

# Two-scale modelling of *Saponaria bellidifolia* Sm. (Caryophyllaceae) abundance on limestone outcrops from its northern range periphery (Southeastern Carpathians)

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**Abstract** We modelled the effect of habitat heterogeneity on the abundance of the submediterranean *Saponaria bellidifolia*, a red list species in Romania. The study was designed at two scales: 100 and 0.5 m<sup>2</sup>. At larger scale, generalized additive models and canonical correspondence analysis were used to model the density of ramets, whereas at microscale, binomial logistic regression was employed to model the species' occurrence. *S. bellidifolia* abundance responded sensitively to habitat type (classified as “grassy”, “rocky” and “scree”), rather than to microclimatic variables. At both scales, habitat type was the best predictor of ramet abundance, followed

by slope and vegetation cover. At 0.5 m<sup>2</sup>, soil depth was also a good predictor of species occurrence. The data revealed that screes are the most suitable habitats for hosting relatively large populations of this rare species, because of occasional natural disturbances and presumably lower interspecific competition.

**Keywords** Rare plants · Generalized additive models · Binomial logistic regression · Habitat heterogeneity · Disturbance · Regeneration niche

## Introduction

Towards the periphery of a species' geographical range, plant populations are likely to approach the limit of their ecological tolerance and may face higher extinction risk than in populations nearer to the centre of the range (Antonovics 1976; Lesica and Allendorf 1995; Holt and Gomulkiewicz 2004; Antonovics et al. 2006). Despite this evidence, marginal populations can act as local evolutionary arenas, important for survival and possible future expansion of the species (Holt 2003). One of the evolutionary forces acting at the range periphery is the spatio-temporal variation in habitat resources of plant populations, which can initiate adaptation processes and, simultaneously, changes of range boundaries (Brown et al. 1996; Kawecki et al. 1997; Holt 2003; Holt et al. 2004). The most often cited consequence

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of a heterogeneous environment is the clustered spatial pattern of individuals (Dale 1999). Empirical evidence shows that even microscale variation of the abiotic environment can result in detectable abundance pattern of plant individuals (Bell and Lechowicz 1994; Kephart and Paladino 1997; Baack et al. 2006; Kalliovirta et al. 2006). At mesoscale, topographic variability was found responsible for variation in plant species distribution (Greig-Smith 1961), sometimes acting through soil microclimate or nutrient availability (Burke et al. 1989). Local vegetation mosaics also markedly influence the distribution pattern of individuals within plant populations (Rabotnov 1969; Şuteu et al. 2003; Röder and Kiehl 2006; Baack et al. 2006). However, the importance of these environmental factors in detecting plant species distributions varies with spatial scale (Wiser et al. 1998; Scott et al. 2002; Thuiller et al. 2003). For instance, complex parameters like aspect, altitude or soil type are likely to be important at mesoscale (Thomas et al. 2002), whereas soil depth, vegetation height, competition and open microsite availability exert more influence on microscale processes (Wiser et al. 1996; Pausas et al. 2006).

In the light of this evidence, one would expect that, because of narrowed tolerance, marginal populations would respond more sensitively to local environmental heterogeneity in terms of species abundance. Although exploration of relationship between species ecological tolerances and their landscape-level range margins is an extensive research area in ecology (review in Gaston 2003), small-scale level determinants of distribution and abundance patterns within isolated marginal populations have remained rather unexplored. However, we have evidence for several factors acting at small scale and limiting abundance within marginal populations. These factors are competition with dominant species (Baack et al. 2006), variation in soil chemistry and accumulated litter (Baack et al. 2006), drought and light availability (Arrieta and Suárez 2006), absence of open microsites (Moretti et al. 2008), dispersal (Pausas et al. 2006), etc. A great many of the spatial patterns observed in peripheral plant populations suggest the importance of local, spatial or temporal disturbance regimes to their survival (Meilleur et al. 1997; Nantel and Gagnon 1999; Stokes et al. 2004; Angert 2006; Baack et al. 2006; Moretti et al. 2008). Most

frequently, disturbance events create a “regeneration niche” (Grubb 1977), which facilitates the successful establishment of new recruitment. Its renewal might therefore play a crucial role in persistence of peripheral populations, similarly to other rare plants (Kephart and Paladino 1997; Garcia and Zamora 2003; Kalliovirta et al. 2006).

