



Managing climate change microrefugia for vascular plants in forested karst landscapes

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ABSTRACT

Microrefugia are small areas that support favourable climate and allow species to persist during regional and global climate changes. Dolines in karst landscapes may provide such areas for many climate change-vulnerable species. Here we provide a better understanding on how plant species indicate changes in their environment (temperature, soil moisture and light availability) after a few years of partial canopy removal from dolines and their close surroundings (logged areas: >1 ha). We place our results in the context of the most widely used forest management practices within the study area (Mecsek Mts, Hungary), in addition to presenting a general framework for the maintenance of doline microrefugia in forested karst landscapes. Three types of habitats were investigated: dolines before logging, dolines after logging, and the forested plateau. Three large dolines and three sites on the plateau were selected for vegetation sampling. All dolines were sampled before logging and 5–10 years after partial canopy removal. Logging resulted in a 50–80% reduction of canopy cover in the dolines and their close surroundings. We established a transect across each doline from north to south passing through doline bottoms, and across each plateau site. We estimated the percentage cover of vascular plant species (tree saplings – up to 1 m in height, shrubs and herbs) along the transects using 1 m × 1 m vegetation plots, determined the diagnostic species of the doline and plateau habitats, and used multivariate methods and linear mixed-effects models during analyses. Plant species indicated clear gradients of the main microclimatic factors within the dolines and that significant changes took place after logging. Canopy removal caused substantial changes in the main microclimatic factors of most doline microhabitats (e.g., south-facing slopes). The vegetation of the dolines before logging indicated moister conditions than that of the plateau and cooler and shadier conditions than that of the dolines after logging. These and our previous results suggest that logging may directly and indirectly influence dolines to be microrefugia under global warming. By applying our framework to refugia conservation and management for the karst landscape in the Mecsek Mts, we can conclude that the protection of old forests and natural forest dynamics in as many large dolines as possible and the implementation of close-to-nature forestry practices may be essential to maintain regional biodiversity in the long run.

1. Introduction

Climate change microrefugia are small areas with special environmental conditions where species persist during regional climate changes with the potential to re-expand in the future (Keppel et al., 2012; Meineri and Hylander, 2017). Because such areas provide important information about past climates due to the presence of climate relicts and will likely play key roles in retaining biodiversity under future climate

changes, they are among the most fascinating study systems in biogeography (Dobrowski, 2011; Lenoir et al., 2017; McLaughlin et al., 2017). In recent years, there has been intense interest in developing approaches for identifying and understanding refugia, highlighting the importance of physical and topographic features, climate exposure, environmental gradients and species-based information (e.g., physiological and functional traits) in microrefugia (Meineri and Hylander, 2017; Keppel et al., 2018; Michalak et al., 2020; Barrows et al., 2020). For instance, a

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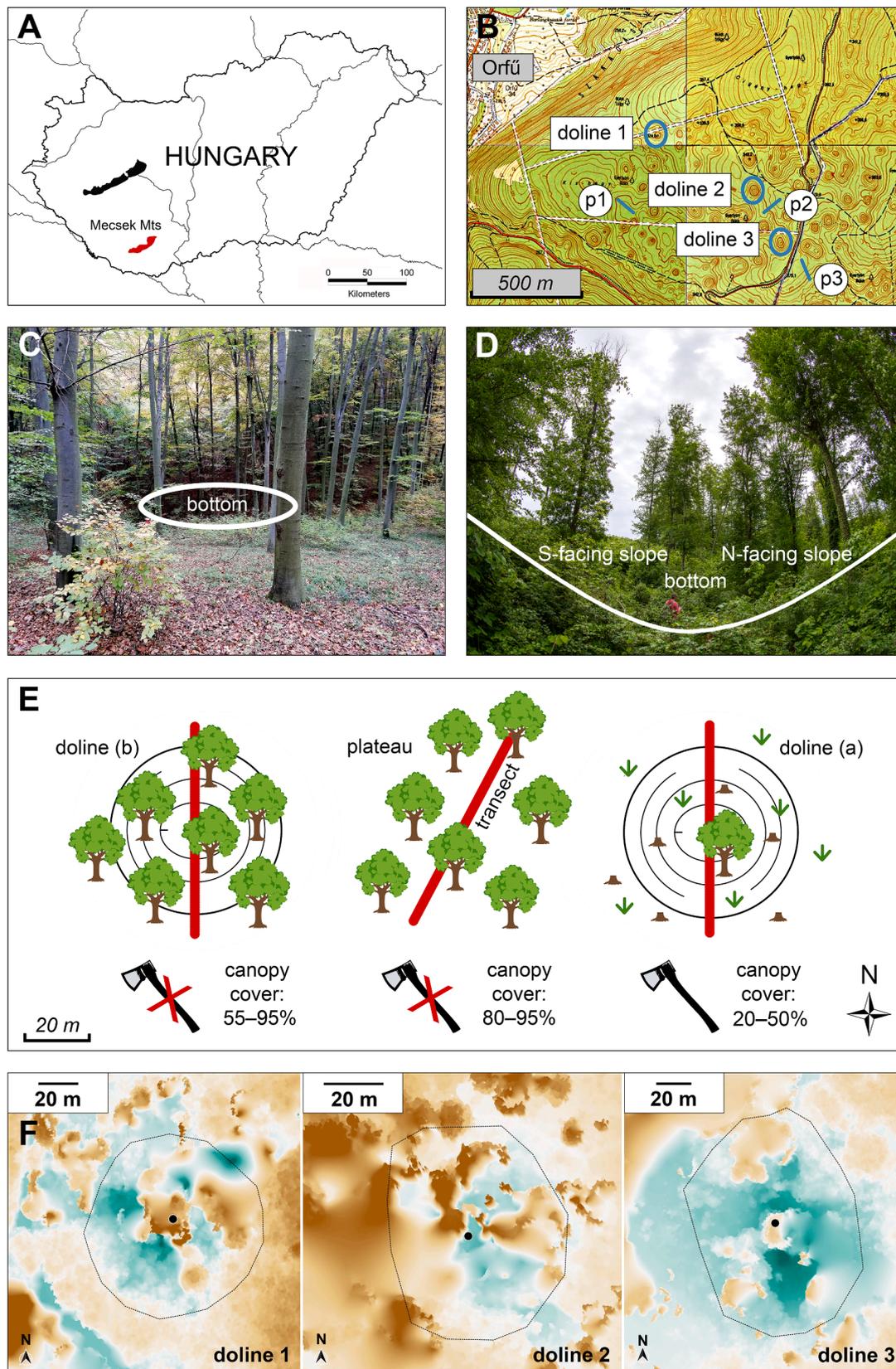


Fig. 1. Study region, study area and sampling design. (A) Location of the study region (Mecsek Mts) in Hungary. (B) Location of the study area in the Mecsek Mts (adapted from www.mepar.hu); p1, p2 and p3 indicate the investigated sites on the plateau. (C) Large doline covered by older beech and ravine forests (photo: Zoltán Batori). (D) Doline 2 about nine years after logging (photo: Gábor Li). (E) Set-up of transects on the plateau and in the dolines before and after logging. (F) Digital surface models (DSMs) of the dolines and their surroundings from May 2021. The intensity of colours indicates the height of vegetation (from dark brown to dark blue; where brown represents taller vegetation, and blue represents shorter vegetation). Black dots indicate the deepest part of the dolines. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

number of studies have demonstrated that the presence of sharp temperature gradients and cold air pooling in topographically complex regions may decrease an organism's vulnerability to warming, indicating that these regions can function as microrefugia under on-going climate change (Bátori et al., 2017, 2019; Deák et al., 2020, 2021; García et al., 2020). Although the need to integrate disturbance responses into climate change modelling of species distributions has been strongly emphasised by recent investigations, it is still poorly understood how anthropogenic disturbances affect the distribution patterns of organisms within microrefugia (Syphard and Franklin, 2010; Serra-Diaz et al., 2015).

Besides incorporating the effects of disturbances into the evaluation of refugia, the prioritisation of current and potential climate change microrefugia is also needed to achieve the most suitable conservation and management measures (Keppel et al., 2015; Bátori et al., 2020a). According to the 'climate change refugia conservation cycle' (Morelli et al., 2016), the first three steps of managing/maintaining refugia are to determine purposes and scopes, to assess the vulnerability of the resource (e.g., a species' range) to climate change, and to review/revise conservation goals and objectives (steps 1–3). Following these assessments, one has to identify and map key refugia features (step 4), followed by the evaluation and prioritisation of refugial areas for specific management (step 5) and the identification/implementation of priority actions to manage these areas (step 6). Finally, the effectiveness of identified refugia should be monitored and locations and management practices should be realigned, if needed (step 7). In this study, we characterise the biotic and environmental changes caused by forest management in karstic microrefugia and provide an example of how the abovementioned steps can be adapted for the conservation and management of forested karst landscapes.

Refugial areas in karst landscapes have played a key role in maintaining global biodiversity during Quaternary climate oscillations (Culver and Sket, 2000; Clements et al., 2008; Bátori et al., 2017; Su et al., 2017), e.g., during warmer interglacial or post-glacial periods (as 'warm-stage' microrefugia). A number of relict species have also maintained viable populations within cooler and moister spots (Vilissics et al., 2011; Raschmanová et al., 2018), such as in karst depressions (dolines, sinkholes, or tiankengs). Dolines are the main geomorphological features in many karst landscapes that not only provide suitable habitats for many climate change-vulnerable species but also play an important role in preserving various functional groups of species (Bátori et al., 2020b). However, anthropogenic disturbances have the potential to alter the conservation value of dolines by changing the physical environment, microclimate and finally, the number of vulnerable species in them (Kovačič and Ravbar, 2013; Aguilon et al., 2020). For instance, Kermavnar et al. (2020) showed that the short-term responses of microclimatic variables to various forest management intensities within dolines differ significantly between uncut areas, intermediate management intensity (50% canopy removal) and high management intensity (100% canopy removal). Specifically, the temperature and vapour pressure deficit increased, while the relative humidity decreased with management intensity. In addition, canopy removal may cause changes in the refugial capacity (i.e. their potential for facilitating species persistence, Keppel et al., 2015) and the naturalness of doline microhabitats (Bátori et al., 2020a; Kiss et al., 2020).

