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The conservation value of karst dolines for vascular plants in woodland habitats of Hungary: refugia and climate change

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Abstract: Limestone (karst) surfaces in Hungary are rich in dolines, in which many endangered vascular plant species occur. To date, the majority of studies dealing with doline vegetation have focused on the local rather than the landscape level, without using comparative data from other areas. However, in this study we aimed to compare the vegetation pattern and species composition of dolines under different climate regimes of Hungary with regard to regional species pools. The fieldwork was carried out between 2005 and 2012. Twenty dolines were selected in the Mecsek Mountains (southern Hungary) and nine dolines in the Aggtelek Karst area (northern Hungary). More than 900 vascular plants and more than 2000 plots were included in the study. The moving split window (MSW) technique, nestedness analysis and principal coordinates analysis (PCoA) were used to reveal the vegetation patterns in dolines. Although we found remarkable differences between the species composition of the two regions, dolines of both regions play a similar role in the preservation of different groups of species. Many plants, in particular mountain species, are restricted to the bottom of dolines where appropriate environmental conditions exist. In addition, depending on the doline geometry, many species of drier and warmer forests have colonized the upper slopes and rims. Thus, we can conclude that karst dolines of Hungary can be considered as reservoirs for many vascular plant species, therefore they are particularly important from a conservation point of view. Moreover, these dolines will likely become increasingly indispensable refugia for biodiversity under future global warming.

Keywords: Aggtelek Karst area; global warming; Mecsek Mountains; relict species; transects

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INTRODUCTION

Habitat destruction together with climate induced species extinction and surface contamination are the main threats to the biological and geological diversity of karst surfaces (cf. Schilthuizen et al., 2005; Breg, 2007). Although karst ecosystems are usually diverse and are very important in many aspects of ecological research (e.g. Cardoso, 2012; Novak et al., 2012), there are still many open questions about how karst surfaces will change under future global warming.

Based on previous studies, we expect remarkable differences between the role of subsurface cavities (e.g. caves) and surface forms (e.g. dolines) in the preservation of different groups of species. Caves and wells serve as habitats for many subterranean species (Culver et al., 1973; Culver & Sket, 2000; Dixon, 2011), while dolines may preserve relicts (Horvat, 1953; Stuckey, 1983; Bátori et al., 2009), mountain species (Beck v. Mannagetta, 1906; Vojtkó, 1997; Bátori et al., 2006), endemic species (Egli, 1991; Barnard et al., 1998) and endemic plant communities (Redžić et al., 2011). The biological literature contains many excellent examples where dolines have been mentioned as key habitats for scientifically important plant species. From a biogeographical perspective, for instance, *Biebersteinia orphanidis* (Peloponnisos, Greece), *Cerastium dinaricum* (Dinarian Mountains, Slovenia), *Dracocephalum ruyschiana* (Pešter plateau, Serbia; Bükk Mountains, Hungary), *Horstrissea dolinicola* (Crete, Greece), *Pulsatilla vernalis* (Julian Alps, Slovenia) and *Stachys alpina* (Mecsek Mountais,

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Hungary) are especially good examples (Bartha, 1933; Egli et al., 1990; Wraber, 1995; Yannitsaros et al., 1996; Dakskobler et al., 2008; Bátori et al., 2009; Lazarević et al., 2009). Since dolines harbour many vascular plant species that are missing or are very rare in the surrounding habitats, they can be considered habitat islands (Bátori et al., 2012). The different amount of solar radiation on the different parts of the slopes has resulted in local environmental gradients (e.g. air temperature, air humidity and soil moisture), which in turn strongly influence the composition of flora and vegetation on the slopes with different orientation at the same altitude (Beck v. Mannagetta, 1906; Horvat, 1953; Gargano et al., 2010; Bátori et al., 2011). It also means that a high species diversity within short distances can be observed (Özkan et al., 2010).

While many studies on the ecological role of dolines have focused mainly on local vegetation changes (e.g. floristic composition and vegetation inversion) (e.g. Lausi, 1964), relatively few studies have been designed to evaluate the correspondences between the local and regional flora (e.g. Egli, 1993). The relationship between the local species pool (i.e., the flora of a doline) and the regional species pool (i.e., the flora of a karst surface) informs us about how dolines play a role in the preservation of different groups of species. Our aims were: to investigate how regional climate influences the flora of dolines and their surroundings; to investigate what correspondence can be detected between the species composition of dolines and the landscape; to examine how the vascular plant species composition changes in different-sized dolines.

MATERIAL AND METHODS

Study regions and study sites

The fieldwork was carried out on a karst surface of 30 km^2 in the Mecsek Mountains (southern Hungary), and on a karst surface of 5 km^2 in the Aggtelek Karst area (northern Hungary) between 2005 and 2012 (Fig. 1).

On the karst surface of the Mecsek Mountains, there are more than 2000 solution dolines located between 250 and 500 m above sea level. Most of them are very small (diameter < 20 m). The average diameter is between 20 and 40 m. The diameter of the largest doline is over 200 m and its depth exceeds 30 m (Lovász, 1971). Due to these topographic differences, the ecological conditions (e.g. soil moisture, air humidity) of the dolines are highly variable (Bátori et al., 2011). The average annual rainfall of the study region exceeds 700 mm. Due to the sub-Mediterranean climate, the monthly maximum values during summer (77 mm in both May and June) and autumn (72 mm in October). The annual mean temperature is about 9.5 °C, with the highest mean temperature of 19.3 °C in July. Winters are moderately cold with a mean temperature of -1.1 °C between December and February (Ádám et al., 1981; Marosi & Somogyi, 1990). The investigated dolines are situated in the oak-hornbeam belt of the mountain range, in the mosaics of Illyrian type oak-hornbeam (*Asperulo taurinae-Carpinetum*) and beech forests (*Helleboro odori-Fagetum*) with the age of 70-110 years. The bottom of larger dolines is often covered by fragments of ravine forests (*Scutellario altissimae-Aceretum*) (Bátori et al., 2012). Some dry grassland and hay meadow patches, moist habitats and trampled places also occur both on the plateaus and in the valleys of the study region.

Vecsembükk is a part of the Aggtelek Karst area characterised by more than 150 solution dolines located between 400 and 600 m above sea level. The average doline size is much larger (80 to 100 m in diameter) than in the Mecsek Mountains. The diameter of the largest doline is over 350 m and its depth exceeds 50 m. Average annual rainfall is more than 650 mm with the monthly maximum during summer (85 mm in June). Annual mean temperature is about 9.1 °C, with the highest mean temperature of 20.3 °C in July. Due to the continental climate, winters are cold with a mean temperature of -2.5 °C from December to February (Ujvárosy, 1998). The investigated dolines are often surrounded by 60-110 years old Central European type oak-hornbeam (*Carici pilosae-Carpinetum*) and beech forests (*Melittio-Fagetum*) consisting of some high mountain plant species like *Dryopteris expansa*, *Polygonatum verticillatum* or *Rosa pendulina*. Dolines are often covered by scree forests (*Mercuriali-Tilietum* and *Tilio-Fraxinetum*) or fragments of ravine forests (*Scolopendrio-Fraxinetum*) (Vojtkó, 2003; 2004).

