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## Large- and small-scale environmental factors drive distributions of cool-adapted plants in karstic microrefugia

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- **Background and aims** Dolines are small- to large-sized bowl-shaped depressions of karst surfaces. They may constitute important microrefugia, as thermal inversion often maintains cooler conditions within them. This study aimed to identify the effects of large- (macroclimate) and small-scale (slope aspect and vegetation type) environmental factors on cool-adapted plants in karst dolines of East-Central Europe. We also evaluated the potential of these dolines to be microrefugia that mitigate the effects of climate change on cool-adapted plants in both forest and grassland ecosystems.
- **Methods** We compared surveys of plant species composition that were made between 2007 and 2015 in 21 dolines distributed across four mountain ranges (sites) in Hungary and Romania. We examined the effects of environmental factors on the distribution and number of cool-adapted plants on three scales: (1) regional (all sites); (2) within sites and; (3) within dolines. Generalized linear models and non-parametric tests were used for the analyses.
- **Key Results** Macroclimate, vegetation type and aspect were all significant predictors of the diversity of cool-adapted plants. More cool-adapted plants were recorded in the coolest site, with only few found in the warmest site. At the warmest site, the distribution of cool-adapted plants was restricted to the deepest parts of dolines. Within sites of intermediate temperature and humidity, the effect of vegetation type and aspect on the diversity of cool-adapted plants was often significant, with more taxa being found in grasslands (versus forests) and on north-facing slopes (versus south-facing slopes).
- **Conclusions** There is large variation in the number and spatial distribution of cool-adapted plants in karst dolines, which is related to large- and small-scale environmental factors. Both macro- and microrefugia are therefore likely to play important roles in facilitating the persistence of cool-adapted plants under global warming.

**Key words:** Capacity of refugia, East-Central Europe, environmental gradient, high-mountain plants, karst dolines, migration processes, refugia, relicts, slope aspect.

### INTRODUCTION

Anthropogenic climate change poses one of the greatest threats to biodiversity on our planet (Bellard *et al.*, 2012; Foden *et al.*, 2013). Studying the effects of past and recent climate change on biodiversity can help us predict the likely impact of future change (Walther *et al.*, 2002; Lenoir *et al.*, 2008). Species responded to past and ongoing climate change by range-shifting (Holt, 1990; Wilson *et al.*, 2005; Chen *et al.*, 2011) and by persisting in habitats that are environmentally more stable (Willis *et al.*, 2000). As a result of these processes in response to Pleistocene and Holocene climatic fluctuations, many species, such as the mountain avens (*Dryas octopetala* s.l.) in arctic/alpine regions of the northern hemisphere, have highly fragmented distributions (Skrede *et al.*, 2006).

Range shifts in response to climate change are well documented and facilitated the persistence of species at lower latitudes during the last glacial maximum (Taberlet *et al.*, 1998; Davis and Shaw, 2001; Hampe and Petit, 2005). Similarly, more recent increases in temperature as a result of ongoing climate change have led to upward shifts in species distributions (Peñuelas and Boada, 2003; Gottfried *et al.*, 1999; Walther *et al.*, 2002). Lenoir *et al.* (2008) found that mountainous and small grassy species showed a larger shift in the optimum elevation than ubiquitous and large woody ones in the last century, highlighting that montane (cool-adapted) species are especially sensitive to climate change (Thuiller *et al.*, 2005; Engler *et al.*, 2011).

Cool-adapted species tend to occur in climatically diverse regions, where they would have survived previous climatic fluctuations by tracking their preferred habitat (Ohlemüller *et al.*,

2008). Many cool-adapted species in East-Central Europe have relatively wide distributions (Theurillat and Guisan, 2001), but their occurrence is often restricted to specific habitats (e.g. to ravine forests and north-facing rock-swards) (cf. Király, 2009). The majority of cold-adapted species prefer non-forested habitats (cf. Totland and Alatalo, 2002; Skrede et al., 2006), which provide cooler temperature extremes (Bárány-Kevei, 1999).

Cool- and cold-adapted endemic plant taxa are especially vulnerable to climate change (e.g. Kutnjak et al., 2014). Species distribution models suggest that many cool-adapted plant species in East-Central Europe will undergo range shifts and are likely to disappear from lower altitudes as a response to ongoing climate change (Theurillat and Guisan, 2001). For example, the population size of the one-sided wintergreen (*Orthilia secunda*) and yellow bird's nest (*Monotropa hypopitys*), which are considered good indicators of cool habitats in Hungary and Romania (Borhidi, 1995; Sárbu et al., 2013), are predicted to significantly decrease in the Carpathian Basin by 2100 (Beatty and Provan, 2011).

