IDŐJÁRÁS

Microclimate-vegetation relationships in natural habitat islands: species preservation and conservation perspectives

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Abstract— Information about the relationship between the spatial and temporal patterns of different climatic parameters and the vegetation is especially important from a nature conservation perspective. We studied the influence of microclimatic parameters (air temperature and air humidity) on certain natural habitat islands (karst sinkhole and sand dune slack) and on their plant species composition and vegetation pattern in Hungary. Vegetation data together with topographic variables were collected along transects to reveal the vegetation patterns on the slopes. Microclimatic parameters were measured with wireless sensor motes equipped with air temperature and humidity sensors. Interactions were examined using distance-based redundancy analysis. We found that the species composition of natural habitat islands varied markedly within short distances, depending on the prevailing microclimatic conditions. Elements of microclimate (daily, daytime, and nighttime averages) have different effects on vegetation pattern and species composition. The observed patterns can be interpreted based on our knowledge on the structure of plant communities and on the role of geomorphology. Future temperature increase, droughts, and forestry activities are the main threats to the habitat diversity and hence to the species diversity of habitat islands in Hungary.

Key-words: air humidity, air temperature, climate change, habitat island, Hungary, refugium, vegetation inversion, wireless sensor

1. Introduction

Microclimate is a suite of climatic conditions measured usually directly on the ground or very close to it (*Geiger*, 1965). The effects of different microclimatic parameters (e.g., air temperature and air humidity) on animals and plants have been widely studied because they are essential to individual organisms for reproduction (e.g., germination) and ecological processes (e.g., evapotranspiration, microbial activity, nutrient cycling, photosynthesis, and regeneration) (*Bátori et al.*, 2012a; *Forseth* and *Teramura*, 1987; *Holl*, 1999; *Marlatt*, 1961; *Schimel* and *Parton*, 1986). The interactions between microclimate and vegetation have been studied both at local and regional scales. Local-scale studies have focused mainly on individuals and stands, providing important information about the local ecological processes and sometimes, based on the extension and generalization of the results, about larger-scale ecological processes (*Antonić et al.*, 1997; *Bátori et al.*, 2011; *Herrera*, 1995). The number of landscape studies examining microclimate and its relationship with flora, vegetation, and related ecological processes in the context of landscape is much lower (*Xu et al.*, 2004).

The interaction between topography and climate is complex and its details are not completely understood (*Dobrowski*, 2011). There is no doubt, however, that topography and related terrain effects strongly affect the local environmental and climatic conditions (*Bátori et al.*, 2009; *Geiger*, 1950; *Whiteman et al.*, 2004). The effect of geomorphology on temperature inversion strengths, diurnal temperature regimes, and vertical temperature gradients has a great impact on vegetation pattern and plant survival. However, vegetation cover usually has a mitigating effect on air and soil temperatures (*Allen* and *Burton*, 1993; *Fetcher et al.*, 1985; *Oliver et al.*, 1987); therefore, elements of microclimate are usually less extreme in forests than in grasslands. In addition, many studies suggest that not only the diurnal or monthly average temperature and humidity values but also the differences between the daytime and nighttime averages as well as their changes affect markedly species composition, vegetation pattern, and ecological processes (*Liu et al.*, 2006; *Mohammed* and *Tarpley*, 2009; *Shiu et al.*, 2009). It is important to note that management related variables often explain more variation in vegetation than any other variables together, indicating the importance of management as determining species composition (*Aude* and *Lawesson*, 1998). Therefore, the effects of microclimate must be interpreted differently under different disturbance regimes, various topographical features, and vegetation covers.

The spatial distribution of microclimate is an essential factor for habitat suitability for many species (*Mantilla-Contreras et al.*, 2011; *Rich* and *Weiss*, 1991). Since climate change apparently affects the occurrences of species and the phenology of animal and plant activity (*Molnár et al.*, 2012; *Rijnsdorp et al.*, 2009; *Thomas et al.*, 2004; *Walther et al.*, 2002) by shifting the overall

temperature distribution, changing the precipitation regime and increasing the frequency of extreme weather events (*Easterling et al.*, 2000; *Parmesan et al.*, 2000), the investigation of the habitats suitable for providing refugia for affected species is of crucial importance. One of the most important insights that scientists can offer for conservation biology is how species are expected to respond to changes in regional and local climate. Hence, an increasing number of species distribution models have recently been reported (*Rasztovits et al.*, 2012; *Schwartz et al.*, 2006). From the point of view of an ecologist, investigations of island-like habitats can offer many possibilities to answer the above question (*Bátori et al.*, 2012b; *Körmöczi et al.*, 1981). According to the well accepted theory, 'islands' should not necessarily be land masses in water but may be particular geological types, soil types, or vegetation types surrounded by dissimilar types of rock, soil or vegetation (*Begon et al.*, 2006). However, we must distinguish between (semi)natural habitat islands and artificially created habitat islands (e.g., agricultural fields, cities, secondary grasslands), because environmental conditions (e.g., microclimate, nutrient availability, water supply), ecological processes, and organism responses are fundamentally different in the two types (*Pinke et al.*, 2012; *Unger*, 1999).

Several previous studies focused on relatively small areas with special temperature and humidity properties that harbor many species that once occurred in larger and more continuous populations (*Müller et al.*, 2006; *Turlure et al.*, 2010). For example, the lowland fens of the Carpathian Basin serve as refuges for many boreal plants (e.g., *Menyanthes trifoliata* L., *Potentilla palustris* (L.) Scop., *Trollius europaeus* L.), and the karst sinkholes and deep ravines of hill and mountain ranges preserved high-mountain species (e.g., *Rubus saxatilis* L., *Stachys alpina* L., *Viola biflora* L.) (*Király*, 2009; *Simon*, 2000). Most of these plants are climatic relicts, whose populations persist in isolated enclaves of suitable climate space surrounded by areas where the climate is not suitable for them (*Hampe* and *Jump*, 2011). Therefore, these habitats can be used for vegetation history studies as well, because their flora reflects cooler climatic periods (*Bátori et al.*, 2012b). Not only climate relicts but also other groups of species may be good indicators for microclimatic conditions of different habitats. For example, *Erdős et al.* (2013) revealed that the vascular plants of the mosaic of lowland xeric grasslands and mesic forests indicate very different climatic conditions along an edge to interior gradient. They also pointed out that the species composition of these habitat complexes may be very diverse and may contain many rare and endangered mesic forest plants, which are more characteristic of the hill and mountain ranges of the Carpathian Basin. In these cases, the local climatic conditions allow many species to maintain their populations in places where the surrounding environmental conditions (e.g., warmer climate) are not suitable for them.

The objective of this study is to examine and compare the species composition and vegetation pattern of natural habitat islands in Hungary, and to

make an attempt to explain these phenomena with microclimatic variables including the daily, daytime and nighttime air temperature and air humidity regimes. We also discuss the potential role of these habitats in preserving different groups of plant species under future climate change.

