Preslia 95: 297–310, 2023
doi: 10.23855/preslia.2023.297

Preslia

Do threatened species occur in species-rich vegetation?

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Abstract: Conservation strategies often assume that the total number of species at a specific location can be used as a proxy for other biodiversity dimensions, such as, the presence of rare and threatened species. However, the validity of this assumption remains unclear, particularly at the plot scale. Here, we used ~17,000 vegetation plots sampled across the Czech Republic to examine the relationship between the occurrence of threatened plant species and species richness in temperate forest and grassland communities. For each individual species, the median, range, and skewness of species richness in the plots in which it occurred were used to define its distribution along the community species richness gradient. These parameters were then compared for threatened and non-threatened species. We also compared the observed values with those obtained under a null expectation to test whether threatened species occurred at random with respect to species richness. On average, threatened species occurred in species-richer plots than non-threatened species. In addition, threatened species assembled non-randomly with respect to species richness, as they occurred more often in species-richer forests but species-poorer grasslands than expected by chance. The occurrence pattern of threatened species in relation to species richness was driven by the species-pool sizes of individual habitats. Threatened species associated with low species richness were thus found in extreme habitats, such as bogs, salt marshes, peat forests, and alpine grasslands characterized by small species pools. In contrast, threatened species associated with high species richness were often found in subcontinental semi-dry grasslands and dry thermophilous forests with large species pools. Threatened species also occurred over shorter species richness gradients and were more symmetrically distributed along these gradients than non-threatened species. These patterns may reflect a high habitat specialization of threatened species or strict requirements for habitat quality. We therefore suggest that species richness is a poor indicator of conservation value when comparing habitats and geographic regions. Targeting specific habitats and using the presence or percentage of threatened or specialized species as indicators may provide better assessment of conservation value.

Keywords: community ecology, conservation, Czech Republic, endangered species, Red List, species richness, vascular plants

Received: 15 Sep 2022; Revised: 11 Jan 2023; Accepted: 14 Jan 2023; Published: 5 Jun 2023

Introduction

Protecting biodiversity from the effects of environmental change is a major global goal (Díaz et al. 2019). However, despite the adoption of numerous international agreements to address the biodiversity crisis, biodiversity continues to decrease (Watson & Venter 2017). Safeguarding and restoring ecosystems requires setting global conservation priorities so that limited resources can be focused on the areas and groups of organisms with the highest conservation value (Brooks et al. 2006, Pimm et al. 2018). Conservation strategies are often based on information on overall or endemic species richness, assuming this measure is a proxy for other biodiversity dimensions (Myers et al. 2000). Global biogeographic studies have, however, demonstrated that spatial patterns in species richness only partially explain the distribution of threatened species (Orme et al. 2005, Jenkins et al. 2013, Veach et al. 2017). In land-use planning, the occurrence of threatened species is one of the most commonly used criteria for prioritizing sites for conservation (Prendergast et al. 1993).

Red Lists of threatened organisms, which classify species into different threat categories established by the International Union for Conservation of Nature (IUCN), are important tools for the conservation of threatened species. The IUCN Red List categories and criteria provide an objective framework for classifying the risk of global extinction. Criteria for assessing threat status include ecological factors such as population size, range size, trends in abundance, and human impacts (Gärdenfors et al. 2010, IUCN 2014). The IUCN Red List criteria have inspired several national and regional agencies and research institutions to develop similar regional systems. Both international and national Red Lists have been widely used to develop databases of the occurrences of rare species to provide information for conservation planning.

Threatened and non-threatened species generally occur in communities shaped by many different factors, including environmental filtering, biotic interactions, dispersal, history of speciation and migration, and stochasticity (Götzenberger et al. 2012). The combined effects of these factors ultimately determine the number of species co-occurring in a given area. Although our understanding of community assembly has advanced considerably in recent decades, questions remain about the circumstances under which certain species groups (e.g. rare threatened species) assemble at random or under the influence of niche processes. This knowledge can inform conservation plans aimed at preserving communities and habitats where threatened species are most likely to occur.

Here, we examine the relationship between the occurrence of individual threatened plant species and species richness using a model system of temperate forest and grassland plant communities. Our study is based on ~17,000 vegetation plots sampled across the Czech Republic. Using two complementary methods, we address the following questions: (i) Does the relationship between species occurrence and diversity parameters of the plots in which they occur differ for threatened and non-threatened species in forests and grasslands? (ii) Do threatened species assemble randomly into forest and grassland communities in relation to species richness gradients?