Sampling

Investigations were performed at two different levels: (1) at the level of each doline and (2) at the level of the karst surfaces. A total of 29 dolines were studied: 20 in the Mecsek Mountains and 9 in the Aggtelek Karst area. Dolines were selected randomly from two size classes of dolines (diameter ≤ 100 m and diameter > 100 m). Dolines ranked by diameter are identified with capital letters from A_m to T_m for the Mecsek Mountains, and A_a to I_a for the Aggtelek Karst area (Table 1).

Vascular plant species lists were compiled between 2005 and 2012 for 20 dolines (A_m to T_m) of the Mecsek Mountains and 8 dolines (A_a to C_a; E_a to I_a) of the Aggtelek Karst area. Species data were collected from early March to late October for the total area of dolines. The total area included the area of the slopes (where the slope angle was over 10°) and the area of the rims, an approximately 1 to 5 m wide strip around

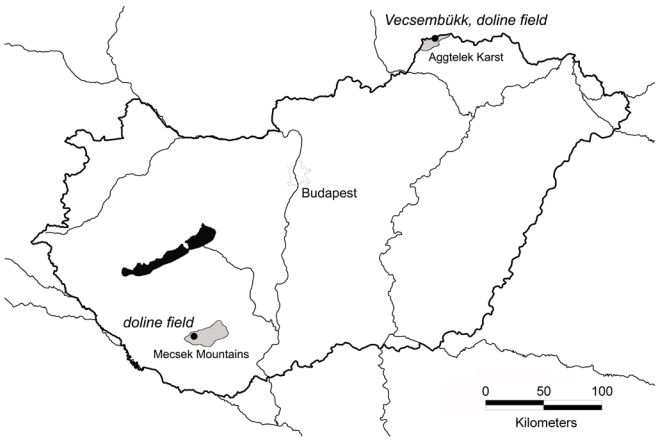

Fig. 1. Location of the study regions in Hungary.

Table 1. Diameter and depth values and depth/diameter ratios of the studied dolines of the Mecsek Mountains (A_m-T_m) and the Aggtelek Karst area (A_a-I_a).

Dolines	A_m	B_m	C_m	D_m	E_m	F_m	G_m	H_m	I_m	J_m	K_m	L_m	M_m
diameter	5	8	10	15	20	20	25	40	60	60	70	70	75
depth (m)	0.5	2	2	3	4.5	3	5.5	10	11	11	14	14	11
depth/diameter	0.10	0.25	0.20	0.20	0.23	0.15	0.22	0.25	0.18	0.18	0.20	0.20	0.15

N_m	O_m	P_m	Q_m	R_m	S_m	T_m	A_a	B_a	C_a	D_a	E_a	F_a	G_a	H_a	I_a
100	100	135	135	135	150	190	40	60	70	70	90	120	120	120	150
15	16	24	20	20	18	28	15	15	15	15	20	20	20	30	40
0.15	0.16	0.18	0.15	0.15	0.12	0.15	0.38	0.25	0.21	0.21	0.22	0.17	0.17	0.25	0.27

the smaller dolines, and an approximately 10 to 20 m wide strip around the larger dolines where the slope angle was less than 10°. Each doline was visited at least 10 times during the investigation period. Finally, a species list for both karst surfaces (Aggtelek Karst area, Vecsembükk: 5 km^2, Mecsek Mountains: 30 km^2) was obtained from the database of the Central European Flora Mapping Programme (CEU) and from detailed field observations. During field studies, the most typical habitat type of each species was also recorded (i.e., the habitat preferred by a species in the study regions).

Transects for sampling the herb layer were established across the 20 dolines (A_m to T_m) of the Mecsek Mountains in a north-south direction, passing through the deepest point of the depressions. Transects begun and ended in the surrounding forests, according to our former study (Bátori et al., 2012). In the case of the Aggtelek Karst area, 4 dolines (B_a; D_a; E_a; G_a) were sampled with the same method. Each transect consisted of a series of 1 m × 1 m contiguous plots. Percentage cover of each vascular herb and tree sapling was estimated visually in the plots. A total of 2220 plots were recorded.

The diameter and depth values of dolines were also measured in both regions (without considering the doline rim) (Table 1), from which depth/diameter ratios were determined.

Species grouping

All vascular plant species found in the karst surfaces were classified according to their coenological preferences (Soó, 1980). Finally, 13 large groups of species were established: (Sg_1) species of dry oak forests (e.g. *Acer tataricum*, *Betonica officinalis*, *Quercus cerris*, *Sorbus torminalis*, *Viola hirta*), (Sg_2) species of mesic oak forests (e.g. *Acer campestre*, *Convallaria majalis*, *Galium schultesii*, *Ligustrum vulgare*, *Melica uniflora*), (Sg_3) species of Central European beech forests (e.g. *Acer pseudoplatanus*, *Allium ursinum*, *Carex pilosa*, *Fagus sylvatica*, *Milium effusum*), (Sg_4) species of Illyrian beech forests (e.g. *Asperula taurina* subsp. *leucanthera*, *Helleborus odorus*, *Ruscus aculeatus*, *Ruscus hypoglossum*, *Tamus communis*), (Sg_5) species of deep ravines and gorges (e.g. *Aruncus dioicus*, *Asplenium scolopendrium*, *Lunaria rediviva*, *Polystichum aculeatum*, *Silene dioica*), (Sg_6) species of wet forests (e.g. *Alnus glutinosa*, *Carex remota*, *Chrysosplenium alternifolium*, *Festuca gigantea*, *Salix alba*), (Sg_7) species of dry grasslands (e.g. *Achillea pannonica*, *Festuca rupicola*, *Fragaria viridis*, *Salvia pratensis*, *Vicia angustifolia*), (Sg_8) species of mesic hay meadows (e.g. *Alopecurus pratensis*, *Arrhenatherum elatius*, *Holcus lanatus*, *Pastinaca sativa*, *Poa pratensis*), (Sg_9) species of marshes (e.g. *Carex acutiformis*, *Galium palustre*, *Lycopus europaeus*, *Phragmites australis*, *Typha latifolia*), (Sg_{10}) weeds (e.g. *Ballota nigra*, *Capsella bursa-pastoris*, *Chenopodium album*, *Hordeum murinum*, *Poa bulbosa*), (Sg_{11}) adventive species (e.g. *Acer negundo*, *Amorpha fruticosa*, *Ambrosia artemisiifolia*, *Quercus rubra*, *Robinia pseudoacacia*), (Sg_{12}) indifferent species (e.g. *Achillea collina*, *Carex hirta*, *Coronilla varia*, *Plantago media*, *Urtica dioica*), (Sg_{13}) species of other habitats (e.g. species of acidic forests) (e.g. *Betula pendula*, *Castanea sativa*, *Luzula luzuloides*, *Lychnis viscaria*, *Veronica officinalis*) (Table 2). The group of Sg_5 together with other plant species of high altitudes that are classed in various other groups are referred to as „mountain" species throughout this paper.

