Ecological niche conservatism shapes the distributions of lichens: geographical segregation does not reflect ecological differentiation

Ekologický konzervatismus nik určuje rozšíření lišejníků – geografická segregace neodpovídá ekologické diferenciaci

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We studied the ecological requirements of two closely related species of lichens, *Solenopsora cesatii* and *S. candicans*, which grow predominantly on basic rocks in natural habitats. We determined the ecological niches they occupy at the centre of their distribution (Mediterranean Basin) where they occur sympatrically and in areas with a continental climate (Western Carpathians and Pannonia) at the limits of their ranges, where they are geographically segregated, in order to assess the level of differentiation across their distributions. Tests of niche equivalency and similarity revealed that the species colonize similar habitats both in the centre and the margin of their ranges, which indicate niche conservatism across their distribution. Geographical segregation between populations of *S. cesatii* and *S. candicans* at the range margin does not reflect niche differentiation, but a lower availability of suitable habitats. For the Western Carpathians, we developed predictive habitat suitability maps using a Climate Space Model based on presence-absence data, which indicated the potential distribution of suitable sites. The reconstruction of habitat suitability under past climatic scenarios indicates presence of suitable sites in Last Inter-Glacial and Mid-Holocene and absence in Last Glacial Maximum. Predictions for the years 2050 and 2070 show horizontal habitat tracking and far fewer suitable sites. This case study is an example of how the conditions at the limits of their range can contribute to the finetuning of the ecological requirements of species.

Keywords: ecological niche, habitat suitability map, Mediterranean, niche overlap, Pannonia, spatial prediction, Western Carpathians

Introduction

The limits of ranges, which can be viewed as barriers, challenge species to face certain ecological disequilibria. These areas may offer habitats with different climatic regimes compared to those at the centre of their range, to which the species respond by niche evolution (Wiens & Donoghue 2004). Hence, differentiation in geographically and ecologically peripheral populations may contribute to the diversification of new biological entities (Thompson et al. 2005). On the other hand, if the areas offer the same or very similar habitats compared to the centre of the range, species can survive over a long evolutionary

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period and their ecological niches do not change. Ecological niche conservatism is defined as the retention of niche-related ecological traits over time and it has many implications for the understanding of fundamental patterns and processes, such as species richness and fitness, and invasions (Wiens et al. 2010). Different perspectives of ecological niche conservatism has already been studied, such as assessment of niche characteristics across species distributional ranges or over different time periods, and by using phylogenetic comparative methods and comparing the native and invaded ranges of invasive species (Peterson 2011). Therefore, understanding species ecological requirements in terms of ecological conservatism or innovation is important. Moreover, identification of species ecological niches is also important for applied ecology and conservation biology.

The projection of ecological niches into geographic space enables one to construct habitat suitability maps (HSMs), which indicate habitats that are potentially suitable for a particular species (Franklin 2009, Sillero 2011). The detection of environments that are suitable for rare taxa could be beneficial for identifying areas where these species could potentially exist (Pfab & Witkowski 1997, Edwards et al. 2005, Khimoun et al. 2013). Moreover, its projection into a different time frame may help in the reconstruction or predict possible pathways for species dispersal or extinction in the past and future (Wiens & Donoghue 2004).

Lichens are symbiotic organisms that have large geographic ranges and wide ecological niches; however many of them are associated with microsite characteristics that are themselves rare and patchy in time and space (Edwards et al. 2005). There are predictive HSMs for various rare and widespread lichens (Edwards et al. 2005, Bolliger et al. 2007, McCune & Printzen 2011, Wiersma & Skinner 2011, Carlsen et al. 2012, Shrestha et al. 2012, Szczepańska et al. 2015), which have been used to predict the response of lichens to future climate changes (Ellis et al. 2007a, b).

In this study we model the ecological niches of two closely related species: *Solenopsora cesatii* (A. Massal.) Zahlbr. and *S. candicans* (Dicks.) J. Steiner (*Leprocaulaceae*). Their distribution is mainly confined to the Mediterranean and Mediterranean-Atlantic region, but they also occur in areas with more continental conditions in the Western Carpathians and Pannonian Basin (Guttová et al. 2014). In the centres of their distributions, both species are fairly abundant and mostly share the same habitats and localities. On the other hand, at the limits of their ranges in areas with continental climates (RL_c) they are scarcer and tend to occur in different sites reflecting parapatry. We aim to determine the width of ecological plasticity of these species; whether they are associated with different habitat conditions in RL_c and whether this influences their parapatric distribution. Therefore, in order to determine the diversity of ecological niches occupied by the central and marginal populations, their overlap, equivalency and similarity, we selected two regions: Mediterranean (centre) vs. Western Carpathians and Pannonian Basin (RL_c). We address the following questions: (i) Do these two closely related taxa show niche differentiation across their distributional ranges? (ii) Do these species colonize novel habitats in RL_c or do they show niche conservatism? (iii) What is the current spatial extent of suitable environmental conditions for these species; how were these conditions distributed in the past and what can be expected under future climatic scenarios?

Material and methods

Species studied

The genus *Solenopsora* includes up to 25 species, which occur predominantly in the Mediterranean, Macaronesian and Madrean floristic regions. With eight species and two subspecies, the Mediterranean Basin is considered as a diversity hotspot for this genus (Guttová et al. 2014). The distribution of the majority of these species is restricted only to the Mediterranean region, but some taxa have a wider biogeographic amplitude extending to European regions with a more continental climate. Such examples are the two species studied, *S. cesatii* and *S. candicans.*

These species form a placodioid thallus with crustose centre and extended marginal, radiating lobes without lower cortex, not firmly attached to the substrate. The fungal partner is an ascomycete reproducing sexually by means of one-septate ascospores. Vegetative reproduction is unknown. The photosynthetic partner belongs to the green chlorococcoid algae (Ryan & Timdal 2002). The species grow on basic rocks (limestone, dolomite, conglomerate; in case of *S. candicans* also basalt) on steep slopes with rocky outcrops, cliffs or towers. Their distribution is predominantly confined to Mediterranean-type ecosystems (Ochoa-Hueso et al. 2011). In the case of *S. cesatii*, current distribution data indicate that its overall range is essentially disjunctive. *Solenopsora cesatii* has been recorded from the European part of the Mediterranean with outposts in the Western Carpathians and Black Sea coast (Fig. 1A). *Solenopsora candicans* has wider distribution. It has been reported from the largest of the world's five Mediterranean-climate regions: Mediterranean Basin, California and Australia. It is also known from European areas with continental (e.g. the Western Carpathians, Pannonia, Central European Highlands) or oceanic temperate climates (e.g. the Black Sea coast, British Isles) (see Fig. 1B).

