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Karstic Microrefugia Host Functionally Specific Ant Assemblages

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Karst landscapes are among the topographically most complex systems with various microhabitats, where species can persist despite unfavourable macro-environmental changes. These microhabitats can also function as stepping stones during range shifts. Although the enclosed depressions (dolines, sinkholes or tiankengs) of karst landscapes may act as such safe havens, data on the functional diversity of their animal assemblages are scarce. Here, we investigate the functional diversity (i.e., certain functional groups and functional traits) of ant assemblages in dolines and study whether dolines surrounded by resource-poor environments (i.e., *Fagus sylvatica* forests) may function as safe havens for different kinds of ants. We found that dolines have the potential to maintain distinctive ant assemblages characterised by specific functional groups and traits that are rare in the surrounding habitats. Although continuous *Fagus sylvatica* cover in dolines had a detrimental impact on ant assemblages, grassland dolines surrounded by grasslands or *Fagus sylvatica* forests supported the presence of some specific functional groups and traits. These results suggest that conservation management needs to consider the influence of vegetation characteristics not only in dolines but also on the surrounding plateau. Moderate grazing and/or mowing would be desirable in order to prevent shrub encroachment into grasslands to ensure optimal vegetation structure for ants in the long run. Therefore, proper management and conservation of these safe havens may mitigate the rate of biodiversity loss under global warming. There is a need to explore a wide variety of taxonomic groups and taxon-specific traits in parallel with the quality of the surrounding habitats when evaluating current and potential microrefugia.

Keywords: doline, functional group, functional trait, hostile environment, microhabitat, refugia, safe haven, tiankeng

INTRODUCTION

Microrefugia are small areas that retain locally favourable environments where species can survive during regional environmental changes (Keppel et al., 2012, 2015; 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; Dobrowski, 2010; de Aguiar-Campos et al., 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 emphasise 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).

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, covering nearly 20% of the Earth's land surface, and constituting one of the topographically most complex terrains (White et al., 1995; Culver, 2000; Bátori et al., 2020). These landscapes support several habitats, such as caves, limestone pavements, valleys, and enclosed depressions (dolines, sinkholes or tiankengs), where species composition and diversity vary with environmental heterogeneity (Whiteman et al., 2004; Bátori et al., 2009; Mammola et al., 2019). Botanists have long recognised the valuable role of these habitats as ideal natural laboratories in which to study multiple environmental gradients, thermal stability and their effects on plant species composition and vegetation patterns. Studies have shown that dolines may provide microhabitats for unique plants that are rare or absent from the surrounding landscape (Beck von Mannagetta, 1906; Horvat, 1953; Kobal et al., 2015), further reinforcing the idea that these depressions can function as habitat islands (Özkan et al., 2010; Bátori et al., 2014, 2017; Su et al., 2017). In addition, the accumulation of cold-adapted plants (e.g., high montane and glacial relict species) within certain microhabitats of dolines – such as poleward-facing slopes and bottoms – is a prime indicator of the presence of current warm-stage microrefugia. Although recent investigations have indicated that dolines may also provide safe havens for various functional groups of animals from different phyla (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 taxa is scarce or completely lacking. Furthermore, most of these studies do not provide information about the effects of habitat heterogeneity and related vegetation patterns on the functional diversity of animal assemblages within dolines. In this paper, we focus on the distribution patterns of ants in habitats inside and outside of forested and grassland dolines in a mountainous landscape in northern Hungary.

Ants are particularly sensitive to changes in resources, moisture and temperature (Sanders, 2002; Dolek et al., 2009), which makes them reliable 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). 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 changes 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 (e.g., *Fagus sylvatica* forests with low resource availability) create unfavourable conditions for many ants (Dolek et al., 2009; Wiezik et al., 2015). Results of the abovementioned studies suggest that habitat 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).

