Forest Ecosystems 12 (2025) 100278

Contents lists available at ScienceDirect

Forest Ecosystems

journal homepage: www.keaipublishing.com/cn/journals/forest-ecosystems

Topographic complexity drives trait composition as well as functional and phylogenetic diversity of understory plant communities in microrefugia: New insights for conservation

Kata Frei [a,b,*], Anna E-Vojtkó [c], Csaba Tölgyesi [d,e], András Vojtkó [f], Tünde Farkas [g], László Erdős [e,h], Gábor Li [a,b], Ádám Lőrincz [a,i], Zoltán Bátori [a,d]

[a] Department of Ecology, University of Szeged, Közép fasor 52, 6726, Szeged, Hungary
[b] Doctoral School of Environmental Sciences, University of Szeged, Rerrich Béla tér 1, 6720, Szeged, Hungary
[c] Institute of Botany, Czech Academy of Sciences, Dukelská 135, 379 82, Třeboň, Czech Republic
[d] MTA-SZTE 'Lendület' Applied Ecology Research Group, University of Szeged, Közép fasor 52, 6726, Szeged, Hungary
[e] HUN-REN–UD Functional and Restoration Ecology Research Group, Egyetem tér 1, 4032, Debrecen, Hungary
[f] Department of Botany and Plant Physiology, Eszterházy Károly Catholic University, Leányka utca 6, 3300, Eger, Hungary
[g] Aggtelek National Park Directorate, Tengerszem oldal 1, 3758, Jósvafő, Hungary
[h] Institute of Ecology and Botany, HUN-REN Centre for Ecological Research, Alkotmány utca 2-4, 2163, Vácrátót, Hungary
[i] Doctoral School of Biology, University of Szeged, Közép fasor 52, 6726, Szeged, Hungary

A R T I C L E I N F O

Keywords:
Doline
Forest herbs
Functional diversity
Microclimate
Microhabitat
Phylogenetic diversity
Species trait
Vegetation

A B S T R A C T

Topographic complexity supports the maintenance of a high diversity of microhabitats, which may act as important 'safe havens' – or microrefugia – for biodiversity. Microrefugia are sites with specific environmental conditions that facilitate the persistence of species during environmental changes and exhibit unique eco-evolutionary dynamics. However, our knowledge about how topographic complexity and related eco-evolutionary selective forces influence the functional and phylogenetic signatures of species assemblages in microrefugia is very limited. Although the conceptual framework on the systematic integration of plant functional traits into the study of refugia is well established, more empirical studies on functional trait composition and functional diversity in refugia are urgently needed for more effective conservation. Here we analyzed the distribution of various plant functional traits and phylogenetic patterns in microhabitats (south- and north-facing slopes, and bottoms) of 30 large topographic depressions (i.e. doline microrefugia) and microhabitats of the surrounding plateaus in two distant forested karst regions. We found that plant assemblages in the understory of dolines and their surroundings are characterized by unique functional values and combinations of traits. Doline bottoms had the highest functional diversity among doline microhabitats and supported plant assemblages with considerably different trait compositions from the plateaus. Bottoms also had the highest phylogenetic diversity. These results suggest that topographic complexity in forested dolines has a significant effect on the distribution of plant functional traits in the understory. High functional and phylogenetic diversity in doline bottoms can have important consequences for the long-term survival of plant populations, highlighting that these microhabitats may provide a higher resilience and support an adaptive community-level response to natural and anthropogenic stressors. Understanding mechanisms that drive the survival of species within microrefugia is required to determine the best conservation and management strategies.

1. Introduction

Topographically complex regions provide microhabitats with clearly different environmental conditions and feature hotspots of biodiversity (Badgley et al., 2017). These microhabitats may be colder or warmer, drier or moister, and more nutrient-rich or nutrient-poor than their surroundings, allowing species to survive changes in their environment by tracking their preferred microhabitats (Frei et al., 2023). In addition, topographic complexity creates environmental stability and therefore may support the formation of microrefugia. Microrefugia are sites that

* Corresponding author. Department of Ecology, University of Szeged, Közép fasor 52, 6726, Szeged, Hungary.
E-mail address: freikata98@gmail.com (K. Frei).

https://doi.org/10.1016/j.fecs.2024.100278
Received 10 June 2024; Received in revised form 29 October 2024; Accepted 11 November 2024

remain relatively buffered from regional environmental changes and therefore provide important 'safe havens' for biodiversity (Rull, 2009; Keppel et al., 2012). The persistence of such refugia is facilitated by a wide range of biophysical factors, supporting the long-term survival of populations and ecological communities by ecosystem-protected (e.g., vegetation cover) and/or terrain-mediated (e.g., topography) mechanisms (Stralberg et al., 2020). For instance, local depressions in topographically complex landscapes promote cold-air pooling, and water and nutrient retention that support the persistence of various species (Dobrowski, 2011; McLaughlin et al., 2017; Frei et al., 2023). Such buffering may be more pronounced due to the combined effects of forest canopy cover and topographic complexity (Lenoir et al., 2017). A better understanding of the effects of these biophysical factors and refugia-promoting processes on local populations and ecological communities can provide important insights for the conservation and management of microrefugia (Morelli et al., 2016; Selwood and Zimmer, 2020).

Approaches for studying microrefugia are wide-ranging, including biogeographic (e.g., evaluating species distribution models), climatic (e.g., measuring thermal stability), ecological (e.g., assessing species–environment relationships) and taxonomic (e.g., describing new species) studies (Dobrowski, 2011; Finocchiaro et al., 2024). Nonetheless, our knowledge is still very limited about how eco-evolutionary selective forces influence the functional signature of ecological communities in microrefugia, compared to their surroundings (Keppel et al., 2018; Marcantonio et al., 2021). As functional traits (i.e. morphological, physiological, and phenological characteristics of organisms that influence performance or fitness) can relay how species respond to their environment (Weiher et al., 1999; McGill et al., 2006), functional trait studies may reveal how contemporary ecological mechanisms drive community assembly (Violle et al., 2007; Götzenberger et al., 2012). Coupling functional traits and phylogeny may offer different and complementary information about the various eco-evolutionary processes shaping the organization and composition of communities (de Bello et al., 2017; Keppel et al., 2018). According to the conceptual framework proposed by Keppel et al. (2018), continuously favorable environmental conditions and strong biotic interactions in refugia may facilitate the persistence of species and specific trait combinations that are purged from the less stable surrounding landscapes. Although the systematic integration of plant functional traits into the study of refugia is well established, more empirical studies on functional trait composition and functional diversity in these entities are urgently needed (Keppel et al., 2018). This is also highlighted by Ottaviani et al. (2019), who found that plants in resource-rich microrefugia are characterized by distinct functional signatures and have more diverse ecological strategies compared to the surrounding resource-impoverished landscape, enabling them to be more resilient to environmental changes.

In this study we sought to provide an empirical account of how topographic depressions (dolines or sinkholes) influence the plant trait distributions, and functional and phylogenetic diversity of forested karst areas, highlighting that the studied mechanisms can provide a deeper insight into the eco-evolutionary dynamics of microrefugia. As karst landscapes cover large portions (ca 15%) of the Earth's land surface and dolines are the dominant landforms in these landscapes (White et al., 1995), understanding the mechanisms that drive community assembly in dolines is crucial for conserving global biodiversity.

Previous studies have demonstrated that dolines may provide local biodiversity hotspots and microrefugia for a number of vascular plant species, as they support high microhabitat diversity and have the capacity to maintain microhabitats of high environmental stability (Kobal et al., 2015; Bátori et al., 2017; Čarni et al., 2022). The presence of permanently cold, moist, and resource-rich microhabitats in the bottom of dolines may considerably enhance their refugial capacity, which facilitates the long-term persistence of plant species associated with cold and/or moist conditions (e.g., montane species) (Keppel et al., 2015; Frei et al., 2023). Although the mechanisms that drive species composition and vegetation patterns in topographic depressions have been analyzed in detail over recent decades (e.g., Kobal et al., 2015; Bátori et al., 2017, 2023), to date no study has compared plant functional trait composition, functional diversity, and phylogenetic diversity within and adjacent to doline microrefugia. To fill this knowledge gap, here we compare the distribution of plant functional traits (dispersal, floral, leaf–height–seed or LHS, and life form traits) and the functional and phylogenetic patterns in the understory within and adjacent to 30 forested doline microrefugia in two distant karst regions in Hungary. Based on the conceptual framework proposed by Keppel et al. (2018), we hypothesized that (i) topographic complexity in dolines creates microhabitats that are characterized by different values and combinations of plant functional traits and that (ii) doline bottoms have greater functional diversity compared to the other microhabitats. We also hypothesized that (iii) plant assemblages in doline bottoms have functionally similar traits belonging to distantly related lineages. Finally, we integrate our observations into a framework that extends to the conservation and management of such microrefugia.

2. Materials and methods

2.1. Study regions and sampling design

We studied dolines in the Aggtelek Karst (northern Hungary, 48°30′37″ N, 20°33′59″ E; between 400 and 600 m a.s.l.) and in the Mecsek Mountains (southern Hungary, 46°7′18″ N, 18°8′21″ E; between 300 and 600 m a.s.l.) (Fig. 1a). The climate is sub-continental in the Aggtelek Karst (mean annual rainfall: 640–700 mm, and mean annual temperature: 8 °C), and sub-continental with sub-Mediterranean influences in the Mecsek Mts (mean annual rainfall: 700–750 mm, and mean annual temperature: 9.5 °C) (Dövényi, 2010). The cool and moist conditions of dolines provide 'safe havens' for a number of plant species and forest vegetation types in both regions (Fig. 1b, c and d). In the Aggtelek Karst, the dominant vegetation types on the plateaus are oak-hornbeam (*Carici pilosae-Carpinetum*) and rocky forests (*Tilio-Fraxinetum excelsioris*), while dolines are covered by scree (*Mercuriali-Tilietum*) and/or beech forests (*Melittio-Fagetum*) (Virók et al., 2016). In the Mecsek Mts, the dominant vegetation type on the plateaus is oak-hornbeam forest (*Asperulo taurinae-Carpinetum*), while dolines are covered by beech (*Helleboro odoro-Fagetum*) and/or ravine forests (*Scutellario altissimae-Aceretum*) (Bátori et al., 2021). The structure of these forests was similar within a region.

