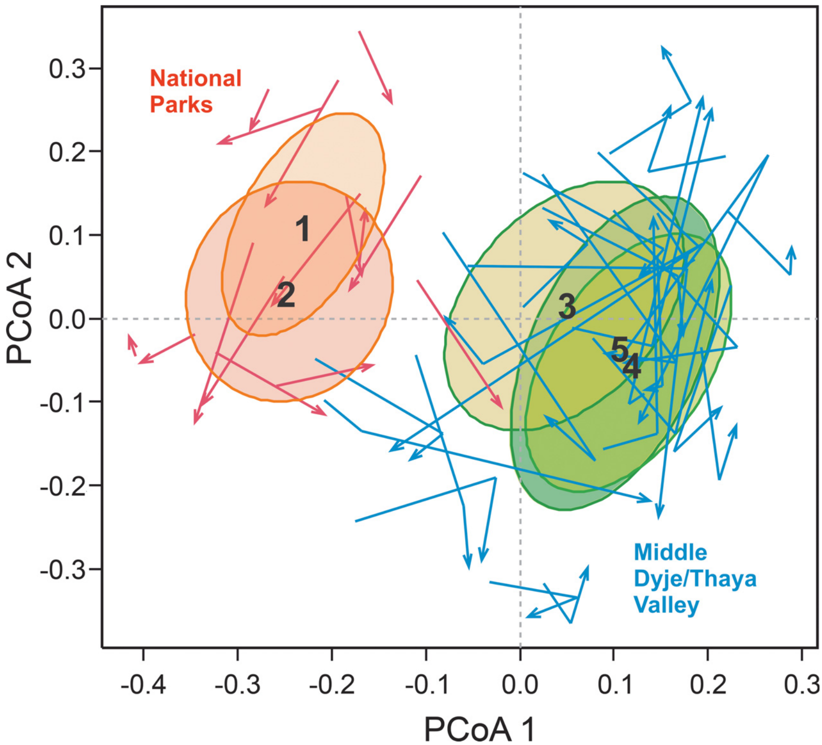

Fig. 6. Ordination diagram of Principal Coordinates Analysis (PCoA) of the herb layer for both datasets: National Parks (red arrows; Group 1: Sampling years 1991–1992, Group 2: 2022) and Middle Dyje/Thaya valley (blue arrows; Group 3: 1993–1994, Group 4: 2020–2021, Group 5: 2024). Ellipses represent the confidence intervals, illustrating the dispersion of plots within each group. Arrows indicate the direction of vegetation change within the same plot sampled at different times. Note that the blue arrows are segmented because they represent trajectories across three time points.

Species-level paired quantitative data analyses revealed remarkably consistent directional changes between the baseline and both recent resurveys in the Middle Dyje/Thaya valley dataset. The most consistent trends, supported by at least $P < 0.1$ in both resurveys, were increases in *Achillea nobilis*, *Echium vulgare*, *Elymus hispidus*, *Fallopia convolvulus*, *Galium mollugo* agg., *Hypericum perforatum*, *Poa pratensis* agg., *Silene latifolia*, *Teucrium chamaedrys*, *Trifolium arvense*, *Verbascum lychnitis* and *Verbascum thapsus*, whereas *Cota tinctoria*, *Lactuca viminea*, *Seseli osseum* and *Stipa pennata* consistently declined. Although none of these changes remained significant after false discovery rate correction, their consistency across independent resurveys suggests non-random vegetation shifts. By contrast, in the National Parks dataset, *Genista tinctoria* and *Sedum sexangulare* increased, whereas *Sanguisorba minor* decreased significantly ($P < 0.05$). Weaker increasing trends ($P < 0.1$) were observed in *Elymus hispidus* and *Hypericum perforatum*, whereas decreasing trends were detected in *Alyssum alyssoides* and *Arenaria serpyllifolia*. None of these changes remained significant after false discovery rate correction.