Here, we investigate how certain functional groups and traits of ant assemblages change with habitat diversity (dolines vs. plateau) and forest cover (*Fagus sylvatica* cover). We hypothesized that (1) habitat 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 would otherwise be eliminated in a warming climate, and that (2) the increasing cover of resource-poor environments (e.g., *Fagus sylvatica* forests) may compromise the capacity of dolines to act as functional refugia for ants within karst landscapes. We predicted that the extreme microclimatic conditions (i.e., warm and dry microhabitats on south-facing slopes vs. cool and moist microhabitats on north-facing slopes) within dolines (Bátori et al., 2019) favour species adapted to very different environmental conditions, while less extreme conditions on the plateau favour species adapted to intermediate conditions. The island-like attributes (e.g., funnel-shaped geometry of dolines) and the presence of *Fagus sylvatica* forests on the plateau may reinforce the spatial isolation of grassland microhabitats within dolines, resulting in the coexistence of less aggressive species or species with different social structure (cf. Tavella et al., 2018). We believe that this study provides further evidence to the hypothesis that heterogeneous karst landscapes may maintain functionally diverse animal assemblages and will play an important role in buffering the negative effects of global warming.

MATERIALS AND METHODS

Study Area

Our study area is located on the karst plateau of the Bükk Mountains in northern Hungary (48°04′31″ N, 20°29′57″ E; altitude: between 780 and 950 m), within the Bükk National Park (**Figures 1a,b**). Mean annual temperature is 6.3°C and mean annual precipitation is 800 mm (Dövényi, 2010). Solution dolines are characteristic landforms of the area, having high topographic complexity (**Figures 1c,d**) and unique microclimate (Bárány-Kevei, 1999). The north-facing slopes of dolines receive less insolation than bottoms, south-facing slopes and the plateau, and therefore are consistently cooler and moister than their surroundings. 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 is a