2. Methods

2.1. Study sites and vegetation survey

Study sites were selected in two different parts of Hungary (*Fig. 1*), where the landscapes contain many natural habitat islands. The fieldwork was conducted between 2009 and 2012 in a large karst sinkhole of the Mecsek Mountains (46°7'17" N, 18°12'11" E; 498 m above sea level) and in a deep sand-dune slack of Bugac (46°41'46" N, 19°36'9" E; 111 m above sea level). All samples were taken in summer, when the influence of spatial microclimatic properties was expected to be the greatest on the habitat islands. Neither site showed signs of considerable human or animal disturbance.
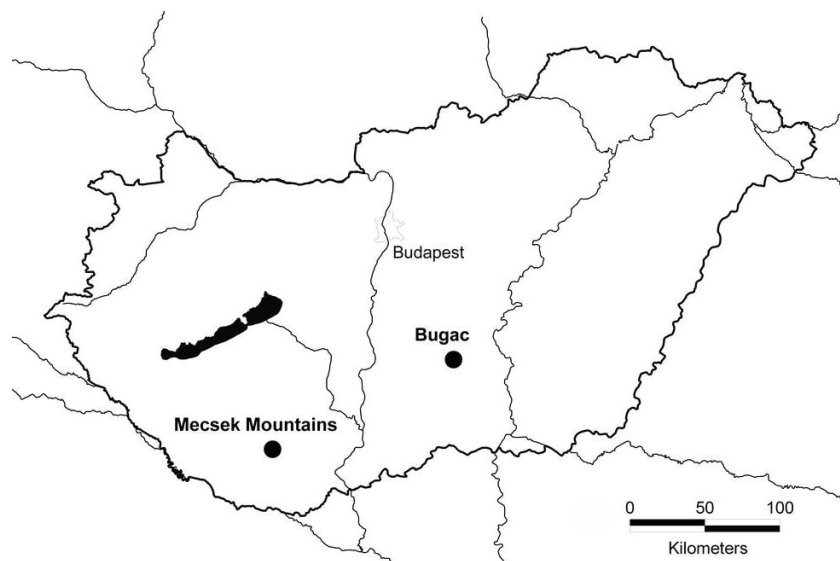
Fig. 1. Location of the study sites in Hungary.

Transect sampling was applied in both sites. Plot sizes were optimized according to our former studies and experiences (*Bátori et al.*, 2012b; *Tölgyesi* and *Körmöczi*, 2012).

In the Mecsek Mountains, a sub-Mediterranean type, middle-aged mesic oak-hornbeam (*Asperulo taurinae-Carpinetum*) and beech forests (*Helleboro odori-Fagetum*) covered the north-facing, east-facing, and west-facing slopes of the approximately 30 m deep sinkhole. A transition between a xeric turkey oak-sessile oak forest (*Potentillo micranthae-Quercetum dalechampii*) and an oak-

hornbeam forest occurred on the south-facing rim and an oak-hornbeam forest on the south-facing slope. The sinkhole bottom was covered by a ravine forest (*Scutellario altissimae-Aceretum*) (*Bátori et al.*, 2011). Herb layer was sampled along a 2 m wide and 243 m long transect consisting of 50 plots, 2 m × 1 m each. The transect was established in a north to south direction traversing the deepest point of the sinkhole.

At Bugac, a xeric grassland (*Festucetum vaginatae*) occupied the major part of the investigated sand dune (*Körmöczi* and *Balogh*, 1990), which is part of the Kiskunság Sand Ridge. The lower parts of the dune were covered by a remnant of a wet interdune vegetation patch (*Molinio-Salicetum rosmarinifoliae*). The vegetation was sampled along a 1 m wide and 14 m long transect consisting of 14 plots, 1 m × 0.25 m each. The transect was established in a northeast to southwest direction (following the orientation of the dune) traversing the deepest point of the dune slack. The elevation difference between the highest and deepest points was approximately 1.7 m.

Presence/absence of all vascular plant species (including tree saplings and low shrubs), mosses and lichens of the summer aspect was recorded in all plots (see *Appendix*). According to the topographic profiles of each transect, the plots were classified into two groups: plots of the upper slopes and plots of the bottoms. The different habitats (the bottom and upper transect sections) were compared based on vegetation and microclimatic parameters during subsequent analyses.

Plant community names are used according to *Borhidi et al*. (2012), the nomenclature of mosses and lichens follow *Simon* (1991), while the names of vascular plant taxa follow *Király* (2009).

2.2. Microclimate measurement

We used 50 IRIS (XM2110CA) wireless sensor motes from Crossbow, each of which was equipped with an MTS400 (SN21140CA) weather sensor board, which included air temperature and air humidity sensors. We measured air temperature (°C) and air humidity (%) for 24 hours 25 cm above the ground surface in the plots of the 2 transects. The signals from the sensors were recorded once every minute, therefore, 1440 temperature and 1440 humidity datapoints (24 × 60, respectively) were obtained from each mote. From these data, the daily minimum air temperature (DMinAT), daily maximum air temperature (DMaxAT), daily minimum air humidity (DMinAH), daily maximum air humidity (DMaxAH), mean daily air temperature (MDAT), mean daily air humidity (MDAH), mean daytime air temperature (MDtAT), mean daytime air humidity (MDtAH), mean nighttime air temperature (MNtAT), and mean nighttime air humidity (MNtAH) were calculated. 'Daytime' is defined as the time interval between 7 a.m. and 7 p.m., while 'nighttime' is the interval between 7 p.m. and 7 a.m. Microclimate measurements were carried out after a dry period, under clear weather conditions.

2.3. Analysis

Percentage frequencies for the species were determined with the JUICE 7.0.25 program (*Tichý*, 2002). After testing normality, one-way ANOVA and subsequent Tukey's HSD post hoc tests were applied in order to reveal the differences in species number between the different habitats, using the stats package of R 2.10.1 (*R Development Core Team*, 2009).

Detrended correspondence analysis (DCA) (*Hill* and *Gauch*, 1980) was used to detect the major gradients of floristic variation of the plots within the study sites. DCA is an ordination technique, which is able to identify gradients in community composition. Its advantage over other unconstrained ordination methods is that it is theoretically free from the so-called 'arch effect', thus, DCA axes correspond better to gradients with high turnover (*Legendre* and *Legendre*, 1998). The procedure was computed using Past 1.18 (*Hammer et al.*, 2001).

Variation of species presence/absence data was related to temperature and humidity measurements using distance-based redundancy analysis (db-RDA) (*Legendre* and *Anderson*, 1999). db-RDA is an ordination method, which arranges data objects in a space defined by the linear combinations of explanatory (environmental) variables and, at the same time, quantifies the variation in species composition explained by the environmental variables. The variation of species composition in db-RDA has to be expressed on the basis of a dissimilarity measure between pairs of community sample units. Here we applied the complement of Sörensen index as a dissimilarity measure, with the formula

$$D_{\text{Sörensen}} = 1 - 2*a/(2*a+b+c),$$

where a is the number of species present in both members of the pair, b and c are the number of species present in one and the other plot (*Legendre* and *Legendre*, 1998). Considering our previous results (*Bátori et al.* 2011), the following measurements were used as explanatory variables: MDAT, MDtAT, MNtAT, MDAH, MDtAH, and MNtAH. For each study site, the gross effect of each climatic variable was calculated by constructing a db-RDA model with the tested variable as the only predictor and the compositional data as the dependent variables (hereafter called 'one-predictor model'). Effect strengths of each climatic variable were quantified by the percentage explained variance and F value of the respective db-RDA model, and their significance was assessed by a permutation test (see *Table 1*). Then, for each study site, the most effective temperature and humidity variables were selected based on the lowest P and the highest F values. With these two as background variables, a new db-RDA was performed ('two-predictor model') in order to assess the cumulative effect of the best climatic variables (see *Table 2*). There was high collinearity within temperature variables and humidity variables, thus, the other 2–2 variables of

these climatic factors were not involved in the model. 'Two-predictor models' were visualized on biplots. Ordinations were performed using the vegan R package (*Oksanen et al.*, 2009; *R Development Core Team*, 2009).

