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Environmental heterogeneity increases the conservation value of small natural features in karst landscapes

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HIGHLIGHTS

- Depressions in karst landscapes (dolines) may function as small natural features.
- Dolines maintain various components of environmental heterogeneity.
- Dolines promote a high diversity of microhabitats with unique species composition.
- Each microhabitat contains species that are rare or absent in other microhabitats.
- Conservation of dolines is crucial to maintain Earth's biodiversity.

GRAPHICAL ABSTRACT
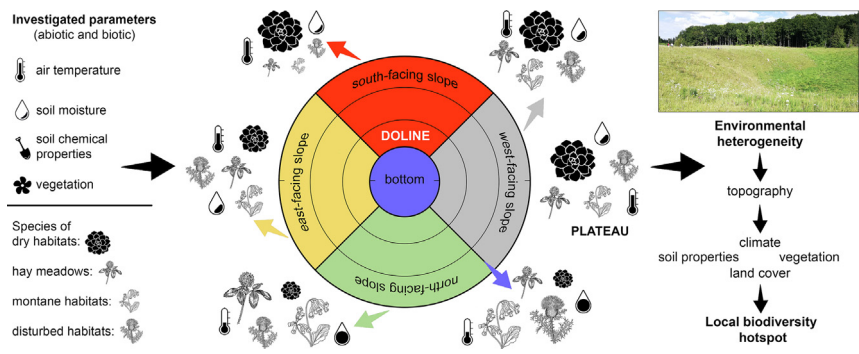
ABSTRACT

Local biodiversity hotspots are often located within regions where extreme and variable environmental – e.g., climatic and soil – conditions occur. These areas are conservation priorities. Although environmental heterogeneity is recognised as an important determinant of biodiversity, studies focusing on the effects of multiple environmental heterogeneity components in the same ecosystem are scarce. Here we investigate how topography and related microclimatic variables and soil properties may influence the biodiversity and conservation value of karst landscapes. Karst landscapes of the world contain millions of dolines (i.e. bowl- or funnel-shaped depressions) that may function as 'small natural features' with a disproportionately large role in maintaining biodiversity relative to their size. We assessed the diversity of microclimates, soils and vegetation and their relationships in six microhabitats (south-facing slopes, east-facing slopes, west-facing slopes, north-facing slopes and bottoms of dolines, and the adjacent plateau) for nine large dolines in a grassland ecosystem. Although there were remarkable differences among the conservation value of these microhabitats (e.g., representation of different species groups, presence of 'climate relicts'), each microhabitat had an important role in maintaining species that are rare or absent in other microhabitats in the landscape. We found

that the studied dolines exhibited highly variable environmental conditions and promoted a high diversity of vegetation types with unique species composition, contributing to the topographic, climatic, soil, vegetation and land cover heterogeneity of karst landscapes. Therefore, our findings highlight that dolines may function as local biodiversity hotspots and have a crucial conservation importance. As dolines are widespread topographic features in many karst landscapes throughout the world, our results could be directly applied to other regions as well. An integrated approach is urgently needed to provide guidelines for landscape management, promoting the retention of the microhabitat diversity of small natural features for species vulnerable to climate change and/or various disturbances.

1. Introduction

Linking spatial environmental heterogeneity (henceforth EH) and species diversity is a fundamental topic in conservation biology, biogeography, and evolution (Lundholm, 2009; Yang et al., 2015; Udy et al., 2021). EH encompasses spatial and temporal variation in biotic and abiotic components from local to continental scales (Tamme et al., 2010), involving topographic, climatic, soil, vegetation and land cover EH (Stein and Kreft, 2015). In addition to the accumulating evidence highlighting positive relationships between EH and species diversity across taxa and spatial scales (Stein et al., 2014; Erdős et al., 2018), negative relationships have also been reported (Gazol et al., 2013; Bar-Massada and Wood, 2014). The positive relationships have been explained by various mechanisms. Environmentally heterogeneous areas may contain larger environmental gradients, more habitat types and resources, and may provide safe havens for a number of species during unfavourable environmental changes (Stein et al., 2014; Bátori et al., 2020a; Deák et al., 2021). In addition, these areas may enhance the probability of speciation due to adaptation to diverse environmental conditions (Antonelli and Sanmartín, 2011). Together, these mechanisms imply that the spatial variation in abiotic and biotic components increases the available niche space and therefore, allows the coexistence of many species (Stein and Kreft, 2015). This is the main reason why areas with high EH are often the focus of conservation efforts (e.g., Costanza et al., 2011; Breg Valjavec et al., 2018a, 2022; Carvalho et al., 2021). Although many studies have assessed the effects of individual EH components on species diversity (Stein et al., 2014; Breg Valjavec et al., 2018b), studies focusing on the effects of multiple EH components in the same ecosystem are scarce (Deák et al., 2021). Here we aimed to assess how topography and related microclimatic variables and soil properties may influence the biodiversity and conservation value of karst landscapes.

Topographically complex karst landscapes – covering about 20 % of the Earth's terrestrial surface (Ford and Williams, 2007) – provide an opportunity to establish relationships among climatic and soil EH, vegetation cover and species diversity (Oliver et al., 2017; Shui et al., 2022). Karst surfaces of the world contain millions of dolines (i.e. bowl- or funnel-shaped depressions), which are the most widespread landforms of karst landscapes (Bátori et al., 2019; Čarni et al., 2022). Dolines may function as 'small natural features' (henceforth SNFs) as they are special landscape elements with a disproportionately large role in maintaining biodiversity relative to their size (cf. Hunter et al., 2017). As SNFs may provide resources for the long-term survival of key populations and support the occurrence of specific ecological or evolutionary phenomena (Bauer et al., 2017; Hunter et al., 2017), implementing steps toward their conservation is important to retain biodiversity (Lindenmayer, 2017; Lundquist et al., 2017). Examples of SNFs include prehistoric burial mounds in agricultural landscapes (Deák et al., 2016), granite outcrops in flat landscapes (Ottaviani and Marcantonio, 2021), caves (Medellin et al., 2017), large old trees in wood-pastures (Hartel et al., 2013), and isolated peat bogs (Gallé et al., 2021).

Dolines are formed by various processes, such as dissolution or collapse, and vary in diameter from a few meters to a few hundreds of meters (Ford and Williams, 2007). The formation of a shallow and cool air layer in the bottom of dolines during night-time (i.e. cold-air pooling) and the role of their poleward-facing (as opposed to equator-facing) slopes in creating a relatively cool and humid microclimate are well-documented (Bárány-Kevei, 1999; Whiteman et al., 2004). Previous studies demonstrated that the bottom and poleward-facing slopes of dolines may serve as

microrefugia for cool-adapted species (Kobal et al., 2015; Bátori et al., 2017; Marcin et al., 2021). For instance, dolines in central and southern Europe have maintained a high richness of boreal, cold-temperate and montane plant species (e.g., Tan et al., 1997; Bátori et al., 2017), including relict populations of *Dracocephalum ruyschiana* in Hungary and Serbia (Lazarević et al., 2009). Dolines in Turkey play a crucial role in maintaining many endangered endemic species (Öztürk and Savran, 2020), while deep dolines in China (called tiankengs) provide safe havens for old-growth forests and their associated wildlife (Su et al., 2017). Although microclimate is recognised as having a major influence on species distributions within dolines, most studies have only focused on its effects on poleward- vs. equator-facing slopes and bottoms (e.g., Bátori et al., 2019; Marcin et al., 2021). Furthermore, spatial variation in soil properties may greatly affect vegetation structure and species composition within dolines (Gargano et al., 2010), but the links between soil properties and vegetation patterns have rarely been studied.

In this study we investigate these links using a comprehensive framework, involving topography, microclimate, soil properties and vegetation. Specifically, we addressed the following questions: 1) How do doline microhabitats (south-, east-, west-, north-facing slopes, and bottoms) and the surrounding plateau contribute to the components of climatic and soil EH in karst landscapes? 2) Do these microhabitats and related environmental factors maintain distinct vegetation patterns contributing to the vegetation and land cover EH? 3) Are there any differences in the conservation value of microhabitats within dolines? By answering these questions, we also hope to further advance our understanding of the role of SNFs with high EH as biodiversity hotspots and potential microrefugia in karst landscapes.