The species studied occur in two types of biomes, open habitats including gorges, rocky macchia, steppe and forest steppe biotopes, or/and broadleaved, mixed and evergreen forests of Mediterranean and temperate zones. They especially inhabit natural rocky outcrops, but can colonize also man-made surfaces (e. g. rocky walls, monuments or castle ruins). In RL_c, the species are geographically separated abutting only in one contact zone. In contrast to the Mediterranean, their continental habitats are exclusively natural, mostly inaccessible, unsuitable for management and stable regarding succession. *Solenopsora cesatii* is distributed along the central belt of the Western Carpathians with extensions into northern parts. It especially inhabits calcareous ridges and rocky cliffs in highland relief, which is forested by natural oak, beech or pine woods. It occurs frequently in relictual calcareous habitats that have been glacial refugia for numerous moisture demanding temperate organisms: snails, small mammals, trees and herbaceous plants (Ložek 1980, 2006, Deffontaine et al. 2005, Kuneš et al. 2008, Kramp et al. 2009, Slovák et al. 2012, Kučera et al. 2013). The species *S. candicans* is fairly rare in the area of RL_c. It is confined to southern foothills of the Western Carpathians and Pannonian Basin, especially, well-developed karst landscapes with sun-exposed outcrops and cliffs. The species grows in dry/steppic grassland and scrubland habitats surrounded by oak and beech woods, and less in relictual fragments of natural pine stands. Despite the habitats of these two species differing in some features, most of the localities are contact zones for the occurrence of montane (e.g. *Arabis alpina* L., *Clematis alpina* (L.) Mill., *Campanula carpatica* Jacq., *Cyclamen purpurascens* subsp. *immaculatum* (Hrabětová) Halda et

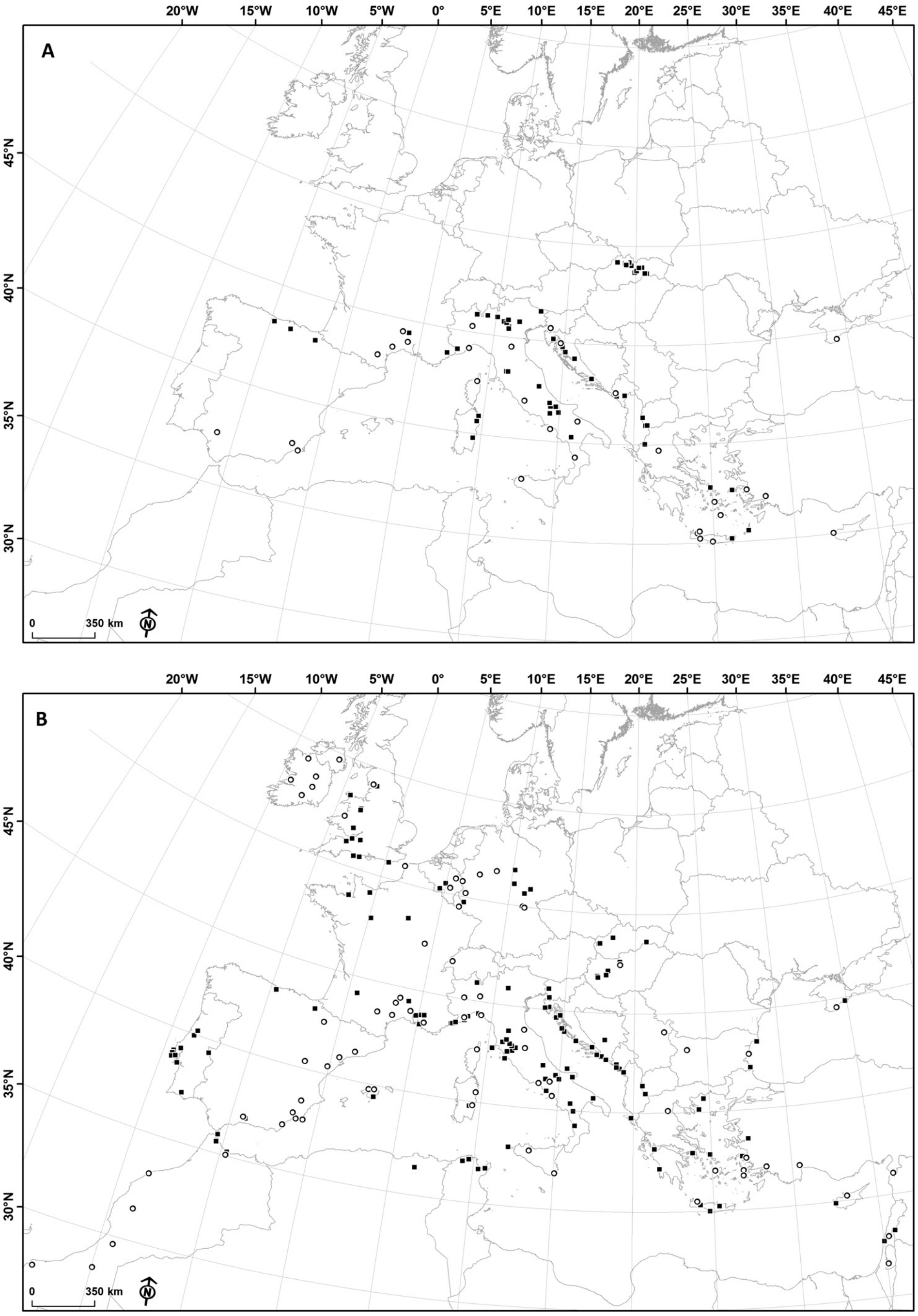

Fig. 1. – Distribution of *Solenopsora cesatii* (A) and *S. candicans* (B) based on revised herbarium specimens (solid squares) and published data (empty circles). For the detailed description of data sources see Material and methods – Species records and Electronic Appendix 1.

Soják, etc.) and thermophilous species (e.g. *Allium flavum* L., *Berberis vulgaris* L., *Cephalanthera rubra* (L.) Rich., *Dianthus praecox* subsp. *lumnitzeri* (Wiesb.) Kmeťová, *Dracocephalum austriacum* L., *Pulsatilla grandis* Wender., etc.).

Study area

The study area is divided into two main regions based on the aims of this study: distributional centre of species of *Solenopsora* covering the Mediterranean Basin and limits of their ranges with a continental climate (RL_c), including the Western Carpathians (Bielczyk et al. 2004), the westernmost parts of the Eastern Carpathians (with western Carpathian flora according to Futák 1984) and Pannonia mountains in the orographic units Bakony, Balaton-felvidék, Budai-hegység and Keszthelyi-hegység. The Mediterranean Basin is considered to be the area of geographic distribution of olive, *Olea europaea* L. (Ponti et al. 2014), with characteristics of Mediterranean-type ecosystem (Ochoa-Hueso et al. 2011). The borders of the regions studied were defined based on recently recorded occurrences of species of *Solenopsora*.

For modelling maps of habitat suitability, for reconstructing the past and predicting the future, we focused on a restricted part of the Western Carpathians covering the area of Slovakia as there are high-resolution data available for this area. We excluded marginal regions biogeographically belonging to the Western Carpathians or the Pannonia (Austria, Czech Republic, Poland and Hungary), for which there are no published references of the occurrence of species of *Solenopsora*, and (i) where only absence data were collected during field surveys in 2010–2014 and (ii) where the geological bedrock is unsuitable.

Species records

The distributional ranges of *Solenopsora candicans* and *S. cesatii* (Fig. 1) were assessed based on our own field surveys from 1999 up to the present (specimens deposited in SAV), on a revision of herbarium specimens (BC, BM, BP, BR, CLU, FH, FI, G, GZU, LISU, PRA, PRC, PRM, SAV, O, TO, TSB, VER, W, herb. I. Pišút, herb. J. Malíček) and published records (see Electronic Appendix 1). Published records are included in order to complete a general overview of the distribution of the species, therefore data from unspecified localities or from localities for which there were already revised herbarium specimens were not reported. Regarding the overseas occurrence of *S. candicans* in California, USA (Hasse 1913, 1914, Millspaugh & Nuttall 1923) and New South Wales, Australia (McCarthy 2016), this species is mentioned as occurring in these regions but these records are rare, uncertain and importantly, there are no herbarium specimens associated with them (Knudsen & Kocourková 2010, Brendan Lepschi CANB and Skye C. Coffey PERTH, personal communication). Therefore, these data were not included in this study.