Stable habitats buffered from regional environmental change are known as 'refugia' (Ashcroft, 2010; Stewart et al., 2010; Keppel et al., 2012). While 'refugia' initially referred to places where species survived the effects of glaciations during the Last Glacial Maximum (Dahl, 1946), the term has also been applied to safe havens from recent and future climate change (e.g. Loarie et al., 2008; Keppel et al., 2012). Furthermore, the term 'microrefugia' has been used to refer to sites with locally favourable environmental conditions amidst unfavourable regional environments, which allow species to maintain viable populations outside of their main distributions (Rull, 2009, 2010; Gentili et al., 2015a). Such microrefugia may result from convergent environments, such as basins, local depressions and deep valleys (Fridley, 2009; Dobrowski, 2010; Gentili et al., 2015b). Similarly, vegetation may modify regional climatic trends to provide more buffered environmental conditions (De Frenne et al., 2013; Scheffers et al., 2014).

Karst dolines (sinkholes), small to large-sized bowl-shaped depressions of karst surfaces (Li et al., 2007), may constitute important microrefugia (Bátori et al., 2014a), as thermal inversion maintains cooler conditions within them and north-facing slopes receive less sunlight (cf. Geiger, 1950; Whiteman et al., 2004; Bátori et al., 2011). As a result, more cool-adapted plants should be found on the north-facing slopes and bottoms of dolines (Beck v. Mannagetta, 1906; Özkan et al., 2010; Surina and Surina, 2010; Kobal et al., 2015). In addition, the bottoms of dolines receive more water and nutrients, producing higher humidity and soil moisture (Bátori et al., 2009, 2011). Because some refugia would have a higher capacity to act as safe havens for biodiversity in changing climates (Keppel et al., 2015; Keppel and Wardell-Johnson, 2015), it is important to understand what factors make some dolines better refugia for cool-adapted plants than others.

In this study we focus on the capacity of dolines to provide cooler microclimates, which would make them crucial refugia for the survival of cool-adapted plants under ongoing global warming. We investigate the effects of both large- (macroclimate) and small-scale (slope aspect and vegetation type) factors on the number and distribution of cool-adapted plant taxa in dolines of four mountainous ranges [in the submontane and montane zones, up to 1400 m above sea level (m.a.s.l.)] along a

natural gradient of decreasing temperature and increasing humidity in Hungary and Romania. We predicted that the number of cool-adapted plants would increase with cooler macroclimatic conditions. If karst dolines do constitute microrefugia, cool-adapted species should be more restricted to cooler microhabitats in warmer than in cooler mountainous ranges.

## MATERIALS AND METHODS

### Study sites and sampling

Fieldwork was done in East-Central Europe during the summers between 2007 and 2015 in forested and non-forested dolines of three Hungarian mountainous areas (Aggtelek Karst area, Bükk Mountains and Mecsek Mountains) and one Romanian (Bihar Mountains) mountainous area, surrounding the Hungarian Great Plain (Fig. 1A). The sites can be arranged according to their macroclimatic conditions as follows: Mecsek, moderately warm and moderately humid [altitude (A) 300–500 m.a.s.l.; average temperature ( $T_a$ ) 9.5 °C; average precipitation ( $P_a$ ) 740 mm]; Aggtelek, moderately cool and moderately humid (A 500–600 m.a.s.l.;  $T_a$  8.3 °C;  $P_a$  680 mm); Bükk, cool and humid (A 700–900 m.a.s.l.;  $T_a$  6.3 °C;  $P_a$  800 mm) and Bihar, cold and very humid (A 1200–1400 m.a.s.l.;  $T_a$  5 °C;  $P_a$  1400 mm) (Feurdean and Willis, 2008; Dövényi, 2010). They hence constitute a natural gradient of decreasing temperature and increasing humidity.

Forested dolines were covered by beech, oak–hornbeam and ravine forests in Mecsek, oak–hornbeam and scree forests in Aggtelek, montane beech forests in Bükk and montane beech and spruce forests in Bihar. Non-forested dolines were covered by semi-dry to dry grasslands and mountain hay meadows in Aggtelek and Bükk and by semi-dry and mountain hay meadows and pastures in Bihar. Non-forested dolines were absent in Mecsek. Forest canopy cover was 75–90 % in forested dolines and grassland cover 75–100 % in non-forested dolines. The cover of the herb layer in forested dolines was variable.

We selected 21 solution dolines (Williams, 2004) that met the following criteria: (1) diameters were between 60 and 150 m and depths between 10 and 25 m, shapes were uniformly round or slightly elliptic with similar (range 0.11–0.24) depth/diameter ratios (vegetation characteristics are similar within this size range; Bátori et al., 2009, 2014a) (Supplementary Data Table S1); (2) vegetation cover was semi-natural (no signs of logging, low abundance of non-native species); and (3) signs of disturbance were few (e.g. low current grazing pressure with negligible effect on vegetation composition and structure, low rate of game damage and wind-induced tree mortality). At each site three forested and three non-forested dolines were selected except at Mecsek, where only three forested dolines were chosen (non-forested dolines were absent). We defined non-forested dolines as having a total tree cover <25 % and transects were established to pass through only non-forested (i.e. grassland) vegetation (Fig. 1B, G).

Because the greatest differences in species composition were expected between the north- and south-facing doline slopes (Bátori et al., 2014a, b), we established a transect with north-to-south orientation across each doline, traversing the deepest points (Fig. 1G). Transects began and ended on doline rims. Each transect consisted of 1 × 1-m plots spaced at 2-m intervals. We recorded the presence/absence of all herbs and shrubs in all plots.