According to Keppel et al. (2015), the environmental and microclimatic suitability of a habitat and its accessibility to species are the main determinants of refugial capacity. Thus, detrimental changes in these attributes may lead to decreased refugial capacity and – as a result – a decline in the number of 'good' indicator species living within a microrefugium. Although an increasing number of studies have reported on the decline of climate change-vulnerable plant species triggered by various anthropogenic disturbances, the usefulness of different indicator species for monitoring potential environmental changes in karstic microrefugia has remained largely unknown (but see Breg Valjavec et al., 2018a, b; Bátori et al., 2020a; Ferré et al., 2020). Here we aim to

provide a better understanding on how plant species indicate changes in their environment after 5–10 years of partial (but significant) canopy removal from dolines and their close surroundings using the Ellenberg indicator values (EIVs) of vascular plant species (Ellenberg et al., 1992). We focus on the changes in the main microclimatic factors (temperature, soil moisture and light availability) caused by forest management, which, we assume, would indicate changes in the refugial capacity of dolines. We also present a general framework for managing/maintaining doline microrefugia in forested karst landscapes based on the steps proposed by Morelli et al. (2016). The following specific questions are addressed: 1) Do plant species indicate any difference in the main microclimatic factors between dolines and the plateau? 2) How do these factors change after a few years of canopy removal within dolines? We believe that our results will provide a firm basis for the conservation and management of microrefugia in karst landscapes and may act as an interface between conservationists and forest managers.

2. Material and methods

2.1. Study area

The study area was selected in a limestone karst landscape of about 30 km² in the western part of the Mecsek Mts (altitude: 250–500 m), near the village of Orfű, Hungary (Fig. 1A, B), where more than 2000 solution dolines are scattered on a relatively flat plateau (Hoyk, 1999a). The climate is continental with strong sub-Mediterranean influences (mean annual temperature: 9.5 °C, mean annual precipitation: 740 mm) (Dövényi, 2010). Although most dolines are small (diameter < 20 m) and do not substantially modify the microclimate of the area, large dolines provide cooler and more humid microclimates than the karst plateau (Bátori et al., 2011). The limestone is covered by weathered loess. Due to this loess cover, soil formation processes are mostly independent of limestone and, as a result, Rendzic Leptosols (WRB 2015) occur only around rocky outcrops and steep south-facing slopes. The dominant soil type is a Haplic Luvisol (Jones et al., 2005; Mezósi, 2017) with relatively thick A and E horizons (40–60 cm), 1–2% humus content and a pH between 5 and 6. The soil texture is mainly clay loam, secondly loam or clay. The B horizon can extend to 90–120 cm and it can be characterised by higher clay content than the topsoil. Carbonate content and coarse fragment are low (under 3%) along the whole soil profile (Hoyk, 1999b). The thinnest soils can be found on the steepest slopes of dolines, valleys and rocky outcrops, while doline bottoms are covered by deep soils with a high water retention capacity (Bátori et al., 2011).

Sub-Mediterranean type oak-hornbeam and beech forests cover the plateau and the upper slopes of dolines (Fig. 1C), while ravine forests with *Acer campestre*, *A. platanoides*, *A. pseudoplatanus*, *Ulmus glabra*, *Tilia cordata* and *T. platyphyllos* occur at the bottoms of larger dolines (Bátori et al., 2012). A relatively high number of dolines are covered by 70–120 year-old forests. Canopy cover on the upper slopes varies between 75% and 95%, while it is generally lower (55–75%) at the bottom of larger dolines. Canopy cover within some larger dolines has decreased significantly in the last 5–15 years, due to commercial forest management (i.e. rotation forestry, Fig. 1D–F; Supplementary Fig. 1). The first cutting intervention (preparation cutting) in the investigated dolines and/or their close surroundings was in 2007 (doline 1) and between 2011 and 2012 (dolines 2 and 3, respectively). Canopy cover within doline 1 had decreased significantly (logged area: > 1 ha) by 2012, while the canopy was removed from about 0.1–0.2 ha patches adjacent to dolines 2 and 3. Selective cutting was also implemented in doline 2 and its close surroundings (logged area: > 1 ha). Only some smaller patches of mature trees had survived in doline 3 by 2016. As a result of these forestry activities, canopy cover within dolines had decreased to approximately 20–50% of its original extent by 2017 and 2019 (Fig. 1D–F). Canopy cover in the older (70–120 years old) oak-hornbeam and beech forests of the plateau ranges between 80% and 95%.

Our previous studies indicated that the bottom of larger dolines may

provide potential microrefugia for a number of climate change-vulnerable species, such as *Aconitum vulparia* Rchb., *Chrysosplenium alternifolium* L., *Dryopteris dilatata* (Hoffm.) A. Gray, *D. pseudomas* (Woll.) Holub bis & Pouzar, *Polystichum aculeatum* (L.) Roth ex Mert., *P. setiferum* (Forssk.) Moore ex Woy., *Stachys alpina* L. and *Veronica montana* L., which are rare in or absent from the plateau habitats (Bátori et al., 2012). The south-facing slopes provide habitats for species adapted to warmer and drier conditions [e.g., *Dioscorea communis* (L.) Caddick & Wilkin and *Fraxinus ornus* L.].

2.2. Sampling

Three types of habitats were investigated: 1) dolines before logging, 2) dolines 5–10 years after logging, and 3) the plateau, covered by intact forests. Three large dolines (dolines 1, 2 and 3; Fig. 1B) and three sites on the plateau were selected for vegetation sampling. Dolines were about 70–100 m in diameter and about 13–14 m deep. All dolines were sampled before logging in 2007 (covered by about 110-year-old forests) and about 5–10 years after partial canopy removal in 2017 (dolines 1 and 2) and 2019 (doline 3). The sites on the plateau were sampled in 2007. No signs of logging were detected during the sampling in 2007, either in the investigated dolines and their close surroundings, or in the sites on the plateau.

We used the same sampling method for the doline and plateau habitats. A transect was established across each doline from north to south passing through the doline bottom (length of transects: 87 m, 78 m, and 114 m, respectively) (Fig. 1E). Transects were placed at approximately the same location before and after logging. Three 100-m-long transects were also established on the plateau. The distance between these transects was at least 100 m. All transects consisted of 1 m × 1 m vegetation plots spaced at 2-m intervals. The survey was conducted in summer (June–August), at the peak of the growing season. We recorded the percentage cover of each vascular plant species (tree saplings – up to 1 m in height, shrubs and herbs) in each plot. We surveyed 294 plots (dolines: 96 plots before and after logging, respectively; plateau: 102 plots). Nomenclature follows The Plant List (www.theplantlist.org/).

2.3. Indicator values

Ellenberg-type indicator values (EIVs) express the realized optimum of the plant species on an ordinal scale defined along environmental gradients. They have been developed for the characterisation of Central European habitats (Ellenberg et al., 1992); the system has been adapted and fine-tuned to the floras of several countries [e.g., Czech Republic (Chytrý et al., 2018), Hungary (Borhidi, 1995) and Romania (Sárbu et al., 2013)], and has become a widespread tool of agriculture, plant ecology and forestry for comparing the habitat conditions of two or more areas and for monitoring environmental changes (Tölgyesi et al., 2014). In order to characterise microclimatic differences between the habitats (dolines before logging, dolines after logging and the plateau), unweighted mean EIVs for temperature (T), soil moisture (W) and light availability (L) were calculated for each plot using the system of Borhidi (1995). Despite the ordinal nature of EIVs, several studies have shown that mean EIVs give reliable estimates of the environmental conditions and thus provide useful ecological information (Lengyel et al., 2012; Wildi, 2016).

2.4. Statistical analysis

The diagnostic species of the habitats (dolines before logging, dolines after logging and the plateau) were determined by using the phi (Φ) coefficient of association (JUICE program, Tichý, 2002). Species with $\Phi \geq 0.2$ were considered diagnostic (Fisher's exact test, $p < 0.05$) (Tichý and Chytrý, 2006). Analysis of similarities (ANOSIM) based on the presence/absence data of species, Jaccard dissimilarity and 5000

Table 1

List of diagnostic plant species on the plateau and in the dolines before and after logging in the Mecsek Mts (Hungary). The temperature (T), moisture (W) and light (L) indicator values of these species are shown in parenthesis (Borhidi, 1995). Within blocks, species are listed by decreasing values of the phi (Φ) coefficient ($\Phi \times 100$, values in boldface).

