Ph.D. thesis

The effect of habitat heterogeneity and human disturbance on ant and plant assemblages of karst dolines

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Szeged
2021

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1 Introduction

1.1 Karst regions in Hungary

Karst areas constitute about 20% of the earth's terrestrial surface (White et al., 1995). Karst topography has been largely shaped by the dissolving action of water on carbonate bedrock made up of either limestone, dolomite, or marble. Geomorphological process which occurred over many thousand years resulted into unique surface and subsurface features such as enclosed depressions (sinkholes, dolines and tiankengs); caves and caverns; underground drainage systems (streams and springs); pavement; pinnacle; and towers (haystacks).

In Hungary, karst areas cover 1.45% of the total land area or around 1,350 square kilometers (km^2) with geological ages ranging from the Early Cretaceous to the Pleistocene (Jakucs, 1977). Karst regions in Hungary are made up of Late Triassic limestone and dolomite which can be grouped into two major types, Transdanubian and Aggletek types (Jakucs, 1977; Bárány-Kevei, 1998). The Transdanubian-type karst arises from the movement of the plate tectonics, while the Aggletek-type karst is more of less disturbed tectonically and characterized by typical karst features. Typical karst features in the Aggletek type include dolines, sinkholes, karren fields, caves, and springs. These karst surface and subsurface features can be found in some parts of Bakony, Vértes, Buda, Mecsek and Villány Mountains which are nature conservation areas, while most of the karst areas are in Aggletek and Bükk Mountains which are national parks (Bárány-Kevei, 2005) (**Fig. 1**). These Hungarian karst areas are highly protected landscapes.

Throughout the century, Hungarian karst areas have been extensively used for agriculture (Bárány-Kevei, 2003). Therefore, it is not spared of the consequences of human-induced disturbances which made these landscapes highly vulnerable. Quarrying, mining, agriculture, forestry, tourism, urban land use and water use usually are the prevailing anthropogenic pressures threatening these karst environments (Bárány-Kevei, 1998). There are no doubt karsts are environmentally sensitive systems. Nowadays, karst ecosystems are undergoing degradation due to these anthropogenic activities (Parise and Pascali, 2003). These human disturbances comprise environmental pressures leading to polluted aquifers, destroyed caves and dolines, denuded landscapes and declining biodiversity which will further lead to the extinction of rare species (Van Beynen et al., 2012).

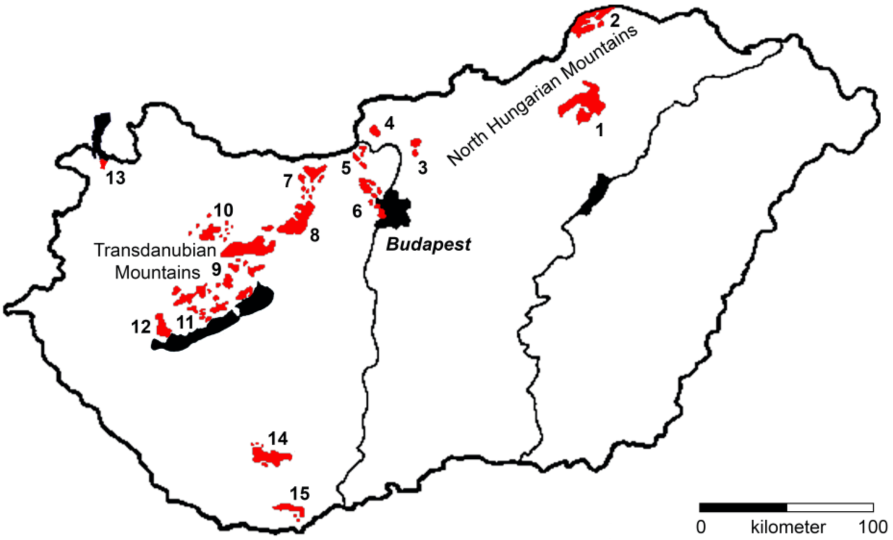

Figure 1. Different karst regions in Hungary. (1) Bükk Mts., (2) Aggtelek Mts., (3) Region of Western Cserhát Mts., (4) Szokolya Basin and Törökmező in the Börzsöny Mts., (5) Pilis Mts., (6) Buda Mts., (7) Gerecse Mts., (8) Vértes Mts., (9–10) Bakony Mts., (11) Balaton Upland, (12) Keszthely Mts., (13) Fertőmellék Hills, (14) Mecsek Mts., (15) Villány Mts. (adapted from Jakucs, 1977).

Karst areas are highly valuable ecosystems as they provide several services. Karsts offer vital ecosystem services such as drinking water provision, soil formation, habitat and biodiversity function, timber production, climate regulation, recreation, and aesthetic value (Kiss et al., 2011). Karsts served as water-reservoirs, whereas springs often provide water for some parts of remote urban areas. These karst landscapes are crucial local biodiversity hotspots comprising of various endangered species of fauna and flora. More importantly, several studies have shown that karst areas in Europe have supported the population of climate relicts during the past Quarternary climate oscillations (Reisch, 2008; Erdős et al., 2011; Kováč et al., 2016; Redžić et al., 2011). Furthermore, karstic dolines are considered to form a significant link between surface and underground ecosystems and play a key role in the geological and ecological processes of karst surfaces (Gams, 2000).

Among these karst landscapes, one of their characteristic features are enclosed depressions such as dolines, sinkholes or tiankengs. These karstic depressions were formed due to several factors such as climate, elevation, slope aspect, lithology, and tectonics (Gams, 2000). Dolines vary in forms and sizes and considered as the most common diagnostic of these karst landscapes (Ford and Williams, 2007). Common types of categories of dolines based on genesis are solution and collapse dolines. Solution dolines arise gradually through dissolution of the bedrock (Sauro, 2003), while collapse dolines originate from catastrophic phenomena such as collapse of cave roofs (Šušteršič, 2000).

Dolines in Hungary can be found mostly in Aggtelek, Bükk and western Mecsek Mountains. Varying sizes of funnel-shaped solution dolines small to large mostly occur in these areas. Smallest solution dolines have a diameter of 5–10 m and depth of 1–3 m, while the largest ones range from 100–300 m in diameter and 20–40 m in depth (Jakucs, 1977).

1.2 Habitat and environmental heterogeneity in karst dolines

The potential of different landscapes to maintain high habitat diversity largely depends on the bedrock type and its physical and chemical properties. For instance, dissolution processes on limestone surfaces contribute to the formation of karst landscapes constituting one of the topographically most complex systems (White et al., 1995; Culver, 2000; Bátori et al., 2020). These landscapes such as caves, limestone pavements, valleys, and enclosed depressions (dolines, sinkholes or tiankengs) support several habitats where species composition and diversity vary with environmental heterogeneity (Whiteman et al., 2004; Bátori et al., 2009; Mammola et al., 2019). Botanists have long recognized the importance of these habitats as ideal natural laboratories which serve as areas for study of multiple environmental gradients, thermal stability and their effects on plant species composition and vegetation patterns.

Environmental heterogeneity is often positively related to biodiversity (Burnett et al., 1998; Stein et al., 2014; Keppel et al., 2016; Fitzsimons and Michael, 2017). Topographical and biological structures can create microhabitats with unique microclimates (Ashcroft et al., 2012; Keppel et al., 2017a; Meineri and Hylander, 2017) on which species may depend for their survival (Schmalholz and Hylander, 2011; Keppel et al., 2017b). These microhabitats may be warmer, drier, cooler and/or moister than the prevailing regional climate (Scherrer and Körner, 2010; Ashcroft et al., 2012). As such, they create a mosaic of microclimates that can allow species to survive changes in their environment by migrating short distances between these microhabitats (Scherrer and Körner, 2010; Gaüzère et al., 2017). These fine-scale mosaics improve species' chances to persist in a landscape, which is contradictory to the results of large-scale (resolutions ≥1 km^2) species distribution models (Franklin et al., 2013; Keppel et al., 2017b; Maclean et al., 2017; Meineri and Hylander, 2017). In relation to this, attempts to regionally model climatic data at 50–100 m resolution has been made (Maclean et al., 2017; Meineri and Hylander, 2017).

Moreover, topographic complexity can create habitats that remain environmentally more stable through time, even as regional climate changes. Such habitats may therefore facilitate the persistence of biodiversity known as refugia (Taberlet and Cheddadi, 2002; Keppel et al., 2012a; Tapper et al., 2014a). Refugia are important for conservation planning and may offer the only chance of in situ survival for many species (Keppel et al., 2012b; Tapper et al., 2014b; Morelli et al., 2016).

1.3 Karst dolines as potential microrefugia and their biodiversity

Small areas that provide suitable pockets of relatively stable microclimate are called microrefugia (Rull, 2009; Dobrowski, 2010; Keppel et al., 2015a). Good examples of these are local depressions (dolines, sinkholes or tiankengs) and valleys in karst areas possessing high topographic convergence (Telbisz et al., 2016; Hoferka et al., 2018; Šegina et al., 2018). Dolines and surrounding habitats retain cooler microclimates when regional climates warm through drainage of cold air currents at night (Whiteman et al., 2004; Daly et al., 2010; Novick et al., 2016). Specifically, their bottoms and north-facing slopes maintain cooler, moister, and more humid environments than the surrounding plateaus (Bátori et al., 2019). These microrefugia, where locally favorable environments are sustained, enable species to survive during regional environmental changes (Keppel et al., 2012a; Gentili et al., 2015). Although microrefugia are generally taxon-specific (Stewart et al., 2010), those that maintain the populations of various taxa are particularly important from a biogeographic and conservation point of view. There has recently been substantial progress in determining the location of such areas, demonstrating the importance of environmental heterogeneity (Ashcroft, 2010; Ashcroft et al., 2012; Dobrowski, 2010; de Aguiar-Campos, 2020) and interactions between geomorphology, climatic change, and the ecological tolerances of species (Bátori et al., 2017; Gentili et al., 2020; Michalak et al., 2020). Recent studies also emphasize the need to integrate functional trait analyses into the study of refugia, highlighting that more data on functional diversity from these areas are needed (Keppel et al., 2018; Ottaviani et al., 2020).

Many studies have shown that dolines may provide microhabitats for unique species that are rare or absent from the surrounding landscape (Beck von Mannagetta, 1906; Horvat, 1953; Kobal et al., 2015). Doline habitats may serve as refuges (for decades) or refugia (for millennia) for vulnerable taxa, such as endemic, montane, and relict species (Vilisics et al., 2011; Bátori et al., 2012; Kemencei et al., 2014; Raschmanová et al., 2015). Many of these species can be under threat because of global warming (Bátori et al., 2019). The occurrence of cold-adapted plants (e.g., high montane and glacial relict species) within certain microhabitats of dolines – such as in north-facing slopes and bottoms – is a primary indicator of the presence of current warm-stage microrefugia.

The complex topography of dolines may play a crucial role in maintaining world's biodiversity providing innumerable ecological niches for various plants and wildlife (Culver, 2000; Clements et al., 2008; Öztürk and Savran 2020). These dolines harbor unique taxa (e.g., endemic, and relict species) (Sánchez et al., 2002; Surina and Surina, 2010; Bátori et al., 2014a, 2014b), and are characterized by high plant, genetic and habitat diversity (Favretto et al., 1985; Özkan et al., 2010; Kobal et al., 2015; Su et al., 2017). Cool-adapted species from various phyla (e.g., Bryophyta, Tracheophyta, Mollusca, Arthropoda) have been documented from dolines (Beck v. Mannagetta, 1906; Pericin and Hürlimann, 2001; Kemencei et al., 2014; Raschmanova et al., 2015). Dolines may also provide key habitats for warm-adapted species (Růžička et al., 2016).

Although recent investigations have indicated that dolines may provide safe havens for various functional groups of animals (Vilisics et al., 2011; Kemencei et al., 2014; Raschmanová et al., 2015, 2018; Růžička et al., 2016; Battisti et al., 2017; Bátori et al., 2019), data on many other taxa is scarce or completely lacking.

1.4 Ants as bio-indicators

Ants are highly sensitive to changes in resources, moisture, and temperature (Sanders, 2002; Dolek et al., 2009), which makes them good indicators of environmental changes Andersen, 1997; Arnan et al., 2014; Gallé, 2017), ecosystem health and functioning (Folgarait, 1998; Ottonetti et al., 2006; Eldridge et al., 2020). These insects inhabit several niches and play essential role in many ecosystems as predators, defoliators, seed, pollen and nectar collectors, and decomposers (Fowler et al., 1991; Silva and Brandão, 1999, 2010; Brandão et al., 2012).

Generally, the species richness of ants is positively associated with habitat diversity cf. Andersen, 1986; Báldi, 2008; Hortal et al., 2009, Pacheco and Vasconcelos, 2012), which may also affect the functional diversity of their assemblages (Gallé, 2017; Heinze, 2017). Topographically complex areas may contain a higher diversity of microhabitats providing suitable nesting sites and a higher amount of exploitable resources for different functional groups of ants (Ribas et al., 2003, Fayle et al., 2013). Ant assemblages are also strongly affected by variations in vegetation cover and structure. For instance, the presence of grassland patches in forested landscapes may support the maintenance of high ant diversity and facilitates the persistence of several species that cannot survive in shady habitats (Dolek et al., 2009). In contrast, homogenous habitats such as European beech (*F. sylvatica*) forests with low resource availability create unfavorable conditions for many ants (Dolek et al., 2009; Wiezik et al., 2015). Results from the abovementioned studies suggest that environmental heterogeneity and related vegetation patterns may influence the composition of ant assemblages in current and potential microrefugia by filtering their functional traits, resulting in a relationship between the functional diversity of assemblages and small-scale environmental conditions (cf. Guilherme et al., 2019).

1.5 Similarities between ants and plants

Ants and plants share various similarities (Brian, 1965). Similar attributes shared by both groups such as their modularity, fixedness and foraging strategies, and interference competition arise to significant implications when it comes to community organization (Andersen, 1991, 1995). For example, in terms of their modularity, both ants and plants usually ‘nest’ in or on the ground and use their modules (e.g., plant roots and ant workers) to forage in the surrounding habitat (Andersen, 1991; López et al.,1994). Foraging strategies of polydomous ant colonies (i.e., colonies occupying multiple nesting sites) have been known to be highly analogous to clonal plants' strategy in acquiring resources especially for the case of Argentine ant colonies (Holway and Case, 2000). In addition, due to the relatively fixed location of ant colonies and plants, competition in both groups is usually confined in well-defined zones.

Similarly, parallels also exist in their functional roles in each community (e.g., subordinate, specialist, and cryptic species). Moreover, ant foundresses (i.e., colony-founding queens) can be considered comparable to dispersing plant seeds in which having larger size for both species can be advantageous in coping under stressful or disturbed conditions (Andersen, 1991; Johnson, 1998).

1.6 Anthropogenic disturbance of karst dolines

Dolines have been cultivated extensively, providing sites for various traditional activities such as arable farming, gardening, pasturing and water extraction (Breg, 2007). The degradation of dolines is among the most pressing issues in karst environments worldwide (Parise and Pascali, 2003; De Waele, 2009; North et al., 2009; Kovačič and Ravbar, 2013). Serious degradation due to urbanization and disposal of a variety of waste materials have been widely documented in the dolines of Central and Southern Europe (Kovačič and Ravbar, 2013; Breg Valjavec et al., 2018a, 2018b). Human-induced activities, one of which is intensive logging, may compromise the capacity of dolines to act as safe havens for species during future climate oscillations (Kiss et al., 2020), and, as a result, may also reduce the naturalness of their habitats. In Hungary through the years, deforestation and grazing drastically affected doline habitats (Bárány-Kevei, 1998). Among all the karst features, dolines are the most common and diagnostic (Sauro, 2003; Ford and Williams, 2007; Li et al., 2007). These local depressions are highly valuable and sensitive systems, thus the need to evaluate the effects of different disturbances on their biota is crucial for improving current management and developing appropriate conservation strategies.

It has been recognized that plants can be used as bio-indicators and are able to indicate the naturalness of their habitat (Ellenberg, 1950). The approach of naturalness indicator values is like that of the original Ellenberg-type indicator values and has been used successfully to study disturbance (Erdős et al., 2017a, b). Some species indicate disturbed sites, while others prefer less disturbed or natural habitats. Usually, the presence of many endemics, habitat specialists and endangered species within a habitat may indicate higher naturalness leading to higher conservation value of the area (Angermeier and Karr, 1994; Trombulak et al., 2004). Recent studies have shed light on the role of climate, geometry, slope aspect and vegetation cover on the distribution of different taxa in dolines (Bátori et al., 2012, 2014a, 2014b, 2017). However, data on the effects of human activity on the naturalness of doline vegetation is sparse.

2 Aims

The general aim of the doctoral study was to assess how habitat heterogeneity and human disturbance influence ant and plant assemblages in two Hungarian karst areas (**Fig. 2**). Specifically, the following questions were addressed in the study.

