RESEARCH ARTICLE

# Topographic depressions provide potential microrefugia for ground-dwelling arthropods

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Species can survive periods of unfavorable conditions in small areas that are protected from climate-related disturbances, such as increasing temperature and severe drought. These areas are known as "microrefugia" and are increasingly recognized by conservationists. Although some studies suggest that the in situ survival of invertebrate species may be mediated by topographically complex environments, there is little information about the main environmental factors that drive species distributions within such areas. Here, we investigate the spatial patterns and species trait composition (moisture preference, body size, dispersal capacity, and feeding habit) of five groups of ground-dwelling arthropods—spiders, woodlice, ants, ground beetles, and rove beetles—in topographic depressions (i.e., "solution dolines" or "solution sinkholes") and on the surrounding plateau within a forested karst landscape and analyze the microhabitat conditions that affect these arthropod assemblages. We found that dolines have the capacity to maintain characteristic arthropod assemblages—including species that may be particularly vulnerable to climate change (e.g., species associated with moist habitats)—and thus, they may contribute to the landscape-scale biodiversity of karst landscapes. We also found that doline bottoms have the potential to maintain permanently moist conditions not only in spring and autumn but also during drier periods of the year. This ability of dolines may indicate the presence of potential hydrologic microrefugia. Furthermore, dolines displayed specific sets of species traits (e.g., more small-bodied spiders, more carnivorous ground beetles, and more rove beetles with high dispersal capacity occurred in dolines than on the plateau), highlighting that they may facilitate the persistence of some species and traits that are purged from the surrounding landscape. Future studies may reveal the long-term ecological consequences of different climatic and anthropogenic factors on the distribution and functional traits of arthropod taxa within microrefugia and on the refugial capacity of these safe havens under a warming climate.

## Introduction

Microrefugia are small areas with favorable environmental conditions that support populations of species while the

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surrounding climate deteriorates (Keppel et al., 2012; Gentili et al., 2020). In addition to microclimatic heterogeneity, environmental stability is a key concept often applied when identifying microrefugia for species under current and future climate change (Ashcroft, 2010; Keppel et al., 2015). The potential of landscapes to maintain environmentally stable habitats largely depends on their geomorphological features, such as topographic complexity (Gubler et al., 2018). For instance, convergent environments (e.g., ravines, valleys, and topographic depressions) help decouple local climate trends from regional climates, serving as potential microrefugia (Dobrowski, 2011; Lenoir et al., 2017).

Botanists have long recognized that topographic depressions—such as dolines/sinkholes/tiankengs in karst landscapes—may act as safe havens for a number of plant species (Beck von Mannagetta, 1906; Kobal et al., 2015; Bátori et al., 2017), as they exhibit thermal inversion, maintaining permanently cool conditions

(Whiteman et al., 2004). Previous studies also demonstrated that the accumulation of cool-adapted plant species in certain microhabitats of dolines (e.g., bottoms and poleward-facing slopes) can indicate the presence of warm-stage microrefugia (Bátori et al., 2017; Bátori et al., 2019). Although field measurements of microclimate have shown bottoms and poleward-facing slopes of dolines to be cooler and more humid than the surrounding plateau (Bátori et al., 2019), the number of published studies measuring microclimatic conditions in dolines over longer time periods is limited (see Whiteman et al., 2004; Marcin et al., 2021). Before we can fully understand how these depressions function as safe havens for different animal taxa, we have to differentiate between "collapse" and "solution" dolines. Collapse dolines are depressions with near-vertical walls, associated with cavity roof breakdown, while solution dolines are bowl- or funnel-shaped depressions formed by the dissolution of rock at the bedrock–soil interface (Ford and Williams, 2007). As a result, collapse dolines usually exhibit steeper environmental gradients, leading to a larger turnover in species composition (Raschmanová et al., 2018), compared to the more gradual environmental gradients of solution dolines. The distinct habitat patches formed by collapse dolines have made them important targets for ecological and biodiversity studies. It has been shown that collapse dolines provide refuge areas or microrefugia for different functional-groups of animal taxa, such as arthropods adapted to cooler/moister or warmer/drier environments (the Czech Republic and Slovakia; Růžička et al., 2016; Raschmanová et al., 2017; Marcin et al., 2021); endemic crustaceans and fishes (Mexico; Schmitter-Soto et al., 2002; Angyal et al., 2020); omnivorous, insectivorous, and carnivorous birds (Italy; Battisti et al., 2017); and endangered terrestrial mammals (China; Pu et al., 2017). However, we have only a very limited understanding of the mechanisms that drive the distributions of animal taxa in solution dolines (see Nagy and Sólymos, 2002; Vilisics et al., 2011; Kemencei et al., 2014; Bátori et al., 2019; Bátori et al., 2020a). As karst lands cover about 20% of the Earth's terrestrial surface and solution dolines are the most prominent geomorphological features in many karst landscapes (White et al., 1995; Veress, 2019), assessment of their animal species composition, functional characteristics, and refugial capacity is particularly important from a conservation point of view (cf. Lewis et al., 2020). Here, we focus on the distribution patterns of ground-dwelling arthropods in solution dolines and analyze the microhabitat conditions that may constrain arthropod assemblages.

Arthropods are important components of ecosystems, acting as key players in ecosystem processes, health, and recovery (Maleque et al., 2006; Corcos et al., 2021). They have a crucial role in granivory, herbivory, pollination, and predator–prey interactions, contributing to the decomposition, turnover, and transport of organic matter (Coleman and Rieske, 2006; Yang and Gratton, 2014; Torma et al., 2019). Arthropods are reliable indicators of local and regional climate fluctuations (Høye, 2020), as many of their species are sensitive to changes in moisture and temperature, and their life cycles and community

composition are closely timed with seasonal climate patterns (Bátori et al., 2019; Murphy et al., 2020). Long-term studies suggest that increasing temperature and drought may have negative consequences on arthropod species richness, as well as on the associated multitrophic interactions (e.g., Lister and Garcia, 2018). For instance, Gallé (2017) compared 37 years of ant distribution data between sand dune and dune slack habitats to find that dune slack species disappeared from the depressions and were replaced with dune species, leading to the impoverishment and homogenization of ant assemblages across habitats. Parmesan et al. (1999) provided evidence of poleward shifts in the species ranges of nonmigratory European butterflies during the 20th century. Recent studies predict a decline in habitat suitability for many subterranean spiders and changes in their distributions in the future (Mammola et al., 2018), suggesting that karst-dwelling species are also vulnerable to climate change. Such changes in species distributions can have far-reaching effects on the strength of species interactions and, therefore, may lead to disruptions within the broader food web with potential consequences on biodiversity and ecosystem functioning (González-Megías and Menéndez, 2012; Jamieson et al., 2012; Murphy et al., 2020). More recently, an increasing number of studies suggest that the in situ survival of at least some arthropod species during unfavorable climate periods is mediated by microrefugia (Bryson et al., 2014; Millar et al., 2014; Marcin et al., 2021).

Although the conservation of microrefugia should be based on a deep ecological understanding of their functioning (Keppel et al., 2018), so far only a limited number of studies have examined the functional trait composition of species assemblages within them. Functional traits, such as morphological, physiological, and behavioral features of species, are closely related to ecosystem processes through evolutionary adaptation, providing valuable information about species interactions and environmental changes (Cadotte et al., 2015; Hébert et al., 2016; Marcisz et al., 2016). Therefore, identifying certain species traits that contribute to the unique functional signature of topographically complex environments may help us to make predictions about the location and function of potential future microrefugia (cf. Stralberg et al., 2020; Halsch et al., 2021). In the present study, we also compare the functional characteristics of arthropod assemblages inside and outside of doline habitats using a multitaxa approach.

It is increasingly acknowledged that understanding biodiversity responses to environmental changes requires a multitaxa approach and that evaluating the predictive power of biodiversity indicators is needed to determine which taxonomic groups should be included in an ecological assessment (Valkó et al., 2016; Lingbeek et al., 2017; Lehmitz et al., 2020; Lewis et al., 2020). It has also been highlighted that the location of refugia varies according to macroclimate (Bátori et al., 2017) as well as to the adaptations of individual taxa, implying that microrefugia are generally taxon-specific (Stewart et al., 2010). This also means that microrefugia that can preserve multiple taxa are particularly important from a conservation point of

view. Here, we investigate the microhabitat conditions, the distribution patterns, and the species traits of 5 groups of ground-dwelling arthropods (spiders, woodlice, ants, ground beetles, and rove beetles) in forested solution dolines. We selected 4 species traits (moisture preference, body size, dispersal capacity, and feeding habit) to identify possible differences between the plateau and doline habitats. We hypothesized (1) that topographic complexity provided by solution dolines may create suitable habitats for characteristic arthropod assemblages with the potential to provide important safe havens for at least some arthropod species and species traits in the present and future climate and (2) that microhabitat conditions (i.e., air temperature, relative air humidity, soil moisture, and amount of deadwood) should have a significant effect on the distribution of arthropod assemblages in dolines. If forested solution dolines have the potential to maintain environmentally stable microhabitats, distinctive arthropod assemblages, and populations of arthropod species that may be particularly vulnerable to climate change, more effective conservation efforts are needed to preserve and maintain the diversity and refugial capacity of such karst landscapes.

## Material and methods
### Study area
The study was conducted in an about 30 km$^2$ karst area of the Mecsek Mountains (near the village of Orfű, southern Hungary), at an altitude between 300 and 420 m a.s.l. (**Figure 1**). The karst plateau has typical karst landform features such as more than 2,000 funnel-shaped dolines (http://karst.elte.hu/maps/SinkholesHungaryMap_HU .html). Most dolines are small (diameter < 20 m and depth < 5 m), while the diameter of the largest doline is over 200 m and its depth exceeds 30 m. The climate is continental with sub-Mediterranean influences: moderately warm and moderately humid (Dövényi, 2010). The average annual rainfall is about 750 mm, and the average annual temperature is 9.5°C. Oak-hornbeam forests are the dominant vegetation types of the plateau with *Carpinus betulus* L., *Fagus sylvatica* L., *Quercus cerris* L., and *Quercus petraea* (Matt.) Liebl. trees. The bottom of larger dolines is covered by small ravine forest patches, where *Acer campestre* L., *Acer platanoides* L., *Acer pseudoplatanus* L., *Carpinus betulus*, *Fagus sylvatica*, and *Fraxinus excelsior* L. are the dominant trees (Bátori et al., 2020b; Bátori et al., 2021). These doline bottoms are believed to be potential microrefugia for a number of cool- and/or moist-adapted plant species, such as *Aconitum vulparia* Rchb., *Actaea spicata* L., *Chrysosplenium alternifolium* L., *Dryopteris affinis* Fraser-Jenk., *Dryopteris carthusiana* (Vill.) H.P. Fuchs, *Dryopteris dilatata* (Hoffm.) A. Gray, *Dryopteris expansa* (C. Presl) Fraser-Jenk. & Jermy, *Polystichum aculeatum* (L.) Roth ex Mert., *Polystichum setiferum* Forssk., and *Stachys alpina* L. (Bátori et al., 2012). The study area is part of the protected area network of the Danube-Drava National Park and the Natura 2000 network (site code: HUDD10007)—an EU-wide network of nature protection areas (https://natura.2000.hu/hu/teruletek/m/HUDD10007).

### Sampling design
Two habitat types were considered in this study: dolines and the surrounding plateau. Twelve large solution dolines (diameter: 100–120 m, depth: 12–15 m, and forest age: approximately 70 years old) were randomly selected for sampling. Two sampling sites were established per doline: one on the plateau about 20–30 m from the edge of the doline and one in the doline bottom (12 dolines × 2 sites [plateau and doline bottom] = 24 sites in total; **Figure 1**). Both plateau and doline sites were at least 100 m apart, respectively.