Table 2. Species group characteristics used to analyze changes in vegetation composition and cover. These characteristics reflect various life forms, reproductive strategies, ecological preferences based on Ellenberg-type indicator values (EIV) for light, temperature, moisture, and nutrients, as well as species rarity, disturbance tolerance, successional status, and species abundance. Values in the columns 'Change (%)' represent the relative mean change between the baseline and the last survey. Numbers in parentheses for the Middle Dyje/Thaya valley dataset indicate the corresponding change between the baseline and the first resurvey. Values in bold indicate statistically significant changes. The column 'Trend' indicates the direction and statistical significance of changes between the baseline and the last survey (n.s. P ≥ 0.1; . P < 0.1; * P < 0.05; ** P < 0.01; *** P <0.001).

Ecological groups and functional traits	Middle Podyjí/Thayatal				National Parks			
	Species presence		Cumul. cover		Species presence		Cumul. cover	
	Change (%)	Trend	Change (%)	Trend	Change (%)	Trend	Change (%)	Trend
Graminoids	**(2.6)** **4.3**	↑ *	**(–6.1)** –5.5	↓ n.s.	**5.3**	↑ **	3.4	↑ n.s.
Legumes	(1.1) 0.0	↑ n.s.	**(2.3)** 1.6	↑ n.s.	2.4	↑ n.s.	1.9	↑ n.s.
Annual species	**(–3.9)** 1.7	↑ n.s.	**(–2.8)** 3.8	↑ n.s.	**–9.3**	↓ ***	**–5.0**	↓ ***
Perennial non-clonal species	(0.5) 0.2	↑ n.s.	(9.8) 1.2	↑ n.s.	–3.4	↓ n.s.	0.5	↑ n.s.
Dwarf shrubs	**(–1.6)** **–2.7**	↓ **	**(5.8)** **6.6**	↑ *	**4.1**	↑ **	**5.0**	↑ ***
Clump-forming clonal species	(0.5) 1.3	↑ n.s.	**(–8.5)** –7.5	↓ n.s.	**2.1**	↑ *	–0.4	↓ n.s.
Vegetatively spreading clonal species	(0.2) 0.0	↑ n.s.	(2.3) 1.8	↑ n.s.	**4.8**	↑ *	5.0	↑ n.s.
Species with ruderal tendency (>10% occurrences)	**(6.0)** **7.1**	↑ **	**(10.2)** **10.8**	↑ ***	**–2.1**	↓ *	**–3.4**	↓ **
Frequent species from the 1990s	**(–5.5)** **–7.5**	↓ **	**(–2.5)** –2.2	↓ n.s.	1.3	↑ n.s.	0.2	↑ n.s.
Light-demanding species (EIV-L > 6)	(–0.4) –2.2	↓ n.s.	(2.8) 2.4	↑ n.s.	2.7	↑ n.s.	**6.9**	↑ .
Thermophilous species (EIV-T > 6)	**(–3.6)** –2.6	↓ n.s.	(–2.0) 0.4	↑ n.s.	–1.2	↓ n.s.	0.6	↑ n.s.
Drought-tolerant species (EIV-H < 4)	**(–3.8)** **–4.9**	↓ .	**(–8.1)** **–9.9**	↓ *	2.9	↑ n.s.	4.7	↑ n.s.
Nutrient-demanding species (EIV-N > 4)	**(3.3)** **5.4**	↑ *	**(4.9)** **6.0**	↑ *	–3.3	↓ n.s.	**–4.1**	↓ .
Rare species (< 300 quadrants of CZ)	(–2.5) **–4.7**	↓ **	**(–8.4)** **–10.4**	↓ **	**–3.9**	↓ *	**–9.0**	↓ **
Species of severely disturbed sites (> 0.3)	**(4.9)** **7.9**	↑ **	**(9.2)** **11.4**	↑ **	**–6.5**	↓ *	**–5.8**	↓ *
Species of frequently disturbed sites (> –0.3)	**(–1.9)** 1.0	↑ n.s.	**(–2.5)** 1.6	↑ n.s.	**–3.9**	↓ .	**–2.1**	↓ *
Ecological specialists (index > 5)	(–0.7) –1.6	↓ n.s.	(–0.1) –0.1	↓ n.s.	**–4.7**	↓ *	**–9.0**	↓ *
Species of successionally young vegetation (ICS > 6)	**(7.9)** **5.8**	↑ **	**(4.8)** 1.7	↑ n.s.	0.5	↑ n.s.	1.5	↑ n.s.
Invasive and expansive species (herb layer)	(0.7) **2.3**	↑ *	**(0.2)** **1.3**	↑ *	0.3	↑ n.s.	0.0	↓ n.s.
Shrubs	(–0.7) –0.2	↓ n.s.	(–0.4) –0.2	↓ n.s.	0.7	↑ n.s.	0.4	↑ n.s.
Juveniles	(1.7) **4.1**	↑ ***	(1.3) **3.0**	↑ ***	**2.3**	↑ .	1.2	↑ n.s.