1. How doline microhabitats (south-facing slopes, north-facing slopes, bottoms, and plateau) determine the species distribution patterns of ant and plant assemblages? (Study 1)
2. How microhabitat heterogeneity and vegetation structure in dolines influence the occurrence of specific functional groups and traits of ant assemblages? (Study 2)
3. How different types of human activities, i.e., human-mediated invasion of reed grass (*Calamagrostis epigeios*) and intensive forestry management affect the naturalness of doline vegetation? (Study 3)

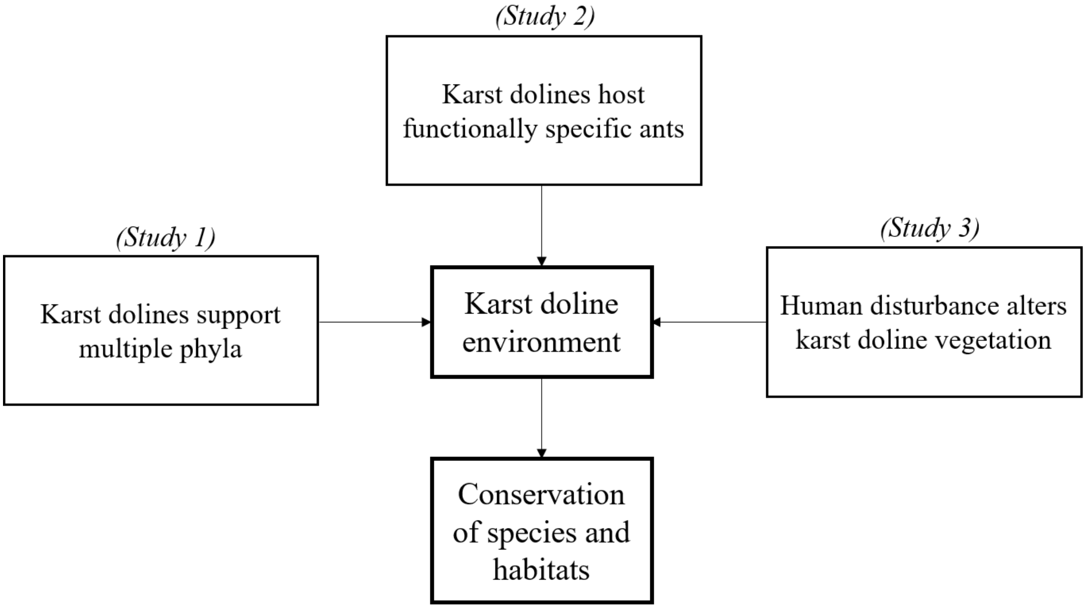

Figure 2. General framework of the doctoral study.

In connection with these questions, it was hypothesized that (1) the north-facing slopes and bottoms of dolines harbor ant and plant species adapted to cooler and/or moister conditions, the south-facing slopes harbor species adapted to warmer and/or drier conditions, while the plateau harbor species adapted to intermediate temperature and/or moisture conditions, (2) microhabitat heterogeneity within dolines has a positive, while the increasing cover of resource-poor environments, e.g. European beech (*Fagus sylvatica*) forests has a negative effect on the functional diversity of ant assemblages, and (3) anthropogenic disturbance negatively affect the naturalness of doline vegetation.

3 Materials and Methods

3.1 Study area

3.1.1 Study 1 and Study 2

Study 1 and Study 2 were conducted in the karst plateau of the Bükk Mountains, Northern Hungary (48°04′31″N, 20°29′57″E) with an altitude between 780 m and 950 m (**Fig. 3**). This mountain range is believed to be an important refugial area in Hungary which supports relict plant populations from both warmer (e.g., *Clinopodium thymifolium*, *Cotinus coggygria* and *Ferula sadleriana*) and cooler (e.g., *Aconitum variegatum*, *Bupleurum longifolium* and *Dracocephalum ruyschiana*) periods (Vojtkó, 2001; Lazarević et al., 2009).

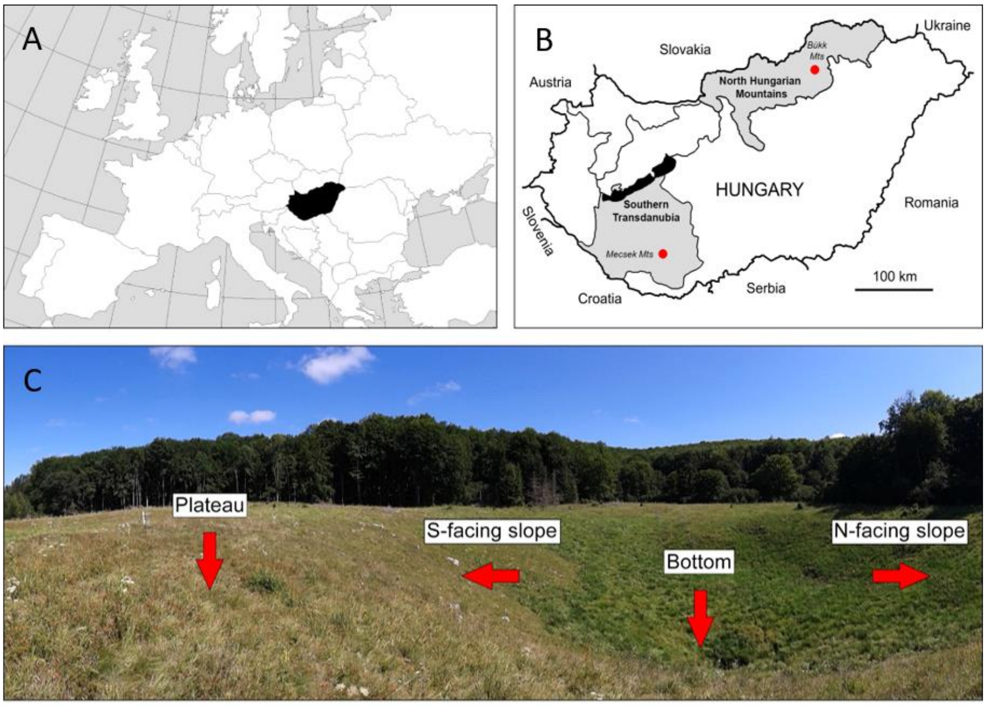

Figure 3. (A) Location of Hungary in Europe; (B) Location of the study areas in Hungary. (C) The different parts of a doline (photo taken by Noémi Kántor).

The plateau has a cool and humid climate with a mean annual temperature of 6.3 °C and a mean annual precipitation of 800 mm. Solution dolines are the typical karst landform features in this area (Williams, 2004; De Waele et al., 2009; Veress, 2017), with bowl-shaped geometry and unique microclimate. In these dolines, the north-facing slopes receive less insolation than bottoms, while the south-facing slopes and the plateau are consistently cooler and moister than the surrounding areas (**Fig. 3C**). However, higher insolation and temperature can be observed on south-facing slopes compared with other slopes and the plateau, providing warm “habitat islands” for many species (Bátori et al., 2019). At night, cold-air pooling occurs in doline bottoms, creating cool or possible occurrence of frost or fog all year round and moist conditions (Lehner et al., 2017). The coldest areas in Hungary can be found in the non-forested dolines of the Bükk Mountains (Bacsó and Zólyomi, 1934).

European beech (*F. sylvatica*) is the dominant tree species within the study area, but dense Norway spruce (*Picea abies*) plantations also occur close to the investigated dolines. Non-forested dolines maintain diverse grassland communities, including dry rocky swards on the south-facing slopes, and mesic wet meadows on the north-facing slopes and bottoms. Semi-dry grasslands and wet meadows are the dominant vegetation types within the fenced area (Borhidi et al., 2012) (**Fig. 4**). The entire area is fenced to prevent overgrazing, soil erosion and the illegal collection of wild plants. In addition, the study area is well known for its unique wildlife and is part of the strictly protected area network of the Bükk National Park.

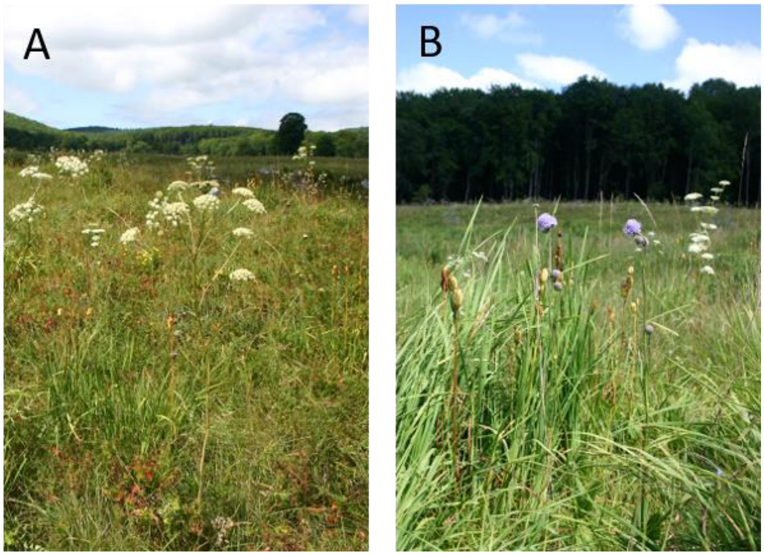

Figure 4. (A) A semi-dry grassland on the plateau, and (B) a wet meadow in the bottom of a doline in the Bükk Mountains (photos taken by Zoltán Bátori).

3.1.2 Study 3

Study 3 was conducted in the Bükk Mountains, Northern Hungary (700–800 m a.s.l.; mean average temperature: 6.3 °C; mean average precipitation: 800 mm) and in the Mecsek Mountains, Southern Hungary (300-500 m a.s.l.; mean average temperature: 9.5 °C; mean average precipitation: 750 mm) (Dövényi, 2010) (**Fig. 3**).

The study sites in the Bükk Mountains are covered with various grassland types as aforementioned. Previous cultivation and lime burning have led to the invasion of *C. epigejos* in many dolines (Bátori et al., 2020). On the otherhand, the study sites in the Mecsek Mountains are covered with oak hornbeam forests (*Carpinus betulus*, *F. sylvatica*, *Quercus petraea* and *Quercus cerris* are the dominant tree species), beech forests (*F. sylvatica* is the dominant tree species) and ravine forests (*Acer campestre*, *Acer platanoides*, *Acer pseudoplatanus*, *C. betulus*, *F. sylvatica* and *Fraxinus excelsior* are the dominant tree species) (**Fig. 5**). Due to forestry practices, current forest stands comprise of 40–50, 60–80 or 90–120-year-old trees. Forest thinning is frequent in the younger (<50-year-old) forests.

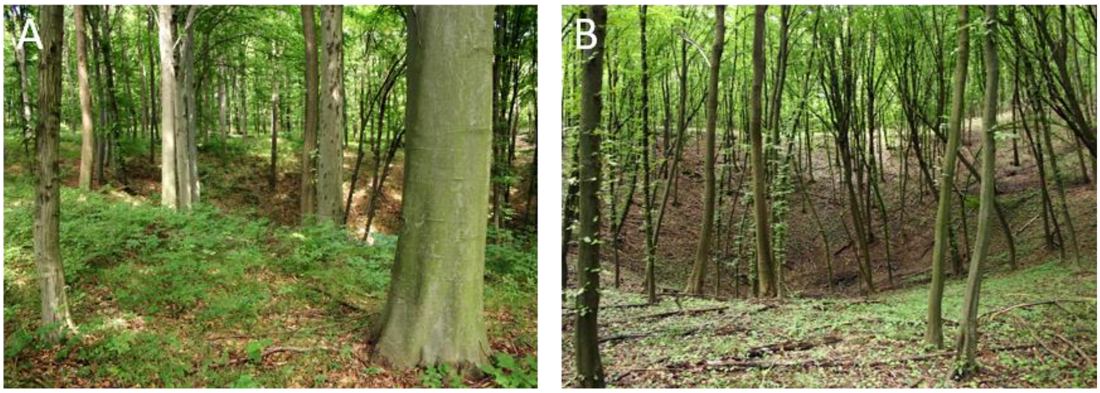

Figure 5. (A) An old (>90 years) beech forest, and (B) a young (<50 years) ravine forest in a doline in the Mecsek Mountains (adapted from Bátori et al., 2020).

3.2 Sampling design

3.2.1 Study 1

For Study 1, three large solution dolines were selected. Dolines 1 and 2 had diameters of 100 m and 70 m, and depths of 17 m and 15 m, respectively. The longer diameter of doline 3 was 190 m, while the shorter was 65 m, and its depth was 13 m. Six sampling sites were established for each doline (18 sites in total), one on the south-facing slope, one in the bottom, one on the north-facing slope and three on the surrounding plateau (**Fig. 6A**). The sites were located at least 20 m from each other. Microclimate measurements and sampling (ants and plants) were carried out in August 2017 under clear weather conditions at the peak of the growing season.

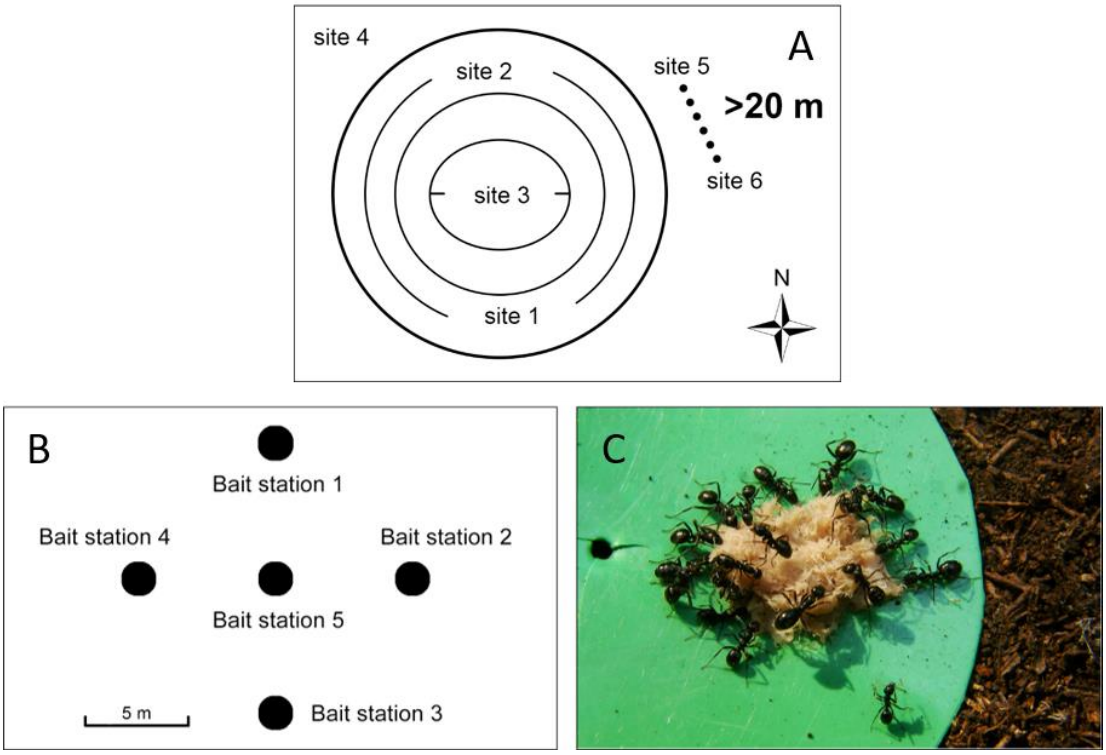

Figure 6. Sampling design for Study 1. (A) Location of study sites inside and outside of dolines. (B) Set-up of ant bait stations in a cross-shaped pattern. (C) Ants feeding on the bait (photo taken by Gábor Lőrinczi).

To provide information on the microclimate of the study area, air temperature (T) and relative air humidity (RH) were recorded every minute for 24 hours using Voltcraft DL-121 TH data loggers. Sensors were suspended 10 cm above the ground to allow enough wind flow to ensure that no humidity was trapped by the sensor casing and actual air temperature and humidity were measured.

Since the study area is a strictly protected nature reserve, we used only non-destructive sampling methods such as baiting and hand collecting to assess the species diversity and relative abundance of ants. At each site, we placed five bait stations in a cross-shaped pattern at 5-m intervals (90 bait stations in total) (**Fig. 6B**). Baits were comprised of plastic discs (8 cm in diameter) with a quarter teaspoon of a mixture of tuna and honey as a food reward (**Fig. 6C**). Foraging activity on baits was monitored every 40 minutes from 7:00 to 10:20 am, overlapping with the daily period of peak ant activity. During each observation, we recorded the presence and number of workers of each ant species on the bait. Baits were replenished as necessary. In addition, we also performed hand collecting to sample those ant species that may have not visited the baits. We visually searched the ground surface in each site for 5 minutes, hand collecting any individuals (workers, incipient queens, etc.) found.

Ants were identified to morphospecies or genus level in the field, and representatives were collected and preserved in 95% ethanol for later species determination. Field-collected specimens were identified in the laboratory using the keys of Seifert (2007) and Czechowski et al. (2012). All the collected specimens were deposited at the Department of Ecology, University of Szeged. We used Bolton’s catalogue (2017) and the Hymenoptera Name Server (Johnson, 2007) to determine the valid names of all ant species.

