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Contents

Hasan BASRI, Tuti MUTIA, Abdul RASYAD, Ahmad TOHRI, Hanapi HANAPI, Muhamad ALI
The impacts of tourism on shifting mountain climbing ritual tradition in geopark Rinjani, Indonesia 7

Rok TURNIŠKI, Helena GRČMAN
Soils of the Dinaric karst in Slovenia: properties, pedogenesis and land use 21

Klemen COF, Uroš STEPIŠNIK, Manja ŽEBRE, Matej LIPAR
Hierarchical cluster classification and analysis of cirques in Slovenian Alps 39

Danijel DAVIDOVIĆ, Jure ČUŠ, Danijel IVAJNŠIČ
Land-use dynamics and grassland succession challenges in the Natura 2000 site Kras: The socioeconomic perspective 61

Zoltán BÁTORI, Kata FREI, Gábor LI, Orsolya VALKÓ, András VOJTKÓ, Csaba TÖLGYESI, Tünde FARKAS, Alida Anna HÁBENCZYUS, Ágnes TÓTH, László ERDŐS, Zsófia KRIVÁCS, Balázs DEÁK
Karstic microrefugia reflect diverse biogeographic affinities of vascular plant species 81

Boudjemline FOUZIA
Mapping and assessing forest fire severity using remote sensing indices: A case study of Tizi Ouzou, Algeria 99

Peter FRANTAR, Frank HERRMANN, Mišo ANDJELOV
National-scale water balance in Slovenia (1972–2024): Long-term trends and variability in water balance components 121

Juš GAŠPARIČ, Ana POTOČNIK BUHVALD, Dušan PETROVIČ
Satellite-based analysis of light pollution in Slovenia for the period 2013–2022 147

Entin HIDAYAH, Mokhammad Farid MARUF, Siti Norafida JUSOH, Joko WIDODO, Afif AMILUDDIN
Machine learning-based landslide susceptibility assessment for shallow landslide mitigation in the Gumitir Mountain Area, Indonesia 179

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KARSTIC MICROREFUGIA REFLECT DIVERSE BIOGEOGRAPHIC AFFINITIES OF VASCULAR PLANT SPECIES

Zoltán Bátori, Kata Frei, Gábor Li, Orsolya Valkó, András Vojtkó, Csaba Tölgyesi, Tünde Farkas, Alida Anna Hábenczyus, Ágnes Tóth, László Erdős, Zsófia Krivács, Balázs Deák



GÁBOR LI

Early-morning view of a doline field on the Bükk Plateau.

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Karstic microrefugia reflect diverse biogeographic affinities of vascular plant species

ABSTRACT: Microrefugia are small areas that allow species to persist in changing environments. Dolines in karst landscapes may function as such safe havens. By analysing vegetation data from 270 plots collected within nine large dolines and on the surrounding plateau in Northern Hungary, we found that topographic complexity in dolines has the potential to support a wide array of plant species with diverse biogeographic affinities. To safeguard the large number of endangered plant species and the high biodiversity associated with dolines, conservation management should take into account the complex interactions among topographic complexity, environmental conditions, and species distributions in karstic microrefugia and their surrounding areas.

KEYWORDS: doline, environmental heterogeneity, grassland, mountain species, topography, Bükk Plateau, Hungary

Kraški mikrorefugiji odražajo biogeografsko raznolikost vaskularnih rastlinskih vrst

POVZETEK: Mikrorefugiji so majhna območja, ki omogočajo vrstam preživetje v spreminjajočih se okoljih. Vrtače v kraških pokrajinah lahko delujejo kot takšna varna zatočišča. Z analizo vegetacijskih podatkov iz severne Madžarske, zbranih na 270 popisnih ploskvah v devetih velikih vrtačah in na planoti izven njih, smo ugotovili, da topografska kompleksnost vrtač omogoča rast široke palete rastlinskih vrst z raznolikimi biogeografskimi značilnostmi. Da bi zaščitili veliko število ogroženih rastlinskih vrst in visoko biotsko raznovrstnost v vrtačah, bi morali v upravljanju in varstvu vrtač upoštevati kompleksne interakcije med topografsko kompleksnostjo, okoljskimi pogoji in razporeditvijo vrst v kraških mikrorefugijih in njihovi okolici.

KLJUČNE BESEDE: vrtače, okoljska heterogenost, travniki, gorske vrste, topografija, planota Bükk, Madžarska

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1 Introduction

Topographically complex landscapes often feature hotspots of biodiversity and promote ecosystem stability during large-scale environmental changes (Badgley et al. 2017). Microclimatic and edaphic gradients in such landscapes not only enable species to track regional climate changes, but also support the persistence of some populations by providing favourable local environmental conditions (Bátori et al. 2017; Ottaviani et al. 2019; Keppel et al. 2024). Therefore, range contraction is often not complete and, during episodes of changing climate, isolated (relict) populations can be left behind in enclaves with environmental conditions resembling the former ones (Hampe and Jump 2011). Such enclaves are known as microrefugia that may constitute the only chance of survival for a variety of species in many landscapes across the globe (Rull 2009; Dobrowski 2011; Keppel et al. 2012). For instance, Stewart and Lister (2001) highlighted that the European southern and eastern refugia for warm-adapted species were supplemented by microrefugia in Northern Europe during the Late Pleistocene. These microrefugia were likely associated with areas of sheltered topography that provided suitable climatic conditions for the long-term persistence of these species. On the other hand, specific topographic features (e.g., basins and valleys) promote cold-air pooling, supporting the survival of geographically restricted populations of cold-adapted plant and animal species during warmer climatic periods (Gentili et al. 2015). Some species may migrate towards areas at higher elevations (Walther et al. 2002), if there is no dispersal limitation (Willner et al. 2009).

Recent studies have demonstrated that specific microclimatic and soil conditions in topographically complex karst depressions (dolines) have the capacity to support an extremely high biodiversity with high turnover of species associated with different environmental conditions (Bátori et al. 2022a; Bátori et al. 2023; Marcin et al. 2024). As dolines are widespread topographic features in many karst landscapes worldwide, they play a key role in supporting global biodiversity, including many rare and endangered species (Su et al. 2017; Čarni et al. 2022; Bátori et al. 2023; Frei et al. 2023). For instance, the endangered rainforest-dwelling cycad species *Zamia decumbens* Calonje, Meerman, M.P. Griff. & Hoese frequently occurs in the dolines of the Maya Mountains (Belize) (Herrera-Blitman et al. 2022; Calonje et al. 2024). The pristine patches of moist evergreen broadleaf forests in the bottom of large dolines (i.e., tiankengs) in China provide safe havens for a high number of pteridophytes, such as *Diplazium maximum* (D.Don) C.Chr. (Shui et al. 2022). Dolines in Central and Southern Europe have provided safe havens for plant species associated with colder and/or moister conditions during warmer and drier periods of the Quaternary (Lazarević et al. 2009; Bátori et al. 2023). The continuous persistence of these populations is associated with unique microsites in dolines, maintained by cold-air pooling and/or water and nutrient retention (Bátori et al. 2022a; Pastore et al. 2022; Frei et al. 2023). For instance, the critically endangered endemic plant species *Horstrissea dolinicola* Greuter, Gerstb. & Egli (Apiaceae) in Crete (Greece) only occurs in the bottom of some dolines that are frequently flooded in springtime (Egli et al. 1990). The persistent cold and moist conditions on the north-facing slopes and bottoms of dolines in Hungary provide habitats for rare and endangered plant species associated with a colder and/or moister microclimate compared to the surrounding regional climate, such as *Aconitum vulparia* Rchb., *Arabidopsis halleri* (L.) O'Kane & Al-Shehbaz, *Daphne mezereum* L., *Dracocephalum ruyschiana* L., *Dryopteris borreri* Newman, *Ophioglossum vulgatum* L., *Ribes alpinum* L., and *Rosa pendulina* L. (Vojtkó 1999; Virók and Farkas 2008; Lazarević et al. 2009; Bátori et al. 2017). Although these examples clearly demonstrate the role of cool and moist north-facing slopes and bottoms of dolines as current and potential future microrefugia, few studies have proposed that slopes with other aspects may also serve as crucial habitats for the survival of certain plant species (cf. Bátori et al. 2023). Moreover, there is no evidence indicating whether dolines serve as important microsites for vascular plant species representing diverse biogeographic affinities.