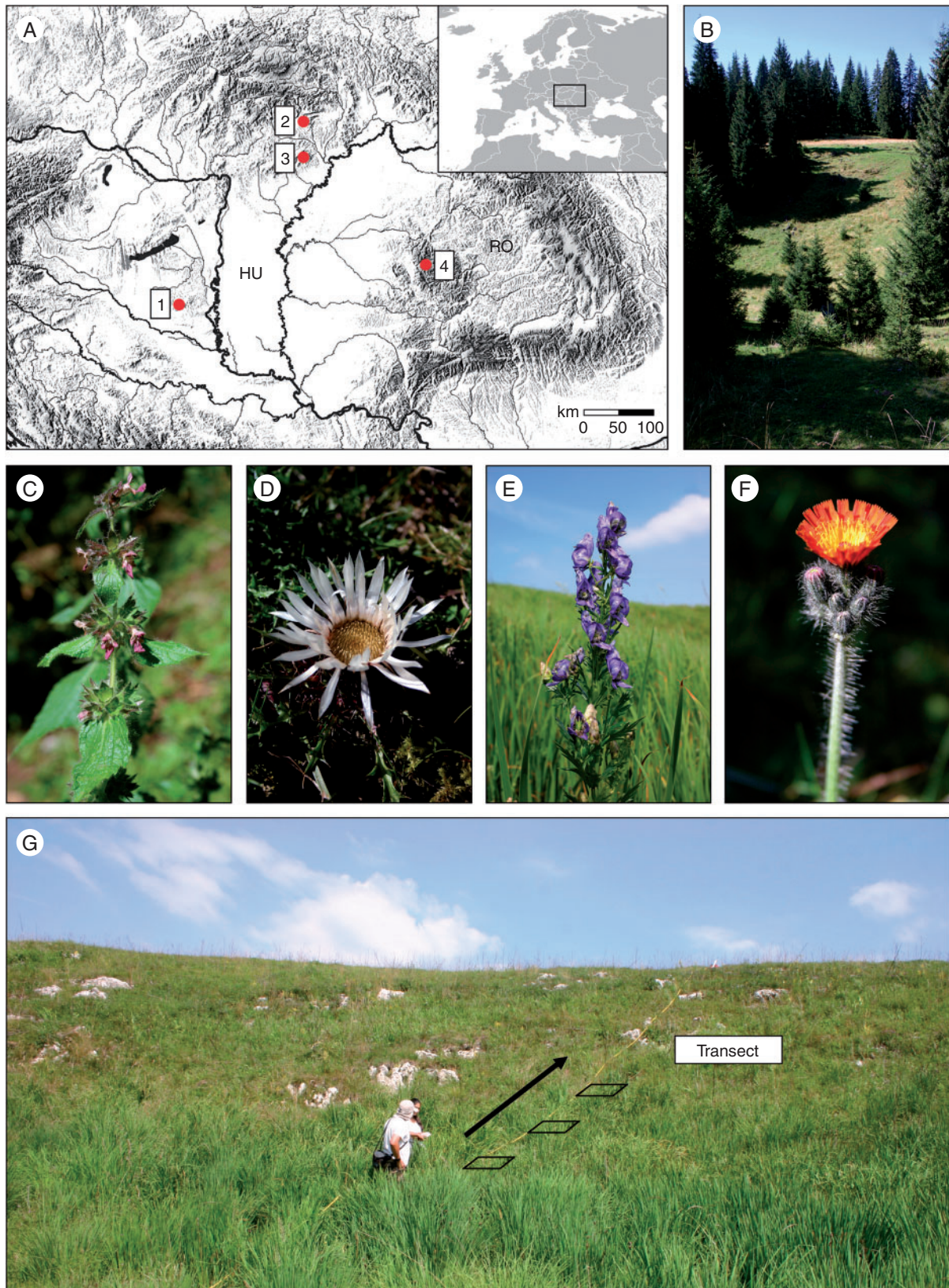


FIG. 1. (A) Location of the study sites in Hungary and Romania. 1, Mecsek Mountains; 2, Aggtelek Karst area; 3, Bükk Mountains; 4, Bihor Mountains. (B) A non-forested doline with Norway spruce (*Picea abies*) individuals in Bihor. (C–F) Some cool-adapted plants in the investigated dolines. (C) Alpine woundwort (*Stachys alpina*), Mecsek. (D) Carline thistle (*Carlina acaulis*), Aggtelek. (E) Wolfsbane (*Aconitum variegatum* s.l.), Bükk; (F) Orange hawkweed (*Pilosella aurantiaca* ssp. *aurantiaca*), Bihor. (G) Transect sampling in a non-forested doline of Bükk.