Frei et al. (2023) have previously studied the microclimate and various soil parameters within and adjacent to these dolines and found that doline bottoms consistently promote cold-air drainage and pooling, as well as high relative air humidity. Due to the concave topography of dolines (Fig. 1e), bottoms also have the capacity to retain more water and accumulate higher amounts of nutrients than their surroundings. Steep moisture and nutrient gradients may be observed along the doline slopes (from the relatively dry and nutrient-poor plateau toward the wet and nutrient-rich doline bottoms). As a result, topographic complexity in karst landscapes has a profound effect on the interactions among microclimate, soil properties, and hydrologic mechanisms, which in turn influences plant distributions. A more detailed description of the soil, microclimate, and species composition in these dolines and their surroundings is provided in Frei et al. (2023).

We selected 15 large dolines (diameters: 80–150 m, depths: 10–20 m, forest age: 100–120 years in the Aggtelek Karst, and 70–80 years in the Mecsek Mts) for vegetation sampling in each region (30 dolines in total). Six sampling locations were established for each doline: one on the central part of the south-facing slope, one in the doline bottom, one on the central part of the north-facing slope, and three on the surrounding plateau (180 locations in total) (Fig. 1b). We sampled the vegetation in each location using three randomly placed 2 m × 2 m permanent plots in two seasons (before canopy closure in spring, and after canopy closure in summer). The cover of herbs, shrubs, and tree saplings was estimated

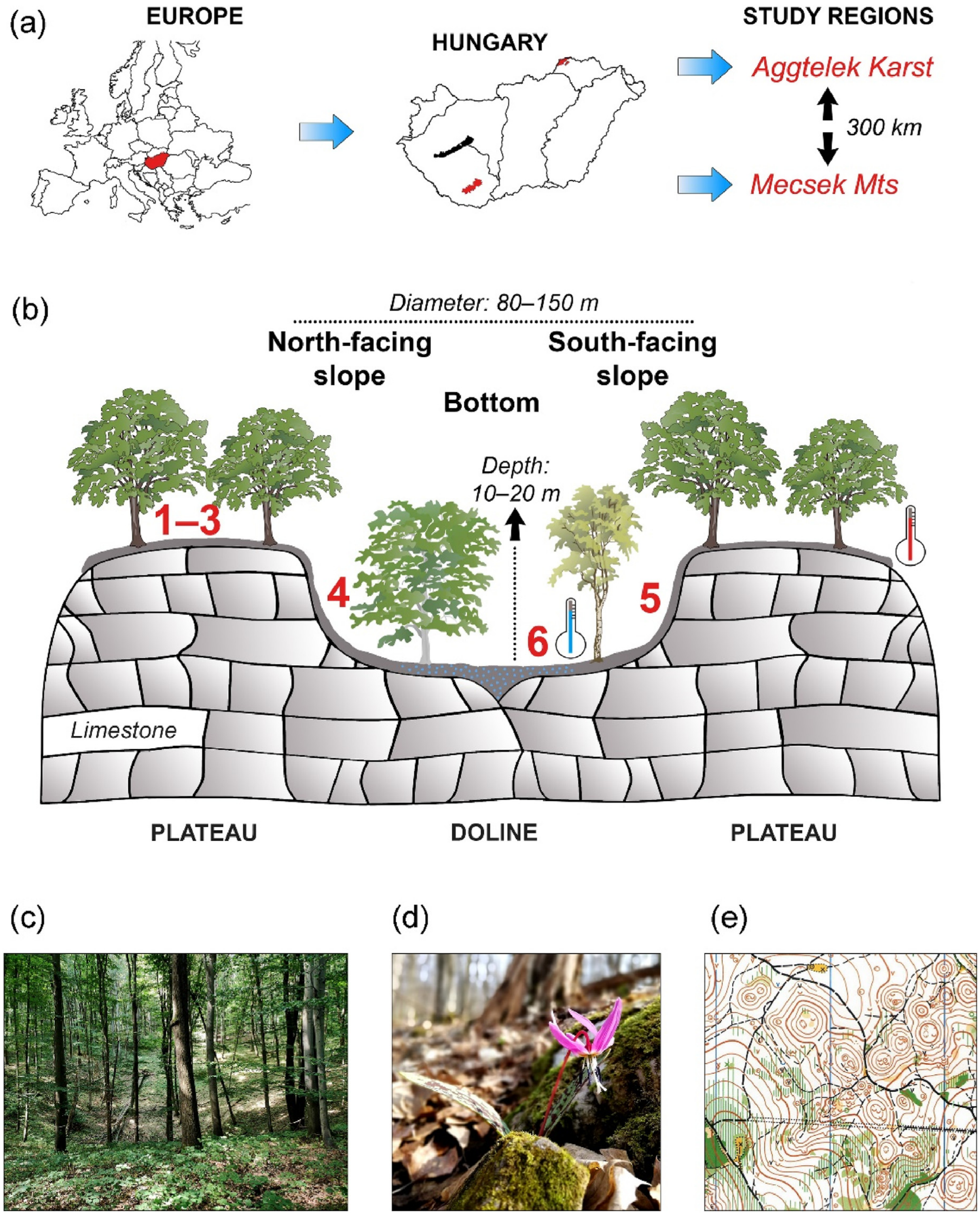

Fig. 1. Study regions and study design. **(a)** Location of the two study regions (Aggtelek Karst and Mecsek Mts), indicated by red color, **(b)** sampling locations in the plateau (1–3) and doline microhabitats (4–6), **(c)** an oak-hornbeam forest on the edge of a large doline in the Mecsek Mts, **(d)** *Erythronium dens-canis*, a rare spring geophyte on the north-facing slope of a large doline in the Aggtelek Karst, and **(e)** contour lines of some dolines in the Mecsek Mts (source: orienteering map of the Mecsek Mts at a scale of 1:7500). Images: http://ian.umces.edu/symbols/. Photos by Zoltán Bátori. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

visually in each plot. If a species had both spring and summer cover values, we used the larger value of each species for data analyses. Plot data are provided in the supplemental material of Frei et al. (2023).

2.2. Plant functional traits

We selected nine plant functional traits that capture the main ecological strategies of plants in the studied understory communities and are widely used in functional trait studies. These are 1) plant height, 2) specific leaf area (SLA), 3) leaf area (LA), 4) seed mass, 5) start of flowering, 6) duration of flowering, 7) pollination type, 8) dispersal distance class, and 9) life form (Table S1). Leaf–height–seed (LHS) traits, including SLA, LA, plant height and seed mass, may provide a useful gauge of habitat characteristics and ecosystem functioning (Westoby, 1998; Díaz et al., 2004). Floral traits, such as start and duration of flowering, and pollination type provide information about the reproduction strategy and floral resources of plant assemblages (Kremen et al., 2007), while dispersal ability may provide important insights into the spatial dynamics of plant populations and the structure of plant assemblages (Lososová et al., 2023). We did not consider dispersal distance class 7 (anthropochorous species) in our study, as only the first six classes (which correspond to natural dispersal) are appropriate for such landscape-scale studies (Lososová et al., 2023). We used the modified Ellenberg–Müller–Dombois life form system (i.e. life form traits), adapted to the vascular plants of Hungary (Botta-Dukát et al., 2023). Subcategories were taken into account only in the case of phanerophytes, differentiating trees and shrubs. Similar to Conti et al. (2023) and E-Vojtkó et al., (2023), we excluded tree saplings from all analyses due to the following reasons: 1) most of the saplings will likely perish over the next few years, and 2) the vegetative and generative traits of trees are measured on fully mature individuals. Trait data were collected from regional data sources, and if these were not available, we used European databases (Table S1). We calculated the average trait values for traits with multiple records. If more than one pollination type occurred for a species, we considered the most common one.

2.3. Statistical analysis

Species cover values were averaged for the three plots of each sampling location in each doline before analysis, resulting in 120 averaged vegetation samples in total (samples hereafter). In order to decrease the importance of the most dominant species, we log-transformed the plant cover data. We also log-transformed the quantitative traits (plant height, start and duration of flowering, seed mass, specific leaf area, and leaf area) before analyses to improve normality. To describe the functional structure of the studied plant assemblages, we calculated community-weighted means (CWMs) on the microhabitat level (plateau, south-facing slope, north-facing slope, and bottom) for quantitative traits, while we evaluated nominal and ordinal traits (life form, pollination type, and dispersal distance class) by analyzing the cover of each level or class separately. We used linear mixed-effects models (LMMs) to test the effects of microhabitats on the CWM values. In the models, CWMs for each trait for each sample were used as response variables, microhabitats were included as fixed factors, while doline ID nested within region was used as a random factor.