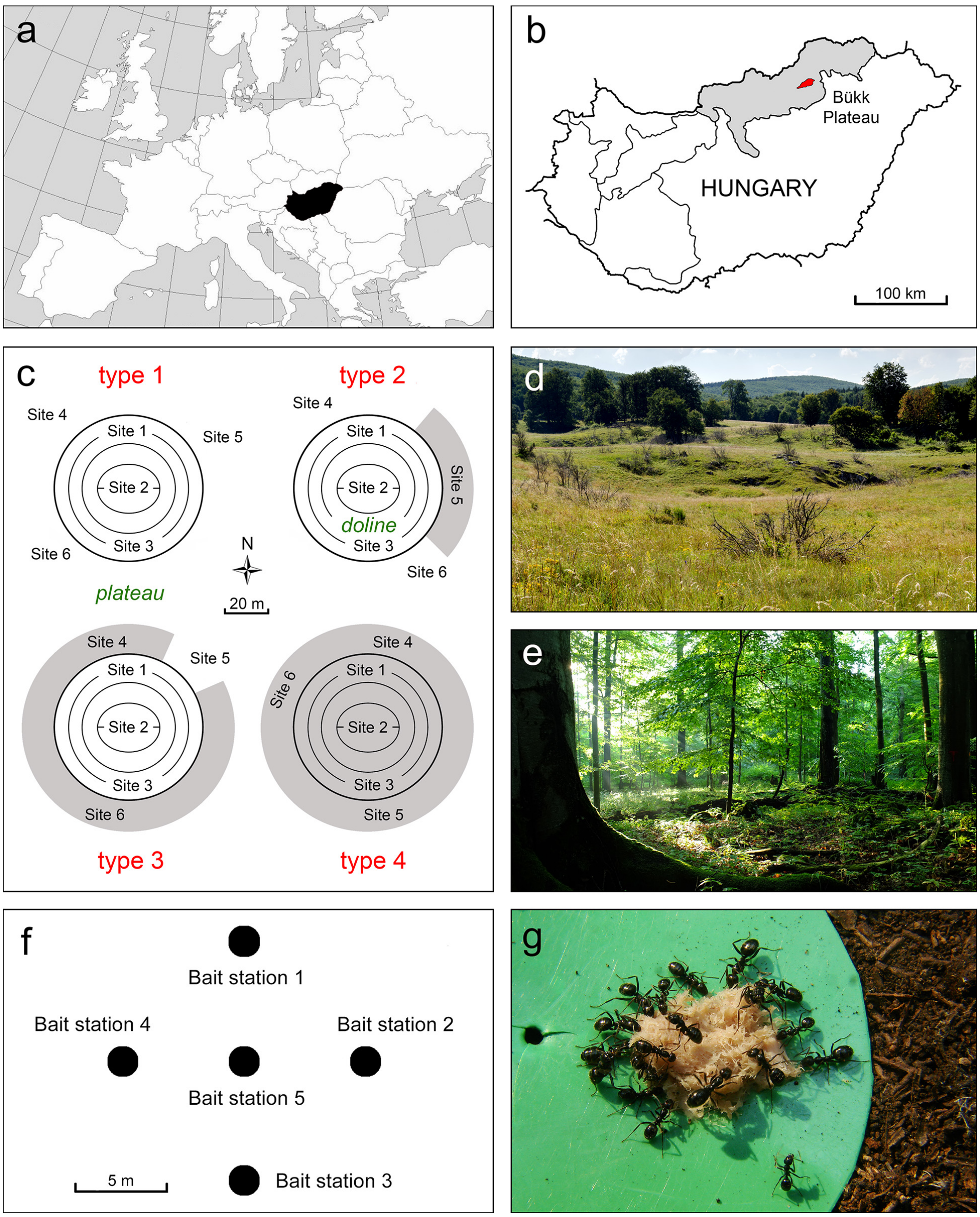

FIGURE 1 | Study region, study sites and sampling design. **(a)** Location of Hungary within Europe. **(b)** Location of the study region in Hungary. **(c)** Location of the study sites (site 1–6) in and around dolines. Forest cover is indicated by grey shading (doline types 2–4). **(d)** Grassland doline surrounded by grasslands. **(e)** *Fagus sylvatica* forest on the plateau. **(f)** Set-up of bait stations in a cross-shaped pattern. **(g)** Ants feeding on a bait.

typical phenomenon in doline bottoms, creating cool and moist conditions (Lehner et al., 2017).

European beech (*Fagus sylvatica*) is the dominant tree species within the study area (**Figure 1e**), 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. Mesic and semi-dry meadows are the most common grassland types on the plateau (Vojtkó, 2001). The concentration of high montane and glacial relict plants (e.g., *Aconitum moldavicum*, *Bupleurum longifolium*, and *Dracocephalum ruyschiana*) on the bottom and north-facing slopes of these dolines indicates the presence of current warm-stage microrefugia (Bátori et al., 2017).

Sampling Design

According to the vegetation cover (grassland vs. forest) inside and surrounding (i.e., plateau) the dolines, four doline types were identified as follows: 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%) (**Figure 1c**). Forested dolines surrounded by different amounts of grassland were absent from the study area. Three large solution dolines (diameter: 80–100 m, depth: 10–15 m) were selected from each type (12 dolines in total) to assess the species composition and relative abundance of ants. Six sampling sites were selected for each doline (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 located at least 20 m from each other. In types 2 and 3, the number of forest and grassland sites on the plateau corresponded to the relative proportions of the two habitat types.

The species composition and relative abundance of ants were assessed by non-destructive sampling methods such as baiting and hand collecting (cf. Bátori et al., 2019). Five bait stations were established at each site in a cross-shaped pattern at 5-m intervals (360 bait stations in total: 220 bait stations in grasslands, and 140 bait stations in forests) (**Figures 1f,g** and **Supplementary Table 1**). We used plastic discs (8 cm in diameter) with a quarter-teaspoon of tuna and honey mixture (1:3) as baits, and observed the foraging activity of ants every 40 min in five observation periods; the first observation started at 7:00 a.m., while the last started at 9:40 a.m. (overlapping with the daily peak activity period of ants). The presence and number of individuals belonging to different ant species were recorded at the baits during each observation period. Additionally, hand collecting was also employed to validate the species identity of occurring ants and to register those species that potentially avoided the baits. During hand collecting, we visually searched the ground surface at each site for 5 min, collecting any individuals (workers, gynes, etc.) found. Sampling was carried out in August 2018 in clear weather.