Transects were coded using capital letters for the study area (A, Aggtelek; BI, Bihar; BÜ, Bükk; M, Mecsek), small letters for the vegetation types (f, forest; g, grassland), and numbers: M<sub>f1</sub>–M<sub>f3</sub>; A<sub>g1</sub>–A<sub>g3</sub>; A<sub>f1</sub>–A<sub>f3</sub>; BÜ<sub>g1</sub>–BÜ<sub>g3</sub>; BÜ<sub>f1</sub>–BÜ<sub>f3</sub>; BI<sub>g1</sub>–BI<sub>g3</sub>; BI<sub>f1</sub>–BI<sub>f3</sub> (Table S1).

#### Defining cool-adapted plant taxa with relative temperature indicator values

Relative ecological indicators (values providing an indication about the niche of a species relative to other plant species in the area) are frequently used to assess the environmental characteristics of an area (Tölgyesi et al., 2014). The concept was developed for the characterization of Central European habitats with seven factors (continentality, light, productivity/nutrients, soil acidity, soil moisture, soil salt content and temperature) (Ellenberg et al., 1992). Each species has a value for each factor, which expresses the realized optimum of the species on a nine-degree ordinal scale (except soil moisture, with a 12-degree scale) defined along environmental gradients. The system has been adapted for the floras of several countries, such as Great Britain (Hill et al., 1999), Hungary (Borhidi, 1995), Poland (Zarzycki, 1984) and Romania (Sârbu et al., 2013).

Prior to our analyses, we classified each plant taxon according to its relative temperature indicator (*T*) value, ranging from 1 (affinity for the coolest habitats) to 9 (affinity for the warmest habitats). We considered both the Hungarian (Borhidi, 1995) and Romanian (Sârbu et al., 2013) systems, which are mostly similar (Supplementary Data Table S2). In this study, we used the term ‘cool-adapted plant’ for plants that have an indicator value of 3 or 4 for temperature in at least one of the two systems (Fig. 1C–F). Species with *T* indicator values of 1 or 2 were not present in the studied dolines. The scientific names of cool-adapted plants found along the transects are listed in Supplementary Data Table S3.

Taxonomy and species information (e.g. distribution) follow Sârbu et al. (2013).

#### Statistical analyses

Analyses were conducted at various scales: across all sites (regional); within sites; and within dolines (see below). All analyses were carried out in R (R Development Core Team, 2015). A generalized linear model (GLM) was performed using the `glm.nb` function from the MASS package (Venables and Ripley, 2002), generalized mixed effect models (GLMMs) with the `glmmadmb` function from the `glmmADMB` package (Fournier et al., 2012; Skaug et al., 2013), and automated model selection with the help of the `dredge` function from the MuMIn package (Bartoń, 2013). When an averaged best model was used, the effects of different explanatory factors were averaged across the models with  $\Delta < 4$  (Grueber et al., 2011). The `relevel` function was used to carry out *post hoc* sequential comparisons among the different factor levels when performing GLM and GLMMs. We applied sequential Bonferroni–Holm corrections to determine the exact significance levels in these cases.

**Regional scale** A GLM (negative binomial error) was used to test the effect of macroclimate on the number of cool-adapted plants in the different dolines, with macroclimate as the sole

explanatory variable ( $N = 4$ ). Because available climatic data for the study area are based on few climate stations, limiting the reliability of available, extrapolated climate layers (cf. Soria-Auza et al., 2010), we coded the macroclimate in broad categories of increasing coolness and humidity (moderately warm and moderately humid, moderately cool and moderately humid, cool and humid, and cold and very humid) according to Dövényi (2010). The number of cool-adapted plants found in each plot was summed for each doline ( $N_{\text{total}} = 21$ ), and included in the model as dependent variable.

We used GLMMs (negative binomial errors) to test the global and site-level effect of vegetation type (grassland and forest) and slope aspect (south- and north-facing) on the number of cool-adapted plants of dolines except Mecsek, where the data were not overdispersed and a Poisson error term was used. In the global model the different variables, such as vegetation type and aspect, were included as explanatory variables (i.e. fixed factors) and the mountain range (= macroclimate) as random factor. The number of cool-adapted plants found in each plot was summed for each slope ( $N_{\text{total}} = 42$ , 21 south-facing and 21 north-facing slopes), and included in the model as dependent variable.

**Within sites** Separate GLMMs were built for each site, with vegetation type (grassland and forest) and aspect (south- and north-facing) as fixed factors and the different dolines as random factors. The dependent variable was the summed number of cool-adapted plants found in the plots of a slope ( $N_{\text{total}} = 12$ , 6 south- and 6 north-facing slopes in all sites but Mecsek;  $N_{\text{total}} = 6$ , 3 south- and 3 north-facing slopes). We also compared the number of cool-adapted plants of both the forested and non-forested south- and north-facing doline slopes of each site using Mann–Whitney *U* tests on the number of cool-adapted plants within each plot.

**Within dolines** The local differences between the south- and north-facing slopes within each doline were compared with Mann–Whitney *U* tests, using the number of cool-adapted plants within each plot. In addition, the occurrences of cool-adapted plants were plotted using kite diagrams, which indicate the diversity of cool-adapted plants along the transect through the thickness of the shaded area.