The biogeographic affinities of plant species indicate the geographic regions or climatic zones to which these species are historically or ecologically linked. In other words, they reflect where a species originated, evolved, or where it typically thrives under natural conditions. Here we compare the distribution of vascular plant species within dolines (south-, east-, west-, and north-facing slopes, and bottoms) and on the surrounding plateau in Hungary in relation to their biogeographic affinities (Mediterranean, mountain, endemic, European, continental, and cosmopolitan groups). Specifically, we addressed the following question: How do the number and cover of plant species with different biogeographic affinities differ between dolines and the surrounding plateau, as well as among various microsites within dolines? By addressing this question, we aim to improve our understanding of the role of dolines as local biodiversity hotspots and potential future microrefugia.

2 Materials and Methods

2.1 Study region and sampling design

We studied dolines covered by grasslands on the Bükk Plateau (Bükk Mountains, Northern Hungary, 48°04'31" N, 20°29'57" E, between 750–800 m asl) (Figure 1). The region has a warm-summer humid continental climate (Dfb type according to the Köppen–Geiger classification) (Peel et al. 2007), with a mean annual temperature of 6.3°C and a mean annual precipitation of 800 mm (Dövényi 2010). The dominant grassland vegetation types in dolines and on the surrounding plateau are *Arrhenatherum elatius* hay meadows, *Festuca rubra* hay meadows, semi-dry rocky grasslands, and wet meadows. In addition, *Fagus sylvatica* L. stands and *Picea abies* (L.) H. Karst. plantations also occur in the surroundings of dolines (Bátori et al. 2023).

We selected five microsites (south-, east-, west-, and north-facing slopes, and bottoms) in nine large dolines (diameter: 80–100 m, depth: 10–15 m) for vegetation sampling (Figure 1). For each doline, we also sampled a microsite on the surrounding plateau. We established five randomly placed 1 m × 1 m vegetation plots at each microsite (nine dolines × six microsites × five vegetation plots: 270 plots in total). We visually estimated and recorded the percentage cover of each vascular plant species in the plots in August 2021, at the peak of the growing season (plot-level data are provided in Bátori et al. (2023)). Nomenclature follows 'The World Flora Online' (https://www.worldfloraonline.org).

2.2 Temperature and moisture indicator values

In order to compare the microclimatic differences among the microsites (plateau, south-, east-, west-, and north-facing slopes, and bottoms), we calculated the unweighted mean Ellenberg-type indicator values (EIVs) for temperature (T) and moisture (F) at the plot level, using the system of Borhidi (1995). Each species is assigned a value for T and F, representing its realised optimum on a nine-point (T) or twelve-point (F) ordinal scale, defined along environmental gradients. The primary distinction between the Borhidi and Ellenberg systems is that the Borhidi system is specifically adapted to the Hungarian flora and assigns an indicator value to every species, with no allowance for an indifferent category. We performed the calculation of plot-level EIV values by dividing the sum of the indicator values – corresponding to a specific EIV – of the plant species occurring in the given plot by the number of plant species in the plot. Previous studies have shown that, despite the ordinal nature of EIVs, mean EIVs provide reliable estimates of the environmental conditions of a habitat (Tölgyesi et al. 2014; Wildi 2016).

2.3 Biogeographic affinities of species

We classified all vascular plant species according to their biogeographic affinities (Table 1, examples are also shown in Figure 1) and assigned them to six biogeographic groups using the PADAPT 1.0 database (Sonkoly et al. 2023) as follows: 1) Mediterranean group, such as *Silene viridiflora* L., *Teucrium chamaedrys* L., and *Waldsteinia geoides* Willd.; 2) mountain group, such as *Aconitum variegatum* L., *Astrantia major* L., and *Bupleurum longifolium* L.); 3) endemic group: *Centaurea scabiosa* subsp. *sadleriana* (Janka) Asch. & Graebn, and *Dianthus giganteiformis* subsp. *pontederae* (A. Kern.) Soó (both species are Pannonian endemics); 4) European group, such as *Allium scorodoprasum* L., *Origanum vulgare* L., and *Vicia cracca* L.; 5) continental group, such as *Anemonoides sylvestris* (L.) Galasso, Banfi & Soldano, *Iris variegata* L., and *Pulsatilla grandis* Wend.; and 6) cosmopolitan group, such as *Achillea millefolium* L., *Convolvulus arvensis* L., and *Trifolium repens* L.

2.4 Statistical analyses

We determined the diagnostic species of the plateau and doline microsites by calculating the phi (Φ) coefficient of all individual species, using the JUICE software (Tichý 2002). Only species having a phi value higher than 0.15 were considered diagnostic species (Fisher's exact test, $p < 0.05$) (Tichý and Chytrý 2006). Diagnostic species of the microsites were compared according to their biogeographic affinities.