We performed a functional principal coordinate analysis (PCoA) to visually assess the compositional differences in trait values among microhabitats (plateau, south-facing slope, north-facing slope, and bottom). For this we prepared a sample × trait matrix, with the values being the CWMs of the microhabitats for each trait (cf. Tölgyesi et al., 2019). Levels of the nominal and ordinal traits were handled as dummy variables with fuzzy coding. As the range of CWM values differed considerably, we log-transformed them before analysis. Two levels of life form traits (parasites and saprophytes) were excluded from the analysis, as they were absent in almost all samples. We then calculated a distance matrix using Gower distance to prepare the functional PCoA. Using this distance matrix, we also calculated pairwise permutational multivariate analysis of variance (PERMANOVA) among the microhabitats to test their effects on the functional composition, based on 999 permutations. The *p*-values were adjusted for multiple comparisons with the FDR method. To gain a deeper insight into the possible changes in the functional strategies of species, we explored the potential functional space across all communities in each region as an addition to the functional PCoA. For this we first identified the number of dimensions needed to build our functional trait space and ran a principal component analysis (PCA) on the species × trait matrix using only quantitative traits. Then we built functional trait spaces for each region separately by using kernel density estimations. Microhabitat was used as a grouping vector, thus we could build a functional trait space for each habitat (plateau *vs.* doline) and microhabitat in each region and contrast them with the functional trait space of the whole community.

To test whether overall functional diversity was different among the four microhabitats (plateau, south-facing slope, north-facing slope, and bottom), we computed Gower distances between pairs of species to produce multi-trait dissimilarity. Using this dissimilarity matrix, we calculated a functional diversity index – mean pairwise distance (MPD) – for each microhabitat by combining the nine traits (de Bello et al., 2021a). To measure the phylogenetic diversity in the microhabitats, we first prepared a dated, ultrametric phylogeny for the studied plant species by pruning the DaPhnE supertree, which is highly resolved for the Central European flora (Durka and Michalski, 2012). Then we calculated a distance matrix, where phylogenetic distances were acquired as the sum of the branch lengths that separate two species in the pruned tree. Using this distance matrix, we calculated a phylogenetic diversity index – mean pairwise distance (MPD) – between all species pairs. We used LMMs to test the effects of microhabitats on both the functional and phylogenetic MPD values, similarly as before.

To determine whether the microhabitats (plateau, south-facing slope, north-facing slope, and bottom) are functionally and phylogenetically over- or underdispersed and thus draw inferences regarding the dominant assembly processes in the studied plant assemblages, we measured the standardized effect size of MPD (SES.MPD) as follows:

$$\mathrm{SES.MPD} = \frac{\mathrm{MPD_{obs}} - \mathrm{mean}(\mathrm{MPD_{null}})}{\mathrm{sd}(\mathrm{MPD_{null}})}$$

where $\mathrm{MPD_{obs}}$ is the observed MPD within assemblages, and $\mathrm{MPD_{null}}$ is the null expectation (de Bello et al., 2021a). For functional SES.MPD, null models were generated using 999 randomizations of the species names in the trait dissimilarity matrix. For phylogenetic SES.MPD, we generated the null models by shuffling the species names across the branch tips of the full tree. Positive SES values indicate that the species coexisting in the studied plant assemblages are functionally more different or phylogenetically more distantly related than expected by chance (trait divergence or phylogenetic overdispersion), while negative SES values indicate the opposite, i.e. species coexisting in the studied plant assemblages are functionally more similar or phylogenetically more closely related than expected by chance (trait convergence or phylogenetic clustering) (de Bello et al., 2021a). We used LMMs to test the effects of microhabitats on the SES.MPD values, similarly as before. To test whether SES.MPD values differed significantly from zero (i.e. from null expectations), we performed one-sample *t*-tests ($\mu = 0$).

All analyses were performed in R (v. 4.2.2, R Core Team, 2022). We calculated CWMs with the *functcomp* function of the 'FD' package (Laliberté et al., 2014), and LMMs with the *lmer* (Gaussian error term) function of the 'lme4' package (Bates et al., 2015). We used the *Anova* function of the 'car' package to test model significances (Fox and Weisberg, 2011), and the *emmeans* function of the 'emmeans' package to calculate pairwise comparisons (Lenth, 2021). Gower distance was calculated using the *gawdis* function of the 'gawdis' package (de Bello et al., 2021b). Pairwise PERMANOVAs were calculated with the *adonis2* function, and functional PCoA was prepared with the *wcmdscale* function of the 'vegan' package (Oksanen et al., 2018). We used the *princomp* function of the 'vegan' package and the *funspace* function of the 'funspace' package for preparing the functional trait spaces (Carmona et al., 2024). We used the *match_data* function provided by de Bello et al. (2021a) to prune the DaPhnE supertree, and the *cophenetic* function of the 'ape' package to calculate the phylogenetic distance matrix. In both cases, MPD values were abundance-weighted and calculated with the *melodic* function provided by de Bello et al. (2016), while null models were generated using the R code provided by de Bello et al. (2021a) and Swenson (2014).

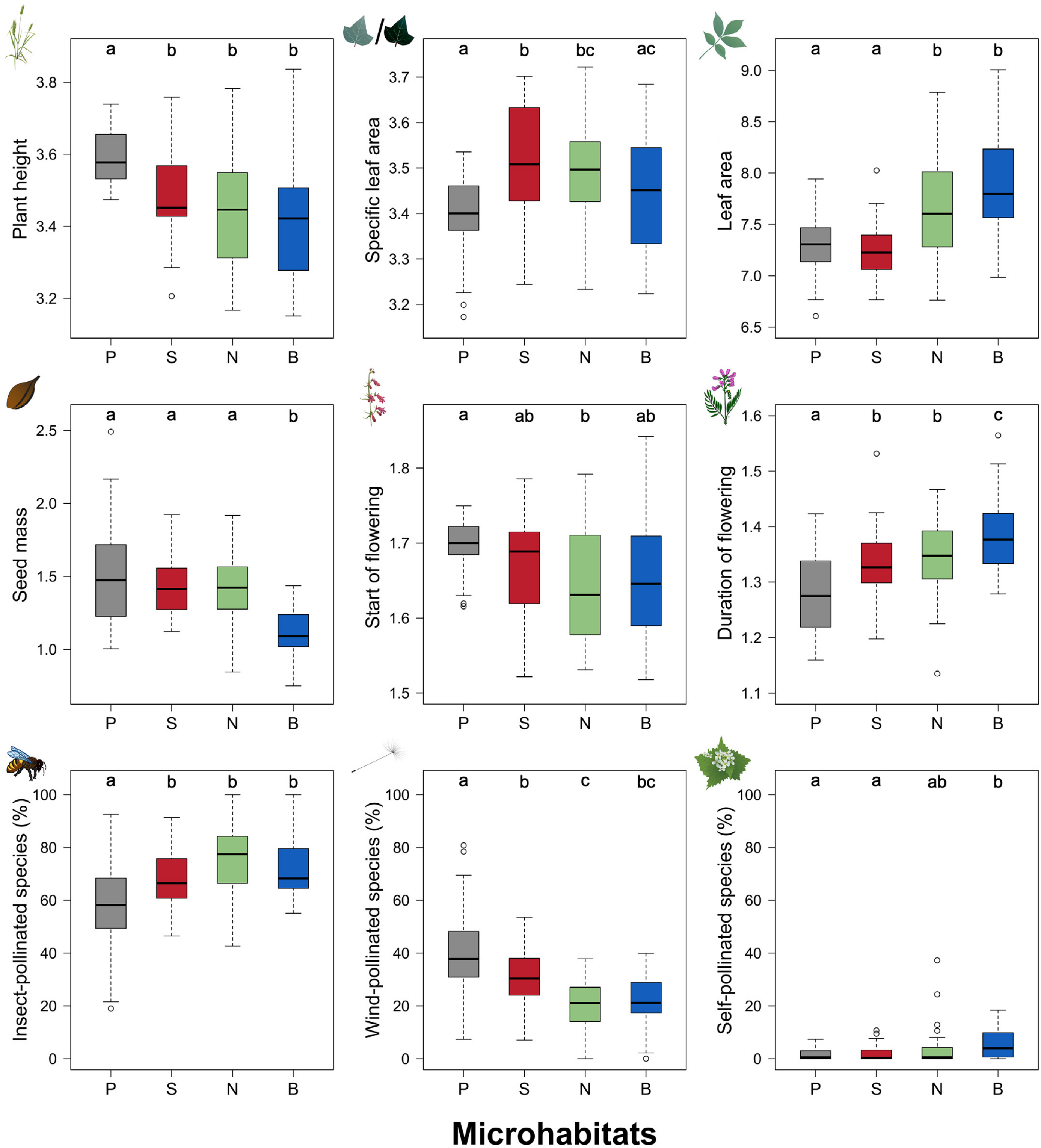

Fig. 2. Community-weighted means (CWMs) of quantitative traits (plant height, specific leaf area, leaf area, seed mass, and start and duration of flowering), and percentage cover values of species with different pollination types (insect-pollinated species, wind-pollinated species, and self-pollinated species) in the four microhabitats (P: plateaus, S: south-facing doline slopes, N: north-facing doline slopes, and B: doline bottoms) in the Aggtelek Karst and the Mecsek Mts. All quantitative traits (from plant height to duration of flowering) are log-transformed. Different lowercase letters (a–c) indicate significant differences ($p < 0.05$) among microhabitats. Images: http://ian.umces.edu/symbols/ and https://publicdomainvectors.org/.