Synoptic table	
Plateau	Φ (T, W, L)
<i>Lathyrus vernus</i> (L.) Bernh.	39.9 (6, 6, 4)
<i>Melica uniflora</i> Retz.	38.1 (5, 5, 4)
<i>Hedera helix</i> L.	37.6 (5, 5, 4)
<i>Carex pilosa</i> Scop.	37.2 (6, 5, 4)
<i>Tilia cordata</i> Mill.	31.0 (5, 5, 4)
<i>Polygonatum multiflorum</i> (L.) All.	21.6 (5, 5, 3)
<i>Fraxinus excelsior</i> L.	21.2 (5, 6, 3)
<i>Alliaria petiolata</i> (M.Bieb.) Cavara & Grande	20.0 (6, 5, 5)
Dolines before logging	Φ (T, W, L)
<i>Acer pseudoplatanus</i> L.	36.6 (5, 6, 4)
<i>Veronica montana</i> L.	34.3 (5, 6, 4)
<i>Lamium galeobdolon</i> (L.) L. s.l.	23.1 (5, 6, 3)
<i>Lamium maculatum</i> (L.) L.	20.6 (5, 6, 4)
Dolines after logging	Φ (T, W, L)
<i>Rubus hirtus</i> Waldst. et Kit. agg.	47.1 (6, 5, 6)
<i>Urtica dioica</i> L.	43.4 (6, 7, 6)
<i>Calamagrostis epigejos</i> (L.) Roth	39.7 (5, 5, 7)
<i>Vinca minor</i> L.	32.0 (6, 5, 4)
<i>Carex sylvatica</i> Huds.	30.3 (5, 6, 3)
<i>Hypericum hirsutum</i> L.	29.8 (6, 5, 7)
<i>Stenactis annua</i> (L.) Cass.	28.2 (5, 7, 5)
<i>Veronica chamaedrys</i> L.	26.6 (5, 5, 6)
<i>Carpinus betulus</i> L.	25.2 (6, 6, 4)
<i>Erechtites hieracifolia</i> (L.) Raf.	23.9 (8, 5, 7)
<i>Fragaria vesca</i> L.	23.9 (5, 5, 7)
<i>Lactuca muralis</i> (L.) Fresen.	23.9 (5, 5, 4)
<i>Dactylis glomerata</i> L.	22.3 (5, 6, 7)
<i>Athyrium filix-femina</i> (L.) Roth	20.8 (5, 7, 4)
<i>Salix caprea</i> L.	20.6 (5, 5, 7)

permutations were applied to test the effect of habitats on the plant species composition. Detrended correspondence analysis (DCA) was used to visually illustrate compositional differences between the habitats (detrending with 26 segments). ANOSIM and DCA were calculated in R (R Core Team, 2021) using the *anosim* and the *decorana* functions of the 'vegan' package (Oksanen et al., 2019). To assess the relationships between mean EIVs and habitats, smooth surfaces and environmental vectors were fitted onto the DCA ordination space using the *ordisurf* and *envfit* functions and correlations between ordination scores and fitted vectors were calculated.

Violin plots were used to illustrate the distribution of mean EIVs in the habitats. To test differences between habitats we used linear mixed-effects models (LMMs) with a Gaussian error term. LMMs were performed in R using the *lme* function of the 'nlme' package (Pinheiro et al., 2021). Habitat (three levels: dolines before logging, dolines after logging and the plateau) was included as the fixed factor, mean EIVs of the plots as dependent variables, and location (i.e. dolines 1, 2 and 3, and sites 1, 2 and 3 on the plateau) as a random factor. Full models were tested for significance with the *Anova* function of the 'car' package (Fox and Weisberg, 2019). Pairwise comparisons of factor levels were carried out with Tukey's HSD post-hoc test, using the *emmeans* function of the 'emmeans' package (Lenth, 2021). Additional models (LMMs, Gaussian error term) were built to test differences in each doline microhabitat before and after logging. We defined microhabitats as follows: south-facing slope – upper two-third of plots along the south-facing slope; bottom – lower third of plots along the slopes, and north-facing slope – upper two-third of plots along the north-facing slope. Time was used as the fixed factor (two levels: before and after logging) in the models, mean EIVs of the plots as dependent variables, and location (i.e. dolines 1, 2 and 3) as a random factor. Separate models were built for each microhabitat.

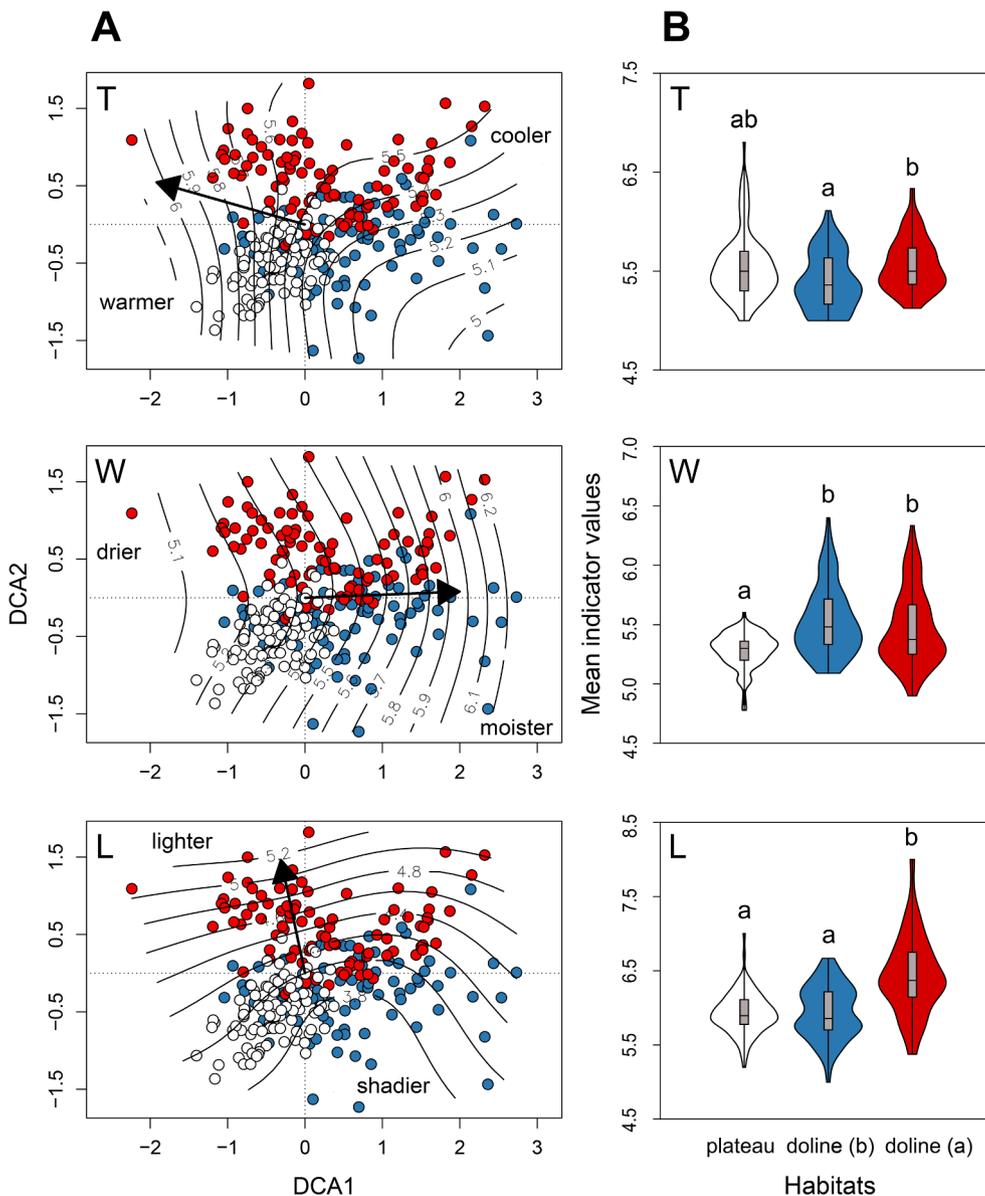


Fig. 2. Species composition differences and mean indicator values in different habitats of the Mecsek Mts (Hungary). Colour code: white – plateau, blue – doline (b): dolines before logging, and red – doline (a): dolines after logging. (A) Detrended correspondence analysis (DCA) ordination diagram of vegetation plots with the fitted smooth surfaces and environmental vectors of the main microclimatic factors (T: temperature, W: soil moisture and L: light availability). Eigenvalues for the first two DCA axes were 0.417 and 0.334, respectively. (B) Violin plots of the mean indicator values. Significant differences ($p < 0.05$) are indicated by different lowercase letters (a and b). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

2.5. Framework for managing/maintaining doline microrefugia

To provide a general framework for managing/maintaining doline microrefugia in forested karst landscapes, published case studies and reviews were identified in peer-reviewed sources using a Google Scholar search on the terms ‘refugium’/‘refugia’, ‘karst’, ‘forest’ and ‘doline’/‘sinkhole’/‘tiankeng’. This search resulted in more than 500 papers. After reading the titles and/or abstracts, we identified a subset of 42 papers about dolines that incorporated relevant conservation and/or management information. Eventually, we used the results of 28 papers (Supplementary Table 1) and our current analysis to build a framework, based on the steps of the ‘climate change refugia conservation cycle’ proposed by Morelli et al. (2016).

3. Results

3.1. Diagnostic species

A total of 97 plant species were recorded in the 294 plots of the three habitats. Four diagnostic species were identified for dolines before logging and 15 diagnostic species for dolines after logging, while the plateau had eight diagnostic species (Table 1). All diagnostic species of dolines before logging were submontane species (T5) and indicators of fresh-humid soils (W6). Three of them were shade-semi-shade plants (L4, 75%) and one was a shade plant (L3, 25%). The plateau contained both colline (T6, 37%) and submontane species (63%), and most of its diagnostic species were shade-semi-shade plants (63%) and indicators of fresh soils (W5, 75%). Although most diagnostic species of dolines after logging were submontane species (60%), five colline species (33%) and one warm-adapted species (T8, 7%) were also identified. Most of

Table 2

Comparisons of the main microclimatic factors (temperature, soil moisture and light availability) among the plateau, doline (b) – dolines before logging, and doline (a) – dolines after logging in the Mecsek Mts (Hungary) using the fitted mixed-effects models. Significant differences ($p < 0.05$) are indicated with boldface.