Material and methods

The methods of this study largely follow Padullés Cubino et al. (2022).

Vegetation data

We obtained vegetation-plot data recorded in the Czech Republic from the Czech National Phytosociological Database (Chytrý & Rafajová 2003). For each vegetation plot, we used information on the presence or absence of taxa. Taxon concepts and nomenclature follow the second edition of the Key to the Flora of the Czech Republic (Kaplan et al. 2019). We classified vegetation plots into phytosociological vegetation types (associations) following the expert system for automatic classification developed by Chytrý (2007–2013). From this classification, plots that could not be unequivocally assigned to any vegetation type were excluded. The database was stratified in terms of phytosociological vegetation types and geographically to reduce differences in sampling intensity among vegetation types and areas. Stratification was done using a geographical grid with cells sized 1.25 minutes of longitude × 0.75 minutes of latitude, i.e. ~1.5 × 1.4 km. If two or more plots assigned to the same phytosociological vegetation type occurred in the same grid cell, only one of them was selected at random. This stratified resampling resulted in 30,115 plots sampled between 1922 and 2012 including all of the main vegetation types in the country. Plot records for aquatic vegetation, and of unknown size were excluded. The final dataset consisted of 18,188 plots, which were grouped into two major vegetation formations dominated by either trees and shrubs or herbaceous plants and dwarf shrubs (Supplementary Table S1). For simplicity, we refer to these vegetation formations as "forests" (n = 4,492) and "grasslands" (n = 13,696). The plot sizes ranged from 20 to 625 m^2 for forests and from 1 to 100 m^2 for grasslands.

All bryophytes, lichens, algae, and fungi records were excluded, because they were not systematically sampled in all plots. We also excluded taxa identified only at the genus level. Some commonly misidentified groups of related species were combined into aggregates. The final dataset included 1,830 species of vascular plants.

Classification of threatened species

We classified species as "threatened" following the Czech national Red List of vascular plants (Grulich 2017). This Red List includes 1,720 taxa, representing ~60% of this country's native flora. It contains two species classifications, one based on national threat categories and the other based on international categories as defined in the IUCN Red List (IUCN 2014). For the national categories, we considered species threatened if they were classified as A (extinct or missing), C1 (critically threatened), C2 (endangered) or C3 (vulnerable). For the IUCN categories, we considered threatened those species classified as EX (extinct), EW (extinct in the wild), CR (critically endangered), EN (endangered) or VU (vulnerable). We also assigned each threatened species to the most typical habitat type in which it occurs based on habitat affinity information provided by Chytrý (2007–2013) and Sádlo et al. (2007).

Calculation of the corrected species richness (S_c)

We computed the corrected species richness (S_c) for each plot to account for variable plot size in the database. S_c was calculated for each vegetation type (i.e. forests, scrub, alpine, grasslands, rocks, screes and walls, and anthropogenic vegetation) by fitting a species-area relationship (Preston 1962):

$$S = c \cdot A^Z$$

where S is species richness (i.e. the number of vascular plant species) in the plot, A is the plot area, z is the slope of the species-area relationship in log-log space, and c is a constant that depends on the unit used for area measurement and corresponds to the number of species that would occur in a unit-sized plot. We then corrected species richness to the same plot size (A_m; the median plot size in each vegetation type; Supplementary Table S1):

$$S_c = S \cdot (A_m / A)^Z$$

Statistical analyses

We performed all the analyses in R v. 4.1.0 (R Core Team 2021). First, we described the tendency of individual species to occur in communities with low or high species richness by assigning the S_c value of each plot to each species present in the plot. Then, we calculated the median, range, and skewness of each species' S_c value separately for forests and grasslands (Supplementary Fig. S1).

The median indicates the central position of the species on the species richness gradient (50th percentile). The range indicates the spread or dispersion of S_c values around the median, while skewness indicates whether S_c values are asymmetrically distributed around the median. The standardized range was calculated as the interquartile range (IQR = 75th percentile (Q3) – 25th percentile (Q1)) divided by the square root of the median. Range was standardized by using the square root of the median because the distribution of S_c approximates a Poisson distribution and thus the IQR depends on the mean and median. Without standardization, the results for the range would follow this mathematical relationship. Range depends linearly on the standard deviation, which is the square root of the mean in a Poisson distribution. As with the central distribution of species richness, we used the median, which is roughly linearly dependent on the mean.