2. Material and methods

2.1. Study area

Investigations were carried out on the Bükk Plateau (Bükk Mountains, northern Hungary, Fig. 1a), at an altitude of approximately 750–800 m (48°04′31″ N, 20°29′57″ E), where solution dolines are a widespread type of karst depression (De Waele, 2009). Solution dolines are bowl- or funnel-shaped depressions formed by the dissolution of rock at the bedrock–soil interface (Ford and Williams, 2007; Čarni et al., 2022). The climate of the Bükk Plateau is cool and humid (mean annual temperature: 6.3 °C, mean annual precipitation: 800 mm, Dövényi, 2010), and doline bottoms consistently promote cold-air pooling during night-time (Bárány-Kevei, 1999). The prevailing soil types of the study area are Rendzic Leptosols and (Leptic) Luvisols (Bárány-Kevei, 1987; IUSS Working Group WRB, 2015). The plateau is characterised by a mosaic of grassland and forest patches. The dominant tree species is *Fagus sylvatica* (European beech), but dense *Picea abies* (Norway spruce) plantations also cover large areas. *Arrhenatherum elatius* and *Festuca rubra* hay meadows, semi-dry rocky grasslands and wet meadows are the most common grassland communities within the study area, consisting of many rare and endangered species such as *Aconitum moldavicum*, *A. variegatum*, *Botrychium lunaria*, *Bupleurum longifolium*, *Gladiolus imbricatus*, *Gymnadenia conopsea*, *Dracocephalum ruyschiana*, *Iris variegata*, *I. sibirica*, *Lilium bulbiferum*, *Primula elatior*, and *Pulsatilla grandis* (Vojtkó, 2001, Fig. 1b). These grasslands were extensively grazed in the past decades. Dolines are covered by either grasslands or forests (Bátori et al., 2020b). The study area is part of the Bükk National Park and the Natura 2000 network (site code: HUBN20001) – a
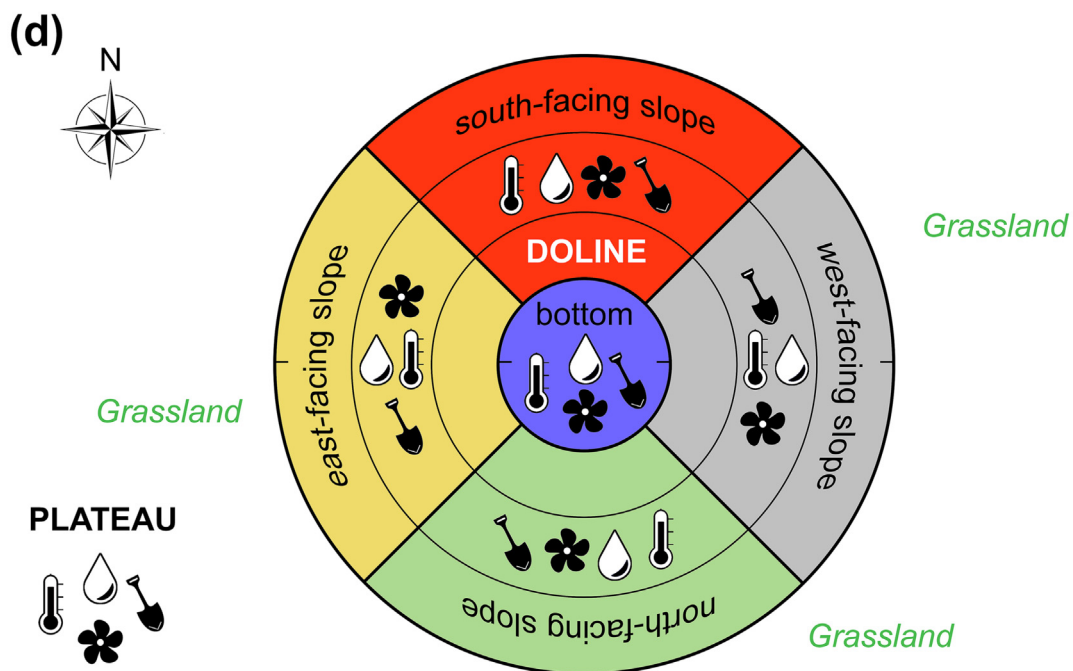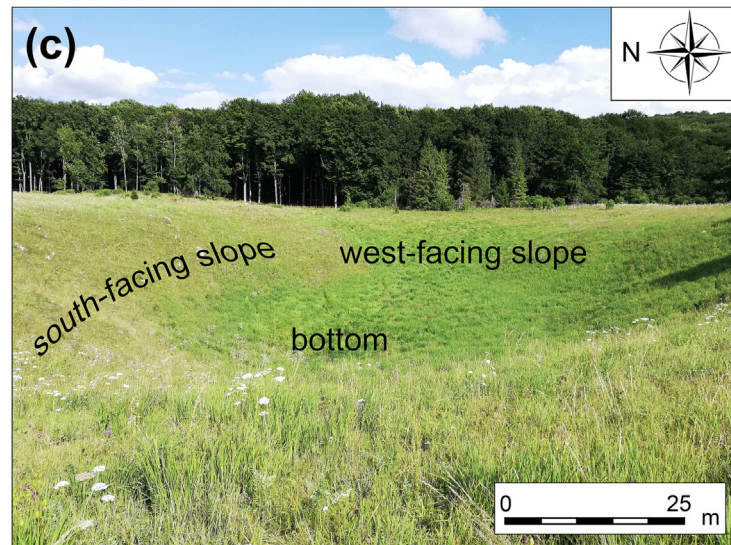
Fig. 1. Study area and study design. (a) Location of the study area in the Bükk Mountains, Hungary, (b) *Dracocephalum ruyschiana*, a relict species in a doline microrefugium, (c) Different grassland types in a doline, (d) Sampling design for dolines and the surrounding plateau.

European Union-wide network of sites for selected species and habitats (https://natura2000.eea.europa.eu/).

2.2. Sampling design

Nine large solution dolines were randomly selected (diameter: 80–100 m, depth: 10–15 m) from the dolines of the Bükk Plateau. Six microhabitats (south-facing slope, east-facing slope, west-facing slope, north-facing slope, bottom, and the adjacent plateau; Fig. 1c and d) were sampled for each doline. All studied microhabitats were covered by grasslands. Investigations were carried out in August 2021, at the peak of the growing season.

At each microhabitat, five randomly placed 1 m × 1 m vegetation plots were established (9 dolines × 6 microhabitats × 5 vegetation plots: 270 plots in total, Fig. 1d). We recorded the percentage cover of each vascular plant species in all plots (Table S1). Nomenclature follows 'The World Flora Online' (http://www.worldfloraonline.org/). To provide information on the microclimate of the study area, we recorded air temperature (°C) and relative air humidity (%) of each microhabitat every 5 min for 24 h using Optin Ambient Data Loggers (ADL) (9 dolines × 6 microhabitats × 1 data logger: 54 data loggers in total, Fig. 1d, Table S1). Loggers were suspended 10 cm above the ground and they were encased in a radiation shield. We measured soil moisture (volumetric water content – VWC%) in the upper 12.2 cm (i.e. rod length) of the soil at 10 locations within each microhabitat using a FieldScout TDR 350 Soil Moisture Meter (9 dolines × 6 microhabitats × 10 measurements: 540 measurements in total, Fig. 1d, Table S1). Measurements were carried out under partly cloudy conditions, representing the typical weather of the study area in summer. Soil samples were taken using a soil probe from the upper 15 cm of the soil at three random locations in each microhabitat (9 dolines × 6 microhabitats × 3 soil samples: 162 samples in total, Fig. 1d, Table S1). Soil samples from a certain microhabitat were pooled and homogenised before soil chemical analysis. Soil chemical properties – pH (H_2O), $CaCO_3$ (m/m%), humus (m/m%), P_2O_5 (mg/kg), K_2O (mg/kg), and nitrogen ($NO_2^- + NO_3^-$)-N (mg/kg) (henceforth N) – were analysed in an accredited laboratory (NAH-1-1437/2018). In addition, the cover of bare rocks (%) within each plot was estimated visually.