For plants, five randomly selected plots of 1 m × 1 m were established in each site (90 plots in total). We recorded the presence/absence of all vascular plant species in all plots. Nomenclature for plants follows ‘The Plant List’ (www.theplantlist.org).

3.2.2 Study 2

For Study 2, four doline types were identified based on vegetation cover (grassland vs. forest): type 1 – grassland dolines surrounded only by grasslands (forest cover in their surroundings: 0%), type 2 – grassland dolines surrounded by low amounts of forest (30–40%), type 3 – grassland dolines surrounded by large amounts of forest (90–100%), and type 4 – forested dolines surrounded only by forests (100%) (**Fig. 7**). The different types of dolines were used for ant sampling. Forested dolines surrounded by different amounts of grassland were absent from the study area.

Ant sampling were adapted from Study 1 with slight modifications. Three large solution dolines (diameter: 80–100 m, depth: 10–15 m) were selected from each doline type (12 dolines in total) for the ant assessment. Six sampling sites were selected for each doline types (72 sites in total), one on the north-facing slope, one in the bottom, one on the south facing slope, and three on the surrounding plateau. The sites were at least 20 m apart from each other. In dolines types 2 and 3, the number of forest and grassland sites on the plateau corresponded to the relative proportions of the two habitat types. Methods for baiting and hand collecting, as well as ant identification and preservation methods were the same as in Study 1. Data collection was done in August 2018 on good weather condition.

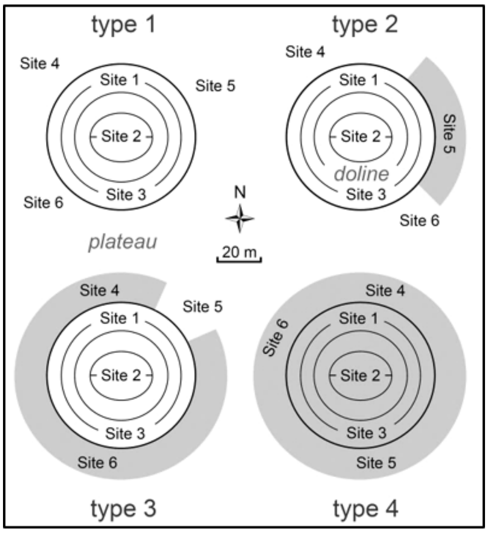

Figure 7. The different types of dolines used for ant sampling in Study 2.
Forest cover is indicated by grey shading (doline types 2–4).

3.2.3 Study 3

In Study 3, six dolines (three ‘natural’ and three ‘disturbed’) were sampled in the Bükk and Mecsek Mountains. Large solution dolines with a diameter of 60‒85 m and depth of 7‒15 m was sampled in the Bükk Mountains, while dolines with a diameter of 55‒105 m and depth of 10‒16 m was sampled in the Mecsek Mountains. Natural dolines in the Bükk Mountains are covered by semi-dry, dry, and wet grasslands, while disturbed dolines can be characterized with a high cover of *C. epigejos*. Natural dolines in the Mecsek Mountains are covered with 90‒120-year-old trees, while disturbed dolines, which are characterized by a markedly higher intensity of forest management, are covered mostly with 40‒50-year-old trees.

We established transects consisting of 1 m × 1 m plots spaced at 2 m intervals from north to south orientation across each doline traversing their deepest point (**Fig. 8**). We recorded the presence/absence of all herbs, shrubs and tree seedlings and saplings in each plot. Plant nomenclature follows ‘The Plant List’ (www.theplantlist.org). Fieldwork was carried out from June to August at the peak of the growing season.

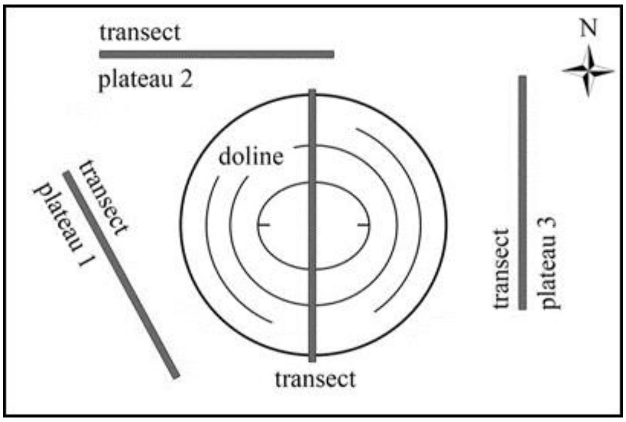

Figure 8. Sampling design for Study 3 (adapted from Bátori et al., 2020).

3.3 Species grouping and data analysis

3.3.1 Species grouping

For Study 1, all ant and plant species were classified according to their temperature and moisture requirements following the methods of Czechowski et al. (2012) for ants and Borhidi (1995) for plants. These were reduced to six functional groups applied to both ants and plants: (1) species adapted to warmer conditions, (2) species adapted to cooler conditions, (3) species adapted to intermediate temperature conditions, (4) species adapted to drier conditions, (5) species adapted to moister conditions, and (6) species adapted to intermediate moisture. We did not analyze combined groups (temperature + moisture) because that would have made the interpretation of results difficult (with many groups), especially in the case of plants. All six main groups of plants and five main groups of ants (groups 1–4 and 6; ants adapted to moister conditions were absent in our study) were analyzed. Because the temperature and moisture requirements of ant and plant species are not the same, direct comparisons between them were not possible.

For Study 2, all sampled ant species (22 species in total) were classified into four main functional groups that relate to (1) temperature preference, (2) moisture preference, (3) habitat preference, and (4) habitat plasticity following Czechowski et al. (2012) and Seifert (2018). Species were also classified according to three main functional traits that relate to (1) dispersal ability, (2) aggressiveness, and (3) social structure (i.e., monogynous or polygynous colonies). Because the number of species and species occurrences were low in all forested sites (only one species, *Myrmica ruginodis*, was found at only eight baits), type 4 dolines were excluded from the statistical analyses (**Table 1**).

For Study 3, all plant species were classified according to their social behavior types. We used the “Social Behavior Types” (SBT) of Borhidi (1995), which are defined for the Pannonian biogeographical region to characterize the naturalness of dolines. Four main functional groups of species were analyzed: (1) specialist species, (2) competitor species, (3) generalist species, and (4) species of disturbed habitats (disturbance tolerant species, natural pioneers, weeds, and ruderal competitors).

Table 1. Functional groups and traits of ants used in Study 2.

Functional groups and traits	Levels
Temperature preference	1: species adapted to warmer conditions 2: species adapted to intermediate temperature conditions 3: species adapted to cooler conditions
Moisture preference	1: species adapted to drier conditions 2: species adapted to intermediate moisture conditions 3: species adapted to moister conditions
Habitat preference	1: species associated primarily with grassland habitats 2: habitat generalists (species associated with forest and grassland habitats) 3: species associated primarily with forest habitats
Habitat plasticity	1: polytopic species 2: oligotopic species 3: stenotopic species
Aggressiveness	1: aggressive species 2: moderately aggressive species 3: subordinate species
Social structure	1: mainly polygynous species 2: both polygynous and monogynous species 3: mainly monogynous species
Dispersal ability	1: flying ability: good 2: flying ability: poor

3.3.2 Data analysis

The temperature and relative humidity data were averaged over 10-minute intervals across all sites of south-facing slopes, bottoms, north-facing slopes, and the plateau, respectively, and plotted using a line graph. Extreme environmental values are generally more informative regarding the distribution of organisms, but maximum relative humidity values in our case often reached 100%, therefore we considered mean values more suitable for differentiating between the microclimatic properties of microhabitats than extreme values. From the site-averaged data, we calculated the mean daily temperature (T_{24}) and relative humidity (RH_{24}), mean daytime temperature (T_d) and relative humidity (RH_d), and mean night temperature (T_n) and relative humidity (RH_n). We also calculated these microclimate variables separately for each site and used them in multivariate analyses.

For Study 1, the diagnostic ant and plant species of the microhabitats were determined by calculating the phi coefficient (Φ) of association between species and habitat. Calculations for ants were based on data from bait stations. Species with $\Phi > 0.2$ were considered diagnostic for ants, and species with $\Phi > 0.3$ for plants. Different threshold values for ants and plants were used due to the differences in the total number of species within each of these taxonomic groups. Non-diagnostic species were excluded with Fisher's exact test ($p < 0.05$) following Tichý and Chytrý (2006). Fidelity measures were calculated using the JUICE program Tichý (2002).

We used permutational multivariate analysis of variance (PERMANOVA) to test the effect of microhabitats (south-facing slopes, bottoms, north-facing slopes, and the plateau) on the species composition of ant and plant assemblages. We used the raw presence/absence data of species for each sampling plot in the source matrices. We applied the Jaccard dissimilarity, performed 5,000 permutations and accounted for the nested design of the data set. When a PERMANOVA yielded significant results, we calculated pairwise PERMANOVAs among the microhabitat types. PERMANOVAs were calculated in R (R Development Core Team, 2018) using the *adonis* function of the 'vegan' package (Oksanen et al., 2019). We used the FDR (false discovery rate) method to adjust *p* values for multiple comparisons (*p. adjust* function).

We prepared non-metric multidimensional scaling (NMDS) ordinations to visually illustrate compositional differences. To remove the confounding effect of the nested data structure on the resulting point clouds, we lumped data from the different sampling plots of each site of each doline together and used the frequency data, ranging from one to five, of the species in the source matrices. We used Euclidean distances and two dimensions (after assessing stress factors for one to five dimensions). NMDS ordinations were done using the metaMDS function of the 'vegan' package. To assess the relationships between microclimate variables (T_{24}, RH_{24}, T_d, RH_d, T_n and RH_n) and species assemblages, we fitted environmental vectors onto the ordination space using the *envfit* function and calculated correlations between ordination values and fitted vectors.

We used mean-and-whisker plots to illustrate the distribution of the various functional groups in different microhabitats. To test if these differences were significant, we used generalized linear mixed-effects models (GLMM). Calculations for ants were based on data from bait stations. Five models were built for ants (three for temperature and two for moisture) and six models for plants (three for temperature and three for moisture). In the full models, different microhabitats were included as fixed factors, the number of ant and plant species as dependent variables, and locations (i.e., doline 1, 2 and 3) as random factors. We transformed the data of ants to binary scale (presence/absence) and used a binomial error term because each functional group had a high preference for one or a few sites and were very rare in other sites, leading to zero inflation of the data. No transformation was needed for plants, and we used Poisson or, if overdispersion was detected, negative binomial error term. GLMMs were performed in R using the *glmer* function of the ‘lme4’ package (Bates et al., 2013). Full models were tested for significance with analysis of variance, using the *ANOVA* function of the ‘car’ package (Fox and Weisberg, 2011). Pairwise comparisons of factor levels were undertaken with the *relevel* function, and the false discovery rate (FDR) method (*p. adjust* function) was used to correct *p* values for multiple comparisons.

For Study 2, the diagnostic species of habitats (doline vs. plateau) and doline types (types 1-3) were determined by fidelity calculations using the phi coefficient (Φ) of association, which ranges from -1 to +1 (Tichý and Chytrý, 2006). Calculations were based on data from baits, and species with $8 > 0.1$ were considered diagnostic (Fisher’s exact test, $p < 0.05$). The highest value of phi was 0.3 in our case. The value of +1 would mean that a given ant species occurred on all baits of the target habitat or doline type and was absent from the baits of the other habitat or doline types. Fidelity measures were calculated using the JUICE program (Tichý, 2002). Because many baits were visited by only one or a few species, we focused on the distribution of single functional groups and traits, and we did not use multi-trait approaches.

We used generalized linear mixed-effects models (GLMMs) to analyze the effects of habitat (doline vs. plateau) and doline type (types 1–3) on the functional groups and traits of ants visiting the baits. The number of species occurrences belonging to each category of the studied functional groups and traits was the response variable, while site was used as a random factor. We used a Poisson error distribution (maximum likelihood fit), but in some cases, where 0 and 1 scores predominated the dataset, we transformed the data to binary scale and used binomial error distribution. GLMMs were performed in R (R Development Core Team, 2017) using the *glmer* function of the ‘lme4’ package (Bates et al., 2013). Full models were tested for significance with the *ANOVA* function of the ‘car’ package (Fox and

Weisberg, 2011). We used the false discovery rate (FDR) method (*p. adjust* function) to account for multiple comparisons when performing pairwise comparisons.

For Study 3, diagnostic species analysis was performed to identify species that prefer one specific habitat type (natural or disturbed dolines). The phi coefficient (Φ) was applied as an indicator of the fidelity of a species to a certain habitat (Chytrý et al., 2002). The phi coefficient varies between -1 and +1, and higher phi values indicate higher diagnostic values. In this study, species with phi values higher than 0.2 were considered. Significant diagnostic species were identified by Fisher's exact test ($p < 0.01$). Analyses were performed with JUICE 7.0.45 (Tichý, 2002).

The differences in the vegetation composition of the two habitat types (natural vs. disturbed dolines) were assessed by non-metric multidimensional scaling ordinations (NMDS, Jaccard index) and one-way analysis of similarities (ANOSIM, Jaccard index) using 9,999 permutations. The analyses were performed in R (R Core Team, 2018) using the *metaMDS* and *anosim* functions of the 'vegan' package (Oksanen et al., 2019). Generalized linear mixed models (GLMMs) with a Poisson distribution were used to compare the social behavior types of the habitats. In each model, the habitat type (natural vs. disturbed) was used as a fixed factor, the number of species with different social behavior types as a response variable, while the sampling location (i.e., transect) as a random factor. GLMMs were prepared in R using the *glmer* function of the 'lme4' package (Bates et al., 2013; R Core Team, 2018). The percentage frequency of each species was determined both for the natural and disturbed dolines.

4 Results

4.1 Study 1

4.1.1 Microclimate

Dolines are known to have unique microclimatic inversion. Climatic variables such as temperature (T) and relative humidity (RH) were recorded on the different parts of dolines during the day and night at a 24-hour duration. North-facing slopes and bottoms of dolines are consistently cooler and moister, while south-facing slopes are consistently warmer and drier than the surrounding plateau (**Fig. 9**).

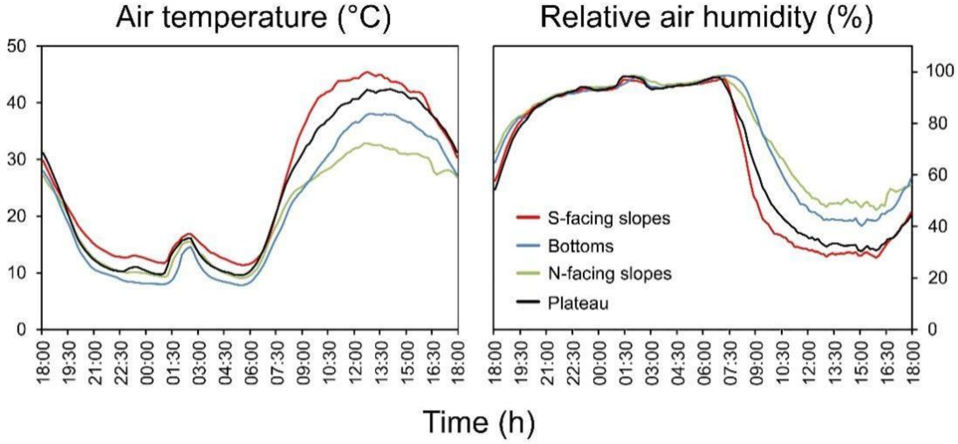

Figure 9. Microclimate in the different microhabitats of dolines in the Bükk Mountains.

The temperatures were higher on south-facing slopes (T_{24} = 25.9 °C; T_d = 33.8 °C; T_n = 13.8 °C) than in other microhabitats. The mean daily temperature was similar on north-facing slopes (T_{24} = 20.1 °C) and in doline bottoms (T_{24} = 20.6 °C), while night temperatures were lowest in bottoms (T_n = 9.78 °C). The night temperatures were similar on north-facing slopes (T_n = 11.5 °C) and plateau (T_n = 11.8 °C). The mean daytime temperature was higher in bottoms (T_d = 27.7 °C) than on north-facing slopes (T_d = 25.7 °C). The temperatures on the plateau were intermediate (T_{24} = 24.0 °C; Td = 31.8 °C; T_n = 11.8 °C). The mean daily relative humidity was lowest on south-facing (RH_{24} = 68.0%) and highest on north-facing slopes (RH_{24} = 78.4%). The values were intermediate in bottoms (RH_{24} = 76.2%) and on the plateau (RH_{24} = 70.0%). At night, relative humidity was similar (RH_n = 92.9-94.0%) in all microhabitats. However, during daytime relative humidity was usually higher on north-facing slopes ($RH_d = 68.2\%$) than in bottoms ($RH_d = 65.2\%$), on south-facing slopes ($RH_d = 51.7\%$) and on the plateau ($RH_d = 55.1\%$). A small intermittent temperature increase in all microhabitats was recorded around 1:30 hours and indicated an inflow of warmer air from the surrounding lower altitudes.