For the modelling of niche overlap, occurrence data from the Mediterranean Basin, the Western Carpathians and Pannonia were collected in the field and during the revision of the herbarium material mentioned above. For this analysis, 79 records of *S. candicans* and 49 records of *S. cesatii* were used (see Electronic Appendix 1).

For the modelling of HSMs in the Western Carpathians, we verified the presence or absence in potential areas of the species studied based on expert assessment during recent field surveys from 2010 to 2015. Apart from the recorded presence data, the absence data were carefully considered to avoid false absences due to insufficient exploration before they were used in the modelling. In the case of larger potential areas, we visited the localities several times and inspected suitable microniches carefully. For models with high predictive abilities the presence/absence approach is preferred over presence-only approaches (Brotons et al. 2004, MacLeod et al. 2008). The dataset for *S. cesatii* consists of 25 presences, 20 absences and that of *S. candicans* of 6 presences and 39 absences (see Electronic Appendix 2).

Environmental variables used to model niche overlap

For modelling niche overlap, we used the following environmental variables (Table 1):

Climate. A primary dataset consisting of long-term monthly and yearly averages of air temperature and long-term monthly and yearly averages of vertical atmospheric precipitation, preprocessed by GeoModel Solar (Bratislava, Slovakia, www.solargis.info). For a detailed description of data sources and resolution (air temperature and precipitation) see Zozomová-Lihová et al. (2015). Primary data are summarized as means, standard deviations, minimum and maximum values, which were used in the analyses.

Continentality. Thermal and ombrical continentality were calculated to reveal how the regional climate is affected by continental or oceanic air masses. The continentality is expressed as a percentage, where 100% indicates the most continental climate. Thermal continentality was calculated according to the Gorczyński index (Gorczyński 1920) and ombrical continentality according to the index proposed by Hrudička (1933).

Geomorphology. Altitude, aspect and inclination were derived from terrain altitude models (source: The Shuttle Radar Topography Mission data [SRTM3], available at http://srtm.usgs.gov) with a resolution of 30 arc-sec (~90 m). For the purpose of the analysis, aspect values were linearized and rescaled to range from 0 to 1 such that: S = 0, SE and SW = 0.25, E and W = 0.5, NE and NW = 0.75, N = 1.

Modelling of environmental niche overlap, niche equivalency and similarity

We defined the realized environmental niches of the species studied in the centre of their distribution (Mediterranean Basin), in RL_c (the Western Carpathians and Pannonia) and in the entire area. We compared niche overlap between species (within regions) and within species (between regions) using the techniques developed by Warren et al. (2008) and Broennimann et al. (2012). As a first step, principal component analysis (PCA) of the correlation matrix was used to define the environmental space. Among numerous ordination techniques or species distribution models, this approach is the most accurate for quantifying niche overlap (Broennimann et al. 2012). The environmental space was bounded by the minimum and maximum values of environmental parameters recorded in the area and depicted by the first two principal components since only these accounted for a nontrivial amount of variance in the data, as indicated by a broken-stick model. Subsequently, the environmental space was divided into a grid of 100 × 100 cells with each cell corresponding to a unique combination of environmental conditions recorded for one or more sites in the area. The recorded occurrences of species were converted into densities (occurrences grouped per grid cell) and a kernel density function used to calculate the smoothed density of occurrences in each cell. The kernel density estimates considerably

Table 1. – List of environmental variables used to model the niche overlap of *Solenopsora cesatii* and *S. candicans* in the Mediterranean and at the limits of their range with continental climate (RL$_c$) and their minimal (min), maximal (max) and mean (ā) values. The same abbreviations (Abbrev.) for the variables are also used in Figs 4 and 5.

Environmental variable	Abbrev.	Unit	RL$_c$						Mediterranean					
			cesatii			*candicans*			*cesatii*			*candicans*		
			min	max	ā	min	max	ā	min	max	ā	min	max	ā
Altitude	ALT	m	169	1028	681	156	480	338	51	1650	634	–14	1146	531
Aspect	ASPECT	–	0.02	0.10	0.43	0.02	0.99	0.45	0.14	1.00	0.49	0.00	1.00	0.46
Inclination	SLOPE	°	2.9	35.2	22.0	6.0	31.9	14.7	1.5	48.9	18.3	0.0	50.2	14.1
Mean annual temperature	TYEAR	°C	5.2	9.3	6.9	8.0	11.1	9.8	4.7	18.4	12.1	9.0	19.4	14.0
Minimum annual temperature	TMIN	°C	–4.0	–1.6	–3.1	–2.6	0.5	–0.8	–2.9	11.6	3.6	–0.1	13.2	5.8
Maximum annual temperature	TMAX	°C	14.8	20.1	17.0	18.5	21.7	20.2	13.0	26.6	21.6	18.7	30.9	23.6
Standard deviation of monthly temperatures	TSD	°C	7.2	8.2	7.7	7.7	8.0	7.9	5.0	7.7	6.7	5.0	8.2	6.6
Mean annual precipitation	PYEAR	mm	655	1076	818	580	708	646	466	2206	1165	186	2206	865
Minimum annual precipitation	PMIN	mm	31	58	42	32	42	35	1	79	46	2	79	28
Maximum annual precipitation	PMAX	mm	92	138	109	71	98	82	78	317	155	27	317	121
Standard deviation of monthly precipitations	PSD	mm	19	28	22	11	22	16	18	88	33	6	88	29
Thermal continentality	GOR	%	15.2	37.2	26.8	15.8	37.2	24.0	11.3	47.6	37.7	34.4	74.63	44.53
Ombrical continentality	OMB	%	15.2	27.8	20.0	14.4	39.9	30.1	–11.2	13.4	3.6	–9.4	16.0	0.8

improve bias by calculating niche overlap and may help to avoid unrealistic gaps in species niches due to low sampling effort (Broennimann et al. 2012, Guisan et al. 2012). The smoothed densities of occurrences were plotted into the PCA grid to visualize the realized niches of the species.

To calculate niche overlap, Schoener's D index (Schoener 1968) was chosen for its simplicity, comparability and good performance in estimating niche overlaps from species occurrences (Warren et al. 2008, Rödder & Engler 2011). Schoener's D measures the overall match between two species occupancies across all cells in the gridded environmental space and varies from 0 (no overlap) to 1 (complete overlap). We calculated Schoener's D using densities of species corrected for environmental availability in order to ensure unbiased comparison between regions where environments are not equally available (Broennimann et al. 2012). The measures of niche overlap were used to test the hypotheses of niche equivalency and niche similarity (Warren et al. 2008) using the randomization procedures outlined by Broennimann et al. (2012). Test of niche equivalency assesses the null hypothesis that two environmental niches are identical by random reshuffling of occurrences between species or regions. This process was repeated 100 times to create a null distribution of Schoener's D. We rejected the null hypothesis when the recorded value of niche overlap was smaller than would be expected by chance, i.e. when the overlap value was smaller than 95% of simulated values (a one-sided test). A rejection of the niche equivalency hypothesis means that two niches are not statistically identical. When the equivalency hypothesis was rejected, we used a less stringent test of niche similarity. The test addresses the null hypothesis that two ecological niches are no more similar than expected by chance, which is defined by the null distribution of Schoener's D generated from 100 random reallocations of one of the two niches among available environments. Again, one-tailed probability was calculated while the null hypothesis was rejected when the recorded overlap was greater than 95% of simulated values. A rejection of niche similarity indicates that niches are more similar than random expectation based on the availability of habitats. The niche similarity test can be constructed in two directions, either the first niche predicts the second one (the second niche is randomized) or vice versa. We report both versions of the test except for the comparisons between regions where we tested whether the overlap between the Mediterranean and RL_c is greater than a random distribution at the edge of the species range. Analyses were performed in R v3.2.0 (R Core Team 2015) using the library ecospat (Broennimann et al. 2015).