Ants were identified to morphospecies or species level whenever possible in the field, and representatives were collected and preserved in 95% ethanol for later species validation. All the collected specimens were identified using the keys of Czechowski et al. (2012) and Seifert (2018), and deposited at the Department of Ecology, University of Szeged. Nomenclature follows the Bolton's catalog (Bolton, 2020) and the Hymenoptera Name Server (Johnson, 2007).

Species Grouping and Data Analysis

Before analysis, 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 (Czechowski et al., 2012; 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) (**Table 1** and **Supplementary Table 2**). 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.

The diagnostic species of habitats (doline vs. plateau) and doline types (types 1–3) were determined by fidelity calculations using the phi (Φ) coefficient of association, which ranges from –1 to + 1 (Tichý and Chytrý, 2006). Calculations were based on data from baits, and species with $\Phi > 0.1$ were considered diagnostic (Fisher's exact test, $p < 0.05$). The highest value of phi was 0.3 in our case (see section "Results"). The value of + 1 would mean that the ant species occurred on all baits of the target habitat or doline type and was absent from the baits of the other habitat or

TABLE 1 | Functional groups and traits used in the study.

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

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 did not use multi-trait approaches. We used generalized linear mixed-effects models (GLMMs) to analyse 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

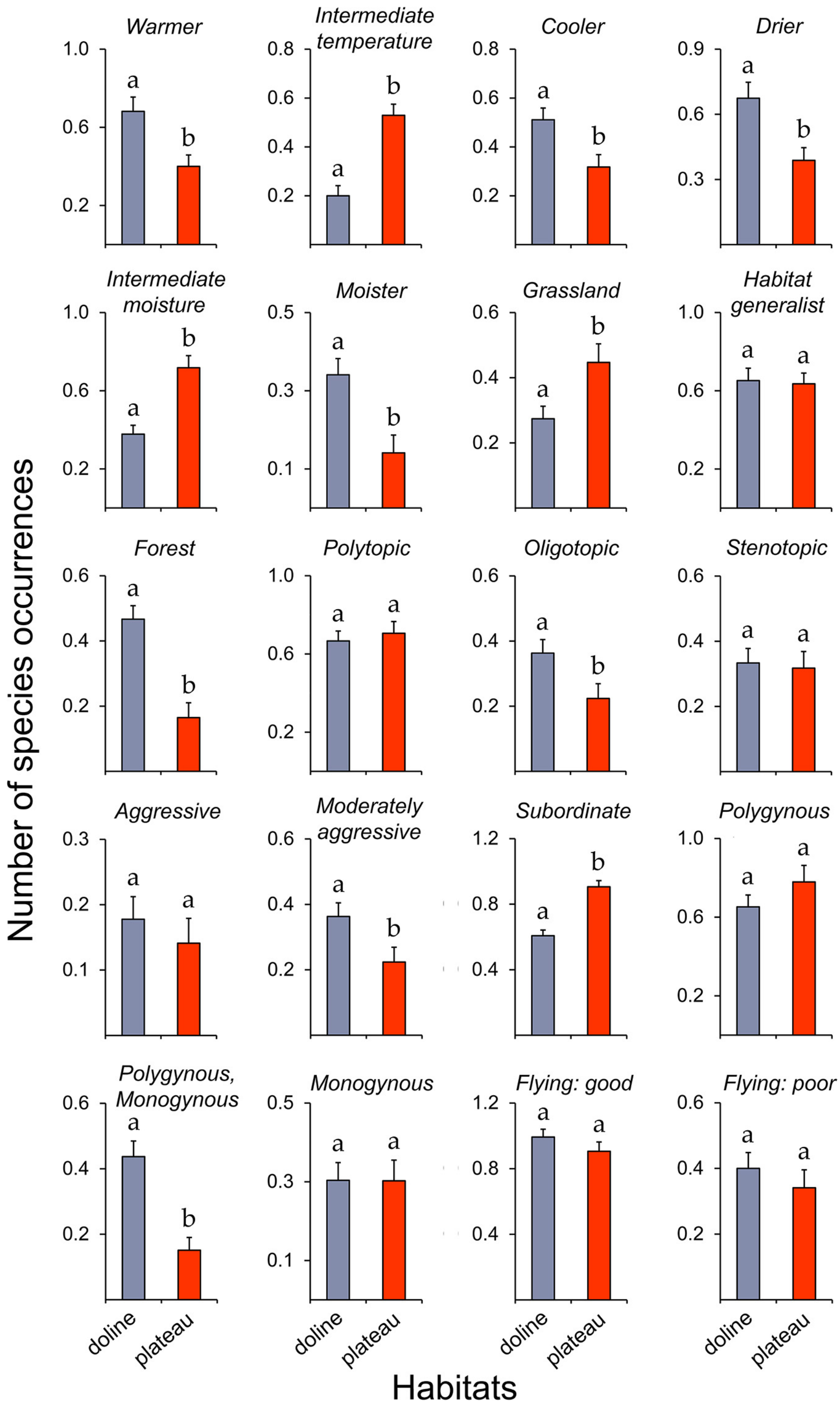

FIGURE 2 | Occurrences of the different functional groups and traits (see **Table 1**) of ant species (mean ± SE) between dolines and the plateau. Different lowercase letters indicate significant differences between the two habitats (see **Table 2**).

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 a 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.

RESULTS

Diagnostic Species

A total of 22 ant species were found in the study area (**Supplementary Table 2**). Baiting yielded 21 species, while 15 species were obtained by hand collecting. *Lasius platythorax* (fidelity value: 0.18), *Myrmica ruginodis* (0.23), *M. sabuleti* (0.27), and *Tetramorium* cf. *caespitum* (0.16) were diagnostic for dolines, while *L. niger* (0.24) and *M. 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 *Tetramorium* cf. *caespitum* (0.26) for types 1, 2 and 3, respectively.