Moreover, we also used the coenological preferences of the plant species (*Soó*, 1980) to characterize each habitat.

Table 1. Summary statistics for the 'one-predictor' db-RDA models. MDAT: mean daily air temperature, MDtAT: mean daytime air temperature, MNtAT: mean nighttime air temperature, MDAH: mean daily air humidity, MDtAH: mean daytime air humidity, MNtAH: mean nighttime air humidity

Predictors	Var. %	F value	P value
Mecsek Mountains: sinkhole			
MDAT	18.7	9.160	<0.001
MDtAT	17.5	8.478	<0.001
MNtAT	17.7	8.592	<0.001
MDAH	16.8	8.039	<0.001
MDtAH	14.9	7.028	<0.001
MNtAH	16.7	7.994	<0.001
Bugac: sand-dune slack			
MDAT	32.5	5.071	<0.005
MDtAT	24.1	3.387	<0.05
MNtAT	30.2	4.560	<0.005
MDAH	34.8	5.578	<0.001
MDtAH	31.9	4.935	<0.001
MNtAH	29.0	4.328	<0.005

Table 2. Summary statistics for the 'two-predictor' db-RDA models. MDAT: mean daily air temperature, MDAH: mean daily air humidity

Predictors	Var. %	F value	P value
Mecsek Mountains: sinkhole			
MDAT + MDAH	21.0	6.249	<0.001
Bugac: sand-dune slack			
MDAT + MDAH	37.8	3.342	<0.005

3. Results

3.1. Microclimate and flora of the karst sinkhole

The MDAT changed from 19.9 to 17.6 °C along a microclimatic gradient in the sinkhole (*Fig. 2*).
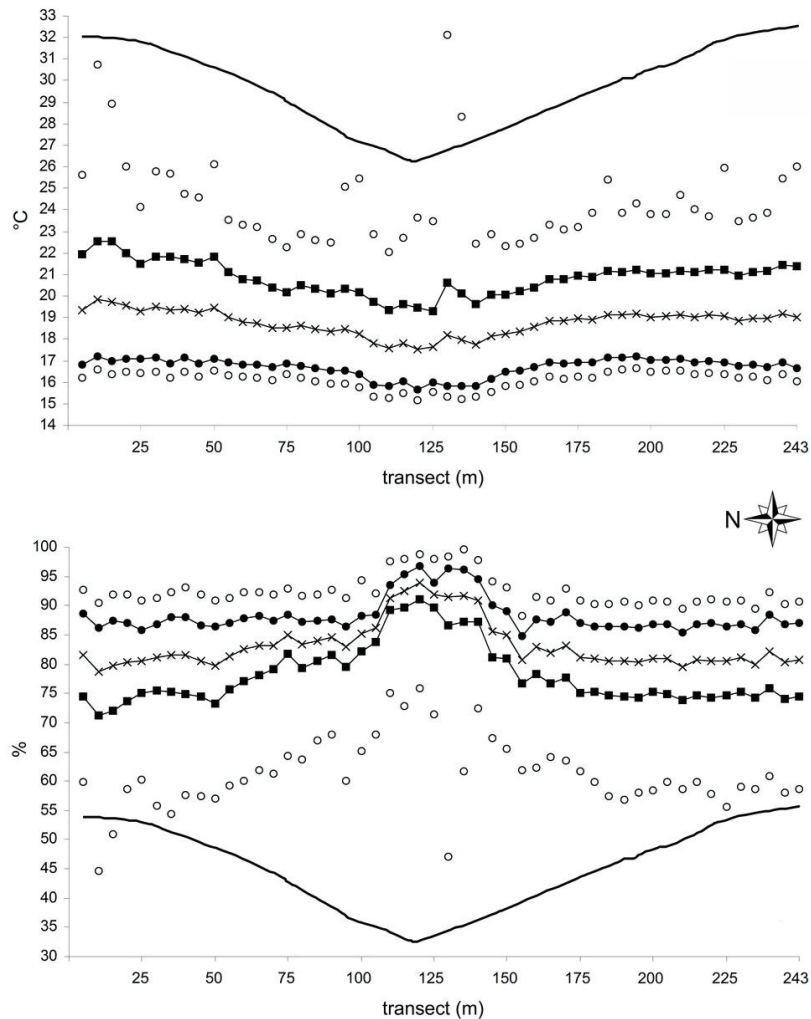
Fig. 2. Air temperature and air humidity values along the transect of the sinkhole of the Mecsek Mountains (August 9–10, 2010). Notations: ○: minimum and maximum air temperature (DMinAT, DMaxAT) and air humidity (DMinAH, DmaxAH) values; ■: mean daytime air temperature (MDtAT) and air humidity (MDtAH) values; ×: mean daily air temperature (MDAT) and air humidity (MDAH) values; ●: mean nighttime air temperature (MNtAT) and air humidity (MNtAH) values.

The maximum MDAT (19.9 °C) was detected in a plot of the south-facing rim where the transition between a turkey oak-sessile oak forest and an oak-hornbeam forest situated consisting of many dry oak forest and mesic oak forest species. The lowest MDAT (17.6 °C) and the DMinAT (15.1 °C) were recorded