As a measure of skewness, we calculated the Pearson moment coefficient of skewness, which is the third central moment divided by the cube of the standard deviation (Zar 2010):

$$\left(\frac{\sum (x-\bar{x})^3}{n}\right) / \left(\frac{\sum (x-\bar{x})^2}{n}\right)^{3/2}$$

Skewness was calculated using the R package 'moments' (Komsta & Novomestky 2022). This metric was then standardized by subtracting the expected skewness based on a Poisson distribution (1/√mean). After this standardization, positive values indicate a greater skewness and negative values indicate a smaller skewness than for a Poisson distribution with the same mean. In this case, we used a parametric measure of skewness in order to account for the effects of outliers and extreme values in the calculations as standardized non-parametric alternatives sensitive to these were not available. Correlations between the median and the standardized range and skewness of S_c can be found in Supplementary Fig. S2.

We used Mann-Whitney U tests to test for significant differences in the distribution of the observed mean of the median, range, and skewness of S_c of the threatened species compared to all other (non-threatened) species in forests and grasslands.

Because we assume that species richness relationships are primarily driven by diversity gradients in plant communities, the three parameters representing different features of the distribution of community species richness associated with threatened species were also combined with a null model approach to test whether threatened species assemble similarly as non-threatened species into plant communities, thus removing the effects of species richness gradients on vegetation. To obtain random S_c values for each parameter, the community matrix (species presence/absence in plots) was randomized without changing row and column totals, thus maintaining species richness in the plots and species frequency across all plots. We used the "curveball algorithm" (Strona et al. 2014) for randomizations, which can uniformly sample the set of all possible matrix configurations and requires much less computational effort than other methods. This step was repeated 999 times to generate the null distribution of random means of median, range, and skewness of S_c. Finally, the observed mean S_c of each parameter was compared with the respective null distribution of the random mean S_c and the P-values determined using the quantiles of the null distribution quantiles. The P-values were calculated as the proportion of the random mean S_c that was lower than the observed mean S_c. P-values below 0.025 indicated that the observed mean S_c of each parameter was significantly lower than expected by chance, whereas P-values above 0.975 indicated that the observed mean S_c of each parameter was significantly higher than expected by chance. The null model approach was implemented independently for forests and grasslands. The analyses separating threatened from non-threatened species based on national and IUCN threat categories were also repeated in order to test the effects of different classifications on the results.

We calculated the median, range, and skewness of S_c values for all of the species occurring in more than five plots and in more than 5% of plots in forests (126/45 species according to national/IUCN Red List categories) and grasslands (394/233 species) to avoid the influence of rare species on the analyses. However, because threatened species can be particularly rare in nature (Gärdenfors et al. 2010, IUCN 2014), we also repeated the analyses considering all threatened species (329/161 species in forests; 632/420 species in grasslands). In this case, only the median S_c values were calculated, because the range and skewness of the S_c values are not informative for small numbers (< 5).

Results

Comparison of corrected species richness (S_c) of threatened and non-threatened species

Threatened species occurred in communities with a higher species richness than other species, both in forests (Fig. 1A) and grasslands (Fig. 1C, D). However, in forests, these differences were not significant when species were classified based on the IUCN Red List categories (Fig. 1B). Virtually identical results were obtained when all threatened species (including very rare ones) were included in the analysis (Supplementary Fig. S2).