Statistical analyses

The moving split window (MSW) technique (Webster, 1978), based on percent cover data, was used as a quantitative identification of boundary location along the transects (Fig. 2). This method calculates dissimilarity coefficients between split windows by moving a sampling unit from one end of a transect to the other end. The complement of the Renkonen index (DREN) was applied as the comparative function, since it is sensitive to species composition changes (Zalatnai & Körmöczi, 2004; Körmöczi, 2005). Significance of the boundaries was tested using the *z*-score transformation:

$$z = (d_{i,k} - d_{exp,k})/SD_{exp,k}$$

where *z* is the *z*-score, $d_{i,k}$ is the DREN at position *i* if the half-window size is *k*, $d_{exp,k}$ is the overall mean of DREN from randomized data for the half-window size *k* (expected mean), and $SD_{exp,k}$ is the standard deviation of the DREN values from the randomized data for the half-window size *k*. Random reference was made with plot randomization and 1000 randomizations were done. Z-scores were plotted against the window midpoint position. In this profile, vegetation boundaries appear

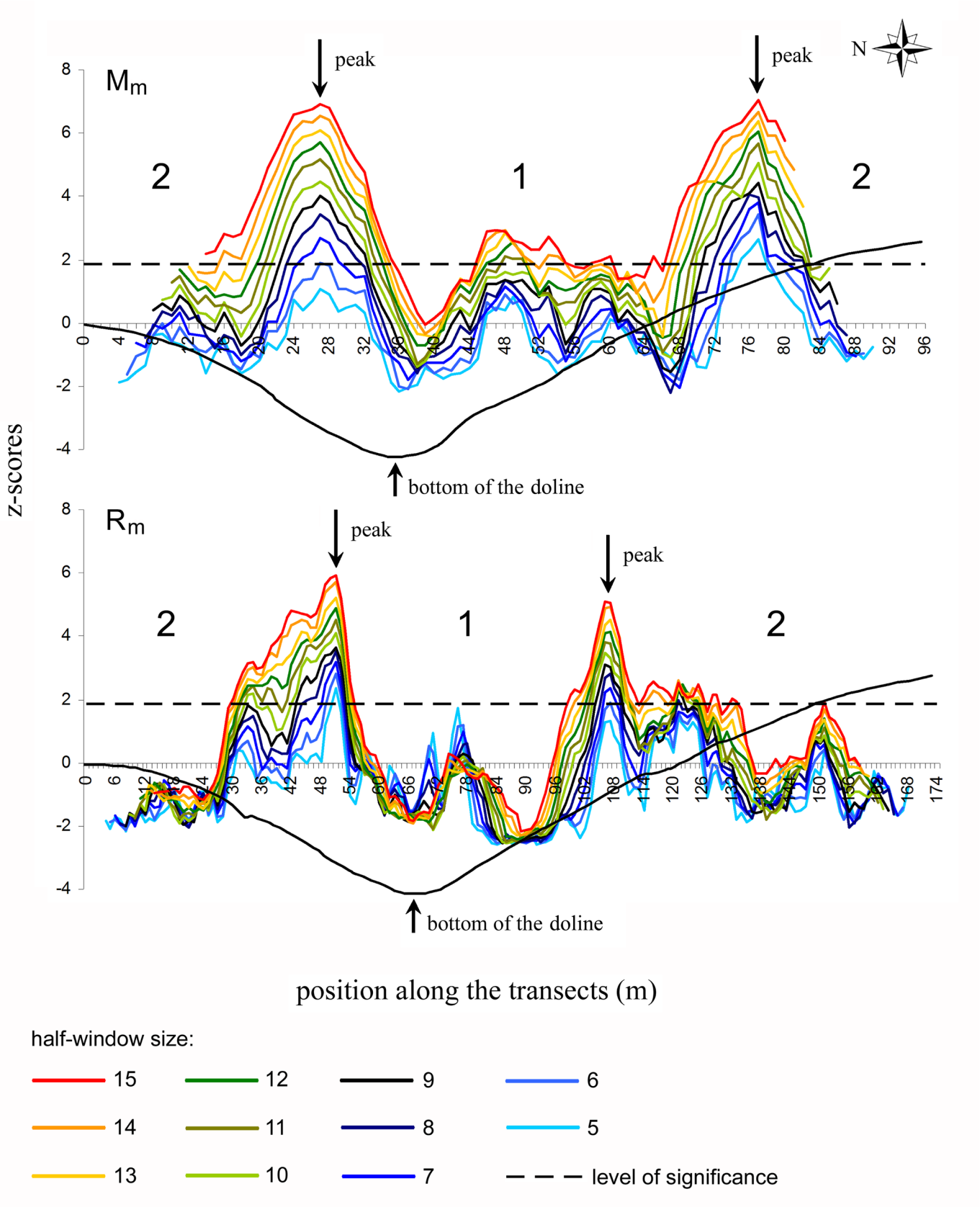

Fig. 2. Representative z-score profiles of transects in two dolines (M_m, R_m) of the Mecsek Mountains with the different doline parts (No. 1 and No. 2) and morphological profiles.

as peaks. Z-scores for each window midpoint position were calculated from 1 to 5 half-window sizes for smaller dolines and from 5 to 15 half-window sizes for larger dolines. Z-scores above 1.85 were considered indicative of significant ($p < 0.05$) boundaries (Körmöczi, 2011). Positions where most of the z-score profiles were above 1.85 were considered real vegetation boundaries (Fig. 2). MSW computations were done using the statistical language R 2.10.1 (R Development Core Team, 2009).

Each transect was divided into two parts according to the results of MSW (Fig. 2). The first part always consisted of the bottom of the dolines and the lower parts of the slopes (No. 1 in the profile), while the second part consisted of the upper parts of the slopes and the rims (No. 2 in the profile). Finally, the proportions of the species groups (weighted by species occurrences in the plots) of both parts were calculated and used to assess the floristic differences between them (Fig. 3, 4). In many cases, the species composition of the upper doline slopes and the rims is the same as (or very similar to) that of the surrounding forests (cf. Bátori et al., 2012; Vojtkó, 2003), therefore this division is appropriate to compare the vegetation of the doline bottoms with that of their surroundings.

Principal coordinates analysis (PCoA), based on presence-absence data and Euclidean distance, was carried out to reveal the vegetation patterns in the dolines (Fig. 5, 6). Vegetation types in the scatter plots were identified according to the results of MSW and field observations.