4.1.2 Species composition

A total of 14 ant (nine from baiting and five from hand collecting) and 145 plant species (from the plots) were recorded in our sites. Hand collection yielded 52 ant individuals, 13 of which were found on south-facing slopes, five in bottoms, 11 on north-facing slopes and 23 on the plateau. In terms of diagnostic species, the south-facing slopes had two ant and 13 plant species, while two ant and 20 plant species were identified on the plateau. North-facing slopes and bottoms had 15 and nine plant species, respectively, and one ant species (**Fig. 10; Table 2**). Dry grasslands dominated the south-facing slope of dolines 1 and 3, while semi-dry grasslands covered the south-facing slope of doline 2 and major parts of the plateau. North-facing slopes and doline bottoms were dominated by wet meadows.

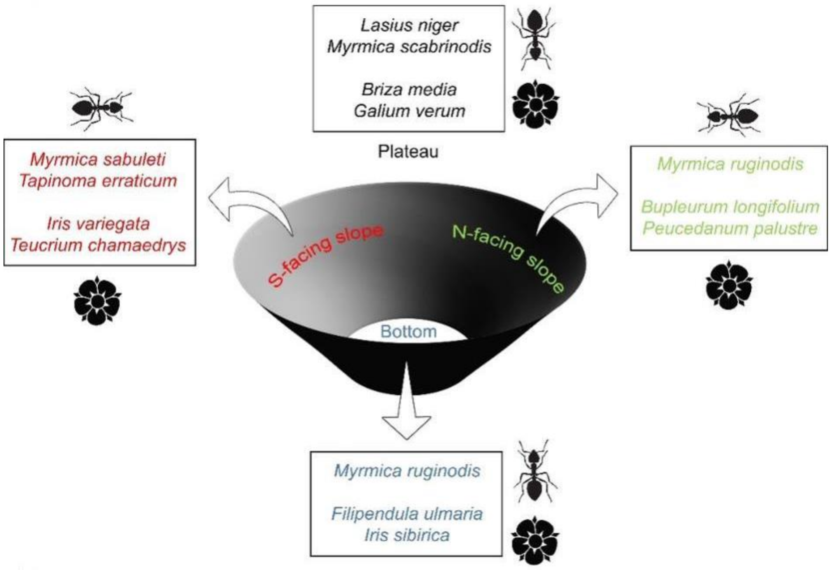

Figure 10. Characteristic ant and plant species in the different microhabitats of dolines in the Bükk Mountains.

Table 2. Synoptic table of ants and plants associated with different microhabitats (south-facing slopes, bottoms and north-facing slopes of dolines, and the plateau) in the Bükk Mountains. Within blocks, species are listed by increasing values of the phi (*Φ*) coefficient of association between species and habitat (in parenthesis). Four of the species marked with an asterisk (*) were diagnostic for two different microhabitats.

Ants	Plants
S-facing slopes	
Tapinoma erraticum (0.30), *Myrmica sabuleti* (0.79)	*Polygonatum odoratum* (0.32), *Digitalis grandiflora* (0.39), *Waldsteinia geoides* (0.40), *Brachypodium pinnatum* (0.43), *Anemone sylvestris* (0.47), *Sedum maximum* (0.50), *Verbascum austriacum* (0.51), *Festuca rupicola* (0.52) *, *Origanum vulgare* (0.53), *Fragaria viridis* (0.55) *, *Geranium sanguineum* (0.61), *Teucrium chamaedrys* (0.66), *Iris variegata* (0.83)
Bottoms	
Myrmica ruginodis (0.25) *	*Potentilla erecta* (0.35), *Filipendula ulmaria* (0.38), *Iris sibirica* (0.39), *Festuca ovina* (0.40), *Agrostis canina* (0.45), *Aconitum variegatum* s.l. (0.46) *, *Molinia caerulea* (0.50), *Geranium palustre* (0.51), *Urtica dioica* (0.57)
N-facing slopes	
Myrmica ruginodis (0.41) *	*Thalictrum lucidum* (0.32), *Senecio integrifolius* (0.32), *Stellaria holostea* (0.32), *Galium mollugo* (0.36), *Primula elatior* (0.36), *Aconitum variegatum* s.l. (0.38) *, *Aconitum moldavicum* (0.40), *Bupleurum longifolium* (0.40), *Carex pilosa* (0.40), *Peucedanum palustre* (0.45), *Astrantia major* (0.46), *Euphorbia lucida* (0.48), *Calamagrostis arundinacea* (0.52), *Aegopodium podagraria* (0.52), *Luzula luzuloides* (0.57)
Plateau	
Lasius niger (0.29), Myrmica *scabrinodis* (0.34)	*Ranunculus polyanthemos* (0.32), *Valeriana officinalis* subsp. *collina* (0.32), *Cirsium pannonicum* (0.34), *Carex michelii* (0.35), *Koeleria pyramidata* (0.35), *Linum catharticum* (0.35), *Primula veris* (0.37), *Galium verum* (0.37), *Seseli libanotis* (0.39), *Poa pratensis* s.l. (0.41), *Centaurea scabiosa* subsp. *sadleriana* (0.42), *Filipendula vulgaris* (0.42), *Helictotrichon alpinum* (0.44), *Phleum phleoides* (0.46), *Briza media* (0.47), *Carex filiformis* (0.47), *Thesium linophyllon* (0.49), *Festuca rupicola* (0.52)*, *Fragaria viridis* (0.55) *, *Hypericum perforatum* (0.58)

The NMDS ordinations of bait stations (stress factor: 0.119) and vegetation plots (stress factor: 0.064) showed that the species composition of ant and plant assemblages differed among microhabitats (**Fig. 11A, B**). These differences were significant, except between ant assemblages of bottoms and north-facing slopes (**Table 3**). Plant assemblages of all microhabitats displayed highly significant differences ($p < 0.001$). T_{24}, T_d and RH_d were significantly related to the ordination of ant assemblages and T_{24}, T_d, RH_{24} and RH_d to the ordination of plant assemblages, with assemblages on south-facing slopes being associated with higher temperatures and lower humidity, and assemblages on north-facing slopes and in doline bottoms being related to lower temperatures and higher humidity.

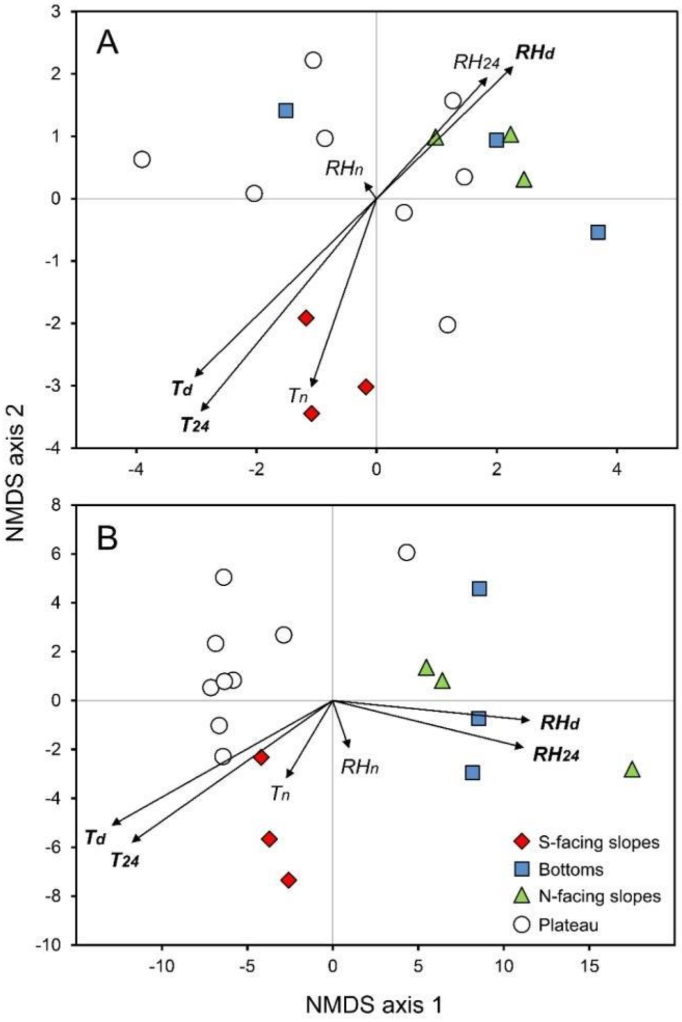

Figure 11. Non-metric multidimensional scaling (NMDS) ordination for (A) ant and (B) plant assemblages in different microhabitats (south-facing slopes, bottoms, and north-facing slopes of dolines, and the plateau) with fitted vectors of mean daily temperature (T_{24}) and relative humidity (RH_{24}), mean daytime temperature (T_d) and relative humidity (RH_d), and mean night temperature (T_n) and relative humidity (RH_n). Vector length indicates the strength of correlation. Microclimate variables that were significantly correlated to the ordination (T_{24}, T_d, RH_{24} and RH_d) are indicated in boldface.

Table 3. Comparisons of ant and plant assemblages in different microhabitats (south-facing slopes, bottoms and north-facing slopes of dolines, and the plateau) with permutational multivariate analysis of variance (PERMANOVA). The *p* values were corrected with the FDR (false discovery rate) method. Significant differences are indicated by bold *p* values.

	Ants			**Plants**		
	F	***R*²**	***p***	***F***	***R*²**	***p***
S-facing slopes vs. Bottoms	20.96	0.327	<**0.001**	10.88	0.279	<**0.001**
S-facing slopes vs. N-facing slopes	15.70	0.389	<**0.001**	7.82	0.349	<**0.001**
S-facing slopes vs. Plateau	11.37	0.171	<**0.001**	5.34	0.169	<**0.001**
N-facing slopes vs. Bottoms	1.35	0.034	**0.261**	2.86	0.164	<**0.001**
N-facing slopes vs. Plateau	8.83	0.141	<**0.001**	6.84	0.204	<**0.001**
Bottoms vs. Plateau	4.89	0.071	**0.004**	5.08	0.237	<**0.001**

4.1.3 Functional groups of species

Functional groups of both ants and plants showed significant preferences for certain microhabitats (**Figs. 12** and **13**). On north-facing slopes, 64% of the hand-collected ants were species adapted to cooler conditions, and 82% of the collected individuals were species adapted to intermediate moisture conditions. In other microhabitats, most of the hand-collected ants (100% on south-facing slopes, 80% in bottoms and 52% on the plateau) were species adapted to warmer and drier conditions. Ants collected from bait stations and plant species adapted to warmer and/or drier conditions occurred more frequently on south-facing slopes than on north-facing slopes and in doline bottoms **(Figs. 12** and **13**). Conversely, ant and plant species adapted to cooler and/or moister conditions were generally most frequent on north-facing slopes and in doline bottoms compared to south-facing slopes and the plateau. We did not find either ant species adapted to moister conditions or plant species adapted to cooler conditions on south-facing slopes.

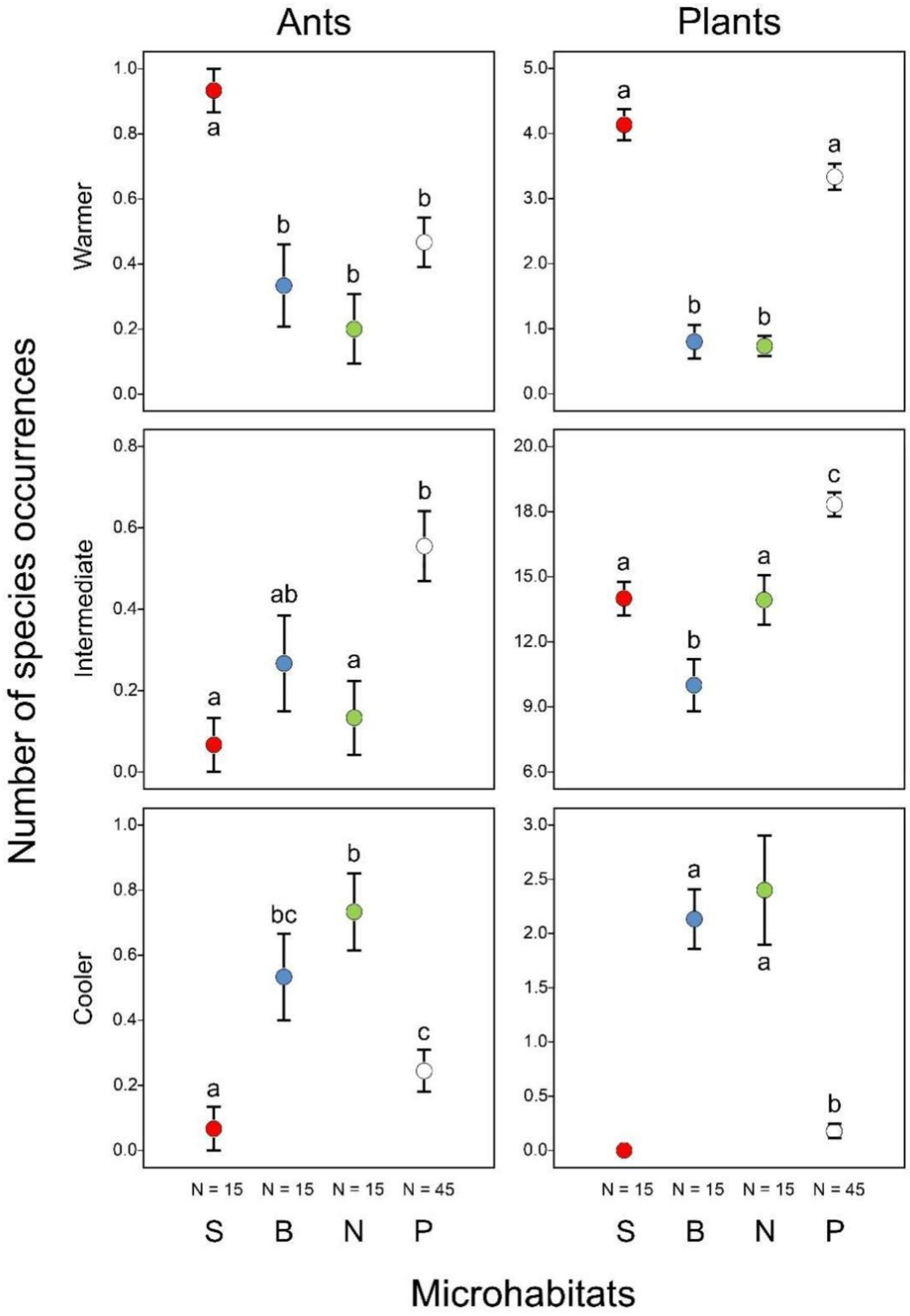

Figure 12. Occurrences of ant and plant species (mean ± SE) belonging to different functional groups of temperature requirements (warmer, intermediate, and cooler) in different microhabitats (S: south-facing slopes of dolines, B: bottoms of dolines, N: north-facing slopes of dolines, P: plateau). Significant differences detected using mixed-effect models are indicated by different lower-case letters (a-c).

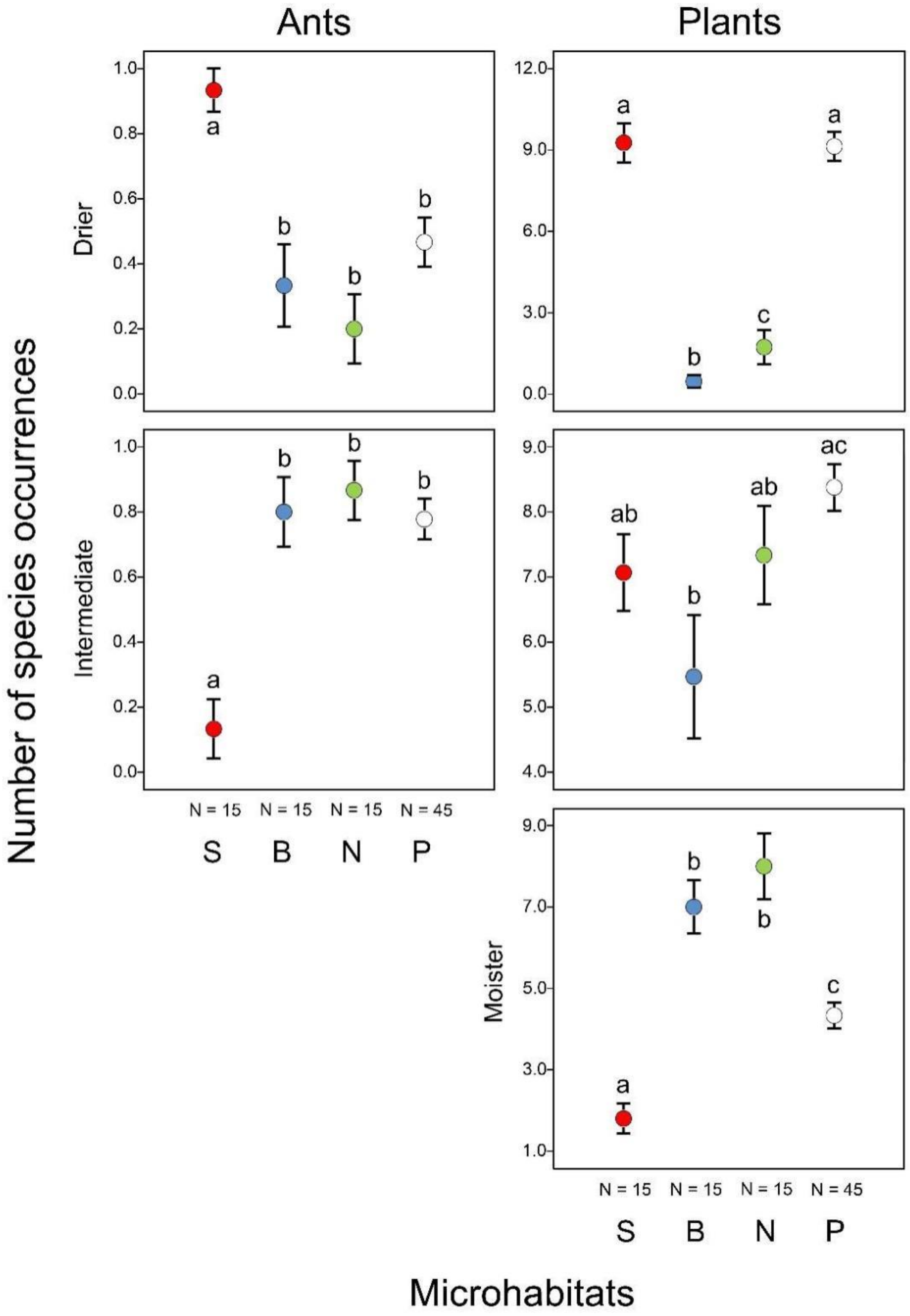

Figure 13. Occurrences of ant and plant species (mean ± SE) belonging to different functional groups of moisture requirements (drier, intermediate, and moister) in different microhabitats (S: south-facing slopes of dolines, B: bottoms of dolines, N: north-facing slopes of dolines, P: plateau). Significant differences detected using mixed-effect models are indicated by different lower-case letters (a-c).