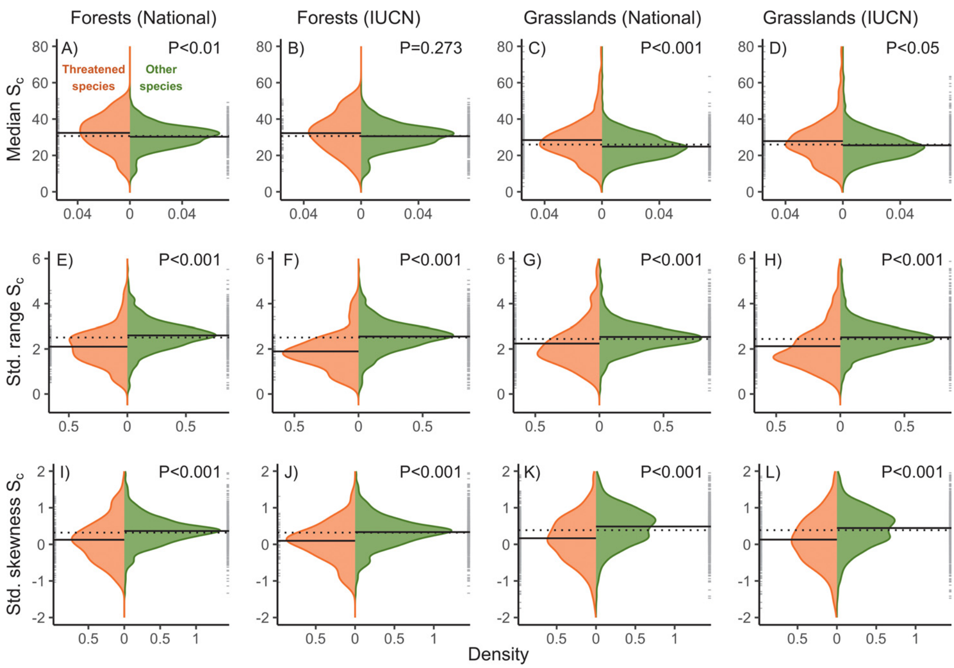

Fig. 1. Density curves for the median (1st row), range (2nd row), and skewness (3rd row) of plot-size adjusted species richness (S_c) of threatened species compared with those of all other species in forests and grasslands. Species are classified as threatened based on the Czech national Red List, using national and IUCN Red List categories. The dotted black line indicates the mean S_c value of each parameter for all species (i.e. threatened and non-threatened). The solid black line indicates the mean S_c value of each parameter for threatened and non-threatened species separately. The tick marks in the left and right margins indicate the S_c values of individual species. The range and skewness of S_c were standardized (Std.) as described in Materials and methods. P-values correspond to Mann-Whitney U tests.

Regardless of the Red List categories considered, threatened species also occurred across significantly narrower standardized ranges of richness than non-threatened species in forest and grassland communities (Fig. 1E–H). Similarly, threatened species had a more symmetric distribution of richness values than non-threatened species in both forests and grasslands (Fig. 1I–L).

In forests, the threatened species associated with the highest median S_c values occurred mainly in thermophilous oak forests (Table 1). In contrast, threatened species associated with the lowest median S_c values occurred in a variety of habitats, such as bog woodlands, mountain spruce forests, and pine forests. In grasslands, threatened species associated with the highest median S_c values occurred mainly in semi-dry grasslands (Table 2). In contrast, threatened species associated with the lowest median S_c values also occurred in a variety of habitats, such as saline habitats, alpine grasslands, or bogs. The median and quantiles of S_c for each threatened species can be found in Supplementary Table S2.

Table 1. Threatened species associated with the highest and lowest median S_c values in forest plots. For each species, the status is based on the national Red List (Grulich 2017) expressed in national and IUCN categories, the median, standardized (Std.) range, and standardized skewness of S_c, and typical habitat are given. Red List category descriptions can be found in Supplementary Data S1. Only species occurring in more than five plots are listed.

Species names	National Red List category	IUCN Red List category	Median S_c	Std. range S_c	Std. skewness S_c	Typical habitat
Species with the highest median S_c:						
Inula ensifolia	C3	NT	51.27	2.79	–0.16	thermophilous oak forests
Lathyrus pannonicus	C2b	EN	50.90	1.93	–0.21	thermophilous oak forests
Adonis vernalis	C2b	VU	49.95	2.46	–0.88	thermophilous oak forests
Orchis mascula	C2t	EN	49.03	1.65	0.32	thermophilous oak forests
Melampyrum cristatum	C3	VU	48.33	1.85	0.22	thermophilous oak forests
Pulmonaria angustifolia	C2b	VU	48.27	2.36	0.23	thermophilous oak forests
Aster amellus	C3	NT	48.11	2.48	–0.23	thermophilous oak forests
Phyteuma nigrum	C3	LC	47.97	0.68	1.41	oak-hornbeam forests
Carex umbrosa	C3	NT	47.90	1.66	0.71	swamp and floodplain forests
Orchis pallens	C2b	EN	47.62	1.98	0.26	oak-hornbeam forests
Thalictrum minus	C3	NT	46.27	2.90	–0.27	thermophilous oak forests
Platanthera chlorantha	C3	VU	44.49	0.63	–0.03	thermophilous oak forests
Thymus glabrescens	C3	NT	44.36	1.63	–0.10	thermophilous oak forests
Staphylea pinnata	C3	NT	44.32	2.76	0.26	ravine forests
Euphorbia epithymoides	C3	NT	44.32	2.74	0.37	thermophilous oak forests
Species with the lowest median S_c:						
Pyrola minor	C3	NT	20.43	1.32	–0.68	pine forests
Arabidopsis petraea	C2r	VU	20.18	1.59	0.28	pine forests
Prunus tenella	C1r	EN	19.48	2.03	0.49	low steppic scrub
Monotropa hypopitys	C3	VU	18.39	3.43	0.69	beech forests
Drosera rotundifolia	C3	VU	16.82	1.78	0.06	bog woodlands
Streptopus amplexifolius	C2t	VU	16.62	2.54	1.53	mountain spruce forests
Huperzia selago	C3	NT	15.09	2.43	0.54	mountain spruce forests
Erica carnea	C3	NT	14.67	1.48	0.35	pine forests
Carex pauciflora	C3	NT	14.14	2.16	0.31	bog woodlands
Lycopodium annotinum	C3	LC	14.14	2.63	1.37	mountain spruce forests
Vaccinium oxycoccos agg.	C3	LC	12.56	1.54	1.92	bog woodlands
Pinus uncinata subsp. *uliginosa*	C2b	EN	12.33	1.34	–0.09	bog woodlands
Andromeda polifolia	C2b	VU	11.32	1.00	0.69	bog woodlands
Rhododendron tomentosum	C3	NT	11.15	1.38	0.08	bog woodlands
Arnica montana	C3	NT	10.37	2.05	1.47	bog woodlands

