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# Forest age and topographic position jointly shape the species richness and composition of vascular plants in karstic habitats

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## Abstract

**Key message** Dolines may provide important safe havens for many plant species and play a key role in maintaining biodiversity. The combined effects of forest age and topographic position influence the biodiversity patterns of these unique habitats. Forest managers, conservationists, and researchers need to work together in order to maintain the species richness and composition of these habitats under environmental changes.

**Context** Dolines are the most prominent geomorphological features in many karst landscapes that may provide important microhabitats for many species.

**Aims** We aim to contribute to a better understanding of how forest age and topographic position influence the plant species richness and composition of vascular plants within doline habitats.

**Methods** We studied the effects of forest age (four age classes: from 5- to 10-year-old stands to more than 90-year-old stands), topographic position (south-facing slope, bottom, and north-facing slope), and their interaction on the distribution of vascular plants and mean Ellenberg indicator values in dolines using detrended correspondence analysis and mixed-effects models. Diagnostic species for the forest age classes and topographic positions were also determined.

**Results** Different groups of vascular plant species usually showed significant preferences for certain topographic positions and/or forest age classes in dolines. In general, the number of species in all studied groups of plants increased after a few years of canopy removal. The number of plant species in almost all groups was lowest in dolines covered with 40–45-year-old forests. The moist and nutrient-rich doline bottoms covered with 90–120-year-old forests harboured many climate change vulnerable plant species.

**Conclusions** Forest age and topographic position considerably influence the species richness and composition of vascular plants in dolines; therefore, forest managers and conservationists need to consider their potential impacts when evaluating the effects of climate warming on karst landscapes.

**Keywords** Doline, Sinkhole, Forest management, Karst landscape, Microrefugia, Topographic complexity, Vegetation

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## 1 Introduction

Topographically complex landscapes — such as karst landscapes — may create habitats that remain environmentally more stable through time, supporting the maintenance of species diversity (Bátori et al. 2017; Lenoir et al. 2017). For instance, dolines (sinkholes) — small- to large-sized depressions of karst landscapes with a funnel-shaped geomorphology (Ford and Williams 2007) — can be considered such safe havens as their microhabitats may protect species from becoming extinct at local or regional scales (Bátori et al. 2022a). Therefore, they are considered important potential microrefugia under climate changes (Keppel et al. 2012; Bátori et al. 2017). Microrefugia are small areas that support populations during periods of unfavourable environmental changes, such as abrupt climate oscillations (Rull 2009; Dobrowski 2011; Keppel et al. 2012; Keppel and Wardell-Johnson 2015). In addition to topographic complexity, vegetation cover may also play an important role in mitigating the effects of climate changes. For instance, microclimate in forests contrasts strongly with the climate outside forests, and forest canopy cover supports the maintenance of distinct below-canopy microclimatic conditions, in which many organisms can survive during macroclimatic changes (Grimmond et al. 2000; De Frenne et al. 2021).

A number of studies have indicated that cool and humid topographic positions (i.e. air temperature is lower, while relative air humidity and soil moisture are higher in bottoms and on north-facing slopes than on the plateau) in dolines (Bárány-Kevei 1999; Whiteman et al. 2004; Bátori et al. 2022a) have the capacity to maintain the populations of plant species vulnerable to climate change, such as climate relicts (i.e. species from colder periods), montane, wet woodland, and marshland species (Egli 1991; Yannitsaros et al. 1996; Dakskobler et al., 2008; Bátori et al. 2012). For instance, dolines in northern Hungary provide suitable microhabitats for the northern dragonhead (*Dracocephalum ruyschiana* L.), stone bramble (*Rubus saxatilis* L.), and alpine currant (*Ribes alpinum* L.) (Lazarević et al. 2009; Király 2009), while dolines in southern Hungary maintain the populations of the hard shield-fern (*Polystichum aculeatum* (L.) Roth ex Mert.), scaly male fern (*Dryopteris affinis* (Lowe) Fraser-Jenk.), and alpine woundwort (*Stachys alpina* L.) (Bátori et al. 2012). Similar examples can be found for other taxa, such as arthropods (Marcin et al. 2021; Bátori et al. 2022a) and land snails (Kemencei et al. 2014). More recently, some studies have been published showing that dolines and their climate change vulnerable plant species are also sensitive to anthropogenic disturbances (Breg Valjavec et al. 2018; Jian et al. 2018; Bátori et al. 2020). Examples include overgrazing (Brullo and Giusso del Galdo 2001) and commercial forest management (Kermavnar et al.

2020; Bátori et al. 2021). Therefore, assessing the potential of dolines to support the populations of climate change vulnerable species requires a deep understanding of the effects of different anthropogenic disturbances (cf. Keppel and Wardell-Johnson 2015; Lenoir et al. 2017; Su et al. 2017), such as changes in forest cover.

The climatic debt of understory plant communities is greater in forest stands with higher basal areas or older trees that may provide more time for plant species to locally adapt (Richard et al. 2021). However, commercial forest management affects the main environmental factors within forests, and therefore, it may change the climatic debt and refugial capacity of forest microhabitats (De Frenne et al., 2013, Zellweger et al., 2020). Intensive logging may cause severe and long-lasting effects in the microclimatic (e.g. light penetration, daily temperature, and vapour pressure) and soil factors (e.g. soil moisture and soil organic carbon content) and may lead to significant changes in species composition, species–environment relationships, and species interactions (Brown and Gurevitch 2004; Dean et al. 2016; Kovács et al. 2018), accelerating the thermophilisation rates and reducing the climatic debt of understory plant communities (Stevens et al. 2015; Richard et al. 2021). The survival of species in such landscapes depends on the geomorphologic features (e.g. slope characteristics), the level of disturbance, and the species' attributes (Johst and Drechsler 2003). For instance, the presence of poleward-facing slopes within a disturbed area may buffer the negative effects of disturbances on the distribution of some cool-adapted species (Olivero and Hix 1998). In a previous study, we have found that plant species on the north-facing slopes in forested dolines indicated a similar mean temperature after some years of logging to that which existed before the logging, while species on the south-facing slopes indicated an appreciable temperature increase (Bátori et al. 2021). We also found that some cool-adapted fern species have colonised the north-facing slopes shortly after logging. Disturbances may have far-reaching consequences for the biota (Brice et al. 2019; Richard et al. 2021). Although some ecosystems may return to their pre-disturbance state within a short period of time, some will never recover fully (Similä et al. 2002). As previous studies have demonstrated, the relationships between forest age and species composition may act as important indicators for the regeneration potential of forest habitats (Richard et al. 2021). For instance, Dunn (2004) found that the species richness of animal taxa in secondary tropical forests may resemble that of mature forests roughly 20–40 years after land abandonment; however, recovery of species composition may be considerably longer than recovery of species richness. Olivero and Hix (1998) identified 21 plant species as potential indicators

of forest age when comparing 70–90-year-old and more than 150-year-old forests in Ohio (USA). Although the need to integrate the effects of anthropogenic disturbances in the identification of refugia has been strongly emphasised by recent studies (Serra-Diaz et al. 2015; Bátori et al. 2020), there is little information about the effects of forest management on the species richness, species composition, and refugial capacity of microhabitats (see Richard et al. 2021). As climate change has already affected and will continue to affect many forest ecosystems worldwide (Hisano et al. 2017; Tewari et al. 2017; Devi et al. 2020), understanding the synergistic effects of topography, environmental changes, and forest management practices is likely to become increasingly important when planning future conservation strategies (Keenan 2015).

In our previous study, we found that forest age can be a good indicator for the number of cool- and moist-adapted species in doline habitats (Bátori et al. 2020). However, this study considered only three forest age classes and did not consider the potential effects of topographic position and the possible interaction between forest age and topographic position. In this paper, we aim to contribute to a better understanding of how forest age (four different age classes) and topographic position (south-facing slope, bottom, and north-facing slope) influence the plant species richness and species composition within dolines, which may help us to predict changes in the refugial capacity of these special habitats under anthropogenic climate change. Therefore, we test the respective effects of forest age and topographic position on the understory vegetation of dolines and compare them to determine their influence on plant communities. We hypothesised that (1) canopy removal and subsequent forest regeneration processes may alter the environmental conditions, species richness, and species composition of vascular plants in dolines, and that (2) forest age, topographic position, and their interaction exert a strong influence on the distribution of different ecological groups of plant species in dolines, contributing to the rise of species associated with more open and/or disturbed habitats in early successional stages and their fall with long-term forest recovery. In addition, we expect the accumulation of climate change vulnerable species in later successional stages on cooler topographic positions, such as doline bottoms.