4.2 Study 2

4.2.1 Species composition

A total of 22 ant species were found in the study area. Baiting yielded 21 species, while 15 species were obtained by hand collecting. *Lasius platythorax* (fidelity value: 0.18), *M. ruginodis* (0.23), *Myrmica sabuleti* (0.27), and *Tetramorium* cf. *caespitum* (0.16) were diagnostic for dolines, while *Lasius niger* (0.24) and *Myrmica scabrinodis* (0.30) for the plateau. All doline types (types 1-3) had their diagnostic species: *Tapinoma erraticum* (fidelity value: 0.24), *Formica pratensis* (0.21), and *T.* cf. *caespitum* (0.26) for types 1, 2 and 3, respectively.

4.2.2 Functional groups and traits of species

There was no significant difference between the total number of ant species in dolines and the plateau (**Table 4**). However, dolines and the plateau differed significantly from each other with respect to many functional groups and traits (**Fig. 14**). Dolines had a significantly higher number of species adapted to cooler, warmer, drier, or moister conditions, while the plateau had more species adapted to intermediate temperature and intermediate moisture conditions. The number of species associated primarily with forest habitats was higher in dolines, while the number of species associated primarily with grassland habitats was higher on the plateau. Dolines had more moderately aggressive and both polygynous and monogynous species, while the number of subordinate species was higher on the plateau (**Table 4**). The total number of species and most functional groups and traits did not differ significantly among the different doline types (**Fig. 15**). However, the number of species adapted to intermediate moisture conditions was higher in type 3 than in type 1, and types 2 and 3 contained more aggressive and monogynous species than type 1 (**Table 5)**.

Hand collecting confirmed the results of baiting. For instance, the proportion of ant species adapted to cooler (34.5%), warmer (52.7%), drier (52.7%) or moister (7.3%) conditions was much higher in dolines, while the plateau contained a higher proportion of species adapted to intermediate temperature (42.3%) or moisture (65.4%) conditions. Generally, only small differences in functional group and trait proportions were observed among the different doline types.

Table 4. Comparisons of species numbers and species occurrences of ants related to different functional groups and traits in different habitats (doline vs. plateau) in the Bükk Mountains using the fitted generalized linear mixed-effect models. Significant differences are indicated by bold *p* values.

	Model	
Species number, functional groups and traits	χ^2	***p***
Total number of species	0.77	0.381
Warmer	6.95	**0.008**
Intermediate temperature	21.29	**<0.001**
Cooler	5.17	**0.023**
Drier	7.29	**0.007**
Intermediate moisture	17.62	**<0.001**
Moister	10.09	**0.001**
Grassland	4.13	**0.042**
Habitat generalist	0.02	0.882
Forest	14.81	**<0.001**
Polytopic	0.12	0.732
Oligotopic	4.67	0.031
Stenotopic	0.04	0.841
Aggressive	0.01	0.948
Moderately aggressive	30.75	**<0.001**
Subordinate	6.49	**0.011**
Polygynous	0.72	0.396
Polygynous, Monogynous	14.71	**<0.001**
Monogynous	1.87	0.178
Flying: good	0.41	0.523
Flying: poor	0.49	0.485

Table 5. Comparisons of species occurrences of ants related to different functional groups and traits in doline types (types 1–3) in the Bükk Mountains using the fitted generalized linear mixed-effect models (only statistically significant models are shown). The *p* values were corrected with the false discovery rate (FDR) method. Significant differences are indicated by bold *p* values.

Model	**Functional groups and traits**	
	Intermediate moisture	
Full model	χ^2	***p***
	6.30	**0.043**
Pairwise comparisons	***z***	***p***
type 1 vs. type 2	1.70	0.134
type 1 vs. type 3	2.51	**0.036**
type 2 vs. type 3	0.92	0.356
	Aggressive	
Full model	χ^2	***p***
	21.47	**<0.001**
Pairwise comparisons	***z***	***p***
type 1 vs. type 2	2.56	**0.027**
type 1 vs. type 3	3.91	**<0.001**
type 2 vs. type 3	0.89	0.632
	Monogynous	
Full model	χ^2	***p***
	8.44	**0.015**
Pairwise comparisons	***z***	***p***
type 1 vs. type 2	2.56	**0.028**
type 1 vs. type 3	2.76	**0.016**
type 2 vs. type 3	0.24	0.968

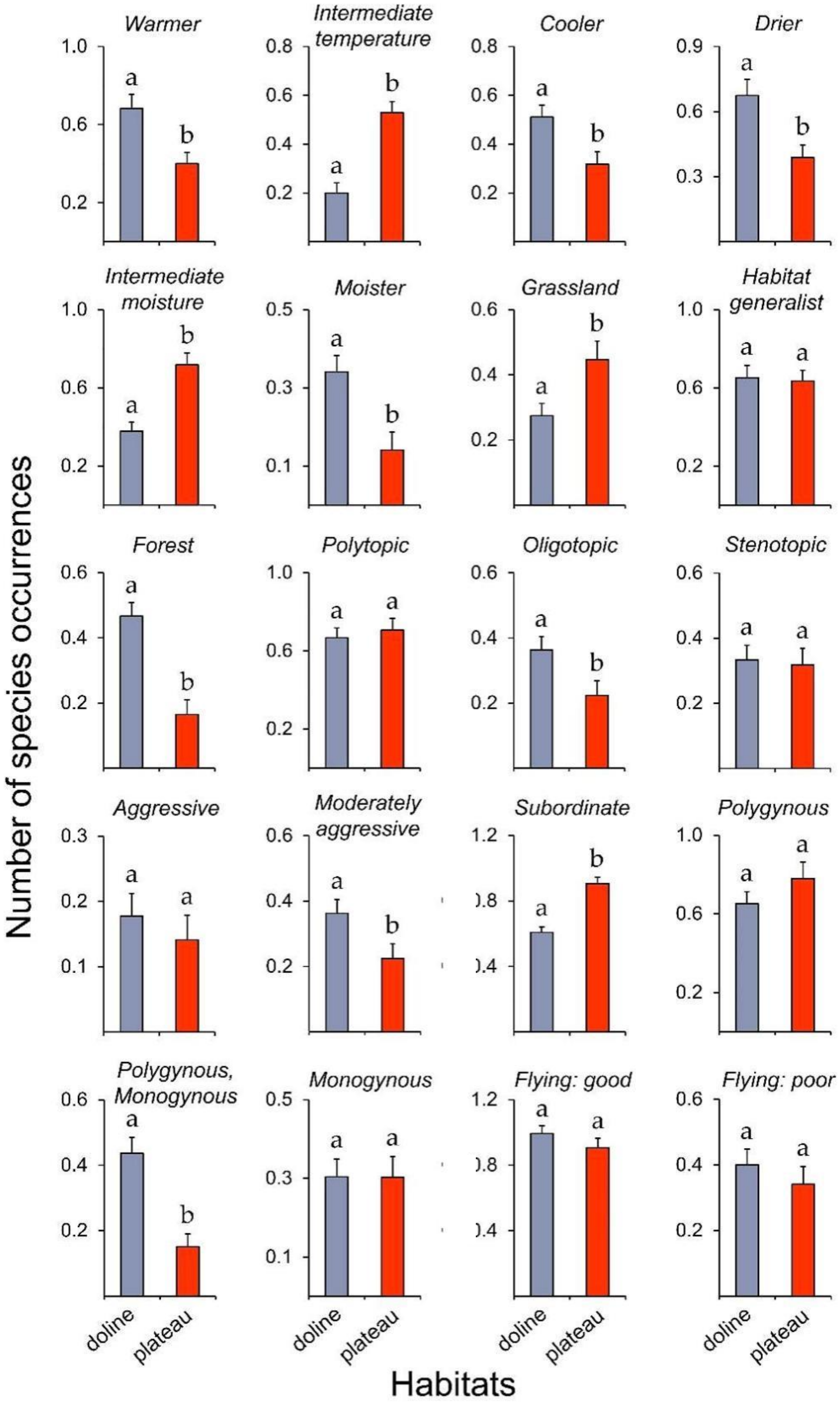

Figure 14. Occurrences of the different functional groups and traits of ant species (mean ± SE) between dolines and the plateau. Different lowercase letters indicate significant differences between the two habitats.

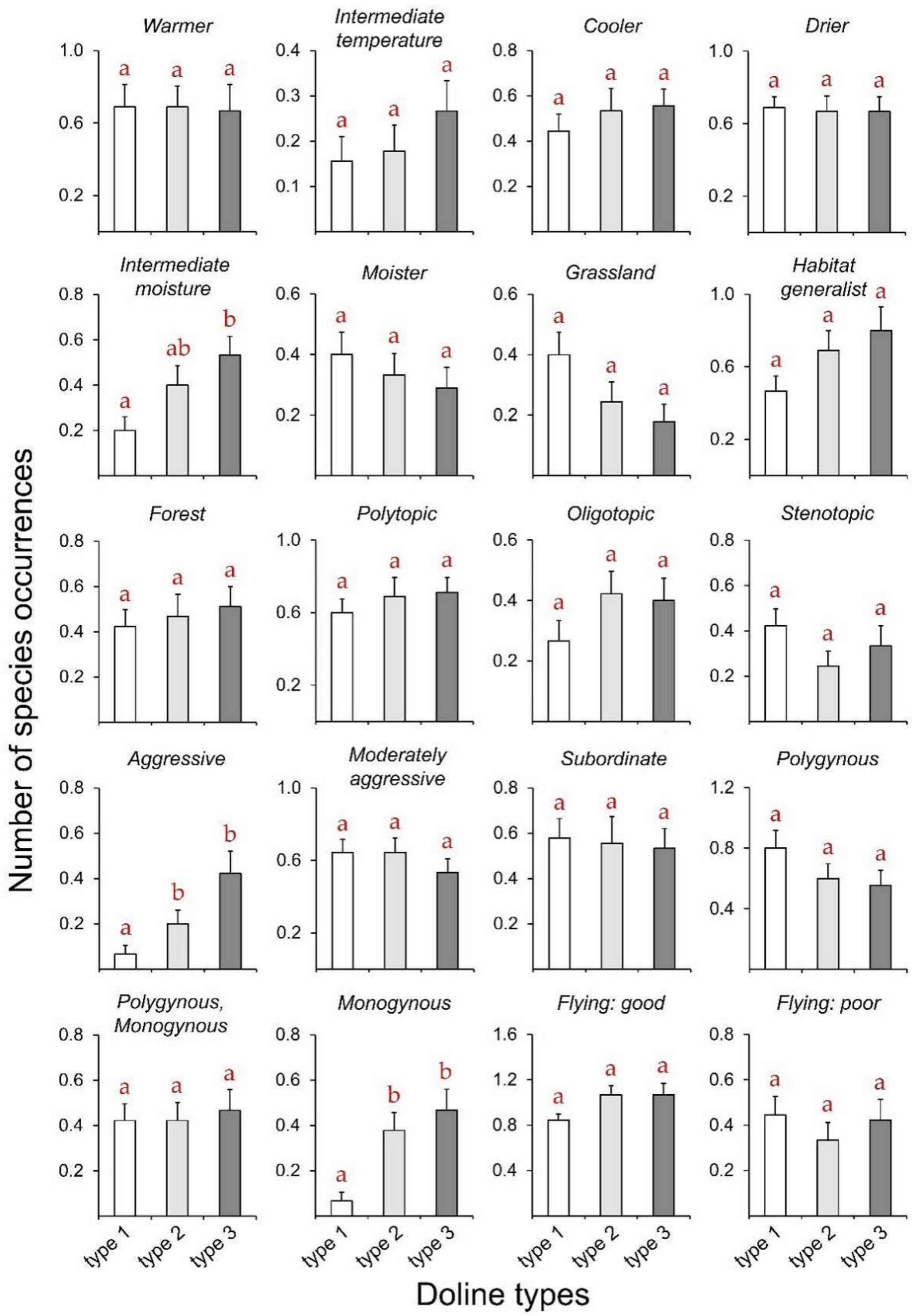

Figure 15. Occurrences of the different functional groups and traits of ant species (mean ± SE) among the different doline types (types 1–3). Different lowercase letters indicate significant differences between the doline types.

4.3 Study 3

4.3.1 Species composition

The most frequent plant species of the natural dolines in the Bükk Mountains were *Arrhenatherum elatius* (66%), *Iris sibirica* (57%), *Stachys officinalis* (54%), *Festuca rupicola* (52%) and *Brachypodium pinnatum* (51%), while in the disturbed dolines *C. epigejos* (72%), *A. elatius* (71%), *Fragaria viridis* (62%), *Galium mollugo* (56%), *F. rupicola* (44%), *Cruciata glabra* (44%) and *Veronica chamaedrys* (44%) were the most frequent (**Table 6**). In the Mecsek Mountains, *Lamium galeobdolon* (88%), *Hedera helix* (64%), *A. pseudoplatanus* (59%), *Mercurialis perennis* (54%), *Galium odoratum* (43%) and *Viola reichenbachiana* (43%) were the most frequent species in the natural dolines, while *H. helix* (74%), *A. pseudoplatanus* (69%), *C. betulus* (63%), *L. galeobdolon* (54%) and *V. reichenbachiana* (31%) were the most frequent species in the disturbed dolines (**Table 7**). In total, we could identify 43 diagnostic species in the dolines of the Bükk Mountains (**Table 6**). Twenty-five species were diagnostic for natural dolines (e.g., *I. sibirica*, *Euphorbia lucida* and *Peucedanum palustre*) and 18 species for disturbed dolines (e.g., *C. epigejos, Carex hirta* and *Cirsium eriophorum*). In the Mecsek Mountains, we found 12 diagnostic species for natural dolines (e.g., *Circaea lutetiana*, *M. perennis* and *Tilia tomentosa*) and only one diagnostic species for disturbed dolines (*C. betulus*) (**Table 7**).

Based on the NMDS analysis, there was a defined gradient between the plots of disturbed and natural dolines in the Bükk Mountains (stress value: 0.33), while a slight overlap of the plots was observed in the Mecsek Mountains (stress value: 0.35) (**Fig. 16**). Plots belonging to the two habitats were significantly different in their species composition in both areas according to the similarity analysis (Bükk Mountains: ANOSIM R = 0.49, $p < 0.001$; Mecsek Mountains: ANOSIM R = 0.30, $p < 0.001$).

Table 6. List of diagnostic plant species for natural (N) and disturbed (D) dolines in the Bükk Mountains. Capital letters in parentheses (S, C, G and D) indicate the four main groups of species, such as S: specialist species, C: competitor species, G: generalist species and D: species of disturbed habitats (disturbance tolerant species, natural pioneers, weeds, and ruderal competitors), bold numbers indicate fidelity values ($\Phi \times 100$), while numbers in parentheses indicate the percentage frequency of species.