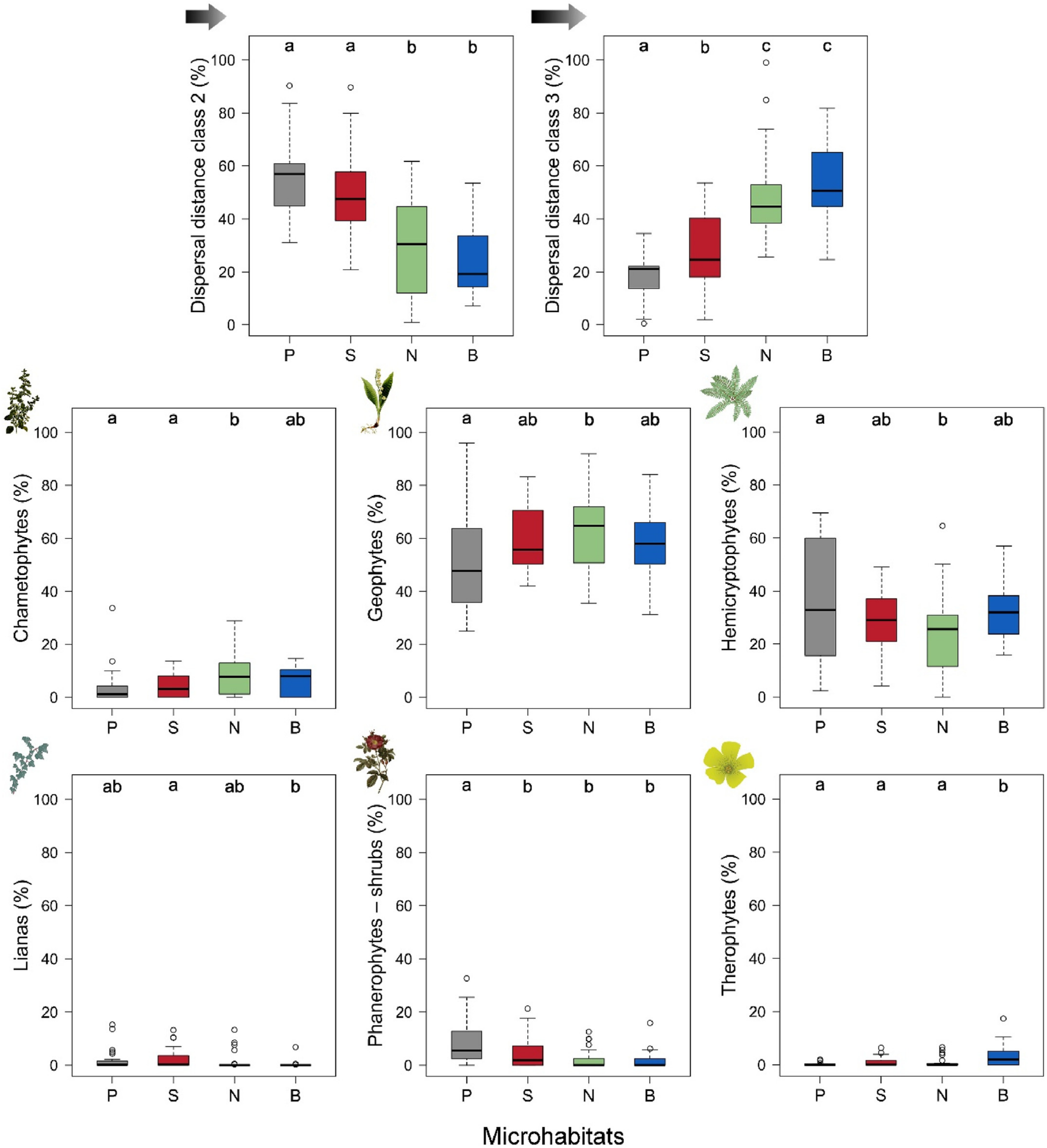

Fig. 3. Percentage cover values of species belonging to different dispersal distance classes (classes 2 and 3) and life forms (chametophyte, geophyte, hemicryptophyte, liana, shrub, and therophyte) in the four microhabitats (P: plateaus, S: south-facing doline slopes, N: north-facing doline slopes, and B: doline bottoms) in the Aggtelek Karst and Mecsek Mts. Different lowercase letters (a–c) indicate significant differences ($p < 0.05$) among microhabitats. Images: http://ian.umces.edu/symbols/ and https://publicdomainvectors.org/.

3. Results

3.1. Single trait characteristics

We recorded a total of 189 vascular plant species in the samples of the two regions, of which 169 were herbaceous and shrub species. Microhabitat (plateau, south-facing doline slope, north-facing doline slope, and doline bottom) had a significant effect on the distribution of almost all traits (18 out of 22 traits – considering each level and class separately) (Table S2). Plant assemblages tended to be taller on the plateaus than in dolines, while we found no significant differences among doline microhabitats considering plant height (Fig. 2). Plants in doline microhabitats were characterized by higher SLA than plants on the plateaus. Plants in doline bottoms and on north-facing slopes had higher LA compared to south-facing slopes and the plateaus. Bottoms hosted proportionally more plants with light seeds than the other microhabitats. Flowering of plants on north-facing slopes started earlier than on the plateaus, while south-facing slopes and bottoms did not differ from the other microhabitats considering the start of flowering. Plants in doline bottoms had the longest, while plants on the plateaus had the shortest duration of flowering. Insect-pollinated species were significantly more abundant in doline microhabitats than on the plateaus, while wind-pollinated species were significantly more abundant on the plateaus than in dolines. Bottoms had the highest cover of self-pollinated species.

We did not find any species in our samples belonging to the dispersal distance class 4 (less efficient wind-dispersed woody plants and tumbleweeds). Although we recorded some species belonging to the dispersal distance classes 1 (species with local non-specific dispersal strategy shorter than 0.3 m), 5 (anemochorous herbs and dwarf shrubs of open habitats), and 6 (dyszoochorous, endozoochorous, and epizoochorous species), their cover did not differ significantly among microhabitats. Plants belonging to the dispersal distance class 2 (species with local non-specific dispersal strategy taller than 0.3 m) were abundant on the plateaus and south-facing slopes, while they had significantly lower covers on north-facing slopes and in bottoms (Fig. 3). Plants belonging to the dispersal distance class 3 (myrmecochorous and anemochorous species with short dispersal distance) had the highest cover in bottoms and on north-facing slopes, and the lowest cover on the plateaus. The cover of chametophytes was highest on north-facing slopes and lowest on south-facing slopes and the plateaus. Geophytes had the highest cover on north-facing slopes and the lowest cover on the plateaus. The cover of hemicryptophytes was generally higher on the plateaus than in doline microhabitats, while the lowest values were observed on north-facing slopes. Lianas had the highest cover on south-facing slopes and the lowest cover in bottoms. Plateaus were characterized by a relatively high cover of shrub species, while all doline microhabitats had a significantly lower cover of shrubs. The cover of therophytes was significantly higher in bottoms compared to the other microhabitats. We did not observe significant differences in the cover of saprophyte and parasite life forms among the microhabitats.

3.2. Functional and phylogenetic diversity

According to the functional PCoA (Fig. 4), samples in bottoms and on north-facing slopes had much more diverse trait compositions than samples on south-facing slopes and the plateaus. Samples in bottoms and on the plateaus showed only a small overlap, while samples in bottoms and on north-facing slopes showed a considerable overlap in the ordination space. Samples on the plateaus indicated the most similar trait compositions, occupying the smallest area in the ordination space. Pairwise PERMANOVAs revealed significant compositional differences among microhabitats in all cases (Table S3). These findings were supported by the functional trait space analyses, where dolines occupied larger areas of the space and had higher functional richness than the plateaus. Moreover, each doline microhabitat occupied quite different parts of the functional space in both regions. The potential functional space was largest in doline bottoms in the Aggtelek Karst and on north-facing slopes in the Mecsek Mts (Figs. S1 and S2; Tables S4 and S5).

Functional diversity expressed by MPD was highest in doline bottoms and lowest on south- and north-facing slopes (Fig. S3; Table S6). There were no significant differences in the SES.MPD values among the microhabitats (Fig. S3; Table S6). All microhabitats had mean SES.MPD values below zero and differed significantly from random assembly (i.e. from zero scores), indicating functional trait convergence in each microhabitat (Table S7).

Phylogenetic diversity expressed by MPD was highest in doline

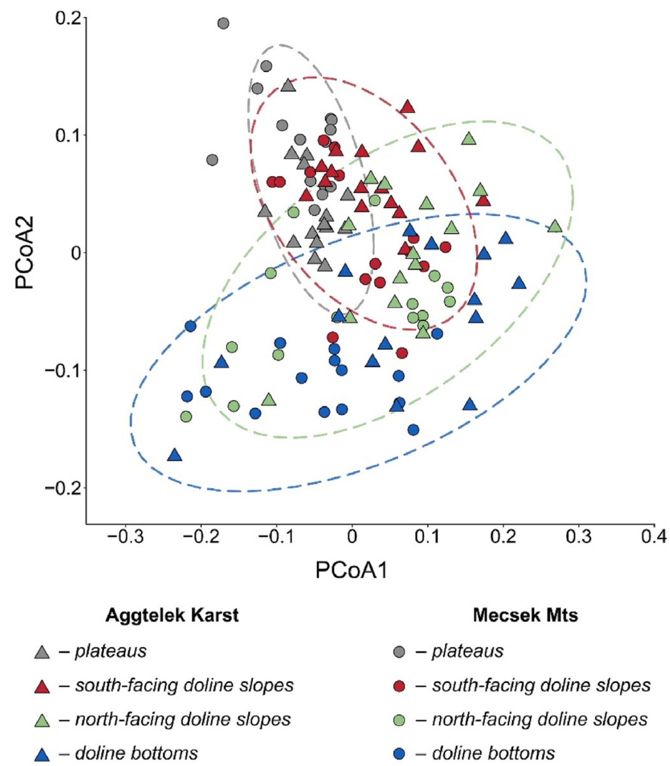

Fig. 4. Principal coordinate analysis (PCoA) scatterplot for the functional composition of all plant functional traits in the doline and plateau microhabitats (Aggtelek Karst and Mecsek Mts). Eigenvalues for the first and second ordination axes were 1.20 and 0.73, respectively. Ellipses were drawn at the 95% confidence intervals.

bottoms and lowest on the plateaus and south-facing slopes, while north-facing slopes had intermediate values (Fig. S4; Table S6). North-facing slopes and bottoms had significantly higher SES.MPD values than the plateaus and south-facing slopes. Bottoms had mean SES.MPD values above zero and differed significantly from random assembly, indicating phylogenetic overdispersion (Table S7). The other microhabitats had mean SES.MPD values below zero. Plateaus and south-facing slopes differed significantly from random assembly, indicating phylogenetic clustering, while north-facing slopes did not differ significantly from random assembly.