Species-area relations (Arrhenius, 1921) were assessed for all plant species, as well as for the groups of Sg_1 and Sg_2 (i.e., oak forest) species, Sg_3 and Sg_4 (i.e., beech forest) species and Sg_5, Sg_6 and Sg_9 (i.e., cool-adapted) species (Fig. 7, 8). The Nestedness Temperature Calculator (NTC) of Atmar & Patterson (1993, 1995) was used to explore various features of nestedness of the flora of dolines (http://aics-research.com/nestedness/tempcalc.html). The degree of nestedness of the presence/absence matrix was quantified by using the matrix's temperature (T) and by assessing the statistical significance of nestedness. T ranges

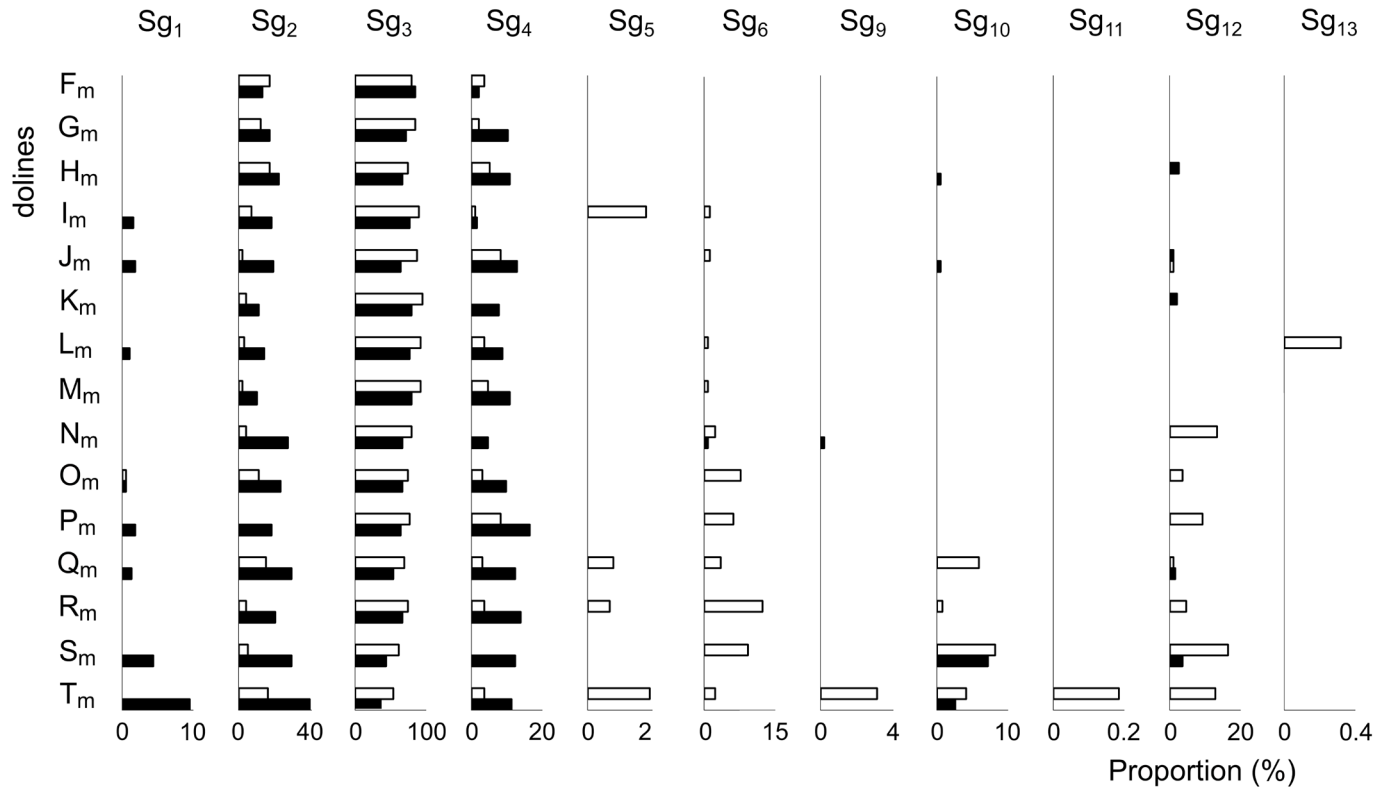

Fig. 3. Proportions of the different species groups in the dolines of the Mecsek Mountains. White and black bars refer to the proportions of the 1st and 2nd vegetation units, respectively.

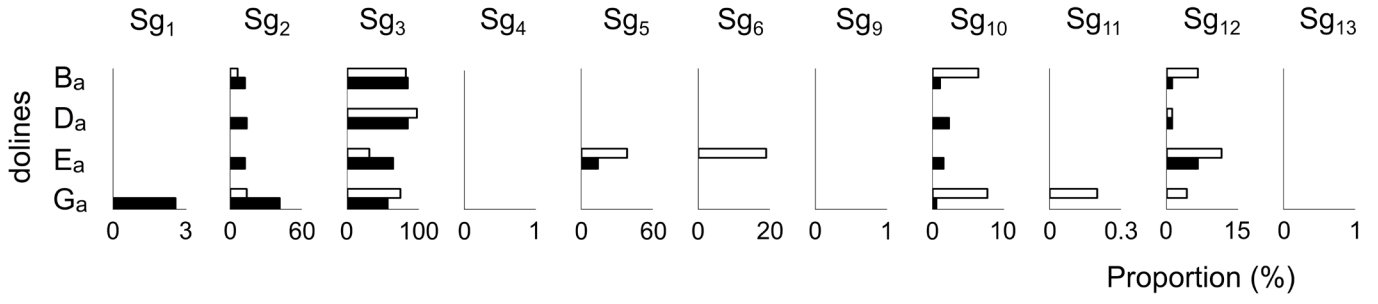

Fig. 4. Proportions of the different species groups in the dolines of the Aggtelek Karst area. White and black bars refer to the proportions of the 1st and 2nd vegetation units, respectively.

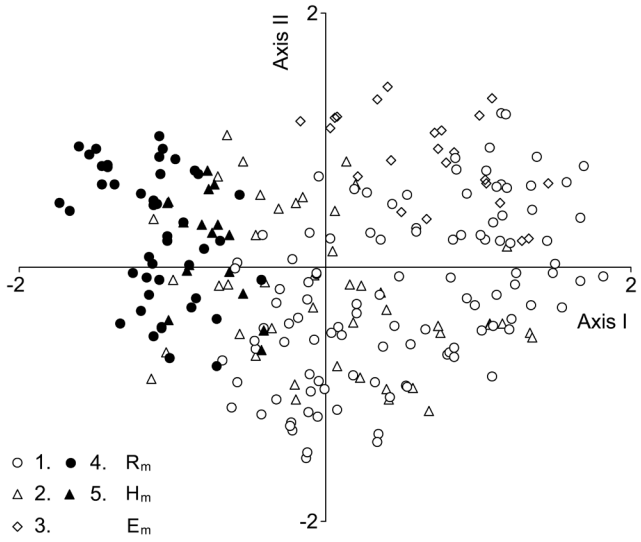

Fig. 5. Representative PCoA scatter diagram for the plots of three dolines (E_m, H_m, R_m) of the Mecsek Mountains. Notation: 1. plots of the beech forest (*Helleboro odori-Fagetum*) and oak-hornbeam forest (*Asperulo taurinae-Carpinetum*) of doline R_m; 2. plots of the beech forest and oak-hornbeam forest of doline H_m; 3. plots of the beech forest and oak-hornbeam forest of doline E_m; 4. plots of the ravine forest (*Scutellario altissimae-Aceretum*) of doline R_m; 5: plots of the ravine forest of doline H_m. Variance explained by the first and second axes was 19.9% and 10.8%, respectively.