	N	**D**
Iris sibirica (S)	**61.8** (57)	(0)
Stachys officinalis (G)	**59.3** (54)	(0)
Brachypodium pinnatum (C)	**56.8** (50)	(0)
Filipendula vulgaris (G)	**49.5** (41)	(0)
Geranium sanguineum (C)	**43.7** (34)	(0)
Molinia caerulea (C)	**43.7** (34)	(0)
Seseli libanotis (G)	**42.0** (32)	(0)
Calamagrostis arundinacea (G)	**41.1** (31)	(0)
Euphorbia lucida (G)	**39.4** (29)	(0)
Aconitum variegatum (S)	**38.6** (28)	(0)
Phleum phleoides (G)	**38.6** (33)	(3)
Potentilla erecta (D)	**35.1** (41)	(10)
Filipendula ulmaria (G)	**34.1** (22)	(0)
Centaurea phrygia subsp. *indurata* (G)	**33.1** (21)	(0)
Gentiana pneumonanthe (S)	**32.2** (20)	(0)
Thalictrum lucidum (G)	**30.3** (18)	(0)
Helictotrichon alpinum (G)	**30.1** (23)	(3)
Peucedanum palustre (G)	**29.3** (17)	(0)
Cirsium pannonicum (G)	**28.2** (16)	(0)
Waldsteinia geoides (G)	**28.2** (16)	(0)
Verbascum lychnitis (G)	**28.0** (21)	(3)
Iris variegata (G)	**27.2** (15)	(0)
Luzula luzuloides (C)	**25.6** (21)	(4)
Digitalis grandiflora (G)	**25.0** (13)	(0)
Veronica austriaca subsp. *dentata* (G)	**25.0** (13)	(0)
Calamagrostis epigejos (D)	(9)	**64.0** (72)
Veronica chamaedrys (D)	(12)	**35.6** (44)
Euphorbia cyparissias (D)	(0)	**34.5** (23)
Carex hirta (D)	(0)	**33.4** (22)
Colchicum autumnale (G)	(6)	**32.6** (33)
Cirsium eriophorum (D)	(0)	**32.2** (20)
Thymus pulegioides subsp. *pannonicus* (G)	(2)	**29.0** (22)
Carex pallescens (D)	(15)	**28.2** (41)
Bromus erectus (C)	(0)	**27.5** (15)
Ranunculus polyanthemos (G)	(7)	**27.4** (29)
Sanguisorba minor (G)	(2)	**26.5** (19)
Alchemilla monticola (G)	(0)	**26.2** (14)

Rhamnus cathartica (G)	(1)	**26.2** (16)
Trifolium montanum (G)	(9)	**25.8** (29)
Cardamine pratensis (G)	(0)	**24.9** (13)
Euphorbia salicifolia (D)	(0)	**24.9** (13)
Trifolium alpestre (G)	(13)	**24.8** (34)
Primula veris (G)	(1)	**23.5** (14)

Table 7. List of diagnostic species for natural (N) and disturbed (D) dolines in the Mecsek Mountains. Capital letters in parentheses (S, C, G and D) indicate the four main groups of species, such as S: specialist species, C: competitor species, G: generalist species and D: species of disturbed habitats (disturbance tolerant species, natural pioneers, weeds, and ruderal competitors), bold numbers indicate fidelity values ($\Phi \times 100$), while numbers in parentheses indicate the percentage frequency of species.

	N	**D**
Mercurialis perennis (C)	**58.3** (54)	(0)
Galium odoratum (C)	**49.8** (43)	(0)
Tilia tomentosa (C)	**44.0** (38)	(1)
Lamium galeobdolon (G)	**38.2** (88)	(54)
Rubus hirtus agg. (D)	**37.6** (30)	(1)
Melica uniflora (C)	**34.6** (29)	(3)
Fraxinus excelsior (C)	**32.3** (21)	(0)
Fagus sylvatica (C)	**31.4** (30)	(5)
Hepatica nobilis (S)	**29.6** (18)	(0)
Circaea lutetiana (G)	**26.8** (15)	(0)
Carex pilosa (C)	**25.6** (37)	(14)
Carpinus betulus (C)	(16)	**47.0** (63)

4.3.2 Functional groups of species

Significant differences ($p < 0.05$) were observed in all Social Behavior Type (SBT) groups except for the generalist species ($p = 0.097$) in the Bükk Mountains (**Fig. 17**). Specifically, specialist and competitor species had a significantly higher ($p < 0.001$) prevalence in natural than in disturbed dolines, while the number of species of disturbed habitats was higher in disturbed dolines ($p = 0.001$). In addition, species of disturbed habitats comprised 41% of all species in the disturbed dolines (total number of species: 120) and 22% in the natural dolines (total number of species: 127). However, in the Mecsek Mountains, all SBT groups of natural dolines contained significantly higher number of species than those of disturbed dolines ($p < 0.05$) (**Fig. 17**). Unexpectedly, the number of species of disturbed habitats was significantly higher ($p < 0.05$) in natural than in disturbed dolines. In addition, species of disturbed habitats comprised 24% of all species in the disturbed dolines (total number of species: 24) and 17% in the natural dolines (total number of species: 42).

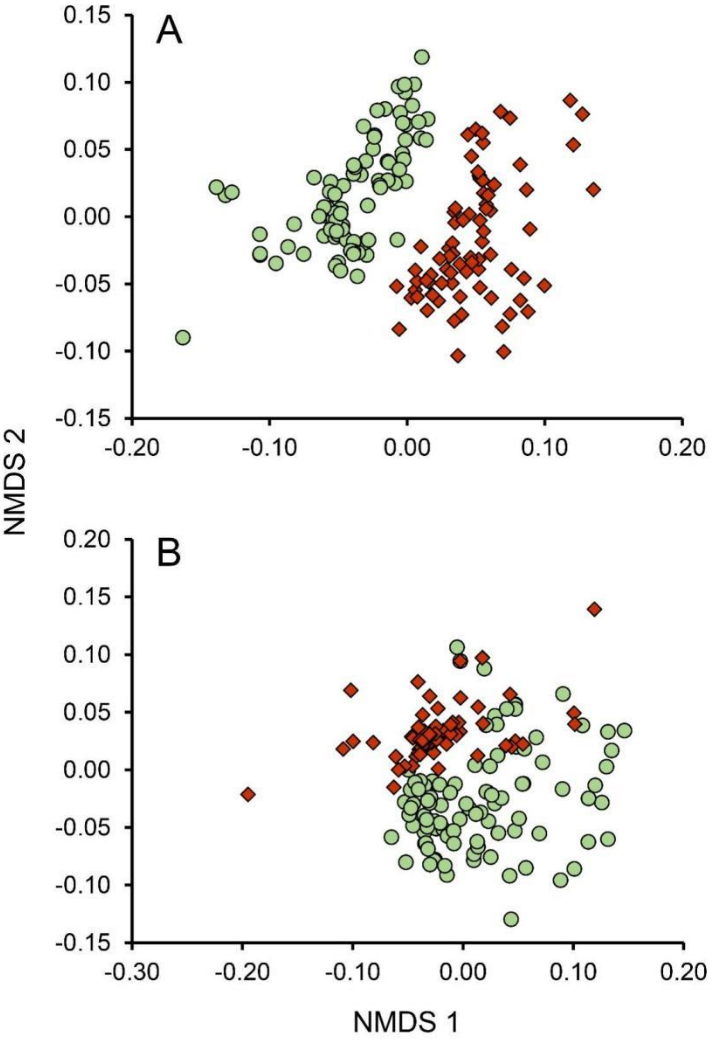

Figure 16. Non-metric multidimensional scaling (NMDS) ordinations of the plots in natural and disturbed dolines in (a) the Bükk and (b) the Mecsek Mountains. Different colors indicate different habitat types (green: natural, red: disturbed).

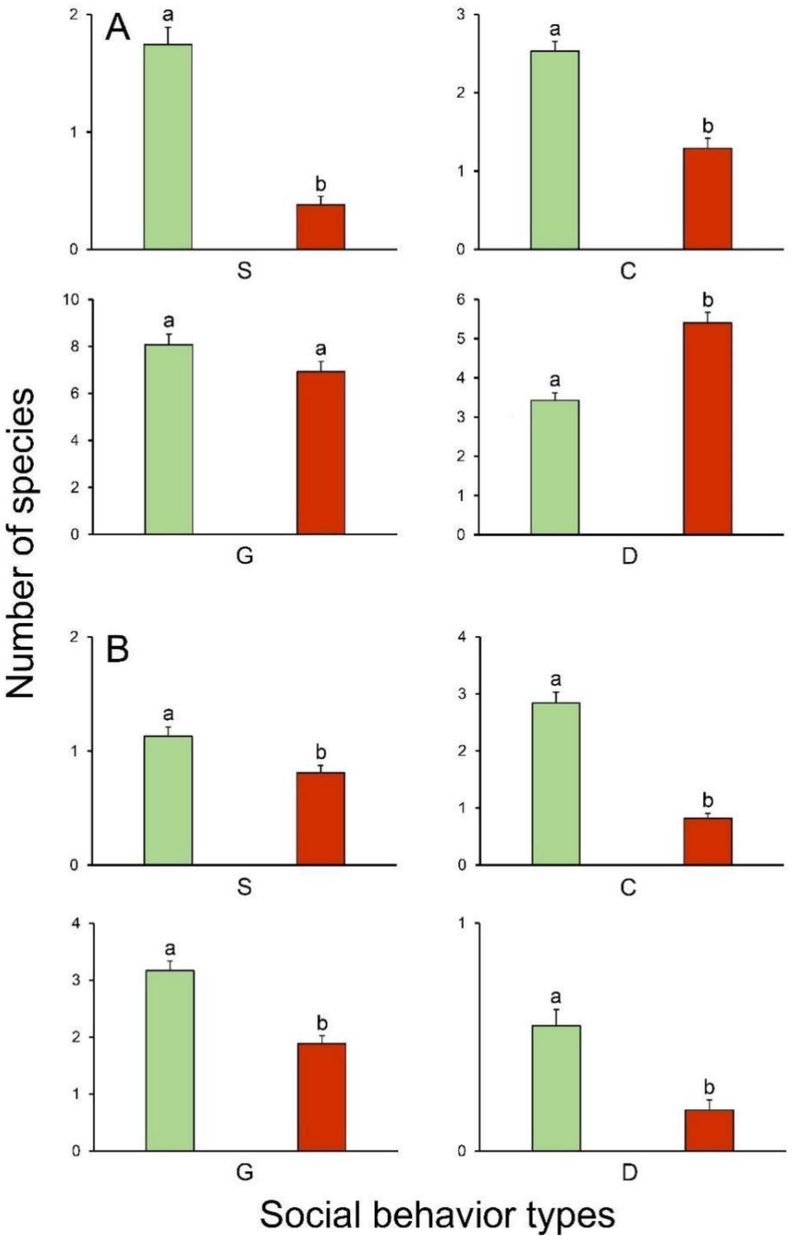

Figure 17. Number of plant species of the different social behavior types (SBT) in natural and disturbed dolines in (A) the Bükk and (B) the Mecsek Mountains. Different letters (a and b) above the boxes indicate significant differences, while colors indicate different habitat types (green: natural, red: disturbed). S: specialist species, C: competitor species, G: generalist species and D: species of disturbed habitats (disturbance tolerant species, natural pioneers, weeds, and ruderal competitors).

5 Discussion

5.1 Study 1

Karst depressions (dolines) having very high topographic complexity support a wide array of microhabitats for various organisms. Our study has shown that these depressions possess highly heterogenous microclimatic conditions (e.g., temperature and moisture). These doline habitats are unique because they can be cooler and moister or warmer and drier than the surrounding areas creating a fine-scale environmental heterogeneity. Our study further demonstrated that the distribution of functional groups on ants and plants correspond to these different microhabitats. To date, this was the first attempt done to illustrate within tens of meters that fine-scale topography of dolines provides microhabitats for different functional groups in two different phyla (i.e., Arthropoda and Tracheophyta).

Studies have been shown that over fine scales, topographic complexity induces climatic variability in an area (Bennie et al., 2008; Lenoir et al., 2013; Hofierka et al., 2018). Even though we have recorded temperature and relative humidity for only a relatively short period of time (24 hours), we found that karst dolines present wide variation in microclimates. In these dolines, mean daytime temperatures were more than 8 °C warmer on south-facing slopes than on north-facing slopes. Microclimatic studies done previously over long periods of time (i.e., from a few days to a year), also indicated that north-facing slopes and bottoms of dolines tend to be cooler and more humid than south-facing slopes and the surrounding plateau (Shanks and Norris, 1950; Wagner, 1963; Jakucs, 1971; Bárány-Kevei, 1999; Clements et al., 2003; Růžička et al., 2016; Šegina et al., 2018). In addition, doline bottoms usually receive less solar radiation but receive more water (Bátori et al., 2011), likely contributing to the higher relative humidity and lower temperatures recorded in these habitats (Fridley, 2009; Ashcroft and Gollan, 2013). Furthermore, north-facing slopes and bottoms of dolines may retain snow cover longer than south-facing slopes and plateaus (Gargano et al., 2010).

Distribution patterns of organisms are directly related to small-scale environmental changes (Schmalholz and Hylander, 2011; Bátori et al., 2014a, 2014b; Frey et al., 2016). Similarly, ant and plant species both responded to the microclimatic variability in our study. The cooler and moister north-facing slopes and bottoms of dolines in the Bükk Mountains acted as key habitats for plants adapted to cooler and/or moister conditions (e.g., *B. longifolium* and *I. sibirica*) and ants adapted to cooler conditions (e.g., *M. ruginodis*). On the other hand, south-facing slopes acted as key habitats both for ants (e.g., *M. sabuleti*) and plants (e.g., *Iris variegata*) adapted to warmer and/or drier conditions, while many ant (e.g., *L. niger*) and plant species (e.g., *Galium verum*) found on the plateau indicated intermediate temperature and/or moisture conditions. Since the recorded ant species are not known to form strict trophic relationships with plants, the main drivers of the observed patterns seem more of their temperature and moisture preferences. These salient findings underline the importance of considering fine-scale environmental variation when investigating the distribution patterns of biodiversity (Bátori et al., 2014a, 2014b; 2017).

Our study has demonstrated that the distributions of microclimate and species in two major taxa, i.e., ants (Arthropoda) and vascular plants (Tracheophyta) showed strong concerted response to fine-scale topography. Though, other taxa also display distribution patterns reflecting changes in environmental conditions in dolines over short distances. The increased soil moisture content on the north-facing slopes and bottoms of solution dolines in the Aggtelek Karst area in Hungary has been shown to provide suitable habitats as well for several cool-adapted species of land snails (Mollusca: Gastropoda) (Kemencei et al., 2014*)* and terrestrial isopods (Arthropoda: Crustacea) (Vilisics et al., 2011). Dolines in Mexico, Australia, and China (‘cenotes’ and ‘tiankengs’) have also been shown to maintain populations of rare taxa in various phyla (Wilkens, 1982; Jaume et al., 2001, Boxshall et al., 2014, Su et al., 2017), highlighting dolines as important safe havens for biodiversity on a global scale. Species may respond to climate changes by range-shifting (Wilson et al., 2005) or by persisting in environmentally stable habitats (Willis et al., 2000; McLaughlin et al., 2017).

In karst dolines, species could potentially track suitable microclimates over a wide range of regional climatic changes with minimal movement because cooler/moister and warmer/drier microclimates vary over very short distances. As few areas can buffer opposing trends in environmental conditions (Mokany et al., 2017) karst dolines may be particularly important for maintaining biodiversity through time. Hence, they could be considered as high-capacity microrefugia (Keppel et al., 2015b). The highest-capacity microrefugia for cool-adapted taxa can usually be found in cold, humid and topographically complex areas (Totland and Alatalo, 2002; Gentili et al., 2015).

Karst dolines may play important roles in facilitating the persistence of different phyla under global warming, which poses a serious threat to global biodiversity (Bellard et al., 2012). Regional predictions of climate change suggest that warming in East-Central Europe will continue in the coming decades (Bartholy et al., 2008). These changes are already impacting the distributions of ants (Gallé, 2017) and vascular plants (Tölgyesi and Körmöczi, 2012) in a sand-dune area in Hungary, with drought-tolerant species replacing dune slack species over the last decades. Therefore, species adapted to warmer and/or drier conditions are expected to expand their distribution from south-facing slopes of dolines to surrounding areas. However, north-facing slopes and bottoms of dolines could provide important microrefugia during global warming by facilitating the persistence of species adapted to cooler and/or moister and to intermediate conditions. The retention of cooler microclimates in these habitats may be facilitated by lower solar radiation, thicker soil layer, higher soil moisture and cool-air pooling (Iijima and Shinoda, 2000; Fridley, 2009; Daly et al., 2010).

Our data supports that dolines are vital safe havens for relict plants (e.g., *A. variegatum*, *B. longifolium* and *D. ruyschiana* in the Bükk Mountains) in the current climate. However, future studies are needed to further confirm the role of dolines as refugia (i.e., places providing environmental conditions that are comparatively stable over long time periods) under global warming. While our 24-hour data demonstrate that dolines are currently providing cooler and warmer microclimates than the surrounding plateau, this does not necessarily prove stability. Thus, long-term monitoring would be required for more accurate data. Available data in the Northern Hemisphere does suggest that habitats in the north-facing slopes undergo slower changes under global warming (Maclean et al., 2015; Winkler et al., 2016). Otherwise, the microclimate of dolines could be investigated along a temperature gradient using a space-for-time substitution approach to determine if north-facing slopes and bottoms of dolines indeed retain more stable microclimates. Lastly, functional traits can be reflective of long-term environmental stability and, therefore, could provide important eco-evolutionary information about refugia (Keppel et al., 2018).