## 2 Material and methods

### 2.1 Study area

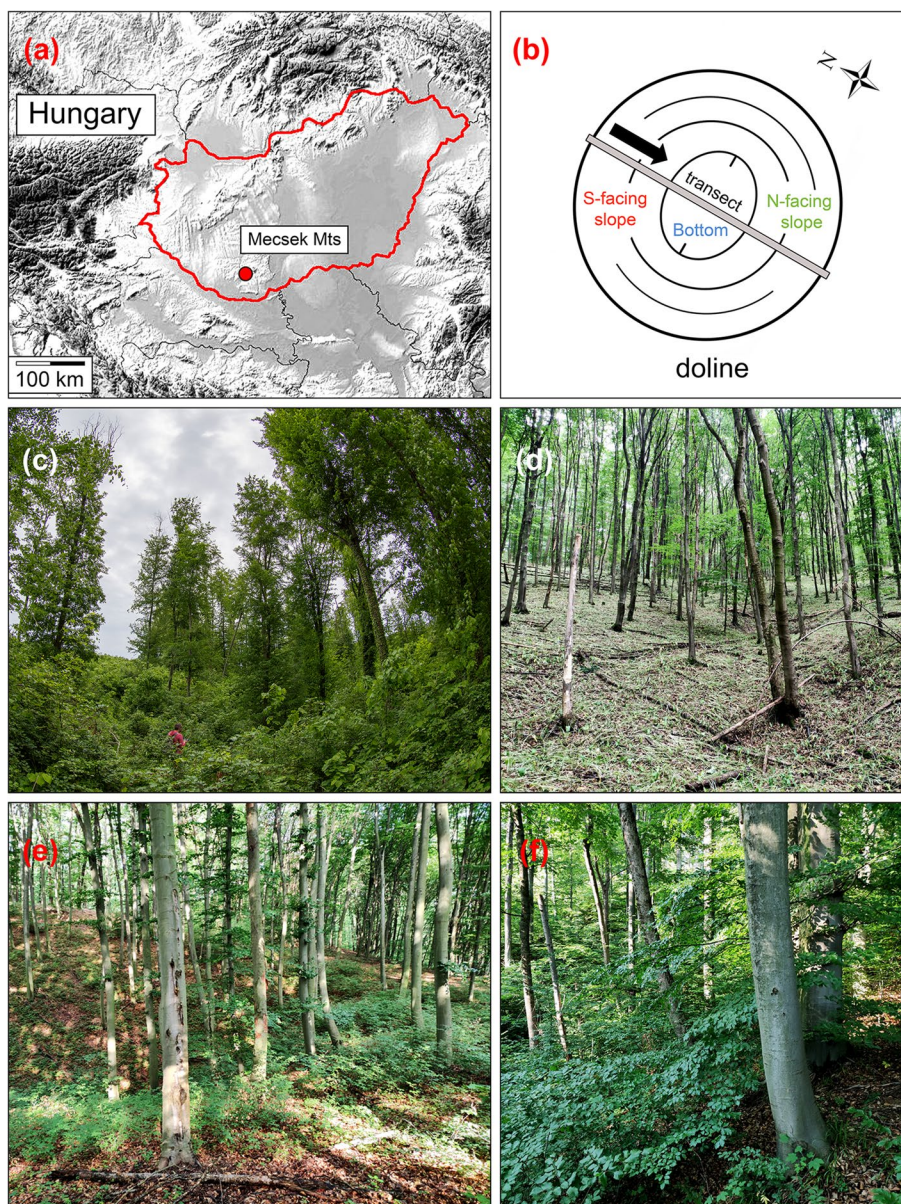
The study was carried out in a limestone karst landscape of the Mecsek Mountains (southern Hungary) (Fig. 1), where more than 2000 dolines occur at an altitude between 250 and 500 m (Hoyk 1999). In this study,

we investigated larger solution dolines that are bowl- or funnel-shaped depressions formed by the dissolution of rock at the bedrock–soil interface (Ford and Williams 2007). The climate is continental with strong sub-Mediterranean influences. The mean annual temperature is about 8.8 °C, and the mean annual precipitation is 740 mm (Dövényi 2010).

Commercial logging has shaped the karst landscape in the Mecsek Mts for decades. Current forest stands mainly include 40–50, 60–80, or 90–120-year-old trees both on the plateau and in dolines (canopy cover on the slopes: 75–90%) (Fig. 1), but the proportion of cut areas has significantly increased in the last 10 years (Bátori et al. 2020). As a result of these forestry activities, canopy cover within some dolines has decreased to approximately 20–50% of its original extent, and only smaller patches of mature trees have survived (where timber harvesting is not feasible). These dolines are dominated by 5–10-year-old saplings [the detailed description of these forestry activities is provided in Bátori et al. (2021)]. Common hornbeam (*Carpinus betulus* L.), European beech (*Fagus sylvatica* L.), and oak species (*Quercus cerris* L. and *Quercus petraea* (Matt.) Liebl.) are dominant on the plateau and the upper slopes of dolines, while common hornbeam, European ash (*Fraxinus excelsior*), and European beech and maples (*Acer campestre* L., *Acer platanoides* L., *Acer pseudoplatanus* L.) are the dominant tree species on the bottoms and lower slopes of larger dolines (Bátori et al. 2012). The shrub and herb layers are rich in sub-Mediterranean species, such as bastard-agrimony (*Aremonia agrimonoides* (L.) DC.), black bryony (*Dioscorea communis* (L.) Caddick & Wilkin), butcher's-broom (*Ruscus aculeatus* L.), and fragrant hellebore (*Helleborus odoratus* Waldst. & Kit. ex Willd.). Doline bottoms are cooler and moister and retain more nutrient-rich soils than slopes and the surrounding plateau; therefore, they may provide important safe havens for a number of plant species (Bátori et al., 2014a).

### 2.2 Sampling design

We studied dolines covered with forests of one of four different age classes (class 1: 5–10-year-old forest stands with mature forest patches, class 2: 40–45-year-old forests, class 3: 60–65-year-old forests, and class 4: more than 90-year-old forests). Tree density (excluding saplings) was  $753 \pm 42$  (mean  $\pm$  SD) trees/ha in age class 2,  $460 \pm 53$  trees/ha in age class 3, and  $280 \pm 20$  trees/ha in age class 4. Only smaller patches of mature trees were found in age class 1. Three dolines from each age class were sampled during vegetation sampling (12 dolines in total). The morphological features (diameter and depth) of dolines were similar across the forest age classes; each



**Fig. 1** Study area, sampling design, and dolines. **a** Location of the study area in Hungary. **b** Position of transects within dolines. **c** Doline dominated by 5–10-year-old forests. **d** Doline covered with 40–45-year-old forests. **e** Doline covered with 60–65-year-old forests. **f** Doline covered with more than 90-year-old forests (photos: Gábor Li and Zoltán Bátori)

contained one large (diameter: 80–100 m, depth: 13–15 m) and two medium-sized (diameter: 60–80 m and depth: 10–13 m) dolines.

As our previous studies showed that the greatest differences in plant species composition occur between the north- and south-facing slopes within dolines (Bátori et al. 2012), we established a transect with north to south orientation across each doline, traversing their deepest point (Fig. 1). Transects began and ended on doline rims and consisted of 1 m × 1 m plots spaced at

2-m intervals (94, 89, 90, and 99 plots in the different forest age classes, respectively; 372 plots in total). We recorded the presence/absence data of all vascular plant species (tree saplings — up to 1 m in height, shrubs, and herbs) in each plot (saplings were excluded before analyses) (Bátori et al. 2022b). Fieldwork was carried out between 2007 and 2019 from June to August, at the peak of the growing season (i.e. one flora survey). Nomenclature follows the ‘World Flora Online’ (<http://www.worldfloraonline.org/>) database.

### 2.3 Species classification

We classified all plant species according to their habitat preferences following the system of Soó (1980). We used the following three groups of plant species during analyses: (1) species primarily associated with beech forests within the study area (order *Fagetalia sylvaticae* — beech forest species hereafter), (2) species primarily associated with oak forests within the study area (class *Querco-Fagetea* — oak forest species hereafter), and (3) species primarily associated with disturbed forests within the study area (e.g. adventives, cosmopolites, and weeds — species of disturbed forests hereafter). Beech forest species were considered as the main target group, as temperature increase and the duration and severity of climate change-related droughts threaten their populations in many hilly and mountainous areas of Europe (cf. Saltré et al. 2015; Kasper et al. 2021; Satoh et al. 2022).

### 2.4 Statistical analyses

Based on previous observations, we defined topographic positions as follows: south-facing slope — upper two-third of plots along the south-facing slope (age class 1: 37 plots, age class 2: 26 plots, age class 3: 31 plots, and age class 4: 31 plots); bottom — lower third of plots along the slopes (age class 1: 29 plots, age class 2: 30 plots, age class 3: 28 plots, and age class 4: 35 plots); and north-facing slope — upper two-third of plots along the north-facing slope (age class 1: 28 plots, age class 2: 33 plots, age class 3: 31 plots, and age class 4: 33 plots).

Diagnostic species for the forest age classes (classes 1–4), diagnostic species for the topographic positions (south-facing slope, bottom, and north-facing slope), and diagnostic species for the different topographic positions in the different forest age classes were determined by calculating the phi ( $\Phi$ ) value of species, using the JUICE programme (Tichý 2002). Species with  $\Phi \times 100 > 14.0$  were considered diagnostic species (Fisher's exact test,  $p < 0.05$ ) (Tichý and Chytrý 2006). In the rare case when a species appeared to be diagnostic for more than one forest age class or topographic position, only the occurrence with the higher phi value was considered.

Unweighted mean Ellenberg indicator values (EIVs hereafter) for light availability (L), temperature (T), soil moisture (W), soil reaction (R), and nutrient availability (N) were calculated for each plot using the system of Borhidi (1995). A number of studies have demonstrated that, despite the ordinal nature of EIVs, mean EIVs provide reliable estimates of the environmental conditions of an area (Lengyel et al., 2012; Tölgyesi et al., 2014); therefore, they are useful for monitoring environmental changes. We used one-way analysis of similarities (ANOSIM) to compare the species composition of plots among the forest age classes, applying the Jaccard dissimilarity

and 9999 permutations. We applied a Bonferroni correction to give a corrected  $p$ -value in pairwise comparisons. We used detrended correspondence analysis (DCA) to illustrate compositional differences in dolines (detrending with 26 segments). As compositional differences between the plots of age class 2 and the plots of the other age classes were rather large — resulting in considerable overlap of the plots of age classes 1, 3, and 4 in the ordination space — an additional DCA was performed excluding the plots of age class 2. ANOSIM and DCA were calculated in R (R Core Team 2019) using the *anosim* and the *decorana* functions of the 'vegan' package (Oksanen et al., 2019).