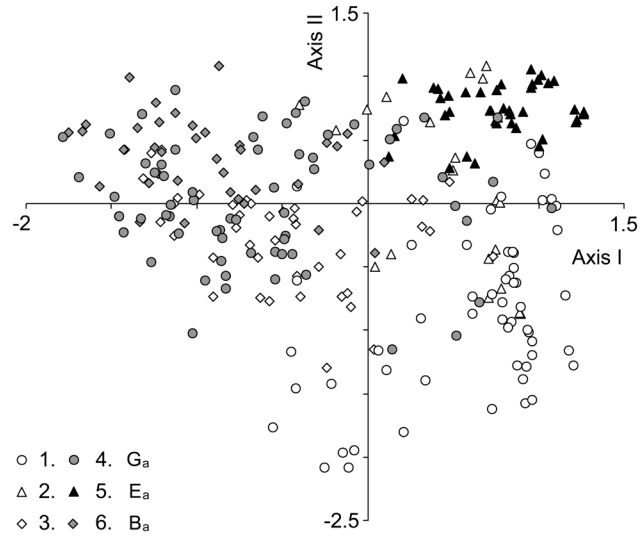

Fig. 6. Representative PCoA scatter diagram for the plots of three dolines (B_a, E_a, G_a) of the Aggtelek Karst area. Notation: 1. plots of the beech forest (*Melittio-Fagetum*) and oak-hornbeam forest (*Carici pilosae-Carpinetum*) of doline G_a; 2. plots of the beech forest and oak-hornbeam forest of doline E_a; 3. plots of the beech forest and oak-hornbeam forest of doline B_a; 4. plots of the scree forest (*Mercuriali-Tilietum*) of doline G_a; 5: plots of the ravine forest (*Scolopendrio-Fraxinetum*) of doline E_a; 6: plots of the scree forest of doline B_a. Variance explained by the first and second axes was 15.7% and 10.5%, respectively.

from 1 (cold) to 100 (hot), where 1 indicates the perfect nestedness, and 100 indicates the complete disorder. Since our matrix was not square (i.e., equal number of rows and columns) and fill was less than 50%, the matrix has been randomized using Monte Carlo simulations by 500 times to get the average T of the random matrices (T_{rand}). Plant species that contributed to the matrix disorder the most were also determined.

Plant species names were used according to Király (2009).

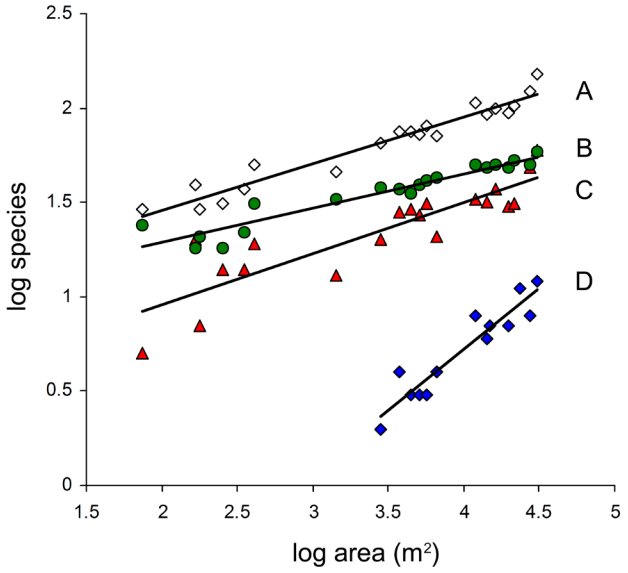

Fig. 7. Relationship between doline area (log_{10}transformed) and species number (log_{10} transformed) for the vascular vegetation of the Mecsek Mountains. Species-area lines were determined for all plant species (A: $y = 0.2491x + 0.9588$, $R = 0.9694$) and for the groups of beech forest species (B: $y = 0.1819x + 0.9247$, $R = 0.9506$), oak forest species (C: $y = 0.273x - 0.4083$, $R = 0.8789$) and cool-adapted species (D: $y = 0.6507x - 1.8830$, $R = 0.9405$).

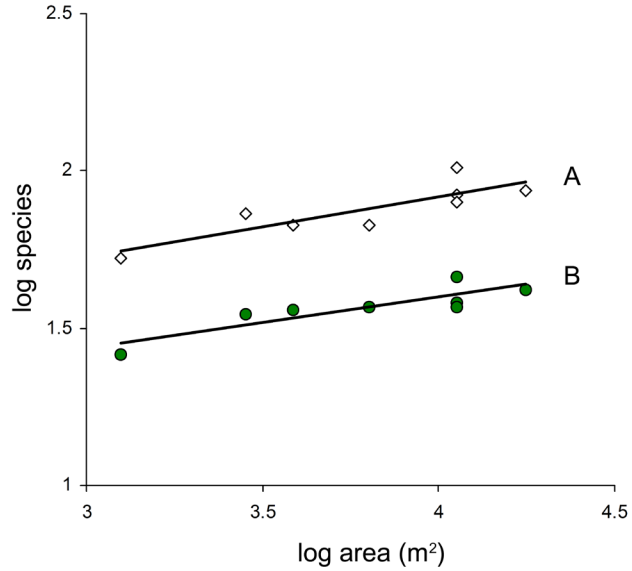

Fig. 8. Relationship between doline area (log_{10}transformed) and species number (log_{10} transformed) for the vascular vegetation of the Aggtelek Karst area. Species-area lines were determined for all plant species (A: $y = 0.1926x + 1.1463$, $R = 0.8590$) and for the groups of beech forest species (B: $y = 0.1614x + 0.9524$, $R = 0.8698$).

RESULTS

The species composition of the karst surface in the Mecsek Mountains (30 km²) was rather diverse (Table 2) with a total of 750 vascular plant species from 13 species groups. Many of the forests were dominated by Sg_2, Sg_3 and Sg_4 species, while Sg_1 species occurred mainly on warm, south-facing slopes and Sg_6 species in cool and moist habitats (e.g. valleys and dolines). Sg_7 species were dominant on rocky outcrops and in dry grasslands, Sg_8 species in meadows and Sg_9 species in small lakes and marshes. Sg_{10} and Sg_{11} species inhabited the roadsides, the plantations and other disturbed places of the karst surface. Sg_5

Table 2. Proportions of the species groups and total number of plants in the dolines of the Mecsek Mountains (A_m-T_m) and in the Aggtelek Karst area (A_a-I_a). Framed rectangles indicate the highest proportions. Abbreviations: Sr_m: study region of the Mecsek Mountains (30 km²); Sr_a: study region of the Aggtelek Karst area (5 km²); tns: total number of species.