5.2 Study 2

Karst dolines have the capacity to maintain microhabitats which enable persistence of several ant functional groups and functional traits which are not common in the surrounding habitats. This further highlights the potential of dolines to function as safe havens during various environmental changes. We confirmed that continuous cover of European beech (*F. sylvatica*) in dolines had a negative effect on the species composition of ant assemblages, drastically reducing the number of functionally different species. However, higher cover of *F. sylvatica* on the plateau did not hinder the functional diversity in grassland dolines. Our findings underline the importance of dolines as local biodiversity hotspots in karst landscapes by supporting specific functional group patterns of ant assemblages. Grassland dolines in the study area acted as key habitats for ants adapted to cooler and/or moister conditions (e.g., *Myrmica lobicornis, M. ruginodis,* and *L. platythorax*), while species on the plateau indicated intermediate temperature and/or moisture conditions (e.g., *Lasius bombycina*, *L. niger*, and *M. scabrinodis*). This can be attributed to the high microhabitat heterogeneity within dolines, presenting great variation in microclimates and soil moisture (Whiteman et al., 2004; Raschmanová et al., 2013; Bátori et al., 2019).

Previous microclimatic studies indicated that the north-facing slopes in grassland dolines tend to be much cooler and more humid than the south-facing slopes, bottoms, and plateaus during daytime, while cool-air pooling, which exist in the doline bottoms, may provide higher humidity and extremely low temperatures at night (Bárány-Kevei, 1999). Although only a few studies have been published on the distribution of animal taxa in European dolines which mostly focused on collapse dolines with cave entrances, dolines' ability to support species adapted to cooler and/or moister conditions has been widely accepted (Kemencei et al., 2014; Bátori et al., 2017; Su et al., 2017). For instance, studies of Růžička et al. (2016) showed that cold adapted mountain species such as *Vitrea transsylvanica* (Mollusca: Gastropoda), *Micrargus georgescuae* (Chelicerata: Araneae), and *Ligidium germanicum* (Crustacea: Isopoda) occur in the lower parts of a collapse doline in the Moravian Karst in Czech Republic. Similar results were published by Raschmanová et al. (2018) showing that collapse dolines in Slovakia harbor disproportionately high biodiversity of cold-adapted springtail species (Collembola). We also found that dolines may act as key habitats for various ants adapted to warmer and/or drier (e.g., *Formica cunicularia*, *M. sabuleti*, and *Tapinoma subboreale*) conditions. The main reason for this is that the south-facing slopes of dolines receive more insolation during daytime than the other microhabitats (Bárány-Kevei, 1999). This is in line with Růžička et al. (2016) who found that south-facing slopes and edges of dolines may provide habitats for warm-adapted steppe species, e.g., *Danacea pallipes* (Insecta: Coleoptera). Our results suggest that dolines in Europe have the potential to buffer climate fluctuations. Since only few areas have the potential to act as refugia with important ecological functions during both cooler and warmer climate periods (Harrison and Noss, 2017; Mokany et al., 2017), dolines may be particularly important for maintaining biodiversity through time (Bátori et al., 2017). We found that the number of ant species associated primarily with forest habitats (e.g., *Formica truncorum*, *M. ruginodis*, and *L. platythorax*) was highest in grassland dolines, whereas only one species (*M. ruginodis*) with few occurrences was observed in the forested sites.

In Central Europe, *F. sylvatica* forests with low resource availability are among the most species poor habitats usually with only a few ant species and very low population densities (Dolek et al., 2009; Wiezik et al., 2015). In our previous study (Bátori et al., 2019), we detected a significant effect of slope exposure on ant species composition within the grassland dolines in the Bükk Mountains (e.g., *M. ruginodis* dominated the north-facing slopes). This indicates that certain microhabitats in dolines have the potential to maintain suitable microclimate and resource availability for ant species associated primarily with forest habitats in landscapes where the dominant forest type is unfavorable for them. Considering that the study area in the Bükk Mountains is dominated by *F. sylvatica* forests, these dolines may also function as stepping stones for some ant species, playing a crucial role for species' dispersal among distant habitats (cf. Saura et al., 2014). Similar patterns can also be observed in other island-like systems, such as under scattered trees in wood pastures (Tölgyesi et al., 2018) or on rocky outcrops and slopes in agricultural landscapes (Bellemare et al., 2002).

Environmental heterogeneity generally has beneficial impact on distribution of ants (Ribas et al., 2003; Fagundes et al., 2015; Tavella et al., 2018). For instance, in heterogenous environments, monopolization of space by behaviorally dominant ant species decreases, thereby, providing more hiding places and foraging opportunities for subordinate ant species (Gibb and Parr, 2010; Koptur et al., 2010). Some of our results is not in conjunction with other studies indicating that baits in dolines were visited more frequently by moderately aggressive (e.g., *M. ruginodis*) and less frequently by subordinate species (e.g., *M.*

scabrinodis) than those on the plateau. Part of the explanation may be that despite the greater environmental heterogeneity, the restricted space within dolines favors ant species that are more aggressive and better competitors. However, the influence of some environmental factors such as higher resource availability within dolines, may relax interspecific competition and can increase the probability of species coexistence (Ribas et al., 2003; Blüthgen et al., 2004).

Assessing the influence of surrounding habitat patterns on the species composition of island-like habitats and microrefugia can be daunting because of many possible interactions between environmental variables and species distributions (Deák et al., 2020; Gentili et al., 2020). The species composition of ant assemblages in habitat fragments is not only influenced by several abiotic and biotic factors but also by colonization-extinction dynamics and dispersal limitation (Crist, 2009). In our study, we investigated how certain functional groups and traits in ant assemblages of dolines change with *F. sylvatica* cover outside the dolines. We found that the number of species adapted to intermediate moisture conditions was the highest in grassland dolines surrounded by large amounts of forests (type 3 dolines). These patterns are likely associated with the ecological effects of these forests (i.e., the edge effect) on the habitat structure, microclimate, and resource availability of doline microhabitats. As key components of landscapes, edges have received considerable attention both in anthropogenic and natural ecosystems (Erdős et al., 2019), because they may control the flows of organisms (Wiens, 1992; Cadenasso et al., 2003), influence species interactions (Fagan et al., 1999), functional characteristics (Gallé et al., 2018) and evolutionary processes (Kevey and Borhidi, 1998), and serve as refuges for a wide range of organisms (Erdős et al., 2014). It can also be assumed that at least some environmental factors are intermediate at forest edges providing habitats for many species adapted to intermediate environmental conditions (e.g., moisture or temperature). In relation to this, we observed that *L. platythorax*, *M. lobicornis*, and *M. scabrinodis* were relatively frequent in type 3 dolines. We also found that the number of aggressive species with mostly monogynous colonies was highest in type 3 dolines. A probable explanation for this is that queens of monogynous colonies tend to disperse by flying to establish a new colony, inhabiting semi-isolated habitats more easily than queens of polygynous colonies that tend to disperse by budding or nest splitting (Czechowski et al., 2012; Seifert, 2018). Furthermore, considering that *F. sylvatica* forests provide unfavorable habitats for ants (Dolek et al., 2009; Wiezik et al., 2015), some aggressive species associated with forest habitats like *F. truncorum* and *L.*

platythorax could find suitable habitats via fallen twigs and abundant moss cover in these dolines for their foraging and nesting activities.

Continued global warming is expected to alter vegetation and landscape patterns in karst areas (Walther et al., 2002). Likewise, it may also pose substantial alterations in the species composition of arthropod assemblages (Wise and Lensing, 2019; Prather et al., 2020). Given their past and present capacity to sustain habitats for various species (Bátori et al., 2017; Raschmanová et al., 2018), dolines in Europe will likely provide important safe havens, where different functional groups of species can survive for long period of time. However, changes to the biological environment (e.g., surrounding vegetation cover and forest height) caused by anthropogenic activities (e.g., changes in forestry activity or in grazing/mowing regimes) may alter the species composition of dolines and their capacity to provide microrefugia for vulnerable species (cf. Liu et al., 2019; Bátori et al., 2020; Kermavnar et al., 2020). For instance, overgrazing is threatening the survival of vulnerable plants in the dolines of the Greek Archipelago (Egli et al., 1990). Therefore, careful conservation and management planning would be essential to maximize the resilience of karst landscapes to global warming. Specifically, in the Bükk Mountains, moderate grazing and/or mowing would be necessary to prevent shrub encroachment into the grassland microhabitats of dolines to safeguard optimal habitat and vegetation structure for ants. Preserving the current distribution of forests and grassland patches may ensure that diverse ant assemblages are maintained in these doline microhabitats.

5.3 Study 3

Karst dolines covered by natural vegetation consistently harbor many valuable plant species and indicate high naturalness. In our study, we compared the naturalness of grassland (invaded by *C. epigejos* vs. non-invaded) and forested habitats (young forests vs. old forests) in the dolines of two Hungarian karst areas using the naturalness indicator values of plants. High numbers of competitors and stress tolerant species (specialist and generalist species) were observed in natural dolines (i.e., in non-invaded grassland dolines and dolines covered with old forests), indicating high naturalness in their vegetation. This is in line with other studies that the high number of certain species (e.g., endemic, habitat specialist and endangered species) within a habitat may indicate higher naturalness (Angermeier and Karr, 1994; Trombulak et al., 2004). Our findings further support that dolines with undisturbed habitats have distinct species composition as compared to disturbed dolines (Bátori et al., 2020).

Interestingly, in the forested dolines of the Mecsek Mountains more disturbed habitat species (e.g., disturbance tolerant species, natural pioneers, and weeds) were observed in the dolines covered with old growth forests than in the dolines covered with young forests. The unexpected occurrence of these species might be a result of natural disturbance in the forest area. The natural forest dynamic processes such as tree-fall gaps or canopy openings created during the falling of old trees led to more light penetration into the lower depths of the canopy and the herb layer, contributing to the presence of disturbed habitat species (e.g., some gap species) such as *Galium aparine*, *Hypericum hirsutum* and *Urtica dioica* within the old forest stands. Similarly, previous studies showed that light conditions strongly affect different plant groups thriving in the understory (Tinya et al., 2009). Furthermore, small-scale natural disturbances resulting in single or multiple tree-fall gaps may also play an important role in driving natural stand dynamics in temperate forests (Pickett and White, 1985; Paillet et al., 2010). Plant species that predominantly or exclusively occur in forest gaps are often described as shade intolerant species, which are typical in non-forested habitats (Goldblum, 1997; Anderson and Leopold, 2002). If the number of these species is not too high in an old forest, their presence may indicate natural processes and contributes to the maintenance of biodiversity in forested landscapes.

Human-induced environmental changes have been shown to influence both ecological and evolutionary processes, leading to population extinctions and biodiversity losses (Palumbi, 2001; Tilman and Lehman, 2001; Stockwell et al., 2003). Karst environments can be prone to such changes. This is also true for dolines, which are known to be highly valuable because of their unique geomorphological feature, microclimate, and habitat structure. In addition, they may act as safe havens for cool adapted species under local and global environmental changes (Bátori et al., 2011). Our results suggest that valuable species in dolines are threatened by different human activities, such as the human-mediated invasion of ruderal competitor species (e.g., the invasion of *C. epigejos*) and high levels of forest management (e.g., clear cutting and frequent logging), and one possible way to evaluate the impacts of such human activities on vegetation is the assessment of the naturalness of habitats. We found that various disturbances decreased the number of specialist and competitor species in dolines, thus reducing the naturalness and conservation value of these special habitats.

Also, our results suggest that the climatically diverse habitats of karst surfaces are extremely sensitive to anthropogenic disturbances and that their recovery from such disturbances may be slow or may not occur at all (Breg Valjavec et al., 2018b; Bátori et al., 2020). To increase the naturalness of these habitats, populations of dominant competitors such as *C. epigejos* should be suppressed through controlled grazing and/or mowing in grassland dolines. On the other hand, in forested dolines adaptation of sustainable forest management by prohibiting logging or reducing intensity of forestry activities should be imposed, which may contribute more for the survival of valuable species under global warming.

6 Conclusion

Study 1: How doline microhabitats (south-facing slopes, north-facing slopes, bottoms, and plateau) determine species distribution patterns of ant and plant assemblages?

In Study 1, we conclude that enclosed depressions (dolines) in karst surfaces provide a diversity of microclimatic habitats that have the capacity to support various taxa in different phyla (Arthropoda and Tracheophyta) under various climatic trends. These highly complex environments topographically present diverse microclimates which are drier and warmer in the south-facing slopes and cooler and moister in the north-facing pole slopes and depression bottoms than the surrounding plateaus. The fine-scale distributions of functional groups of ant and plant assemblages mirror this variation in microclimate. Hence, these dolines may be crucial in facilitating the in-situ persistence of numerous species under local and global climate oscillations. This implies that modelling of climate change impacts on the distribution of biodiversity will need to consider fine-scale topographic variation occurring within tens of meters to arrive at accurate predictions.

Study 2: How vegetation structure and habitat heterogeneity in dolines influence the occurrence of specific functional groups and traits of ant assemblages?

In Study 2, our results demonstrate strong relationships between environmental heterogeneity and the distribution of functional groups and traits among ant assemblages in karst ecosystems. We found that dolines harbor specific functional groups and traits that are rare in the surrounding habitats, and that vegetation structure on the surrounding plateau may have the potential to influence the functional diversity of ant assemblages within dolines. Species for which a given habitat becomes environmentally unsuitable may find shelter in doline microhabitats, but species can also use dolines as stepping stones during their range expansion. Furthermore, our findings indicate that ants are reliable model organisms and possible indicators for identifying those locations that have the capacity to provide safe havens for different functional groups of species. Proper management and conservation of these safe havens may mitigate the rate of biodiversity loss under global warming.

Study 3: How different types of human activities, i.e., human-mediated invasion of reed grass (Calamagrostis epigeios) and intensive forestry management affect the naturalness of dolines vegetation?

In Study 3, our findings indicate that various types of local anthropogenic disturbances such as human mediated invasion of dominant grassland competitors and extensive forestry activities negatively influence the degree of naturalness in dolines and alter the capacity of dolines to support valuable species. On the other hand, dolines with natural vegetation continuously provide unique habitats for a high diversity of valuable species and indicate high naturalness. To maintain the naturalness of vegetation in these doline habitats, the populations of ruderal competitors should be eliminated, and sustainable forest management should be adapted. This just imply that measures for conservation need to put into consideration the various impact of disturbance to these doline habitats. Also, there are still open questions with regards to the effects of different disturbances on the naturalness in dolines that need to be answered to determine which conservation strategies will be particularly suitable for valuable species in a warming climate.

7 Summary

Karst area covers 20% of the earth’s terrestrial surface. Dissolution processes on limestone surfaces contributed to the formation of the karst surface and subsurface features such as caves, limestone pavements, valleys, and enclosed depressions (dolines, sinkholes or tiankengs). Karst areas provide important ecosystem services one of which is the habitat function. Karst depressions (dolines) due to their topographically intricate features and microclimatic inversions may support several habitats where species composition and diversity vary with environmental heterogeneity. Dolines may have the potential to act as safe havens for a high diversity of valuable species. However, nowadays these important doline habitats are altered by various man-made activities that made them highly vulnerable and prone to degradation.

Topographic parameters (e.g., geometry, size, and slope aspect) and related environmental conditions (e.g., air temperature, air humidity and soil moisture) which contributed to heterogeneity of doline habitats are known to play a major role in determining their biodiversity patterns. These topographic and biological attributes can create microhabitats with unique microclimates which species may depend on for their survival. Microhabitats may be warmer, drier, cooler and/or moister than the prevailing regional climate. As such, they create a mosaic of microclimates that can allow species to survive changes in their environment by migrating short distances between these microhabitats. These fine-scale mosaics improve species’ chances also to persist in a certain landscape. Various studies have shown that dolines may provide microhabitats for unique species that are rare or absent from the surrounding landscape. The heterogenous habitats of dolines may serve as refuges (for decades) or refugia (for millennia) for vulnerable taxa, such as endemic, montane, and relict species. Many of these species can be under threat because of global warming and anthropogenic activities.

Dolines have been cultivated extensively, providing sites for various traditional activities such as arable farming, gardening, pasturing and water extraction. The degradation of dolines is among the most pressing issue in karst environments worldwide. Human-induced activities may compromise the capacity of dolines to act as safe havens for species during future climate oscillations, and, as a result, may also reduce the naturalness of their habitats.

In Hungary, for centuries, intensive deforestation and grazing drastically have been affecting doline habitats.