Environmental variables used to model HSMs

We constructed habitat suitability maps of the species in the Western Carpathians using high-resolution data on climate, geology, geomorphology and land cover (Table 2):

Climate. The primary dataset consists of the long-term monthly and yearly averages of air temperature and long-term monthly and yearly averages of vertical atmospheric precipitation based on available records for the period 1961–1990 with a resolution of 500 m horizontally and approximately 100 m vertically. The data were provided by the Slovak Hydrometeorological Institute (Bratislava, Slovakia).

Geology. Out of the complete list of layers of geological structure (Digital geological map of the Slovak Republic at scale 1: 50 000; Káčer 2005), we selected a grid layer of calcareous substrates. We further included particular volcanic substrates due to the tendency of *S. candicans* to colonize these substrates (Farkas et al. 2011). In total, we selected 851 units (limestone, dolomite, conglomerate, basalt) for *S. candicans* and 830 units (limestone, dolomite, conglomerate) for *S. cesatii*.

Geomorphology. Digital elevation model (DEM; Geodetic and Cartographic Institute 2004) with resolution of 10 m (scale 1: 10 000) was used to obtain data on altitude, aspect and slope in the Geographic Resources Analysis Support System (GRASS) of the Geographic Information System (GIS) environment version 7.1. To obtain more accurate HSMs, we used the thematic layer of rock outcrops occurrence generated from forest stand maps (provided by National Forest Centre, www.nlcsk.org).

Land cover. Vegetation and other bio-physical surface types and human activity, such as the use of a parcel of land generated by CORINE Land Cover 2000 (valid to 2006, data provided by Slovak Environmental Agency) at a scale of 1:50 000. The map includes minimum cartographic units of 25 ha with a grid resolution 3 arc-sec (on average 70 to 90 m).

Table 2. – List of environmental variables used to produce maps of habitat suitability (HSMs) of *Solenopsora cesatii* and *S. candicans* in the Western Carpathians.

Environmental variable	Unit
Geological substrate	qualitative data
Rock outcrops occurrence	qualitative data
Land cover	qualitative data
Altitude	m
Aspect	°
Inclination	°
Mean annual temperature	°C
Monthly average temperature	°C
Mean annual precipitation	mm
Monthly average precipitation	mm

Modelling of current HSMs

We predicted a distribution of the suitable habitats of these species in the Western Carpathians. The maps were developed using the Climate Space Model (CSM; Robertson et al. 2001), with modification for the presence-absence approach (absence model subtracted from real presence model). CSM is a correlative modelling technique that produces a probability response surface in terms of a suite of predictor environmental variables. It is regarded as an efficient PCA-based modelling method for predicting environmental suitability based on small sample sizes (Stockwell & Peterson 2002). The selection process in this algorithm implementation is based on the broken-stick cutoff, where any component with an eigenvalue less than two standard deviations above a randomized sample is discarded (Robertson et al. 2001). Redundant, strongly correlated climatic variables ($|r| \geq 0.8$) were excluded prior to the analysis. The final model included the following variables: annual averages of air temperature and vertical precipitation, mean temperature in the coldest month (January), in the warmest month (July) and mean precipitation in the wettest month (February). The raster maps of geology and rock outcrops occurrence, as well as land cover data were applied using the module r.mask (GRASS GIS) to filter out the areas with suitable substrates for analysis. The results of this modelling algorithm are presented as probability values for each grid cell implemented into a geographical space. For better clarity of display, we divided pixels of the final maps with occurrence probability of 1-100 into 1/3 standard deviation. The last field of pixels are shown on the maps as points.

Accuracy of the predicted HSMs was evaluated using AUC (Area Under the Curve) derived from ROC (Receiver Operating Characteristics) plots, which provides an effective indicator of model performance independent of a particular decision threshold (Fielding & Bell 1997). The value of the AUC ranges between 0.5 and 1, where 0.5 indicates randomness and 1 indicates a high prediction success (Robertson et al. 2001).

Reconstruction of HSMs for the past and prediction of the future

Using a combination of climatic data based on current species distributions in the Western Carpathians, we reconstructed the distribution of suitable habitats in the past and predicted their future distribution within this area. Climatic suitability was projected onto mapped estimates of historical and future climates with a resolution of 30 arc-sec. The data were obtained from CMIP5 of the World Climate Research Program (Taylor et al. 2012) and calibrated using WorldClim 1.4 as a baseline (Hijmans et al. 2005), except for the Last Inter-Glacial climate model (source: Otto-Bliesner et al. 2006). For projection of the current climatic niches to the past, we used climate estimates for the Mid-Holocene (~ 6000 years BP), the Last Glacial Maximum (~ 22,000 years BP) and the Last Inter-Glacial period (~ 120,000–140,000 years BP). For predictions of the future, we used climate estimates for the years 2050 (average for 2041–2060) and 2070 (average for 2061–2080) based on two possible greenhouse gas scenarios: minimal rcp2.6 (Weyant et al. 2009) and maximal rcp8.5 (Riahi et al. 2011). Assuming that geology and rock outcrop occurrences remain similar over time, for all models we used their raster maps to filter out the areas with suitable substrates using the module r.mask in GRASS GIS environment. The final maps display points indicating climatic suitability within the range of likelihood 91–100% for *S. cesatii* and 92–99% for *S. candicans*. All reconstructions were made based on current species niches and the analyses do not take into account the possibility of their altering over time as consequence of evolution.

Results

Ecological niches in the Mediterranean central part and at the limits of the ranges with a continental climate (RL_c)

The ecological niches of both species are wider at the centre of their range than at RL_c (Table 1). Almost all parameters reach their minimal and maximal limits in the Mediterranean except for mean annual temperatures (TYEAR), minimum annual temperatures (TMIN), maximum annual temperatures (TMAX), thermal continentality (GOR) and ombrical continentality (OMB), which reaching their extreme values for one or both species at RL_c. Mean values of most parameters are lower at RL_c than at the centre of their range, except for OMB, which reaches higher mean values at RL_c. Considering RL_c, *Solenopsora cesatii* grows mainly in the foothills of higher mountain systems such as Tatry Mts and Nízke Tatry Mts (mean value 681 m), with mean TYEAR 6.9 °C, mean