Table 2. Threatened species associated with the highest and lowest median S_c values in grassland plots. For each species, the status is based on the national Red List (Grulich 2017) expressed in national and IUCN categories, the median, standardized (Std.) range, standardized skewness of S_c, and typical habitat are shown. Red List category descriptions can be found in Supplementary Material S3. Only species occurring in more than five plots are listed.

Species names	National Red List category	IUCN Red List category	Median S_c	Std. range S_c	Std. skewness S_c	Typical habitat
Species with the highest median S_c:						
Scorzonera purpurea	C2b	VU	80.00	9.48	–1.23	semi-dry grasslands
Euphorbia illirica	C3	VU	73.00	1.11	–0.95	semi-dry grasslands
Traunsteinera globosa	C2b	EN	65.93	2.14	–0.52	semi-dry grasslands
Trifolium rubens	C3	VU	65.93	2.51	–0.51	semi-dry grasslands
Pulmonaria angustifolia	C2b	VU	63.40	3.93	–0.32	semi-dry grasslands
Lathyrus latifolius	C3	NT	62.00	3.68	–0.53	semi-dry grasslands
Clematis recta	C3	NT	59.53	3.65	–0.08	semi-dry grasslands
Astragalus danicus	C3	NT	58.00	4.59	–0.28	semi-dry grasslands
Crepis praemorsa	C2b	EN	57.86	4.01	–0.48	semi-dry grasslands
Melampyrum cristatum	C3	VU	55.14	3.98	–0.04	semi-dry grasslands
Lathyrus pannonicus	C2b	EN	54.79	6.20	0.19	semi-dry grasslands
Neotinea ustulata	C1t	CR	53.93	6.03	–0.06	semi-dry grasslands
Cirsium pannonicum	C3	NT	53.00	4.28	0.04	semi-dry grasslands
Pulmonaria mollis	C3	NT	52.00	4.32	0.26	semi-dry grasslands
Potentilla alba	C3	VU	51.96	4.37	0.22	intermittently wet to semi-dry grasslands
Species with the lowest median S_c:						
Festuca supina	C3	VU	11.04	-6.89	1.07	alpine grasslands
Sclerochloa dura	C2b	VU	10.80	2.01	1.67	trampled habitats
Woodsia ilvensis	C2r	EN	10.77	2.39	0.54	rock outcrops
Vaccinium oxycoccos agg.	C3	LC	10.32	1.61	1.44	bogs
Carex bigelowii subsp. *dacica*	C2r	EN	9.84	1.60	2.12	alpine grasslands
Koeleria glauca	C1t	CR	9.59	1.74	1.04	sandy grasslands
Huperzia selago	C3	NT	9.58	1.50	0.95	alpine grasslands
Asplenium adulterinum	C1r	VU	9.42	0.62	–0.11	rock outcrops
Suaeda prostrata	A1	RE	8.66	1.59	0.80	saline habitats
Spergularia media	C1t	CR	8.66	1.44	0.62	saline habitats
Festuca psammophila subsp. *psammophila*	C1t	EN	8.47	2.47	1.20	sandy grasslands
Lycopodium annotinum	C3	LC	7.83	0.78	–0.22	heathlands
Salicornia prostrata	A1	RE	7.22	0.93	0.85	saline habitats
Rhododendron tomentosum	C3	NT	4.98	-0.20	–0.66	bogs
Crypsis aculeata	C1t	CR	2.89	3.30	0.86	saline habitats