Functional Group and Trait Composition

We did not find significant difference between the total number of species in dolines and the plateau (**Table 2**). However, dolines and the plateau differed significantly from each other with respect to many functional groups and traits (**Figure 2**). 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 2**).

The total number of species and most functional groups and traits did not differ significantly among the different doline types (**Figure 3**, **Table 3**, and **Supplementary Table 3**). 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.

Hand collecting confirmed the results of baiting. For instance, the proportion of 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 2 | Comparisons of species numbers and ant species occurrences related to different functional groups and traits (see **Figure 2** and **Table 1**) in different habitats (doline vs. plateau) in the Bükk Mts (Hungary) using the fitted generalized linear mixed-effect models.

Species number, functional groups and traits	Model	
	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

Significant differences are indicated by bold p values.

DISCUSSION

Dolines provide microhabitats for a number of ant functional groups and traits that are rare in the surrounding habitats. This highlights the potential of dolines to function as safe havens during various environmental changes. We further demonstrated that continuous *Fagus sylvatica* cover in dolines had a detrimental impact on the species composition of ant assemblages, drastically reducing the number of functionally different species. However, higher *Fagus sylvatica* cover 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 *Lasius platythorax*), while species on the plateau indicated intermediate temperature and/or moisture conditions (e.g., *L. bombycina*, *L. niger*, and *M. scabrinodis*). This is due to the high habitat heterogeneity within dolines, introducing great variation in microclimates and soil moisture (Whiteman et al., 2004; Raschmanová et al., 2013; Bátori et al., 2019). Previous microclimatic studies indicated north-facing slopes of grassland dolines to be cooler and more humid than south-facing slopes, bottoms and plateaus during daytime, while cool-air pooling may provide higher humidity and extremely low temperatures