	Sg_1	Sg_2	Sg_3	Sg_4	Sg_5	Sg_6	Sg_7	Sg_8	Sg_9	Sg_{10}	Sg_{11}	Sg_{12}	Sg_{13}	tns.
A_m		17.2	72.4	10.3										29
B_m	7.7	43.6	30.8	15.4								2.6		39
C_m		24.1	58.6	13.8								3.4		29
D_m	6.5	35.5	48.4	9.7										31
E_m	2.7	35.1	54.1	5.4								2.7		37
F_m		38.0	56.0	6.0										50
G_m	2.2	26.1	63.0	8.7										46
H_m	4.6	26.2	50.8	7.7		3.1				4.6		3.1		65
I_m	2.7	34.7	38.7	10.7	2.7	2.7				2.7	1.3	4.0		75
J_m	2.7	36.0	40.0	6.7		4.0				2.7		6.7	1.3	75
K_m	5.5	31.5	46.6	6.8	2.7	1.4				2.7		2.7		73
L_m	3.8	35.0	42.5	8.8	1.3	2.5				3.8		2.5		80
M_m	1.4	28.2	53.5	7.0	1.4	4.2				2.8		1.4		71
N_m	3.8	27.4	35.8	11.3	1.9	3.8		0.9	1.9	3.8	1.9	6.6	0.9	106
O_m	2.2	32.6	44.6	7.6	1.1	5.4				2.2		4.3		92
P_m	6.0	31.0	42.0	8.0	2.0	5.0				2.0		4.0		100
Q_m	4.2	27.4	41.1	9.5	2.1	5.3				4.2	1.1	4.2	1.1	95
R_m	2.9	27.2	43.7	7.8	2.9	6.8			1.0	1.9	1.0	4.9		103
S_m	7.4	32.0	30.3	10.7	1.6	4.9				4.1	0.8	8.2		122
T_m	8.6	30.3	30.3	8.6	3.9	2.6	0.7		1.3	4.6	1.3	6.6	1.3	152
Sr_m	9.7	10.9	9.5	2.1	1.5	3.9	11.9	5.9	6.9	14.3	7.1	14.0	2.4	750
A_a		28.3	49.1		9.4	3.8				3.8		5.7		53
B_a	1.4	37.0	47.9		4.1		1.4			4.1		4.1		73
C_a	1.5	32.8	53.7		3.0	1.5				3.0		4.5		67
E_a		20.9	55.2		10.4	3.0				4.5		6.0		67
F_a		33.3	54.8		4.8					3.6		3.6		84
G_a	7.8	45.1	37.3		2.9					3.9		2.9		102
H_a	2.5	42.5	46.3		2.5					3.8	1.3	1.3		80
I_a		42.5	48.3		3.4					3.4		2.3		87
Sr_a	12.0	16.5	13.4		1.6	1.8	18.3	7.4	3.3	11.4	2.5	11.8		552

species such as *Aconitum vulparia*, *Actaea spicata*, *Aruncus dioicus*, *Asplenium scolopendrium*, *Asplenium trichomanes*, *Cystopteris fragilis*, *Dryopteris affinis*, *Lunaria rediviva*, *Polystichum aculeatum*, *Polystichum* × *bicknelli,* and *Silene dioica* were restricted mainly to mountain "islands" (e.g. doline bottoms and deep valleys) within the "ocean" of oak-hornbeam and beech forests. Only a few of the mountain species (*Daphne mezereum*, *Luzula pilosa*, and *Stachys alpina* (Sg_3)) occurred also in the forests surrounding dolines.

Sg_4 and Sg_{13} species were absent from the flora of the investigated karst surface of the Aggtelek Karst area (5 km²), therefore its 552 vascular plants belonged to 11 species groups (Table 2). Similar to the study region of the Mecsek Mountains, Sg_2 and Sg_3 species played an important role in structuring forest communities. Sg_7, Sg_8, Sg_9, Sg_{10} and Sg_{11} species occupied similar habitats as in the Mecsek Mountains. Sg_5 species (*Adoxa moschatellina*, *Arabis turrita*, *Asplenium scolopendrium*, *Asplenium trichomanes*, *Cystopteris fragilis*, *Festuca altissima*, *Lunaria rediviva*, *Polypodium interjectum,* and *Ribes alpinum*) primarily occurred within the deep and rocky dolines of the karst surface. The number of other mountain species (*Carex brevicollis* (Sg_1), *Actaea spicata*, *Astrantia major*, *Daphne mezereum*, *Dryopteris dilatata*, *Dryopteris expansa*, *Polygonatum verticillatum*, *Prenanthes purpurea*, *Rosa pendulina,* and *Senecio ovatus* (Sg_3)) occurring also on the plateaus among dolines, was much higher than in the Mecsek Mountains.

Species composition changed markedly depending on the size of dolines (Table 2). In the small and shallow dolines (A_m to G_m), only species belonging to Sg_1, Sg_2, Sg_3, Sg_4 and Sg_{12} were found. In the case of larger and deeper dolines (H_m to M_m), the spectra were wider, and several species of other groups, especially of Sg_5 and Sg_6, were found (see Fig. 9). The large dolines (N_m to T_m) contained the highest number of species groups with the highest proportions of Sg_5, Sg_6, Sg_7, Sg_8, Sg_9 and Sg_{12} species. In contrast, many Sg_5, Sg_{10} and Sg_{12} species occurred in the dolines of the Aggtelek Karst area, independently of the doline diameter. Moreover, in most cases, the proportion of Sg_5 species was much higher in the Aggtelek Karst area with the maximum of 10.4% occurring in doline E_a as compared with that of the Mecsek Mountains, where the maximum (3.9%) occurred in the largest doline. In all cases, Sg_2 and Sg_3 species had higher proportions in dolines than in the total flora of the karst surfaces. It is important to note that larger dolines of both regions hold many Sg_5 and Sg_6 species that are restricted mainly to them.

Results of the MSW analysis indicated the presence of more vegetation units (i.e., No. 1 and No. 2 in the profiles) in dolines F_m to T_m and B_a, D_a, E_a and G_a. In contrast, in the case of A_m to E_m no significant differences were found along the transects. In all but the F_m doline, Sg_1, Sg_2 and Sg_4 species (if they occurred in the doline) had a higher proportion in the 2nd unit than in the 1st unit; however, in most cases Sg_3 and Sg_{12} showed the reverse distribution (Fig. 3, 4). From a floristic point of view, the 1st unit showed a marked mountain character due to the occurrence of numerous Sg_5 and Sg_6 species.