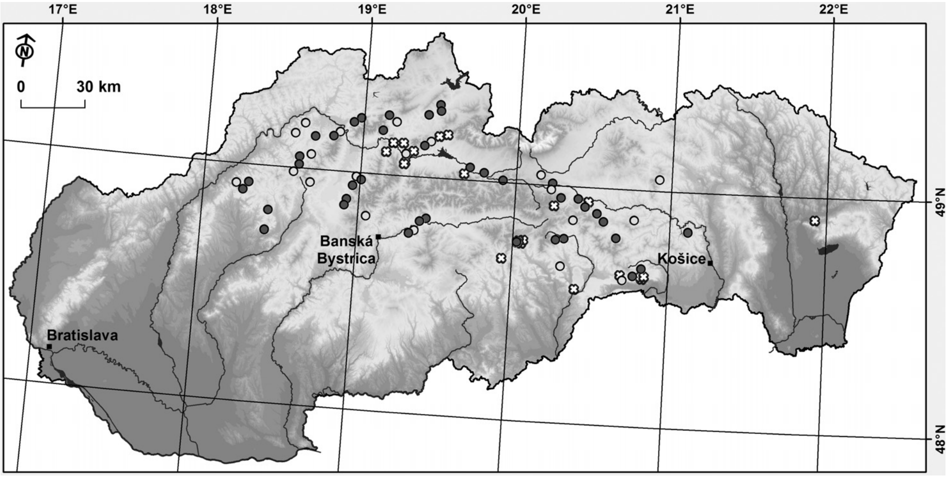

Fig. 2. – Recent habitat suitability map of *Solenopsora cesatii* in the Western Carpathians. White crosses correspond to real occurrence data; solid circles represent modelled localities (probability of occurrence: light grey colour 91–95%, dark grey colour 96–100%).

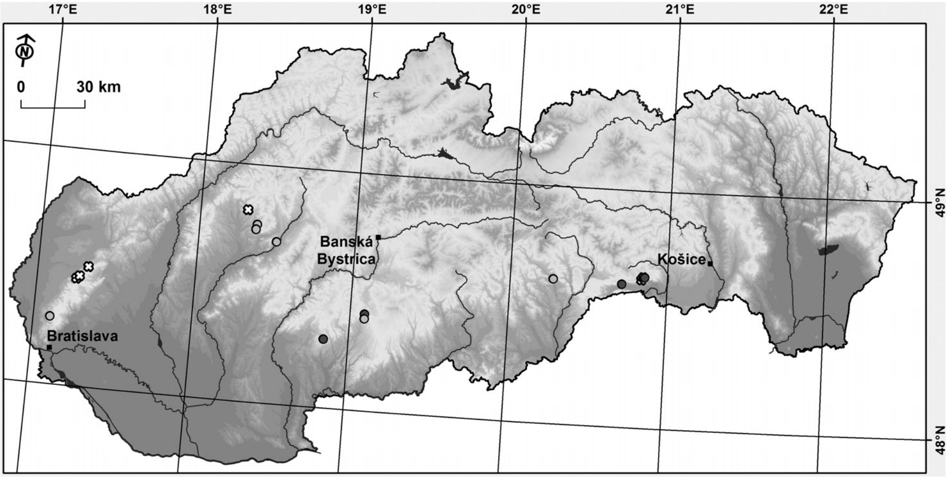

Fig. 3. – Recent habitat suitability map of *Solenopsora candicans* in the Western Carpathians. White crosses correspond to real occurrence data; solid circles represent modelled localities (probability of occurrence: light grey colour 92–95%, dark grey colour 96–99%).

TMIN –3.1 °C and mean annual precipitation (PYEAR) 818 mm (Table 1), and is geographically concentrated in the north-central part of Slovakia (white crosses in Fig. 2). *Solenospora candicans* occurs mainly at lower altitudes, in uplands with a mean altitude of 338 m in the south and western part of the country (white crosses in Fig. 3). These sites are warmer (mean TYEAR 9.8 °C, mean TMIN –0.8 °C) and less humid (mean PYEAR 646 mm; Table 1) compared to the localities of *S. cesatii*.

Table 3. – Results of niche equivalency and similarity tests for pairwise comparisons between and within *Solenospora* species in the centre of their distribution (Mediterranean), at the limits of their range with a continental climate (RL$_c$) and in the entire area. Observed niche overlaps (Schoener's D), ranges of simulated overlap values under null hypothesis and one-tailed probabilities (in parentheses) are displayed. Results significant at $\alpha = 5\%$ are highlighted in bold.

Between species	D	Equivalency	Similarity (*S. candicans* predicting *S. cesatii*)	Similarity (*S. cesatii* predicting *S. candicans*)
Entire area	0.53	**0.75–0.93 (0.010)**	**0.05–0.30 (0.010)**	**< 0.01-0.29 (0.010)**
Mediterranean	0.55	**0.70–0.92 (0.010)**	**< 0.01–0.27 (0.010)**	**< 0.01-0.21 (0.010)**
RL$_c$	0.32	**0.59–0.88 (0.010)**	0.18–0.51 (0.624)	0.02-0.43 (0.287)
Between regions	D	Equivalency	Similarity (Mediterranean predicting RL$_c$)	
S. candicans	0.01	**0.69–0.96 (0.010)**	**<0.01–0.01 (0.010)**	
S. cesatii	0.03	**0.59–0.93 (0.010)**	**<0.01–0.02 (0.010)**	

Niche overlap, niche equivalency and similarity

The niche overlap between species was intermediate over the whole area (D = 0.52) and Mediterranean centre of distribution (D = 0.55) and relatively low at RL$_c$ (D = 0.32). Regardless of region, niche equivalency tests revealed that the species occupied statistically non-identical ecological niches (Table 3). The niches were separated mainly along the temperature-continentality gradient (Fig. 4). In general, *S. candicans* prefers sites with higher temperatures and lower values of ombrical continentality, while the niche of *S. cesatii* is shifted towards a colder environment and higher values of ombrical continentality (see Electronic Appendix 3). However, niche similarity tests showed that niches of the species over the entire area and the Mediterranean, respectively, were more similar to each other than random expectation (Table 3). For the remaining comparison, the overlap of ecological niches at RL$_c$ was not significantly different from the null expectation. Failure to reject the null hypothesis does not, however, indicate niche divergence but that the two niches cannot be distinguished from each other relatively to the available environment in the region; i.e. the niche overlap between species is explained by differences in the available environmental conditions.

Testing differences between regions (range centre vs. RL$_c$), niche equivalency hypothesis was rejected for both species (Table 3). The very low values of niche overlap (D = 0.03 and 0.01) evidently result from the restricted environmental conditions available at RL$_c$ (Fig. 5). Despite the low D values, niches in the regions are significantly more similar than expected by chance, meaning that the environmental conditions at the sites occupied by the species at RL$_c$ are more similar to the conditions occupied at the centre of their range than expected given the habitat availability (rejection of the null hypothesis in similarity tests). Apparently, the species do not colonize novel habitats at RL$_c$, which indicates conservatism of their ecological niches.