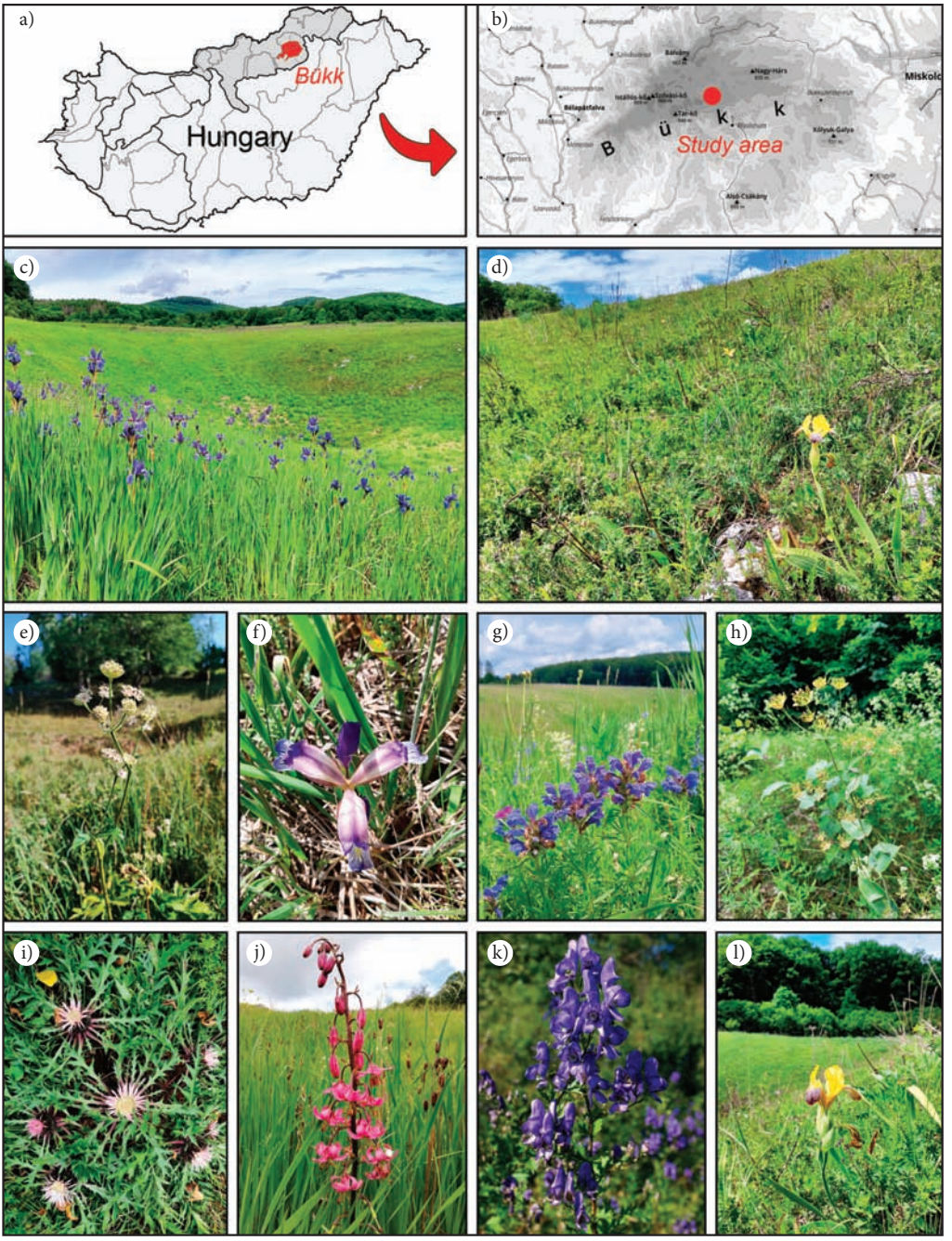


Figure 1: Map of the study region and study area, along with photos of microsites and characteristic rare and protected plant species. a) Study region in Hungary, b) study area in the Bükk Mountains, c) north-facing doline slope with a high cover of *Iris sibirica* L., d) south-facing doline slope with a high cover of *Iris variegata* L. and *Sempervivum globiferum* subsp. *hirtum* (L.) 't Hart & Bleij, e) *Astrantia major* L. in a doline bottom, f) *Iris graminea* L. on the plateau, g) *Dracocephalum ruyschiana* L. on an east-facing doline slope, h) *Bupleurum longifolium* L. on a north-facing doline slope, i) *Carlina acaulis* L. in a doline bottom, j) *Lilium martagon* L. in a doline bottom, k) *Aconitum variegatum* L. on a north-facing doline slope, and l) *Iris variegata* on a south-facing doline slope.

Table 1: A list of plant species assigned to the six biogeographic groups (Mediterranean, mountain, endemic, European, continental, and cosmopolitan groups).

Mediterranean group

Carex michelii
Colchicum autumnale
Cornus sanguinea
Cruciata glabra
Cruciata laevipes
Cruciata pedemontana
Geranium sanguineum
Muscari racemosum
Salvia verticillata
Sedum album
Silene viridiflora
Teucrium chamaedrys
Tragopogon dubius
Trifolium ochroleucon
Verbascum chaixii subsp. *austriacum*
Waldsteinia geoides

mountain group

Aconitum variegatum
Allium lusitanicum
Astrantia major
Bupleurum longifolium
Carlina acaulis
Centaurea phrygia subsp. *indurata*
Sempervivum globiferum subsp. *hirtum*

continental group

Ajuga genevensis
Anemonoides sylvestris
Asperula cynanchica
Carex montana
Cirsium pannonicum
Coronilla varia
Elymus hispidus
Euphorbia lucida
Geranium palustre
Gladiolus imbricatus
Glechoma hirsuta
Iris graminea
Iris variegata
Nonea pulla
Phleum phleoides
Potentilla recta
Pulsatilla grandis
Ranunculus polyanthemos
Scabiosa ochroleuca
Tanacetum corymbosum
Thalictrum lucidum
Trifolium montanum
Veronica austriaca subsp. *dentata*

cosmopolitan group

Achillea millefolium
Asplenium trichomanes
Botrychium lunaria
Briza media
Convolvulus arvensis
Dactylis glomerata
Deschampsia caespitosa
Koeleria cristata
Luzula campestris
Poa compressa
Poa pratensis s.l.
Potentilla reptans
Prunella vulgaris
Trifolium repens
Urtica dioica

endemic group

Centaurea scabiosa subsp. *sadleriana*
Dianthus giganteiformis subsp. *pontederae*

European group

Arrhenatherum elatius
Asplenium ruta-muraria
Astragalus glycyphyllos
Betonica officinalis
Betula pendula
Brachypodium pinnatum
Calamagrostis arundinacea
Calamagrostis epigejos
Campanula glomerata
Campanula patula
Campanula persicifolia
Cardamine pratensis
Carex caryophyllea
Carex hirta
Carex leporina
Carex pallescens
Carex pilosa
Carex praecox
Carex spicata
Carex tomentosa
Centaurea jacea agg.
Cerastium arvense subsp. *matrense*
Cirsium arvense
Cirsium eriophorum
Cirsium vulgare
Clinopodium acinos
Clinopodium vulgare
Genista tinctoria
Gentiana cruciata
Gentiana pneumonanthe
Gymnadenia conopsea
Helianthemum nummularium
Helictochloa praeusta
Helictotrichon pubescens
Hieracium umbellatum
Hylotelephium maximum
Hypericum hirsutum
Hypericum perforatum
Hypochaeris maculata
Iris sibirica
Jacobaea vulgaris
Knautia arvensis
Lathyrus pratensis
Leontodon hispidus
Leucanthemum vulgare
Lilium martagon
Linaria vulgaris
Linum catharticum
Lotus corniculatus
Luzula luzuloides
Lysimachia nummularia
Medicago falcata
Medicago lupulina
Mercurialis perennis
Pulmonaria mollis
Pulmonaria obscura
Ranunculus acris
Ranunculus auricomus
Ranunculus repens
Ribes uva-crispa
Rosa canina agg.
Rubus idaeus
Rumex acetosa
Salvia pratensis
Sanguisorba minor
Saponaria officinalis
Scorzoneroides autumnalis
Sedum acre
Selinum carvifolia
Seseli libanotis
Silene vulgaris
Solidago virgaurea
Stellaria graminea
Stellaria holostea
Succisa pratensis
Symphytum tuberosum
Taraxacum officinale
Thesium linophyllon
Thymus pulegioides subsp. *pannonicus*
Trifolium alpestre
Trifolium aureum

Dianthus deltoides
Digitalis grandiflora
Dracocephalum ruyschiana
Elymus repens
Euphorbia cyparissias
Fallopia convolvulus
Festuca heterophylla
Festuca pratensis
Festuca rubra
Festuca rupicola
Filipendula ulmaria
Filipendula vulgaris
Fragaria vesca
Galanthus nivalis
Galeopsis pubescens
Galium boreale
Galium mollugo
Galium schultesii
Galium verum
Molinia caerulea
Myosotis ramosissima
Nardus stricta
Ophioglossum vulgatum
Origanum vulgare
Parnassia palustris
Peucedanum palustre
Phleum pratense
Pimpinella saxifraga
Plantago media
Polygala comosa
Polygonatum odoratum
Potentilla argentea
Potentilla erecta
Potentilla heptaphylla
Primula elatior
Primula veris
Prunella grandiflora
Prunus spinosa
Trifolium medium
Trifolium pratense
Tussilago farfara
Valeriana officinalis subsp. *collina*
Verbascum thapsus
Veronica chamaedrys
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Vicia sepium
Vicia tetrasperma
Vincetoxicum hirundinaria
Viola canina
Viola hirta
Viola mirabilis
Viola reichenbachiana