The field sampling was performed in the summers of 2019 and 2020. Arthropod sampling was conducted using pitfall traps following the methodology described by Császár et al. (2018), which has proven effective in reducing bycatches of small vertebrates. The traps were 500-mL plastic cups with transparent plastic funnels (8.5 and 2.4 cm in upper and lower diameters, respectively) filled with 50% ethylene glycol dissolved in water, to which we added a few drops of odorless detergent to reduce the surface tension. Five traps were placed in a line at 5-m intervals at each site (12 dolines × 2 sites × 5 traps × 2 years = 240 traps in total; **Figure 1**). The duration of arthropod sampling was 2 weeks in both years of the study. The first 2-week sampling period was during the summer of 2019 (June 7–21) and the second was during the summer of 2020 (June 26–July 10). In 2019, only 94 of the 120 traps remained in operation due to wild boar digging and heavy rains. In 2020, however, 114 traps remained intact. The collected arthropods were sorted in the laboratory and preserved in 70% ethanol. Spiders (Araneae), woodlice (Isopoda: Oniscidea), ants (Hymenoptera: Formicidae), ground beetles (Coleoptera: Carabidae), and rove beetles (Coleoptera: Staphylinidae) were chosen as target taxa due to their high abundance in the investigated forest types. Sorted specimens were identified to species level by taxonomic experts using the keys of Nentwig et al. (2020) for spiders, Gruner (1966) and Farkas and Vilisics (2013) for woodlice, Czechowski et al. (2012) and Seifert (2018) for ants, Freude et al. (2004) for ground beetles, and Lohse (1974) and Assing and Schülke (2007) for rove beetles (Table S1). All the collected specimens were deposited at the invertebrate collection of the Department of Ecology, University of Szeged. Only adult individuals were included in the analyses. The nomenclature follows Nentwig et al. (2020) for spiders, Schmalfuss (2003) for woodlice, Bolton (2020) for ants, Freude et al. (2004) for ground beetles, and Assing and Schülke (2007) for rove beetles.

We recorded the microclimate, that is, air temperature (°C) and relative air humidity (%), of all sampling sites every 5 min (with no missing data) during the second 2-week sampling period in 2020 (for 10.5 days; Table S2) using Optin Ambient Data Loggers (ADL). Loggers were encased in a radiation shield and they were suspended 10 cm above the ground. Soil moisture (volumetric water content—VWC%) was also measured in 2020 in the upper 10 cm of the soil at five locations within each site with a FieldScout TDR 350 Soil Moisture Meter. The amount of downed deadwood (%) within each site was
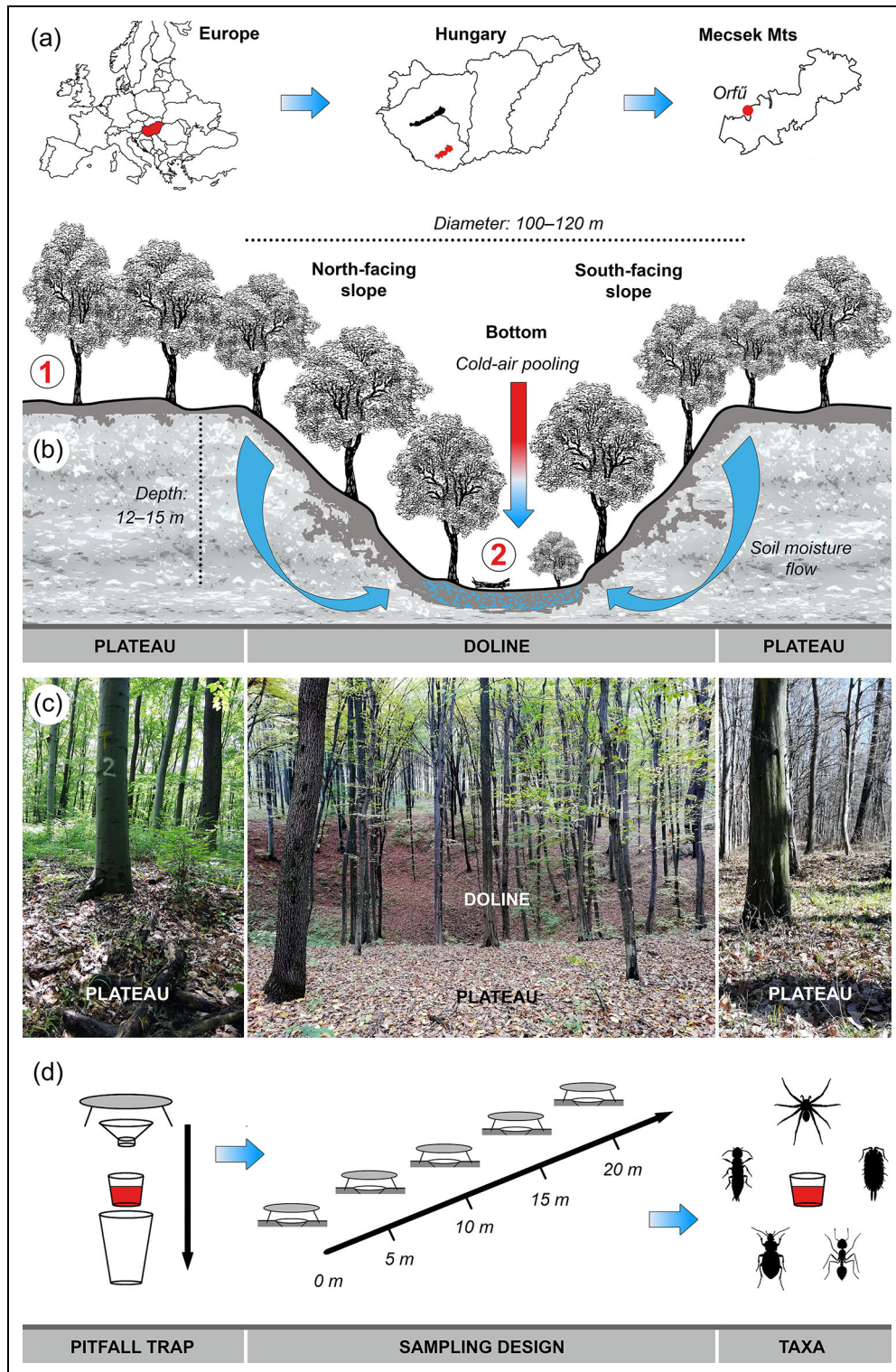
**Figure 1. Study area, study sites, and study design.** (a) Location of the Mecsek Mountains in Europe and Hungary. (b) Location of the study sites on the plateau (1) and in a doline (2). (c) Photos of the plateau and doline habitats. (d) Setup of pitfall traps in a line at 5-m intervals and the target taxa (spiders, woodlice, ants, ground beetles, and rove beetles). DOI: https://doi.org/10.1525/elementa.2021.00084.f1

estimated visually. In order to test the potential of dolines to maintain permanently moist microhabitats during the growing season, soil moisture (VWC%) was continuously measured (with no missing data) in the bottom of five dolines as well as at five sites on the plateau with Optin ADL Soil sensors (from mid-March to late October 2020; Table S2). The sensors were placed 10 cm below the soil surface and soil moisture was measured at 1-h intervals. Prior to deployment, all loggers were checked for calibration accuracy in the lab. At the end of the measurements, microclimate and soil moisture data were exported into an Excel spreadsheet (Microsoft Excel 2010) for further

analysis. To provide information on the macroclimate of the study area, daily mean temperature and daily precipitation data were obtained from the nearest climate station (Pécs, from mid-March to late October 2020; see "Data accessibility statement").

### Species classification

We selected four species traits (moisture preference, body size, dispersal capacity, and feeding habit) for spiders, woodlice, ants, ground beetles, and rove beetles (Table S1) that accurately reflect the adaptation of species to environmental conditions (Gallé and Batáry, 2019). As we did not find any differences in the dispersal capacity of ants and the feeding habits of woodlice, these were excluded from the analysis.

All arthropod species were classified according to their moisture requirements (coded as 1: species associated with moister habitats, 0.5: mesophilous species, and 0: species associated with drier habitats) following Buchar and Růžička (2002) for spiders, Hornung et al. (2008) for woodlice, Czechowski et al. (2012) for ants, Freude et al. (2004) for ground beetles, and Koch (1989) and Ádám (2004) for rove beetles. The average body size—"cephalic size" for ants (Seifert, 2002)—of each species was given as a continuous variable (in millimeter or in micrometer for ants) using the data of Nentwig et al. (2020) for spiders, Farkas and Vilisics (2013) for woodlice, Seifert (2018) for ants, Freude et al. (2004) for ground beetles, and Assing and Schülke (2007) for rove beetles. We ranged body size values between 0 and 1 to down weight the influence of large-bodied species (cf. Gallé et al., 2019). All spider (1: frequently ballooning, 0.5: rarely ballooning, and 0: nonballooning; Blandenier, 2009), woodlouse (1: "eurydynamic"—faster and 0: "steneodynamic"—slower; Sutton et al., 1984), ground beetle (1: macropterous—fully developed wings, 0.5: dimorph—either with developed or with reduced wings, and 0: apterous/brachypterous—reduced or no wings; Homburg et al., 2014), and rove beetle (1: high dispersal ability, 0.5: moderate dispersal ability, and 0: low dispersal ability; Ádám, 2004; Lott, 2009; Lott and Anderson, 2011) species were classified according to their dispersal capacity. Finally, we classified spider (1: active hunting, 0.5: burrowing, and 0: web-building; Cardoso et al., 2011), ant (1: zoophagous and 0: both zoophagous and phytophagous; Seifert, 2018), ground beetle (1: carnivorous, 0.5: carnivorous, but consumes other materials as well, and 0: granivorous, but consumes other materials as well; Homburg et al., 2014), and rove beetle (1: carnivorous, 0.5: carnivorous or coprophagous, and 0: saprophagous or mycetophagous; Arnett and Thomas, 2001; Lott, 2009; Nitzu and Olenici, 2009; Lott and Anderson, 2011; Lutska and Sirenko, 2020) species according to their feeding habits.

### Data analysis

Species richness and abundance

Pitfall trap data from both sampling periods (2019 and 2020) were used to analyze the total number of species and specimens between the two habitats (plateau vs. doline).

We calculated the total number of species and specimens of each taxon for both habitats. To test whether the number of species and specimens differed between the two habitats, we used generalized linear mixed-effects models with a Poisson (for species number) or negative binomial (for specimen number) error distribution. Separate models were calculated for each taxon using the *glmer* function of the *lme4* package (Bates et al., 2015). In the models, the number of species or specimens sampled by each trap in 2019 (94 traps) and 2020 (114 traps) was used as a response variable, habitat type (plateau vs. doline) was included as a fixed factor, and doline ID (dolines 1–12) and sampling year as random factors. Analyses were carried out in R 3.6.2 (R Core Team, 2019).

### Microclimate, soil moisture, and deadwood

Mean air temperature, mean relative air humidity, mean soil moisture (FieldScout TDR 350 Soil Moisture Meter), and the average amount of deadwood were calculated across all sites and for each site (except in the case of deadwood) of the plateau and doline habitats. Paired $t$ tests were used to compare these means between the plateau and doline habitats using the $t$ test function from the *stats* package (R Core Team, 2019).

We standardized microclimatic data to the mean plateau values, that is, mean plateau data across all plateau sites were subtracted from the data of dolines for every measurement time point. Soil moisture values (Optin ADL Soil sensors) were averaged over 1-h intervals (from mid-March to late October 2020) across all five sites of the plateau and doline habitats, respectively. The results were plotted using a line graph.

### Compositional differences and species—environment relationships

We used data collected in the second sampling period (2020) to determine compositional differences and species–environment relationships, as (1) the number of sites where all the five traps remained in operation was low in the first sampling period, and (2) we possess environmental data only from the second sampling period. Species data from traps for those sites where all the five traps remained in operation (11 plateau and 9 doline sites) were pooled before these analyses.

The identification of species primarily associated with the plateau or doline habitats was made using the indicator value (IndVal) procedure (Dufrêne and Legendre, 1997), considering the relative frequency and abundance of species. This method provides an IndVal value for each species, based on the degree of specificity of a species to an ecological state (e.g., a habitat type) and its fidelity within that state. We used the *indval* function in the *labdsv* package (Roberts, 2019). The statistical significance of the IndVal statistics was evaluated by a Monte Carlo permutation procedure (999 permutations).