4. Discussion

We found that plant assemblages in doline microrefugia are characterized by unique trait values and trait combinations. Doline bottoms had the highest functional diversity among doline microhabitats and supported plant assemblages with considerably different functional trait compositions compared to the surrounding plateaus. Bottoms also had the highest phylogenetic diversity among the microhabitats. To the best of our knowledge, this is the first study to analyze the functional and phylogenetic characteristics of plant assemblages inside and outside dolines using a large set of plant data and functional traits from geographically distant regions.

4.1. Single trait characteristics

Our results confirmed that microhabitats in dolines and their surroundings are characterized by markedly different values and combinations of plant functional traits (supporting hypothesis 1). Topography and related environmental conditions (e.g., higher light availability and air temperature during summer) resulted in taller vegetation on the plateaus than in dolines (Bátori et al., 2021; Frei et al., 2023). We found that SLA in doline microhabitats (south- and north-facing slopes, and bottoms) was generally higher than on the plateaus. This pattern mirrors the prevalent microclimatic and soil conditions in dolines (Frei et al., 2023), as high-SLA plants are productive, short-lived, and are associated with resource-rich environments (Lavorel and Garnier, 2002). Another possible explanation for the pattern of SLA is the mass-ratio effect (Grime, 1998), as *Allium ursinum* – a fast-growing species with short-lived leaves and rapid resource acquisition strategy (Eggert, 1992) – was the most dominant spring geophyte in some dolines. Previous studies conducted in the temperate climate zone have highlighted that many forest communities with a high proportion of spring geophytes can be characterized by relatively high SLA (Muller, 2014; Rawlik et al., 2021). We also found higher LA on north-facing slopes and bottoms that retain more moisture than south-facing slopes and the plateaus (Frei et al., 2023), confirming that LA is positively associated with moisture (Díaz et al., 2016).

Doline bottoms hosted proportionally more light-seeded plant species than the other microhabitats. As small and light seeds can be easily carried by wind and are advantageous in long-distance dispersal (Kreft et al., 2010), doline bottoms, like a large pitfall, can trap a high number of small and light seeds (similarly to small-bodied spiders and ground beetles; Bátori et al., 2022). In addition, light seeds might buffer the negative effect of isolation and fragmentation (Kreft et al., 2010). The other microhabitats (south- and north-facing doline slopes, and the plateaus) hosted proportionally more large-seeded species, which can be linked with greater resilience to environmental stress (such as heat and drought), as large seeds can retain more metabolic reserves (Westoby, 1998; Maes et al., 2020). The cover of spring geophytes (e.g., *Allium ursinum* and *Erythronium dens-canis*) was generally higher in doline microhabitats than on the plateaus, presumably because the combined effects of topography and canopy structure result in more pronounced temporal changes in light conditions in dolines than on the plateaus (microhabitats in dolines are darker during summer than microhabitats on the plateaus; Bátori et al., 2021). This results in earlier flowering in dolines, providing possible food sources for early-season pollinators. The longer duration of flowering in doline microhabitats may be the result of a complex set of interactions among topographic complexity, temperature and moisture (cf. Olliff-Yang and Ackerly, 2020; Deák et al., 2021). Longer duration of flowering is associated with longer periods of pollination and higher chance of successful pollination (Bock et al., 2014). Pollinators typically avoid locations with high wind speed and prefer wind-sheltered areas (Kühn et al., 2006). As dolines are less exposed to wind than their surroundings (Whiteman et al., 2004), all doline microhabitats had proportionally higher cover of insect-pollinated species than the plateaus. This indicates that doline microhabitats provide relatively stable environmental conditions not only for plant species but also for their insect pollinators, and also explains why the plateaus hosted the highest cover of wind-pollinated species (cf. Friedman and Barrett, 2009). The high cover of self-pollinated species in island-like doline bottoms confirms the results of previous studies that self-pollinated species are characteristic of insular ecosystems as species capable of self-fertilization are more likely to be successful island colonists (Ottaviani et al., 2020; Deák et al., 2021).

We found that plants belonging to the dispersal distance class 2 had higher cover values on the plateaus and south-facing doline slopes than in the other microhabitats (e.g., *Carex pilosa* and *Melica uniflora*). Many of these species are clonal and generally disperse between 1 and 5 m (Lososová et al., 2023), forming large patches on the plateaus in both karst regions. Plants belonging to the dispersal distance class 3 are myrmecochorous (e.g., *Ajuga reptans* and *Ranunculus ficaria*) or anemochorous species (e.g., *Dryopteris filix-mas* and *Athyrium filix-femina*) with special dispersal-related diaspore features, such as elaiosome or pappus. The majority of seeds in this class generally disperse between 2 and 15 m (Lososová et al., 2023). These plants had the highest cover on north-facing slopes and in doline bottoms. Myrmecochorous plants comprise a considerable part of the herbaceous layer in deciduous forests and usually grow in stable environments (Warren II et al., 2021), such as certain doline microhabitats. Most of the anemochorous species we recorded were ferns. Previous studies have pointed out that the majority of fern spores disperse only relatively short distances and only a few spores are carried long distances during periods of strong wind (Friedman and Barrett, 2009). We also found differences in plant life forms among microhabitats, reflecting local environmental conditions and natural disturbances (e.g., more geophytes occurred on the cool north-facing slopes than in the other microhabitats, and more therophytes occurred in bottoms where soil profile inversion due to tree uprooting is more frequent than in the other microhabitats) (Jakob et al., 2022; Frei et al., 2023; Šipek et al., 2023).

4.2. Functional and phylogenetic diversity and community assembly

Our results showed that plant assemblages in doline bottoms had more diverse trait compositions than on the plateaus, and doline bottoms maintained greater functional diversity than the other doline microhabitats (supporting hypothesis 1 and partially supporting hypothesis 2). Functional PCoA revealed marked differences between doline bottoms and the plateaus, demonstrating the potential effects of topographic complexity and related refugia-promoting processes (cold-air pooling, air temperature and soil moisture gradients, and soil resource availability) on trait composition (Ottaviani et al., 2019; Frei et al., 2023; Marcin et al., 2024). Although we did not find significantly greater functional diversity (expressed by MPD) in dolines than on the plateaus, the much broader functional space (expressed by PCoA and functional trait spaces) in doline bottoms or on north-facing slopes indicates that plant species in these microhabitats can employ more diversified ecological strategies than in their surroundings (Keppel et al., 2018; Ottaviani et al., 2019). These processes may also have important consequences for the long-term persistence of plant populations, providing greater resilience and supporting an adaptive community-level response to environmental changes (Keppel et al., 2018). All microhabitats had negative SES.MPD values, indicating that these microhabitats are characterized by trait convergence. This might be a result of the specific environmental conditions of each microhabitat, filtering species distributions in a similar way (Mouchet et al., 2010; Götzenberger et al., 2012; Frei et al., 2023). We found that phylogenetic diversity was greater in doline bottoms and on north-facing slopes than in the other microhabitats (supporting hypothesis 3), due to the co-occurrence of ferns and angiosperms in these cooler and more humid microhabitats. The large phylogenetic distances of these ancient taxa from the modern angiosperms may result in a considerable increase in MPD (Lososová et al., 2015). Doline bottoms had positive SES.MPD values, indicating that this microhabitat is characterized by phylogenetic overdispersion, which might be a result of two possible evolutionary processes. Firstly, ancient lineages are well adapted to stable refugial habitats, where they are still not outcompeted by angiosperms. Secondly, some ancient lineages successfully readapted to modern habitats, such as leptosporangiate ferns (e.g., *Dryopteris* spp.), which adaptively radiated into new niches in angiosperm-dominated forests (Schneider et al., 2004; Lososová et al., 2015). Plateaus and south-facing slopes had negative SES.MPD values, indicating that these microhabitats are phylogenetically underdispersed, which might be due to the fact that many species occurring in these microhabitats belong to two phylogenetically closely related families (Poaceae and Cyperaceae).