We tested the effects of microsites (plateau, south-, east-, west-, and and bottoms) on the mean Ellenberg-type indicator values (temperature and moisture), and on the number and cover of species within each biogeographic group (Mediterranean, mountain, endemic, European, continental, and cosmopolitan groups). We used linear mixed-effects models (LMMs) with Gaussian error distribution for the mean indicator values and species cover data, and generalised linear mixed-effects models (GLMMs) with Poisson error distribution for the species number data – except for the species number data of the endemic group, for which we used a binomial error distribution because only two species with low frequency belonged to this group. In the models, the mean indicator values, as well as the number and cover of species in the vegetation plots were used as response variables, with microsite (plateau, south-, east-, west-, and north-facing slopes, and bottoms) included as a fixed factor, and doline ID as a random factor. We performed all analyses in R v. 4.2.2 (R Foundation … 2022) using the *lmer* and *glmer* functions of the 'lme4' package (Bates et al. 2015), the *Anova* function of the 'car' package to test model significances, and the *emmeans* function of the 'emmeans' package to calculate pairwise comparisons (Lenth 2023).

3 Results

A total of 211 vascular plant species were recorded in the plots. Vegetation on south-facing slopes indicated significantly warmer conditions than all other microsites, except for east-facing slopes, while vegetation on north-facing slopes and bottoms indicated the coldest conditions (Figure 2, Table 2). A similar pattern was observed for moisture conditions among the microsites, with vegetation on south-facing slopes indicating significantly drier, and on north-facing slopes and in bottoms significantly moister conditions compared to all other microsites.

We recorded 16 species (7.6%) belonging to the Mediterranean group, eight species belonging to the mountain group (3.8%), two species (0.9%) belonging to the endemic group, 147 species belonging to the European group (69.7%), 23 species (10.9%) belonging to the continental group, and 15 species belonging to the cosmopolitan group (7.1%) in the vegetation plots.

Considering the diagnostic species of the microsites, we found 13 diagnostic species for the plateau, 20 species for south-facing slopes, 18 species for east-facing slopes, 10 species for west-facing slopes, 23 species for north-facing slopes, and 20 species for bottoms. In terms of the distribution of biogeographic groups, south-facing slopes exhibited the highest diversity (six groups), while east-facing slopes and bottoms showed the lowest (three groups). The proportion of the Mediterranean group was highest on east-facing slopes (17%), while the proportion of the mountain group was highest on south- and north-facing slopes (5% and 4%, respectively) (Figure 3, Table 3). The proportions of the endemic and continental groups were highest on the plateau (8 and 31%, respectively), while the European group had the lowest proportion in this microsite (46%). Bottoms had the highest proportion of cosmopolitan species (15%).

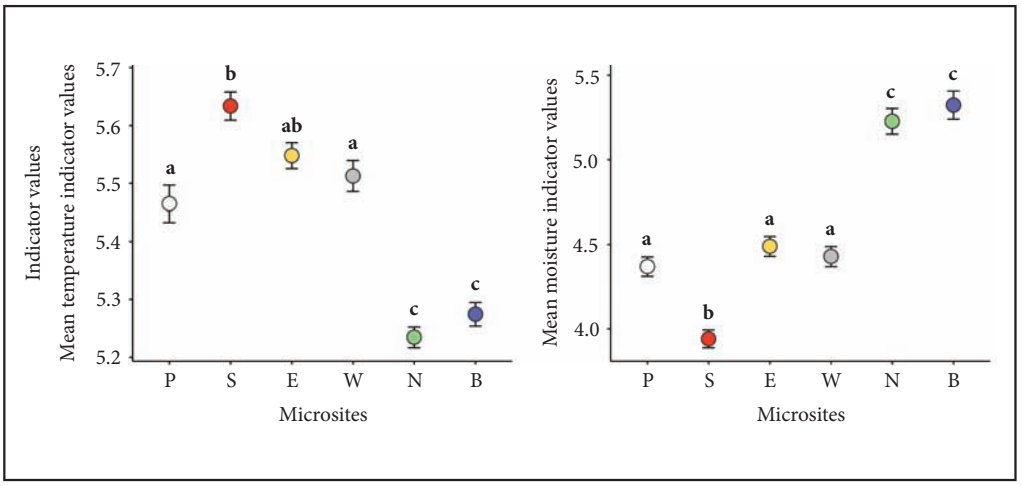


Figure 2: Mean Ellenberg-type indicator values for temperature and moisture (mean ± SE). Lowercase letters (a–c) indicate significant differences (LMMs, $p < 0.05$) among the microsites (P: plateau, S: south-facing slopes of dolines, E: east-facing slopes of dolines, W: west-facing slopes of dolines, N: north-facing slopes of dolines, and B: doline bottoms).

Table 2: Test results of linear mixed-effects models (LMMs) used for the mean Ellenberg-type indicator values (temperature and moisture) across the microsites (P: plateau, S: south-facing slopes of dolines, E: east-facing slopes of dolines, W: west-facing slopes of dolines, N: north-facing slopes of dolines, and B: doline bottoms). Pairwise differences ($p < 0.05$) are marked with boldface.

	Mean temperature indicator values		Mean moisture indicator values	
Microsite	F 47.56	*p* **<0.001**	F 73.47	*p* **<0.001**
	t	*p*	t	*p*
B – E	–8.45	**<0.001**	9.42	**<0.001**
B – N	1.23	0.820	1.08	0.888
B – P	–5.88	**<0.001**	10.77	**<0.001**
B – S	–11.10	**<0.001**	15.61	**<0.001**
B – W	–7.36	**<0.001**	10.10	**<0.001**
E – N	9.68	**<0.001**	–8.34	**<0.001**
E – P	2.57	0.110	1.35	0.755
E – S	–2.65	0.090	6.19	**<0.001**
E – W	1.09	0.887	0.68	0.984
N – P	–7.12	**<0.001**	9.69	**<0.001**
N – S	–12.33	**<0.001**	14.53	**<0.001**
N – W	–8.60	**<0.001**	9.02	**<0.001**
P – S	–5.21	**<0.001**	4.84	**<0.001**
P – W	–1.48	0.678	–0.68	0.984
S – W	3.73	**0.003**	–5.51	**<0.001**

Figure 3: Biogeographic affinities of the diagnostic species across the microsites (plateau, south-, east-, west-, and north-facing slopes of dolines, and doline bottoms). The numbers indicate the number and proportion of diagnostic species belonging to each group. ► p. 89