on the bottom of the sinkhole, under the ravine forest. The MNtAT and MDtAT showed a very similar pattern, however, the DMaxAT (32.1 °C) was detected on the bottom of the sinkhole. Air humidity values also changed markedly along the transect with the lowest MDAH (79%) on the higher zone of the sinkhole slopes and with the highest MDAH (94%) in the sinkhole bottom (*Fig. 2*). The rest of the air humidity values followed a similar pattern. The 24-hour pattern of air temperature and air humidity also differed markedly between the upper sinkhole slopes and the sinkhole bottom (*Figs. 3–4*).
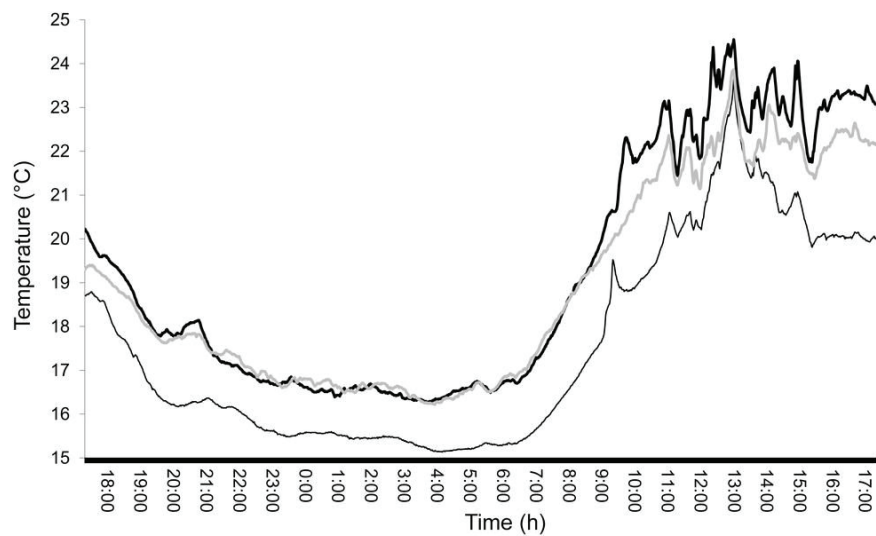
Fig. 3. Air temperature values in three plots along the transect (south-facing sinkhole slope: thick black line; sinkhole bottom: thin line; north-facing sinkhole slope: thick grey line) of the sinkhole of the Mecsek Mountains, measured over a 24-hour period (August 9–10, 2010).
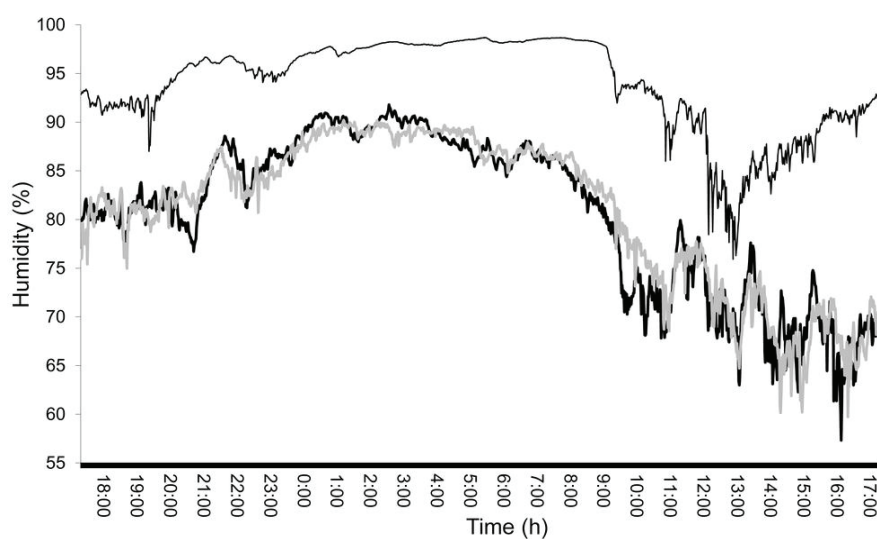
Fig. 4. Air humidity values in three plots along the transect (south-facing sinkhole slope: thick black line; sinkhole bottom: thin line; north-facing sinkhole slope: thick grey line) of the sinkhole of the Mecsek Mountains, measured over a 24-hour period (August 9–10, 2010).

The most frequent (>80%) species were *Fraxinus excelsior* L. on the upper sinkhole slopes and *F. excelsior* and *Galeobdolon luteum* s.l. on the sinkhole bottom. Species that occurred only in the sinkhole bottom include *Aconitum vulparia* Rchb., *Athyrium filix-femina* (L.) Roth, *Atropa belladonna* L., *Carex sylvatica* Huds., *Circaea lutetiana* L., *Dryopteris filix-mas* (L.) Schott, *Eupatorium cannabinum* L., *Paris quadrifolia* L., *Polystichum aculeatum* (L.) Roth, *P. setiferum* (Forssk.) Woyn., *Pyrus pyraster* (L.) Burgsd., *Rubus fruticosus* agg., *Solanum dulcamara* L., *Stachys sylvatica* L., *Urtica dioica* L., and *Veronica montana* L. According to the ANOVA, species number in the upper slopes and in the sinkhole bottom did not differ significantly (P=0.710). The proportions of the different species groups are shown in *Fig. 5*. Species of mesic oak forests (38%) and Central European beech forests (40%) had the highest proportions on the sinkhole slopes, but species of dry oak forests (9%) and Illyrian beech forests (9%) also had an important role in structuring the plant communities. The sinkhole bottom was covered mainly by beech forest species (54%), but the proportions of mesic oak forest species (14%) and indifferent species (12%) were also considerable. It is important to note that the sinkhole bottom held some species of deep ravines and gorges (e.g., *Aconitum vulparia* and *Polystichum aculeatum*) (2%), which were restricted to them.
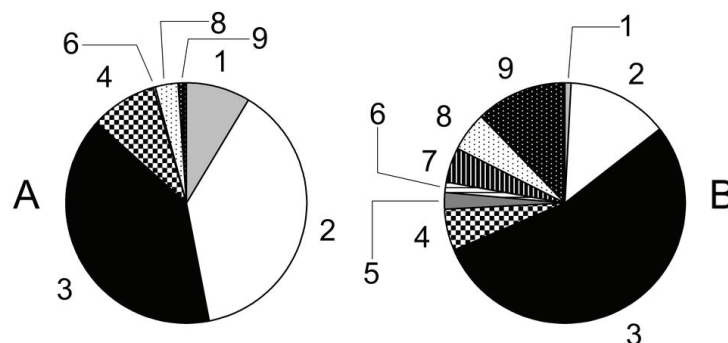
Fig. 5. Proportions of the different species groups of the sinkhole slopes (A) and of the sinkhole bottom (B). 1: species of dry oak forests; 2: species of mesic oak forests; 3: species of Central European beech forests; 4: species of Illyrian beech forests; 5: species of deep ravines and gorges; 6: species of wet forests; 7: species of marshes; 8: weed species; 9: indifferent species.

3.2. Microclimate and flora of the sand-dune slack

Air temperature and air humidity changed markedly along the transect of Bugac (*Fig. 6*). The lowest MDAT (15.8 °C) was recorded in the bottom of the dune slack where a remainder of the association *Molinio-Salicetum rosmarinifoliae* occurred. The highest MDAT (20.2 °C) was recorded in the open sandy