One-way analysis of similarities (ANOSIM) was used to test the effect of the plateau and doline habitats on the compositional differences of arthropod assemblages. We used the *anosim* function in the *vegan* package, applied the Bray–Curtis dissimilarity and performed 999
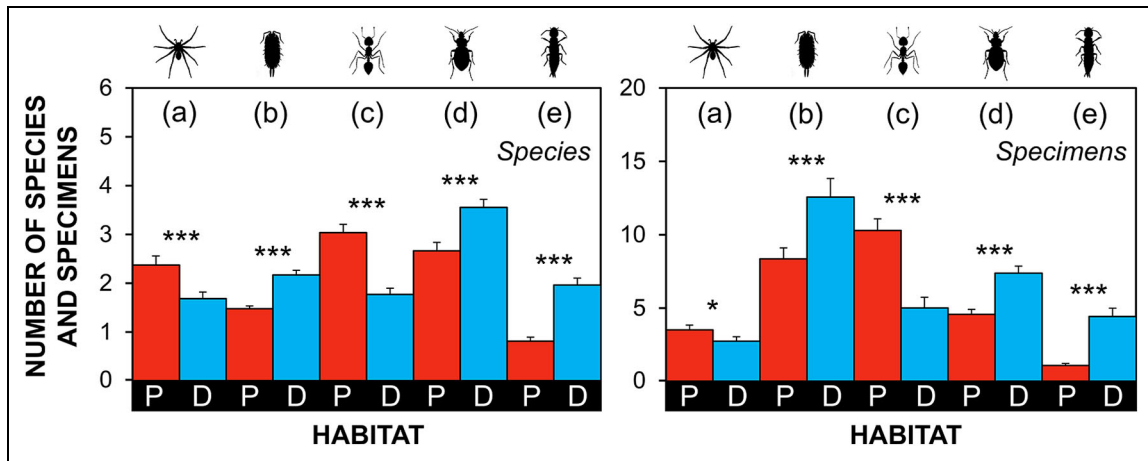
**Figure 2. Number of species and specimens (mean $\pm$ *SE*) in the pitfall traps.** Lowercase letters indicate different arthropod taxa as follows: (a) spiders, (b) woodlice, (c) ants, (d) ground beetles, and (e) rove beetles. Asterisks indicate significant differences (*$P < 0.05$; ***$P < 0.001$) between the plateau (P) and doline (D) habitats. DOI: https://doi.org/10.1525/elementa.2021.00084.f2

permutations (Oksanen et al., 2019). Nonmetric multidimensional scaling (NMDS) ordinations were used to visually illustrate compositional differences for each taxon applying the *metaMDS* function in the *vegan* package. A Hellinger transformation was applied to the matrix of species abundance data before the ordination. To assess the relationships between environmental factors (mean air temperature, mean relative air humidity, mean soil moisture, and the amount of deadwood; see "Data analysis—Microclimate, soil moisture, and deadwood" subsection) and arthropod assemblages, we fitted environmental vectors onto the ordination space using the *envfit* function, calculated correlations between ordination values and fitted vectors, and defined the significance of each environmental factor with a permutation procedure (999 permutations). All analyses were carried out in R 3.6.2 (R Core Team, 2019).

### Species traits
Pitfall trap data from both sampling periods (2019 and 2020) were used to analyze the species trait (moisture preference, body size, dispersal capacity, and feeding habit) distributions between the two habitats (plateau vs. doline). We calculated community-weighted means (CWMs)—the average of trait values weighted by the relative abundances of each species for each single trait—for each trap (Lavorel et al., 2008; Ricotta and Moretti, 2011).

To test whether the trait distributions differed between the two habitats, we used linear mixed-effects models (LMMs). Separate models were calculated for each trait of each taxon using the *lmer* function of the *lme4* package (Bates et al., 2015). In the models, the CWM of each trait calculated for each trap (2019: 94 traps and 2020: 114 traps) was used as a response variable, habitat type (plateau vs. doline) was included as a fixed factor, and doline ID (dolines 1–12) and sampling year as random factors. Analyses were carried out in R 3.6.2 (R Core Team, 2019).

## Results
### Species richness and abundance
A total of 74 spider (653 specimens), 5 woodlouse (2,163 specimens), 18 ant (1,606 specimens), 32 ground beetle (1,234 specimens), and 49 rove beetle (563 specimens) species were captured in the 208 traps (Table S1). Dolines contained more woodlouse (5 species and 1,269 specimens in dolines, while 4 species and 894 specimens on the plateau), ground beetle (28 species and 745 specimens in dolines, while 21 species and 489 specimens on the plateau), and rove beetle (40 species and 447 specimens in dolines, while 25 species and 116 specimens on the plateau) species and specimens than the plateau. In contrast, the plateau contained more spider (58 species and 376 specimens on the plateau, while 40 species and 277 specimens in dolines) and ant (16 species and 1,101 specimens on the plateau, while 11 species and 505 specimens in dolines) species and specimens than dolines.

The number of woodlouse, ground beetle, and rove beetle species and specimens found in the pitfall traps was higher ($P < 0.001$ in both cases) in dolines (woodlice: $z = 3.68$ and 4.43, respectively; ground beetles: $z = 3.51$ and 4.89, respectively; rove beetles: $z = 6.93$ and 9.24, respectively), while the number of spider and ant species and specimens was higher ($P < 0.001$ and $P < 0.05$, respectively) on the plateau (spiders: $z = 3.32$ and 2.17, respectively; ants: $z = 5.66$ and 6.92, respectively; **Figure 2**; Table S3).

### Microclimate, soil moisture, and deadwood
Mean air temperature was higher on the plateau (20.48°C $\pm$ 4.35°C; mean $\pm$ *SD*) than in dolines (19.46°C $\pm$ 3.68°C), while mean relative air humidity, mean soil moisture, and the average amount of deadwood showed higher values in dolines (78.73% $\pm$ 11.08%, 41.97% $\pm$ 6.71%, and 7.59% $\pm$ 3.42%, respectively) than on the plateau (70.34% $\pm$ 13.62%, 12.68% $\pm$ 4.20%, and 1.08% $\pm$ 0.51%, respectively). These differences were statistically significant (mean air temperature: $t = 5.68$, $P < 0.001$, mean relative air humidity: $t = 3.96$, $P = 0.002$, mean soil moisture:

**Table 1.** Indicator values and species occurrence and abundance data for arthropod species in the plateau and doline habitats. DOI: https://doi.org/10.1525/elementa.2021.00084.t1

| Taxa | Abbr. | IndVal Value | P | Occurrence/Abundance Plateau | Doline |
|---|---|---|---|---|---|
| Spiders (Araneae) | | | | | |
| *Apostenus fuscus* Westring, 1851 | *Apo_fus* | 0.455 (P) | 0.035 | 5/5 | 0/0 |
| *Diplostyla concolor* (Wider, 1834) | *Dio_con* | 0.893 (D) | 0.007 | 5/10 | 9/68 |
| *Harpactea saeva* (Herman, 1879) | *Har_sae* | 0.455 (P) | 0.016 | 5/5 | 0/0 |
| *Tenuiphantes tenebricola* (Wider, 1834) | *Ten_ten* | 0.846 (D) | 0.001 | 1/1 | 8/16 |
| Woodlice (Isopoda) | | | | | |
| *Hyloniscus vividus* (Koch, 1841) | *Hyl_viv* | 0.540 (D) | 0.037 | 2/2 | 6/7 |
| *Ligidium germanicum* Verhoeff, 1901 | *Lig_ger* | 0.889 (D) | 0.001 | 0/0 | 8/229 |
| *Protracheoniscus politus* (C. Koch, 1841) | *Pro_pol* | 0.818 (P) | 0.001 | 11/231 | 9/42 |
| *Trachelipus rathkii* (Brandt, 1833) | *Tra_rath* | 0.862 (D) | 0.006 | 8/38 | 9/194 |
| *Trachelipus ratzeburgii* (Brandt, 1833) | *Tra_ratz* | 0.749 (D) | 0.002 | 1/1 | 7/21 |
| Ants (Hymenoptera: Formicidae) | | | | | |
| *Lasius platythorax* (Seifert, 1991) | *Las_pla* | 0.799 (P) | 0.004 | 5/32 | 3/3 |
| *Myrmecina graminicola* (Latreille, 1802) | *Myr_gra* | 0.740 (P) | 0.008 | 11/68 | 3/14 |
| *Stenamma debile* (Foerster, 1850) | *Ste_deb* | 0.717 (P) | 0.011 | 10/41 | 4/9 |
| *Temnothorax crassispinus* (Karawajew, 1926) | *Tem_cra* | 0.939 (P) | 0.001 | 11/225 | 4/12 |
| Ground beetles (Coleoptera: Carabidae) | | | | | |
| *Abax parallelepipedus* (Piller & Mitterpacher, 1783) | *Aba_par* | 0.718 (D) | 0.038 | 9/24 | 9/50 |
| *Carabus nemoralis* (O. F. Muller, 1764) | *Car_nem* | 0.455 (P) | 0.035 | 5/13 | 0/0 |
| *Carabus ullrichii* (Germar, 1824) | *Car_ull* | 0.444 (D) | 0.031 | 0/0 | 4/5 |
| *Limodromus assimilis* (Paykull, 1790) | *Lim_ass* | 0.889 (D) | 0.001 | 0/0 | 8/27 |
| *Pterostichus ovoideus* (Sturm, 1824) | *Pte_ovo* | 0.667 (D) | 0.004 | 0/0 | 6/12 |
| *Trechus pilisensis* (Csiki, 1918) | *Tre_pil* | 0.667 (D) | 0.003 | 0/0 | 6/25 |
| Rove beetles (Coleoptera: Staphylinidae) | | | | | |
| *Carpelimus corticinus* (Gravenhorst, 1806) | *Car_cor* | 0.444 (D) | 0.026 | 0/0 | 4/6 |
| *Philonthus decorus* (Gravenhorst, 1802) | *Phi_dec* | 0.883 (D) | 0.001 | 1/1 | 8/131 |
| *Platydracus chalcocephalus* (Fabricius, 1801) | *Pla_cha* | 0.455 (P) | 0.031 | 5/9 | 0/0 |

Only species with statistically significant values ($P < 0.05$) are shown. IndVal values represent the higher value for the target species in either the plateau (P) or doline (D) habitats, respectively. Abbr. = abbreviated species names.

$t = 14.16$, $P < 0.001$, and average amount of deadwood: $t = 6.82$, $P < 0.001$).

Dolines were cooler (maximum difference: 3.1°C) and more humid (maximum difference: 16%) than the plateau during the investigated period (Figure S1). Daytime temperatures in dolines were much lower than those on the plateau. However, differences in nighttime temperatures were less pronounced. Soil moisture in dolines had remained relatively stable (36%–43%) from mid-March to late October 2020. However, soil moisture on the plateau had changed substantially with the highest value of 34% in late March and the lowest value of 12% in late September (Figure S1).

### Compositional differences and species—environment relationships

According to the IndVal procedure, there were 2 spider, 1 woodlouse, 4 ant, 1 ground beetle, and 1 rove beetle species that were primarily associated with the plateau. In contrast, there were 2 spider, 4 woodlouse, 5 ground beetle, and 2 rove beetle species that were primarily associated with dolines (**Tables 1** and S4). No characteristic ant species was identified for dolines by the IndVal procedure.