Model	Microclimatic factors	
	<i>Mean temperature values</i>	
<i>Full model</i>	χ^2	<i>p</i>
	18.66	<0.001
Pairwise comparisons	<i>t</i>	<i>p</i>
doline (b) vs. plateau	-1.17	0.527
doline (b) vs. doline (a)	-4.30	< 0.001
doline (a) vs. plateau	0.27	0.962
	<i>Mean moisture values</i>	
<i>Full model</i>	χ^2	<i>p</i>
	49.85	< 0.001
Pairwise comparisons	<i>t</i>	<i>p</i>
doline (b) vs. plateau	6.80	< 0.001
doline (b) vs. doline (a)	1.62	0.237
doline (a) vs. plateau	5.28	0.002
	<i>Mean light values</i>	
<i>Full model</i>	χ^2	<i>p</i>
	91.64	<0.001
Pairwise comparisons	<i>t</i>	<i>p</i>
doline (b) vs. plateau	0.11	0.994
doline (b) vs. doline (a)	-8.67	< 0.001
doline (a) vs. plateau	7.27	< 0.001

their diagnostic species were indicators of fresh soils (60%), but indicators of fresh–humid soils (20%) and humid soils (W7, 20%) were also identified. Six diagnostic species of dolines after logging were half-light plants (L7, 40%), three were semi-shade–half-light plants (L6, 20%), and four were shade–semi-shade plants (27%). The proportion of other groups [L3 and L5 (semi-shade plants)] was low (6.7%, respectively). In 2007, we detected three species (*Chrysosplenium alternifolium*, *Dryopteris pseudomas* and *Veronica montana*) along the slopes of dolines that are rare or absent on the plateau, but we did not detect them in 2017.

3.2. Species compositional and environmental changes

The ANOSIM revealed significant differences ($R: 0.24, p < 0.001$) among the plot-level species composition of the habitats. All the pairwise comparisons were also clearly significant ($0.15 < R < 0.33, p < 0.001$). DCA axis 1 separated plots of the plateau and plots of the dolines before logging, while DCA axis 2 separated plots of the dolines after logging and plots of the other two habitats (Fig. 2A). Vegetation indicated a clear gradient of temperature ($r^2 = 0.25; p < 0.001$), moisture ($r^2 = 0.56; p < 0.001$) and light availability ($r^2 = 0.54; p < 0.001$) along DCA axes (axis 1: temperature and moisture, axis 2: light availability). The first DCA axis had a gradient length of 4.96 standard deviation (SD) units, while the second axis had a gradient length of 3.55 SD units.

According to the LMMs (Table 2), the vegetation of the dolines before logging indicated moister ($p < 0.001$) conditions than that of the plateau, and cooler ($p < 0.001$) and shadier ($p < 0.001$) conditions than that of the dolines after logging (Fig. 2B). In addition, vegetation in the dolines after logging indicated moister ($p < 0.005$) and lighter ($p < 0.001$) conditions than that of the plateau. EIVs of the plots on the south-facing slopes indicated significantly warmer ($t = 2.39, p = 0.02$), drier ($t = 2.1, p = 0.04$) and lighter ($t = 7.79, p < 0.001$) conditions after logging than before logging (Fig. 3). Doline bottoms became warmer ($t = 6.06, p < 0.001$) and lighter ($t = 3.74, p < 0.001$), while north-facing slopes became lighter ($t = 3.57, p < 0.001$) after logging.

3.3. Framework

In our framework we defined the seven steps that are considered important for managing/maintaining doline microrefugia in forested karst landscapes (Table 3).

4. Discussion and conclusions

Dolines can act as important microrefugia where species may survive for long periods during regional climate oscillations with the potential to re-expand in the future. We demonstrated that canopy removal within dolines may cause substantial changes in the understory vegetation and refugial capacity of doline microhabitats. Plant species indicated clear gradients of the main microclimatic factors (temperature, soil moisture and light availability) within dolines and their significant changes after partial canopy removal. By applying our framework to refugia conservation and management for the karst landscape in the Mecsek Mts, we can conclude that the protection of old forests and natural forest dynamics in as many large dolines as possible and the implementation of close-to-nature forestry practices may be essential to maintain regional biodiversity in the long run. Therefore, forest management and conservation actions within and adjacent to karstic microrefugia need to consider the possible effects of global climate change on the refugial capacity of microhabitats during the regeneration phase of forest stands.

Of particular importance in the face of climate changes is that dolines may provide a wide range of ecological conditions (both cooler and moister, and warmer and drier microhabitats) in which climate change-vulnerable species can maintain viable populations (Raschmanová et al., 2018; Bátori et al., 2019; Ferré et al., 2020). We found that plant species within larger forested dolines in the Mecsek Mts indicated diverse microclimatic conditions and steep gradients of temperature, soil moisture and light availability, suggesting the refugial capacity of these depressions to be higher than that of the plateau (Fig. 2, Table 2). This is in line with the findings of previous microclimatic studies that south-facing slopes in dolines receive more solar radiation than bottoms and north-facing slopes and that the lower parts of dolines retain more water (Whiteman et al., 2004; Kemencei et al., 2014; Bátori et al., 2019). If the regional climate becomes warmer and drier, those species of the upper slopes that indicate cooler and moister conditions would shift their distributions downslope to track their climatic niche. Contrarily, in a cooling climate, the upper slopes of dolines (especially the south-facing slopes) might provide important microhabitats for the reestablishment of these species. Similar conclusions can be drawn by considering and analysing the results of other studies in which the distribution of different species from various phyla (e.g., indicators of cool and moist or warm and dry habitats) indicates the presence of steep environmental gradients within dolines (Raschmanová et al., 2013; Battisti et al., 2017; Bátori et al., 2017). Although plant species indicated clear gradients of the main microclimatic factors after canopy removal as well, there were significant differences in gradient patterns before and after logging.

Logging may cause significant changes in the main microclimatic patterns of forests corresponding to the degree of canopy removal. For instance, clear-cutting often has severe and long-lasting effects by increasing light penetration, daily temperature and vapour pressure deficit that may lead to the changes of understory microhabitats (Jokela et al., 2019; Koivula et al., 2019; Kermavnar et al., 2020). Although less severe disturbances (e.g., 30–50% canopy removal or thinning) can still cause significant changes in at least some microclimatic factors, their total effect appears to be lower (Elek et al., 2018; Kovács et al., 2020; Zellweger et al., 2020). We found that partial (50–80%) canopy removal in the oak-hornbeam, beech and ravine forests of dolines stimulated and promoted the germination and growth of many plant species in the understory that indicated significant shifts toward a warmer and lighter environment (Fig. 2, Table 1). These changes were especially pronounced on the south-facing slopes and the bottoms (Fig. 3). Although we found no apparent shifts in soil moisture when comparing plant

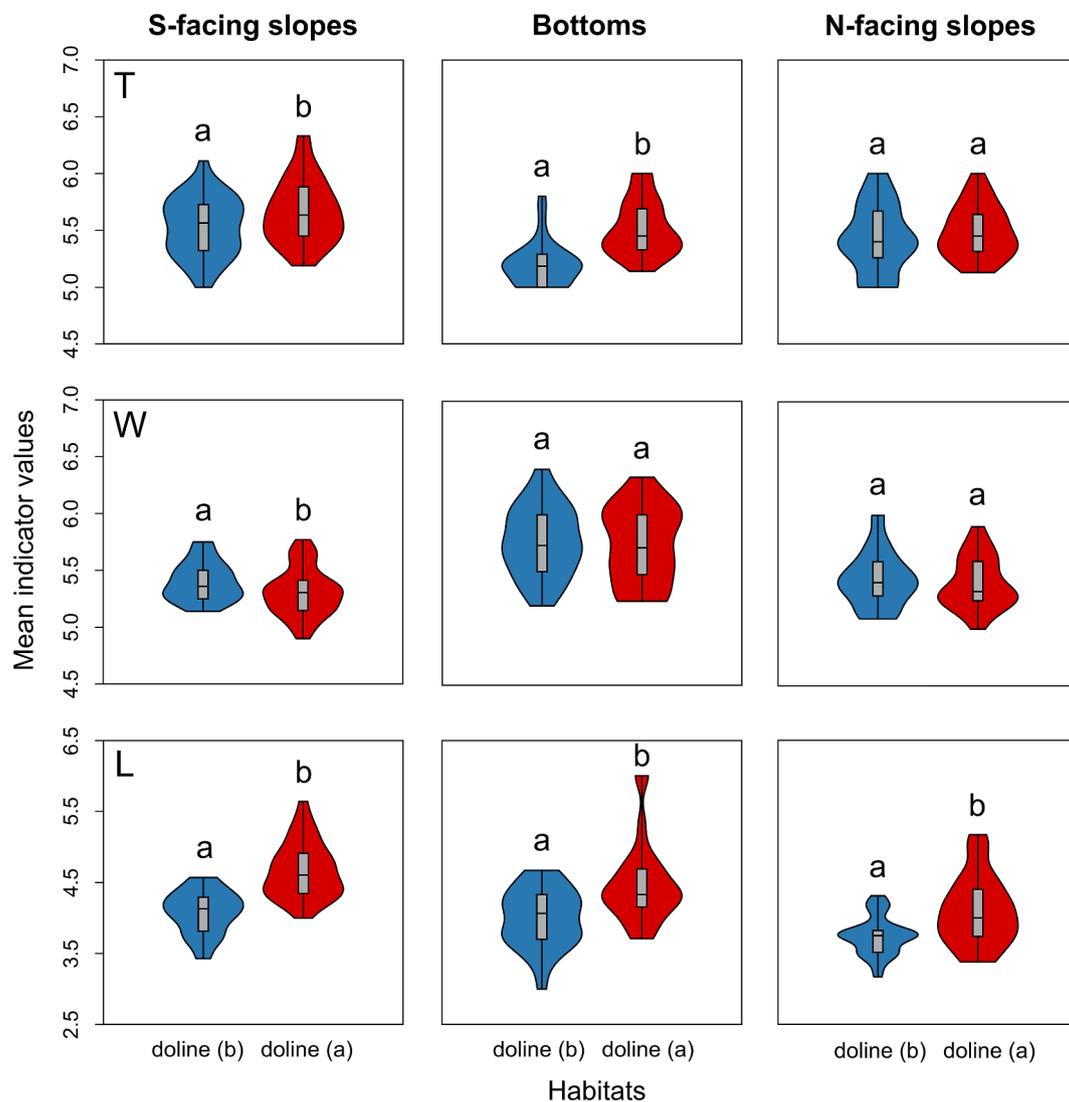


Fig. 3. Violin plots of the mean indicator values (T: temperature, W: soil moisture and L: light availability) in different doline microhabitats (south-facing slopes, bottoms and north-facing slopes) before and after logging. Colour code: blue – doline (b): dolines before logging, and red – doline (a): dolines after logging. Significant differences ($p < 0.05$) are indicated by different lowercase letters (a and b). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

indicators before and after logging at the doline level, the appearance of some moisture indicators (W7 species) after canopy removal may refer to community reorganisation. Previous studies conducted in different ecosystems showed that woody vegetation removal may increase soil moisture due to reduced transpiration and interception (Ritter et al., 2005; Özkan and Gökbulak, 2017; Kovács et al., 2020). It appears evident that the funnel-shaped topography of dolines interacts with the effects of canopy removal promoting a shift from climatically buffered microhabitats to climatically extreme microhabitats (cf. Kermavnar et al., 2020). Similar patterns may be observed in grassland dolines, where differences between the main microclimatic factors of microhabitats (e.g., north- and south-facing slopes and bottoms) are greater than those in forested dolines (Bárány-Kevei, 1999; Bátori et al., 2019).