## RESULTS

#### Cool-adapted plant taxa

A total of 83 cool-adapted plants (6 in Mecsek, 15 in Aggtelek, 21 in Bükk and 66 in Bihar) were recorded in the 21 dolines (Table S3). These included 18 circumpolar, 16 Eurasian, 8 European, 6 Carpathian (endemic or subendemic), 6 Central European, 5 Alpine and Carpathian, 5 Alpine, Carpathian and Balkan, 4 Central European and sub-Mediterranean, and 3 cosmopolitan plants. The remaining 12 taxa belonged to various groups (e.g. European and North European plants).

#### Regional scale

The effect of macroclimate on the number of cool-adapted plants was significant (GLM  $3.96 < z < 9.16$ ,  $P < 0.001$ ), except between Aggtelek and Bükk ( $z = 1.31$ ). The coolest site (Bihar) had the most and the warmest site (Mecsek) had the

least cool-adapted plants. Considering the effects of slope aspect and vegetation type, the best model contained both variables (i.e. full model), so no model averaging was needed. The global effect of vegetation type and aspect was significant (GLMM  $z = 3.01$ ,  $P < 0.01$  and  $z = 2.9$ ,  $P < 0.01$ , respectively). The number of cool-adapted plants was higher in the non-forested dolines and on the north-facing slopes.

*Within sites*

For the three sites with forested and non-forested dolines (Aggtelek, Bükk, Bihor), the averaged best GLMMs contained both aspect and vegetation type (Tables 1–3). The number of

cool-adapted plants on the south- and north-facing slopes differed significantly in Aggtelek (GLMM  $z = 2.1$ ,  $P = 0.03$ ), but not in Mecsek ( $z = -1.05$ ), Bükk ( $z = 1.8$ ) and Bihor ( $z = 1.9$ ). The effect of vegetation type on the number of cool-adapted plants was significant in Bükk ( $z = 2.06$ ,  $P = 0.039$ ) but not in Aggtelek ( $z = 1.45$ ) and Bihor ( $z = 0.88$ ). Differences between the number of cool-adapted plants on south- and north-facing slopes were significant in the non-forested dolines of Aggtelek (Mann–Whitney  $W = 430.5$ ,  $P < 0.001$ ) and Bükk ( $W = 446.5$ ,  $P < 0.001$ ) and in the forested dolines of Bihor ( $W = 596.5$ ,  $P < 0.05$ ) (Fig. 2).

*Within dolines*

Aspect did not have a significant effect on the number of cool-adapted plants in Mecsek (Mann–Whitney  $219.5 < W < 390.5$ ). In Aggtelek, however, the difference between the south- and north-facing slopes was significant in each non-forested doline ( $A_{g1}$ – $A_{g3}$ ) ( $26 < W < 66.5$ ,  $P < 0.001$ ) and not significant in forested dolines ( $A_{f1}$ – $A_{f3}$ ) ( $77.5 < W < 153$ ). We did not find any significant difference in the forested dolines of Bükk ( $BÜ_{f1}$ – $BÜ_{f3}$ ) ( $43 < W < 131$ ), but in two non-forested dolines

TABLE 1. Average best GLMM explaining the number of cool-adapted plants in the dolines of the Aggtelek Karst area

Model	d.f.	logLIK	AICc	$\Delta$	Weight
Slope aspect	3	-39.57	88.14	0	0.59
Null	2	-42.14	89.62	1.47	0.28
Slope aspect + vegetation type	4	-38.69	91.1	2.96	0.13

TABLE 2. Average best GLMM explaining the number of cool-adapted plants in the dolines of the Bükk Mountains

Model	d.f.	logLIK	AICc	$\Delta$	Weight
Vegetation type	3	-43.65	96.29	0	0.45
Null	2	-45.91	97.14	0.85	0.29
Slope aspect + vegetation type	4	-42.2	98.11	1.81	0.18
Slope aspect	3	-45.46	99.93	3.63	0.07

TABLE 3. Average best GLMM explaining the number of cool-adapted plants in the dolines of the Bihor Mountains

Model	d.f.	logLIK	AICc	$\Delta$	Weight
Vegetation type	3	-56.07	121.14	0	0.46
Null	2	-58.11	121.55	0.41	0.37
Slope aspect + vegetation type	3	-57.69	124.38	3.24	0.09
Slope aspect	4	-55.44	124.59	3.45	0.08