grassland of the upper slope. MDtAt and MNtAT values showed a marked decrease from the slopes to the bottom indicating a clear temperature gradient between them. Air humidity showed an opposite pattern with the highest values (MDAH: 79%; MNtAH: 96%; MDtAH: 62%) in the bottom of the dune slack and the lowest values (MDAH: 64%; MNtAH: 81%; MDtAH: 42%) on the upper slopes. The 24-hour pattern of air temperature and air humidity also differed markedly between the upper dune slopes and the bottom of the dune slack (*Figs. 7–8*).
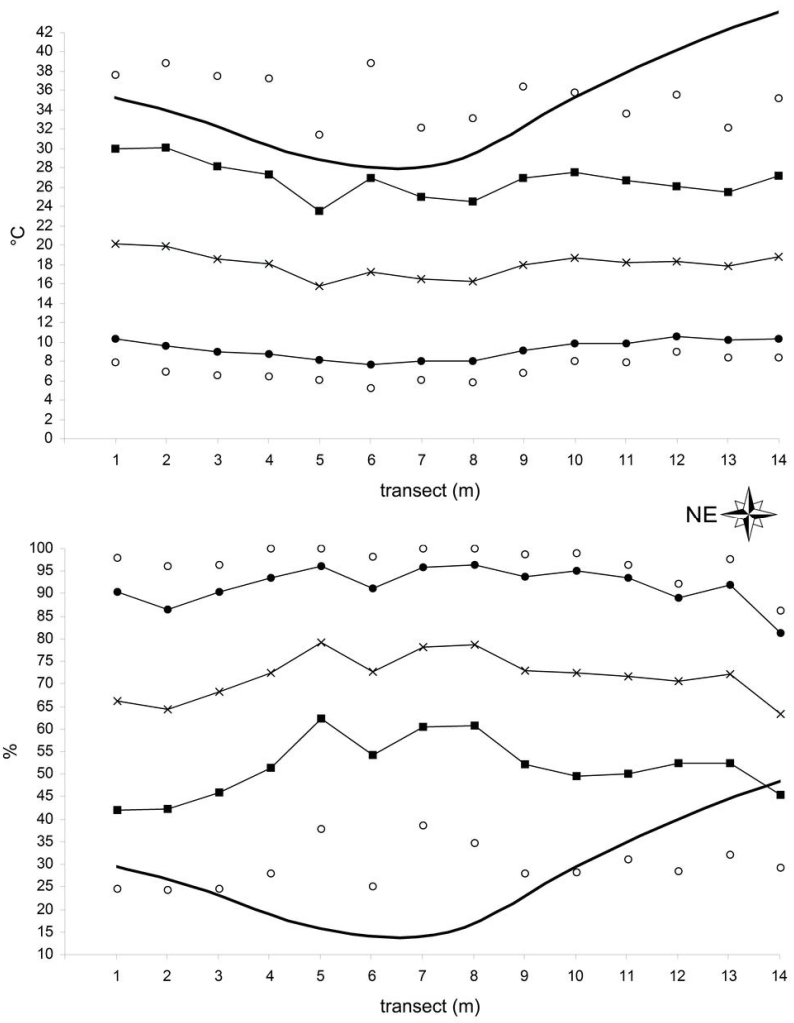
Fig. 6. Air temperature and air humidity values along the transect of the dune slack of Bugac (September 25–26, 2012). Notations: ○: minimum and maximum air temperature (DMinAT, DMaxAT) and air humidity (DMinAH, DmaxAH) values; ■: mean daytime air temperature (MDtAT) and air humidity (MDtAH) values; ×: mean daily air temperature (MDAT) and air humidity (MDAH) values; ●: mean nighttime air temperature (MNtAT) and air humidity (MNtAH) values.
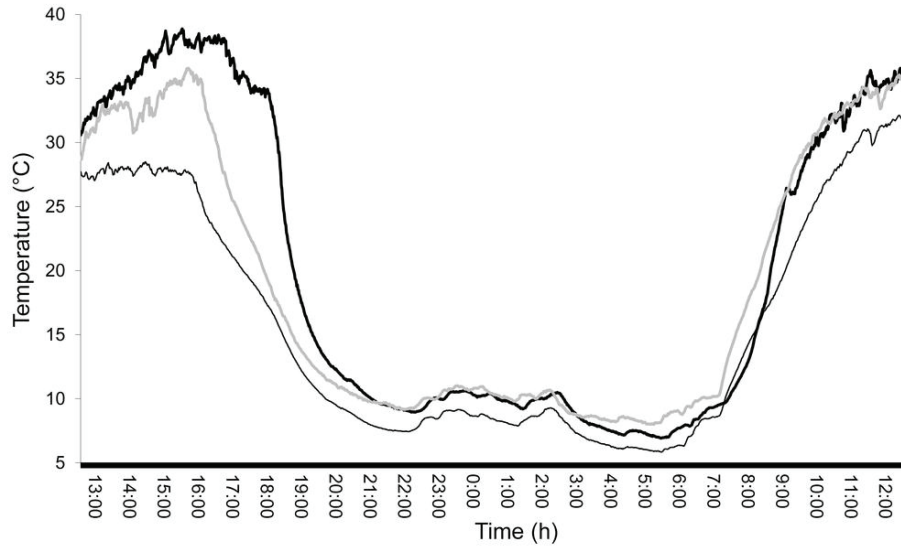
Fig. 7. Air temperature values in three plots along the transect (southwest-facing dune slope: thick black line; bottom of the dune slack: thin line; northeast-facing dune slope: thick grey line) of the dune slack of Bugac, measured over a 24-hour period (September 25–26, 2012).
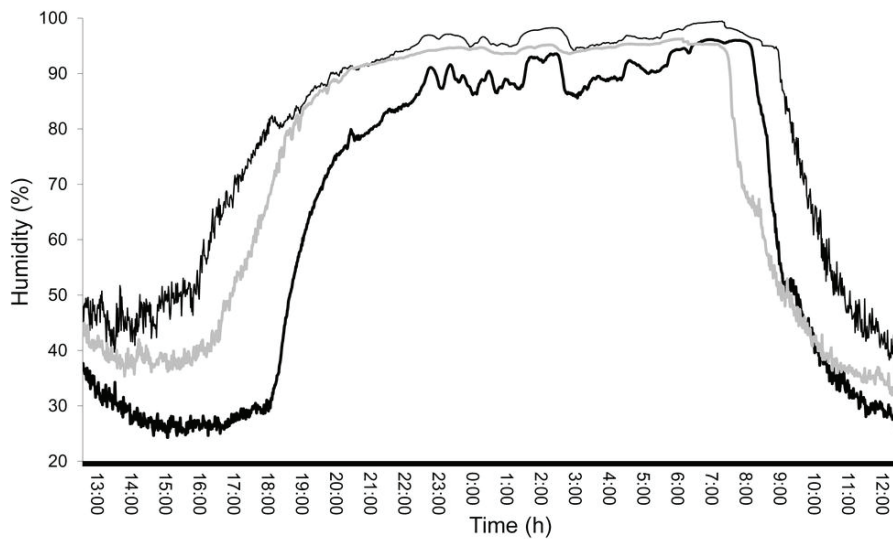
Fig. 8. Air humidity values in three plots along the transect (southwest-facing dune slope: thick black line; bottom of the dune slack: thin line; northeast-facing dune slope: thick grey line) of the dune slack of Bugac, measured over a 24-hour period (September 25–26, 2012).