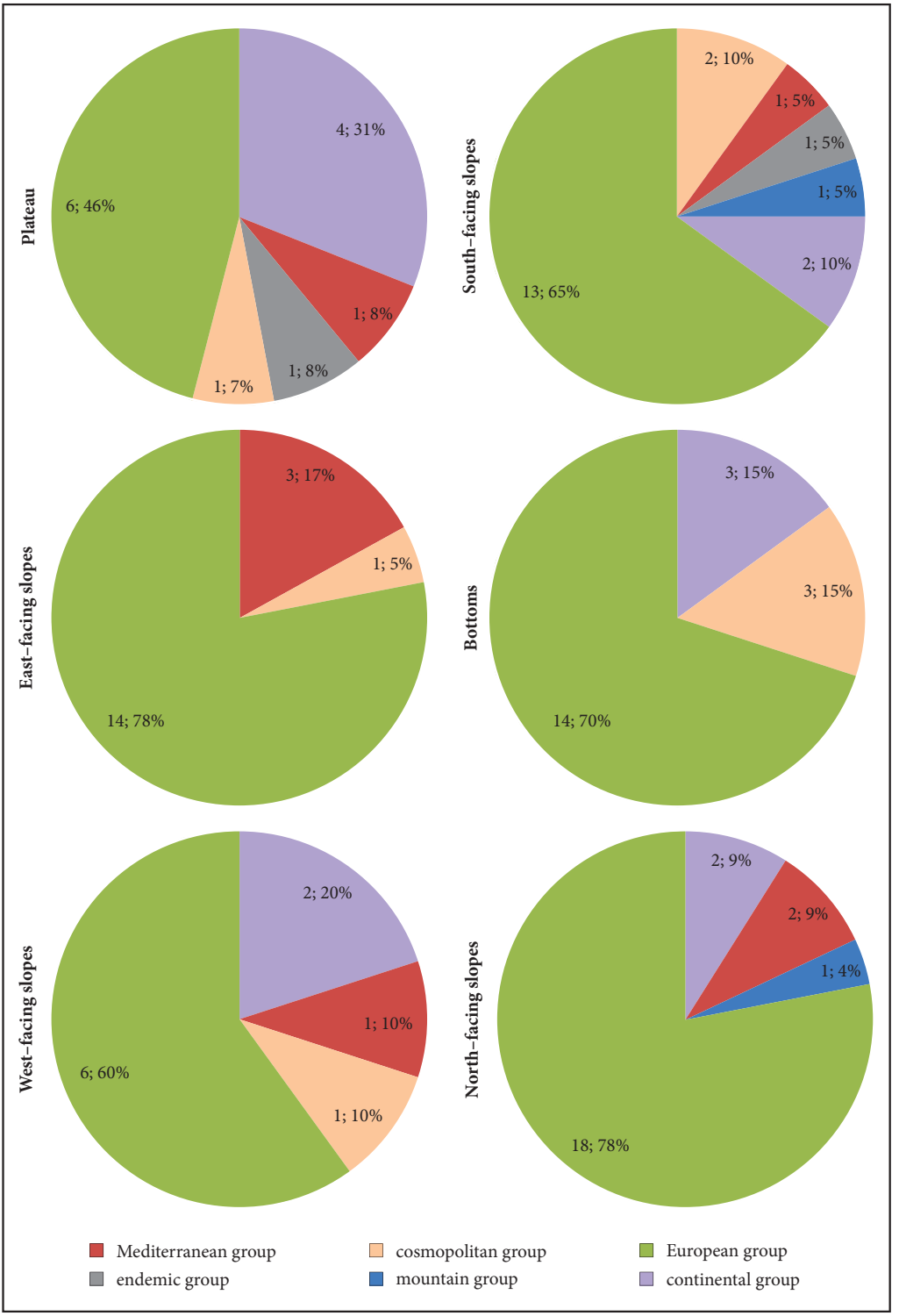

Plateau
4; 31%
6; 46%
1; 8%
1; 8%
1; 7%
South–facing slopes
2; 10%
1; 5%
1; 5%
1; 5%
2; 10%
13; 65%
East–facing slopes
3; 17%
1; 5%
14; 78%
Bottoms
3; 15%
3; 15%
14; 70%
West–facing slopes
2; 20%
1; 10%
6; 60%
1; 10%
North–facing slopes
2; 9%
2; 9%
1; 4%
18; 78%
Mediterranean group
cosmopolitan group
European group
endemic group
mountain group
continental group

Table 3: Diagnostic species of the plateau and doline microsites (south-, east-, west- and north-facing slopes, and bottoms) according to their biogeographic affinities (phi (Φ) coefficients of association between species and microsites are provided in Bátori et al. (2023)).

Plateaus

Mediterranean group: *Carex michelii*; **endemic group:** *Centaurea scabiosa* subsp. *sadleriana*; **European group:** *Seseli libanotis*, *Allium oleraceum*, *Galium verum*, *Filipendula vulgaris*, *Carex pallescens, Helictotrichon pubescens*; **continental group:** *Trifolium montanum*, *Phleum phleoides*, *Veronica austriaca* subsp. *dentata, Thalictrum lucidum*; **cosmopolitan group:** *Briza media*

South-facing doline slopes

Mediterranean group: *Teucrium chamaedrys*; **mountain group:** *Sempervivum globiferum* subsp. *hirtum*; **endemic group:** *Dianthus giganteiformis* subsp. *pontederae*; **European group:** *Polygonatum odoratum*, *Medicago lupulina*, *Arabis hirsuta*, *Digitalis grandiflora*, *Clinopodium acinos*, *Carex praecox*, *Thymus pulegioides* subsp. *pannonicus*, *Carex caryophyllea*, *Potentilla heptaphylla*, *Hylotelephium maximum*, *Festuca rupicola*, *Euphorbia cyparissias*, *Sedum acre*; **continental group:** *Iris variegata, Coronilla varia*; **cosmopolitan group:** *Koeleria cristata*, *Poa compressa*

East-facing doline slopes

Mediterranean group: *Verbascum chaixii* subsp. *austriacum*, *Cruciata laevipes*, *Waldsteinia geoides*; **European group:** *Viola hirta*, *Rosa canina* agg., *Galium mollugo*, *Veronica chamaedrys*, *Clinopodium vulgare*, *Acer platanoides*, *Lilium martagon*, *Veronica spicata*, *Hypericum hirsutum*, *Digitalis grandiflora*, *Origanum vulgare*, *Agrimonia eupatoria*, *Fallopia convolvulus*, *Stellaria holostea*; **cosmopolitan group:** *Convolvulus arvensis*

West-facing doline slopes

Mediterranean group: *Salvia verticillata*; **continental group:** *Carex montana*, *Tanacetum corymbosum*; **European group:** *Cirsium arvense*, *Trifolium alpestre*, *Pimpinella saxifraga*, *Salvia pratensis*, *Prunella grandiflora*, *Carex tomentosa*; **cosmopolitan group:** *Luzula campestris*

North-facing doline slopes

Mediterranean group: *Cruciata glabra*, *Colchicum autumnale*; **mountain group:** *Bupleurum longifolium*; **European group:** *Helictochloa praeusta*; *Luzula luzuloides*, *Alchemilla monticola*, *Filipendula ulmaria*, *Veronica chamaedrys*, *Leontodon hispidus*, *Rubus idaeus*, *Hypochaeris maculata*, *Trifolium aureum*, *Cirsium eriophorum*, *Dianthus deltoides*, *Agrostis capillaris*, *Potentilla erecta*, *Festuca pratensis*, *Ranunculus auricomus*, *Stellaria graminea*, *Rumex acetosa*, *Aegopodium podagraria*; **continental group:** *Ranunculus polyanthemos*, *Glechoma hirsuta*