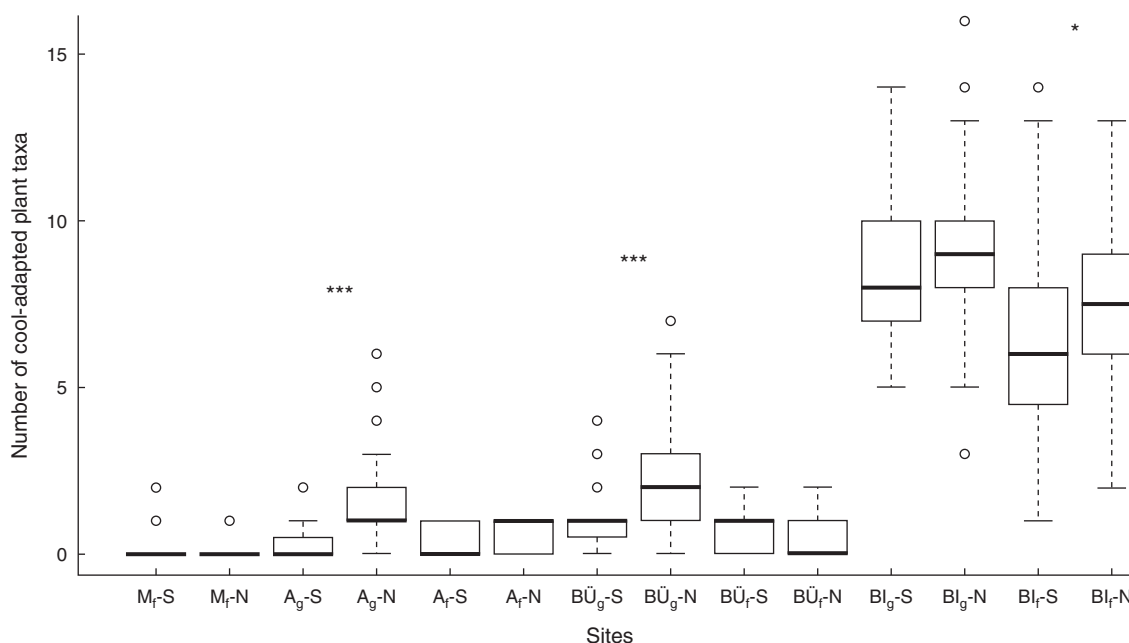


FIG. 2. Number of cool-adapted plant taxa in the dolines ( $M_f$ – $Bl_f$ ) of Hungary and Romania in site-level comparison. Boxes indicate the interquartile ranges, horizontal lines in the boxes are the medians, whiskers include all points within one interquartile range from the boxes and open circles indicate outliers from this range. Lower-case letters f and g indicate forested and non-forested dolines, respectively. Capital letters S and N indicate slope aspects (N, north-facing; S, south-facing). Significant differences in the number of cool-adapted plants on the forested and non-forested south- and north-facing slopes are indicated by asterisks (\* $P < 0.05$ ; \*\*\* $P < 0.001$ ).

the difference was significant ( $B\ddot{U}_{g2}$  and  $B\ddot{U}_{g3}$ ) ( $19 < W < 85$ ,  $P = 0.03$  and  $P < 0.001$ , respectively). In Bihar, differences between the south- and north-facing slopes were not significant in the non-forested dolines ( $BI_{g1}$ – $BI_{g3}$ ) ( $23 < W < 71.5$ ), but they were in one forested doline ( $BI_{f3}$ ) ( $W = 53.5$ ,  $P = 0.01$ ). As shown in the kite diagrams (Fig. 3), the distribution of cool-adapted plants in the dolines of Mecsek was restricted to the deepest parts of the depressions. In the non-forested dolines of Aggtelek, cool-adapted plants predominantly occurred on north-facing slopes, while in Bükk and Bihar, cool-adapted plants colonized all parts of doline slopes.

## DISCUSSION

### *The role of large- and small-scale environmental factors*

Our results show that the number and distribution of cool-adapted plant taxa in karst dolines are determined by both

large- and small-scale environmental factors. As predicted, sites with cooler and more humid macroclimates had higher numbers of cool-adapted plants. Similarly, a greater number of cool-adapted plants occurred on north-facing slopes, which receive less solar radiation and as a result have cooler microclimates (Jakucs, 1971; Rorison *et al.*, 1986). This aspect-related effect was particularly strong at the non-forested sites of intermediate suitability (Aggtelek and Bükk, with regard to macroclimate), as the least suitable site (Mecsek) had very few and the most suitable site (Bihar) had uniformly abundant numbers of cool-adapted plants (Fig. 3).

In the least suitable site, cool-adapted plants were restricted to the lowest parts of depressions (i.e. in doline bottoms), while they occurred on both upper and lower slopes in the cooler and more humid climates of North Hungary and Romania (Fig. 3). Indeed, cool-adapted plant taxa occur almost exclusively in dolines, deep valleys and sometimes on north-facing slopes in Mecsek (Bátori *et al.*, 2012) and Aggtelek (Bátori *et al.*, 2014b;