2.3. Species classification

We classified all vascular plant species according to their habitat preferences following the systems of Soó (1980) and Mucina et al. (2016). We used the following five groups of plant species during analyses: (1) species of dry grasslands and dry forests (species of Asplenio-Festucion pallentis, Festuco-Brometea, Festucetalia valesiacae, Prunetalia spinosae, Quercetalia roboris and Quercetea pubescentis) – henceforth 'species of dry habitats', (2) 'species of hay meadows' (species of Arrhenatherion elatioris and Molinio-Arrhenatheretea), (3) 'species of mesic forests' (species of Querco-Fagetea), (4) species of fen meadows, montane grasslands and montane forests (species of Fagetalia sylvaticae, Filipendulo-Petasition, Molinio juncetea and Nardetea strictae) – henceforth 'species of montane habitats', and (5) 'species of disturbed habitats' (e.g., adventives, cosmopolitan species and weeds – such as species of Epilobietea angustifolii and Onopordion acanthii). We also analysed the distribution of protected and red-listed species (henceforth 'species of high conservation value'). To identify these species, we used the 'Database of Hungarian Natural Values' (https://termeszetvedelem.hu/) and Király (2007).

2.4. Statistical analysis

We standardised microclimatic data to the mean plateau values, that is, mean plateau values across all plateau microhabitats were subtracted from the mean values of doline microhabitats (south-facing slopes, east-facing slopes, west-facing slopes, north-facing slopes, and bottoms, respectively) for every measurement time point.

To test the effects of microhabitats on microclimatic variables (mean daily air temperature and relative air humidity) and soil properties (soil

moisture, pH, $CaCO_3$, humus, K_2O, N, and P_2O_5 contents), we fitted Gaussian mixed-effects models. Before analysis, we excluded an extreme outlier $CaCO_3$ value from the dataset (doline bottom 5: 19.7 m/m%). As the occurrence of bare rocks within the microhabitats was low (in 37 out of the 270 plots), only their mean cover values were calculated and compared. We also tested the effects of microhabitats on the total number of species, total cover of species (estimated total vegetation cover, as well as summarised cover of all recorded species) and on the species number and cover of the specific species groups (number and cover of species of dry habitats, species of hay meadows, species of mesic forests, species of montane habitats, species of disturbed habitats, and species of high conservation value). We used negative binomial (for species number, with linear parametrisation) or log-linked gamma (for species cover) generalized mixed-effects models. When species-cover datasets included 0 values, we added one to every cover value to be able to fit the gamma models. In the models, microclimate variables, soil parameters and the number and cover of species and specific species groups were used as response variables, microhabitat was included as a fixed factor, and site ID (doline 1–9) as a random factor. We applied a Bonferroni correction to give a corrected p value in pairwise comparisons. All data handling and statistical analysis were carried out in R (v. 4.2.0, R Core Team R, 2022), using the 'glmmTMB' package (Brooks et al., 2017). Pairwise comparisons of microhabitats were undertaken using the 'emmeans' package (Lenth, 2019).

Diagnostic species for the plateau and doline microhabitats were determined by calculating the phi (Φ) value of all individual species, using the JUICE program (Tichý, 2002). Species with Φ ≥ 0.15 were considered diagnostic species (Fisher's exact test, $p < 0.05$) (Tichý and Chytrý, 2006). In the rare case when a species appeared to be diagnostic for more than one microhabitat, only the occurrence with the higher phi value was considered.

Comparisons of vegetation composition were made (1) at the level of each doline and (2) at the level of all dolines. (1) To compare the compositional differences of the microhabitats for each doline (30 plots for each doline: 25 plots in dolines and 5 plots on the adjacent plateau), we used one-way analysis of similarities (ANOSIM) based on Bray–Curtis distance and 1000 permutations. We used non-metric multidimensional scaling (NMDS) ordinations with Bray–Curtis distances to visually illustrate compositional differences among the microhabitats in each doline (nine ordinations in total). (2) To compare the compositional differences of the microhabitats of all dolines (270 plots), we used one-way analysis of similarities (ANOSIM) based on Bray–Curtis distance and 1000 permutations. We applied a Bonferroni correction to give a corrected p value in pairwise comparisons. We used a non-metric multidimensional scaling (NMDS) ordination based on Bray–Curtis distance to visually illustrate compositional differences among the microhabitats. We averaged the species cover data of the five sampling plots of each microhabitat of each doline and used these site-averaged data in the source matrix. To assess the relationships among environmental conditions (microclimatic variables: mean air temperature and relative air humidity, and soil properties: cover of bare rocks, soil moisture, pH, $CaCO_3$, humus, K_2O, N, and P_2O_5 contents) and compositional differences, we fitted environmental vectors onto the ordination space and calculated correlations between ordination values and fitted vectors. NMDS ordinations and related calculations were done using the 'vegan' package in R (v. 4.2.0, R Core Team R, 2022; Oksanen et al., 2018).

3. Results

3.1. Microclimatic and soil conditions

Air temperature and relative air humidity considerably changed in the microhabitats during the day (Fig. 2). East-facing slopes were considerably warmer than the plateau in the morning, while west-facing slopes were warmer than the plateau in the mid- and late afternoon. Temperature was highest on south-facing slopes around noon. Temperature was lowest in bottoms during night-time (frost was observed in all doline bottoms between 2:30 a.m. and 5:45 a.m.), while temperature was lowest on north-
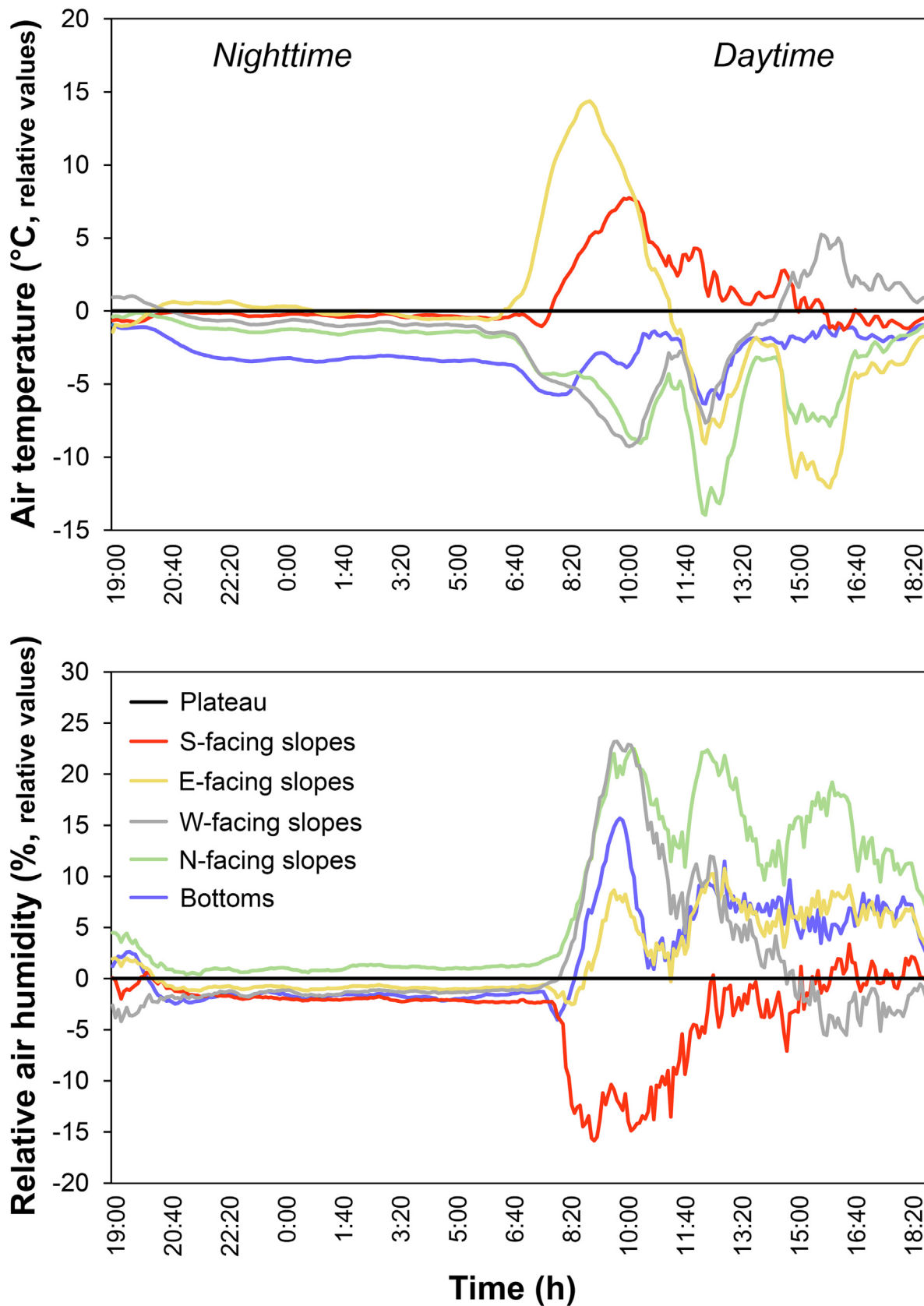
Fig. 2. Differences in mean air temperature and relative air humidity between the plateau and doline microhabitats in the Bükk Mountains, Hungary. Air temperature and relative air humidity values were averaged across the same microhabitats of dolines, respectively. Negative and positive temperature and relative air humidity values indicate that doline microhabitats had lower or higher values, respectively, than the plateau at particular times of the investigation period.