Doline bottoms

European group: *Gentiana pneumonanthe*, *Selinum carvifolia, Plantago media*, *Calamagrostis epigejos*, *Vicia cracca*, *Ophioglossum vulgatum*, *Alopecurus pratensis*, *Carex pilosa*, *Leucanthemum vulgare*, *Calamagrostis arundinacea*, *Molinia caerulea*, *Lathyrus pratensis*, *Vicia sepium*, *Carex hirta*; **continental group:** *Gladiolus imbricatus*, *Elymus repens*, *Geranium palustre*; **cosmopolitan group:** *Deschampsia caespitosa*, *Potentilla reptans*, *Urtica dioica*

At the plot level, the number of species belonging to the Mediterranean group tended to be highest on east- and west-facing slopes and lowest in bottoms (Figure 4, Table 4). Their cover was similarly high on the plateau, as well as on south-, east-, and west-facing slopes, and lowest on north-facing slopes and in bottoms. The number of species belonging to the mountain group tended to be highest on north-facing slopes, while their cover tended to be highest in bottoms. The number of species belonging to the endemic group tended to be highest on south-facing slopes, while no endemic species occurred on north-facing slopes or in bottoms. The number and cover of species belonging to the European group tended to be lowest on south-facing slopes, and their cover was highest on north-facing slopes (Figure 5, Table 4). The number and cover of species belonging to the continental group tended to be lowest on north-facing slopes or in bottoms. The cover of species belonging to the cosmopolitan group tended to be lowest on the plateau and south-facing slopes, and highest in the bottoms.

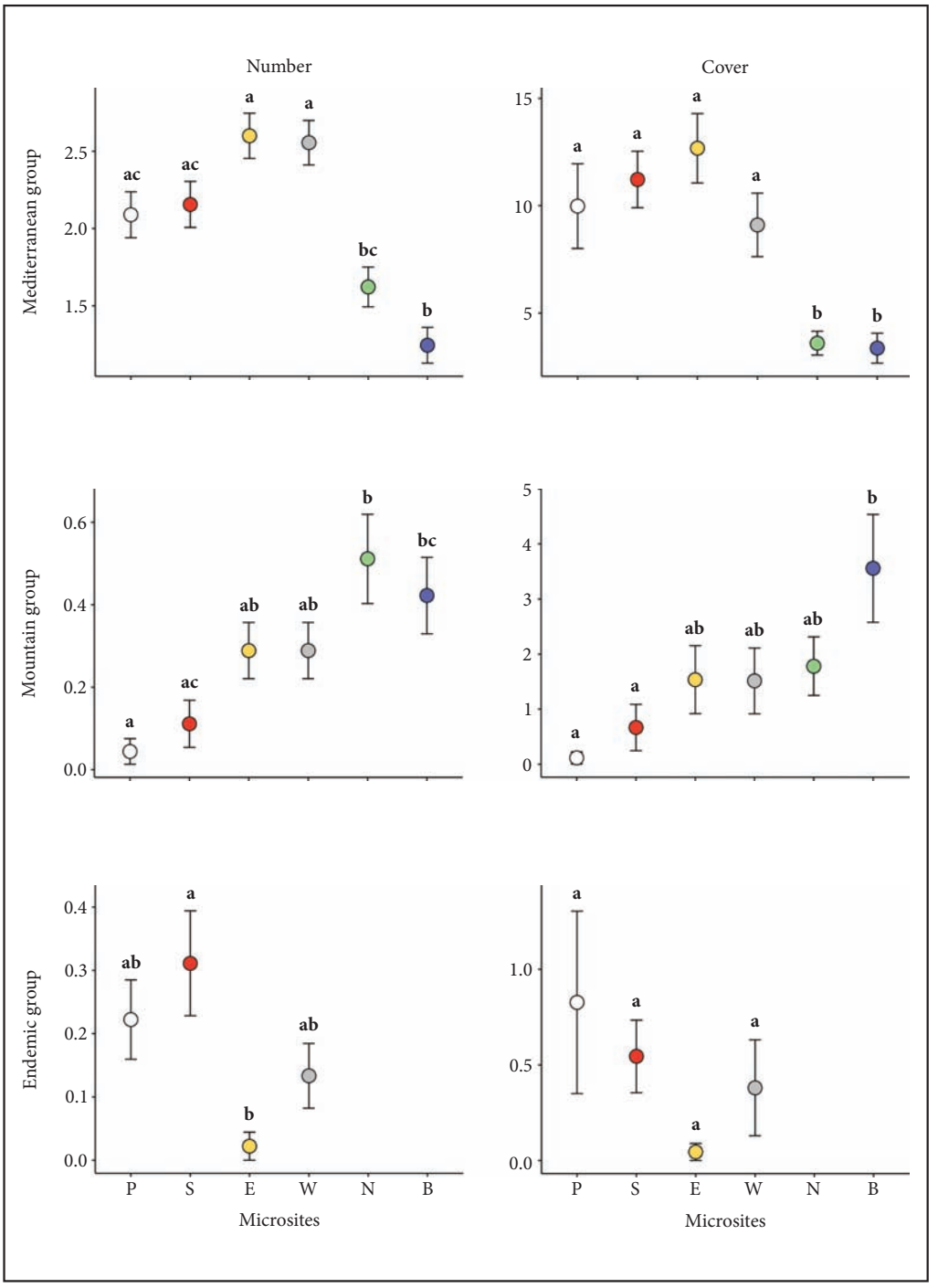


Figure 4: Number and cover of species belonging to the Mediterranean, mountain and endemic groups (mean ± SE) across the microsites. Lowercase letters (a–c) indicate significant differences (LMMs and GLMMs, $p < 0.05$) among the microsites (P: plateau, S: south-facing slopes of dolines, E: east-facing slopes of dolines, W: west-facing slopes of dolines, N: north-facing slopes of dolines, and B: bottoms).