4.3. Conclusions and implications for conservation policy and practice

We revealed that topographic complexity in doline microrefugia contributes to the presence of unique functional trait compositions in the understory and that doline bottoms have a relatively high functional and a high phylogenetic diversity. We also found that plants in dolines are generally shorter than plants on the plateaus, presumably due to the ecological limits imposed by temperature (i.e. cooler microclimates; Frei et al., 2023), have higher SLA, presumably as a result of more acquisitive

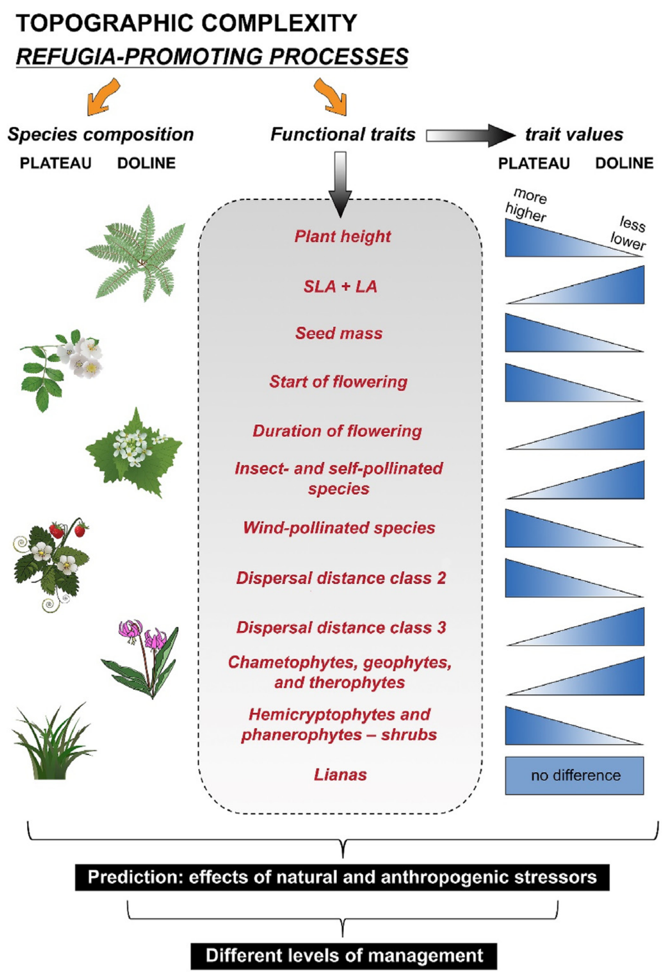

Fig. 5. Understanding and managing doline microrefugia in karst landscapes. Topographic complexity and related refugia-promoting processes drive species composition (Frei et al., 2023), community assembly and ecosystem functioning in contemporary and future microrefugia, such as in topographic depressions (dolines). Plant species composition and the patterns of functional traits differ considerably between dolines and their surroundings. Predicting the potential effects of natural and anthropogenic stressors on the biota of dolines may enable the selection of the optimal level of management, opening the possibility to restore the populations and ecosystem functions (in degraded landscapes) in such microrefugia (Keppel et al., 2024). Images: http://ian.umces.edu/symbols/and https://publicdomainvectors.org/.

nutrient uptake strategies (Copeland and Harrison, 2015; Govaert et al., 2024), and invest more in on-spot persistence (low proportion of wind-dispersed species) (Keppel et al., 2018). This corresponds well with the observation that plant functional trait composition in the understory of temperate forests across Europe is strongly determined by multiple environmental drivers, such as temperature, moisture, soil, and forest structure (Maes et al., 2020; Chelli et al., 2024). The high cover of spring geophytes in dolines may indicate more pronounced temporal changes in light conditions in doline microhabitats and may refer to more natural stand structures (Šipek et al., 2023). In addition, the presence of dolines may have positive consequences for the pollination services of wild pollinators, as topographic complexity in dolines may contribute to longer duration of flowering.

Understanding the influence of topographic complexity on community assembly and ecosystem functioning in forested landscapes may assist in predicting the potential effects of environmental stressors (natural and anthropogenic disturbances) on their plant assemblages and may enable the selection of the most suitable management practices (Fig. 5). Different levels of management may be required to support biodiversity in the understory of doline microrefugia (cf. Bátori et al., 2021; Keppel et al., 2024). Such management practices not only need to consider vegetation patterns (e.g., canopy closure and height) and species composition (e.g., endangered species), but also the dominant eco-evolutionary processes that drive community assembly and ecosystem functioning in dolines. Without these considerations, the resilience of ecosystems in doline microrefugia and their ability to adapt to new environmental conditions may be eroded in the long run.

CRediT authorship contribution statement

Kata Frei: Writing – original draft, Visualization, Investigation, Formal analysis, Data curation, Conceptualization. **Anna E-Vojtkó:** Writing – review & editing, Investigation, Formal analysis. **Csaba Tölgyesi:** Writing – review & editing, Validation, Methodology, Investigation, Formal analysis, Conceptualization. **András Vojtkó:** Writing – review & editing, Investigation, Conceptualization. **Tünde Farkas:** Writing – review & editing, Investigation. **László Erdős:** Writing – review & editing, Investigation. **Gábor Li:** Writing – review & editing. **Ádám Lőrincz:** Writing – review & editing, Visualization. **Zoltán Bátori:** Writing – original draft, Visualization, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization.

Availability of date and materials

Not applicable.

Funding

This research was funded by the National Research, Development and Innovation Office (NKFIH FK 142428 grant). The contribution of Z.B. was supported by the János Bolyai Research Scholarship of the Hungarian Academy of Sciences and by the New National Excellence Program of the Ministry for Culture and Innovation from the source of the National Research, Development and Innovation Fund (ÚNKP-23-5-SZTE-697). K.F. was supported by the New National Excellence Program of the Ministry for Culture and Innovation from the source of the National Research, Development and Innovation Fund (ÚNKP-23-3-SZTE-441). C.T. was supported by the NKFIH K 146137 grant. A.E-V. was supported by the long-term research development project of the Czech Academy of Sciences (RVO 67985939).

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.fecs.2024.100278.

References

Badgley, C., Smiley, T.M., Terry, R., Davis, E.B., DeSantis, L.R., Fox, D.L., Hopkins, S.S.B., Jezkova, T., Matocq, M.D., Matzke, N., McGuire, J.L., Mulch, A., Riddle, B.R., Roth, V.C., Samuels, J.X., Strömberg, C.A.E., Yanites, B.J., 2017. Biodiversity and topographic complexity: modern and geohistorical perspectives. Trends Ecol. Evol. 32, 211–226. https://doi.org/10.1016/j.tree.2016.12.010.

Bates, D., Mächler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4. J. Stat. Softw. 67, 1–48. https://doi.org/10.18637/jss.v067.i01.

Bátori, Z., Vojtkó, A., Farkas, T., Szabó, A., Havadtői, K., E-Vojtkó, A., Tölgyesi, C., Cseh, V., Erdős, L., Maák, I.E., Keppel, G., 2017. Large- and small-scale environmental factors drive distributions of cool-adapted plants in karstic microrefugia. Ann. Bot. 119, 301–309. https://doi.org/10.1093/aob/mcw233.

Bátori, Z., Erdős, L., Gajdács, M., Barta, K., Tobak, Z., Frei, K., Tölgyesi, C., 2021. Managing climate change microrefugia for vascular plants in forested karst landscapes. For. Ecol. Manag. 496, 119446. https://doi.org/10.1016/j.foreco.2021.119446.

Bátori, Z., Gallé, R., Gallé-Szpisjak, N., Császár, P., Nagy, D.D., Lőrinczi, G., Torma, A., Tölgyesi, C., Maák, I.E., Frei, K., Hábenczyus, A.A., Hornung, E., 2022. Topographic depressions provide potential microrefugia for ground-dwelling arthropods. Elementa 10, 00084. https://doi.org/10.1525/elementa.2021.00084.

Bátori, Z., Valkó, O., Vojtkó, A., Tölgyesi, C., Farkas, T., Frei, K., Hábenczyus, A.A., Tóth, Á., Li, G., Rádai, Z., Dulai, S., Barta, K., Erdős, L., Deák, B., 2023. Environmental heterogeneity increases the conservation value of small natural features in karst landscapes. Sci. Total Environ. 872, 162120. https://doi.org/10.1016/j.scitotenv.2023.

Bock, A., Sparks, T.H., Estrella, N., Jee, N., Casebow, A., Schunk, C., Leuchner, M., Menzel, A., 2014. Changes in first flowering dates and flowering duration of 232 plant species on the island of Guernsey. Glob. Change Biol. 20, 3508–3519. https://doi.org/10.1111/gcb.12579.

Botta-Dukát, Z., Bartha, D., Dancza, I., Lukács, B.A., Pinke, G., 2023. Adaptation of life form categorization of Ellenberg and Mueller-Dombois to the Hungarian flora. Acta Bot. Hung. 65, 1–34. https://doi.org/10.1556/034.65.2023.1-2.1.

Carmona, C.P., Pavanetto, N., Puglielli, G., 2024. funspace: An R package to build, analyse and plot functional trait spaces. Divers. Distrib. 30, e13820. https://doi.org/10.1111/ddi.13820.

Čarni, A., Čonč, Š., Breg Valjavec, M., 2022. Landform-vegetation units in karstic depressions (dolines) evaluated by indicator plant species and Ellenberg indicator values. Ecol. Indic. 135, 108572. https://doi.org/10.1016/j.ecolind.2022.108572.

Chelli, S., Bricca, A., Tsakalos, J.L., Andreetta, A., Bonari, G., Campetella, G., Carnicelli, S., Cervellini, M., Puletti, N., Wellstein, C., Canullo, R., 2024. Multiple drivers of functional diversity in temperate forest understories: climate, soil, and forest structure effects. Sci. Total Environ. 916, 170258.

Conti, L., Valencia, E., Galland, T., Götzenberger, L., Lepš, J., E-Vojtkó, A., Carmona, C.P., Májeková, M., Danihelka, J., Dengler, J., Eldridge, D.J., Estiarte, M., García-González, R., Garnier, E., Gómez, D., Hadincová, V., Harrison, S.P., Herben, T., Ibáñez, R., Jentsch, A., Juergens, N., Kertész, M., Klumpp, K., Krahulec, F., Louault, F., Marrs, R.H., Ónodi, G., Pakeman, R.J., Pärtel, M., Peco, B., Peñuelas, J., Rueda, M., Schmidt, W., Schmiedel, U., Schuetz, M., Skalova, H., Šmilauer, P., Šmilauerová, M., Smit, C., Song, M.H., Stock, M., Val, J., Vandvik, V., Ward, D., Wesche, K., Wiser, S.K., Woodcock, B.A., Young, T.P., Yu, F.-H., Zobel, M., de Bello, F., 2023. Functional trait trade-offs define plant population stability across different biomes. P. Roy. Soc. B – Biol. Sci. 290, 20230344. https://doi.org/10.1098/rspb.2023.0344.