facing slopes from mid-morning to mid-afternoon. Relative air humidity was generally higher in all doline microhabitats than on the plateau during daytime. Relative air humidity was generally higher on north-facing slopes than in the other microhabitats throughout the day, while it was generally lowest on south-facing slopes.

Mean daily air temperature was highest on south-facing slopes and the plateau, and lowest on north-facing slopes and bottoms, while mean daily relative air humidity was highest on north-facing slopes and lowest on the plateau, south-facing slopes and east-facing slopes (Fig. 3, Table S1). Soil moisture was similarly high on north-facing slopes and bottoms, while it was lowest on south-facing slopes.

Soil pH was highest on south-facing slopes and lowest on north-facing slopes (Fig. 3, Table S1). Soil nutrient content (K_2O, N, and P_2O_5) on south-facing slopes was slightly higher than that on north-facing slopes and the plateau; however, these differences were not statistically significant. The mean cover of bare rocks was also highest on south-facing slopes (mean ± SD: 8.8 ± 9.1 %). The plateau, east-facing slopes and west-facing slopes generally indicated intermediate conditions in respect to microclimate and soil properties.

3.2. Species composition

A total of 211 vascular plant species were recorded in the study area. The total number of species was lowest in the plots of south-facing slopes and bottoms, while the other microhabitats showed similarly high values (Fig. 4). In terms of diagnostic species, the plateau had 13, south-facing slopes had 20, east-facing slopes had 18, west-facing slopes had 10, north-facing slopes had 23, and bottoms had 20 species, respectively

(Table 1). The total cover of species (estimated total vegetation cover, as well as summarised cover of all recorded species) was similarly high in the microhabitats, except on the south-facing slopes, where the lowest values were observed (Fig. 4). The number and cover of species of dry habitats were highest on south-facing slopes and lowest on north-facing slopes and bottoms, while the number and cover of species of hay meadows were lowest on south-facing slopes (Table S1). We did not find a consistent pattern in the distribution of species of mesic forests. North-facing slopes had the highest number of species of montane habitats, and north-facing slopes and bottoms had the highest cover of species of high conservation value. The cover of species of disturbed habitats was highest in bottoms.

3.3. Vegetation–environment relationships

NMDS ordinations of plots (stress factors: 0.14–0.26) showed that there were differences in the vegetation patterns of microhabitats in each doline (Fig. 5a). These differences were significant (ANOSIM $R = 0.51–0.87$, $p < 0.001$). Plots of the south-facing slopes and north-facing slopes and/or bottoms were usually separated from each other, revealing clear environmental gradients in the ordination space. However, in many cases, plots of the plateau, west-facing slopes and/or east-facing slopes strongly overlapped in the ordination space. NMDS ordination of the averaged species cover data (Fig. 5b, stress factor: 0.12) also showed clear differences in vegetation patterns (ANOSIM $R = 0.23$, $p < 0.001$). Differences in vegetation patterns were significant ($p < 0.05$), except between the plateau and west-facing slopes ($p = 0.375$), east-facing-slopes and west-facing slopes ($p = 0.300$), and north-facing slopes and bottoms ($p = 0.200$). Mean air temperature, mean relative air humidity, the cover of bare rocks, soil moisture, soil pH,
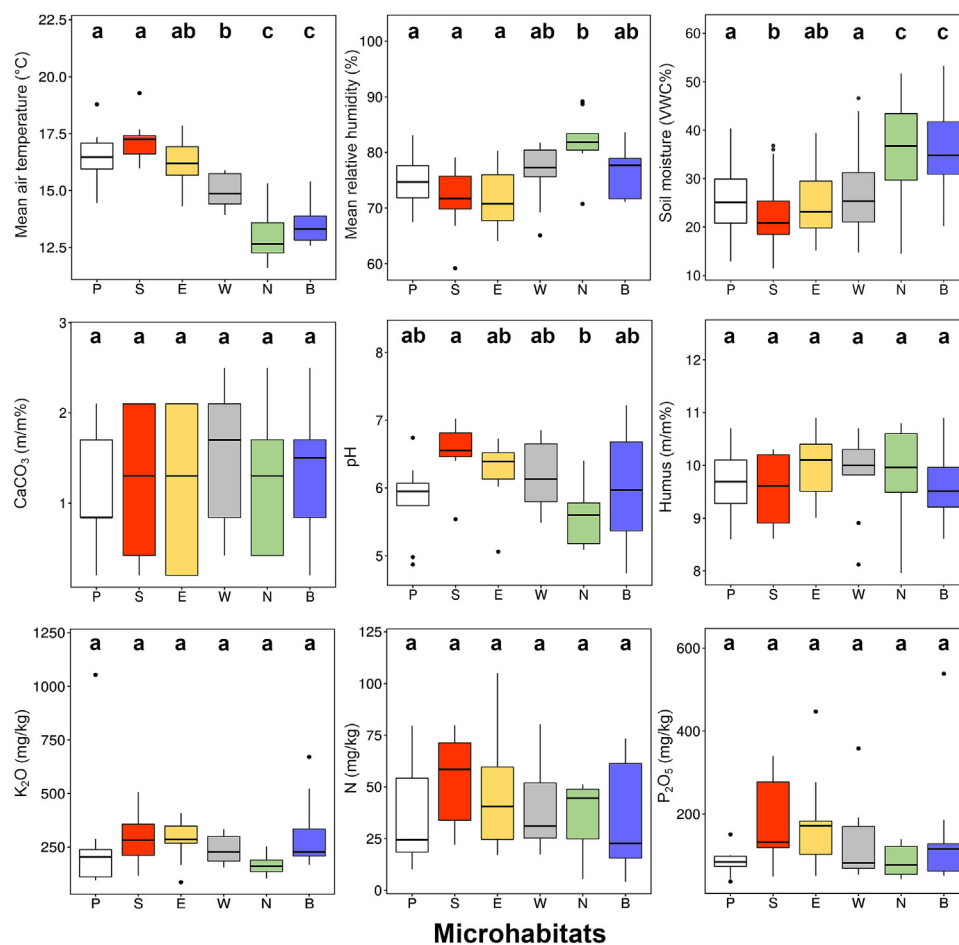