When all vascular plants were taken into consideration, the correlation between species number (log_{10}transformed) and doline area (log_{10}transformed) was positive and significant ($R = 0.97$, $P < 0.001$ in the Mecsek Mountains and $R = 0.86$, $P < 0.01$ in the Aggtelek Karst area). This relationship was also significant when the oak forest species ($R = 0.88$, $P < 0.001$), beech forest species ($R = 0.95$, $P < 0.001$) and cool-adapted species ($R = 0.94$, $P < 0.001$) of the Mecsek Mountains and the beech forest species ($R = 0.87$, $P < 0.005$) of the Aggtelek Karst area were considered (Fig. 7, 8). However, no such significant correlation was established for cool-adapted species and oak forest species in the Aggtelek Karst area. The slope of the species-area curves (z-values) for all vascular plant species was 0.25 in the Mecsek Mountains and 0.19 in the Aggtelek Karst area, while the slope was higher for oak forest species ($z = 0.27$) and cool-adapted species ($z = 0.65$) in the Mecsek Mountains. The slope was relatively low in the case of beech forest species for both regions ($z = 0.18$ in the Mecsek Mountains; $z = 0.16$ in the Aggtelek Karst area).

The distribution of plant species in the dolines was significantly nested for both regions: $T = 14.08°$, $T_{rand} = 71.38°$, SD = 1.96°, $P < 0.001$ in the Mecsek Mountains; $T = 35.32°$, $T_{rand} = 56.54°$, SD = 3.11°, $P < 0.001$ in the Aggtelek Karst area. Species that contributed greatest to the matrix disorder include: *Fraxinus excelsior*, *Tilia cordata* (Sg_2), *Acer platanoides*, *Allium ursinum*, *Arum maculatum*, *Euphorbia amygdaloides*, *Galanthus nivalis*, *Hepatica nobilis*, *Mercurialis perennis* (Sg_3) and *Ruscus hypoglossum* (Sg_4) in the Mecsek Mountains; *Melica nutans* (Sg_2), *Daphne mezereum*, *Lathraea squamaria*, *Ribes uva-crispa*, *Stachys sylvatica* (Sg_3), *Asplenium scolopendrium*, *Lunaria rediviva* (Sg_5), *Circaea lutetiana*, *Dryopteris carthusiana* (Sg_6), and *Sambucus nigra* (Sg_{12}) in the Aggtelek Karst area.

PCoA showed that the vegetation of smaller dolines of the Mecsek Mountains was very similar to that of upper slopes of larger ones (a representative sample is

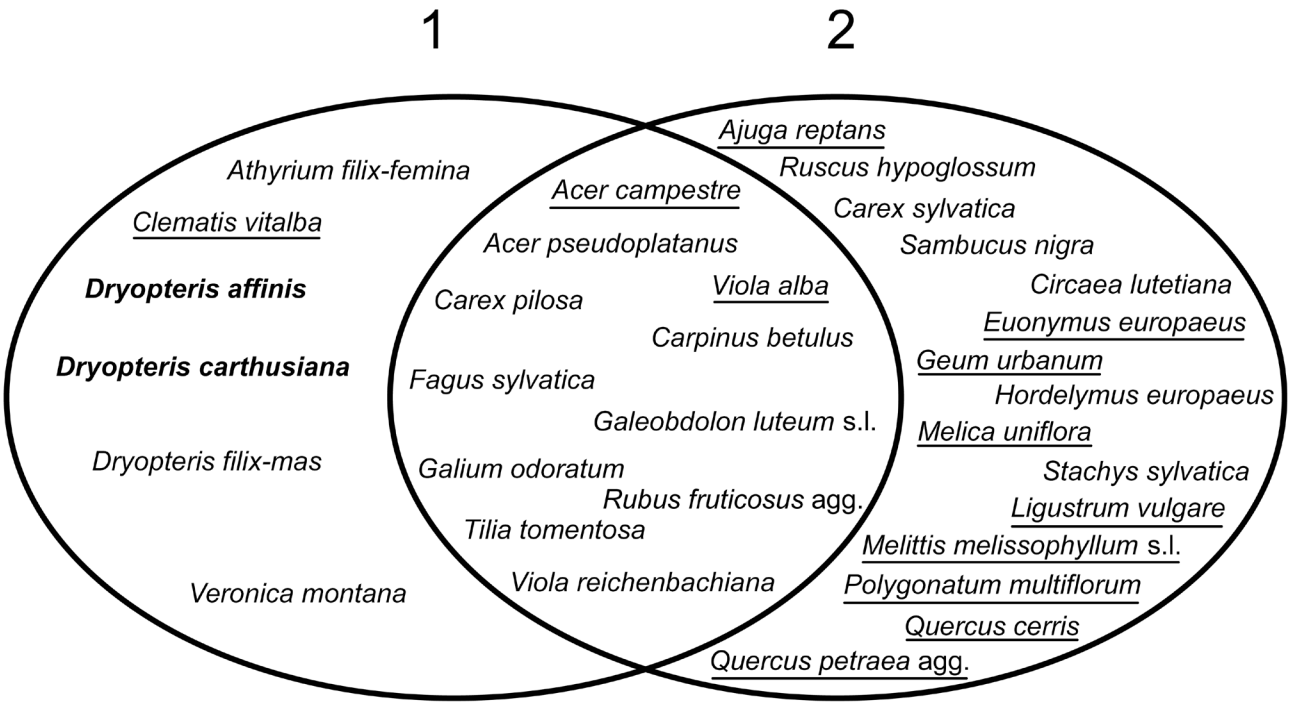

Fig. 9. The species composition of the I_m doline (a representative sample) along the transect divided into two parts (doline bottom: No. 1, upper slopes and rim: No. 2) by the moving split window (MSW) technique. Species names of deep ravines and gorges (Sg_5) and wet forests (Sg_6) are in bold and species names of dry oak forests (Sg_1) and mesic oak forests (Sg_2) are underlined.

shown in Fig. 5). The length of the gradient along the 1st axis was the longest in the largest doline and the slopes were covered by different types of forests. Plots of the ravine forests were on the left side of the scatter in the given sample. However, the plots of beech forests and oak-hornbeam forests were not separated from each other. Despite the relatively high depth/diameter ratios of some smaller dolines (e.g. B_m: 0.25; E_m: 0.23), they did not contain vegetation types that were not present in larger dolines. In contrast, as the representative sample shows (Fig. 6), ordination of the plots of the Aggtelek Karst area indicated a different pattern. Plots of E_a at one end of the gradient showed a relatively distinct vegetation type that was absent from larger dolines and was identified as ravine forest in the field. However, scree forest was absent from this doline. Similarly to the Mecsek Mountains, the length of the gradient along the 1st axis was the longest in the largest doline.