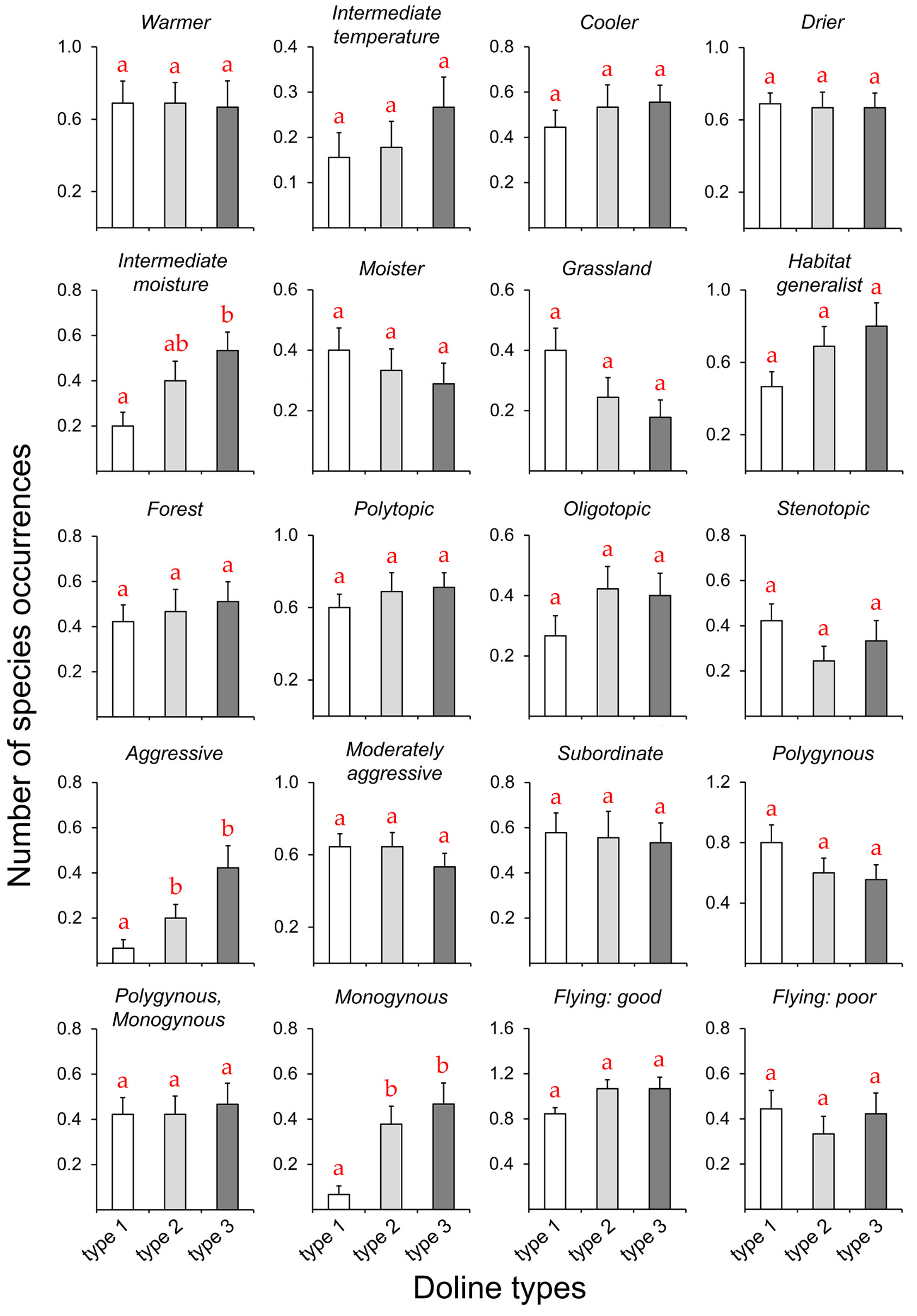

FIGURE 3 | Occurrences of the different functional groups and traits (see **Table 1**) of ant species (mean ± SE) among the different doline types (types 1–3). Different lowercase letters indicate significant differences between the types (see **Table 3** and **Supplementary Table 3**).

TABLE 3 | Comparisons of ant species occurrences related to different functional groups and traits (see **Figure 3** and **Table 1**) in doline types (types 1–3) in the Bükk Mts (Hungary) using the fitted generalized linear mixed-effect models (only statistically significant models are shown).