Our previous studies demonstrated that larger dolines in the Mecsek Mts (covered by 100–120 year-old forests) maintain the populations of climate change-vulnerable plant species that are rare in or absent from the surrounding plateau habitats (Bátori et al., 2012, 2017). A

significant decrease in canopy cover may reduce the number and cover of cool-adapted plant species in dolines within 10 years (Kiss et al., 2020). Our results suggest that north-facing slopes may have the greatest chance of maintaining climate change-vulnerable species after canopy removal, as this microhabitat experienced the lowest rate of environmental changes (Fig. 3). Previous studies also show that slope aspect within topographically complex areas has a significant effect on a number of abiotic and biotic factors, such as microclimate, species composition and biotic linkages in forest ecosystems (Bátori et al., 2012; Gilliam et al., 2014). However, more field-based measurements are required to better understand how abiotic factors change within different microhabitats in dolines in relation to the degree of canopy removal and how long climate change-vulnerable species can survive in the changed environment during the regeneration phase of these forests. Although Bátori et al. (2020a) suggest that the competitive effect of the dense and extremely shady canopy of young trees upon understory herbs may contribute to a further decrease in the refugial capacity of doline

Table 3

Suggested framework for managing/maintaining doline microrefugia in forested karst landscapes applying the steps proposed by [Morelli et al. \(2016\)](#).

For forested dolines and their climate change-vulnerable species in a warming climate
Step 1 – Define planning purpose and objectives Maintain/increase the refugial capacity of doline microhabitats in forested karst landscapes and protect their climate change-vulnerable species; consider at least a 30–40 year planning cycle and 50–80 year climate projections.
Step 2 – Assess climate impacts and vulnerabilities Consider macroclimatic drivers; increases in temperature and interannual precipitation variability; summer heat waves and drought; intense storms; vegetation shifts; changes in forestry policy and practices (e.g., preference for planting non-native warm-adapted tree species); changes in tourism-related effects (e.g., fire ignition, littering and trampling).
Step 3 – Review/revise conservation goals and objectives Maintain sufficient number of cool and moist microhabitats (i.e. current and potential microrefugia) in dolines and their physical properties (e.g., rockiness, slope steepness and soil texture) to protect the biodiversity and critical ecosystem functions over the next 30–40 years (until the next planning cycle).
Step 4 – Identify and map key microrefugia features Potential microrefugia features: environmental stability; high topographic complexity (e.g., diameter, depth, exposure, rockiness and slope angle); cool air pooling; high water retention capacity; microhabitats with a high number of climate change-vulnerable species; presence of highly divergent lineages.
Step 5 – Evaluate and prioritize refugial areas for specific management Prioritize: large and/or deep dolines; high microhabitat diversity; high taxonomic diversity and species richness; high number of cool- and moist-adapted species (e.g., endemic and relict species); spatial and temporal overlap with other climate change-vulnerable species from different phyla.
Step 6 – Identify and implement priority actions to manage climate change microrefugia Maintain old forests and natural forest dynamics in as many doline microrefugia as possible; protect surrounding forests; protect natural and semi-natural grassland patches among forest stands, support the rehabilitation of areas covered by young, dense and homogenous forests; assist colonization; implement close-to-nature forestry practices (e.g., continuous cover forestry); work together with local forest managers in order to obtain the best experience and to determine the most efficient solutions for all stakeholders.
Step 7 – Monitor the effectiveness of designated microrefugia, realign objectives and actions accordingly Monitor: main microclimatic factors (temperature, soil moisture and light availability); habitat and microhabitat patterns; soil characteristics; indicator species; taxonomic diversity and species richness; human impacts.

microrefugia within a few decades after canopy removal ([Supplementary Fig. 1](#)), there are many unresolved questions about the potential ecological effects of different management practices during the regeneration phase of these forest stands ([Fig. 4](#); see also [Battles et al., 2001](#); [Roberts and Gilliam, 2014](#)).

Although a number of studies of early succession in old-growth forests suggest that changes in understory diversity may be fairly short-lived following larger disturbances ([Kermavnar et al., 2021](#)), some species may experience local extinction ([Halpern and Spies, 1995](#)). The main question is how these species will recover and how the refugial capacity of these habitats will change in a warming climate if the current management practices are maintained. We believe that at least some management practices during the regeneration phase of forests have the potential to restore plant community diversity and function in dolines under a warming climate. For instance, gap-based management may facilitate the regeneration of forests via providing optimal temperature, soil moisture and light conditions for species ([Gray et al., 2002](#); [Kern et al., 2013, 2014](#)) and may increase the refugial capacity of doline microhabitats. Shade-tolerant cool-adapted species, which often depend on small gaps for establishment, may benefit from such small-scale disturbances that mimic natural forest dynamics ([Roberts and Gilliam,](#)

[1995](#)). Further investigations are required to determine the optimal number and size of harvest-created gaps and analyse the potential effects of climate warming on regeneration processes (e.g., identifying declining and stable populations) to maintain the biodiversity of forest ecosystems in karst landscapes.

As continuous forest canopy may reduce warming rates and thermophilization inside forests ([De Frenne et al., 2013](#); [Stevens et al., 2015](#); [Lenoir et al., 2017](#); [Kovács et al., 2017, 2018](#); [Zellweger et al., 2020](#)), the establishment of forest reserves or the introduction of continuous cover forestry (CCF, i.e. continuous and uninterrupted maintenance of canopy cover, [Pommerening and Murphy, 2004](#); [Tinya et al., 2020](#)) in at least some parts of karst landscapes may provide a possible way to maintain/increase the refugial capacity of doline microhabitats. Finally, applying the steps of the ‘climate change refugia conservation cycle’ ([Morelli et al., 2016](#)) for forested dolines ([Table 3](#)) may help conservationists and forest managers to identify, manage and monitor the most vulnerable areas (e.g., local biodiversity hotspots and areas with high refugial capacity), taxonomic groups (e.g., cool- and moist adapted species from different phyla) and functional traits (e.g., flowering characteristics and life forms) to maintain regional biodiversity and sustainable forest management in the long run. We believe that our framework may also be easily applied to manage other types of forested microrefugia, such as sinkholes, ravines, valleys, north-facing slopes and rocky habitats.

As refugia often maintain higher species diversity and a higher number of endemic species and relict lineages than the surrounding area ([Keppel et al., 2012](#)), the identification of such areas within a karst landscape may indicate the presence of current and potential microrefugia ([Table 3](#)). In addition, environmental stability in topographically complex landscapes, cool air pooling and high water retention capacity may also be key factors in producing ‘warm-stage’ microrefugia ([Kobal et al., 2015](#); [Bátori et al., 2017](#)). However, anthropogenic disturbances may influence the structure and function of these microrefugia. As karst landscapes are extremely sensitive to human impacts such as agricultural use, quarrying, stone clearing, urban development, pollution and deforestation ([Gargano et al., 2010](#); [Kovačić and Ravbar, 2013](#); [Gutiérrez et al., 2014](#)), considerable progress has been made over the last decades in developing specific vulnerability assessment tools to identify and assess the detrimental effects of these impacts in a comprehensive way. For instance, using different indices (e.g., KDI: Karst Disturbance Index, and KSI: Karst Sustainability Index) may allow conservationists and forest managers to develop and implement methods for sustaining karst ecosystems ([van Beynen and Townsend, 2005](#); [van Beynen et al., 2012](#)) and to protect microrefugia. Monitoring of climate change impacts on the biota of microrefugia in forested karst landscapes will need to consider changes in microclimatic patterns, habitat structure, species composition and taxonomic diversity, as well as various human impacts to arrive at accurate predictions ([Table 3](#)). Further investigations are needed to determine the main steps required to identify and maintain microrefugia in non-forested karst landscapes.