NMDS ordinations of trap data showed that the composition of arthropod assemblages differed between the plateau and doline habitats (stress factors: 0.15, 0.04, 0.14,
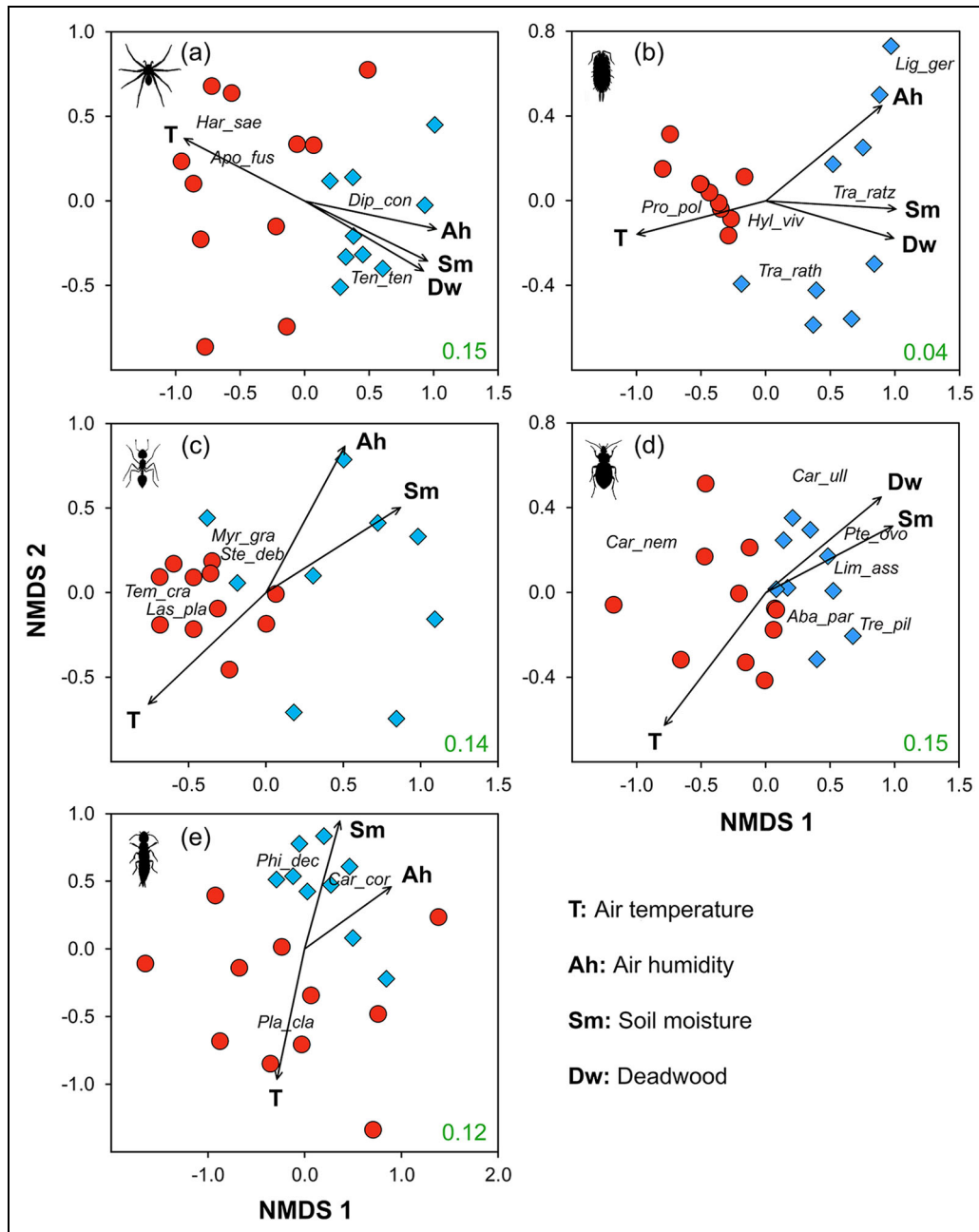
**Figure 3. Compositional differences and species–environment relationships.** Nonmetric multidimensional scaling (NMDS) ordinations for the (a) spider, (b) woodlouse, (c) ant, (d) ground beetle, and (e) rove beetle assemblages of the plateau (red circles) and doline (blue diamond) habitats in the Mecsek Mountains, Hungary. Fitted vectors show correlations between NMDS axial scores and potential predictors (air temperature, relative air humidity, soil moisture, and amount of downed deadwood, $P < 0.05$). Arrow directions indicate the direction of the correlation, while vector length shows the strength of correlation. Green numbers indicate stress values. Abbreviated names of characteristic species are also plotted (**Table 1**). DOI: https://doi.org/10.1525/elementa.2021.00084.f3

0.15, and 0.12 for spiders, woodlice, ants, ground beetles, and rove beetles, respectively; **Figure 3**), and these differences were all statistically significant (ANOSIM; spiders: $R = 0.43$, $P = 0.002$; woodlice: $R = 0.71$, $P = 0.001$; ants: $R = 0.61$, $P = 0.001$; ground beetles: $R = 0.24$, $P = 0.006$; and rove beetles: $R = 0.37$, $P = 0.001$). Air temperature, relative air humidity, soil moisture, and the amount of deadwood were significantly related to the ordination of spider ($r^2 = 0.52$–$0.74$, $P < 0.005$) and woodlouse assemblages ($r^2 = 0.42$–$0.80$, $P < 0.05$), and air temperature,

relative air humidity, and soil moisture were significantly related to the ordination of ant ($r^2 = 0.33$–$0.61$, $P < 0.05$) and rove beetle assemblages ($r^2 = 0.36$–$0.49$, $P < 0.05$), while air temperature, soil moisture, and the amount of deadwood were significantly related to the ordination of ground beetle assemblages ($r^2 = 0.36$–$0.52$, $P < 0.05$; **Figure 3**). Arthropod assemblages on the plateau were associated with higher air temperature, lower relative air humidity and/or soil moisture, and/or lower amount of deadwood, while arthropod assemblages in dolines were
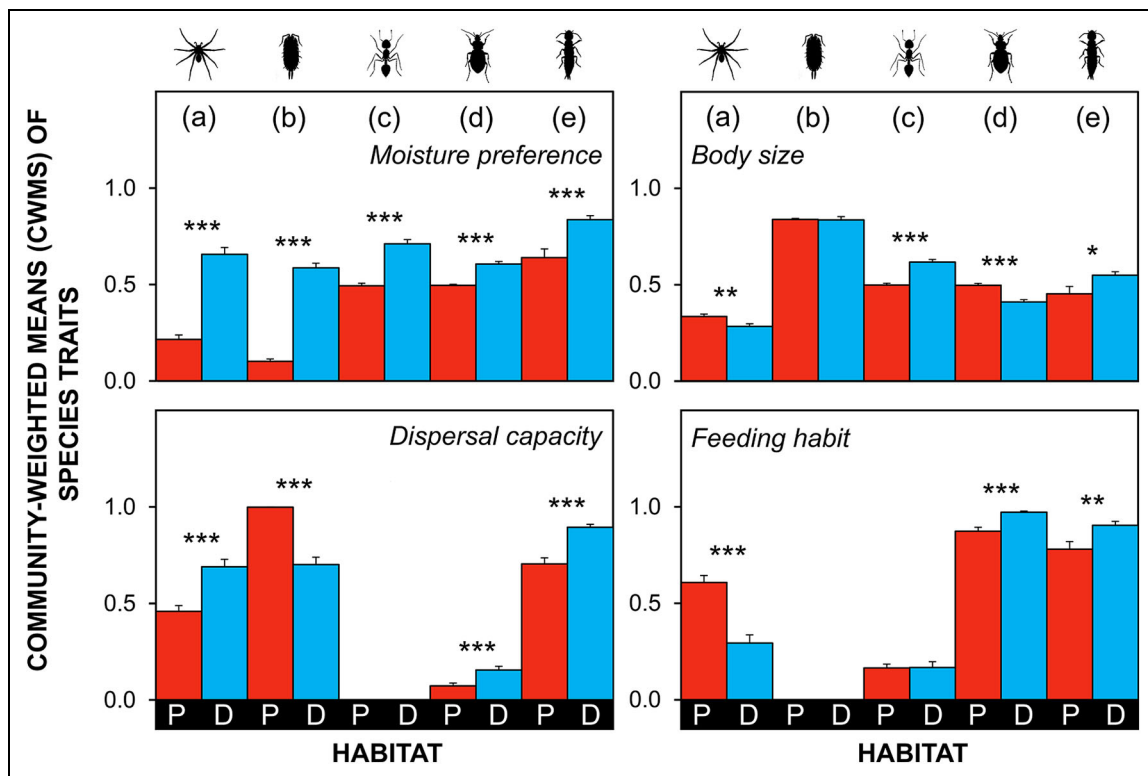
**Figure 4. Community-weighted means of species traits (mean ± *SE*) for the pitfall trap data.** Lowercase letters indicate different arthropod taxa as follows: (a) spiders, (b) woodlice, (c) ants, (d) ground beetles, and (e) rove beetles. As no differences were observed in the dispersal capacity of ants and the feeding habits of woodlice, these were excluded from the analysis. Functional trait values correspond to coded values ranging between 0 and 1 (as described in the Material and methods section). Asterisks indicate significant differences (*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$) between the plateau (P) and doline (D) habitats. DOI: https://doi.org/10.1525/elementa.2021.00084.f4

associated with lower air temperature, higher relative air humidity and/or soil moisture, and/or higher amount of deadwood.

### Species traits

According to the LMMs (**Figure 4**; Table S5), the distribution of arthropod species associated with moister habitats was significantly ($P < 0.001$) related to dolines (spiders: $t = 10.86$, ants: $t = 9.15$, woodlice: $t = 19.63$, ground beetles: $t = 7.67$, and rove beetles: $t = 4.52$). Dolines contained proportionally more large-bodied ants ($t = 8.04$, $P < 0.001$) and rove beetles ($t = 2.49$, $P < 0.05$), and fewer large-bodied spiders ($t = -3.08$, $P < 0.01$) and ground beetles ($t = -5.84$, $P < 0.001$) than the plateau. The distribution of spiders, ground beetles, and rove beetles with greater dispersal capacity was significantly ($P < 0.001$) related to dolines (spiders: $t = 5.26$, ground beetles: $t = 3.37$, and rove beetles: $t = 6.23$). However, we found a significantly greater proportion of woodlice with greater dispersal capacity on the plateau ($t = 9.50$, $P < 0.001$). Dolines contained proportionally fewer active hunting spiders ($t = -6.40$, $P < 0.001$) and more carnivorous ground beetles ($t = 4.91$, $P < 0.001$) and rove beetles ($t = 3.06$, $P < 0.01$) than the plateau.

### Discussion

This study provides a vivid picture of how topographic complexity provided by solution dolines may create suitable habitats for ground-dwelling arthropod assemblages and certain species traits. Our results correspond well with those obtained for different microclimatic habitats in Europe (e.g., kurgans, peat bogs, and cold scree slopes), where habitat diversity provided by topography and/or soil plays a key role in the maintenance of distinct arthropod assemblages (Rendoš et al., 2016; Deák et al., 2020; Gallé et al., 2021).

Our results suggest that forested solution dolines may provide important habitats for many arthropod species that are rare or absent from the surrounding plateau and that they have the capacity to maintain characteristic arthropod assemblages, contributing to the landscape-scale biodiversity in karst landscapes. We further demonstrated that the local habitat features, such as microclimate, soil moisture, and the amount of downed deadwood, may play a significant role in determining the composition of arthropod assemblages in dolines. Increasing topographic complexity generally leads to increased climatic variability and therefore affects the spatial distributions of organisms (Badgley et al., 2017; Graae et al., 2018; Raschmanová et al., 2018; Lewis et al., 2020; Deák et al., 2021). Arthropod species responded to microclimatic variation in the studied landscape (Mecsek Mts, Hungary). To our knowledge, this is the first study illustrating a strong and concerted response of the distribution of five arthropod taxa from various trophic levels (spiders, woodlice, ants, ground

beetles, and rove beetles) to topography and related microclimatic patterns in solution dolines. We found that the relatively cool and humid microclimate and high soil moisture in the bottom of large forested dolines may contribute to the maintenance of characteristic arthropod assemblages, as ANOSIMs confirmed significant differences between the composition of all arthropod assemblages of the plateau and doline habitats. The maintenance of comparatively cool and moist environments in dolines may be facilitated by lower solar radiation, cool-air pooling, thicker soil layer, and higher soil moisture (Whiteman et al., 2004; Bátori et al., 2019). Similar to the rocky slopes and deep ravines, mass soil movements on the steep and wet slopes of dolines uproot large trees allowing an increased amount of deadwood at doline bottoms. Previous studies have demonstrated that deadwood is an important predictor of biodiversity (Magura, 2002; Gallé et al., 2016; Oettel et al., 2020; Öder et al., 2021), as it provides food source and shelter for a number of saproxylic (i.e., deadwood-dependent) species and their predators, parasites, and parasitoids (Verkerk et al., 2011). We also found that the amount of deadwood may be an important predictor of the distribution of at least some arthropod species in dolines (Vilisics et al., 2011), such as *Hyloniscus vividus* (C. Koch, 1841; Isopoda: Oniscidea) and *Limodromus assimilis* (Paykull, 1790; Coleoptera: Carabidae). Some of these species were particularly abundant in dolines. These results also underline the importance of fine-scale variation in environmental conditions and the presence of microclimatic habitats (e.g., caves, north-facing slopes, and topographic depressions) when investigating the distribution of biodiversity in karst landscapes (Bátori et al., 2017; Stralberg et al., 2020; Pavlek and Mammola, 2021). Furthermore, topographic complexity may create conditions that facilitate species persistence (especially for cool-adapted species), even as the regional climate changes (Schmalholz and Hylander, 2011). These cool-adapted species are highly threatened by climate change and therefore have a high conservation priority. However, the recent focus on temperature as a determinant of microrefugia insufficiently accounts for the importance of hydrologic processes with global warming (McLaughlin et al., 2017).