Fig. 3. Microclimatic variables and soil properties in the plateau and doline microhabitats in the Bükk Mountains, Hungary. Lowercase letters (a–c) indicate significant differences ($p < 0.05$) among microhabitats (P: plateau, S: south-facing doline slopes, E: east-facing doline slopes, W: west-facing doline slopes, N: north-facing doline slopes and B: doline bottoms).
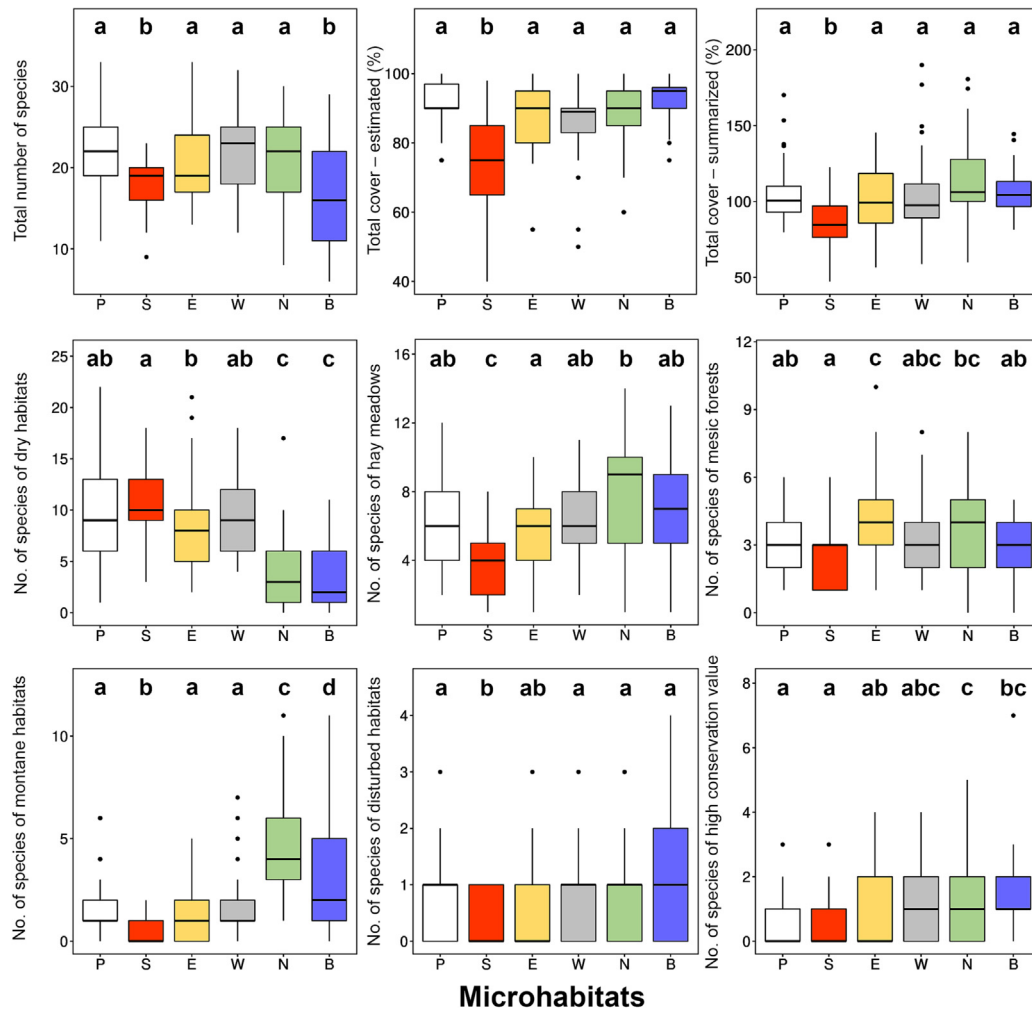
Fig. 4. Species number and cover of vascular plant species in the plateau and doline microhabitats in the Bükk Mountains, Hungary. Lowercase letters (a–d) indicate significant differences ($p < 0.05$) among microhabitats (P: plateau, S: south-facing doline slopes, E: east-facing doline slopes, W: west-facing doline slopes, N: north-facing doline slopes and B: doline bottoms).

and soil N content were significantly related to the ordination (R^2 = 0.12–0.67, $p < 0.05$). Vegetation on south-facing slopes was associated with higher mean air temperature, soil pH and soil N content, and lower relative air humidity and soil moisture, while vegetation on north-facing slopes and bottoms was associated with lower mean air temperature, soil pH and soil N content, and higher relative air humidity and soil moisture than the other microhabitats.

4. Discussion

4.1. Microclimatic and soil heterogeneity in dolines

To our knowledge, this study is the first to assess the complex relationships among topography, climatic and soil EH, and the distribution patterns of different groups of vascular plant species and their conservation value in karstic microrefugia. We found that dolines exhibit high EH due to the presence of different microhabitats (south-, east-, west- and north-facing slopes, and bottoms) and promote a high diversity of vegetation types with unique species composition. Although there are remarkable differences among the conservation value of these microhabitats, each microhabitat has an important role in maintaining species that are rare or absent in other microhabitats in the landscape. Therefore, our results also highlight the conservation importance of east- and west-facing slopes – which are often neglected in EH studies (cf. Deák et al., 2021) – when studying topographically complex landscapes.

We found that the complex topography of dolines increases the climatic EH of karst landscapes over small scales and provides microhabitats with contrasting temperature and humidity regimes (Raschmanová et al., 2015, 2018; Li et al., 2019). Differences in climatic patterns may be especially pronounced between the poleward- vs. equator-facing doline slopes (north-facing and south-facing slopes, from the perspective of the Northern Hemisphere) (Bárány-Kevei, 1999), as the amount of solar radiation received at a given slope over time is much lower on north-facing slopes (Ackerly et al., 2020; Stralberg et al., 2020). For instance, Bátori et al. (2019) found mean daytime temperatures on the south-facing slopes of solution dolines >8 °C warmer than on north-facing doline slopes in a grassland ecosystem. In the current study, we found that mean air temperature was highest on south-facing slopes and lowest in north-facing slopes within dolines, while mean temperature values were intermediate on east-facing and west-facing slopes (Figs. 2 and 3). Diurnal temperature and humidity showed a high variation between the microhabitats, and cold-air pooling and associated air temperature inversions were important features of doline bottoms, where minimum temperatures were below zero during dawn. Previous studies measuring microclimate over longer time periods – i.e. from a few days to more than one year – have also reported north-facing slopes and bottoms of dolines to be colder and more humid than their surroundings (Whiteman et al., 2004; Marcin et al., 2021; Bátori et al., 2022). The main reason for the spatial variation in air temperature and relative air humidity in dolines is due to the movement of the sun through the day and the bowl- or funnel-shaped geometry of these depressions – e.g., east-facing

Table 1
Synoptic table of vascular plants associated with the plateau and doline microhabitats (south-, east-, west- and north-facing slopes, and bottoms) in the Bükk Mountains, Hungary. Within blocks, species are listed by increasing values of the phi (Φ) coefficient of association between species and microhabitat (in parenthesis, Φ × 100). Two of the species, marked with an asterisk, were diagnostic for two different microhabitats (with the same Φ value). The names of species with high conservation value are indicated with boldface.

Plateau
Seseli libanotis (15.3), *Allium oleraceum* (15.7), *Trifolium montanum* (16.2), *Galium verum* (17.6), **Centaurea scabiosa** subsp. **sadleriana** (17.8), *Filipendula vulgaris* (18.4), *Carex michelii* (19.3), *Carex pallescens* (21.0), *Phleum phleoides* (21.0), *Veronica austriaca* subsp. *dentata* (24.8), *Briza media* (26.2), *Helictotrichon pubescens* (27.4), *Thalictrum lucidum* (27.4)

South-facing slopes
Polygonatum odoratum (16.0), *Medicago lupulina* (17.7), **Iris variegata** (19.3), *Coronilla varia* (20.2), *Arabis hirsuta* (20.9), *Digitalis grandiflora* (22.8)*, *Clinopodium acinos* (23.7), *Carex praecox* (23.7), **Sempervivum globiferum** subsp. **hirtum** (23.7), *Thymus pulegioides* subsp. *pannonicus* (24.0), *Carex caryophyllea* (24.1), *Potentilla heptaphylla* (26.7), *Poa compressa* (27.4), *Koeleria cristata* (28.2), *Hylotelephium maximum* (29.2), *Dianthus giganteiformis* subsp. *pontederae* (31.9), *Festuca rupicola* (32.0), *Euphorbia cyparissias* (32.5), *Teucrium chamaedrys* (33.9), *Sedum acre* (43.3)