We also recorded several ruderal, expansive, or alien species in some plots, although their changes did not reach statistical significance: *Alliaria petiolata*, *Ballota nigra*, *Berteroa incana*, *Bromus inermis*, *Bromus sterilis*, *Calamagrostis arundinacea*, *Calamagrostis epigejos*, *Capsella bursa-pastoris*, *Chenopodium album*, *Chenopodium hybridum*, *Convolvulus arvensis*, *Cytisus scoparius*, *Galium aparine*, *Geum urbanum*, *Impatiens parviflora*, *Lactuca serriola*, *Melilotus officinalis*, *Parthenocissus inserta*, *Robinia pseudoacacia*, *Rubus fruticosus* agg., and *Setaria viridis*.

Discussion

Our results indicate that even dry grasslands on rock outcrops in the Dyje/Thaya valley are undergoing consistent changes in vegetation composition despite the extreme environmental conditions of these habitats. While changes at the level of individual species were generally weak and often inconsistent, broader shifts in vegetation composition and structure became apparent when species were evaluated in ecological and functional groups. Described vegetation changes are also consistent with independent field observations of local declines or disappearances of several rare species associated with rock outcrops of the study area during the last decades (e.g. *Stipa dasyphylla* – Sloní hřbet, Podyjí National Park, last recorded by Tichý in 1996, personal observation; *Pulsatilla grandis* – many rock outcrops in national parks, Tichý et al. 2025, population declined by 50–90%).

Interpretation of species-level vegetation changes is complicated by methodological limitations typical of resurveys of historical vegetation plots. The study is constrained by the limited number of isolated non-forest rock outcrops, where colonization events may partly reflect stochastic processes. Since the original vegetation records were collected before the widespread availability of GPS, their locations can only be considered semi-permanent. Another source of potential inaccuracies is cover estimation in repeated sampling (Morrison 2016), although this potential observer bias was partly reduced in our study because the resurveys were conducted by the same authors who carried out the original sampling.

A methodological strength of this study is the repeated resurvey of the same historical Middle Dyje/Thaya valley dataset within a relatively short interval (2020–2021 and again in 2024). This approach allowed us to evaluate the consistency of detected vegetation trends and to distinguish directional changes from short-term fluctuations potentially caused by interannual climatic variability following a period of exceptionally dry years (2016–2019; Zahradníček et al. 2021). The similarity of trends observed in both resurveys supports the robustness of the detected patterns.

While we found significant changes in the structure and composition of dry grassland vegetation on rock outcrops in both parts of the Dyje/Thaya valley, their magnitude and direction differed markedly between them, although they are geographically close, and the character of the river valley is comparable. These differences may partly reflect broader environmental contrasts between the two parts of the valley. The localities in the national parks are situated further downstream at slightly lower elevations and often include higher density of open rocky habitats, which may support greater habitat connectivity and influence species composition. The section of the river valley outside the national parks (Middle Dyje/Thaya valley dataset) with generally smaller and more scattered non-forest patches showed notable changes in community structure, including an increased frequency of invasive and expansive species, accompanied by a decline in rare species, suggesting a reduction in habitat quality. In the following sections, we explore several likely interacting factors driving these temporal changes.

Gradual overgrowing of open areas by woody species

Our results are in accordance with previous studies that have documented broader successional changes across a wide spectrum of dry grassland habitats at both regional and national scales (Klinkovská et al. 2024, 2025). Changes in the most extreme rocky habitats may proceed relatively slowly due to harsh environmental conditions. However, encroachment of woody vegetation in their immediate surroundings may substantially alter local environmental conditions. The presence of tree seedlings and the increase in their cover on open rock outcrops indicate the ongoing succession and decreasing habitat openness.