Our results showed that solution dolines may facilitate the persistence of a number of arthropod species associated with moister habitats, such as *Diplostyla concolor* (Wider, 1834; Araneae), *Ligidium germanicum* (Verhoeff, 1901; Isopoda: Oniscidea), *Limodromus assimilis* (Paykull, 1790; Coleoptera: Carabidae), and *Carpelimus corticinus* (Gravenhorst, 1806; Coleoptera: Staphylinidae). In the present climate, many of these species have a restricted distribution in Hungary (e.g., Hornung et al., 2008; Hornung et al., 2009). Karst landscapes around the world are experiencing particularly rapid climate change, such as temperature increase and severe drought (Zhou et al., 2018; Nerantzaki and Nikolaidis, 2020). Projections of regional climate models show for East-Central Europe that temperature will increase substantially and extreme heat waves and drought will be more frequent and last longer in the next decades (Bartholy et al., 2007; Bartholy and

Pongrácz, 2010). As doline bottoms have the potential to maintain permanently moist conditions (i.e., environmental stability) during the driest periods of the year, we believe that at least some arthropod species associated with moister habitats can survive unfavorable periods within these dolines in the future (**Figure 5**). It also means that these local topographic depressions may need to be accounted for when evaluating climate change impacts on biodiversity in karst landscapes, as they may constitute important hydrologic microrefugia and they increase habitat connectivity for dispersal and migration (Keppel et al., 2015; McLaughlin et al., 2017).

Furthermore, we found that dolines may also host species with specific sets of body size, dispersal, and feeding traits. For instance, dolines hosted proportionally more small-bodied spiders and ground beetles, and more spiders, ground beetles, and rove beetles with higher dispersal capacity than the plateau. The main reason for this appears to be the funnel-shaped topography that can trap good dispersers, such as frequently ballooning spiders and macropterous ground beetles and rove beetles (Bell et al., 2005; Dauber et al., 2005; Hendrickx et al., 2009). We also found that the proportion of carnivorous species was generally positively associated with the doline habitats, meaning that those arthropods that have higher dispersal capacities and consume other animals may significantly influence the dynamics of predator–prey interactions and the structure of food webs within these depressions (cf. Rosenblatt and Schmitz, 2016). In addition, water availability could affect the physiology, dietary preferences, or behaviors of predatory arthropods in many ways (McCluney and Sabo, 2009), also influencing species interactions in karstic microrefugia. Considering the facts above, we believe that solution dolines may act as microrefugia for some arthropods (cf. Marcin et al., 2021), while for others, they may function as stepping stones (Bátori et al., 2020a) or "ecological traps" (cf. Hale and Swearer, 2016). However, further studies are required to confirm these findings, considering the potential effects of environmental changes on functional trait patterns as well. As changes in rainfall and temperature patterns may influence the physiological, reproductive, and behavioral responses of organisms in a different fashion (Lister and Garcia, 2018; Joly et al., 2019), it is important to identify how individual arthropod species and different arthropod assemblages will respond to future climatic events. Previous studies have demonstrated that warming may lead to faster development and smaller adult body sizes in various arthropod groups (Forster and Hirst, 2012; Frances et al., 2017), influence feeding rates and diet selection (Rall et al., 2012; Lemoine and Shantz, 2016), affect plant–herbivore and predator–prey interactions (Frank and Bramböck, 2016; Sentis et al., 2017), and alter the structure and stability of ectotherm-dominated food webs (Boukal et al., 2019). There is an urgent need to focus on the direct and indirect effects of temperature increase and drought on the biotic interactions among arthropods (Walther, 2010; Murphy et al., 2020; Abrego et al., 2021) and to understand the relationships among taxon-specific responses to long-term environmental stability when studying microrefugia. As
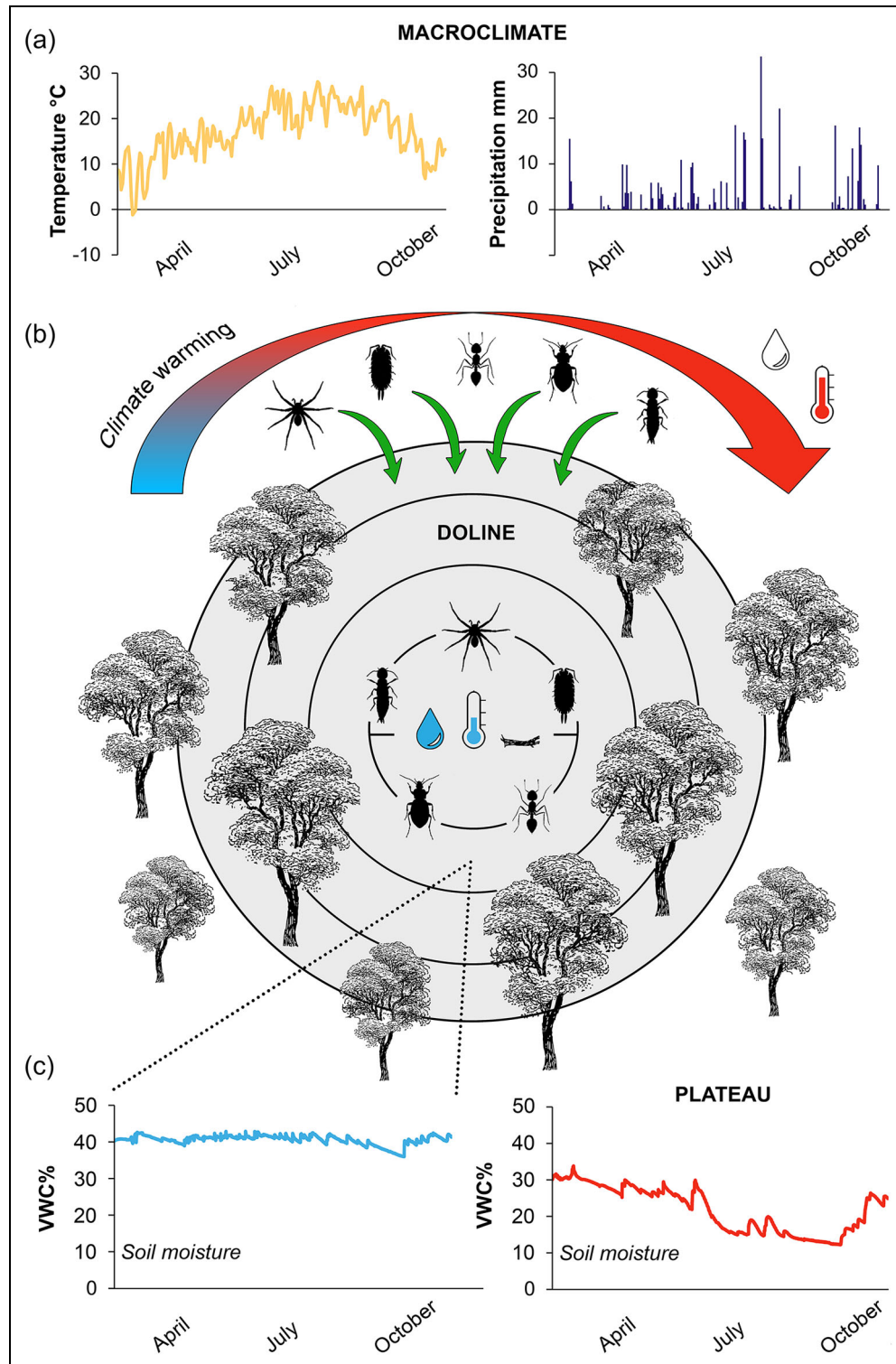
**Figure 5. Macroclimate, soil moisture, and potential future changes in the distribution of arthropods (spiders, woodlice, ants, ground beetles, and rove beetles) in the karst region of the Mecsek Mountains, Hungary.** (a) Daily mean temperature and daily precipitation during the growing season (from mid-March to late October 2020) in the study area. (b) Doline bottoms may provide microrefugia (i.e., permanently cool, humid, and moist microhabitats) for arthropod species during climate warming. (c) Changes in soil moisture in the bottom of dolines and on the plateau from mid-March to late October 2020. DOI: https://doi.org/10.1525/elementa.2021.00084.f5

functional traits may be reflective of long-term environmental stability (Keppel et al., 2018), extensive data collection—including field and laboratory measurements of functional traits within species—would be required to investigate the relationships between functional patterns and environmental factors inside and outside dolines.

Finally, future studies have to reveal the long-term ecological consequences of different anthropogenic disturbances on the distribution of arthropod taxa in dolines under a warming climate (cf. Rojas et al., 2021).

## Conclusions

Our investigations revealed that topographic depressions in karst landscapes (solution dolines) may play an important role in maintaining characteristic arthropod assemblages, arthropod species that may be particularly vulnerable to climate change, and specific species traits. This ability is strongly related to the microhabitat structure and corresponding environmental conditions present in these unique habitats (Kobal et al., 2015). Similar to plants (cf. Bátori et al., 2019), ground-dwelling arthropods (spiders, woodlice, ants, ground beetles, and rove beetles) showed a concerted response to topography and related microclimatic (air temperature, soil moisture, and/or relative air humidity) patterns in dolines. The amount of downed deadwood was also an important predictor of arthropod diversity. Our current results and previous climatic studies over longer time periods indicate that in forested landscapes, doline bottoms are cooler and more humid than the surrounding plateau (Raschmanová et al., 2018; Marcin et al., 2021). We also demonstrated that doline bottoms have the potential to maintain permanently moist conditions not only in spring and autumn but also during drier periods of the year. The ability of dolines to provide soil moisture levels that are no longer available in the surrounding landscape may indicate the presence of future hydrologic microrefugia. Furthermore, dolines may host species with specific sets of body size, dispersal, and feeding traits, highlighting that they may facilitate the persistence of some functional traits that are rare or absent from the surrounding landscape. Considering these findings, we believe that dolines are likely to maintain viable populations of at least some arthropod species that may be vulnerable to climate change (e.g., species associated with moist habitats). However, quantifying the degree to which biotic (e.g., species composition and vegetation pattern) and abiotic (e.g., microclimate and soil moisture) conditions in dolines will change would provide a key indicator of the potential capacity of these special habitats. Future studies might be able to reveal how anthropogenic disturbances affect the arthropod assemblages in dolines and how the main environmental filters (i.e., seasonal drought and temperature increase) may impact functional traits within and among species in these safe havens.

## Data accessibility statement

All data generated during the study are presented in this article or its supplemental material. Information about the macroclimate of the study area is available at http://ogimet.com.

## Supplemental files

The supplemental files for this article can be found as follows:

**Figure S1**. Differences in air temperature, relative air humidity, and soil moisture between the plateau and doline habitats (Mecsek Mountains, Hungary) during the sampling period in 2020.

**Table S1**. Arthropod occurrence and abundance data from pitfall traps and species traits (Mecsek Mountains, Hungary).

**Table S2**. Microclimate, soil moisture, and deadwood data for the plateau and doline habitats (see Supplemental Excel file 2).

**Table S3**. Results of the separate generalized linear mixed-effects models built for each taxon (species number: Poisson error distribution; specimen number: negative binomial error distribution).

**Table S4**. Indicator values of all arthropod species from the plateau and doline habitats.

**Table S5**. Results of the separate linear mixed-effects models built for each taxon.

## Competing interests

The authors declare that they have no conflict of interest.

## Author contributions

Substantial contributions to conception and design: ZB, RG, CT, EH.

Acquisition of data: ZB, RG, NGS, GL, AT, CT, IEM, KF, AAH.

Species identification: RG, NGS, PC, DDN, GL, EH.

Analysis and interpretation of data: ZB, RG, AT.

Wrote and revised this article: All authors.

## References

**Abrego, N**, **Roslin, T**, **Huotari, T**, **Ji, Y**, **Schmidt, NM**, **Wang, J**, **Yu, DW**, **Ovaskainen, O**. 2021. Accounting for species interactions is necessary for predicting how arctic arthropod communities respond to climate change. *Ecography* **44**: 885–896. DOI: http://dx.doi.org/10.1111/ecog.05547.

**Ádám, L**. 2004. *A Bakony és a Vértes holyvafaunája (Coleoptera: Staphylinidae)*. Zirc, Hungary: Bakonyi Természettudományi Múzeum: 28.

**Angyal, D**, **Chávez-Solís, EF**, **Liévano-Beltrán, LA**, **Magaña, B**, **Simoes, N**, **Mascaró, M**. 2020. New distribution records of subterranean crustaceans from cenotes in Yucatan (Mexico). *ZooKeys* **911**: 21–49. DOI: http://doi:10.3897/zookeys.911.47694.

**Arnett, RH, Thomas, MC**. 2001. *American beetles, Volume 1. Archostemata, Myxophaga, Adephaga, Polyphaga: Staphyliniformia*. New York, NY: CRC Press.

**Ashcroft, MB**. 2010. Identifying refugia from climate change. *Journal of Biogeography* **37**: 1407–1413. DOI: http://dx.doi.org/10.1111/j.1365-2699.2010.02300.x.

**Assing, V, Schülke, M**. 2007. Supplemente zur mitteleuropäischen Staphylinidenfauna (Coleoptera, Staphylinidae). III. *Entomologische Blätter* **102**: 1–78.