We used generalised linear mixed-effects models (GLMMs) with a Poisson distribution and linear mixed-effects models (LMMs) to reveal the effect of forest age (classes 1–4) and topographic position (south-facing slope, bottom, and north-facing slope) on species richness and mean EIVs in dolines. Topographic position, forest age class, and their interaction term were treated as fixed factors, while doline (i.e. dolines 1–12) was included as a random factor (random intercept term). Four GLMMs were built for the richness variables, for the number of (1) all plant species, (2) beech forest species, (3) oak forest species, and (4) species of disturbed forests in the plots, while five LMMs were built for the mean EIV variables, for the mean L, T, W, R, and N indicator values in the plots. Bonferroni post hoc tests were used for the comparison of the different levels of the fixed factors, for (1) forest age class, for (2) topographic position, and for (3) the interaction term of forest age and topographic position. Mixed-effects models were performed in R using the *glmer* and *lmer* functions of the 'lme4' package. The significance of the fixed factors was estimated using the *Anova* function of the 'car' package (Fox and Weisberg 2019). Post hoc tests were performed using the *lsmeans* function of the 'lsmeans' package (Lenth 2016), while the *rsquaredGLMM* function of the 'MuMIn' package was also used for calculating conditional and marginal  $R^2$  for the models (R Core Team 2019; Bates et al. 2021; Bartoń 2022).

## 3 Results

### 3.1 Diagnostic species

Altogether, 92 vascular plant species (herbs and shrubs) was found in the plots. Age class 1 had 29 diagnostic species (13 beech forest species — proportion: 45%; seven oak forest species — 24%; and nine species of disturbed forests — 31%), while age classes 2–4 had five (four beech forest species — 80% and one species of disturbed forests — 20%), two (one beech forest species — 50%, and one species of disturbed forests — 50%), and six (beech forest species — 100%) diagnostic species, respectively (Table 1).

**Table 1** List of diagnostic species for the forest age classes (class 1: 5–10-year-old forest stands with mature forest patches, class 2: 40–45-year-old forests, class 3: 60–65-year-old forests, and class 4: more than 90-year-old forests) in dolines. Within blocks, species are listed by decreasing values of the phi ( $\Phi$ ) coefficient. Fidelity values ( $\Phi \times 100$ ) of beech forest species, oak forest species, and species of disturbed forests are indicated with superscripts b, o, and d, respectively. Non-diagnostic species were excluded with Fisher's exact test ( $p < 0.05$ )

	Forest age			
	5–10 years	40–45 years	60–65 years	> 90 years
<i>Urtica dioica</i> <sup>d</sup>	49.1			
<i>Rubus hirtus</i> agg. <sup>d</sup>	41.8			
<i>Calamagrostis epigejos</i> <sup>d</sup>	41.1			
<i>Hypericum hirsutum</i> <sup>o</sup>	34.1			
<i>Vinca minor</i> <sup>b</sup>	34.1			
<i>Mycelis muralis</i> <sup>o</sup>	30.1			
<i>Stenactis annua</i> <sup>d</sup>	30.1			
<i>Erechtites hieracifolia</i> <sup>d</sup>	25.5			
<i>Galium odoratum</i> <sup>b</sup>	25.2			
<i>Hepatica nobilis</i> <sup>b</sup>	24.9			
<i>Carex sylvatica</i> <sup>b</sup>	24.8			
<i>Fragaria vesca</i> <sup>o</sup>	24.2			
<i>Dactylis glomerata</i> <sup>d</sup>	23.9			
<i>Melica uniflora</i> <sup>o</sup>	23.9			
<i>Euphorbia amygdaloides</i> <sup>b</sup>	22.9			
<i>Salix caprea</i> <sup>d</sup>	22.1			
<i>Viola reichenbachiana</i> <sup>b</sup>	22.1			
<i>Veronica chamaedrys</i> <sup>o</sup>	20.6			
<i>Hordelymus europaeus</i> <sup>b</sup>	20.1			
<i>Scrophularia nodosa</i> <sup>o</sup>	20.1			
<i>Dryopteris filix-mas</i> <sup>b</sup>	19.4			
<i>Milium effusum</i> <sup>b</sup>	19.1			
<i>Athyrium filix-femina</i> <sup>b</sup>	18.7			
<i>Pulmonaria officinalis</i> <sup>b</sup>	18.7			
<i>Brachypodium sylvaticum</i> <sup>o</sup>	18.0			
<i>Taraxacum campylodes</i> <sup>d</sup>	18.0			
<i>Torilis japonica</i> <sup>d</sup>	18.0			
<i>Festuca drymeja</i> <sup>b</sup>	17.5			
<i>Stachys sylvatica</i> <sup>b</sup>	15.5			
<i>Veronica montana</i> <sup>b</sup>		30.5		
<i>Veronica hederifolia</i> <sup>d</sup>		27.3		
<i>Hedera helix</i> <sup>b</sup>		22.1		
<i>Paris quadrifolia</i> <sup>b</sup>		20.0		
<i>Cardamine bulbifera</i> <sup>b</sup>		16.0		
<i>Carex pilosa</i> <sup>b</sup>			16.6	
<i>Sambucus nigra</i> <sup>d</sup>			14.8	
<i>Mercurialis perennis</i> <sup>b</sup>				25.5
<i>Lamium maculatum</i> <sup>b</sup>				23.5
<i>Oxalis acetosella</i> <sup>b</sup>				18.5
<i>Circaea lutetiana</i> <sup>b</sup>				17.8
<i>Lamium galeobdolon</i> s.l. <sup>b</sup>				14.9
<i>Dryopteris carthusiana</i> <sup>b</sup>				14.4

South-facing slopes, bottoms, and north-facing slopes had 19 (eight beech forest species — proportion: 42%, eight oak forest species — 42%, and three species of disturbed forests — 16%), five (beech forest species — 100%), and two (beech forest species — 100%) diagnostic species, respectively (Table 2).

South-facing slopes, bottoms, and north-facing slopes in age class 1 had 24, four, and six diagnostic species, respectively (Table 3). Only seven diagnostic species were found in age class 2, four for the south-facing slopes, two for the bottoms, and one for the north-facing slopes. South-facing slopes in age class 3 had five diagnostic species, while bottoms had one diagnostic species. No diagnostic species were found for

the north-facing slopes. Eleven diagnostic species were found for age class 4, two for the south-facing slopes, eight for the bottoms, and one for the north-facing slopes. The proportion of beech forest species was highest (100%) on the north-facing slopes in age class 2 and on the bottoms and north-facing slopes in age class 4 (Fig. 2).

### 3.2 Vegetation patterns

Although the first DCA showed that the plots of the different forest age classes — except age class 2 — overlapped considerably in the ordination space (Fig. 3a), differences in species composition were statistically significant (ANOSIM  $R$ : 0.2,  $p < 0.001$ ; pairwise comparisons:  $R$ : 0.05–0.41,  $p < 0.005$ , Appendix Table 4). Eigenvalues for the first two DCA axes were 0.523 and 0.425, respectively. Plots of the south-facing slopes, north-facing slopes, and bottoms arranged along the first DCA axis (from left to right), revealing clear environmental gradients in the ordination space. The second DCA (eigenvalues for the first two axes: 0.521 and 0.349, respectively) showed that plots of the south-facing slopes in age class 1 differed markedly from the plots of the other topographic positions (Fig. 3b).

### 3.3 Different groups of plant species

Forest age, topographic position, and their interaction term had significant effects on the total number of species (full model:  $R^2_{\text{marginal}}$ : 0.53,  $R^2_{\text{conditional}}$ : 0.57) (Appendix Table 5). Age and the interaction term of age and topographic position affected the number of beech forest species (full model:  $R^2_{\text{marginal}}$ : 0.30,  $R^2_{\text{conditional}}$ : 0.37). Age and topographic position had significant effects on the number of oak forest species (full model:  $R^2_{\text{marginal}}$ : 0.56,  $R^2_{\text{conditional}}$ : 0.63). Age also had a significant effect on the number of species of disturbed forests (full model:  $R^2_{\text{marginal}}$ : 0.97,  $R^2_{\text{conditional}}$ : 0.98).

Both the total number of plant species and the number of beech forest species were highest in age class 1 and lowest in age class 2 (Fig. 4). Across age classes 2–4, the total number of species and the number of beech forest species showed an increasing trend. The number of oak forest species and species of disturbed forests was highest in age class 1, while the number of species of disturbed forests was lowest in age class 2.

The total number of species was highest on south-facing slopes and did not differ between bottoms and north-facing slopes (Fig. 5). The number of oak forest species was highest on south-facing slopes and lowest in bottoms.