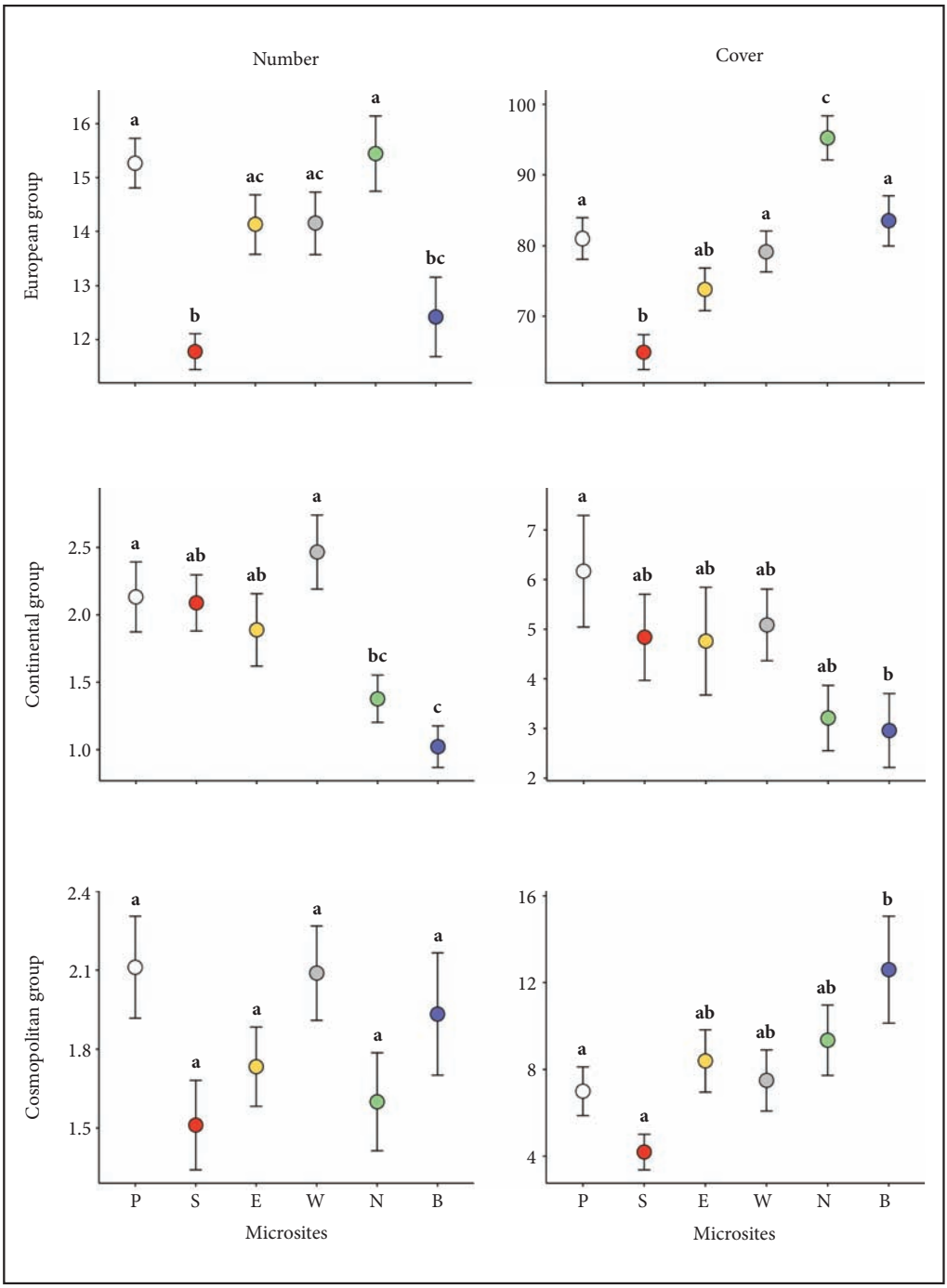


Figure 5: Number and cover of species belonging to the European, continental and cosmopolitan groups (mean ± SE) across the microsites. Lowercase letters (a–c) indicate significant differences (LMMs and GLMMs, $p < 0.05$) or marginally significant differences (LMMs and GLMMs, $0.05 < p < 0.08$) among the microsites (P: plateau, S: south-facing slopes of dolines, E: east-facing slopes of dolines, W: west-facing slopes of dolines, N: north-facing slopes of dolines, and B: bottoms of dolines).

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Table 4: Test results of the linear mixed-effects models (LMMs) used for the cover of species groups and the generalized linear mixed-effects models (GLMMs) used for the number of species groups across the microsites (P: plateau, S: south-facing slopes of dolines, E: east-facing slopes of dolines, W: west-facing slopes of dolines, N: north-facing slopes of dolines, and B: doline bottoms). Significant pairwise differences ($p < 0.05$) are marked with boldface, while marginally significant differences ($0.05 < p < 0.08$) are marked with bold italics.

	Number of species belonging to the Mediterranean group		Cover of species belonging to the Mediterranean group		Number of species belonging to the mountain group		Cover of species belonging to the mountain group	
	F	*p*	F	*p*	F	*p*	F	*p*
Microsite	6.01	**<0.001**	9.44	**<0.001**	3.93	**0.001**	4.05	**0.001**
	t	*p*	t	*p*	t	*p*	t	*p*
B – E	–4.54	**<0.001**	–5.14	**<0.001**	1.06	0.897	2.44	0.145
B – N	–1.49	0.669	–0.13	1.000	–0.62	0.990	2.15	0.266
B – P	–3.07	**0.026**	–3.65	**0.004**	3.05	**0.028**	4.16	**0.001**
B – S	–3.27	**0.014**	-4.33	**<0.001**	2.68	0.080	3.49	**0.007**
B – W	–4.42	**<0.001**	–3.17	**0.021**	1.06	0.897	2.47	0.137
E – N	3.16	**0.020**	5.01	**<0.001**	–1.66	0.561	–0.30	1.000
E – P	1.58	0.612	1.49	0.674	2.48	0.129	1.72	0.521
E – S	1.37	0.748	0.80	0.967	1.83	0.447	1.05	0.900
E – W	0.13	1.000	1.97	0.364	0.00	1.000	0.03	1.000
N – P	–1.62	0.585	–3.52	**0.007**	3.34	**0.011**	2.01	0.337
N – S	–1.84	0.443	–4.20	**0.001**	3.12	**0.023**	1.35	0.759
N – W	–3.04	**0.029**	–3.04	**0.031**	1.66	0.561	0.32	1.000
P – S	–0.22	1.000	–0.68	0.984	–1.10	0.880	–0.67	0.985
P – W	–1.45	0.696	0.48	0.997	–2.48	0.129	–1.69	0.538
S – W	–1.24	0.820	1.17	0.853	–1.83	0.447	–1.02	0.910

	Number of species belonging to the endemic group		Cover of species belonging to the endemic group		Number of species belonging to the European group		Cover of species belonging to the European group	
	F	*p*	F	*p*	F	*p*	F	*p*
Microsite	1.96	0.076	2.42	**0.037**	7.15	**<0.001**	12.21	**<0.001**
	t	*p*	t	*p*	t	*p*	t	*p*
B – E	–0.12	1.000	–0.14	1.000	–2.23	0.225	2.36	0.173
B – N	0.00	1.000	0.00	1.000	–3.83	**0.002**	–2.87	**0.050**
B – P	–0.14	1.000	–2.65	0.090	–3.62	**0.004**	0.61	0.990
B – S	–0.14	1.000	–1.74	0.504	0.88	0.952	4.54	**<0.001**
B – W	–0.13	1.000	–1.22	0.828	–2.26	0.213	1.06	0.897
E – N	0.09	1.000	0.14	1.000	–1.62	0.587	–5.24	**<0.001**
E – P	–2.61	0.094	–2.51	0.127	–1.40	0.726	–1.75	0.498
E – S	–2.90	**0.043**	–1.60	0.599	3.10	**0.024**	2.18	0.252
E – W	–1.88	0.414	–1.08	0.891	–0.03	1.000	–1.30	0.783
N – P	–0.11	1.000	–2.65	0.090	0.22	1.000	3.48	**0.008**
N – S	–0.11	1.000	–1.74	0.504	4.70	**<0.001**	7.41	**<0.001**
N – W	–0.10	1.000	–1.22	0.828	1.59	0.606	3.93	**0.002**
P – S	–0.57	0.993	0.90	0.945	4.49	**<0.001**	3.93	**0.002**
P – W	1.24	0.818	1.43	0.709	1.37	0.743	0.45	0.998
S – W	1.77	0.489	0.53	0.995	–3.13	**0.022**	–3.48	**0.008**