**Badgley, C, Smiley, TM, Terry, R, Davis, EB, DeSantis, LRG, Fox, DL, Hopkins, SSB, Jezkova, T, Matocq, MD, Matzke, N, McGuire, JL, Mulch, A, Riddle, BR, Roth, L, Samuels, JX, Strömberg, CAE, Yanites, BJ**. 2017. Biodiversity and topographic complexity: Modern and geohistorical perspectives. *Trends in Ecology & Evolution* **32**: 211–226. DOI: http://dx.doi.org/10.1016/j.tree.2016.12.010.

**Bartholy, J, Pongrácz, R**. 2010. Analysis of precipitation conditions for the Carpathian Basin based on extreme indices in the 20th century and climate simulations for 2050 and 2100. *Physics and Chemistry of the Earth, Parts A/B/C* **35**: 43–51. DOI: http://dx.doi.org/10.1016/j.pce.2010.03.011.

**Bartholy, J, Pongrácz, R, Gelybó, G**. 2007. Regional climate change expected in Hungary for 2071–2100. *Applied Ecology and Environmental Research* **5**: 1–17.

**Bates, D, Maechler, M, Bolker, B, Walker, S**. 2015. Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* **67**: 1–48. DOI: http://dx.doi.org/10.18637/jss.v067.i01.

**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. *Forest Ecology and Management* **496**: 119446. DOI: http://dx.doi.org/10.1016/j.foreco.2021.

**Bátori, Z, Körmöczi, L, Erdős, L, Zalatnai, M, Csiky, J**. 2012. Importance of karst sinkholes in preserving relict, mountain, and wet-woodland plant species under Sub-Mediterranean climate: A case study from southern Hungary. *Journal of Cave and Karst Studies* **74**: 127–134. DOI: http://dx.doi.org/10.4311/2011LSC0216.

**Bátori, Z, Lőrinczi, G, Tölgyesi, C, Módra, G, Juhász, O, Aguilon, DJ, Vojtkó, A, Valkó, O, Deák, B, Erdős, L, Maák, IE**. 2020a. Karstic microrefugia host functionally specific ant assemblages. *Frontiers in Ecology and Evolution* **8**: 613738. DOI: http://dx.doi.org/10.3389/fevo.2020.613738.

**Bátori, Z, Vojtkó, A, Farkas, T, Szabó, A, Havadtői, K, Vojtkó, AE, Tölgyesi, C, Cseh, V, Erdős, L, Maák, IE, Keppel, G**. 2017. Large- and small-scale environmental factors drive distributions of cool-adapted plants in karstic microrefugia. *Annals of Botany* **119**: 301–309. DOI: http://dx.doi.org/10.1093/aob/mcw233.

**Bátori, Z, Vojtkó, A, Keppel, G, Tölgyesi, C, Čarni, A, Zorn, M, Farkas, T, Erdős, L, Kiss, PJ, Módra, G,** **Valjavec, MB**. 2020b. Anthropogenic disturbances alter the conservation value of karst dolines. *Biodiversity and Conservation* **29**: 503–525. DOI: http://doi:10.1007/s10531-019-01896-4.

**Bátori, Z, Vojtkó, A, Maák, IE, Lőrinczi, G, Farkas, T, Kántor, N, Tanács, E, Kiss, PJ, Juhász, O, Módra, G, Tölgyesi, C, Erdős, L, Aguilon, DJ, Keppel, G**. 2019. Karst dolines provide diverse microhabitats for different functional groups in multiple phyla. *Scientific Reports* **9**: e7176. DOI: http://dx.doi.org/10.1038/s41598-019-43603.

**Battisti, C, Giardini, M, Marini, F, Di Rocco, L, Dodaro, G, Vignoli, L**. 2017. Diversity metrics, species turnovers and nestedness of bird assemblages in a deep karst sinkhole. *Israel Journal of Ecology and Evolution* **63**: 8–16. DOI: http://dx.doi.org/10.1163/22244662-06301009.

**Beck von Mannagetta, G**. 1906. Die Umkehrung der Pflanzenregionen in den Dolinen des Karstes. *Sitzungsberichte der Kaiserliche Akademie der Wissenschaften in Wien* **65**: 3–4.

**Bell, JR, Bohan, DA, Shaw, EM, Weyman, GS**. 2005. Ballooning dispersal using silk: World fauna, phylogenies, genetics and models. *Bulletin of Entomological Research* **95**: 69–114. DOI: http://dx.doi.org/10.1079/BER2004350.

**Blandenier, G**. 2009. Ballooning of spiders (Araneae) in Switzerland: General results from an eleven-year survey. *Arachnology* **14**: 308–316. DOI: http://dx.doi.org/10.13156/arac.2009.14.7.308.

**Bolton, B**. 2020. An online catalog of the ants of the world. Available at http://antcat.org. Accessed 2 June 2020.

**Boukal, DS, Bideault, A, Carreira, BM, Sentis, A**. 2019. Species interactions under climate change: Connecting kinetic effects of temperature on individuals to community dynamics. *Current Opinion in Insect Science* **35**: 88–95. DOI: http://dx.doi.org/10.1016/j.cois.2019.06.014.

**Bryson, RW, Prendini, L, Savary, WE, Pearman, PB**. 2014. Caves as microrefugia: Pleistocene phylogeography of the troglophilic North American scorpion *Pseudouroctonus reddelli*. *BMC Evolutionary Biology* **14**: 9. DOI: http://dx.doi.org/10.1186/1471-2148-14-9.

**Buchar, J, Růžička, J**. 2002. *Catalogue of spiders of the Czech Republic*. Praha, Czech Republic: Peres Publisher.

**Cadotte, MW, Arnillas, CA, Livingstone, SW, Yasui, SLE**. 2015. Predicting communities from functional traits. *Trends in Ecology & Evolution* **30**: 510–511. DOI: http://dx.doi.org/10.1016/j.tree.2015.07.001.

**Cardoso, P, Pekár, S, Jocqué, R, Coddington, JA**. 2011. Global patterns of guild composition and functional diversity of spiders. *PLoS One* **6**: e21710. DOI: http://dx.doi.org/10.1371/journal.pone.0021710.

**Coleman, TW, Rieske, LK**. 2006. Arthropod response to prescription burning at the soil–litter interface in oak–pine forests. *Forest Ecology and Management*

**233**: 52–60. DOI: http://dx.doi.org/10.1016/j.foreco.2006.06.001.

**Corcos, D**, **Lami, F**, **Nardi, D**, **Boscutti, F**, **Sigura, M**, **Giannone, F**, **Pantini, P**, **Tagliapietra, A**, **Busato, F**, **Sibella, R**, **Marini, L**. 2021. Cross-taxon congruence between predatory arthropods and plants across Mediterranean agricultural landscapes. *Ecological Indicators* **123**: 107366. DOI: http://dx.doi.org/10.1016/j.ecolind.2021.107366.

**Császár, P**, **Torma, A**, **Gallé-Szpisjak, N**, **Tölgyesi, C**, **Gallé, R**. 2018. Efficiency of pitfall traps with funnels and/or roofs in capturing ground-dwelling arthropods. *European Journal of Entomology* **115**: 15–24. DOI: http://dx.doi.org/10.14411/eje.2018.003.

**Czechowski, W**, **Radchenko, A**, **Czechowska, W**, **Vepsä-läinen, K**. 2012. *The ants (Hymenoptera, Formicidae) of Poland with reference to the myrmecofauna of Europe.* Warszawa, Poland: MIZ PAS.

**Dauber, J**, **Purtauf, T**, **Allspach, A**, **Frisch, J**, **Voigtländer, K**, **Wolters, V**. 2005. Local vs. landscape controls on diversity: A test using surface-dwelling soil macroinvertebrates of differing mobility. *Global Ecology and Biogeography* **14**: 213–221. DOI: http://dx.doi.org/10.1111/j.1466-822X.2005.00150.x.

**Deák, B**, **Kovács, B**, **Rádai, Z**, **Apostolova, I**, **Kelemen, A**, **Kiss, R**, **Lukács, K**, **Palpurina, S**, **Sopotlieva, D**, **Báthori, F**, **Valkó, O**. 2021. Linking environmental heterogeneity and plant diversity: The ecological role of small natural features in homogeneous landscapes. *Science of the Total Environment* **763**: 144–199. DOI: http://dx.doi.org/10.1016/j.scitotenv.2020.144199.

**Deák, B**, **Valkó, O**, **Nagy, DD**, **Török, P**, **Torma, A**, **Lőrinczi, G**, **Kelemen, A**, **Nagy, A**, **Bede, Á**, **Mizser, S**, **Csathó, AI**, **Tóthmérész, B**. 2020. Habitat islands outside nature reserves—Threatened biodiversity hotspots of grassland specialist plant and arthropod species. *Biological Conservation* **241**: 108254. DOI: http://dx.doi.org/10.1016/j.biocon.2019.108254.

**Dobrowski, SZ**. 2011. A climatic basis for microrefugia: The influence of terrain on climate. *Global Change Biology* **17**: 1022–1035. DOI: http://dx.doi.org/10.1111/j.1365-2486.2010.02263.x.

**Dövényi, Z ed**. 2010. *Magyarország Kistájainak Katasztere.* Budapest, Magyarország: MTA Földrajztudományi Kutatóintézet.

**Dufrêne, M**, **Legendre, P**. 1997. Species assemblages and indicator species: The need for a flexible asymmetrical approach. *Ecological Monographs* **67**: 345–366. DOI: http://doi.org/10.1890/0012-9615(1997)067[0345:SAAIST]2.0.CO;2.

**Farkas, S**, **Vilisics F**. 2013. Magyarország szárazföldi ászkarák faunájának határozója (Isopoda: Oniscidea). *Natura Somogyiensis* **23**: 89–124.

**Ford, DC**, **Williams, PW**. 2007. *Karst hydrology and geomorphology.* Chichester, UK: John Wiley and Sons Ltd.

**Forster, J**, **Hirst, AG**. 2012. The temperature-size rule emerges from ontogenetic differences between growth and development rates. *Functional Ecology* **26**: 483–492. DOI: http://dx.doi.org/10.1111/j.1365-2435.2011.01958.x.

**Frances, DN**, **Moon, JY**, **McCauley, SJ**. 2017. Effects of environmental warming during early life history on libellulid odonates. *Canadian Journal of Zoology* **95**: 373–382. DOI: http://dx.doi.org/10.1139/cjz-2016-0233.

**Frank, T**, **Bramböck, M**. 2016. Predatory beetles feed more pest beetles at rising temperature. *BMC Ecology* **16**: 21. DOI: http://dx.doi.org/10.1186/s12898-016-0076-x.

**Freude, H**, **Harde, KW**, **Müller-Motzfeld, G**, **Lohse, GA**, **Klausnitzer, B**. 2004. *Die Käfer Mitteleuropas, Adephaga 1, Carabidae Laufkäfer.* Munich, Germany: Spektrum Akademischer Verlag.

**Gallé, L**. 2017. Climate change impoverishes and homogenizes ants' community structure: A long term study. *Community Ecology* **18**: 128–136. DOI: http://dx.doi.org/10.1556/168.2017.18.2.2.

**Gallé, R**, **Batáry, P**. 2019. Trait-based paradise—About the importance of real functionality. *Community Ecology* **20**: 314–316. DOI: http://dx.doi.org/10.1556/168.2019.20.3.11.

**Gallé, R**, **Gallé-Szpisjak, N**, **Zsigmond, AR**, **Könczey B**, **Urák, I**. 2021. Tree species and microhabitat affect forest bog spider fauna. *European Journal of Forest Research* **140**: 691–702. DOI: http://dx.doi.org/10.1007/s10342-021-01359-y.

**Gallé, R**, **Happe, AK**, **Baillod, AB**, **Tscharntke, T**, **Batáry, P**. 2019. Landscape configuration, organic management, and within-field position drive functional diversity of spiders and carabids. *Journal of Applied Ecology* **56**: 63–72. DOI: http://dx.doi.org/10.1111/1365-2664.13257.

**Gallé, R**, **Torma, A**, **Maák, I**. 2016. The effect of forest age and habitat structure on the ground-dwelling ant assemblages of lowland poplar plantations. *Agricultural and Forest Entomology* **18**: 151–156. DOI: http://dx.doi.org/10.1111/afe.12148.