CRediT authorship contribution statement

Zoltán Bátori: Conceptualization, Methodology, Formal analysis, Investigation, Writing - original draft, Supervision. **László Erdős:** Conceptualization, Investigation, Writing - review & editing. **Márió Gajdács:** Writing - review & editing. **Károly Barta:** Investigation, Writing - review & editing. **Zalán Tobak:** Investigation, Writing - review & editing. **Kata Frei:** Investigation, Writing - review & editing. **Csaba Tölgyesi:** Conceptualization, Formal analysis, Investigation, Writing - review & editing, Supervision.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

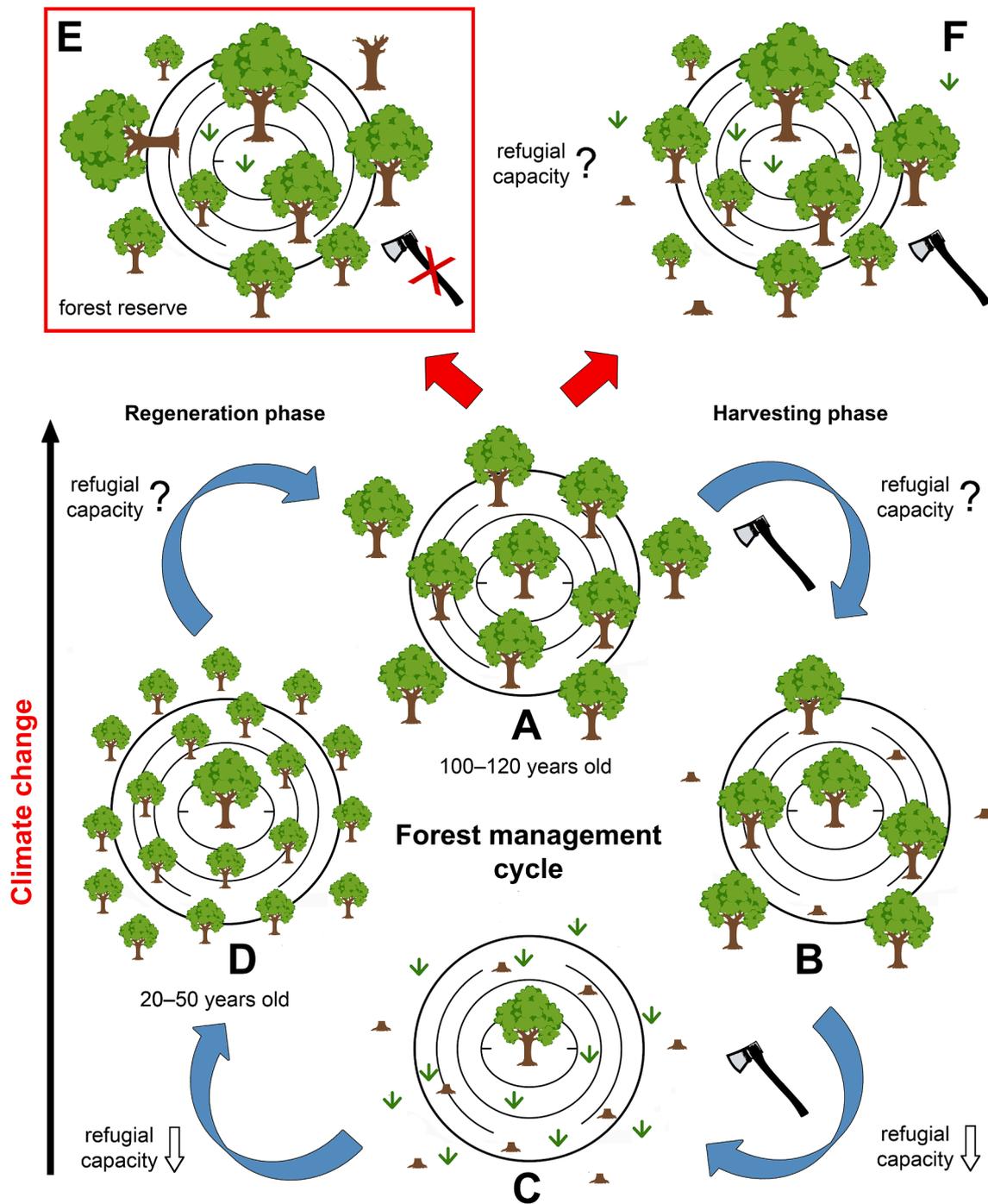


Fig. 4. Forest management cycle in karst dolines and their surroundings in the Mecsek Mts (Hungary). (A) Older forests (100–120 years old, canopy cover: 55–95% in different microhabitats) in larger dolines maintain the populations of many climate change-vulnerable plant species (Batori et al., 2012). (B) A significant decrease in canopy cover due to logging presumably decreases the refugial capacity of dolines within a few years via persistent changes in microclimatic patterns. (C) The number and/or cover of climate change-vulnerable species may decrease within 10 years after canopy removal (Kiss et al., 2020; but see Kermavnar et al., 2021) and species in the understory indicate significantly warmer conditions than before logging (Fig. 2). Although small patches of mature trees may survive in dolines (where timber harvesting is not feasible), their presence does not necessarily prevent the disappearance of at least some climate change-vulnerable species at the doline level. (D) The dense and homogenous canopy in the first decades of the regeneration phase leads to a further decrease of the number and cover of climate change-vulnerable species (Batori et al., 2020a). Finally, the creation of artificial gaps and forest thinning may facilitate the colonisation of different species (including climate change-vulnerable species) and forest regeneration, allowing the potential for the ecosystem to return to a more natural state. However, climate warming in East-Central Europe will continue in the coming decades affecting the regeneration process of forests within and adjacent to microrefugia. The main question is how these forests will recover and how their refugial capacity will change in a warming climate if the current management practices are maintained. (E) Establishment of strictly protected forest reserves would be highly desirable to mitigate the effects of climate change on the biodiversity of karst landscapes. (F) Introducing continuous cover forestry in dolines and their surroundings may also provide a promising alternative to maintain the biodiversity of microrefugia.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2021.119446>.