In general, the different groups of plant species showed significant preferences for certain topographic positions

**Table 2** List of diagnostic species for topographic positions (S: south-facing slope, B: bottom, and N: N-facing slope) in dolines. Within blocks, species are listed by decreasing values of the phi ( $\Phi$ ) coefficient. Fidelity values ( $\Phi \times 100$ ) of beech forest species, oak forest species, and species of disturbed forests are indicated with superscripts b, o, and d, respectively. Non-diagnostic species were excluded with Fisher's exact test ( $p < 0.05$ )

	Topographic position		
	S	B	N
<i>Melica uniflora</i> <sup>o</sup>	47.9		
<i>Carex pilosa</i> <sup>b</sup>	41.4		
<i>Veronica chamaedrys</i> <sup>o</sup>	36.4		
<i>Euphorbia amygdaloides</i> <sup>b</sup>	28.1		
<i>Fragaria vesca</i> <sup>o</sup>	27.9		
<i>Vinca minor</i> <sup>b</sup>	27.9		
<i>Carex sylvatica</i> <sup>b</sup>	24.0		
<i>Milium effusum</i> <sup>b</sup>	22.2		
<i>Hypericum hirsutum</i> <sup>o</sup>	21.8		
<i>Calamagrostis epigejos</i> <sup>d</sup>	20.9		
<i>Dactylis polygama</i> <sup>o</sup>	20.9		
<i>Dactylis glomerata</i> <sup>d</sup>	19.5		
<i>Festuca drymeja</i> <sup>b</sup>	19.3		
<i>Ajuga reptans</i> <sup>o</sup>	17.2		
<i>Viola alba</i> <sup>o</sup>	16.9		
<i>Symphytum tuberosum</i> <sup>o</sup>	16.4		
<i>Carex digitata</i> <sup>b</sup>	14.7		
<i>Rumex sanguineus</i> <sup>b</sup>	14.7		
<i>Torilis japonica</i> <sup>d</sup>	14.7		
<i>Athyrium filix-femina</i> <sup>b</sup>		33.0	
<i>Circaea lutetiana</i> <sup>b</sup>		24.7	
<i>Dryopteris filix-mas</i> <sup>b</sup>		20.1	
<i>Lamium maculatum</i> <sup>b</sup>		19.7	
<i>Veronica montana</i> <sup>b</sup>		15.4	
<i>Hedera helix</i> <sup>b</sup>			24.6
<i>Lamium galeobdolon</i> s.l. <sup>b</sup>			18.1

**Table 3** List of diagnostic species for topographic positions (S: south-facing slope, B: bottom, and N: N-facing slope) in the forest age classes (class 1: 5–10-year-old forest stands with mature forest patches, class 2: 40–45-year-old forests, class 3: 60–65-year-old forests, and class 4: more than 90-year-old forests) in dolines. Within blocks, species are listed by decreasing values of the phi ( $\Phi$ ) coefficient. Fidelity values ( $\Phi \times 100$ ) of beech forest species, oak forest species, and species of disturbed forests are indicated with superscripts b, o, and d, respectively. Non-diagnostic species were excluded with Fisher's exact test ( $p < 0.05$ )

	Forest age and topographic position											
	5–10 years			40–45 years			60–65 years			> 90 years		
	S	B	N	S	B	N	S	B	N	S	B	N
<i>Vinca minor</i> <sup>b</sup>	59.8											
<i>Calamagrostis epigejos</i> <sup>d</sup>	50.1											
<i>Hypericum hirsutum</i> <sup>o</sup>	49.3											
<i>Fragaria vesca</i> <sup>o</sup>	44.7											
<i>Euphorbia amygdaloides</i> <sup>b</sup>	43.5											
<i>Dactylis glomerata</i> <sup>d</sup>	42.0											
<i>Veronica chamaedrys</i> <sup>o</sup>	38.7											
<i>Milium effusum</i> <sup>b</sup>	35.2											
<i>Carex sylvatica</i> <sup>b</sup>	34.7											
<i>Festuca drymeja</i> <sup>b</sup>	34.1											
<i>Torilis japonica</i> <sup>d</sup>	31.6											
<i>Stenactis annua</i> <sup>d</sup>	29.8											
<i>Hordelymus europaeus</i> <sup>b</sup>	26.6											
<i>Scrophularia nodosa</i> <sup>o</sup>	26.6											
<i>Erechtites hieracifolia</i> <sup>d</sup>	24.6											
<i>Mycelis muralis</i> <sup>o</sup>	24.3											
<i>Deschampsia cespitosa</i> <sup>b</sup>	22.3											
<i>Rumex sanguineus</i> <sup>b</sup>	22.3											
<i>Brachypodium sylvaticum</i> <sup>o</sup>	21.9											
<i>Taraxacum campylodes</i> <sup>d</sup>	21.9											
<i>Viola alba</i> <sup>o</sup>	19.0											
<i>Stellaria holostea</i> <sup>o</sup>	16.2											
<i>Salix caprea</i> <sup>d</sup>	15.9											
<i>Helleborus odoratus</i> <sup>b</sup>	14.7											
<i>Urtica dioica</i> <sup>d</sup>		49.6										
<i>Rubus hirtus</i> agg. <sup>d</sup>		32.3										
<i>Athyrium filix-femina</i> <sup>b</sup>		31.8										
<i>Stachys sylvatica</i> <sup>b</sup>		19.5										
<i>Galium odoratum</i> <sup>b</sup>			32.9									
<i>Viola reichenbachiana</i> <sup>b</sup>			27.9									
<i>Hepatica nobilis</i> <sup>b</sup>			26.7									
<i>Geranium robertianum</i> <sup>o</sup>			25.7									
<i>Mercurialis perennis</i> <sup>b</sup>			24.2								24.2	
<i>Atropa belladonna</i> <sup>b</sup>			20.9									
<i>Hedera helix</i> <sup>b</sup>				25.7								
<i>Cardamine bulbifera</i> <sup>b</sup>				21.8								
<i>Ruscus aculeatus</i> <sup>b</sup>				18.4								
<i>Moehringia trinervia</i> <sup>o</sup>				16.8								
<i>Veronica hederifolia</i> <sup>d</sup>					35.5							
<i>Paris quadrifolia</i> <sup>b</sup>					21.8							
<i>Veronica montana</i> <sup>b</sup>						28.9						
<i>Melica uniflora</i> <sup>o</sup>							34.2					
<i>Carex digitata</i> <sup>b</sup>							25.1					



**Table 3** (continued)

	Forest age and topographic position											
	5–10 years			40–45 years			60–65 years			> 90 years		
	S	B	N	S	B	N	S	B	N	S	B	N
<i>Lathyrus venetus</i> <sup>b</sup>							24.4					
<i>Dactylis polygama</i> <sup>o</sup>							22.3			22.3		
<i>Symphytum tuberosum</i> <sup>o</sup>							20.8					
<i>Sambucus nigra</i> <sup>d</sup>								23.7				
<i>Carex pilosa</i> <sup>b</sup>										39.2		
<i>Lamium maculatum</i> <sup>b</sup>											43.2	
<i>Circaea lutetiana</i> <sup>b</sup>											29.4	
<i>Dryopteris carthusiana</i> <sup>b</sup>											27.6	
<i>Pulmonaria officinalis</i> <sup>b</sup>											26.0	
<i>Chrysosplenium alternifolium</i> <sup>b</sup>											22.9	
<i>Dryopteris filix-mas</i> <sup>b</sup>											22.9	
<i>Lamium galeobdolon</i> s.l. <sup>b</sup>											22.1	
<i>Oxalis acetosella</i> <sup>b</sup>												16.8

within the forest age classes, except in age class 2 (Fig. 6). The greatest difference between the topographic positions was observed in age class 1. Bottoms had the lowest, and south-facing slopes had the highest number of species in this age class. This is also true for age class 3. Conversely, the bottoms in age class 4 had higher number of species and beech forest species than the other topographic positions, although these differences were not always statistically significant. If we compare the same topographic positions among the forest age classes, the total number of species and the number of beech forest species were highest on the south-facing slopes in age class 1. The bottoms in age class 4 had more beech forest species than the bottoms in the other forest age classes. The number of beech forest species was highest on the north-facing slopes in age class 1.

### 3.4 Environmental characteristics

Forest age, topographic position, and their interaction term had significant effects on the mean L indicator values (full model:  $R^2_{\text{marginal}}$ : 0.22,  $R^2_{\text{conditional}}$ : 0.31), while topographic position had significant effects on the mean T indicator values (full model:  $R^2_{\text{marginal}}$ : 0.07,  $R^2_{\text{conditional}}$ : 0.12) (Appendix Table 6). Topographic position and the interaction term of age and topographic position had significant effects on the mean W indicator values (full model:  $R^2_{\text{marginal}}$ : 0.28,  $R^2_{\text{conditional}}$ : 0.29). Similarly, topographic position and the interaction term of age and topographic position had significant effects on the mean R indicator values ( $R^2_{\text{marginal}}$ : 0.13,  $R^2_{\text{conditional}}$ : 0.23), while forest age and topographic position affected the mean N

indicator values (full model:  $R^2_{\text{marginal}}$ : 0.37,  $R^2_{\text{conditional}}$ : 0.43).