**Gentili, R**, **Baroni, C**, **Panigada, C**, **Rossini, M**, **Tagliabue, G**, **Armiraglio, S**, **Citterio, S**, **Carton, A**, **Salvatore, MC**. 2020. Glacier shrinkage and slope processes create habitat at high elevation and microrefugia across treeline for alpine plants during warm stages. *Catena* **193**: 104626. DOI: http://dx.doi.org/10.1016/j.catena.2020.104626.

**González-Megías, A**, **Menéndez, R**. 2012. Climate change effects on above- and below-ground interactions in a dryland ecosystem. *Philosophical Transactions of the Royal Society B: Biological Sciences* **367**: 3115–3124. DOI: http://dx.doi.org/10.1098/rstb.2011.0346.

**Graae, BJ**, **Vandvik, V**, **Armbruster, WS**, **Eiserhardt, WL**, **Svenning, JC**, **Hylander, K**, **Ehrlén, J**, **Speed, JDM**, **Klanderud, K**, **Bråthen, KA**, **Milbau, A**, **Opedal, ØH**, **Alsos, IG**, **Ejrnæs, R**, **Bruun, HH**, **Birks, HJB**, **Westergaard, KB**, **Birks, HH**, **Lenoir, J**. 2018. Stay

or go—How topographic complexity influences alpine plant population and community responses to climate change. *Perspectives in Plant Ecology, Evolution and Systematics* **30**: 41–50. DOI: http://dx.doi.org/10.1016/j.ppees.2017.09.008.

Gruner, HE. 1966. Krebstiere oder Crustacea. V. Isopoda. 2. Lieferung, in Dahl, F (Begr.) ed., *Die Tierwelt Deutschlands* (Vol. 53). Jena, Germany: Gustav Fischer: 151–380.

Gubler, M, Henne, PD, Schwörer, C, Boltshauser-Kaltenrieder, P, Brönnimann, S, Tinner, W. 2018. Microclimatic gradients provide evidence for a glacial refugium for temperate trees in a sheltered hilly landscape of Northern Italy. *Journal of Biogeography* **45**: 2564–2575. DOI: http://dx.doi.org/10.1111/jbi.13426.

Hale, R, Swearer, SE. 2016. Ecological traps: Current evidence and future directions. *Proceedings of the Royal Society B* **283**: 20152647. DOI: http://dx.doi.org/10.1098/rspb.2015.2647.

Halsch, CA, Shapiro, AM, Fordyce, JA, Nice, CC, Thorne, JH, Waetjen, DP, Forister, ML. 2021. Insects and recent climate change. *Proceedings of the National Academy of Sciences of the United States of America* **118**: e2002543117. DOI: http://dx.doi.org/10.1073/pnas.2002543117.

Hébert, MP, Beisner, BE, Maranger, R. 2016. A meta-analysis of zooplankton functional traits influencing ecosystem function. *Ecology* **97**: 1069–1080. DOI: http://dx.doi.org/10.1890/15-1084.1.

Hendrickx, F, Maelfait, JP, Desender, K, Aviron, S, Bailey, D, Diekotter, T, Lens, L, Liira, J, Schweiger, O, Speelmans, M, Vandomme, V, Bugter, R. 2009. Pervasive effects of dispersal limitation on within- and among-community species richness in agricultural landscapes. *Global Ecology and Biogeography* **18**: 607–616. DOI: http://dx.doi.org/10.1111/j.1466-8238.2009.00473.x.

Homburg, K, Homburg, N, Schaefer, F, Schuldt, A, Assmann, T. 2014. carabids.org—A dynamic online database of ground beetle species traits (Coleoptera, Carabidae). *Insect Conservation and Diversity* **7**: 195–205. DOI: http://dx.doi.org/10.1111/icad.12045.

Hornung, E, Vilisics, F, Sólymos, P. 2008. Low alpha and high beta diversity in terrestrial isopod assemblages in the Transdanubian region of Hungary, in Zimmer, M, Charfi-Cheikrouha, F, Taiti, S eds., *Proceedings of the International Symposium of Terrestrial Isopod Biology, ISTIB-7*. Aachen, Germany: Shaker Verlag.

Hornung, E, Vilisics, F, Sólymos, P. 2009. Ászkarák együttesek (Crustacea, Isopoda, Oniscidea) felhasználhatósága élőhelyek minősítésében. *Természetvédelmi Közlemények* **15**: 381–395.

Høye, TT. 2020. Arthropods and climate change—Arctic challenges and opportunities. *Current Opinion in Insect Science* **41**: 40–45. DOI: http://dx.doi.org/10.1016/j.cois.2020.06.002.

Jamieson, MA, Trowbridge, AM, Raffa, KF, Lindroth, RL. 2012. Consequences of climate warming and altered precipitation patterns for plant-insect and multitrophic interactions. *Plant Physiology* **160**: 1719–1727. DOI: http://dx.doi.org/10.1104/pp.112.206524.

Joly, FX, Weibel, AK, Coulis, M, Throop, HL. 2019. Rainfall frequency, not quantity, controls isopod effect on litter decomposition. *Soil Biology and Biochemistry* **135**: 154–162. DOI: http://dx.doi.org/10.1016/j.soilbio.2019.05.003.

Kemencei, Z, Farkas, R, Páll-Gergely, B, Vilisics, F, Nagy, A, Hornung, E, Sólymos, P. 2014. Microhabitat associations of land snails in forested dolinas: Implications for coarse filter conservation. *Community Ecology* **15**: 180–186. DOI: http://dx.doi.org/10.1556/ComEc.15.2014.2.6.

Keppel, G, Mokany, K, Wardell-Johnson, GW, Phillips, BL, Welbergen, JA, Reside, AE. 2015. The capacity of refugia for conservation planning under climate change. *Frontiers in Ecology and the Environment* **13**: 106–112. DOI: http://dx.doi.org/10.1890/140055.

Keppel, G, Ottaviani, G, Harrison, S, Wardell-Johnson, GW, Marcantonio, M, Mucina, L. 2018. Towards an eco-evolutionary understanding of endemism hotspots and refugia. *Annals of Botany* **122**: 927–934. DOI: http://dx.doi.org/10.1093/aob/mcy173.

Keppel, G, Van Niel, KP, Wardell-Johnson, GW, Yates, CJ, Byrne, M, Mucina, L, Schut, AGT, Hopper, SD, Franklin, SE. 2012. Refugia: Identifying and understanding safe havens for biodiversity under climate change. *Global Ecology and Biogeography* **21**: 393–404. DOI: http://dx.doi.org/10.1111/j.1466-8238.2011.00686.x.

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. DOI: http://dx.doi.org/10.1371/journal.pone.0122070.

Koch, K. 1989. *Die Käfer Mitteleuropas. Ökologie. Band 1.* Krefeld, Germany: Goecke & Evers Verlag.

Lavorel, S, Grigulis, K, McIntyre, S, Williams, NSG, Garden, D, Dorrough, J, Berman, S, Quétier, F, Thébault, A, Bonis, A. 2008. Assessing functional diversity in the field—Methodology matters! *Functional Ecology* **22**: 134–147. DOI: http://dx.doi.org/10.1111/j.1365-2435.2007.01339.x.

Lehmitz, R, Haase, H, Otte, V, Russell, D. 2020. Bioindication in peatlands by means of multi-taxa indicators (Oribatida, Araneae, Carabidae, Vegetation). *Ecological Indicators* **109**: 105837. DOI: http://dx.doi.org/10.1016/j.ecolind.2019.105837.

Lemoine, NP, Shantz, AA. 2016. Increased temperature causes protein limitation by reducing the efficiency of nitrogen digestion in the ectothermic herbivore *Spodoptera exigua*. *Physiologica Entomology* **41**: 143–151. DOI: http://dx.doi.org/10.1111/phen.12138.

Lenoir, J, Hattab, T, Pierre, G. 2017. Climatic microrefugia under anthropogenic climate change:

Implications for species redistribution. *Ecography* **40**: 253–266. DOI: http://dx.doi.org/10.1111/ecog.02788.

**Lewis, JJ**, **Milne, MA**, **Stephen, CDR**, **Dourson, DC**. 2020. Karst sinkholes as foci of biodiversity in the Hoosier National Forest. *Journal of Cave and Karst Studies* **82**: 276–292. DOI: http://dx.doi.org/10.4311/2020LSC0103.

**Lingbeek, BJ**, **Higgins, CL**, **Muir, JP**, **Kattes, DH**, **Schwertner, T**. 2017. Arthropod diversity and assemblage structure response to deforestation and desertification in the Sahel of western Senegal. *Global Ecology and Conservation* **11**: 165–176. DOI: http://dx.doi.org/10.1016/j.gecco.2017.06.004.

**Lister, BC**, **Garcia, A**. 2018. Climate-driven declines in arthropod abundance restructure a rainforest food web. *Proceedings of the National Academy of Sciences of the United States of America* **115**: 10397–10406. DOI: http://dx.doi.org/10.1073/pnas.1722477115.

**Lohse, GA**. 1974. *Staphylinidae II (Hypocyphtinae und Aleocharinae) Pselaphidae, Band 5. Die Käfer Mitteleuropas.* Krefeld, Germany: Goecke & Evers Verlag.

**Lott, DA**. 2009. *The Staphylinidae (rove beetles) of Britain and Ireland. Part 5: Scaphidiinae, Piestinae, Oxytelinae. Handbooks for the identification of British insects 12: Part 5.* St Albans, UK: Royal Entomological Society.

**Lott, DA**, **Anderson, R**. 2011. *The Staphylinidae (rove beetles) of Britain and Ireland. Parts 7 & 8: Oxyporinae, Steninae, Euaesthetinae, Pseudopsinae, Paederinae, Staphylininae. Handbooks for the Identification of British Insects 12: Part 7.* St. Albans, UK: Royal Entomological Society.

**Lutska, M**, **Sirenko, A**. 2020. Ecological features of groups of rove beetles (Coleoptera: Staphylinidae) in beech forest ecosystems of the lower forest belt of the Gorgan Massif. *Scientific Journal—ScienceRise: Biological Science* **3**: 29–34. DOI: http://dx.doi.org/10.15587/2519-8025.2020.214189.

**Magura, T**. 2002. Comparison of the carabid assemblages of an oak-hornbeam forest and dolines (Coleoptera: Carabidae). *Acta Biologica Debrecina* **24**: 73–79.

**Maleque, MA**, **Ishii, HT**, **Maeto, K**. 2006. The use of arthropods as indicators of ecosystem integrity in forest management. *Journal of Forestry* **104**: 113–117. DOI: http://dx.doi.org/10.1093/jof/104.3.113.

**Mammola, S**, **Goodacre, SL**, **Isaia, M**. 2018. Climate change may drive cave spiders to extinction. *Ecography* **41**: 233–243. DOI: http://dx.doi.org/10.1111/ecog.02902.

**Marcin, M**, **Raschmanová, N**, **Miklisová, D**, **Kováč, Ľ**. 2021. Microclimate and habitat heterogeneity as important drivers of soil Collembola in a karst collapse doline in the temperate zone. *Invertebrate Biology* **140**: e12315. DOI: http://dx.doi.org/10.1093/jof/104.3.113.

**Marcisz, K**, **Colombaroli, D**, **Jassey, VEJ**, **Tinner, W**, **Kołaczek, P**, **Gałka M**, **Karpińska-Kołaczek, M**, **Słowiński, M**, **Lamentowicz, M**. 2016. A novel testate amoebae trait-based approach to infer environmental disturbance in *Sphagnum* peatlands. *Scientific Reports* **6**: 33907. DOI: http://dx.doi.org/10.1038/srep33907.

**McCluney, K**, **Sabo, JL**. 2009. Water availability directly determines per capita consumption at two trophic levels. *Ecology* **90**: 1463–1469. DOI: http://dx.doi.org/10.1890/08-1626.1.

**McLaughlin, BC**, **Ackerly, DD**, **Klos, PZ**, **Natali, J**, **Dawson TE**, **Thompson, SE**. 2017. Hydrologic refugia, plants, and climate change. *Global Change Biology* **23**: 2941–2961. DOI: http://dx.doi.org/10.1111/gcb.13629.

**Millar, CI**, **Westfall, RD**, **Evenden, A**, **Holmquist, JG**, **Schmidt-Gengenbach, J**, **Franklin, RS**, **Nachlingere, J**, **Delanya, DL**. 2014. Potential climatic refugia in semi-arid, temperate mountains: Plant and arthropod assemblages associated with rock glaciers, talus slopes, and their forefield wetlands, Sierra Nevada, California, USA. *Quaternary International* **387**: 106–121. DOI: http://dx.doi.org/10.1016/j.quaint.2013.11.003.