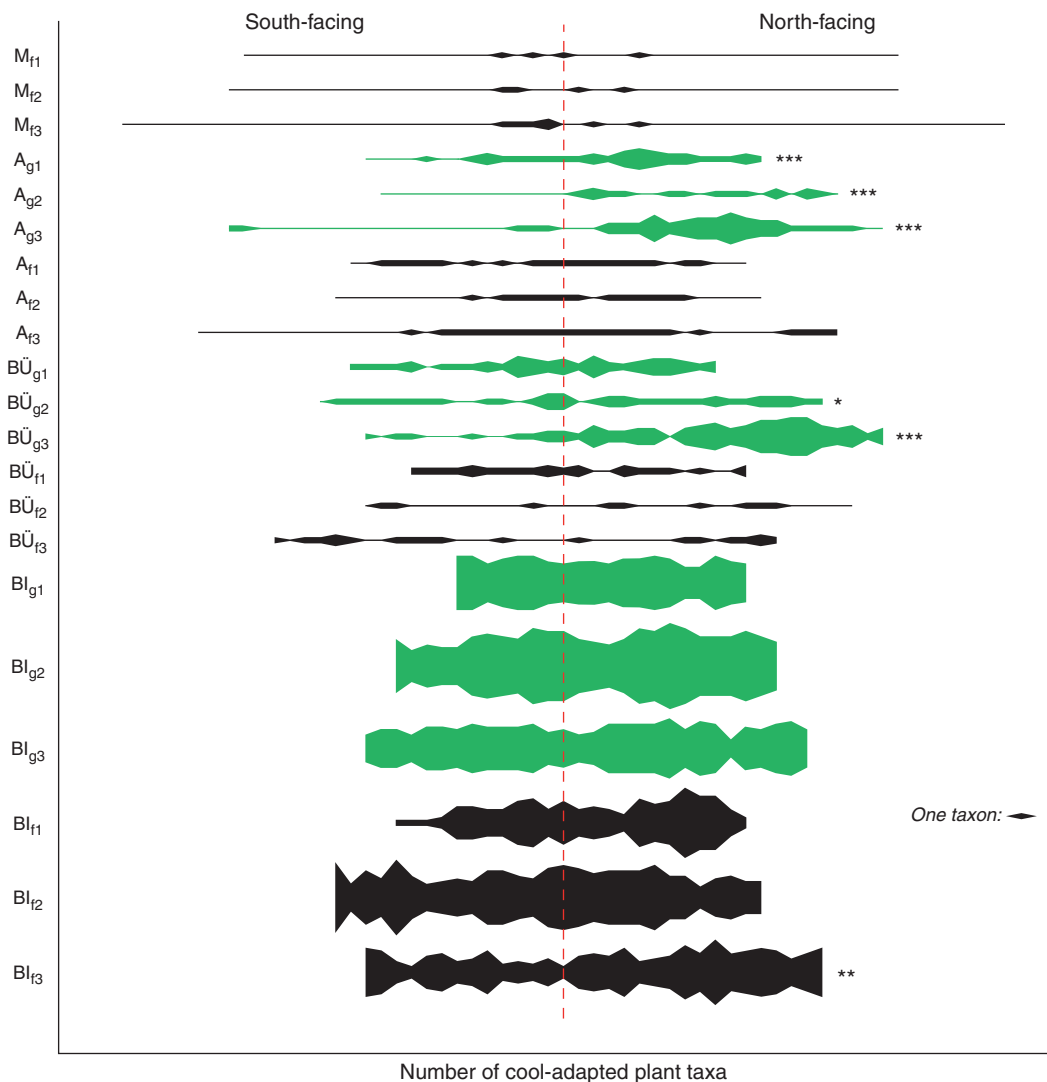


FIG. 3. Kite diagrams of cool-adapted plant taxa along the doline transects in Hungary and Romania ( $M_{f1}$ – $BI_{f3}$ ). Forested dolines are indicated in black and non-forested dolines in green. The red dashed line shows the deepest point of dolines, where slope exposure changes. Significant differences in the number of cool-adapted plants between the south- and north-facing slopes are indicated by asterisks (\* $P < 0.05$ ; \*\* $P = 0.01$ ; \*\*\* $P < 0.001$ ).

Virók *et al.*, 2014), while they also occur in the surroundings of dolines in the cooler macroclimates of Bükk (Vojtkó, 2001) and Bihar (Z. Bátori, pers. commun.). This highlights dolines as important microrefugia under warmer and less humid conditions.

Forested dolines contained fewer cool-adapted plants than non-forested ones. Extreme temperature, humidity and wind occur more frequently in non-forested depressions (cf. Bárány-Kevei, 1999; Bátori *et al.*, 2014c), resulting in a more variable microhabitat structure and presumably greater opportunities for cool-adapted plants. This is supported by other studies finding greater numbers of cool-adapted plants residing in non-forested than in forested habitats (cf. Vanderplank *et al.*, 2014; Mráz *et al.*, 2016).

The explanation for the observed patterns is complex and is related to the combined effects of macro- and microclimate (Bátori *et al.*, 2011, 2014a), individual species responses to climatic variation (Hylander *et al.*, 2015) and vegetation cover (De Frenne *et al.*, 2013; Mráz *et al.*, 2016). Our results correspond well with those for Europe in general, where refugial areas for cool- and cold-adapted species are primarily found at high elevations (mountains) at lower latitudes, and low to high elevation (from lowland to mountains) at higher latitudes (Stewart *et al.*, 2010; Ohlemüller *et al.*, 2012). They also highlight the importance of microhabitats, such as fens and bogs, slopes of V-shaped valleys and deep depressions, where local climatic conditions are similar to those of mountaintops (Rorison *et al.*, 1986; Daly *et al.*, 2010; Dobrowski, 2010).