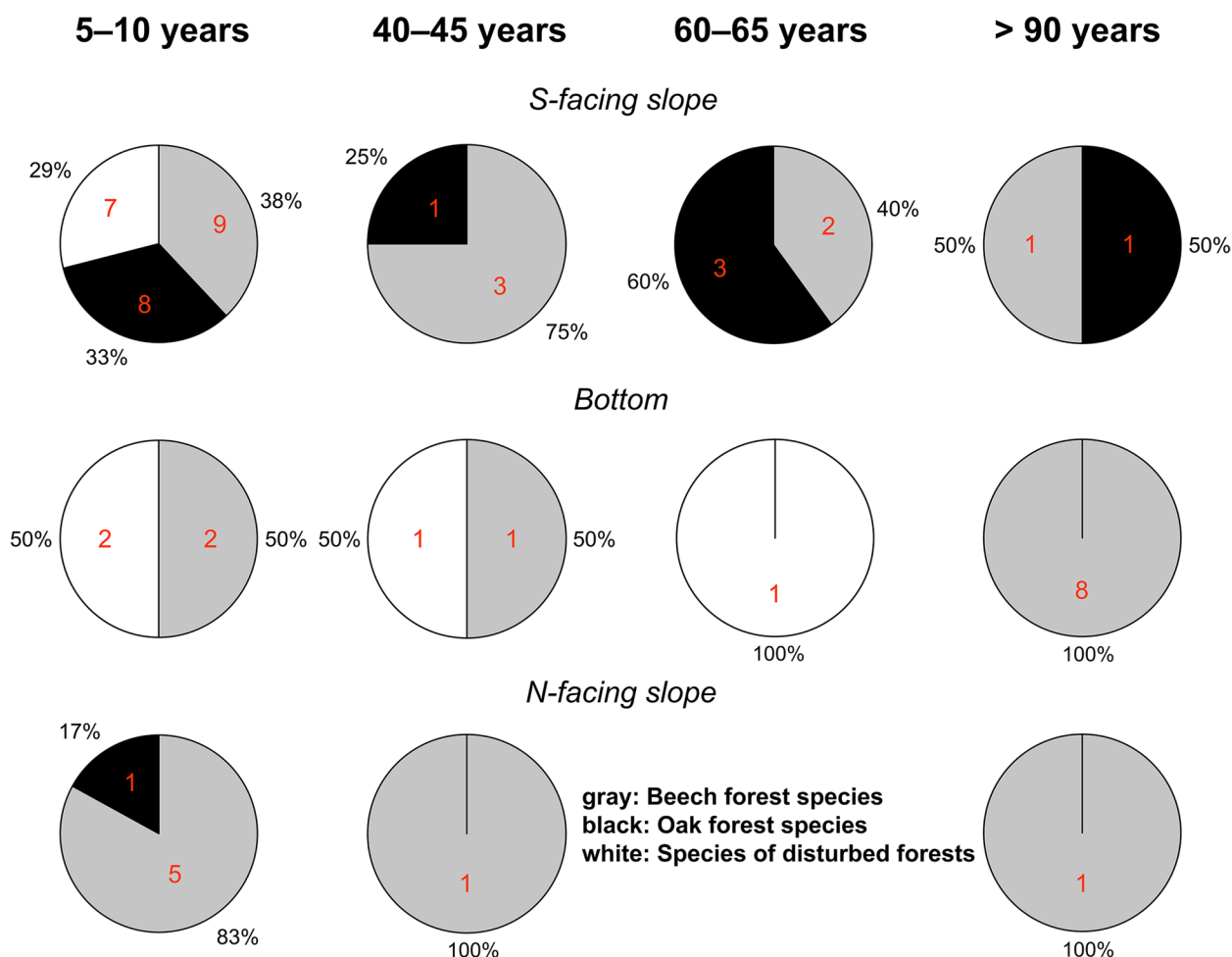
Species in age class 1 indicated higher intensity of light than species in age class 4, and species in age class 3 indicated less nutrients than species in age class 1 (Appendix Figure 8).

Light intensity was higher on south-facing slopes and bottoms than on north-facing slopes (Appendix Figure 9). Species in bottoms indicated colder conditions than on south-facing slopes. Bottoms had the highest, and south-facing slopes had the lowest moisture content, while moisture availability was intermediate on north-facing slopes. All topographic positions differed from each other with regard to soil reaction values. Bottoms showed the highest, and south-facing slopes showed the lowest soil reaction values. Nutrient availability was highest in bottoms and lowest on south-facing slopes, while it was intermediate on north-facing slopes.

Light intensity was lowest on north-facing slopes in age classes 1 and 4, and moisture availability was highest in the bottoms in age classes 1, 3, and 4, while soil reaction values were highest in the bottoms in age class 3 and on the north-facing slopes in age class 4 (Appendix Figure 10). If we compare the same topographic positions among the forest age classes, moisture availability was lowest in the bottoms of age class 2.

## 4 Discussion

Forest age and topographic position play an important role in determining the species composition, species richness, and environmental characteristics of karstic habitats and jointly shape the vegetation patterns in dolines.

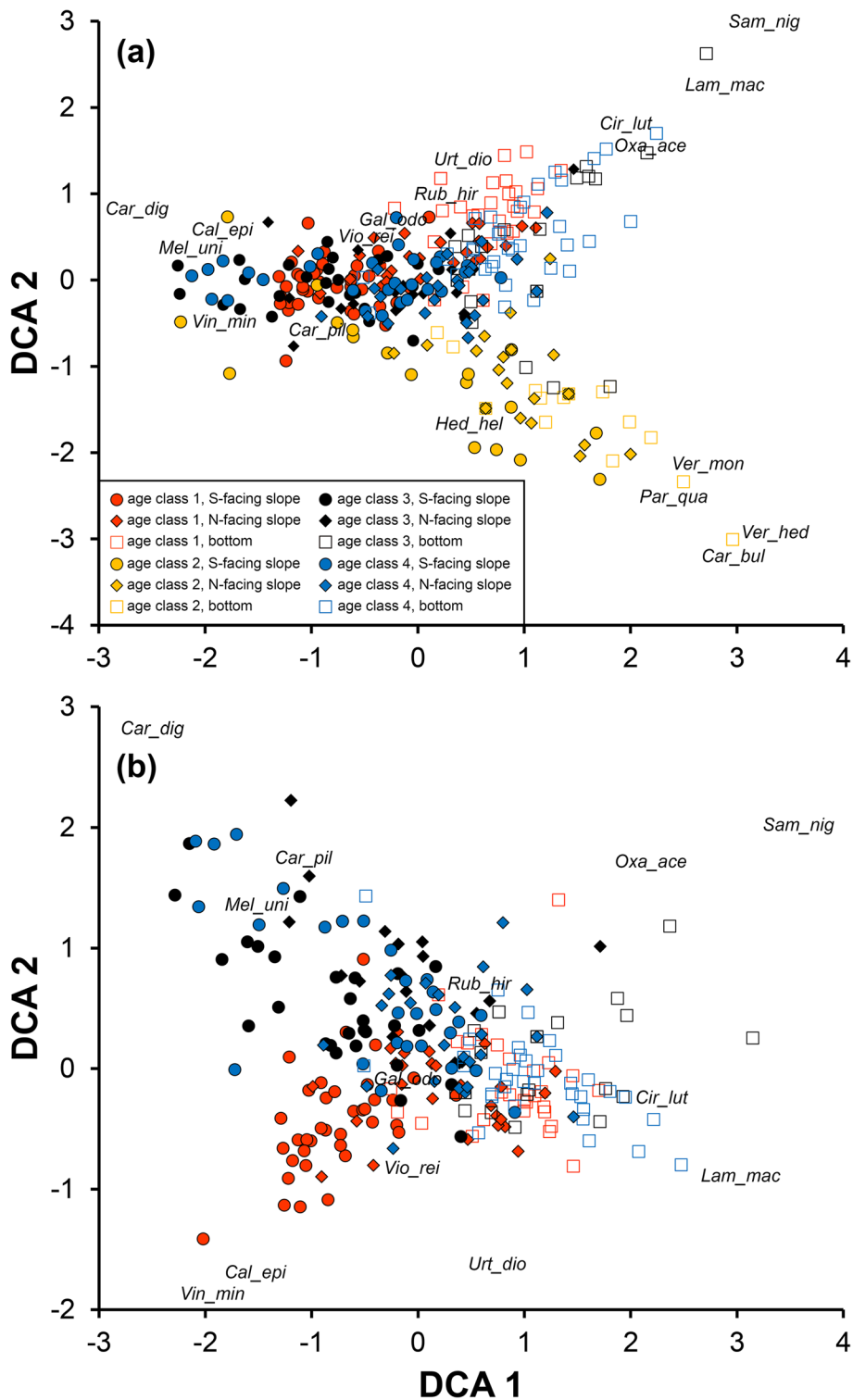


**Fig. 2** Number (in red) and proportion of diagnostic species (beech forest species, oak forest species, and species of disturbed forests) in the plots of topographic positions in dolines (south-facing slope, bottom, and north-facing slope) covered with different forest age classes (class 1: 5–10-year-old forest stands with mature forest patches, class 2: 40–45-year-old forests, class 3: 60–65-year-old forests, and class 4: more than 90-year-old forests) (see Table 3)

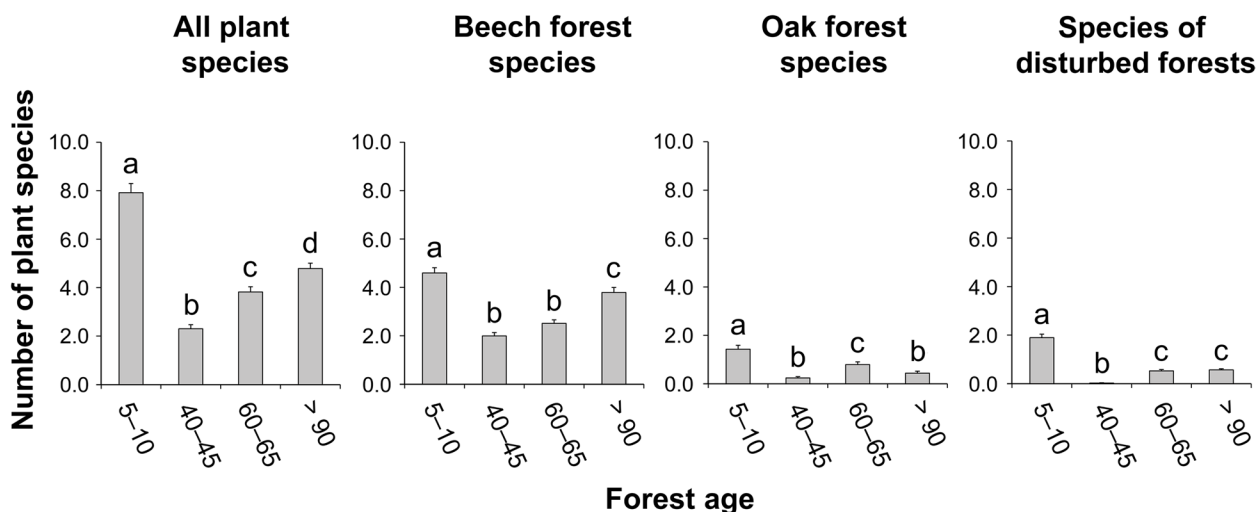
In general, the number of diagnostic species and the number of species in all studied groups of vascular plants (beech forest species, oak forest species, and species of disturbed forests) increased after a few years of canopy removal within dolines. However, the number of plant species in almost all groups was lower in dolines covered with 40–45-year-old forests than in the other forest age classes. We also demonstrated the accumulation of beech forest species in the moist and nutrient-rich doline bottoms covered with more than 90-year-old forests. To our knowledge, this is the first study to illustrate how forest age, topography, and their interaction shape the species richness and composition of vascular plants in potential future microrefugia in karst landscapes.