East-facing slopes
Viola hirta (15.0), *Convolvulus arvensis* (16.7), *Rosa canina* agg. (17.0), *Galium mollugo* (17.5), *Veronica chamaedrys* (17.9)*, *Clinopodium vulgare* (19.0), *Acer platanoides* (19.3), **Lilium martagon** (19.3), *Veronica spicata* (19.3), *Verbascum chaixii* subsp. *austriacum* (20.8), *Hypericum hirsutum* (22.4), *Digitalis grandiflora* (22.8)*, *Origanum vulgare* (23.3), *Agrimonia eupatoria* (23.7), *Fallopia convolvulus* (23.7), *Stellaria holostea* (26.9), *Cruciata laevipes* (29,8), *Waldsteinia geoides* (36.4)

West-facing slopes
Carex montana (15.6), *Cirsium arvense* (15.6), *Trifolium alpestre* (16.5), *Pimpinella saxifraga* (17.0), *Salvia pratensis* (17.8), **Prunella grandiflora** (19.2), *Luzula campestris* (19.3), *Carex tomentosa* (20.6), *Tanacetum corymbosum* (22.4), *Salvia verticillata* (23.7)

North-facing slopes
Helictochloa praeusta (15.2), *Ranunculus polyanthemos* (15.3), *Luzula luzuloides* (15.9), **Alchemilla monticola** (16.6), *Filipendula ulmaria* (17.5), *Veronica chamaedrys* (17.9)*, *Leontodon hispidus* (17.5), *Rubus idaeus* (17.7), **Bupleurum longifolium** (19.3), *Hypochaeris maculata* (19.3), *Trifolium aureum* (19.3), *Cruciata glabra* (19.9), *Cirsium eriophorum* (22.9), **Dianthus deltoides** (23.7), *Agrostis capillaris* (25.4), *Glechoma hirsuta* (25.5), *Potentilla erecta* (26.7), *Festuca pratensis* (27.9), *Ranunculus auricomus* (31.1), *Stellaria graminea*, (31.2), *Rumex acetosa* (31.7), *Aegopodium podagraria* (34.1), *Colchicum autumnale* (35.8)

Bottoms
Gentiana pneumonanthe (15.9), *Selinum carvifolia* (15.9), *Plantago media* (16.4), *Calamagrostis epigejos* (17.1), *Vicia cracca* (17.7), **Ophioglossum vulgatum** (19.1), *Alopecurus pratensis* (19.3), *Carex pilosa* (19.3), *Deschampsia caespitosa* (19.3), **Gladiolus imbricatus** (19.3), *Leucanthemum vulgare* (19.3), *Elymus repens* (20.2), *Calamagrostis arundinacea* (20.9), **Geranium palustre** (20.9), *Potentilla reptans* (23.3), *Molinia caerulea* (25.4), *Lathyrus pratensis* (27.6), *Vicia sepium* (44.4), *Urtica dioica* (46.1), *Carex hirta* (48.2)

slopes receive more solar radiation in the morning, while west-facing slopes receive more solar radiation in the mid- and late afternoon (cf. Kobal et al., 2015). Our results are in line with previous studies suggesting that SNFs may generate substantial environmental heterogeneity providing a suite of different microhabitats (Stein et al., 2014; Stein and Kreft, 2015). As has been shown for prehistoric burial mounds and rocky outcrops, for instance, topography can be an important source of EH resulting in opposing temperature and humidity gradients (Keppel et al., 2017; García et al., 2020; Deák et al., 2021). These SNFs – together with dolines – may provide microhabitats that share similar environmental conditions with habitats at higher latitudes and elevations (cf. Ottaviani et al., 2016; Bátori et al., 2017, 2019; Deák et al., 2021), providing key opportunities for species to persist locally under future environmental changes, such as global warming.

Previous studies have demonstrated that there are strong relationships among slope aspect, microclimate, soil moisture and soil chemical properties in environmentally heterogeneous landscapes (Stein et al., 2014; Stein and Kreft, 2015). In our study system, we found higher soil moisture levels on north-facing doline slopes and doline bottoms than on other slopes

and the plateau, while soil moisture was lowest on south-facing slopes (Figs. 3 and 5). Similar to other SNFs, dolines introduce great variation in soil moisture, creating steep gradients from south-facing, east-facing and west-facing slopes to bottoms. Doline bottoms tend to receive more water due to the runoff of precipitation from the adjacent slopes and may retain snow cover longer than most of the other doline microhabitats (except north-facing slopes) and the plateau (Gargano et al., 2010; Kiss et al., 2020). These effects likely contribute to the higher soil moisture recorded in this microhabitat. As north-facing slopes receive consistently less solar radiation – resulting in lower temperatures and increased air humidity – than adjacent microhabitats, they may also conserve soil moisture through reduced evapotranspiration (Måren et al., 2015; Wang et al., 2022).

We also found that soil pH was highest on south-facing slopes and lowest on north-facing slopes. The main reason for this is that cool north-facing slopes in dolines are moister with a higher intensity of leaching than south-facing slopes, where the highest amount of bare rocks was observed. On the other hand, soils on south-facing slopes have large daily temperature fluctuations and low moisture contents (Bárány-Kevei, 1999). This is also reflected by the presence of some diagnostic species on north-facing slopes, such as *Agrostis capillaris* and *Luzula luzuloides* (Table 1), which are reliable indicators of soils with lower pH (Borhidi, 1995). These results are in line with other SNF studies documenting higher soil pH on south-facing slopes than north-facing ones (e.g., Lisetskii et al., 2014; Deák et al., 2021). There were only slight differences in other soil properties (CaCO$_3$, humus, K$_2$O, N, and P$_2$O$_5$ contents) among microhabitats. Soils on south-facing slopes contained slightly more K$_2$O, N, and P$_2$O$_5$ than soils on north-facing slopes and the plateau. This is presumably due to the moister conditions on north-facing slopes and the plateau supporting the leaching of nutrients into the deeper soil layers and enhancing their uptake by deep-rooted plants (cf. Deák et al., 2021).

To sum up, topographic complexity in dolines maintains a high diversity of microhabitats that are characterised by highly variable environmental conditions, increasing the climatic and soil EH in karst landscapes at different spatial scales. These patterns should also have important consequences for biodiversity, such as for the distribution of plant species.

4.2. Vegetation and land cover heterogeneity in dolines

We found a total of 211 vascular plant species in the microhabitats, sampling a total area of only 270 m^2 (our dataset contained 270 1 m × 1 m vegetation plots). High plant species richness was observed in some vegetation plots of east-facing slopes, west-facing slopes and the plateau, where the most species-rich plots contained >30 plant species (Fig. 4). However, south-facing slopes, north-facing slopes and bottoms had more diagnostic species (20–23 species) than the other microhabitats (10–18 species) (Table 1), indicating their distinctiveness from their immediate surroundings. These results suggest that dolines may act as major biodiversity hotspots in karst landscapes, where vegetation varies along steep environmental gradients (e.g., moisture, temperature and soil pH), resulting in different vegetation types and covers, and a high diversity of microhabitats and species over relatively short distances (Su et al., 2017; Jakob et al., 2022).