Occurrence of suitable habitats in the Western Carpathians

Results of the habitat suitability map (HSMs) modelling are presented in Figs 2 and 3. Concerning the evaluation of their performance, high AUC values (*S. cesatii* 0.82, *S. candicans* 0.87) indicate a good fit of the models to the independent test localities,

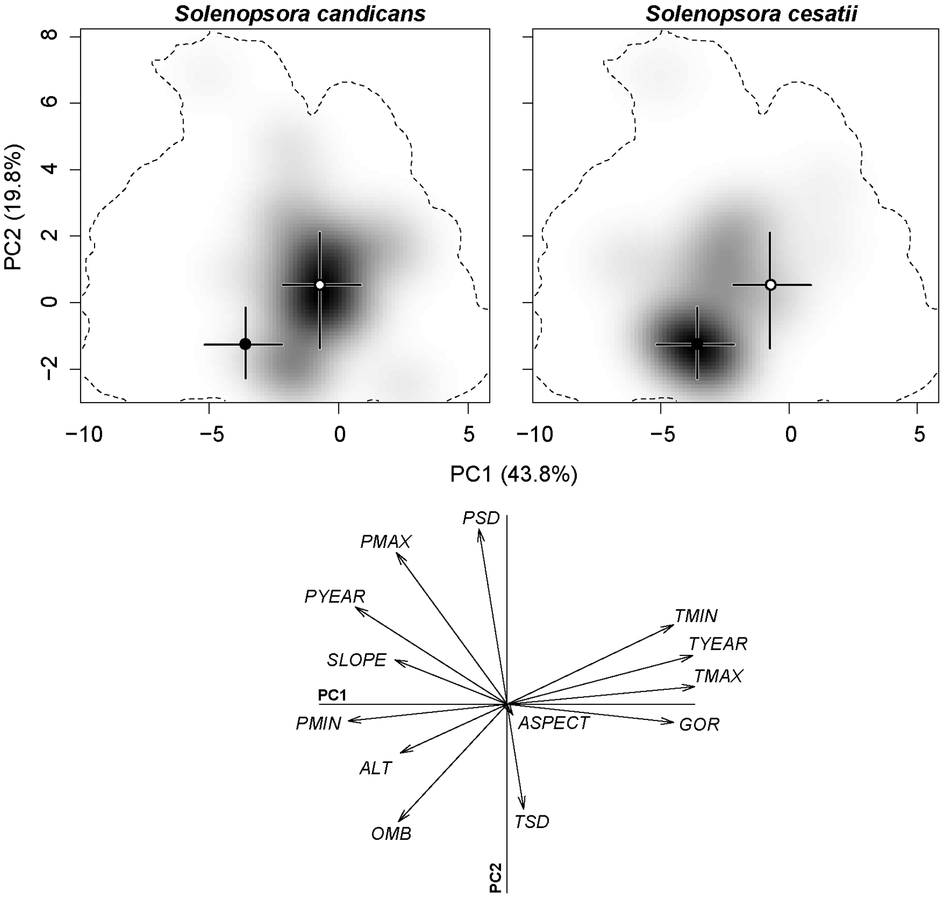

Fig. 4. – Environmental niche of *Solenopsora candicans* (empty circles) and *S. cesatii* (solid circles) in principal component space of the entire area studied. Grey shading is proportional to density of the species occurrence while a white background colour indicates the environmental conditions in which the species were not recorded. Dashed lines indicate available environmental space. Points and whiskers represent centroids (median density) and key habitats (density > 0.5) in which the estimated occurrence densities were recorded, respectively. Arrows indicate the contribution of each variable to the principal components. Variance explained by the components is given in parentheses. The abbreviations of the variables are given in Table 1.

which in turn indicate that the modelling technique performs well. The HSM for *S. cesatii* (Fig. 2) predicts 59 localities as suitable for this species. The predicted localities are broadly distributed in the Inner Western Carpathians with local northern extension to the central Beskydy Mts region. They are mainly in the submontane zone. Most of them are in foothills at altitudes of 510–877 m with all types of aspects. Slope inclination varies from plain surface up to 42°. The localities are characterized by TYEAR 5.6–6.9 °C and PYEAR 672–1090 mm. Predicted HSM for *S. candicans* (Fig. 3) indicates 10 localities with suitable habitats for this species. Unlike the predictions for *S. cesatii*, these sites are restricted to the southern part of the Inner Western Carpathians, close to the border with the Pannonian Basin. The localities are in upland zone at altitudes of 357–581 m, especially

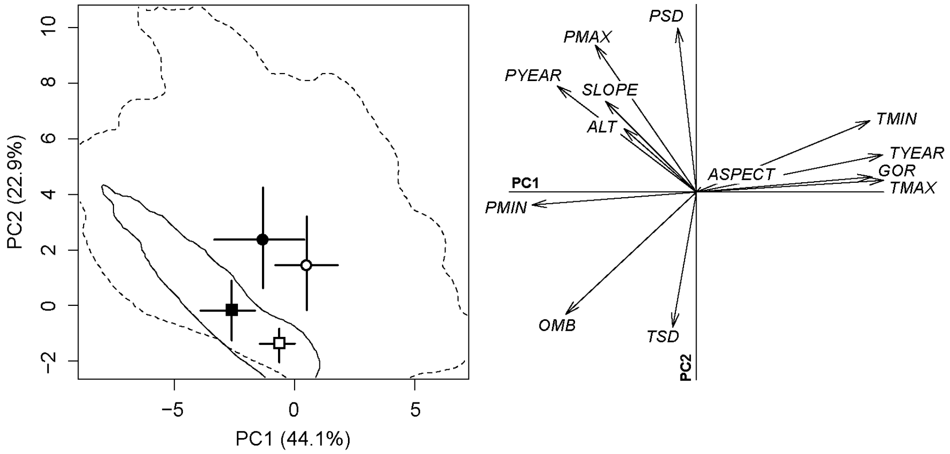

Fig. 5. – Comparison of the environmental niches of *Solenopsora candicans* (empty shapes) and *S. cesatii* (solid shapes) at the centre of their Mediterranean distribution (circles) and RL_c (squares). Lines indicate available environmental space at centre of their Mediterranean distribution (dashed) and RL_c (solid). Points and whiskers represent niche centroids (median density) and key habitats (densities > 0.5) of the estimated occurrence densities, respectively. Arrows indicate the contribution of each variable to the principal components. Variance explained by the components is given in parentheses. The abbreviations of the variables are given in Table 1.

those with south-western and south-eastern aspects and slope inclination from 13.7° to 26.0°. The values of TYEAR and PYEAR vary in range between 7.2–8.3 °C and 643–771 mm, respectively.

These analyses confirmed one real and disclosed two new potential contact zones of the species studied, all on the edges of their potential distributions within upland and submontane belts. These predicted localities are not geographically and ecologically identical. They are distributed approximately from 1.5 km up to 12 km from each other and differ in habitat conditions. Suitable habitats for *S. cesatii* in potential contact zones are at altitudes of 662–828 m with a northern aspect, inclination 1.8–32.9°, TYEAR 6.0–6.6 °C, PYEAR 834–908 mm, and for *S. candicans* at altitudes of 357–581 m with mainly a southern aspect, inclination 19.4–25.5°, TYEAR 7.5–8.3 °C and PYEAR 708–771 mm.

Reconstruction of habitats that were suitable in the past

The projection of the current climatic niches to the Mid-Holocene and Last Inter-Glacial climate revealed the existence of suitable habitats for both species in the Western Carpathians (see Electronic Appendices 4–6). Nevertheless, they were significantly restricted compared to their current distribution. The results of reconstruction for the Last Glacial Maximum revealed no appropriate climatic conditions.