Eryngium campestre L., *Festuca pseudovina* Hack., *Galium verum* L., *Stipa borysthenica* Klokov ex Prokudin, and *Thymus pannonicus* All. were the most frequent (>80%) species on the upper dune slopes, and *Carex liparicarpos* Gaudin, *Galium verum*, *Potentilla arenaria* Borkh., *Stipa borysthenica*, and

Thymus pannonicus in the bottom of the dune slack. Species that occurred only on the bottom of the dune slack include *Elymus repens* (L.) Gould, *Hieracium umbellatum* L., *Poa angustifolia* L., *Scirpoides holoschoenus* (L.) Soják, *Silene conica* L., *Salix rosmarinifolia* L. and *Trinia ramosissima* (Fisch.) W.D.J. Koch. According to the ANOVA, species number of the upper slopes and the dune slack did not differ significantly (P=0.245). Species of open sandy grasslands and closed sandy grasslands dominate all parts of the transect. However, fen species were only detected in the bottom of the dune slack with a proportion of 1.3% (*Fig. 9*).
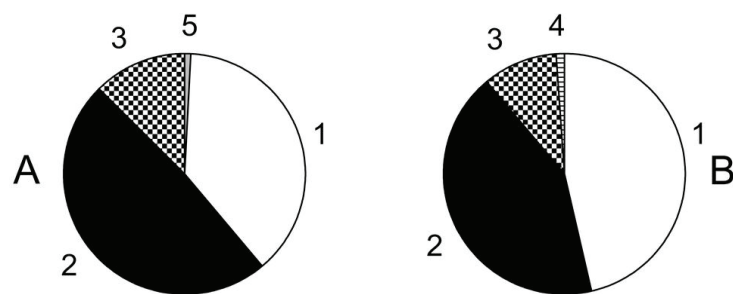
Fig. 9. Proportions of the different species groups of the dune slopes (A) and of the bottom of the dune slack (B). 1: species of closed sandy grasslands; 2: species of open sandy grasslands; 3: indifferent species; 4: fen species; 5: weed species.

3.3. Results of the multivariate analyses

The DCA-ordinations of the samples show a strong gradient along axis 1 with a very high species turnover in the sinkhole (eigenvalue: 0.63, gradient length: 4.4 S.D. units) and lower species turnover along the slopes of the dune slack (eigenvalue: 0.36, gradient length: 2.7 S.D. units).

The explanatory power of climatic variables in the 'one-predictor' db-RDA models is shown in *Table 1*. In Bugac, all of the 6 variables were significant, since they had P values under 0.001, 0.005, or 0.05, even though their F values varied considerably. In the Mecsek Mountains, there were minor differences among the variables in the explained variation, and all of them were found highly significant (<0.001). Both in Bugac and the Mecsek Mountains, MNtAT explained more variation of the vegetation than the daytime measurements, although the difference was negligible in the case of the Mecsek Mountains. MDAT had higher F values than MDtAT or MNtAT. Regarding air humidity, MDAH explained the most variation in both sites.

The 'two-predictor' models included MDAT and MDAH (*Figs. 10–11*). These models explained significant variation in both sites (*Table 2*).
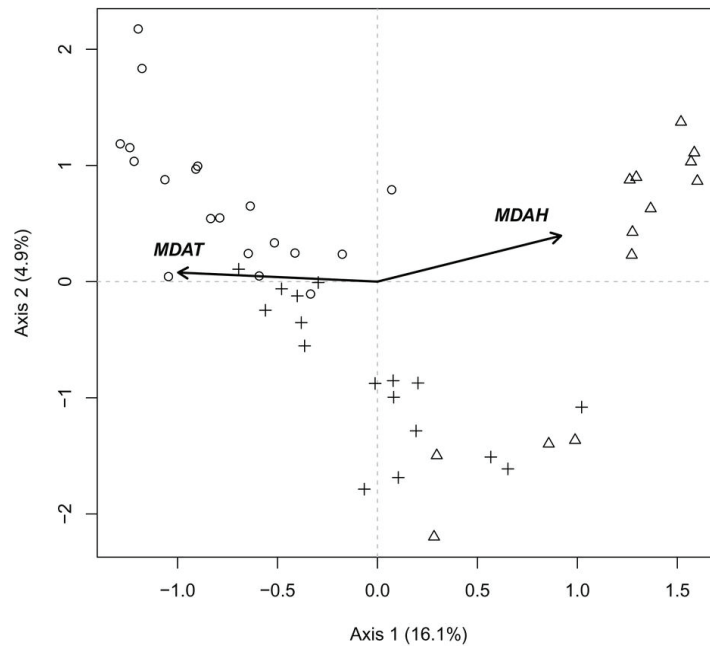
Fig. 10. Distance-based redundancy analysis diagram with 50 plots (○: plots of the south-facing sinkhole slope, +: plots of the north-facing sinkhole slope, △: plots of the sinkhole bottom) and environmental variables (MDAT: mean daily air temperature, MDAH: mean daily air humidity) of the Mecsek Mountains.
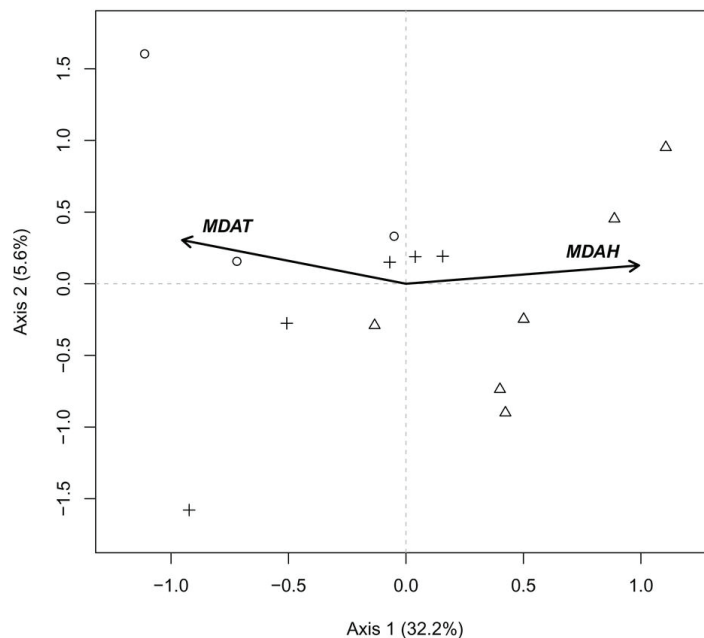
Fig. 11. Distance-based redundancy analysis diagram with 14 plots (○: plots of the southwest-facing dune slope, +: plots of the northeast-facing dune slope, △: plots of the bottom of the dune slack) and environmental variables (MDAT: mean daily air temperature, MDAH: mean daily air humidity) of Bugac.

4. Discussion

We studied the relationship between the spatial pattern of microclimatic parameters and the vegetation of natural habitat islands in Hungary. Our study yielded three main results. Firstly, the investigated habitat islands can be recognized as refugia for many species adapted to various climatic conditions. Secondly, the different elements of microclimate differently influenced the distribution of plant species. Thirdly, forest cover has a strong mitigating effect not only on air temperature but also on air humidity.