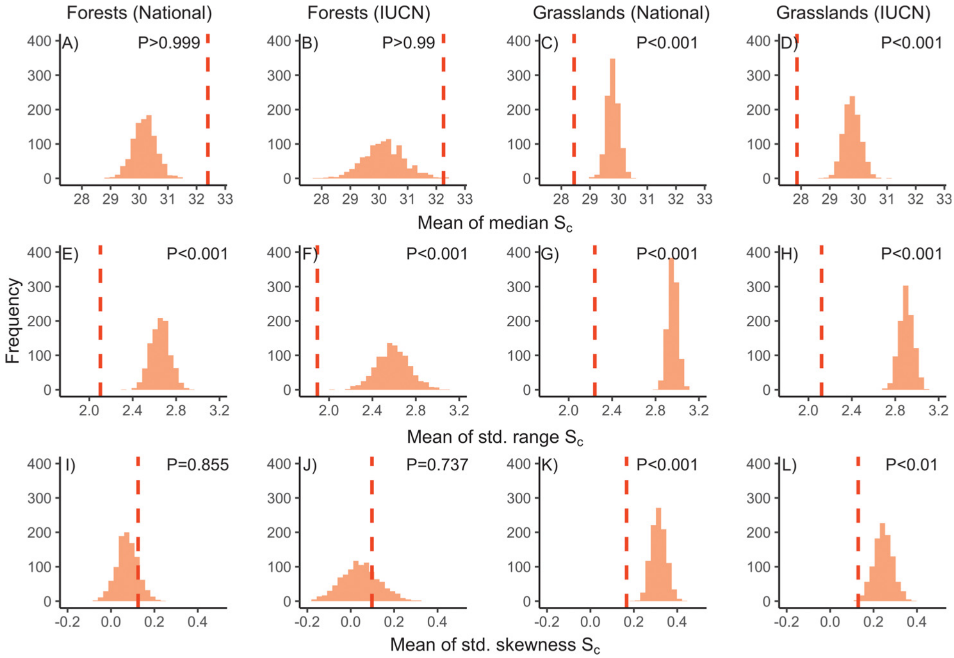

Fig. 2. Comparison of the mean observed values of the median (1st row), range (2nd row), and skewness (3rd row) of S_c of threatened species (dashed red line) with the distributions of mean random values of S_c of the same parameters (orange bars). Results are for threatened species in forests and grasslands based on the Czech national Red List using national and IUCN Red List categories. The range and skewness of S_c were standardized (Std.) as described in Materials and methods. P-values indicate the proportion of randomized parameters that are lower than the observed value.

Comparison of corrected species richness (S_c) of threatened species with the random expectation

Threatened species tended to occur more often in communities with higher species richness than under random expectation in forests (Fig. 2A, B), but with lower species richness than under random expectation in grasslands (Fig. 2C, D). They also tended to occur in communities with a species richness value closer to the median than under random expectation in forests and grasslands (Fig. 2E–H). Threatened species occurred in communities with richness values more symmetrically distributed around the median than under random expectation in forests (Fig. 2I, J), but more positively skewed than under random expectation in grasslands (Fig. 2K, L).

Discussion

The observed patterns were largely consistent between the two Red List types, which indicates that the results do not depend on a particular definition of threatened species. We found only a weak relationship between the occurrence of threatened species and community species richness. This finding contributes the community-scale perspective to global biogeographic studies that identified discrepancies between geographic distributions of total species richness and threatened species (Orme et al. 2005, Jenkins et al. 2013, Veach et al. 2017). Rather than being concentrated in species-rich vegetation, threatened species occur along the entire gradient of plant community species richness. An inspection of median S_c values (Tables 1, 2; Supplementary Table S2) reveals that threatened species associated with low species richness are specialists of extreme habitats, including fens and peat forests, alpine grasslands, oligotrophic forests, oligotrophic and dry sandy grasslands, rocky outcrops, and saline habitats. In contrast, threatened species associated with high species richness are present mainly in subcontinental semi-dry grasslands (Tables 1, 2) and dry thermophilous forests.