References

- Aguilon, D.J., Vojtkó, A., Tölgyesi, C., Erdős, L., Kiss, P.J., Lőrinczi, G., Juhász, O., Frei, K., Batori, Z., 2020. Karst environments and disturbance: evaluation of the effects of human activity on grassland and forest naturalness in dolines. *Biologia* 75, 1529–1535. <https://doi.org/10.2478/s11756-020-00518-7>.
- Barrows, C.W., Ramirez, A.R., Sweet, L.C., Morelli, T.L., Millar, C.I., Frakes, N., Rodgers, J., Mahalovich, M.F., 2020. Validating climate-change refugia: empirical bottom-up approaches to support management actions. *Front Ecol. Environ.* 18, 298–306. <https://doi.org/10.1002/fee.2205>.
- Battles, J.J., Shlisky, A.J., Barrett, R.H., Heald, R.C., Allen-Diaz, B.H., 2001. The effects of forest management on plant species diversity in a Sierran conifer forest. *Forest Ecol. Manage.* 146, 211–222. [https://doi.org/10.1016/S0378-1127\(00\)00463-1](https://doi.org/10.1016/S0378-1127(00)00463-1).
- Bárányi-Kevei, I., 1999. Microclimate of karstic dolines. *Acta Climatologica Universitatis Szegediensis* 32–33, 19–27.
- Batori, Z., Gallé, R., Erdős, L., Körmöczy, L., 2011. Ecological conditions, flora and vegetation of a large doline in the Mecsek Mountains (South Hungary). *Acta Bot. Croat.* 70, 147–155. <https://doi.org/10.2478/v10184-010-0018-1>.
- Batori, Z., Körmöczy, L., Erdős, L., Zaltnai, M.R., Csiky, J., 2012. Importance of karst sinkholes in preserving relict, mountain, and wet-woodland plant species under sub-Mediterranean climate: a case study from southern Hungary. *J. Cave Karst Stud.* 74, 127–134. <https://doi.org/10.4311/2011LSC0216>.
- Batori, Z., Vojtkó, A., Farkas, T., Szabó, A., Havadtói, K., E.-Vojtkó, A., Tölgyesi, C., Cseh, V., Erdős, L., Maák, I.E., Keppel, G., 2017. Large- and small-scale environmental factors drive distributions of cool-adapted plants in karstic microrefugia. *Ann. Bot.-London.* 119, 301–309. <https://doi.org/10.1093/aob/mcw233>.
- Batori, Z., Vojtkó, A., Maák, I.E., Lőrinczi, G., Farkas, T., Kántor, N., Tanács, E., Kiss, P.J., Juhász, O., Módra, G., Tölgyesi, C., Erdős, L., Aguilon, D.J., Keppel, G., 2019. Karst dolines provide diverse microhabitats for different functional groups in multiple phyla. *Sci. Rep.-Uk.* 9, e7176 <https://doi.org/10.1038/s41598-019-43603>.
- Batori, Z., Vojtkó, A., Keppel, G., Tölgyesi, C., Carni, A., Zorn, M., Farkas, T., Erdős, L., Kiss, P.J., Módra, G., Valjavec, M.B., 2020a. Anthropogenic disturbances alter the conservation value of karst dolines. *Biodivers. Conserv.* 29, 503–525. <https://doi.org/10.1007/s10531-019-01896-4>.
- Batori, Z., Lőrinczi, G., Tölgyesi, C., Módra, G., Juhász, O., Aguilon, D.J., Vojtkó, A., Valkó, O., Deák, B., Erdős, L., Maák, I.E., 2020. Karstic microrefugia host functionally specific ant assemblages. *Front. Ecol. Evol.* 8, 613738 <https://doi.org/10.3389/fevo.2020.613738>.
- Battisti, C., Giardini, M., Marini, F., Di Rocco, L., Dodaro, G., Vignoli, L., 2017. Diversity metrics, species turnovers and nestedness of bird assemblages in a deep karst sinkhole. *Isr. J. Ecol. Evol.* 63, 8–16. <https://doi.org/10.1163/22244662-06301009>.
- Borhidi, A., 1995. Social behaviour types, the naturalness and relative indicator values of the higher plants in the Hungarian Flora. *Acta Bot. Hung.* 39, 97–182.
- Breg Valjavec, M., Zorn, M., Čarni, A., 2018a. Bioindication of human-induced soil degradation in enclosed karst depressions (dolines) using Ellenberg indicator values. (Classical Karst, Slovenia). *Sci. Total Environ.* 640–641, 117–126. <https://doi.org/10.1016/j.scitotenv.2018.05.294>.
- Breg Valjavec, M., Zorn, M., Čarni, A., 2018b. Human-induced land degradation and biodiversity of Classical Karst landscape: on the example of enclosed karst depressions (dolines). *Land Degrad. Dev.* 29, 3823–3835. <https://doi.org/10.1002/ldr.3116>.
- Chytrý, M., Tichý, L., Dřevojan, P., Sádlo, J., Zelený, D., 2018. Ellenberg-type indicator values for the Czech flora. *Preslia* 90, 83–103. <https://doi.org/10.23855/preslia.2018.083>.
- Clements, R., Ng, P.K.L., Lu, X.X., Ambu, S., Schilthuizen, M., Bradshaw, C.J.A., 2008. Using biogeographical patterns of endemic land snails to improve conservation planning for limestone karsts. *Biol. Conserv.* 141, 2751–2764. <https://doi.org/10.1016/j.biocon.2008.08.011>.
- Culver, D.C., Sket, B., 2000. Hotspots of subterranean biodiversity in caves and wells. *J. Cave Karst Stud.* 62, 11–17.
- De Frenne, P., Rodríguez-Sánchez, F., Coomes, D.A., Verstraten, G., Vellend, M., Bernhardt-Römermann, M., Brown, C.D., Brunet, J., Cornelis, J., Decocq, G.M., Dierschke, H., Eriksson, O., Gilliam, F.S., Hédl, R., Heinken, T., Hermy, M., Hommel, P., Jenkins, M.A., Kelly, D.L., Kirby, K.J., Mitchell, F.J.G., Naaf, T., Newman, M., Peterken, G., Petřík, P., Schultz, J., Sonnier, G., Van Calster, H., Waller, D.M., Walther, G., White, P.S., Woods, K.D., Wulf, M., Graae, B.J., Verheyen, K., 2013. Microclimate moderates plant responses to macroclimate warming. *PNAS* 110, 18561–18565. <https://doi.org/10.1073/pnas.1311190110>.
- Deák, B., Kovács, B., Rádai, Z., Apostolova, I., Kelemen, A., Kiss, R., Lukács, K., Palpurina, S., Sopotlieva, D., Báthori, F., Valkó, O., 2021. Linking environmental heterogeneity and plant diversity: The ecological role of small natural features in homogeneous landscapes. *Sci. Total Environ.* 734, e144199 <https://doi.org/10.1016/j.scitotenv.2020.144199>.
- Deák, B., Rádai, Z., Lukács, K., Kelemen, A., Kiss, R., Batori, Z., Kiss, P.J., Valkó, O., 2020. Fragmented dry grasslands preserve unique components of plant species and phylogenetic diversity in agricultural landscapes. *Biodivers. Conserv.* 29, 4091–4110. <https://doi.org/10.1007/s10531-020-02066-7>.
- Dobrowski, S.Z., 2011. A climatic basis for microrefugia: the influence of terrain on climate. *Glob. Change Biol.* 17, 1022–1035. <https://doi.org/10.1111/j.1365-2486.2010.02263>.
- Dövényi, Z. (Eds.), 2010. Magyarország kistájainak katasztere. MTA Földrajztudományi Kutatóintézet, Budapest.
- Elek, Z., Kovács, B., Aszalós, R., Boros, G., Samu, F., Tinya, F., Ódor, P., 2018. Taxon-specific responses to different forestry treatments in a temperate forest. *Sci. Rep.-UK* 8, e16990. <https://doi.org/10.1038/s41598-018-35159>.
- Ellenberg, H., Weber, H., Düll, R., Wirth, V., Werner, W., Paulissen, D., 1992. Indicator values of central European plants. *Scr. Geobot.* 18, 1–258.
- Ferré, C., Caccianiga, M., Zanzottera, M., Comolli, R., 2020. Soil–plant interactions in a pasture of the Italian Alps. *J. Plant Interact.* 15, 39–49. <https://doi.org/10.1080/17429145.2020.1738570>.
- Fox, J., Weisberg, S., 2019. *An R companion to applied regression, (second edition)*. Sage publications.
- García, M.B., Domingo, D., Pizarro, M., Font, X., Gómez, D., Ehrlén, J., 2020. Rocky habitats as microclimatic refuges for biodiversity. A close-up thermal approach. *Environ. Exp. Bot.* 170, e103886 <https://doi.org/10.1016/j.envexpbot.2019.103886>.
- Gargano, D., Vecchio, G., Bernardo, L., 2010. Plant–soil relationships in fragments of Mediterranean snow-beds: ecological and conservation implications. *Plant Ecol.* 207, 175–189. <https://doi.org/10.1007/s11258-009-9663-7>.
- Gilliam, F.S., Hédl, R., Chudomelová, M., McCulley, R.L., Nelson, J.A., 2014. Variation in vegetation and microbial linkages with slope aspect in a montane temperate hardwood forest. *Ecosphere* 5, 1–17. <https://doi.org/10.1890/ES13-00379.1>.
- Gray, A.N., Spies, T.A., Easter, M.J., 2002. Microclimatic and soil moisture responses to gap formation in coastal Douglas-fir forests. *Can. J. Forest Res.* 32, 332–343. <https://doi.org/10.1139/X01-200>.
- Gutiérrez, F., Parisse, M., De Waele, J., Jourde, H., 2014. A review on natural and human-induced geohazards and impacts in karst. *Earth-Sci. Rev.* 138, 61–88. <https://doi.org/10.1016/j.earscirev.2014.08.002>.
- Halpern, C.B., Spies, T.A., 1995. Plant species diversity in natural and managed forests of the Pacific Northwest. *Ecol. Appl.* 5, 913–934. <https://doi.org/10.2307/2269343>.
- Hoyk, E., 1999a. Investigations of the vegetation and soil in the dolinas of Mecsek Mountains, South Hungary. *Acta Carsologica* 28, 105–113.
- Hoyk, E., 1999b. Soil and vegetation on karst terraces in the projected protected landscapes of Western Mecsek, Hungary. *Acta Carsologica* 36, 31–39.
- Jokela, J., Siitonen, J., Koivulaa, M., 2019. Short-term effects of selection, gap, patch and clear cutting on the beetle fauna in boreal spruce-dominated forests. 446, 29–37. <https://doi.org/10.1016/j.foreco.2019.05.027>.
- Jones, A., Montanarella, L., Jones, R., 2005. *Soil Atlas of Europe*. European Soil Bureau Network, European Commission. Office for Official Publications of the European Communities, Luxembourg.
- Kemencei, Z., Farkas, R., Páll-Gergely, B., Vilisics, F., Nagy, A., Hornung, E., Sólymos, P., 2014. Microhabitat associations of land snails in forested dolinas: implications for coarse filter conservation. *Community Ecol.* 15, 180–186. <https://doi.org/10.1556/ComEc.15.2014.2.6>.
- Keppel, G., Mokany, K., Wardell-Johnson, G.W., Phillips, B.L., Welbren, J.A., Reside, A.E., 2015. The capacity of refugia for conservation planning under climate change. *Front. Ecol. Environ.* 13, 106–112. <https://doi.org/10.1890/140055>.
- Keppel, G., Ottaviani, G., Harrison, S., Wardell-Johnson, G.W., Marcantonio, M., Mucina, L., 2018. Towards an eco-evolutionary understanding of endemism hotspots and refugia. *Ann. Bot.-London.* 122, 927–934. <https://doi.org/10.1093/aob/mcy173>.
- Keppel, G., Van Niel, K.P., Wardell-Johnson, G.W., Yates, C.J., Byrne, M., Mucina, L., Schut, A.G.T., Hopper, S.D., Franklin, S.E., 2012. Refugia: identifying and understanding safe havens for biodiversity under climate change. *Global Ecol. Biogeogr.* 21, 393–404. <https://doi.org/10.1111/j.1466-8238.2011.00686>.
- Kermavnar, J., Ferlan, M., Marinšek, A., Eler, K., Kobler, A., Kutnar, L., 2020. Effects of various cutting treatments and topographic factors on microclimatic conditions in Dinaric fir-beech forests. *Agr. Forest Meteorol.* 295, e108186 <https://doi.org/10.1016/j.agrformet.2020.108186>.
- Kermavnar, J., Eler, K., Marinšek, A., Kutnar, L., 2021. Post-harvest forest herb layer demography: General patterns are driven by pre-disturbance conditions. *Forest Ecol. Manage.* 491, e119121. <https://doi.org/10.1016/j.foreco.2021.119121>.
- Kern, C.C., D'Amato, A.W., Strong, T.F., 2013. Diversifying the composition and structure of managed, late-successional forests with harvest gaps: What is the optimal gap size? *Forest Ecol. Manage.* 304, 110–120. <https://doi.org/10.1016/j.foreco.2013.04.029>.
- Kern, C.C., Montgomery, R.A., Reich, P.B., Strong, T.F., 2014. Harvest-created canopy gaps increase species and functional trait diversity of the forest ground-layer community. *Forest Sci.* 60, 335–344. <https://doi.org/10.5849/forsci.13-015>.