Previous studies showed that karst sinkholes may considerably affect the flora and vegetation of the karst surfaces (*Antonić et al.*, 2001; *Bátori et al.*, 2013; *Geiger*, 1950). As semi-isolated enclaves, lower sinkhole slopes and sinkhole bottoms are very important from a nature conservation point of view (*Bacsó* and *Zólyomi*, 1934; *Bátori et al.*, 2011; *Beck-Mannagetta*, 1906). Since they often harbor species that are very rare or missing from the surrounding habitats, they can be considered habitat islands (*Bátori et al.*, 2012b). We also found remarkable floristic differences between the bottom and the higher slopes of the investigated sinkhole. Many plants, in particular cool-adapted species, are restricted to the bottom of the sinkhole, where appropriate microclimatic conditions exist. The mean daily, daytime, and nighttime air temperature and air humidity values explained almost the same variation of species composition along the vegetation gradient. This is due to the mitigating effect of the forest, which reduces the differences between daytime and nighttime air temperatures and between daytime and nighttime air humidities at the same altitude (*Lehmann*, 1970; *Antonić et al.*, 1997). The extreme temperature value of the sinkhole bottom (DMaxAT: 32.1 °C) can be explained with the rate of canopy closure. Here, similarly to the ravine forests of deep valleys, frequent mass soil movements on the steep and wet slopes uproot trees allowing increased insolation through the sparse canopy. However, after this short high temperature period, the temperature of the sinkhole bottom decreased significantly, while the upper slopes remained warmer. Since karst surfaces are sensitive to climatic changes (*Loáiciga et al.*, 2000), sinkholes may play an essential role in reducing extinction rate of plant species, as they did in earlier geological times as well. The literature offers many excellent examples where sinkholes are mentioned as key habitats for cold-stage relicts and high mountain species (*Bátori et al.*, 2006; *Horvat*, 1953; *Lazarević et al.*, 2009). If we accept that the beech production optimum will shift in the future toward the pole and from lower elevation to higher elevation, and beech mortality risk will increase in its lower distribution range (*Hlásny et al.*, 2011; *Peñuelas et al.*, 2007; *Sykes* and *Prentice*, 1996), we can conclude that the beech forests of the Mecsek Mountains have a high chance of surviving in deep sinkholes for longer periods. In contrast, oak production and mortality seems almost insensitive to climate change in Central Europe, and in addition, the increasing oak production in elevations above 400 m a.s.l.

suggests a potential upward expansion of oak forests in the future (*Hlásny et al.*, 2011). This also means that the vegetation zones of sinkholes may shift toward the deeper sinkhole parts. This, in the worst scenario, would mean that vegetation types of the lowest parts (unable to shift even more downwards) may disappear from the sinkholes. A study by *Gargano et al.* (2010) on snow-bed vegetation of sinkholes has also showed that climate change would favor the replacement of snow-adapted species with the mesic ones occurring in surrounding habitats. In forest landscapes, climate-induced species replacement may be more striking if the forests are actively managed. Therefore, forest management should focus on maintaining forests not only in sinkholes but also in surrounding areas in order to moderate the potential impacts of climate change on karst surfaces.

Sand-dune slacks of the Kiskunság Sand Ridge play a similar role in preserving plant species as the karst sinkholes of mountain areas. Remnant patches of dune slacks have a high conservation value, since they support ancient steppe and fen vegetation with characteristic species such as *Carex flacca* Schreb., *Carex humilis* Leyss., *Chrysopogon gryllus* (L.) Trin., *Molinia caerulea* (L.) Moench, *Salix rosmarinifolia*, *Scirpoides holoschoenus*, *Schoenus nigricans* L., and *Thalictrum simplex* L. (*Borhidi*, 2012; *Molnár*, 2003). As our results revealed, microclimate is an important factor in structuring dune slack communities, although impacts of the nighttime and daytime air humidity and temperature values differ significantly (*Körmöczi et al.*, 1981). Although the investigated dune slack is much shallower than the karst sinkhole, its air humidity and temperature regimes are more extreme due to the large diurnal temperature variation, which can be explained by the different vegetation physiognomy. In the different parts of the world, several factors have been shown to contribute to the species composition changes of dune vegetation. The most important factors are the climate change- and human-induced drought (*Körmöczi*, 1991; *Muhs* and *Holliday*, 1995). Since the effect of precipitation and its spatial and temporal distribution are of great importance in xeric habitats (*Margóczi et al.*, 2007; *Thomas et al.*, 2005; *Yizhaq et al.*, 2009), the potential impact of precipitation decline on dune slack vegetation must be taken into consideration. For example, between 1981 and 1993, the average annual precipitation decreased by 16.7% on the Kiskunság Sand Ridge, causing a regional groundwater table decline (*Molnár et al.*, 2003). Apart from the climate change-induced drought, local human activities (e.g., afforestation, artesian and groundwater extraction, draining, hydrocarbon extraction, and intensive farming) also have had a strong negative influence on the groundwater table. A long-term vegetation study by *Tölgyesi* and *Körmöczi* (2012) revealed that both the wetter and drier sections of the dune fields of the Kiskunság are influenced by the water table decline, though most of the shifts were more prominent in the wet section (i.e., dune slack). The vegetation of the dune slack was getting more thermophilous, and its continental character was getting more pronounced. Since

climate change scenarios predict a significant temperature increase and a significant decrease in precipitation in summer for the Kiskunság Sand Ridge (*Bartholy et al.*, 2007), climate change could make the area even more vulnerable to drought and fire (*Blanka et al.*, 2013). Hence, conservation biologists must work on presenting arguments for policy makers and water management authorities in order to reduce the potential impact of drought on natural habitats of the Kiskunság.

As a summary, we have demonstrated the current and potential role of natural habitat islands in preserving different groups of plant species. According to our findings, the current vegetation of habitat islands is highly determined by the elements of microclimate, indicating the different importance of the daily, daytime, and nighttime humidity and temperature regimes. Presumably, these habitat islands will play an important role in mitigating species loss under future climate change. Probably the most important question in relation to the vegetation of natural habitat islands is how we can moderate and delay the impacts of climate change on species loss and vegetation replacement.

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Appendix

Table A1. Species composition (presence/absence data) of the plots along the sinkhole transect of the Mecsek Mountains

Part.1.

Plots	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
Species / Sinkhole	South-facing rim and slope																	
Acer campestre						1													
Acer platanoides											1								
Acer pseudoplatanus								1											1
Aconitum vulparia																			
Ajuga reptans							1											1	
Alliaria petiolata												1				1			
Arabis turrita																			
Asarum europaeum						1	1	1								1	1	1	1
Athyrium filix-femina																			
Atropa belladonna																			
Brachypodium sylvaticum		1	1																
Bromus ramosus agg.			1				1		1										
Campanula rapunculoides	1	1				1													
Cardamine impatiens																			
Carex pilosa	1	1	1	1	1	1	1	1	1	1	1	1	1			1	1	1	
Carex sylvatica																			
Carpinus betulus		1				1	1	1	1			1	1	1	1	1		1	1
Circaea lutetiana																			
Clematis vitalba																			1
Clinopodium vulgare							1												
Convallaria majalis			1																
Crataegus laevigata																			
Dactylis polygama	1	1	1	1	1	1	1	1	1			1							1
Dryopteris filix-mas																			
Eupatorium cannabinum																			
Euphorbia amygdaloides	1		1	1		1	1		1										
Fagus sylvatica														1	1			1	1
Fallopia dumetorum		1																	1
Festuca drymeja			1		1	1			1	1	1	1	1	1	1				
Fraxinus excelsior			1		1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Fraxinus ornus	1	1	1	1	1	1	1	1	1			1		1	1	1			
Galeobdolon luteum s.l.																		1	
Galium aparine				1												1	1		
Galium odoratum																		1	
Galium schultesii	1																		
Geranium robertianum																			
Geum urbanum																			
Glechoma hirsuta					1														
Hedera helix	1			1	1	1	1	1	1		1						1	1	
Helleborus odorus	1		1																1
Hepatica nobilis			1																
Lathyrus venetus												1						1	1