These results agree well with the pattern of native species pool sizes in different habitats in the Czech Republic (Sádlo et al. 2007). The largest species pools (> 500 species) are found in grassland habitats (including subcontinental semi-dry grasslands), scrub, and various types of thermophilous forests. In contrast, the extreme habitats hosting threatened species with the lowest S_c values have small species pools (~100 native species or fewer). Thus, the relationship between median S_c values and threatened species occurrence appears to be largely driven by the patterns in the size of habitat species pools rather than a general preference of threatened species for highly diverse communities. The negative relationship between threatened species and species richness found in the null model analysis for grasslands (Fig. 2) seems paradoxical. However, we assume that this result reflects the high diversity of open habitats in extreme environmental conditions in central Europe (Chytrý 2007–2013), some of which harbour a high number of specialized threatened species relative to their total species number (Table 2).

In contrast to the weak pattern found for median species richness, threatened species have narrower ranges of S_c values than non-threatened species, i.e. they occur over shorter diversity gradients. The difference in community assembly rules between threatened and non-threatened species may reflect two aspects of threatened species distribution. First, a narrow range of S_c values may be a consequence of, on average, the higher habitat specialization of threatened species (Zelený & Chytrý 2019: Fig. 1F). Second, the narrow range of S_c values for threatened species may reflect their stricter requirements for habitat quality compared to non-threatened species. While the first mechanism is straightforward and supported by direct empirical evidence (Zelený & Chytrý 2019), the second requires further examination.

Habitat quality and consequently habitat suitability for threatened species may not be related to local species richness in a unidirectional way, with higher richness indicating also higher habitat quality. This positive relationship may only apply to habitats with large species pools. In these habitats, the occurrence of threatened species may be associated with species-rich sites, while many threatened species are sensitive to environmental change and are the first to disappear following a decline in habitat quality. In central Europe, this is especially the case in various grassland or deciduous forest communities (Galvánek & Lepš 2009, Kopecký et al. 2013, Lepš 2014, Roleček & Řepka 2020).

However, in extreme environments, this relationship may be reversed due to the limited species pool (Hillebrand et al. 2018). Therefore, even species-poor habitats can be of high quality and harbour threatened specialist species. Degradation of such habitats may not result in a decrease in total species diversity because the loss of (threatened) specialists is compensated for by the establishment of (non-threatened) generalists. Empirical evidence for such a contrasting pattern between habitat specialists and generalists has been recorded in several types of vegetation. For example, in oligotrophic forests, a decline in specialist species and a general community homogenization by generalists coupled with an increase in local species richness is attributed to eutrophication (Naaf & Wulf 2010, Reinecke et al. 2014). Species richness of alpine snow-bed grasslands was observed to increase with climate warming, but this was associated with a decline in specialist species (Matteodo et al. 2016, Amagai et al. 2018). Degradation of mire communities caused by eutrophication and climate change is also associated with declines in mire specialists, but their local species richness may increase with the establishment of generalist wet-meadow species (Hájek et al. 2020, Kolari et al. 2021).

Threatened species also respond differently to ecological restoration of habitats that differ in the size of their species pool. Restoration of habitats with large species pools, such as dry grasslands, is mainly associated with the establishment of generalist species in the short and medium-term (Lepš et al. 2007, Prach et al. 2014). In contrast, ecological restoration of extreme habitats created by natural disturbance or human activities, such as mining, may be followed by the rapid appearance of threatened specialists of the respective habitats. This trajectory of successional development was reported in several case studies of sandy grasslands (Olsson & Ödman 2014, Řehounková et al. 2021), halophytic vegetation (Danihelka et al. 2022), limestone quarries (Tropek et al. 2010), and fens (Ekrtová et al. 2018). However, this pattern is unlikely to be universal, as the dynamics of the establishment of threatened species can vary considerably depending on type of habitat. Therefore, mapping and targeting habitats with a favourable ecological status can complement floristic surveys aimed at the conservation of threatened plants.

The inferences about the range of S_c values were supported by the patterns of S_c skewness. The comparative analysis revealed that non-threatened species tend to have a positively skewed S_c value distribution (Fig. 1), i.e. they mostly occur in the lower part of their S_c range with occasional occurrences in more species-rich communities. In contrast, the distribution of S_c values was generally more symmetric for the threatened species, which was also confirmed by the null model analysis of grasslands (Fig. 2). This pattern is again consistent with the fact that threatened species either occur in species-rich habitats, where their distribution of S_c values is limited by the general upper limit of species richness or are specialists of species-poor extreme habitat types and cannot establish elsewhere.