For *S. cesatii*, 18 localities were identified as suitable in the Mid-Holocene, representing 21% of their current real and potential distribution. Reconstructed localities occurred within a similar geographical range to the recently recorded localities. They were distributed in the foothills of high mountains and span the altitudinal range from 377 m to 722 m with mainly south-western and eastern aspects and inclination of 2.5–46.5°. For *S. candicans*, seven suitable localities (44% of current real and potential species distribution habitats) were reconstructed for the Mid-Holocene. They were situated in the southern part of the Inner Western Carpathians, mostly in the Pannonian Basin. They range from 174 m to 492 m above sea level, with a predominantly southern and south-eastern aspect and inclination of 10.5–43.4°.

The distribution of suitable habitats during the Last Inter-Glacial is similar to that in the Mid-Holocene, but with lower abundance. For *S. cesatii* and *S. candicans*, 10 and 2 localities, which represent 12% and 13% of the current real and potential distribution, were identified, respectively.

Prediction of suitable habitats in the future

Predicted future distribution of suitable habitats depends on the selected greenhouse gas scenario (rcp2.6 vs. rcp8.5). Compared with the current distribution, all future predictions show spatial shift towards the east. The distribution of suitable sites is restricted and the currently known western, north-western and south-eastern localities are not predicted for the future.

Considering lower values of emissions (rcp2.6), the distribution is very similar for both time horizons, 2050 (see Electronic Appendices 4, 7) and 2070 (see Electronic Appendices 4, 8). Six localities for habitats of *S. cesatii* are confined to altitudinal ranges from 645 m to 984 m with a mainly southern aspect, 3.1–26.5° inclination and six of the localities for *S. candicans* are associated with altitudes from 366 m to 587 m with a mainly eastern aspect and inclination of 8.5–46.5°. This represents 7% of the current real and potential distribution of *S. cesatii* and 38% of that of *S. candicans*.

Regarding higher emission values (rcp8.5), the number of suitable sites significantly decreases (see Electronic Appendices 4, 9, 10). For *S. cesatii*, one locality is predicted for the year 2050 (1% of their current real and potential distribution), none for 2070 and for *S. candicans*, four localities for 2050 (25%) and three for 2070 (19%).

Discussion

The margins of the ranges of species are usually undersampled compared to the range centre (Sagarin & Gaines 2002). This is also the case for the species investigated and despite extensive biodiversity research, these relatively conspicuous lichens were almost unknown from their range margin (RL_c) (Vězda 1970, Guttová 2000). We overcame this methodological bias by systematic sampling their occurrence data since 1999 and thus filled this gap in their geographical pattern. Due to the limited number of occurrence records in this area, we thought the species could be habitat specialists.

Niche overlap based on current distribution

At the limits of their ranges with continental climate (RL_c), we revealed that the species do not colonize novel habitats in comparison to the Mediterranean Basin. Our results indicate that despite the low level of niche overlap between regions, the species inhabit similar environmental conditions at RL_c as at the centre. Thus, the ecological niches of *S. cesatii* and *S. candicans* are conserved across the studied distributional range. In his review, Peterson (2011) points out that this pattern has already been revealed for more than 90% of the 144 taxa studied, including amphibians, birds, fishes, invertebrates, plants, microbes and viruses. A conserved ecological niche is characteristic also for specialists, such as arctic-alpine plants (Wasof et al. 2015). However, this aspect has not yet been studied in lichens (Leavitt & Lumbsch 2016).

The populations of *S. cesatii* and *S. candicans* in the Mediterranean are more abundant than at RL_c and geographical segregation between the species is not so evident there. Their ecological niches overlap moderately and despite *S. cesatii* generally tending to prefer more humid, sheltered environments and reaching higher altitudes than *S. candicans* (Table 1), the species co-occur in localities with suitable conditions for both of them. At the microhabitat scale based on our field observations, *S. candicans* grows preferably at sites exposed to direct solar radiation (sun-exposed surfaces of rocks) and *S. cesatii* is mostly confined to semi-shaded fissures in rocks. If the species colonizes the exposed surfaces of rocks, they are at least partially sheltered by vegetation. This is in line with the observations of Guisan & Zimmermann (2000) that many species tend to compensate for regional differences in climatic conditions by selecting comparable microsites and by changing their topographic position.

Considering RL_c, geographical segregation of the species investigated does not reflect their ecological differentiation, but, a restricted availability of habitats along bioclimatic gradients that are suitable for both species. Despite the northern regions of the Western Carpathian Mountains have suitable conditions for *S. cesatii* and the southern outskirts for *S. candicans*, habitat suitability maps (HSMs) predict two new potential contact zones. All predicted and real contact zones are situated in upland and submontane belts on peri-Carpathian calcareous slopes, known for the occurrence there of thermophilous biotopes with dealpine flora. Hence, these habitats are enriched by subalpine and alpine elements occasionally occurring at lower altitudes with a cooler and moister microclimate (Janišová & Dúbravková 2010). The co-occurrence of our *Solenopsora* species in such contact zones is therefore highly probable.

Nevertheless, HSMs do not necessarily reflect the real presence of the species, since their long-term survival can also be affected by biotic interactions, human impact, limited dispersal, migration barriers and microclimatic conditions (Pulliam 2000, Anderson et al. 2002, Pigot & Tobias 2013, Zozomová-Lihová et al. 2015). In the case of lichens, their symbiotic nature must also be considered. The availability of suitable photobionts may limit the distributional range, as in the case of *Cetraria aculeata* s.l. (Printzen et al. 2013). The mycobionts of *S. cesatii* and *S. candicans* reproduce by means of sexual ascospores, which have to associate with their photobiont during each reproductive cycle. Some authors suggest potential difficulties for the mode of reproduction of the *Solenopsora* mycobiont related to the scarcity of mature, well developed spores in the asci (Kantvilas 2004, Guttová et al. 2014). Despite these potential difficulties of colonizing suitable habitats, a first field verification of nine randomly selected localities indicated by the *S. cesatii* HSM confirmed the presence of the species in eight of them.

Potential past and predicted future distribution

Because palaeoclimatic modelling may provide information about possible pathways of shifts in species distributions at a large-time scale (Richards et al. 2007, Theissinger et al.

2011), we produced maps of suitable habitats in three past periods in order to reveal possible distributions of these species in the Western Carpathians. Our results indicate that climatic conditions during the Last Inter-Glacial and Mid-Holocene period were suitable for both species, but over a smaller range than currently occupied. Interestingly, the analyses indicate an absence of favourable climatic conditions for both *Solenopsora* species at the south-eastern edge, a recent contact zone (Slovenský kras karst), despite known occurrence of thermophilous species (e.g. *Celtis* sp.) in this area during both interglacial periods (Ložek 2007).

The Last Inter-Glacial in central Europe was characterized by warm, humid and evidently more oceanic climate. These conditions favoured wide afforestation, predominantly by mixed broadleaved forest with termophilous elements (Ložek 2007). It is possible that some of the climatically suitable localities predicted for species of *Solenopsora* were so densely forested that they were ecologically unsuitable. Favourable conditions might have occurred in very restricted open and semi-open xerotherms on extensive rocky outcrops or places with a thin layer of soil, where forest vegetation could not dominate (Hendrych 1984, Ložek 2007).