DISCUSSION

Humanity is rapidly destroying habitats that are natural, species-rich and are an important source of knowledge about life-history evolution (Pimm & Raven, 2000). In addition, another adverse factor is the effect of climate change caused by global warming, which has caused distributional shifts towards the poles or higher altitudes accompanied by various behavioural changes in the case of several species (Walther et al., 2002; Erschbamer et al., 2011). However, many species choose other possible migration routes restricting their distribution to sheltered sites such as dolines, fens, ponds, valleys and other cold and humid places (Schindler et al., 1996; Kochjarová et al., 1997; Bátori et al., 2012).

Our study yielded three main results. First, the investigated dolines can be recognized as refugia for many vascular plant species. Second, doline geometry significantly influences the distribution of plant species. Third, species preservation in the dolines is not influenced by the type of regional climate.

The role of dolines in preserving different kinds of species is well-known (Horvat, 1953; Özkan et al., 2010; Bátori et al., 2011), although species preservation is significantly influenced by many factors (Geiger, 1950; Lehmann, 1970; Favretto & Poldini, 1985; Whiteman et al., 2004). Our study revealed that dolines of both investigated regions provide good habitat for many species adapted to different temperature and moisture regimes. According to the results of the MSW analysis, vegetation of smaller dolines of the Mecsek Mountains does not change substantially along the transects, however, the slopes of larger dolines of both regions contain more vegetation units with their own species. When all plant species of the dolines are considered, the *z*-values (z = 0.25 and z = 0.19, respectively) are in good agreement with those obtained previously for oceanic and habitat islands (Begon et al., 2006). Our results suggest that the larger dolines of the Mecsek Mountains have much greater impact on the distribution of oak forest species than the smaller ones. Larger dolines have larger south-facing slopes, which allow increased insolation during daytime. The species-area curve for oak forest species (z = 0.27) is much steeper than that for beech forest species (z = 0.18 in the Mecsek Mountains; z = 0.16 in the Aggtelek Karst area). This means that, for beech forest species, dolines serve as island-like habitats to a lesser degree than for oak forest species (cf. Rockwood, 2006). We did not find linear correlation between the number of oak forest species and doline area in the Aggtelek Karst area. This is due to the fact that some dolines of this region have vertical rocky walls, which modify the effects of solar insolation on species preservation of the south-facing slopes. In our former study (Bátori et al., 2012), we reported that larger dolines of the Mecsek Mountains act as refugia for many cool-adapted plants of the summer flora. If considering the steepness of the species-area curve of cool-adapted species in the Mecsek Mountains (z = 0.65), we can conclude that larger dolines play an essential role in preserving many plant species that are particularly vulnerable to climatic change. This is due to the linear relation between doline diameter and depth, which results in lower temperatures in larger dolines. As the multivariate analyses (MSW, PCoA) and field observations revealed, larger dolines of this region always contain the vegetation types of the smaller dolines. However, cool-adapted species and vegetation types of the Aggtelek Karst area show a very different pattern. Although vascular plant assemblages are significantly nested in both regions, we should always take into consideration those species that appeared in unexpected places (Atmar & Patterson, 1993; Heino et al., 2009). For example, many idiosyncratic species of the Aggtelek Karst area belong to the groups of Sg_5 and Sg_6, highlighting the role of some smaller dolines as refugia. The smallest doline of this region (A_a) contains much more cool-adapted species than some larger ones (e.g. G_a and H_a). This can be explained by the geometry, because this doline is deep relative to its width (depth/diameter ratio is 0.38) and, in addition, has rocky walls. The steep slopes of some smaller dolines are covered by ravine forests, which vegetation type is absent from many large dolines of this region.

Both investigated regions are rich in habitats and plant species. Oak-hornbeam and beech forest communities dominate most of the plateaus and hill slopes (Jakucs & Jurko, 1967; Kevey & Borhidi, 1998), ecologically connecting the numerous dolines scattered in these forests. However, the proportion of different types of species differs markedly between the karst surfaces and individual dolines. The different regional climates of the two regions studied resulted in different species pools from which local communities are drawn (cf. Pärtel et al., 1996). This is in good agreement with the results of former studies, which revealed that many plant species have a high degree of range equilibrium with actual climate (Webb, 1986; Prentice et al., 1991). Considering our study regions, Sg_4 species play an important role in structuring plant communities of the Mecsek Mountains, but they are absent from the study region of the Aggtelek Karst area, although some Illyrian species do occur in other

parts of the Aggtelek Karst area. Obviously, these differences are somewhat understandable if we try to identify and clarify the late glacial and post-glacial evolution of the Carpathian Basin. Investigation of loess profiles, lake sediments and archaeological sites in different parts of the Carpathian Basin revealed that between ca. 32000 and 16000 years BP recurring boreal forest-steppe characterised the area (Willis et al., 1998; Rudner & Sümegi, 2001). After the Younger Dryas (III) (ca. 11000 BP), warming with increasing summer insolation allowed species to expand northward, mainly from the Balkan Peninsula. In the Boreal and Atlantic phases of the Holocene, the limestone flora of Hungary became more diverse with many vascular plant species migrating from the south. After the Holocene climate optimum (ca. 5000 BP), when the climate became cooler, many warm-adapted plants of northern Hungary have been forced into refugia (e.g. south-facing rocky outcrops), but the Mecsek Mountains and its surroundings preserved its sub-Mediterranean character (Borhidi, 2006). Under the present-day climate regime of the Aggtelek Karst area, mountain elements could occupy the karst surface at two levels. First, many mountain species (e.g. *Daphne mezereum*, *Polygonatum verticillatum*) occur in all favourable habitats, both on plateaus among dolines and in dolines; second, other mountain plants (e.g. *Lunaria rediviva*, *Ribes alpinum*) are restricted mainly to rocky dolines (see Fig. 4.). In contrast, due to the warmer climate, mountain species of the Mecsek Mountains occur mainly in dolines (see Fig. 3.) and in deep valleys (cf. Kevey, 1997). However, dolines of both regions play the same role in the preservation of vascular plant species. Since larger dolines of both regions were formed in the Pleistocene (Hoyk, 1999; Telbisz & Ádám, 2011), they might play an important role as refugia for many vascular plants in different periods of geologic time, highlighting the dolines as target objects for vegetation history studies. For example, *Stachys alpina*, a cold-stage relict of the Mecsek Mountains (Simon, 2000), might have survived in the bottom of larger dolines during periods of unfavourable conditions (e.g. in the Atlantic phase of Holocene).

Our results suggest that the effects of doline geometry on temperature inversion strength, latitude, rockiness, vegetation cover and vegetation history exert a major impact on plant growth and survival in dolines. We can conclude that karst dolines of Hungary can be considered as potential refugia for many vascular plant species under future global warming, therefore they are particularly important from a conservation point of view. Due to the recent increases in the degradation of doline vegetation (e.g. deforestation, overgrazing) in some areas of Hungary (Bárány-Kevei, 2011), there is a pressing need to focus conservation efforts on the preservation of the valuable flora of dolines. The classification of species presented in this paper will be used to prioritize species groups on which to focus management and to identify those environmental factors which require further studies.

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