These patterns were detectable even at the most extreme sites included in this study, where woody species occur near the limits of their ecological range. In addition, surrounding trees are a gradual source of nutrient enrichment for the rock outcrop habitats through litter accumulation. This process creates a continuous input of organic matter, likely increasing soil nutrient availability (Frouz et al. 2008), which favours nutrient-demanding and mesophilous species at the expense of dry grassland specialists (Ceulemans et al. 2017). The absence of traditional management practices, such as grazing, burning, or other forms of woodland use, which historically helped maintain this mosaic of open patches in a forested landscape, may further accelerate the degradation of dry grasslands on these treeless habitat islands. Comparable effects of decreasing habitat openness have also been described in other types of open habitats within forested landscapes (Roleček & Řepka 2020). Ongoing succession may contribute to a decline of light-demanding and drought-adapted species while promoting species that prefer more mesic conditions. This pattern was documented mainly in the Middle Dyje/Thaya valley dataset, which represents the more mesic part of the study area. In contrast, some localities in national parks have already been managed over the past two decades to reduce shrub and tree encroachment into open patches of dry grasslands.

Resting sites for wild ungulates

Rock outcrops are likely increasingly used as resting sites by ungulates, particularly by expanding populations of native roe deer, non-native mouflon, and native wild boar (Čermák & Mrkva 2006, Fuchs et al. 2021, VÚLHM 2024). In addition, these ungulates are displaced from other parts of the landscape due to increasing human activities, as the middle course of the Dyje River around the Vranov Reservoir has become a highly frequented recreational area, especially during summer. Large herbivores increase the selective grazing pressure in dry grasslands, while their trampling and resting may disturb perennial plants and create open microsites. In addition, the dung and urine may locally increase nutrient availability and promote the spread of ruderal and nutrient-demanding species (Kolbek 1996). The situation in the Podyjí National Park may be somewhat more favourable. The large mouflon population was systematically and significantly suppressed during the 1990s (Benda et al. 1997). According to the park's management policies, populations of hoofed game are regularly reduced to meet conservation objectives (Reiterová 2022). This could positively affect dry grassland vegetation on rock outcrops within national parks, although signs of animal presence have still been observed in open habitats.

Spread of invasive and expansive species

Invasive alien and native expansive species represent ecologically similar groups – both are characterized by rapid spread, high competitiveness, and a tendency to dominate disturbed or changing habitats. However, they differ in origin. Invasive species (Pyšek et al. 2022) are non-native to the local flora, while expansive species (Axmanová et al. 2024) are native but have recently increased their abundance and distribution range. Invasive and expansive species in our study sites were only rarely dominant, probably because the strong spatial isolation of these habitat islands limits faster colonization. However, we observed spread of these species into ecologically extreme vegetation of rock outcrops, likely due to propagule pressure from the wider surroundings and changing environmental conditions (Brown & Kodric-Brown 1977). Additionally, some other species typical of the ruderal and arable-weed vegetation can also be frequently found there. Their overall spread (Table 2) is statistically significant outside the national parks (Middle Dyje/Thaya valley dataset), likely due to the high number of grassland sites adjacent to cultivated conifer plantations, forest clearings, and arable fields. In contrast, human-disturbed sites in the proximity of rock outcrops are rare within national parks, where seminatural forests prevail in the proximity of all stands, and the presence of alien and expansive species is, therefore, less pronounced.

Repeated periods of drought

Repeated periods of summer drought in Europe in recent years may have significant ecological consequences (Büntgen et al. 2021), particularly when combined with a steadily increasing temperature (Zahradníček et al. 2021). However, the repeated sampling of the Middle Dyje/Thaya valley dataset in 2020–2021, following a period of exceptionally dry years (2016–2019; Zahradníček et al. 2021), and again in 2024 under different weather conditions, did not reveal consistent short-term effects of drought on the analyzed vegetation parameters. Because dry grasslands are dominated by long-lived perennial species, short-term climatic fluctuations may not be immediately reflected in vegetation composition. The overall long-term trends remained similar in both resurveys. A possible effect of drought was observed as the increasing prevalence of certain long-lived drought-tolerant dwarf shrubs, particularly *Teucrium chamaedrys*, which showed a systematic increase in cover in both datasets.