Forest age may determine several abiotic and biotic factors, such as light availability, microclimate, soil characteristics, species composition, and community

composition in forest ecosystems (Brunet et al. 2010; Bátori et al. 2020; Richard et al. 2021; Zema et al. 2021). The degree of canopy removal during forestry operations may range from low levels to complete canopy removal (Roberts and Gilliam 1995), resulting in various changes in the forest environment. In a previous study, we demonstrated that vascular plant species in dolines indicated significant changes in temperature and light availability after a few years of partial (50–80%) canopy removal (Bátori et al. 2021) and opened up niches for a number of plant species associated with warmer temperatures. Similar results were reported by Richard et al. (2021), who found that changes in canopy cover may reshuffle understory communities towards less cold-adapted but more warm-adapted species (i.e. thermophilisation). In the current study, we found that forest age — comparing four different age classes — is an important



**Fig. 3** Detrended correspondence analysis (DCA) for the plots of dolines **(a)** all plots and **(b)** plots of classes 1, 3, and 4) with some important diagnostic species of the topographic positions of the forest age classes (see Table 3). Abbreviations for species are as follows: Cal\_epi, *Calamagrostis epigejos*; Car\_dig, *Carex digitata*; Car\_pil, *Carex pilosa*; Car\_bul, *Cardamine bulbifera*; Cir\_lut, *Circaea lutetiana*; Gal\_odo, *Galium odoratum*; Hed\_hel, *Hedera helix*; Lam\_mac, *Lamium maculatum*; Mel\_uni, *Melica uniflora*; Oxa\_ace, *Oxalis acetosella*; Par\_qua, *Paris quadrifolia*; Rub\_hir, *Rubus hirtus* agg.; Sam\_nig, *Sambucus nigra*; Urt\_dio, *Urtica dioica*; Ver\_mon, *Veronica montana*; Ver\_hed, *Veronica hederifolia*; Vin\_min, *Vinca minor*; Vio\_rei, *Viola reichenbachiana*

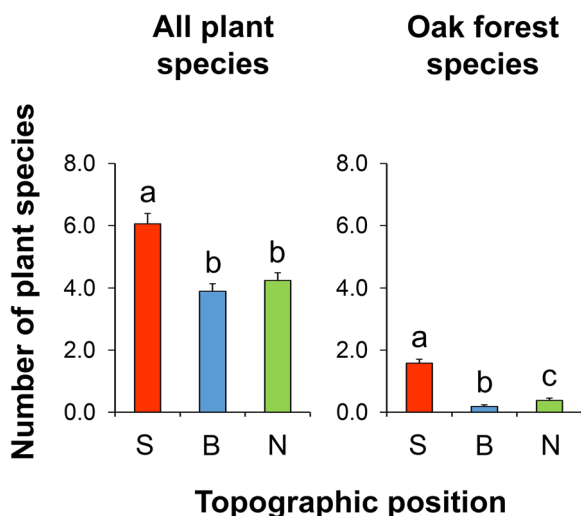


**Fig. 4** Number of vascular plant species (all plant species, beech forest species, oak forest species, and species of disturbed forests) in the plots of dolines covered with different forest age classes (class 1: 5–10-year-old forest stands with mature forest patches, class 2: 40–45-year-old forests, class 3: 60–65-year-old forests, and class 4: more than 90-year-old forests) (mean ± SE). Significant differences ( $p < 0.05$ , based on the GLMMs with Bonferroni post hoc tests), are indicated by different lower case (a–d) letters

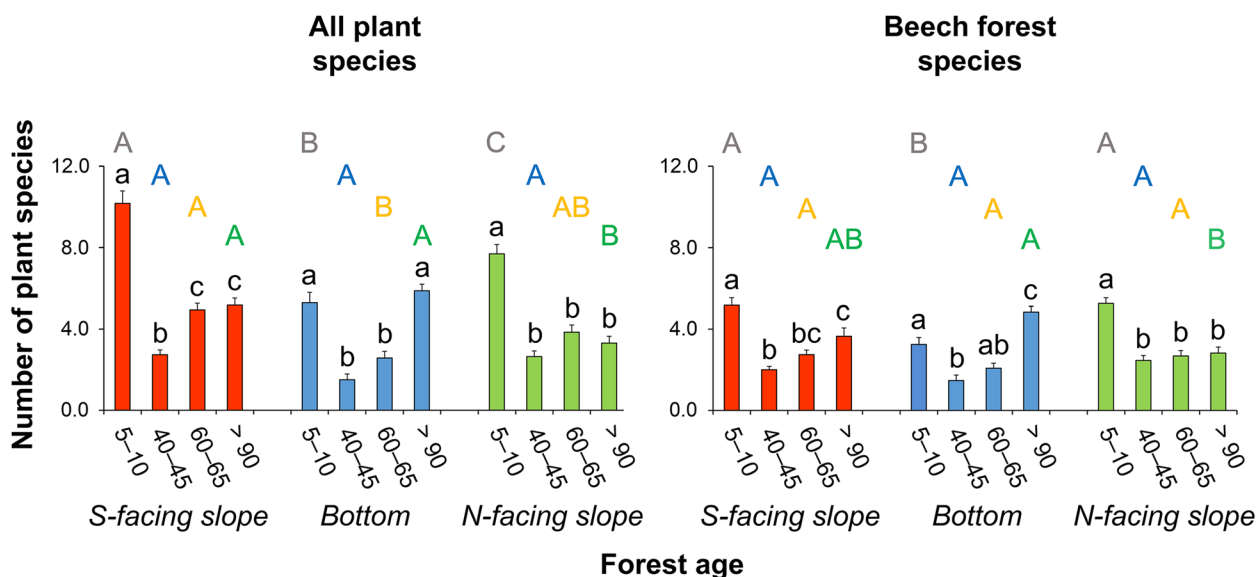
predictor of species compositional changes and community reorganisation within dolines and influences the environmental characteristics, such as light and nutrient availability, not only in dolines after canopy removal but also in different successional stages (Figs. 4 and Appendix Figure 8, Table 1). The number of diagnostic species, the total number of species, and the number of species

in all studied groups of plants (beech forest species, oak forest species, and species of disturbed forests) were higher after a few years of canopy removal than in the other forest age classes. Kermavnar et al. (2021) also found increases in plot-level species richness and overall enrichment of the species pool in dolines in Slovenia over a 6-year period after canopy removal. This also suggests that the environmental changes experienced in these habitats were not detrimental to the survival of most forest-related species within a short period of time (Kermavnar et al. 2019), even though the cover of some climate-change sensitive functional groups may decrease (Kiss et al. 2020). However, the species diversity of forests usually shows a rise in early successional stages and a fall with long-term forest recovery in relation to the distribution of pioneer, early-, and late-successional species (Sheil and Bongers 2020).

We also found that most plant species may disappear from dolines between 10 and 40 years after canopy removal, as both the total number of species and the number of species in almost all studied groups of plants were lowest in dolines dominated by 40–45-year-old forests (Figs. 4 and 6). The competitive effect of the dense and shady thickets of young trees upon understory herbs and shrubs during this successional stage may be responsible for the significant decrease in species richness of dolines (cf. Allen et al. 2002; Gilliam 2007; Roleček and Řepka 2020). Different forest management activities, such as forest thinning and the creation of small artificial gaps, may create more favourable conditions for a number of forest floor species and facilitate the recolonisation of



**Fig. 5** Number of vascular plant species (all plant species and oak forest species) in the plots of topographic positions in dolines (S: south-facing slope, B: bottom, and N: north-facing slope) (mean ± SE). Significant differences ( $p < 0.05$ , based on the GLMMs with Bonferroni post hoc tests) are indicated by different lower case (a–c) letters



**Fig. 6** Number of vascular plant species (all plant species and beech forest species) in the plots of topographic positions in dolines (south-facing slope, bottom, and north-facing slope) covered with different forest age classes (class 1: 5–10-year-old forest stands with mature forest patches, class 2: 40–45-year-old forests, class 3: 60–65-year-old forests, and class 4: more than 90-year-old forests) (mean ± SE). Significant differences (based on the GLMMs with Bonferroni post hoc tests) are indicated by different lowercase (a–c: between the same topographic positions of the different forest age classes,  $p < 0.05$ ) and upper case (A–C in different colours: between the different topographic positions within a forest age class,  $p < 0.05$ ) letters, respectively