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

The p values were corrected with the false discovery rate (FDR) method. Significant differences are indicated by bold p values.

in doline bottoms at night (Bárány-Kevei, 1999). Although only a few studies have been published on the distribution of animal taxa in European dolines (and most of these studies focus on collapse dolines with cave entrances), their ability to support species adapted to cooler and/or moister conditions is widely accepted (Kemencei et al., 2014; Bátori et al., 2017; Su et al., 2017). For instance, Růžička et al. (2016) mention *Vitrea transsylvanica* (Mollusca: Gastropoda), *Micrargus georgescuae* (Chelicerata: Araneae), and *Ligidium germanicum* (Crustacea: Isopoda) as cold-adapted mountain species from the lower parts of a collapse doline in the Moravian Karst (Czech Republic). Similar results were published by Raschmanová et al. (2018), showing that collapse dolines in Slovakia harbour disproportionately high biodiversity and numbers of cold-adapted springtail species (Collembola). We also found that dolines may act as key habitats for a number of 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. Because only a 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., *F. truncorum*, *M. ruginodis*, and *L. platythorax*) was the highest in grassland dolines, whereas only one species (*M. ruginodis*) with few occurrences was observed in forested sites. In Central Europe, *Fagus 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 Mts (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 unfavourable for them. Considering that the study area in the Bükk Mts is dominated by *Fagus 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).

Generally, environmental heterogeneity has a positive effect on ant distribution (Ribas et al., 2003; Fagundes et al., 2015; Tavella et al., 2018), decreasing the monopolisation of space by behaviourally dominant species, thereby, providing more hiding places and foraging opportunities for subordinate species (Gibb and Parr, 2010; Koptur et al., 2010). Our results stand in contrast with these studies to some extent, indicating that baits in dolines were visited more frequently by moderately aggressive (e.g., *M. ruginodis*) and less 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 favours 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).

Gauging the effects of surrounding habitat patterns on the species composition of island-like habitats and microrefugia is challenging because of the many possible interactions between environmental variables and species distributions (Deák et al., 2020; Gentili et al., 2020). For instance, 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 this study, we investigated how certain functional groups and traits in ant assemblages of dolines change with *Fagus 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), as we observed in this study (e.g., *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. One of the possible reasons for this phenomenon 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). Moreover, considering that *Fagus sylvatica* forests provide unfavourable habitats for ants (Dolek et al., 2009; Wiezik et al., 2015), some aggressive species associated with forest habitats (e.g., *F. truncorum* and *L. platythorax*) could find suitable habitats in these dolines (e.g., via fallen twigs and higher moss cover) for their foraging and nesting activities.

Global warming has been predicted to continue altering vegetation and landscape patterns in karst landscapes (Walther et al., 2002), likely resulting in significant changes in the composition of arthropod assemblages (Wise and Lensing, 2019; Prather et al., 2020). Based on their historical and current ability to facilitate the persistence of 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 a longer period of time. However, changes to the biological environment (e.g., surrounding vegetation cover and forest height) caused by anthropogenic impacts (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 maximise the resilience of karst landscapes to global warming. In the Bükk Mts, moderate grazing and/or mowing would be desirable in order to prevent shrub encroachment into the grassland microhabitats of dolines to ensure the optimal habitat and vegetation structure for ants. Preserving the current distribution of forests and grassland patches may ensure that diverse ant assemblages are maintained by doline microhabitats.

CONCLUSION

Our results demonstrate strong relationships between habitat heterogeneity and the distribution of functional groups and traits among ant assemblages in karst ecosystems. We found that dolines may harbour 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. 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.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author.

AUTHOR CONTRIBUTIONS

ZB, GL, AV, and IM conceived and designed the experiment. GL, GM, OJ, DA, and IM conducted the field and lab work. CT performed the statistical analyses. ZB wrote the first draft of the manuscript. All authors contributed to content and editing of the manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2020.613738/full#supplementary-material

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