Conclusions

The rock outcrops with relatively extreme environmental conditions experience the same broad pressures as those affecting European dry grasslands – woody-species encroachment and eutrophication (Stevens et al. 2004, Habel et al. 2013) – but these processes are slower than in less extreme habitats. This has created a perception that such habitats do not require active conservation management, as they were assumed to be sufficiently resistant to pronounced vegetation change. However, observed trends indicate significant long-term change in vegetation composition over the past 30 years, particularly outside the national parks.

One of the primary concerns highlighted by this study is the detection of successional changes in dry grassland vegetation on rock outcrops toward more degraded stages. This degradation can be manifested in various ways – through the retreat of rare, light-demanding, and xerophilous species, an increased proportion of common species, or the new occurrence of nutrient-demanding, ruderal, expansive, or alien species and increasing dominance of shrubs. We have shown that signs of such degradation are not evident at most sites within national parks. The smaller changes recorded at these sites may be attributed to more systematic management, lower pressure from wild ungulates, a well-preserved landscape structure, and possibly also to the presence of larger patches of open rocky habitats. In contrast, non-forest vegetation further upstream is generally more vulnerable to various vegetation changes.

To counter degradation trends, targeted management actions, such as selective clearing of woody plants and extensive grazing by sheep and goats, are needed. These measures have proven effective in reversing degradation in other dry grassland habitats (Dostálek & Frantík 2008, Elias & Tischew 2016). Without such interventions, the unique biodiversity of rock outcrop vegetation may face substantial losses in the coming decades.

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Data availability statement

Both datasets are available through the ReSurveyEurope database
(https://euroveg.org/resurvey/detail/19; https://euroveg.org/resurvey/detail/37).

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Dlouhodobé změny suchých trávníků na skalních ostrožnách v údolí Dyje

Suché trávníky na skalních výchozech v říčních údolích Českého masivu bývají tradičně považovány za relativně stabilní a málo náchylné k sukcesním změnám díky mělkým půdám, oslunění a dlouhodobé kontinuitě otevřených stanovišť. Dosud však nebylo jasné, do jaké míry reagují na současné změny prostředí. V letech 2020–2024 jsme opakovali vegetační snímkování z počátku 90. let 20. století na 42 plochách v údolí řeky Dyje. Studované lokality zahrnovaly jednak střední část údolí Dyje mimo národní parky, jednak území národních parků Podyjí a Thayatal. Změny druhového složení byly hodnoceny ordinací PCoA, pomocí párového testu PERMANOVA a analýzou ekologických a funkčních skupin druhů i jednotlivých druhů. Ve vegetaci suchých trávníků byly zjištěny významné dlouhodobé změny. Opakované snímkování části lokalit navíc potvrdilo, že tyto změny nepředstavují pouze krátkodobé výkyvy způsobené meziroční klimatickou variabilitou, ale odrážejí trvalý posun ve struktuře vegetace. Na lokalitách mimo národní parky došlo zejména k nárůstu ruderálních druhů a druhů náročných na živiny, zvýšení pokryvnosti keřů a semenáčků dřevin a k úbytku vzácných a xerofilních druhů. Lokality v národních parcích vykazovaly pomalejší a méně výrazné změny, přestože i zde byl zaznamenán pokles některých vzácných druhů a zvýšení pokryvnosti keříků. Rozdíly mezi oběma částmi území pravděpodobně souvisejí s odlišným charakterem okolní krajiny, intenzitou managementu, mírou sukcese dřevin, tlakem spárkaté zvěře a šířením expanzivních či invazních druhů. Výsledky ukazují, že i extrémní trávníky na skalních ostrožnách podléhají postupné degradaci a sukcesním změnám, i když pravděpodobně pomaleji než běžné suché trávníky v kulturní krajině. Studie zároveň naznačuje význam dlouhodobé ochrany a aktivního managementu otevřených stanovišť, zejména odstraňování náletových dřevin a případné podpory extenzivní pastvy, pro zachování biodiverzity říčních údolí.

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