➤ p. 94

	Number of species belonging to the continental group		Cover of species belonging to the continental group		Number of species belonging to the cosmopolitan group		Cover of species belonging to the cosmopolitan group	
	F	*p*	F	*p*	F	*p*	F	*p*
Microsite	6.75	**<0.001**	2.31	**0.045**	1.57	0.162	4.09	**0.001**
	t	*p*	t	*p*	t	*p*	t	*p*
B – E	–3.37	**0.010**	–1.60	0.602	0.70	0.982	2.16	0.259
B – N	–1.54	0.638	–0.22	1.000	1.19	0.841	1.67	0.551
B – P	–4.12	**0.001**	–2.85	***0.054***	–0.60	0.991	2.88	**0.049**
B – S	–3.99	**0.001**	–1.67	0.556	1.53	0.646	4.32	**<0.001**
B – W	–5.04	**<0.001**	–1.89	0.413	–0.52	0.995	2.63	0.095
E – N	1.90	0.404	1.37	0.743	0.49	0.997	–0.49	0.997
E – P	–0.82	0.964	–1.25	0.812	–1.30	0.788	0.72	0.979
E – S	–0.68	0.985	–0.07	1.000	0.83	0.962	2.16	0.260
E – W	–1.86	0.428	–0.29	1.000	–1.22	0.826	0.46	0.997
N – P	–2.69	***0.076***	–2.62	0.095	–1.78	0.478	1.21	0.832
N – S	–2.55	0.109	–1.44	0.701	0.34	0.999	2.65	0.089
N – W	–3.69	**0.003**	–1.66	0.557	–1.71	0.526	0.95	0.932
P – S	0.15	1.000	1.18	0.846	2.11	0.280	1.44	0.702
P – W	–1.05	0.902	0.96	0.930	0.07	1.000	–0.26	1.000
S – W	–1.19	0.842	–0.22	1.000	–2.04	0.319	–1.70	0.535

4 Discussion

To our knowledge, this study is among the first to assess the complex relationships between microsite diversity and the biogeographic affinities of plant species across a relatively large number of karstic microrefugia. We demonstrated that dolines have the potential to function as safe havens for plant species with various biogeographic affinities. We also demonstrated that the number and/or cover of species belonging to the Mediterranean group tended to be higher in warmer and drier microsites (i.e., the plateau and the south-, east-, and west-facing doline slopes), whereas those of the mountain group tended to be higher on cooler and moister north-facing slopes and/or in doline bottoms. Therefore, the current species pools and plant distributions in dolines indicate the presence of both 'warmer islands' and 'cooler islands' within short distances, providing habitats for a high diversity of species adapted to different climates.

We found that fine-scale topographic complexity in dolines facilitates the survival of plant species with diverse biogeographic affinities, likely due primarily to the unique microclimatic patterns within these landforms. Previous studies indicate that cold-air pooling and temperature inversions in dolines promote environmental stability and drive other key environmental factors, such as soil temperature, soil moisture, duration of snow cover, and frost frequency (Bárány-Kevei 1999; Bátori et al. 2019; Bátori et al. 2022a; Marcin et al. 2024). On the other hand, south-, east- and west-facing slopes in the Northern Hemisphere receive much more insolation than north-facing slopes, providing warmer and drier microsites than their surroundings (Bátori et al. 2023; Simpson et al. 2024). Due to increased insolation reaching the bottom of grassland dolines during the daytime, these areas experience higher temperatures than north-facing slopes for a certain period (Bátori et al. 2019). These microclimatic differences, resulting from the topographic complexity of dolines, may support the long-term persistence of species with specific climatic requirements during both warmer and cooler climatic periods. For instance, the occurrence of *Dracocephalum ruyschiana* in the dolines of the Bükk Mountains is presumed to date back millennia (Lazarević et al. 2009). During the warmer periods of the Pleistocene (i.e., the interglacials) and the Holocene, plant species migrated northwards in Europe (Stewart et al. 2010) or retreated to higher elevations in the mountains (cf. Walther et al. 2002). These migrations were presumably geographically structured across temperate Europe in relation to geomorphology and vegetation composition (Divíšek et al. 2020; Roleček et al. 2021). For instance, Bátori et al. (2022b) highlighted that both the western and eastern parts of the Carpathian Basin and their vicinity (i.e., eastern part and borderland of the Alps, and the Western Romanian Carpathians) have served as

migration routes for many karst-dwelling species now inhabiting the North Hungarian Mountains (Vojtkó 2001; Vojtkó 2016), including the Bükk Mountains. Warmer climatic periods during the Holocene (e.g., in the early Holocene, between 11,700 and 8,200 BP) might have facilitated both the migration of several sub-Mediterranean plant species from the south and the expansion of plant species with various ecological requirements from local and regional refugia (Willis et al. 2000; Magyari et al. 2010; see also the 'Flora Continuity Hypothesis' for the Carpathian Basin, Molnár et al. 2023). In the current climate, the north-facing slopes and bottoms of dolines serve as 'cool islands' for mountain species, such as *Aconitum variegatum* L., *Bupleurum longifolium* L., and *Carlina acaulis* L., while the other microsites support the persistence of many species belonging to the Mediterranean group, such as *Cruciata pedemontana* (Bellardi) Ehrend., *Teucrium chamaedrys* L., and *Waldsteinia geoides* Willd. The number of species belonging to the Mediterranean group did not differ significantly among the plateau, south-, east-, and west-facing slopes, which may be explained not only by microclimatic effects but also by other factors, such as soil depth and moisture (Bátori et al. 2023). Within the study area, the two Pannonian endemics – *Centaurea scabiosa* subsp. *sadleriana* (Janka) Asch. & Graebn. and *Dianthus giganteiformis* subsp. *pontederae* (A.Kern.) Soó – are xerophilous plants that predominantly inhabit the warmer and drier south-facing slopes and the plateau (Vojtkó 2001). We also found that the warm and dry south-facing doline slopes and the cool and moist doline bottoms did not favour the establishment of many species belonging to the European group, presumably due to the strong abiotic filters (e.g., extreme temperatures) in these microsites (Bátori et al. 2019; Bátori et al. 2023). The environmental stability on north-facing slopes and in bottoms did not favour the persistence of continental species adapted to climatic extremes (warm summers and cold winters) (cf. Spiecker 2003). Moreover, the relatively stable microclimatic conditions in doline bottoms may also result in lower diversity in the distribution of diagnostic species belonging to different biogeographic groups. The distribution of some cosmopolitan species in doline microsites and their surroundings (e.g., *Convolvulus arvensis* L. and *Trifolium repens* L.) may reflect past human disturbances, such as soil contamination, lime burning and overgrazing (cf. Bárány-Kevei et al. 2001; Bátori et al. 2020).

Climate models predict a substantial increase in temperature and summer drought for the Carpathian Basin in the coming decades (Bartholy et al. 2009). We suggest that dolines may play an important role in the long-term persistence of at least some plant species under anthropogenic climate change. Although species will respond individualistically to climate changes (Stewart et al. 2010), most species belonging to the Mediterranean group within our study area are expected to expand their distributions from the warmer and drier microsites to the cooler and moister microsites (i.e., north-facing slopes and doline bottoms). Even after biophysical thresholds are exceeded and the relatively buffered north-facing slopes and doline bottoms no longer function as safe havens for cool-adapted species, these microsites may still be valuable for other species that benefit from climate buffering (cf. Morelli et al. 2020).

5 Conclusion

We can conclude that dolines likely have the capacity to provide safe havens for plant species with different biogeographic affinities in the future. Therefore, management should take into account the complex relationships between microsite structure, environmental conditions, and species distributions in dolines and their surroundings, as well as the magnitude and rate of climate change, and the refugial capacity (cf. Keppel et al. 2024).

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RESEARCH DATA: For information on the availability of research data related to the study, please visit the article webpage: https://doi.org/10.3986/AGS.14564.

6 References

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