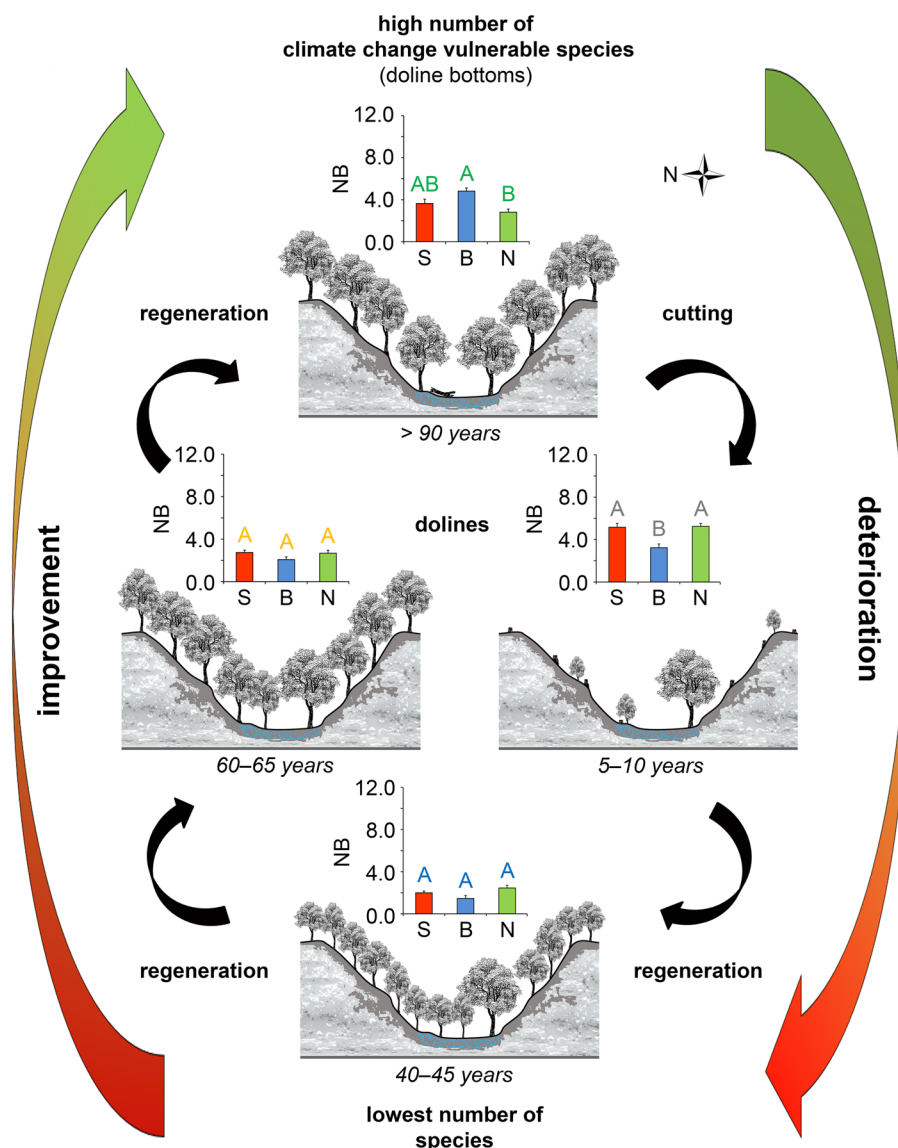
many climate change vulnerable species (e.g. beech forest species) (cf. Govaert et al., 2020; Li et al. 2020; Richard et al. 2021). The above patterns are also strongly related to the high topographic complexity within dolines.

Topographic complexity (e.g. various topographic positions and rockiness) can create microhabitats with unique microclimates [i.e. high thermal variability over short distances, Lenoir et al. (2013)] that may allow species to survive changes in their environment by migrating short distances between microhabitats (Burnett et al. 1998; Deák et al. 2020, 2021). Differences in the microclimate of opposing slope aspects (e.g. north-facing vs. south-facing) are usually larger in grasslands than in forested habitats. For instance, Bátori et al. (2019) found that the mean daytime temperatures on south-facing slopes in grassland dolines can be more than 8 °C higher than on north-facing slopes, while climatic differences in forested dolines are much less pronounced (Bátori et al. 2014b). However, intensive logging may cause significant changes in the habitat characteristics of forest stands, increasing differences in temperature, moisture, soil, and light conditions among microhabitats (Dean et al. 2016; Kovács et al. 2018; Bátori et al. 2021; Richard et al. 2021) and resulting in shifts in the distribution and abundance of forest floor species. We found that the studied groups of vascular plants often showed significant preferences

for certain topographic positions (south-facing slope, bottom, and north-facing slope) and indicated various environmental conditions within the forest age classes in dolines, except in dolines covered with 40–45-year-old forests (Figs. 5, 6, and Appendix Figure 10). We also found that logging may cause significant changes in the environmental conditions of topographic positions. For instance, plants indicated slightly lower soil moistures in doline bottoms covered with 40–45-year-old forests than in the other age classes. This is presumably due to the change in forest structure (i.e. tree density and canopy closure) during the succession of these forests. The dense forest canopy in this successional stage can intercept a substantial fraction of rainfall (reducing the amount of water reaching the soil), contributing to a decrease in soil moisture content (Tölgyesi et al. 2020; Bátori et al. 2021). These patterns show that intensive logging may lead to community changes and a reduction in the species richness of forest floor species and may influence changes in the length of local environmental gradients (e.g. light availability and soil moisture, Appendix Figure 10) within 40 years after canopy removal in dolines, similar to other human-mediated disturbances such as overgrazing and intensive agricultural use (Ren et al. 2015; Buhk et al. 2017). Differences in species richness were often larger between the bottoms and slopes than between the slopes, suggesting

that bottoms provide a unique niche within dolines with cool air pooling and high moisture retention capacity (Raschmanová et al. 2018; Marcin et al. 2021). Results of the current study and previous studies showed that doline bottoms with high refugial capacity (i.e. lower temperature, higher relative air humidity, and deeper and more fertile soil with high water retention capacity) may provide microhabitats for a number of climate change vulnerable species (i.e. diagnostic species), such

as narrow buckler-fern [*Dryopteris carthusiana* (Vill.) H. P. Fuchs] and alternate-leaved golden-saxifrage (*Chrysosplenium alternifolium* L.) in the Mecsek Mts (Hungary) (cf. Table 3) and alpine foxtail (*Alopecurus alpinus* Vill.) in Serra del Prete (Italy) (Gargano et al. 2010), which are rare or absent from the surrounding plateau. Our results also showed that the number and/or proportion of climate change vulnerable species significantly decreased after a few years of canopy removal



**Fig. 7** Effects of forest management on the vegetation in dolines in the Mecsek Mts, Hungary. The total number of species and the number of climate change vulnerable plant species (i.e. beech forest species) may change due to intensive logging. Doline bottoms covered with more than 90-year-old forests may provide important microhabitats for many beech forest species (see bar charts and Fig. 6). The number of these species may decrease at doline bottoms and increase on the slopes after 5–10 years of logging. The competitive effect of the dense and shady thickets of young trees upon understory herbs and shrubs during the forest regeneration phase may be responsible for the significant decrease in species richness of dolines. Most plant species associated with the oldest forest stands may re-establish within 90–120 years after a regeneration felling. Abbreviation: NB, number of beech forest species in the plots

in doline bottoms (Fig. 7), indicating rapid changes in their conservation value. As the climate is changing rapidly, there is an increasing need to understand how the biota of these dolines will respond to these changes during the succession of these forests.

Global warming poses one of the biggest challenges that ecosystems are facing in recent times (Bartholy et al. 2007; Gilman et al. 2010). Studies examining the effects of global warming on European ecosystems revealed a consistent pattern of change; the response to temperature increase and precipitation variations by species distributional shifts is well documented (Gallé 2017; Casado-Amezúa et al. 2019; Lenoir et al. 2020). Although the increasing atmospheric CO<sub>2</sub> content and warmer temperatures may increase forest growth and wood production in northern and western Europe, adverse effects are expected in southern and eastern Europe due to increasing drought and disturbance risks (Lindner et al. 2010). As forest age and topography may jointly influence the species richness and composition of vascular plants as well as the number of climate change vulnerable plant species, conservationists and forest managers need to consider their potential impacts when evaluating the effects of climate warming on the biota of karst landscapes.

### 5 Conclusions

Dolines may provide important microhabitats for a number of vascular plant species for which a given habitat becomes environmentally unsuitable due to climate warming. However, anthropogenic disturbances may alter the environmental characteristics and species composition of these habitats. The main result of our study is that there is a strong relationship between topographic complexity, forest management, and the distribution of different groups of vascular plant species in karstic habitats. We found that topographic position plays an important role in structuring plant communities in dolines, and that the current management practices may change the environmental conditions and vegetation patterns in these unique habitats. Although the investigation of different forest age classes within dolines shows that most plant species associated with the oldest forest stands in our study area have re-established within 90–120 years after a regeneration felling, there is an urgent need to develop guidelines for local forest managers so that they also facilitate the maintenance of such safe havens in a warming climate.