Plots	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
Species / Sinkhole	**South-facing rim and slope**																		
Lathyrus vernus		1															1	1	
Ligustrum vulgare		1		1	1		1												
Luzula forsteri														1					
Melica uniflora	1	1	1	1	1	1	1	1	1	1	1	1	1		1	1	1	1	1
Mercurialis perennis																			1
Milium effusum																			
Moehringia trinervia																			
Mycelis muralis																			
Paris quadrifolia																			
Polygonatum multiflorum	1			1												1	1	1	
Polystichum aculeatum																			
Polystichum setiferum																			
Primula vulgaris																		1	
Pyrus pyraster																			
Quercus cerris				1		1													
Quercus petraea agg.					1	1				1	1	1							1
Rosa arvensis	1	1	1	1															
Rubus fruticosus agg.																			
Rubus hirtus																			
Rumex sanguineus																			1
Ruscus hypoglossum																			
Sambucus nigra																			1
Solanum dulcamara																			
Sorbus torminalis					1														
Stachys sylvatica																			
Stellaria holostea	1	1	1	1		1	1	1	1	1	1					1	1	1	1
Symphytum tuberosum	1																		
Tilia tomentosa							1	1	1	1	1	1	1	1	1	1	1		
Urtica dioica																			
Veronica montana																			
Viola alba							1												
Viola reichenbachiana							1												

Table A1. (cont.)

Part. 2.

Plots	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50
Species / Sinkhole	**Bottom**													**North-facing rim and slope**																	
Acer campestre			1																										1		
Acer platanoides																										1	1	1			
Acer pseudoplatanus	1		1		1	1	1	1	1	1					1	1															
Aconitum vulparia		1																													
Ajuga reptans																															
Alliaria petiolata		1							1	1		1		1		1									1	1	1	1	1	1	1

Plots	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50
Species / Sinkhole							**Bottom**											**North-facing rim and slope**													
Arabis turrita																										1					
Asarum europaeum		1	1			1	1			1	1				1	1										1	1	1	1	1	
Athyrium filix-femina			1			1	1	1	1	1																					
Atropa belladonna	1					1	1	1																							
Brachypodium sylvaticum			1		1																										
Bromus ramosus agg.						1																						1	1		
Campanula rapunculoides																															
Cardamine impatiens			1																								1	1			1
Carex pilosa																										1	1	1	1	1	1
Carex sylvatica						1																									
Carpinus betulus			1			1	1																								
Circaea lutetiana	1			1	1		1	1		1																					
Clematis vitalba	1					1																									
Clinopodium vulgare																															
Convallaria majalis																															
Crataegus laevigata																															1
Dactylis polygama																											1				
Dryopteris filix-mas			1		1			1	1	1	1																				
Eupatorium cannabinum	1						1	1	1																						
Euphorbia amygdaloides																										1					
Fagus sylvatica																		1													
Fallopia dumetorum																										1					1
Festuca drymeja																															
Fraxinus excelsior	1	1	1	1	1	1	1	1	1	1		1	1		1	1	1	1		1	1	1		1	1	1	1	1	1	1	1
Fraxinus ornus															1				1	1	1	1	1	1	1	1	1	1	1	1	1
Galeobdolon luteum s.l.	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1		1		1	1		1	1	1	1	1		1	1	1
Galium aparine	1			1																											
Galium odoratum									1						1																
Galium schultesii																											1				
Geranium robertianum									1																	1		1			
Geum urbanum																															1
Glechoma hirsuta																															
Hedera helix										1	1	1					1					1				1	1	1			
Helleborus odorus		1	1										1			1										1					
Hepatica nobilis																															1
Lathyrus venetus																															
Lathyrus vernus																											1		1		
Ligustrum vulgare																										1			1	1	1
Luzula forsteri																															
Melica uniflora																										1	1	1	1	1	1
Mercurialis perennis	1		1	1	1	1								1	1	1	1					1				1	1	1	1	1	1
Milium effusum																													1		
Moehringia trinervia						1																							1	1	
Mycelis muralis																										1					
Paris quadrifolia			1																												
Polygonatum multiflorum																															
Polystichum aculeatum							1	1																							
Polystichum setiferum			1																												
Primula vulgaris																															

Plots	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50
Species / Sinkhole	Bottom													North-facing rim and slope																	
Pyrus pyraster	1																														
Quercus cerris																															
Quercus petraea agg.																									1						
Rosa arvensis																										1					
Rubus fruticosus agg.	1					1																									
Rubus hirtus					1	1		1																		1					
Rumex sanguineus	1	1																													
Ruscus hypoglossum													1		1	1					1										
Sambucus nigra				1	1																										
Solanum dulcamara						1	1																								
Sorbus torminalis																															
Stachys sylvatica			1	1	1		1		1																						
Stellaria holostea																												1	1	1	1
Symphytum tuberosum																															
Tilia tomentosa	1									1					1											1					
Urtica dioica	1	1	1	1	1	1	1	1	1	1	1																				
Veronica montana			1			1																									
Viola alba																															
Viola reichenbachiana															1														1		

Table A2. Species composition (presence/absence data) of the plots along the dune slack transect of Bugac

Plots	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Species / Dune slack	Southwest-facing slope			Bottom						Northeast-facing slope				
Achillea pannonica			1	1			1	1	1	1	1	1	1	
Calamagrostis epigeios							1	1		1	1			
Carex liparicarpos			1	1	1	1	1	1	1	1	1	1	1	
Cladonia convoluta	1	1												
Cladonia furcata	1	1	1	1						1	1	1	1	1
Cladonia magyarica		1	1	1					1	1	1	1	1	1
Crepis rhoeadifolia												1		1
Crepis setosa														1
Cynodon dactylon	1	1										1		1
Dianthus pontederae		1	1		1			1		1	1		1	
Elymus repens							1							
Eryngium campestre	1	1	1	1						1	1	1	1	1
Erysimum diffusum										1				
Euphorbia cyparissias						1	1	1	1	1	1		1	
Euphorbia seguieriana							1	1					1	
Falcaria vulgaris												1	1	1
Festuca pseudovina	1	1	1	1		1		1	1	1	1	1	1	1
Festuca vaginata										1		1	1	1
Galium verum		1	1	1	1	1	1	1	1	1	1	1	1	1
Hieracium umbellatum							1	1						

Plots	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Species / Dune slack	**Southwest-facing slope**			**Bottom**						**Northeast-facing slope**				
Kochia laniflora	1													
Koeleria glauca		1				1				1	1	1	1	1
Odontites rubra						1					1			
Phleum phleoides												1		
Poa angustifolia						1	1							
Potentilla arenaria		1	1	1	1	1	1	1	1	1	1	1	1	
Salix rosmarinifolia						1								
Scabiosa ochroleuca						1						1		1
Scirpoides holoschoenus						1	1							
Silene conica						1								
Silene otites			1	1	1			1			1			1
Stipa borysthenica	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Stipa capillata			1	1				1	1	1				1
Thymus pannonicus	1	1	1		1	1	1	1	1	1	1	1	1	
Tortula ruralis	1	1	1	1	1									
Tragopogon dubius			1				1	1			1			
Trinia ramosissima				1				1	1					
Verbascum lychnitis		1	1	1	1				1					1