Differences in vegetation cover and plant species composition lead to increased vegetation and land cover EH within dolines, highlighting the conservation value of topographically complex karst landscapes (Bátori et al., 2017; Wang et al., 2019). Furthermore, we found remarkable differences in the distribution of most investigated plant species groups among microhabitats. For instance, species of dry habitats were frequent on south-facing slopes, while north-facing slopes and bottoms contained many species of montane habitats. Considering the results of previous microclimatic studies and our microclimate measurements, doline microhabitats may function as warm and dry 'islands' (south-facing slopes) and cold and moist 'islands' (north-facing slopes and bottoms) in the 'ocean' of habitats (containing several microhabitats) with intermediate temperature and moisture conditions (cf. Čarni et al., 2022). The diversity of microclimates found in dolines may allow relict populations to persist despite regionally unfavourable climate
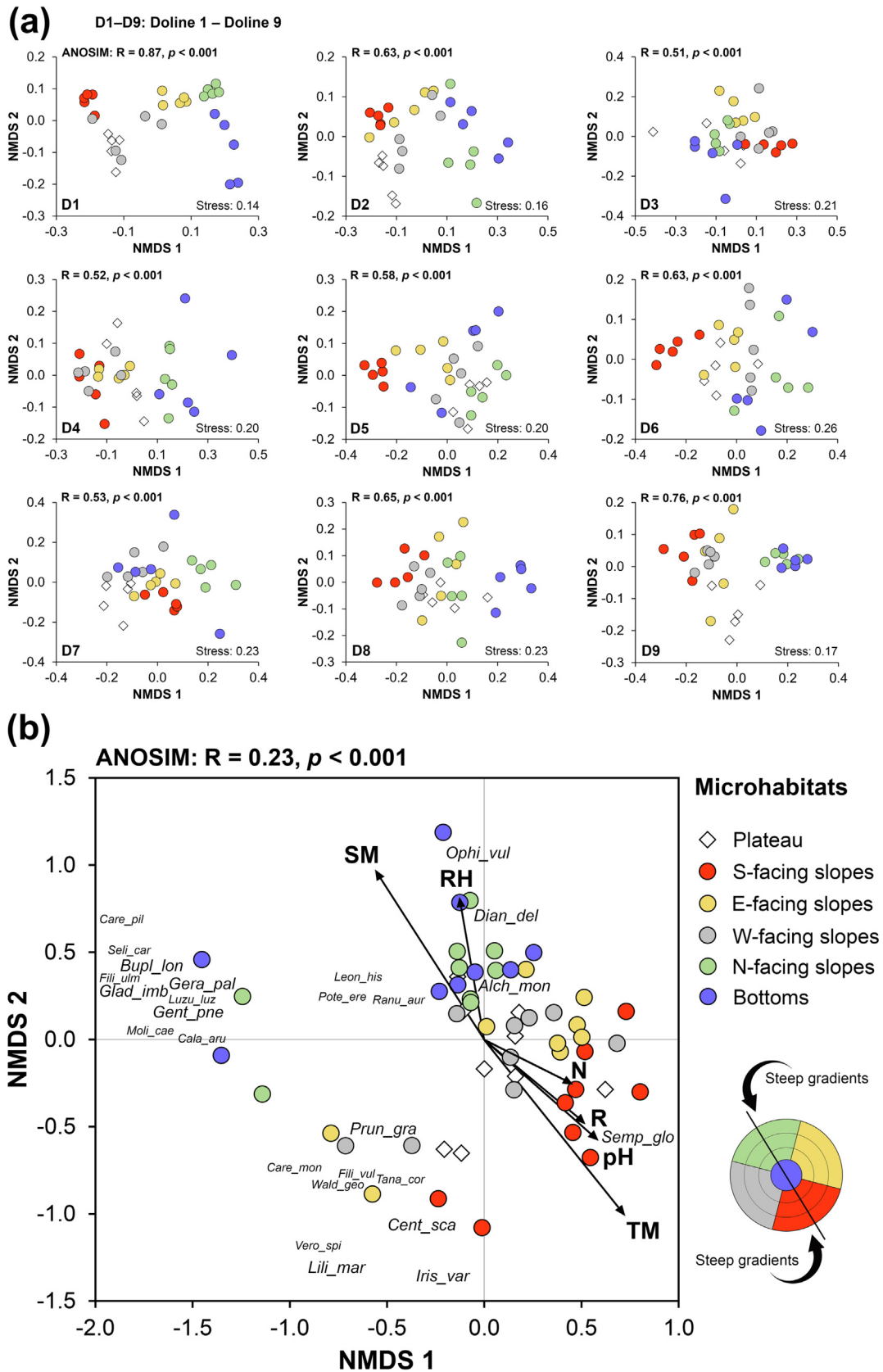
Fig. 5. Compositional patterns and vegetation–environment relationships in the plateau and doline microhabitats (south-, east-, west- and north-facing slopes, and bottoms) in the Bükk Mountains, Hungary. Nonmetric multidimensional scaling (NMDS) ordinations were performed (a) at the level of each doline and (b) at the level of all dolines. Fitted vectors show correlations between NMDS axial scores and potential predictors (TM: mean air temperature, RH: mean relative air humidity, R: amount of bare rocks, SM: soil moisture, pH: soil pH, and N: soil nitrogen (NO_2^- + NO_3^-)-N; $p < 0.05$). Arrow directions indicate the direction of the correlation, while vector length shows the strength of correlation. Abbreviated names of some diagnostic species are also plotted (see Table 1) – the names of species of high conservation value are presented in larger font size.

(e.g., *Bupleurum longifolium* on north-facing doline slopes). Our results correspond well with those for the Northern Hemisphere in general, where refugial areas for species associated with cooler and/or moister conditions are primarily found at high elevations and/or higher latitudes (Stewart et al., 2010; Gentili et al., 2015; Abeli et al., 2018) as well as in special microhabitats at lower elevations, such as microhabitats of basins, fens, local depressions, rocky outcrops, sinks and valleys (Dobrowski, 2011; de Aguiar-Campos et al., 2020; Gallé et al., 2021).

4.3. Conservation value of doline microhabitats

Similar to the distribution of species of montane habitats, the distribution of species of high conservation value was primarily related to the cool and humid north-facing slopes and bottoms of dolines within the study area (Fig. 4). The reason why many protected and/or red-listed species occur predominantly in such microhabitats is due to the geographic characteristics of Hungary. As the majority of the country has an elevation <300 m (the highest point is 1014 m asl) (Lóczy, 2015), species of montane habitats only have a scattered distribution and are highly threatened by climate change and human disturbance. According to climate change models (Lindner et al., 2014; Dyderski et al., 2018), climate warming in East-Central Europe will continue in the forthcoming decades, affecting the distribution of many species within and adjacent to microrefugia. The key questions are how the refugial capacity of doline microhabitats will change in a warming climate and how many species do these environmental changes threaten. We believe that the combined influences of long-term environmental stability (e.g., temperature and soil moisture, Marcin et al., 2021; Bátori et al., 2022) and special topography (e.g., cool and moist north-facing slopes) in dolines will support the long-term persistence of at least some species even in the face of ongoing climate change (cf. Keppel et al., 2012, 2015; Harrison and Noss, 2017). As all doline microhabitats hosted several species that are rare or absent in other microhabitats (including species of high conservation value), conservation efforts must address all microhabitats as a part of the sustainable strategy for karst landscapes.

We also found that the cover of species of disturbed habitats was relatively high in the bottoms of dolines (Fig. 4). One of the main reasons for this is that the bottom of many dolines in this region was used as lime kilns over decades (Bátori et al., 2020a), facilitating the spread of disturbance-tolerant species (e.g., *Calamagrostis epigejos* and *Urtica dioica*) in this microhabitat.

4.4. Implications for management

Doline microhabitats – covered by grasslands – and their diverse biota are particularly vulnerable to the effects of abandonment and also to the invasion of some species that can establish due to past or present anthropogenic activities (Bátori et al., 2020a). These processes may lead to an overall decline of grassland biodiversity and to the disappearance of microhabitat-level differences in many abiotic and biotic factors within dolines.

According to our own observations from the past 40 years in the Bükk Mountains, biomass removal by mowing once a year in autumn can be a sufficient conservation measure for maintaining overall plant diversity in dolines covered by natural (or semi-natural) grassland vegetation. The removal of living and dead biomass may suppress tall-growing species with a good competitive ability, enhancing the diversity of grassland specialist annuals and small perennials (Kahmen et al., 2002). In abandoned dolines, the increased amounts of biomass – even in the short run – may also affect components of EH by altering microclimatic and soil conditions. The disappearance of open soil surfaces that can rapidly heat up during daytime and cool down during night may considerably moderate the magnitude of diurnal changes in air temperature (Löffler and Fartmann, 2017). Abandonment of grasslands may also reduce the rate of evapotranspiration (Rosset et al., 2001); potentially reducing abiotic differences among the microhabitats of dolines and finally leading to the disappearance of vegetation and land cover EH. Taking these into account, we suggest applying a regular but extensive biomass removal in dolines by mowing, as in this way the effect of biotic filters can be suppressed in microhabitats and the filtering effect of abiotic drivers typical to certain microhabitat types can be enhanced. As defoliation and trampling by herbivores may increase soil erosion and therefore microhabitat homogenisation on steep doline slopes, we believe that grazing is not an appropriate management alternative in these dolines.