**Murphy, SM**, **Richards, LA**, **Wimp, GM**. 2020. Editorial: Arthropod interactions and responses to disturbance in a changing world. *Frontiers in Ecology and Evolution* **8**: 93. DOI: http://dx.doi.org/10.3389/fevo.2020.00093.

**Nagy, A**, **Sólymos, P**. 2002. Relationship between microclimate and Orthoptera assemblages in different exposures of a dolina. *Articulata* **17**: 73–84.

**Nentwig, W**, **Blick, T**, **Bosmans, R**, **Gloor, D**, **Hänggi, A**, **Kropf, C**. 2020. Spiders of Europe. Available at https://www.araneae.nmbe.ch. Accessed 30 August 2020.

**Nerantzaki, SD**, **Nikolaidis, NP**. 2020. The response of three Mediterranean karst springs to drought and the impact of climate change. *Journal of Hydrology* **591**: 125296. https://doi.org/10.1016/j.jhydrol.2020.125296.

**Nitzu, E**, **Olenici, N**. 2009. The first study on the beetle fauna in the Giumalău spruce primeval forest (Eastern Carpathians, Romania), mainly based on a quantitative analysis of terrestrial and saproxylic species, in Buse, J, Alexander, KNA, Ranius, T, Assmann, T eds., *Saproxylic beetles—Their role and diversity in European woodland and tree habitats. Proceedings of the 5th Symposium and Workshop on the Conservation of Saproxylic Beetles.* Sofia-Moscow-Lueneburg: Pensoft.

**Öder, V**, **Petritan, AM**, **Schellenberg, J**, **Bergmeier, E**, **Walentowski, H**. 2021. Patterns and drivers of deadwood quantity and variation in mid-latitude deciduous forests. *Forest Ecology and Management* **487**: 118977. DOI: http://dx.doi.org/10.1016/j.foreco.2021.118977.

**Oettel, J**, **Lapin, K**, **Kindermann, G**, **Steiner, H**, **Schweinzer, KM**, **Frank, G**, **Essl, F**. 2020. Patterns and drivers of deadwood volume and composition in different forest types of the Austrian natural forest reserves. *Forest Ecology and Management* **463**:

118016. DOI: http://dx.doi.org/10.1016/j.foreco.2020.118016.

Oksanen, J, Blanchet, FG, Friendly, M, Kindt, R, Legendre, P, McGlinn, D, Minchin, PR. 2019. Vegan: Community ecology package. Available at https://cran.r-project.org/web/packages/vegan/index.html. Accessed 19 June 2021.

Parmesan, C, Ryrholm, N, Stefanescu, C, Hill, JK, Thomas, CD, Descimon, H, Huntley, B, Kaila, L, Kullberg, J, Tammaru, T, Tennent, WJ, Thomas, JA, Warren, M. 1999. Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature* **399**: 579–583. DOI: http://dx.doi.org/10.1038/21181.

Pavlek, M, Mammola, S. 2021. Niche-based processes explaining the distributions of closely related subterranean spiders. *Journal of Biogeography* **48**: 118–133. DOI: http://dx.doi.org/10.1111/jbi.13987.

Pu, G, Lv, Y, Xu, G, Zeng, D, Huang, Y. 2017. Research progress on karst tiankeng ecosystems. *The Botanical Review* **83**: 5–37. DOI: http://dx.doi.org/10.1007/s12229-017-9179-0.

Rall, BC, Brose, U, Hartvig, M, Kalinkat, G, Schwarzmüller, F, Vucic-Pestic, O, Petchey, OL. 2012. Universal temperature and body-mass scaling of feeding rates. *Philosophical Transactions of the Royal Society B: Biological Sciences* **367**: 2923–2934. DOI: http://dx.doi.org/10.1098/rstb.2012.0242.

Raschmanová, N, Miklisová, D, Kováč, Ľ. 2018. A unique small-scale microclimatic gradient in a temperate karst harbours exceptionally high diversity of soil Collembola. *International Journal of Speleology* **47**: 247–262. DOI: http://dx.doi.org/10.5038/1827-806X.47.2.2194.

Raschmanová, N, Žurovcová, M, Kováč, Ľ, Paučulová, L, Šustr, V, Jarošová, A, Chundelová, D. 2017. The cold-adapted population of *Folsomia manolachei* (Hexapoda, Collembola) from a glaciated karst doline of Central Europe: Evidence for a cryptic species? *Journal of Zoological Systematics and Evolutionary Research* **55**: 19–28. DOI: http://dx.doi.org/10.1111/jzs.12150.

R Core Team. 2019. *R: A language and environment for statistical computing.* Vienna, Austria: R Foundation for Statistical Computing. Available at https://www.r-project.org/. Accessed 19 June 2021.

Rendoš, M, Raschmanová, N, Kováč, Ľ, Miklosivá, D, Mock, A, Luptáčik, P. 2016. Organic carbon content and temperature as substantial factors affecting diversity and vertical distribution of Collembola on forested scree slopes. *European Journal of Soil Biology* **75**: 180–187. DOI: http://dx.doi.org/10.1016/j.ejsobi.2016.06.001.

Ricotta, C, Moretti, M. 2011. CWM and Rao's quadratic diversity: A unified framework for functional ecology. *Oecologia* **167**: 181–188. DOI: http://dx.doi.org/10.1007/s00442-011-1965-5.

Roberts, DW. 2019. Labdsv: Ordination and multivariate analysis for ecology. Available at http://cran.r-

project.org/web/packages/labdsv. Accessed 21 June 2021.

Rojas, IM, Jennings, MK, Conlisk, E, Syphard, AD, Mikesell, J, Kinoshita, AM, West, K, Stow, D, Storey, E, De Guzman, ME, Foote, D, Warneke, A, Pairis, A, Ryan, S, Flint, LE, Flint, AL, Lewison, RL. 2021. A landscape-scale framework to identify refugia from multiple stressors. *Conservation Biology.* DOI: http://dx.doi.org/10.1111/cobi.13834.

Rosenblatt, AE, Schmitz, OJ. 2016. Climate change, nutrition, and bottom-up and top-down food web processes. *Trends in Ecology & Evolution* **31**: 965–975. DOI: http://dx.doi.org/10.1016/j.tree.2016.09.009.

Růžička, V, Mlejnek, R, Juřičková, L, Tajovský, K, Šmilauer, P, Zajíček, P. 2016. Invertebrates of the Macocha Abyss (Moravian Karst, Czech Republic). *Acta Carsologica* **45**: 71–84. DOI: http://dx.doi.org/10.3986/ac.v45i1.896.

Schmalfuss, H. 2003. World catalog of terrestrial isopods (Isopoda: Oniscidea). Stuttgarter Beiträge zur Naturkunde, Serie A, Nr. 654. Available at https://isopods.nhm.org/pdfs/27577/27577.pdf.

Schmalholz, M, Hylander, K. 2011. Microtopography creates small-scale refugia for boreal forest floor bryophytes during clear-cut logging. *Ecography* **34**: 637–648. DOI: http://dx.doi.org/10.1111/j.1600-0587.2010.06652.x.

Schmitter-Soto, J, Comín, F, Escobar-Briones, E., Herrera-Silveira, J, Alcocer, J, Suárez-Morales, E, Elías-Gutiérrez, M, Díaz-Arce, V, Marín, LE, Steinich, B. 2002. Hydrogeochemical and biological characteristics of cenotes in the Yucatan Peninsula (SE Mexico). *Hydrobiologia* **467**: 215–228. https://doi.org/10.1023/A:1014923217206.

Seifert, B. 2002. How to distinguish most similar insect species—Improving the stereomicroscopic and mathematical evaluation of external characters by example of ants. *Journal of Applied Entomology* **126**: 445–454. DOI: http://dx.doi.org/10.1046/j.1439-0418.2002.00693.x.

Seifert, B. 2018. *The ants of Central and North Europe.* Tauer, Germany: Lutra Verlags- und Vertriebsgesellschaft.

Sentis, A, Gémard, C, Jaugeon, B, Boukal, DS. 2017. Predator diversity and environmental change modify the strengths of trophic and nontrophic interactions. *Global Change Biology* **23**: 2629–2640. DOI: http://dx.doi.org/10.1111/gcb.13560.

Stewart, JR, Lister, AM, Barnes, I, Dalén, L. 2010. Refugia revisited: Individualistic responses of species in space and time. *Proceedings of the Royal Society B* **277**: 661–671. DOI: http://dx.doi.org/10.1098/rspb.2009.1272.

Stralberg, D, Arseneault, D, Baltzer, JL, Barber, QE, Bayne, EM, Boulanger, Y, Brown, CD, Cooke, HA, Devito, K, Edwards, J, Estevo, CA, Flynn, N, Frelich, LE, Hogg, EH, Johnston, M, Logan, T, Matsuoka, SM, Moore, P, Morelli, TL, Morissette, JJ, Nelson, EA, Nenzén, H, Nielsen, SE, Parisien, MA, Pedlar, JH, Price, DT, Schmiegelow, FKA, Slattery,

SM, **Sonnentag, O**, **Thompson, DK**, **Whitman, E**. 2020. Climate-change refugia in boreal North America: What, where, and for how long? *Frontiers in Ecology and the Environment* **18**: 261–270. DOI: http://dx.doi.org/10.1002/fee.2188.

**Sutton, SL**, **Hassall, M**, **Willows, R**, **Davis, RC**, **Grundy, A**, **Sunderland, KD**. 1984. Life histories of terrestrial isopods: A study of intra- and interspecific variation. *Symposia of the Zoological Society of London* **53**: 269–294.

**Torma, A**, **Császár, P**, **Bozsób, M**, **Deák, B**, **Valkó, O**, **Kiss, O.**, **Gallé, R**. 2019. Species and functional diversity of arthropod assemblages (Araneae, Carabidae, Heteroptera and Orthoptera) in grazed and mown salt grasslands. *Agriculture, Ecosystems & Environment* **273**: 70–79. DOI: http://dx.doi.org/10.1016/j.agee.2018.12.004.

**Valkó, O**, **Deák, B**, **Magura, T**, **Török, P**, **Kelemen, A**, **Tóth, K**, **Horváth, R**, **Nagy, DD**, **Debnár, Z**, **Zsigrai, G**, **Kapocsi, I**, **Tóthmérész, B**. 2016. Supporting biodiversity by prescribed burning in grasslands—A multi-taxa approach. *Science of the Total Environment* **572**: 1377–1384. DOI: http://dx.doi.org/10.1016/j.scitotenv.2016.01.184.

**Veress, M**. 2019. The KARREN and KARREN formation of bare slopes. *Earth-Science Reviews* **188**: 272–290. DOI: http://dx.doi.org/10.1016/j.earscirev.2018.11.006.

**Verkerk, PJ**, **Lindner, M**, **Zanchi, G**, **Zudin**, **S**. 2011. Assessing impacts of intensified biomass removal on deadwood in European forests. *Ecological Indicators* **11**: 27–35. DOI: http://dx.doi.org/10.1016/j.ecolind.2009.04.004.

**Vilisics, F**, **Sólymos, P**, **Nagy, A**, **Farkas, R**, **Kemencei, Z**, **Hornung, E**. 2011. Small scale gradient effects on isopods (Crustacea: Oniscidea) in karstic sinkholes. *Biologia* **66**: 499–505. DOI: http://dx.doi.org/10.2478/s11756-011-0042-1.

**Walther, GR**. 2010. Community and ecosystem responses to recent climate change. *Philosophical Transactions of the Royal Society B: Biological Sciences* **365**: 2019–2024. DOI: http://dx.doi.org/10.1098/rstb.2010.0021.

**White, WB**, **Culver, DC**, **Herman, JS**, **Kane, TC**, **Mylroie, JE**. 1995. Karst lands: The dissolution of carbonate rock produces unique landscapes and poses significant hydrological and environmental concerns. *American Scientist* **83**: 450–459.

**Whiteman, CD**, **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. *Journal of Applied Meteorology* **43**: 1224–1236. DOI: http://dx.doi.org/10.1175/1520-0450(2004)043<1224:MTDTRA>2.0.CO;2.

**Yang, LH**, **Gratton, C**. 2014. Insects as drivers of ecosystem processes. *Current Opinion in Insect Science* **2**: 26–32. DOI: http://dx.doi.org/10.1016/j.cois.2014.06.004.

**Zhou, Q**, **Lou, Y**, **Zhou, X**, **Cai, M**, **Zhao C**. 2018. Response of vegetation to water balance conditions at different time scales across the karst area of southwestern China—A remote sensing approach. *Science of the Total Environment* **645**: 460–470. DOI: http://dx.doi.org/10.1016/j.scitotenv.2018.07.148.