Conclusions

Using a country-wide dataset, we demonstrated that the occurrence of threatened species is weakly associated with community species richness. Threatened species occur across the entire richness gradient. The relationship between the occurrence of individual species and species richness is largely determined by the size of their habitat species pools. At the same time, individual threatened species occur across shorter species richness gradients than non-threatened species. Their occurrence patterns along these gradients also tend to be more symmetric. We interpret this pattern in community assembly as a possible consequence of high habitat specialization or the strict requirements for habitat quality of many threatened species. Therefore, we suggest that species richness is a weak predictor of conservation value at large spatial scales when comparing different habitats or geographical areas. Conservation value may be better estimated from the occurrence or proportion of threatened or specialist species in particular habitat types than from total species richness.

Supplementary material

Data S1. Reference categories for the national and IUCN Red Lists.
Fig. S1. Schematic representation illustrating how the variation in the distribution of community species richness associated with individual species is described by the median, range, and skewness.
Fig. S2. Correlations between the median, range, and skewness of community species richness.
Fig. S3. Results considering all threatened species.
Table S1. Overview of the vegetation plots included in the different vegetation types.
Table S2. The community species richness values of individual threatened species occurring in forests and grasslands.

Supplementary materials are available at www.preslia.cz

Acknowledgments

This study was supported by the Czech Science Foundation projects 19-28491X (JPC, JT, and MC) and 20-02901S (JL).

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Rostou ohrožené druhy rostlin v druhově bohaté vegetaci?

Priority v ochraně přírody se často stanovují na základě druhové bohatosti. To vychází z předpokladu, že biologickou hodnotu dané lokality lze stanovit na základě celkového počtu druhů, s nímž koreluje počet ohrožených nebo vzácných druhů. Pro takovou souvislost mezi výskytem ohrožených druhů a druhovou bohatostí ale chybí empirická podpora. To platí zejména pro malou prostorovou škálu společenstev zachycených fytocenologickým snímkováním. Proto jsme prozkoumali souvislost mezi výskytem ohrožených druhů rostlin a druhovou bohatostí lesních společenstev a bezlesí na souboru přibližně 17 000 fytocenologických snímků z České republiky. Pro každý druh jsme spočítali medián, rozsah a šikmost rozložení hodnot druhové bohatosti snímků, v nichž se daný druh vyskytoval. Tím jsme definovali jeho vztah ke gradientu druhové bohatosti v lese nebo bezlesí. Následně jsme porovnali hodnoty těchto parametrů mezi ohroženými a ostatními druhy. Kromě toho jsme použili nulové modely, abychom otestovali nulovou hypotézu, že se ohrožené druhy vyskytují ve vegetaci nezávisle na parametrech druhové bohatosti. Zjistili jsme, že ohrožené druhy se vyskytují v průměru v druhově bohatších plochách než ostatní druhy. Navíc se ohrožené druhy vyskytují ve vztahu k druhové bohatosti nenáhodně, protože jsou častější v druhově bohatších lesích a druhově chudší travinné vegetaci, než by se dalo předpokládat při náhodném rozložení. Ohrožené druhy se vyskytují jak v druhově bohatých, tak druhově chudých společenstvech, přičemž vztah mezi jejich výskytem a druhovou bohatostí závisí na velikosti zásobníku druhů daného biotopu. Ohrožené druhy druhově chudé vegetace tak rostou v extrémních biotopech ovlivněných stresem, jako jsou např. vrchoviště, slaniska, rašelinné lesy a alpínské bezlesí. Jiné ohrožené druhy najdeme v druhově bohatých společenstvech, jako jsou vysýchavé subkontinentální trávníky a teplomilné lesy. Zjistili jsme ovšem, že se jednotlivé ohrožené druhy vyskytují ve snímcích s menším rozsahem hodnot druhové bohatosti než ostatní druhy. Zároveň vykazovaly i symetričtější rozložení na gradientu druhové bohatosti. To může být odrazem jejich vyšší ekologické specializace nebo vyšších nároků na kvalitu biotopů. Z našich analýz vyplývá, že druhová bohatost není dostatečným indikátorem ochranářské hodnoty vegetace, zejména při srovnání různých biotopů nebo geografických oblastí. Namísto toho je při ochranářském hodnocení potřeba zohlednit spíš počet ohrožených druhů nebo specialistů na daný typ biotopu.

How to cite: Padullés Cubino J., Fibich P., Lepš J., Chytrý M. & Těšitel J. (2023) Do threatened species occur in species-rich vegetation? – Preslia 95: 297–310.

Preslia, a journal of the Czech Botanical Society

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