On rocky south-facing slopes, where management by mowing might be less feasible, prescribed burning might be considered as an alternative management option. However, more experimental studies should be conducted to assess the effects of fire frequency, timing and intensity on species composition and richness before the implementation of prescribed burning (Pereira et al., 2012; Valkó and Deák, 2021) in our study area.

In our study system, the former use of many dolines as lime kilns has facilitated the invasion of *Calamagrostis epigejos* and other disturbance-tolerant species (Bátori et al., 2020a). Being a tall-growing species with a high biomass production and good competitive ability, *Calamagrostis epigejos* may considerably affect the species composition of microhabitats by suppressing most of the grassland species, and due to its high biomass production, it also has the ability to modify the abiotic conditions in the microhabitats where it is established (Rebele and Lehmann, 2001). The suppression of this undesirable competitive species by applying proper management would be important in order to increase the conservation value of dolines and to preserve EH typical of these habitats. As previous studies reported a low efficiency of traditional management measures (such as mowing or grazing) in reducing *Calamagrostis* stands, it is possible that the use of native hemiparasitic plants would be an accessible and efficient tool for targeted biological control of *Calamagrostis epigejos* in dolines and their surroundings (cf. Těšitel et al., 2017). Sowing seed mixtures, hay transfer and translocation of rare plants (from the local species pool, e.g., from dolines with natural or semi-natural vegetation) may allow doline microhabitats to return to a more natural state following the removal of undesirable competitive species (cf. Turnbull et al., 2000; Silcock et al., 2019).

5. Conclusions

Our findings highlight that dolines – that are the most typical SNFs – in karst landscapes have a crucial conservation importance. We demonstrated that dolines introduce a large variation of EH (involving topography, climate, soil, vegetation and land cover) and maintain high plant diversity (Fig. 6). The complex topography of dolines is an important driver of climatic EH over small scales and provides microhabitats with contrasting air temperature and humidity regimes. We found that abiotic EH components are considerably interrelated with biotic EH components. For instance, differences in soil pH, soil moisture, air temperature and relative air humidity patterns among microhabitats may result in high species turnover over small scales and influence the species composition of microhabitats. Doline microhabitats have an important role in maintaining species that are rare or absent in other microhabitats/habitats in the landscape and therefore provide safe havens for species of high conservation value. These findings highlight that dolines may function as local biodiversity hotspots. As dolines are widespread topographic features in many karst landscapes throughout the world, their conservation and management are crucial to maintaining Earth's biodiversity. An integrated approach is urgently needed to provide guidelines for landscape management, promoting the retention (or increase) of the microhabitat diversity of SNFs for species of high conservation value.

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CRediT authorship contribution statement

Zoltán Bátori: Conceptualisation, Data collection, Data analysis, Writing - original draft, Graphical illustration, Project administration

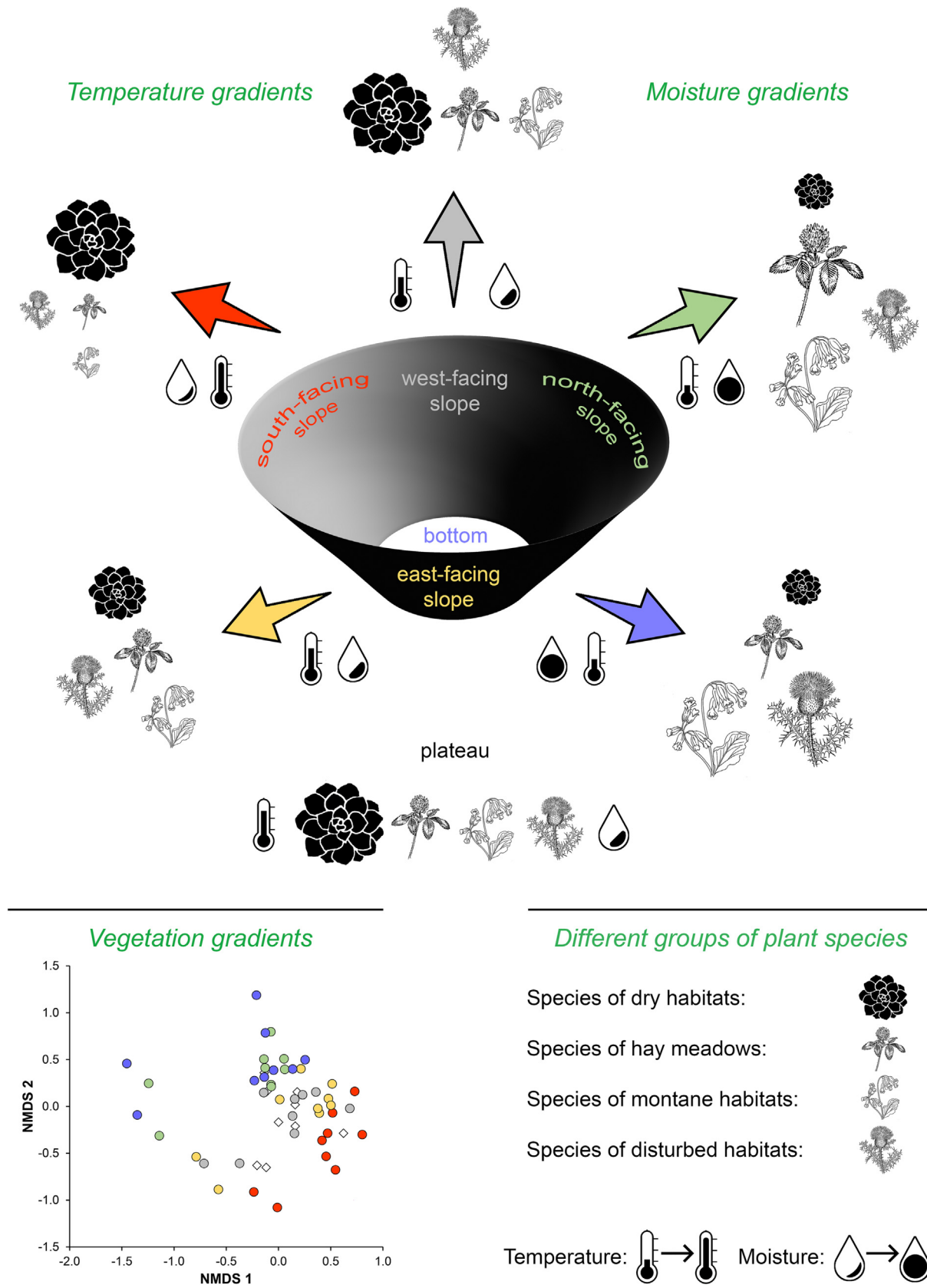Orsolya Valkó: Conceptualisation, Data collection, Writing - Reviewing and Editing

Fig. 6. Schematic illustration of the differentiation of the plateau and doline microhabitats in the Bükk Mountains, Hungary. Different doline microhabitats (south-, east-, west-, north-facing slopes, and bottoms) and the surrounding plateau exhibit high environmental heterogeneity and promote a high diversity of vegetation types with unique species composition. Illustration size for different plant species groups indicates their importance in microhabitats (smaller illustrations: lower importance, and larger illustrations: higher importance) (see also Fig. 5).

András Vojtkó: Conceptualisation, Data collection, Writing - Reviewing and Editing

Csaba Tölgyesi: Data collection, Data analysis, Writing - Reviewing and Editing

Tünde Farkas: Data collection, Writing - Reviewing and Editing

Kata Frei: Data collection, Data analysis, Writing - Reviewing and Editing

Alida Anna Hábenczyus: Data collection, Writing - Reviewing and Editing

Ágnes Tóth: Data collection, Writing - Reviewing and Editing

Gábor Li: Data collection, Writing - Reviewing and Editing

Zoltán Rádai: Data analysis, Graphical illustration, Writing - original draft

Sándor Dulai: Data collection, Writing - Reviewing and Editing

Károly Barta: Data analysis, Writing - Reviewing and Editing

László Erdős: Data collection, Writing - Reviewing and Editing

Balázs Deák: Conceptualisation, Data collection, Data analysis, Writing - original draft, Project administration

Data availability

Data will be made available on request.

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.

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