Copeland, S.M., Harrison, S.P., 2015. Identifying plant traits associated with topographic contrasts in a rugged and diverse region (Klamath-Siskiyou Mts, OR, USA). Ecography 38, 569–577. https://doi.org/10.1111/ecog.00802.

de Bello, F., Carmona, C.P., Leps, J., Szava-Kovats, R., Partel, M., 2016. Functional diversity through the mean trait dissimilarity: resolving shortcomings with existing paradigms and algorithms. Oecologia 180, 933–940. https://doi.org/10.1007/s00442-016-3546-0.

de Bello, F., Šmilauer, P., Diniz-Filho, J.A.F., Carmona, C.P., Lososová, Z., Herben, T., Götzenberger, L., 2017. Decoupling phylogenetic and functional diversity to reveal hidden signals in community assembly. Methods Ecol. Evol. 8, 1200–1211. https://doi.org/10.1111/2041-210X.12735.

de Bello, F., Carmona, C.P., Dias, A.T.C., Götzenberger, L., Moretti, M., Berg, M.P., 2021a. Handbook of Trait–Based Ecology: from Theory to R Tools. Cambridge University Press, Cambridge.

de Bello, F., Botta-Dukát, Z., Lepš, J., Fibich, P., 2021b. Towards a more balanced combination of multiple traits when computing functional differences between species. Methods Ecol. Evol. 12, 443–448. https://doi.org/10.1111/2041-210X.13537.

Deák, B., Rádai, Z., Bátori, Z., Kelemen, A., Lukács, K., Kiss, R., Maák, I.E., Valkó, O., 2021. Ancient burial mounds provide safe havens for grassland specialist plants in transformed landscapes—a trait-based analysis. Front. Ecol. Evol. 9, 619812. https://doi.org/10.3389/fevo.2021.619812.

Díaz, S., Hodgson, J., Thompson, K., Cabido, M., Cornelissen, J.H., Jalili, A., Montserrat-Martí, G., Grime, J., Zarrinkamar, F., Asri, Y., 2004. The plant traits that drive ecosystems: evidence from three continents. J. Veg. Sci. 15, 295–304. https://doi.org/10.1111/j.1654-1103.2004.tb02266.x.

Díaz, S., Kattge, J., Cornelissen, J.H.C., Wright, I.J., Lavorel, S., Dray, S., Reu, B., Kleyer, M., Wirth, C., Prentice, I.C., Garnier, E., Bönisch, G., Westoby, M., Poorter, H., Reich, P.B., Moles, A.T., Dickie, J., Gillison, A.N., Zanne, A.E., Chave, J., Wright, S.J., Sheremet'ev, S.N., Jactel, H., Baraloto, C., Cerabolini, B., Pierce, S., Shipley, B., Kirkup, D., Casanoves, F., Joswig, J.S., Günther, A., Falczuk, V., Rüger, N., Mahecha, M.D., Gorné, L.D., 2016. The global spectrum of plant form and function. Nature 529, 167–171. https://doi.org/10.1038/nature16489.

Dobrowski, S.Z., 2011. A climatic basis for microrefugia: the influence of terrain on climate. Glob. Change Biol. 17, 1022–1035. https://doi.org/10.1111/j.1365-2486.2010.02263.x.

Dövényi, Z., 2010. Magyarország Kistájainak Katasztere (Inventory of Microregions in Hungary). MTA Földrajztudományi Kutatóintézet, Budapest.

Durka, W., Michalski, S.G., 2012. Daphne: a dated phylogeny of a large European flora for phylogenetically informed ecological analyses. Ecology 93, 2297. https://doi.org/10.1890/12-0743.1.

Eggert, A., 1992. Dry matter economy and reproduction of a temperate forest spring geophyte, *Allium ursinum*. Ecography 15, 45–55. https://doi.org/10.1111/j.1600-0587.1992.tb00007.x.

E-Vojtkó, A., de Bello, F., Lososová, Z., Götzenberger, L., 2023. Phylogenetic diversity is a weak proxy for functional diversity but they are complementary in explaining community assembly patterns in temperate vegetation. J. Ecol. 111, 2218–2230. https://doi.org/10.1111/1365-2745.14171.

Finocchiaro, M., Médail, F., Saatkamp, A., Diadema, K., Pavon, D., Brousset, L., Meineri, E., 2024. Microrefugia and microclimate: unraveling decoupling potential and resistance to heatwaves. Sci. Total Environ. 924, 171696. https://doi.org/10.1016/j.scitotenv.2024.171696.

Fox, J., Weisberg, S., 2011. An R Companion to Applied Regression, second ed. SAGE Publications, Thousand Oaks.

Frei, K., Vojtkó, A., Farkas, T., Erdős, L., Barta, K., E-Vojtkó, A., Tölgyesi, C., Bátori, Z., 2023. Topographic depressions can provide climate and resource microrefugia for biodiversity. iScience 26, 108202. https://doi.org/10.1016/j.isci.2023.108202.

Friedman, J., Barrett, S.C., 2009. Wind of change: new insights on the ecology and evolution of pollination and mating in wind-pollinated plants. Ann. Bot. 103, 1515–1527. https://doi.org/10.1093/aob/mcp035.

Götzenberger, L., de Bello, F., Bråthen, K.A., Davison, J., Dubuis, A., Guisan, A., Lepš, J., Lindborg, R., Moora, M., Pärtel, M., Pellissier, L., Pottier, J., Vittoz, P., Zobel, K., Zobel, M., 2012. Ecological assembly rules in plant communities-approaches patterns and prospects. Biol. Rev. 87, 111–127. https://doi.org/10.1111/j.1469-185X.2011.00187.x.

Govaert, S., Meeussen, C., Vanneste, T., Bollmann, K., Brunet, J., Calders, K., Cousins, S.A.O., De Pauw, K., Diekmann, M., Graae, B.J., Hedwall, P.-O., Iacopetti, G., Lenoir, J., Lindmo, S., Orczewska, A., Ponette, Q., Plue, J., Sanczuk, P., Selvi, F., Spicher, F., Verheyen, K., Vangansbeke, P., De Frenne, P., 2024. Trait–micro-environment relationships of forest herb communities across Europe. Global Ecol. Biogeogr. 33, 286–302. https://doi.org/10.1111/geb.13789.

Grime, J.P., 1998. Benefits of plant diversity to ecosystems: immediate, filter and founder effects. J. Ecol. 86, 902–910.

Jakob, A., Breg Valjavec, M., Čarni, A., 2022. Turnover of plant species on an ecological gradient in karst dolines is reflected in plant traits: chorotypes, life forms, plant architecture and strategies. Diversity 14, 597. https://doi.org/10.3390/d14080597.

Keppel, G., Van Niel, K.P., Wardell-Johnson, G.W., Yates, C.J., Byrne, M., Mucina, L., Schut, A.G.T., Hopper, S.D., Franklin, S.E., 2012. Refugia: identifying and understanding safe havens for biodiversity under climate change. Global Ecol. Biogeogr. 21, 393–404. https://doi.org/10.1111/j.1466-8238.2011.00686.x.

Keppel, G., Mokany, K., Wardell-Johnson, G.W., Phillips, B.L., Welbergen, J.A., Reside, A.E., 2015. The capacity of refugia for conservation planning under climate change. Front. Ecol. Environ. 13, 106–112. https://doi.org/10.1890/140055.

Keppel, G., Ottaviani, G., Harrison, S., Wardell-Johnson, G.W., Marcantonio, M., Mucina, L., 2018. Towards an eco-evolutionary understanding of endemism hotspots and refugia. Ann. Bot. 122, 927–934. https://doi.org/10.1093/aob/mcy173.

Keppel, G., Stralberg, D., Morelli, T.L., Bátori, Z., 2024. Managing climate-change refugia to prevent extinctions. Trends Ecol. Evol. 39, 800–808. https://doi.org/10.1016/j.tree.2024.05.002.

Kobal, M., Bertoncelj, I., Pirotti, F., Dakskobler, I., Kutnar, L., 2015. Using lidar data to analyse sinkhole characteristics relevant for understory vegetation under forest cover – case study of a high karst area in the Dinaric Mountains. PLoS One 10, e0122070. https://doi.org/10.1371/journal.pone.0122070.

Kreft, H., Jetz, W., Mutke, J., Barthlott, W., 2010. Contrasting environmental and regional effects on global pteridophyte and seed plant diversity. Ecography 33, 408–419. https://doi.org/10.1111/j.1600-0587.2010.06434.x.

Kremen, C., Williams, N.M., Aizen, M.A., Gemmill-Herren, B., LeBuhn, G., Minckley, R., Packer, L., Potts, S.G., Roulston, T., Steffan-Dewenter, I., Vázquez, D.P., Winfree, R., Adams, L., Crone, E.E., Greenleaf, S.S., Keitt, T.H., Klein, A.-M., Regetz, J., Ricketts, T.H., 2007. Pollination and other ecosystem services produced by mobile organisms: a conceptual framework for the effects of land-use change. Ecol. Lett. 10, 299–314. https://doi.org/10.1111/j.1461-0248.2007.01018.x.

Kühn, I., Bierman, S.M., Durka, W., Klotz, S., 2006. Relating geographical variation in pollination types to environmental and spatial factors using novel statistical methods. New Phytol. 172, 127–139. https://doi.org/10.1111/j.1469-8137.2006.01811.x.

Laliberté, E., Legendre, P., Shipley, B., 2014. FD: measuring functional diversity from multiple traits, and other tools for functional ecology. R package version 1.0-12. https://cran.r-project.org/web/packages/FD/index.html. (Accessed 15 September 2024).