In our studies, ants and plants were selected as focal taxa because ant colonies and plants share many similarities. Both groups usually ‘nest’ in or on the ground and use their modules (e.g., plant roots and ant workers) to forage in the surrounding habitat. In addition, due to the relatively fixed location of ant colonies and plants, competition in both groups is confined to well-defined zones. Similarities also exist in terms of their functional roles (e.g., subordinate, specialist, and cryptic species). Also, ant foundresses (i.e., colony-founding queens) can be considered analogous to dispersing plant seeds. Ants are particularly sensitive to changes in resources, moisture, and temperature, which makes them good indicators of environmental changes, ecosystem health and functioning. Generally, the species richness of ants is positively associated with habitat diversity, which may also affect the functional diversity of their assemblages. Topographically complex areas may contain a higher diversity of microhabitats providing suitable nesting sites and a higher amount of exploitable resources for different functional groups of ants. Plants have long been recognized as bioindicators and can indicate the naturalness of their habitat. The approach of naturalness indicator values is like the original Ellenberg-type indicator values and has been used successfully to study disturbance. Some species indicate disturbed sites, while others prefer less disturbed or natural habitats. For instance, the presence of many endemics, habitat specialists and endangered species within a habitat may indicate higher naturalness and higher conservation value.

Although, recent investigations have indicated that dolines serve as important habitat islands for various taxa, data on influence of these heterogenous microhabitats on the functional diversity of these taxa are lacking. In addition, since man-made activities are known to alter these habitats, the actual effect on naturalness of doline vegetation is sparse. To fill these gaps, the doctoral study was done to assess the effect of habitat heterogeneity and human disturbance on different taxa (ant and plants) in two Hungarian karst areas. Our key findings are summarized below.

In the first study, we hypothesized that dolines could support a wide range of microclimatic conditions and that they have the capacity to support diverse ant and plant assemblages. The influence of four different microhabitats in dolines (south-facing slopes, bottoms, and north-facing slopes) and surrounding plateau on the distribution patterns of ants and plants were investigated in the Bükk Mountains. Our results showed that the distributions of different functional groups of both ants and plants respond to the fine-scale microclimatic differences among the microhabitats in a similar manner. In conclusion, enclosed depressions (dolines) in karst surfaces provide a wide array of microclimatic habitats that have the capacity to support various taxa in different phyla (Arthropoda and Tracheophyta) under various climatic trends. These highly complex environments topographically present diverse microclimates. Hence, these dolines may be crucial in facilitating the in-situ persistence of numerous species under local and global climate oscillations. This implies that modelling of climate change impacts on the distribution of biodiversity will need to consider fine-scale topographic variation occurring within tens of meters to arrive at accurate predictions.

In the second study, we hypothesized that microhabitat heterogeneity within dolines has a positive effect on the functional diversity of ant assemblages by supporting some specific functional groups and traits that are rare on the plateau and possibly could be eliminated during global warming. We also assumed that the increasing cover of resource-poor environments (e.g., *F. sylvatica* forests) may compromise the capacity of dolines to act as functional refugia for ants within karst landscapes. The influence of habitat heterogeneity (dolines vs. plateau) and vegetation structure (*F. sylvatica* cover) on certain functional groups and traits of ant assemblages were investigated in the Bükk Mountains. We found that dolines harbor specific functional groups and traits that are rare in the surrounding habitats, and that vegetation structure on the surrounding plateau may have the potential to influence the functional diversity of ant assemblages within dolines. Our results demonstrate strong relationships between environmental heterogeneity and the distribution of functional groups and traits among ant assemblages in karst ecosystems. Our findings indicate that ants are reliable model organisms and possible indicators for identifying those locations that have the capacity to provide safe havens for different functional groups of species. We provided further evidence to the hypothesis that heterogeneous karst landscapes may maintain functionally diverse animal assemblages and play an important role in buffering the negative effects of global warming. Proper management and conservation of these safe havens may mitigate the rate of biodiversity loss under global warming.

In the last study, we hypothesized that anthropogenic activities may alter the conservation value of dolines. The effects of different human disturbance (human-mediated invasion of

C. epigeios and intensive forestry management) on naturalness of doline habitats were investigated in the Bükk and Mecsek Mountains. Our study further seeks to compare the naturalness of grassland (invaded by *C. epigejos* vs. non-invaded) and forested habitats (young forests vs. old forests) in the dolines of two Hungarian karst areas using the naturalness indicator values of plants. Our results showed that local anthropogenic disturbances such as human mediated invasion of dominant grassland competitors and extensive forestry activities negatively influence the degree of naturalness in dolines and alter the capacity of dolines to support valuable species. On the other hand, dolines with natural vegetation continuously provide unique habitats for a high diversity of valuable species and indicate high naturalness. To maintain the naturalness of vegetation in these doline habitats, the populations of ruderal competitors should be eliminated, and sustainable forest management should be adapted. This just implies that measures for conservation need to put into consideration the various impacts of disturbance to these doline habitats. Also, there are still open questions with regards to the effects of different disturbances on the naturalness in dolines that need to be answered to determine which conservation strategies will be particularly suitable for valuable species in a warming climate.

8 Összefoglalás

A Föld szárazföldi területeinek körülbelül 20%-át karsztos területek borítják. A mészkő területeken az oldási folyamatok jelentősen hozzájárulnak a felszíni és felszín alatti formák képződéséhez, mint pl. barlangok, karrok, völgyek, és felszíni mélyedések (oldásos töbrök, víznyelők, vagy szakadéktöbrök). A karsztterületek fontos ökoszisztéma szolgáltatásokat is nyújtanak. A töbrök sajátos geomorfológiája és mikroklímája számos olyan élőhely fennmaradását teszi lehetővé, ahol a fajösszetétel és a diverzitás jelentősen változik a környezeti heterogenitással. A töbrök menedékhelyként is funkcionálhatnak számos veszélyeztetett faj számára. Azonban bizonyos emberi hatások és beavatkozások jelentősen megváltoztatták e felszínformák fajmegőrző potenciálját.

A töbrök abiotikus tulajdonságai (alak, méret és kitettség) és a kapcsolódó környezeti tényezők (pl. levegő hőmérséklete, páratartalma, s a talajnedvesség) alapvetően meghatározzák a töbrök biodiverzitási mintázatait. Ezek a tulajdonságok a biotikus tényezőkkel közösen olyan mikroélőhelyek kialakulását eredményezik, amelyek alapvetően meghatározzák a fajok túlélését. Ezek a mikroélőhelyek melegebbek, szárazabbak, hűvösebbek és/vagy nedvesebbek lehetnek a terület regionális klíma által meghatározott élőhelyeinél. Ebből az is következik, hogy a regionális környezeti változásokat a fajok rövid távon belüli vándorlással átvészelhetik. Számos tanulmány szerint a töbrök lehetővé teszik olyan fajok fennmaradását, melyek a környező tájban már nincsenek jelen, vagy igen ritkák. Különösen az endemikus, montán és reliktum fajok számára lehetnek fontos refúgiumok, melyek különösen veszélyeztetettek a globális felmelegedés és egyes antropogén behatások miatt.

Számos töbröt jelentősen átalakítottak az elmúlt évszázadokban, pl. mezőgazdasági művelésre, kertészkedésre, legeltetésre vagy vízkitermelésre alkalmas helyeket hoztak bennük létre. Ezek a beavatkozások negatívan befolyásolhatták a töbrök refúgiális kapacitását, s természetességét. Magyarországon pl. az erdőművelés és a legeltetés évszázadokon keresztül jelentősen befolyásolta a töbrök élővilágát.

Disszertációmban a növényeket és hangyákat választottam modell organizmusokként a töbrök fajmegőrző potenciáljának vizsgálatához. Korábbi vizsgálatok alapján a növények és a hangyakolóniák között számos hasonlóság figyelhető meg környezeti igényeik, az egy adott élőhelyre kifejtett ökológiai hatásuk, terjedésük sajátossága, kompetíciós jellemzőik, funkcionális tulajdonságaik, stb. tekintetében. A növényekhez hasonlóan a hangyák szintén érzékenyek a környezeti változásokra, pl. a tápanyagforrás, hőmérséklet és nedvesség változásaira, ezért jó indikátorszervezeteknek tekinthetők, s fontos információkat szolgáltatnak az ökoszisztémák állapotáról. Általánosságban elmondható, hogy a hangyák fajgazdagsága pozitív kapcsolatban áll az élőhelydiverzitással, ami a hangyaközösségek funkcionális diverzitását is befolyásolhatja. A topográfiai szempontból komplex élőhelyek számos olyan mikroélőhelyet nyújtanak, melyek megfelelő fészkelőhelyet, s nagyobb mennyiségű tápanyagforrást biztosítanak a hangyák különböző funkcionális csoportjai számára. A kutatók a növényeket, mint érzékeny indikátorszervezeteket, régóta használják az egyes élőhelyek természetességének jellemzésére. Az Ellenberg-féle indikátorértékekhez hasonlóan a természetességi állapotot jelző indikátorok is széles körben használatosak. A fajok egy része zavart élőhelyet jelez, míg más fajok (pl. endemizmusok) a kevésbé zavart vagy a természetes élőhelyek indikátorai.

Habár a publikációk egy része kiemeli, hogy a töbrök fontos élőhely-szigetekként funkcionálhatnak a karsztos tájakon belül, a közösségek funkcionális diverzitására kifejtett hatásokról keveset tudunk. Emellett a különböző emberi behatásoknak a töbrök természetességére gyakorolt hatásairól is keveset tudunk. Ahhoz, hogy ezeket a hiányosságokat pótoljuk, két hazai karsztterületen végeztünk vizsgálatokat annak megállapítására, hogy a töbrök élőhelydiverzitása és az emberi zavarás miként befolyásolja a töbrök élővilágát.

Az első tanulmányban megvizsgáltuk a bükki töbrök mikroélőhelyeinek és a környező platónak a növény- és hangyaközösségeit. Megállapítottuk, hogy a töbrök számos olyan speciális mikroklimatikus adottsággal rendelkező élőhelyet tartanak fenn, ahol különböző élőlénycsoportok élhetnek túl egy változó klímában. Ezért a töbrök számos faj számára segíthetik a helyben történő fennmaradást a lokális- és regionális klímaingadozások során. Eredményeink azt sugallják, hogy a klímaváltozás hatásait értékelő modellezés során a finom léptékű topográfiai változásokat is figyelembe kell venni, hogy minél pontosabb előrejelzéssel tudjunk élni a fajok előfordulási mintázataiban bekövetkező változásokkal kapcsolatban.

A második tanulmányban azt vizsgáltuk, hogy a töbrök mikroélőhelyei a hangyák milyen funkcionális csoportjai és jellegei számára biztosíthatnak menedéket, s ezek közül melyek azok, amelyek a klímaváltozás miatt különösen veszélyeztetettek. Megvizsgáltuk továbbá, hogy a hangyák számára tápanyagszegény élőhelyek (pl. bükkösök) töbörbeli és töbrök körüli előfordulása hogyan befolyásolja a fenti mintázatokat. Megállapítottuk, hogy a bükki töbrök olyan hangya funkcionális csoportoknak és jellegeknek nyújtanak menedéket, melyek a környező tájban ritkák, s hogy a töbör körüli erdőborítás jelentősen befolyásolhatja a töbrök hangyaközösségeinek funkcionális diverzitását. Alátámasztottuk, hogy a hangyafajok kiváló modellorganizmusoknak és indikátorszervezeteknek tekinthetők a jelenlegi és a potenciális refúgiumok azonosítása során, s hogy a töbrök változatos összetételű állati közösségeknek nyújthatnak menedéket. A töbrök megfelelő kezelésével refúgiális kapacitásuk hosszabb távon is megőrizhető.

A harmadik tanulmányban az emberi tevékenység töbörnövényzetre gyakorolt hatásait vizsgáltuk a Bükkben és a Mecsekben. Különböző típusú ember által indukált zavarások hatásait vizsgáltuk (*Calamagrostis epigeios* inváziója és az erdőművelés) a töbrök természetességére. Eredményeink azt mutatták, hogy az emberi beavatkozások jelentősen módosíthatják a töbrök növényzetét, s annak természetességét. Ezek a beavatkozások gyakran negatívan hatnak, s megváltoztatják a töbrök refúgiális kapacitását. A töbrök természetességének megőrzéséhez a ruderális kompetítorok visszaszorítására és természetközeli erdőgazdálkodásra van szükség. A természetvédelmi intézkedések során a különböző emberi behatások komplex elemzése nélkülözhetetlen. További vizsgálatokra van szükség annak megállapítására, hogy a különböző emberi behatások hogyan befolyásolják a töbrök természetességét, s ezek negatív hatásainak mérséklésére milyen konzervációs stratégiákat szükséges kidolgozni.

9 Acknowledgement

Firstly, I would like to express my deepest love and gratitude to my family for being my best support system during this whole process. My parents Marilyn and Bernard, for constantly checking my well-being and reminding me to take care of myself. My beautiful sisters and closest confidantes Beverly, Liberty, Katrina, and Loren, for helping me cope with my homesickness and encouraging me not to give up especially during the tough times. A special thanks to my boyfriend Zsolt, for always being there for me and for introducing me to the Hungarian culture, and to his mom, for welcoming me in their home and for the hearty homemade Hungarian dishes.

I am highly grateful to my supervisors, Dr. Zoltán Bátori and Dr. Gábor Lőrinczi, for their kindness and full academic support throughout my PhD. Utmost heartfelt thanks to Dr. Zoltán Bátori for giving me the opportunity to take part in his research project, fieldworks, and publications; for introducing me to the interesting world of karst dolines and for willingly and enthusiastically sharing his expertise; for all the scientific and non-scientific discussions; for all the coffee and eating sessions. Sincerest gratitude to Dr. Gábor Lőrinczi for his patience not only in editing this thesis but also in answering all my questions about ants. My special thanks to the head of department, Dr. Zsolt Pénzes, for accepting me as a PhD student at the Department of Ecology, University of Szeged and for all his technical support during my PhD. Special mention to my fellow PhD students in Szeged, Jelena and Vaishali, many thanks for the friendship, for the good and bad times, and for the delicious foods and drinks we have shared together. Thankful as well to my good friends in Budapest, Chopa, Madel, and Glary who are always there to share their small space whenever I will visit Budapest. I want to extend my appreciation too to the students, staffs and faculty members of the Department of Ecology who also played an important role in my PhD journey, to Peti, Gabi and most especially to Orsi, for inviting me to participate in her PhD research and including me in the red wood ant publications; to Anna, for the chitchat during my stay in the ecology lab and always for the willingness to help me whenever I will have any Hungarian-related concerns; to my professors, Dr. István Elek Maák, for tagging me along in his ant fieldworks and sharing his knowledge on ant ecology; to Dr. Attila Torma, Dr. Róbert Gallé, and Dr. Csaba Tölgyesi, for their valuable teachings in Entomology, Ecology, and R course, respectively.

I am very thankful to these institutions for their support in this PhD endeavor. To the Stipendium Hungaricum Scholarship Program of the Tempus Public Foundation and the Ministry of Foreign Affairs and Trade of Hungary for funding my PhD study. To Dr. Zoltán Bátori's research project namely NKFI K 124796 which made it possible for me to conduct my PhD research in Hungary. The research was also supported by the ÚNKP-21-5-581-SZTE New National Excellence Program of the Ministry for Innovation and Technology from the source of the National Research, Development, and Innovation Fund. To the Commission on Higher Education (CHED) of the Philippine government for endorsing me to the Stipendium Hungaricum Scholarship Program and for providing additional financial support (Partial Foreign Scholarship Grant) for my PhD study in Hungary. To the Department of Forest Biological Sciences, College of Forestry and Natural Resources, University of the Philippines Los Baños (UPLB), my home institution, for allowing me to undergo a four-year study leave to pursue my PhD at the University of Szeged.

I want to express my thanks to all the people who contributed and played an important role throughout this PhD endeavor, including the ones I forgot to mention. Additionally, I would like to dedicate this work to those who stayed with me and believed in me regardless of my shortcomings. Lastly, I will be always grateful for everything to GOD ALMIGHTY.

To everyone, Thank you very much! Maraming Salamat po! Nagyon köszönöm szépen!

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11 List of publications

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Publications related to the PhD thesis

Aguilon, D.J., Vojtkó, A., Tölgyesi, C., Erdős, L., Kiss, P.J., Lőrinczi, G., Juhász, O., Frei, K., & Bátori, Z. (2020). Karst environments and disturbance: evaluation of the effects of human activity on grassland and forest naturalness in dolines. *Biologia, 75*, 1529–1535. **IF$_{2020}$: 1.350 (Q3)**

Bátori, Z., Vojtkó, A., Maák, I.E., Lőrinczi, G., Farkas, T., Kántor, N., Tanács, E., Kiss, P.J., Juhász, O., Módra, G., Tölgyes, C., Erdős, L., **Aguilon, D.J.** & Keppel, G. (2019). Karst dolines provide diverse microhabitats for different functional groups in multiple phyla. *Scientific Reports, 9*, 7176. **IF$_{2019}$: 3.998 (D1)**

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Aguilon, D.J., Velasco, L.R.I, & Medina C.D. (2015). Effects of larval rearing temperature and host plant condition on the development, survival, and coloration of African armyworm, *Spodoptera exempta* Walker (Lepidoptera: Noctuidae). *Journal of Environmental Science and Management, 18*, 54–60. **IF$_{2015}$: 0.250 (Q3)**

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