#### *The capacity of karst dolines as future refugia*

Several studies indicate that cool and humid dolines in Europe have supported plant populations outside their species' ranges along both the north-to-south (latitudinal) and oceanic-to-continental (longitudinal) migration axes during past Quaternary climate change (Stewart *et al.*, 2010). For example the dragon's head (*Dracocephalum ruschiana*), a Eurasian floristic element occurring from the boreal–sub-boreal regions to the temperate zone, likely maintained a viable population in a large doline of North Hungary (Bükk), far from its main distribution (Király, 2009; Lazarević *et al.*, 2009). Similar examples have been provided by Horvat (1953) from the Balkan Peninsula and by Atalay (2006) from the Taurus Mountains (Turkey, Asia).

The ongoing regional warming in East-Central Europe is predicted to continue as a result of anthropogenic climate change (Bartholy *et al.*, 2008; Pongrácz *et al.*, 2011). Based on their past and current ability to facilitate persistence, karst dolines are likely to provide important microrefugia that will facilitate the persistence of cool-adapted plant taxa outside their macroclimatic envelope. However, species will respond individually to environmental change (Stewart *et al.*, 2010) and responses will differ from those in the past because past climate changes differ from the one currently experienced (Williams *et al.*, 2007).

Our results suggest that microrefugia at higher elevations and latitudes are likely to play important roles in facilitating species persistence. This corresponds to previous findings that plant responses to climate changes vary across elevational

gradients and forest types (Sykes and Prentice, 1996; Lindner *et al.*, 2010). Therefore, populations of cool-adapted plants in dolines of the least suitable site in South Hungary may be especially vulnerable to climate change. Presumably, they exist at the limits of their environmental tolerances and are unlikely to be able to shift their distribution towards cooler places. More suitable sites (North Hungary and Romania) are likely to provide suitable habitats for a longer time.

Within dolines, north-facing slopes will provide more suitable habitats for longer, corresponding to cooler and more stable microclimate on these slopes (cf. Rorison *et al.*, 1986; Daly *et al.*, 2010; Maclean *et al.*, 2016). This could allow species to shift their distributions towards the cooler and more stable microclimates of north-facing slopes and lower parts of dolines (Bátori *et al.*, 2011). Dolines may also play an important role in facilitating the long-term survival of cool-adapted endemic plant taxa (cf. Table S3). These taxa have a narrow distribution and their survival may therefore largely depend on the presence of appropriate microhabitats (Pauli *et al.*, 2012; Malanson *et al.*, 2015).

However, climate change will influence the distribution not only of cool-adapted species, but also that of other species. The distributions of the tree species oak (*Quercus* spp.), European beech (*Fagus sylvatica*) and Norway spruce (*Picea abies*) in Central Europe are likely to shift upwards (Cuculeanu *et al.*, 2002; Gebler *et al.*, 2007; Czúcz, 2011; Hlásny *et al.*, 2011). Oak distributions are predicted to shift to elevations above 400–500 m.a.s.l., optimum conditions for beech will likely shift to around 1200 m.a.s.l., and spruce production will decline at lower elevations and increase in the elevation range 1250–1550 m. This means that low-lying dolines (300–600 m.a.s.l.) in East-Central Europe could also become refugia for beech, higher-lying dolines (600–1000 m.a.s.l.) for montane beech and high-lying dolines (>1000 m.a.s.l.) for montane beech and pine forest species.

Resource-gaining sites are also sometimes considered refugia (Schut *et al.*, 2014). The doline bottoms are such resource-gaining sites, receiving more nutrients and moisture (Bátori *et al.*, 2009, 2011) and are hence potential microrefugia for a variety of functional groups, in addition to cool-adapted species. For example, marsh and wet-woodland plants (mostly not cool-adapted) do occur at the bottom of dolines, indicating high moisture conditions (cf. Bátori *et al.*, 2012). Further investigations are necessary to determine the effects of the various environmental properties found in dolines on the occurrence of various functional groups in these microhabitats.

Our study confirms karst dolines as important refugia for many plant taxa. The capacity of these microrefugia to enable the persistence of plants depends on both large- and small-scale environmental factors. Our results provide a first indication of what these factors are. They can be used as a space-for-time substitution and suggest that the buffering capacity of the East-Central European karst doline microrefugia increases with cooler macroclimates (higher elevations and latitudes) and with cooler (north-facing) aspects. Determining the potential impacts of climate change on these microrefugia allows their protection and the selection of the most appropriate conservation strategies.



## SUPPLEMENTARY DATA

Supplementary data are available online at [www.aob.oxfordjournals.org](http://www.aob.oxfordjournals.org) and consist of the following. Table S1: location, altitude (alt), diameter (di), depth (de) and depth/diameter ratio (r) of the studied dolines. Capital letters (M–BI) refer to study sites (M, Mecsek; A, Aggtelek; BÜ, Bükk; BI, Bihar) and small letters to vegetation types (f, forest; g, grassland). Table S2: temperature indicator values according to the Hungarian and Romanian systems. Table S3: scientific names of the cool-adapted plant taxa of the doline transects in Hungary and Romania. The names of endemic and subendemic plant taxa are underlined.

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