Lavorel, S., Garnier, E., 2002. Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. Funct. Ecol. 16, 545–556. https://doi.org/10.1046/j.1365-2435.2002.00664.x.

Lenoir, J., Hattab, T., Pierre, G., 2017. Climatic microrefugia under anthropogenic climate change: implications for species redistribution. Ecography 40, 253–266. https://doi.org/10.1111/ecog.02788.

Lososová, Z., Šmarda, P., Chytrý, M., Purschke, O., Pyšek, P., Sádlo, J., Tichý, L., Winter, M., 2015. Phylogenetic structure of plant species pools reflects habitat age on the geological time scale. J. Veg. Sci. 26, 1080–1089. https://doi.org/10.1111/jvs.12308.

Lenth, R., 2021. Emmeans: estimated marginal means, aka least–squares means. R package version 1.6.0. https://cran.r-project.org/web/packages/emmeans/index.html. (Accessed 15 September 2024).

Lososová, Z., Axmanová, I., Chytrý, M., Midolo, G., Abdulhak, S., Karger, D.N., Renaud, J., Van Es, J., Vittoz, P., Thuiller, W., 2023. Seed dispersal distance classes and dispersal modes for the European flora. Global Ecol. Biogeogr. 32, 1485–1494. https://doi.org/10.1111/geb.13712.

Maes, S.L., Perring, M.P., Depauw, L., Bernhardt-Römermann, M., Blondeel, H., Brūmelis, G., Brunet, J., Decocq, G., den Ouden, J., Govaert, S., Härdtle, W., Hédl, R., Heinken, T., Heinrichs, S., Hertzog, L., Jaroszewicz, B., Kirby, K., Kopecký, M., Landuyt, D., Máliš, F., Vanneste, T., Wulf, M., Verheyen, K., 2020. Plant functional trait response to environmental drivers across European temperate forest understorey communities. Plant Biol. 22, 410–424. https://doi.org/10.1111/plb.13082.

Marcantonio, M., Silveira, F.A., Keppel, G., Harrison, S., Ottaviani, G., 2021. Roles and implications of functional traits and phylogenies to characterize refugia under increasing climate variability. Front. Ecol. Evol. 9, 754451. https://doi.org/10.3389/fevo.2021.754451.
Marcin, M., Raschmanová, N., Miklisová, D., Šupinský, J., Kaňuk, J., Kováč, L., 2024. Karst landforms as microrefugia for soil Collembola: open versus forested dolines. Elementa 12, 00107. https://doi.org/10.1525/elementa.2023.00107.
McGill, B.J., Enquist, B.J., Weiher, E., Westoby, M., 2006. Rebuilding community ecology from functional traits. Trends Ecol. Evol. 21, 178–185. https://doi.org/10.1016/j.tree.2006.02.002.
McLaughlin, B.C., Ackerly, D.D., Klos, P.Z., Natali, J., Dawson, T.E., Thompson, S., 2017. Hydrologic refugia, plants, and climate change. Glob. Change Biol. 23, 2941–2961. https://doi.org/10.1111/gcb.13629.
Morelli, T.L., Daly, C., Dobrowski, S.Z., Dulen, D.M., Ebersole, J.L., Jackson, S.T., Lundquist, J.D., Millar, C.I., Maher, S.P., Monahan, W.B., Nydick, K.R., Redmond, K.T., Sawyer, S.C., Stock, S., Beissinger, S.R., 2016. Managing climate change refugia for climate adaptation. PLoS One 11, e0159909. https://doi.org/10.1371/journal.pone.0159909.
Mouchet, M.A., Villéger, S., Mason, N.W., Mouillot, D., 2010. Functional diversity measures: an overview of their redundancy and their ability to discriminate community assembly rules. Funct. Ecol. 24, 867–876. https://doi.org/10.1111/j.1365-2435.2010.01695.x.
Muller, R.N., 2014. Nutrient relations of the herbaceous layer in deciduous forest ecosystems. In: Gilliam, F. (Ed.), The Herbaceous Layer in Forests of Eastern North America, second ed. Oxford University Press, Oxford, pp. 12–34.
Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P.R., 2018. Vegan: community ecology package. https://cran.r-project.org/web/packages/vegan/index.html. (Accessed 15 September 2024).
Olliff-Yang, R.L., Ackerly, D.D., 2020. Topographic heterogeneity lengthens the duration of pollinator resources. Ecol. Evol. 10, 9301–9312. https://doi.org/10.1002/ece3.6617.
Ottaviani, G., Keppel, G., Marcantonio, M., Mucina, L., Wardell-Johnson, G., 2019. Woody species in resource-rich microrefugia of granite outcrops display unique functional signatures. Austral Ecol. 44, 575–580. https://doi.org/10.1111/aec.12745.
Ottaviani, G., Keppel, G., Götzenberger, L., Harrison, S., Opedal, Ø.H., Conti, L., Liancourt, P., Klimešová, J., Silveira, F.A.O., Jiménez-Alfaro, B., Negoita, L., Doležal, J., Hájek, M., Ibanez, T., Méndez-Castro, F.E., Chytrý, M., 2020. Linking plant functional ecology to island biogeography. Trends Plant Sci. 25, 329–339. https://doi.org/10.1016/j.tplants.2019.12.022.
R Core Team R, 2022. A Language and Environment for Statistical Computing (4.2.2). Computer software R Foundation for Statistical Computing. https://cran.r-project.org/. (Accessed 15 September 2024).
Rawlik, K., Nowiński, M., Jagodziński, A.M., 2021. Short life–fast death: decomposition rates of woody plants leaf- and herb-litter. Ann. For. Sci 78, 6. https://doi.org/10.1007/s13595-020-01019-y.
Rull, V., 2009. Microrefugia. J. Biogeog. 36, 481–484. https://doi.org/10.1111/j.1365-2699.2008.02023.x.
Schneider, H., Schuettpelz, E., Pryer, K.M., Cranfill, R., Magallón, S., Lupia, R., 2004. Ferns diversified in the shadow of angiosperms. Nature 428, 553–557. https://doi.org/10.1038/nature02361.
Selwood, K.E., Zimmer, H.C., 2020. Refuges for biodiversity conservation: a review of the evidence. Biol. Cons. 245, 108502. https://doi.org/10.1016/j.biocon.2020.108502.
Šipek, M., Ravnjak, T., Šajna, N., 2023. Understorey species distinguish late successional and ancient forests after decades of minimum human intervention: a case study from Slovenia. For. Ecosyst. 10, 100096. https://doi.org/10.1016/j.fecs.2023.100096.
Stralberg, D., Arseneault, D., Baltzer, J., Barber, Q.E., Bayne, E.M., Boulanger, Y., Brown, C.D., Cooke, H.A., Devito, K., Edwards, J., Estevo, C.A., Flynn, N., Frelich, L.E., Hogg, E.H., Johnston, M., Logan, T., Matsuoka, S.M., Moore, P., Morelli, T.L., Morissette, J.L., Nelson, E.A., Nenzén, H., Nielsen, S.E., Parisien, M.-A., Pedlar, J.H., Price, D.T., Schmiegelow, F.K.A., Slattery, S.M., Sonnentag, O., Thompson, D.K., Whitman, E., 2020. Climate-change refugia in boreal North America: what, where, and for how long? Front. Ecol. Environ. 18, 261–270. https://doi.org/10.1002/fee.2188.
Swenson, N.G., 2014. Functional and Phylogenetic Ecology in R. Springer.
Tölgyesi, C., Török, P., Kun, R., Csathó, A.I., Bátori, Z., Erdős, L., Vadász, C., 2019. Recovery of species richness lags behind functional recovery in restored grasslands. Land Degrad. Dev. 30, 1083–1094. https://doi.org/10.1002/ldr.3295.
Violle, C., Navas, M.L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., Garnier, E., 2007. Let the concept of trait be functional. Oikos 116, 882–892. https://doi.org/10.1111/j.0030-1299.2007.15559.x.
Virók, V., Farkas, R., Farkas, T., Šuvada, R., Vojtkó, A., 2016. A Gömör-Tornai-Karszt Flórája-Enumeráció. Vascular Flora of the Gömör–Torna Carst, Enumeration. Aggteleki Nemzeti Park Igazgatóság, Aggtelek.
Warren, R.J.I.I., Olejniczak, M., Labatore, A., Candeias, M., 2021. How common and dispersal limited are ant-dispersed plants in eastern deciduous forests? Plant Ecol. 222, 361–373. https://doi.org/10.1007/s11258-020-01111-3.
Weiher, E., Van Der Werf, A., Thompson, K., Roderick, M., Garnier, E., Eriksson, O., 1999. Challenging Theophrastus: a common core list of plant traits for functional ecology. J. Veg. Sci. 10, 609–620. https://doi.org/10.2307/3237076.
Westoby, M., 1998. A leaf–height–seed (LHS) plant ecology strategy scheme. Plant Soil 199, 213–227. https://doi.org/10.1023/A:1004327224729.
White, W.B., Culver, D.C., Herman, J.S., Kane, T.C., Mylroie, J.E., 1995. Karst lands. The dissolution of carbonate rock produces unique landscapes and poses significant hydrological and environmental concerns. Am. Sci. 83, 450–459.
Whiteman, C.D., Haiden, T., Pospichal, B., Eisenbach, S., Steinacker, R., 2004. Minimum temperatures, diurnal temperature ranges, and temperature inversions in limestone sinkholes of different sizes and shapes. J. Appl. Meteorol. 43, 1224–1236. https://doi.org/10.1175/1520-0450(2004)043<1224:MTDTRA>2.0.CO;2.