A similar pattern of afforestation is recorded for the postglacial period, during the climatic optimum in the Mid-Holocene, when temperatures reached their peak and were 2–3 °C higher than at present (Ložek 2007). Recent studies (e.g. Dúbravková & Hajnalová 2012) demonstrate that a continuous landscape of forest was interrupted by primary steppe vegetation with light-demanding species in warmer and drier areas at lower altitudes, on the boundary between the Carpathians and Pannonian Basin. A few forest steppe mosaics are documented for open pine-birch forest (Pokorný et al. 2015), which are preserved from the early postglacial period in the Western Carpathians on calcareous screes (e.g. localities in Veľká Fatra Mts; Ložek 2007). Probably, localities with such conditions and rocky enclaves could harbour suitable habitats for species of *Solenopsora*.

Based on our analysis, climatic conditions between these two periods, during the Last Glacial Maximum, were inhospitable for their occurrence. Therefore we assume that if the species occurred here in the Last Inter-Glacial, they became extinct during the glaciation and recolonized this area in post glacial periods. This scenario is presumed for most thermophilous and temperate species, which survived the glacial periods mostly on peninsulas in the Mediterranean area (Hewitt 1996). However, recent paleoecological, palynological and phylogeographic studies also provide evidence for the persistence of moisture demanding temperate species, which are confined to broadleaved and mixed forests, in small sheltered "cryptic" refugia in the Carpathians (Deffontaine et al. 2005, Kotlík et al. 2006, Ložek 2007, Kramp et al. 2009, Schmitt & Varga 2012, Slovák et al. 2012). The current distribution of the species of *Solenopsora* studied (especially *S. cesatii*) is associated with these localities. Hence, it is questionable whether paleoclimatic reconstruction for the Last Glacial Maximum can detect such small microclimatically favourable sites within an extensive inhospitable area. In order to clarify this point, the analyses of genetic data are crucial for revealing the potential colonization by species of *Solenopsora* and their evolutionary history.

Predictions of the future distribution of *Solenopsora* in the Western Carpathians indicate considerable changes due to the predicted changes in climate. Taking into consideration the expected changes in climatic conditions (mostly an increase in mean annual temperature by more than 2 °C), our results indicate horizontal habitat tracking. HSMs revealed a distributional shift towards the eastern part of the mountains and also the southern part in the case of *S. cesatii*. Nevertheless, considering the future predicted localities, a certain shift to higher altitudes is evident for both species (see Electronic Appendix 4).

The potential future loss of the currently important suitable localities for these species in the west, north-west and south-east could be crucial for their survival in this area. The overall abundance of suitable sites is also likely to decrease significantly. In a changing environment the decrease in favourable conditions may reach 93–100% for *S. cesatii* and 62–81% for *S. candicans*, depending on the attributes of the species (e.g. ecological plasticity, ability to survive in suboptimal conditions, dispersal capacity). In general, if the species are able to adapt, they can persist in the same areas despite changes in environmental conditions (Hoffmann & Sgrò 2011), conversely, there are changes in their distributions or locally they may become extinct (Holt & Gomulkiewicz 2004, Eldredge et al. 2005). This is viewed as pattern of niche conservatism when climatic niches are considered over time (Wiens et al. 2010).

We assume that potential future habitat loss may influence the occurrence of these species in the study area. They are considered to be habitat specialists, which are more likely to respond to environmental changes more markedly than widespread species. Moreover, saxicolous species are used as indicators of environmental change along steep climatic gradients (Insarov et al. 1999, Gupta et al. 2014). However, taking into consideration the physiological properties of lichens (such as slow growth rate, slow metabolism) a delayed response to climate change can be expected.

Conclusion

Based on an examination of the ecological niches of the saxicolous lichens *S. cesatii* and *S. candicans*, we revealed niche conservatism throughout their distribution, previously not reported in lichens. The species colonize similar habitats in range limit with continental climate (RL_c) as in the centre of their distribution, despite the environmental variables recorded in localities at RL_c having limiting values. In this area, the occurrence of the species is geographically segregated (only one real contact and two potential zones recorded). However, we revealed that this segregation reflects a restricted availability of suitable habitats at RL_c rather than a differentiation of ecological niches. The reconstruction of the potential distribution of suitable habitats in the Western Carpathians in the Mid-Holocene and Last Inter-Glacial period revealed that it is possible that both species were present. However, compared with their current distributions, they were significantly restricted. On the other hand, the reconstruction for Last Glacial Maximum indicates that there were no localities with suitable conditions for their occurrence. The predictions of the future distributions of the species of *Solenopsora* indicate they are likely to change markedly due to predicted changes in climate. The number of suitable localities, which currently are important centres of species occurrence, could significantly decrease. Moreover, potential horizontal habitat tracking towards the eastern and southern parts of the mountains may also result in changes in the distributions of these species.

See www.preslia.cz for Electronic Appendices 1–10

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Souhrn

Okraje areálů organismů mohou poskytovat stejné nebo podobné ekologické podmínky v porovnání s centrem jejich rozšíření, nebo se mohou lišit natolik, že druhy odpovídají na dané změny prostřednictvím evoluce ekologických nik. Pokud jsou však podmínky zachovány v čase nebo prostoru, můžeme hovořit o jejich konzervatismu. Konzervatismus ekologických nik v celém areálu byl dosud zaznamenán u různých skupin organismů, nikoli však u lišejníků. Tato studie zkoumá, zda blízce příbuzné studované druhy lišejníků *Solenopsora cesatii* a *S. candicans* vykazují na geografickém okraji areálu ekologickou diferenciaci nebo konzervatismus. Studované druhy patří mezi saxikolní lišejníky, rostoucí především na přirozených stanovištích s vápencovými skalními výchozy. Centrem jejich rozšíření je Mediteránní a Mediteránně-Atlantská oblast, avšak vyskytují se i ve střední Evropě – v Západních Karpatech a Panonii, kde dosahují severovýchodní hranice areálu v kontinentálních podmínkách. Na rozdíl od Mediteránu, kde mají sympatrický výskyt, jsou na okraji areálu jejich lokality geograficky oddělené – v současnosti jsme jejich společný výskyt zaznamenali jen na jedné lokalitě v Slovenském krasu. V této studii analyzujeme jejich ekologické nároky a porovnáváme ekologické niky v centru rozšíření (Mediteránu) a na jeho kontinentálním okraji (Západní Karpaty, Panonie). Zjistili jsme, že oba druhy obsazují na okraji areálu podobná stanoviště jako v centru, což svědčí o konzervatismu jejich ekologických nik. Geografická segregace mezi lokalitami *S. cesatii* a *S. candicans* na okraji areálu odráží omezenou dostupnost vhodných podmínek pro jejich sympatrický výskyt. Na základě klimatických, geomorfologických a geologických dat a údajů z lokalit s výskytem a absencí druhů jsme vytvořili mapy vhodných habitatů a zjistili další dvě potenciálně kontaktní zóny těchto druhů (v Strážovských vrších a v oblasti Jelšavy). Také jsme rekonstruovali mapy vhodných habitatů pro jejich rozšíření v předchozím interglaciálu a středním Holocénu, kde jsme zjistili nižší počet potenciálních lokalit v porovnání se současností. Rekonstrukce pro poslední glaciální maximum nezachytila žádné lokality s vhodnými podmínkami. Predikce výskytu vhodných habitatů na základě klimatických scénářů pro období 2050 a 2070 odhalily potenciální posun lokalit směrem na východ a jih, s výrazným úbytkem lokalit, které v současné době patří k významným střediskům výskytu studovaných druhů v Západních Karpatech. Budoucí klimatické změny tak mohou výrazně ovlivnit rozšíření studovaných lišejníků na tomto území.

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