### Appendix

**Table 4** Comparisons of plant species composition between the forest age classes (class 1: 5–10-year-old forest stands with mature forest patches, class 2: 40–45-year-old forests, class 3: 60–65-year-old forests, and class 4: more than 90-year-old forests) with one-way analysis of similarities (ANOSIM) in the dolines of the Mecsek Mts (Hungary)

	R	<i>p</i>
class 1 – class 2	0.41	<b>&lt; 0.001</b>
class 1 – class 3	0.15	<b>&lt; 0.001</b>
class 1 – class 4	0.09	<b>&lt; 0.001</b>
class 2 – class 3	0.27	<b>&lt; 0.001</b>
class 2 – class 4	0.23	<b>&lt; 0.001</b>
class 3 – class 4	0.05	<b>&lt; 0.005</b>

The *p* values in pairwise comparisons were Bonferroni corrected. Significant differences (*p* < 0.005) are indicated by bold *p* values

**Table 5** Results of the generalized linear mixed-effects models for the number of species

	Forest age	Topographic position	Interaction
	F value		
All plant species	<b>25.23***</b>	<b>19.79***</b>	<b>10.08*</b>
Beech forest species	<b>9.48*</b>	NS	<b>7.05*</b>
Oak forest species	<b>21.29**</b>	<b>57.89***</b>	NS
Species of disturbed forests	<b>16.24**</b>	NS	NS

Asterisks indicate statistically significant differences (\*: *p* < 0.05, \*\*: *p* < 0.01, and \*\*\*: *p* < 0.001)

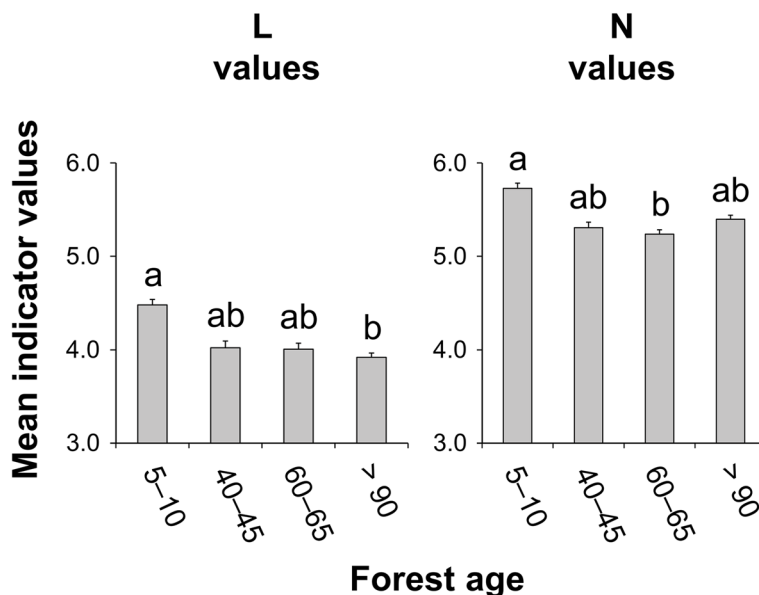
Abbreviation: NS not significant

**Table 6** Results of the linear mixed-effects models for the mean Ellenberg indicator values (L: light availability, T: temperature, W: soil moisture, R: soil reaction, and N: nutrient availability)

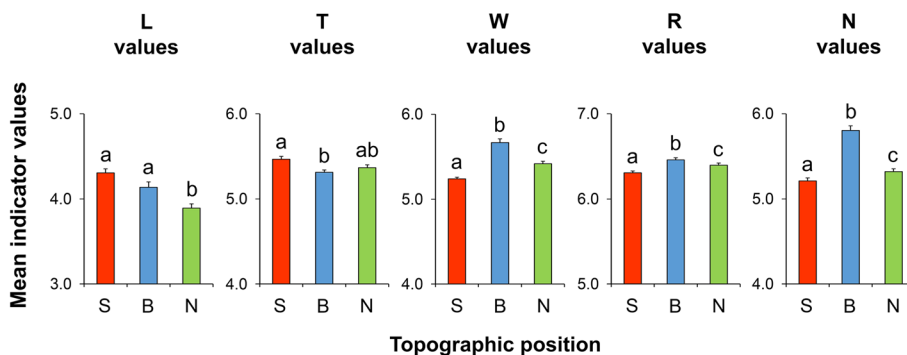
	Forest age	Topographic position	Interaction
	F value		
L	<b>4.23**</b>	<b>15.01***</b>	<b>3.05**</b>
T	NS	<b>5.94**</b>	NS
W	NS	<b>48.08***</b>	<b>4.21***</b>
R	NS	<b>10.92***</b>	<b>5.30***</b>
N	<b>6.48***</b>	<b>70.15***</b>	NS

Asterisks indicate statistically significant differences (\*\*: *p* < 0.01, and \*\*\*: *p* < 0.001)

Abbreviation: NS not significant

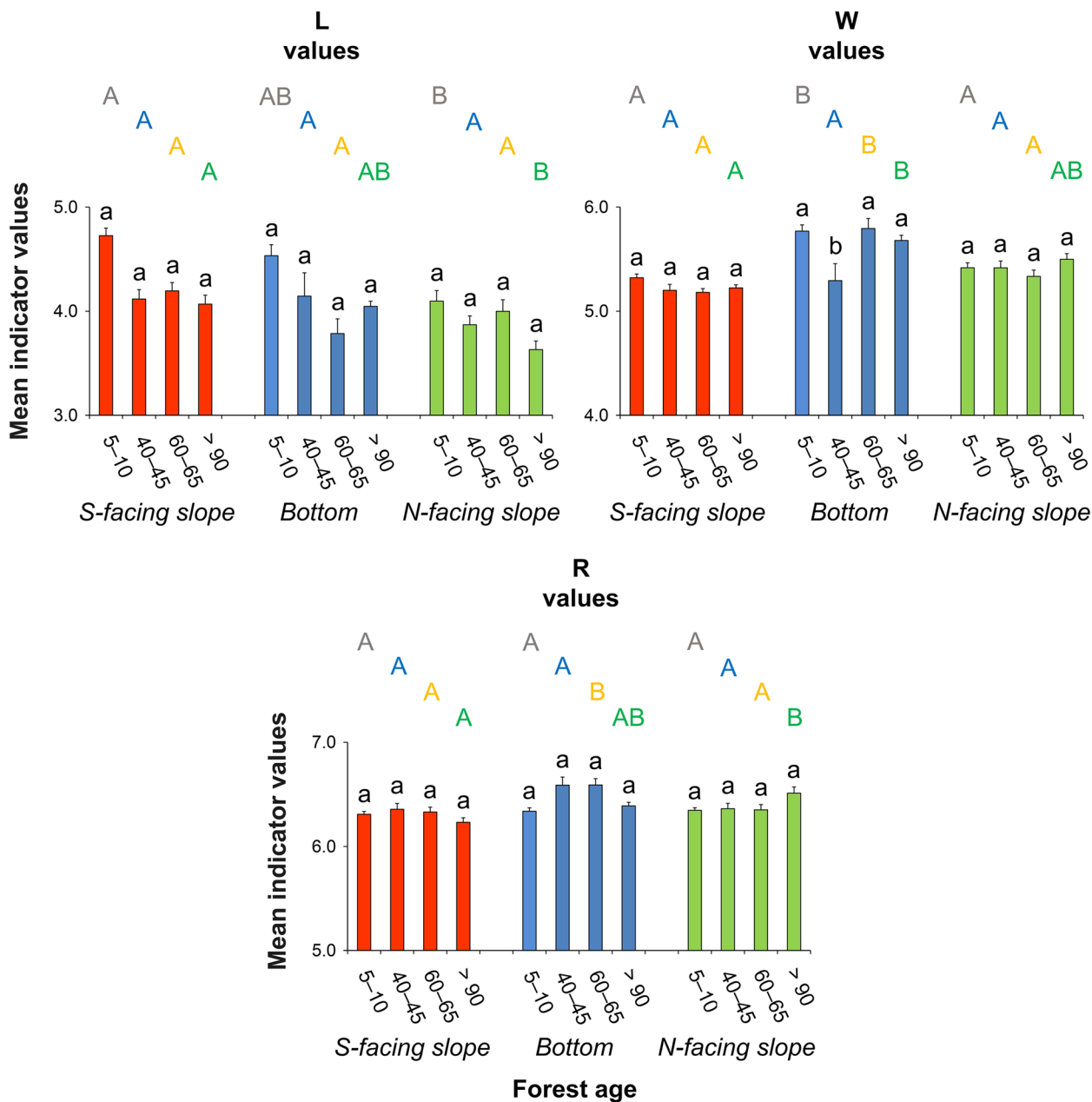


**Fig. 8** Mean Ellenberg indicator values (L: light availability, and N: nutrient availability) in the plots of dolines covered with different forest age classes (class 1: 5–10-year-old forest stands with mature forest patches, class 2: 40–45-year-old forests, class 3: 60–65-year-old forests, and class 4: more than 90-year-old forests) (mean ± SE). Significant differences ( $p < 0.05$ , based on the LMMs with Bonferroni post hoc tests) are indicated by different lower case (a and b) letters



**Fig. 9** Mean Ellenberg indicator values (L: light availability, T: temperature, W: soil moisture, R: soil reaction, and N: nutrient availability) in the plots of topographic positions in dolines (S: south-facing slope, B: bottom, and N: north-facing slope) (mean ± SE). Significant differences ( $p < 0.05$ , based on the LMMs with Bonferroni post hoc tests) are indicated by different lower case (a–c) letters





**Fig. 10** Mean Ellenberg indicator values (L: light availability, W: soil moisture, and R: soil reaction) in the plots of topographic positions in dolines (south-facing slope, bottom, and north-facing slope) covered with different forest age classes (class 1: 5–10-year-old forest stands with mature forest patches, class 2: 40–45-year-old forests, class 3: 60–65-year-old forests, and class 4: more than 90-year-old forests) (mean ± SE). Significant differences (based on the LMMs with Bonferroni post hoc tests) are indicated by different lower case (a and b: between the same topographic positions of the different forest age classes,  $p < 0.05$ ) and upper case (A and B in different colours: between the different topographic positions within a forest age class,  $p < 0.05$ ) letters, respectively

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### Code availability

Not applicable

### Reference to preprint servers

Not applicable

### Authors' contributions

The study was conceived and planned by ZB and AK. ZB, CT, LE, GL, and MG conducted the field work. ZB and GL prepared the datasets. AK, CT, and ZB performed the analysis and wrote the manuscript. The authors read and approved the final manuscript.

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### Availability of data and materials

The datasets generated and/or analysed during the current study are available in the Zenodo data repository: <https://doi.org/10.5281/zenodo.6863694>

### Declarations

#### Ethics approval and consent to participate

Not applicable. All authors gave their informed consent to this publication and its content.

#### Competing interests

The authors declare that they have no competing interests.

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