- Kiss, P.J., Tölgyesi, C., Bóni, I., Erdős, L., Vojtkó, A., Maák, I.E., Bátori, Z., 2020. The effects of intensive logging on the capacity of karst dolines to provide potential microrefugia for cool-adapted plants. *Acta Geogr. Slov.* 60, 37–48. <https://doi.org/10.3986/AGS.6817>.
- Kobal, M., Bertonecclj, I., Pirotti, F., Dakskobler, I., Kutnar, L., 2015. Using lidar data to analyse sinkhole characteristics relevant for understory vegetation under forest cover – case study of a high karst area in the Dinaric Mountains. *PLoS ONE* 10, e0122070. <https://doi.org/10.1371/journal.pone.0122070>.
- Koivula, M.J., Venn, S., Hakola, P., Niemelä, J., 2019. Responses of boreal ground beetles (Coleoptera, Carabidae) to different logging regimes ten years post harvest. *Forest Ecol. Manag.* 436, 27–38. <https://doi.org/10.1016/j.foreco.2018.12.047>.
- Kovačić, G., Ravbar, N., 2013. Analysis of human induced changes in a karst landscape – the filling of dolines in the Kras plateau. *Slovenia. Sci. Total Environ.* 447, 143–151. <https://doi.org/10.1016/j.scitotenv.2013.01.002>.
- Kovács, B., Tinya, F., Guba, E., Németh, C., Sass, V., Bidló, A., Ódor, P., 2018. The short-term effects of experimental forestry treatments on site conditions in an oak–hornbeam forest. *Forests* 9, 406. <https://doi.org/10.3390/f9070406>.
- Kovács, B., Tinya, F., Németh, C., Ódor, P., 2020. Unfolding the effects of different forestry treatments on microclimate in oak forests: results of a 4-year experiment. *Ecol. Appl.* 30, e02043 <https://doi.org/10.1002/eap.20443>.
- Kovács, B., Tinya, F., Ódor, P., 2017. Stand structural drivers of microclimate in mature temperate mixed forests. *Agr. Forest Meteorol.* 234–235, 11–21. <https://doi.org/10.1016/j.agrformet.2016.11.268>.
- Lengyel, A., Purger, D., Csiky, 2012. Classification of mesic grasslands and their transitions of South Transdanubia (Hungary). *Acta Bot. Croat.* 71, 31–50. <https://doi.org/10.2478/v10184-011-0060-7>.
- Lenoir, J., Hattab, T., Pierre, G., 2017. Climatic microrefugia under anthropogenic climate change: implications for species redistribution. *Ecography* 40, 253–266. <https://doi.org/10.1111/ecog.02788>.
- Lenth, R., 2021. emmeans: Estimated Marginal Means, aka Least-Squares Means. R package version 1.6.0. <https://cran.r-project.org/web/packages/emmeans/index.html>.
- McLaughlin, B.C., Ackerly, D.D., Klos, P.Z., Natali, J., Dawson, T.E., Thompson, S.E., 2017. Hydrologic refugia, plants, and climate change. *Glob. Change Biol.* 23, 2941–2961. <https://doi.org/10.1111/gcb.13629>.
- Meineri, E., Hylander, K., 2017. Fine-grain, large-domain climate models based on climate station and comprehensive topographic information improve microrefugia detection. *Ecography* 40, 1003–1013. <https://doi.org/10.1111/ecog.02494>.
- Mezősi, G., 2017. *The Physical Geography of Hungary*. Springer, Cham.
- Michalak, J.L., Stralberg, D., Cartwright, J.M., Lawler, J.J., 2020. Combining physical and species-based approaches improves refugia identification. *Front. Ecol. Environ.* 18, 254–260. <https://doi.org/10.1002/fee.2207>.
- Morelli, T.L., Daly, C., Dobrowski, S.Z., Dulen, D.M., Ebersole, J.L., Jackson, S.T., Lundquist, J.D., Millar, C.I., Maher, S.P., Monahan, W.B., Nydick, K.R., Redmond, K. T., Sawyer, S.C., Stock, S., Beissinger, S.R., 2016. Managing climate change refugia for climate adaptation. *PLoS ONE* 11, e0169725. <https://doi.org/10.1371/journal.pone.0159909>.
- Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlenn, D., Minchin, P.R., 2019. vegan: Community Ecology Package. R package version 2.5-5. <https://cran.r-project.org/web/packages/vegan/index.html>.
- Özkan, U., Gökbülak, U., 2017. Effect of vegetation change from forest to herbaceous vegetation cover on soil moisture and temperature regimes and soil water chemistry. *Catena* 149, 158–166. <https://doi.org/10.1016/j.catena.2016.09.017>.
- Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., R Core Team., 2021. nlme: Linear and nonlinear mixed effects models. R package version 3.1-152. <http://CRAN.R-project.org/package=nlme>.
- Pommerening, A., Murphy, S.T., 2004. A review of the history, definitions and methods of continuous cover forestry with special attention to afforestation and restocking. *Forestry* 77, 27–44. <https://doi.org/10.1093/forestry/77.1.27>.
- R Core Team, 2021. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Raschmanová, N., Miklisová, D., Kováč, L., 2013. Soil Collembola communities along a steep microclimatic gradient in the collapse doline of the Silická ľadnica Cave, Slovak Karst (Slovakia). *Biologia* 68, 470–478. <https://doi.org/10.2478/s11756-013-0172-8>.
- Raschmanová, N., Miklisová, D., Kováč, L., 2018. A unique small-scale microclimatic gradient in a temperate karst harbours exceptionally high diversity of soil Collembola. *Int. J. Speleol.* 47, 247–262. <https://doi.org/10.5038/1827-806X.47.2.2194>.
- Ritter, E., Dalsgaard, L., Einhorn, K.S., 2005. Light, temperature and soil moisture regimes following gap formation in a semi-natural beech-dominated forest in Denmark. *Forest Ecol. Manag.* 206, 15–33. <https://doi.org/10.1016/j.foreco.2004.08.011>.
- Roberts, M.R., Gilliam, F.S., 1995. Patterns and mechanisms of plant diversity in forested ecosystems: implications for forest management. *Ecol. Appl.* 5, 969–977. <https://doi.org/10.2307/2269348>.
- Roberts, M.R., Gilliam, F.S., 2014. Response of the herbaceous layer to disturbance in eastern forests. In: Gilliam, F.S. (Ed.), *The herbaceous layer in forests of eastern North America*. Oxford University Press, New York, pp. 321–339.
- Sârbu, I., Ştefan, N., Oprea, A., 2013. *Plante vasculare din România. Determinator ilustrat de teren*. Victor B Victor, Bucureşti.
- Serra-Diaz, J.M., Scheller, R.M., Syphard, A.D., Franklin, J., 2015. Disturbance and climate microrefugia mediate tree range shifts during climate change. *Landscape Ecol.* 30, 1039–1053. <https://doi.org/10.1007/s10980-015-0173-9>.
- Stevens, J.T., Safford, H.D., Harrison, S., Latimer, A.M., 2015. Forest disturbance accelerates thermophilization of understory plant communities. *J. Ecol.* 103, 1253–1263.
- Su, Y., Tang, Q., Mo, F., Xue, Y., 2017. Karst tiankengs as refugia for indigenous tree flora amidst a degraded landscape in southwestern China. *Sci. Rep.-UK* 7, e4249. <https://doi.org/10.1038/s41598-017-04592>.
- Syphard, A., Franklin, J., 2010. Species traits affect the performance of species distribution models for plants in southern California. *J. Veg. Sci.* 21, 177–189. <https://doi.org/10.1111/j.1654-1103.2009.01133>.
- Tichý, L., 2002. JUICE, software for vegetation classification. *J. Veg. Sci.* 13, 451–453. <https://doi.org/10.1111/j.1654-1103.2002.tb02069>.
- Tichý, L., Chytrý, M., 2006. Statistical determination of diagnostic species for site groups of unequal size. *J. Veg. Sci.* 17, 809–818. <https://doi.org/10.1111/j.1654-1103.2006.tb02504>.
- Tinya, F., Kovács, B., Aszalós, R., Tóth, B., Csépanyi, P., Németh, C., Ódor, P., 2020. Initial regeneration success of tree species after different forestry treatments in a sessile oak-hornbeam forest. *Forest Ecol. Manag.* 459, e117810 <https://doi.org/10.1016/j.foreco.2019.117810>.
- Tölgyesi, C., Bátori, Z., Erdős, L., 2014. Using statistical tests on relative ecological indicator values to compare vegetation units – Different approaches and weighting methods. *Ecol. Indic.* 36, 441–446. <https://doi.org/10.1016/j.ecolind.2013.09.002>.
- van Beynen, P., Brinkmann, R., van Beynen, K., 2012. A sustainability index for karst environments. *J. Cave Karst Stud.* 74, 221–234. <https://doi.org/10.4311/2011SS0217>.
- van Beynen, P., Townsend, K., 2005. A disturbance index for karst environments. *Environ. Manag.* 36, 101–116. <https://doi.org/10.1007/s00267-004-0265-9>.
- Vilicsics, F., Sóllymos, P., Nagy, A., Farkas, K., Kemencei, Z., Hormung, E., 2011. Small scale gradient effects on isopods (Crustacea: Oniscidea) in karstic sinkholes. *Biologia* 66, 499–505. <https://doi.org/10.2478/s11756-011-0042-1>.
- Whiteman, C.D., Haiden, T., Pospichal, B., Eisenbach, S., Steinacker, R., 2004. Minimum temperatures, diurnal temperature ranges, and temperature inversions in limestone sinkholes of different sizes and shapes. *J. Appl. Meteorol.* 43, 1224–1236. [https://doi.org/10.1175/1520-0450\(2004\)043<1224:MTDTRA>2.0.CO;2](https://doi.org/10.1175/1520-0450(2004)043<1224:MTDTRA>2.0.CO;2).
- Wildi, O., 2016. Why mean indicator values are not biased. *J. Veg. Sci.* 27, 40–49. <https://doi.org/10.1111/jvs.12336>.
- Zellweger, F., De Frenne, P., Lenoir, J., Vangansbeke, P., Verheyen, K., Bernhardt-Römermann, M., Baeten, L., Hédl, R., Berki, I., Brunet, J., Van Calster, H., Chudomelová, M., Decocq, G., Dirnböck, T., Durak, T., Heinken, T., Jaroszewicz, B., Kopecký, M., Máliš, F., Macek, M., Malicki, M., Naaf, T., Nagel, T.A., Ortmann-Ajkai, A., Petřík, P., Pielech, R., Reczyńska, K., Schmidt, W., Standovář, T., Świerkosz, K., Telek, B., Vild, O., Wulf, M., Coomes, D., 2020. Forest microclimate dynamics drive plant responses to warming. *Science* 368, 772–775. <https://doi.org/10.1126/science.aba6880>.