On cliffs and rock outcrops, the constraining effect of environmental factors on establishment and survival of plants is very strong. These formations harbour several types of microhabitats (e.g. crevices, ledges, soil pockets, screes), which can be selectively exploited by many plant species with different ecological requirements and therefore have outstanding levels of biodiversity (Davis 1951; Cooper 1997; Larson et al. 2000; Clements et al. 2006). Evidently their variable spatial environment also operates on individual plant populations and might determine clumped distribution and abundance patterns, depending on the ecological requirements and competitive abilities of the species. Microtopography, seed bank availability and biotic interactions are amongst the strongest factors in influencing the assembly of plant communities in these extreme habitats (Davis 1951; Houle and Phillips 1989; Booth and Larson 1998; Kuntz and Larson 2006a, b and references therein).

Scree cones, born at the foot of rockslides, are highly unstable and stressful habitats, where stochastic processes like substrate shifting and rock weathering represent natural disturbance events that shape grasslands heterogeneity (Fisher 1952; Rejmánek et al. 2004). The role of preserving a great number of rare and relict species has been attributed to these habitats, due to their peculiar geomorphological and microclimatic characteristics (Boşcaiu 1971; Kun 1998). Indeed, recent empirical studies have demonstrated that they facilitate the coexistence of both dominant and competitively weaker rare species, depending on the extent of disturbance and their successional maturity (Rejmánek et al. 2004). From a population perspective, disturbance events on screes represent a frequent renewal of the regeneration niche and this would make these habitats suitable for the persistence of peripheral populations.

Therefore, cliffs, rock outcrops and screes are suitable for analysing the small-scale ecological response of peripheral plant populations in terms of their abundance. Detailed microhabitat models for

peripheral populations confined to rocky environments, however, are still very few in number.

In this context, our study aimed to detect the relationships between environmental variables and local distribution patterns of the rupicolous pioneer *Saponaria bellidifolia* on two isolated outcrops from the Southeastern Carpathians (Romania). We looked for limiting or facilitating environmental variables acting within these northernmost peripheral populations. Our hypothesis was that microtopography, naturally disturbed habitats and the absence of dominant competitors should account for most of the spatial variability of the target species within the studied limestone outcrops. At larger scale we expected to reveal mostly the effect of topography, disturbance and topoclimate on ramet abundance. With the small-scale approach we hoped to detect additional factors that could act within the presumed regeneration niche of this rare species.

## Materials and methods

### Study species

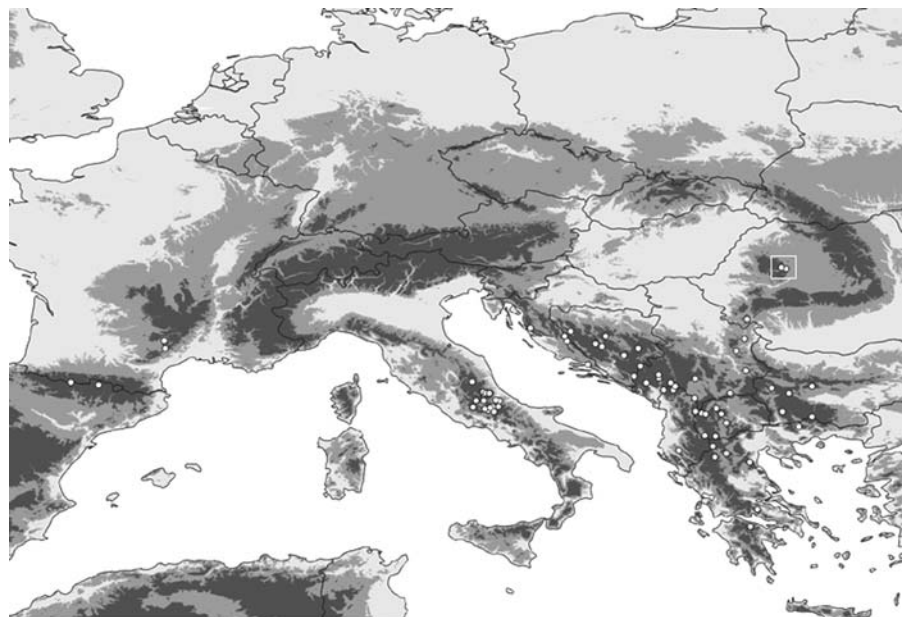
*Saponaria bellidifolia* Sm. (*Caryophyllaceae*) is a submediterranean mountain species with disjunct distribution, but strongly concentrated on the Balkan Peninsula (Jalas and Suominen 1986). The

northernmost isolated populations are in the Apuseni Mountains from Southeastern Carpathians (Romania), where they are confined to warm, south-exposed slopes of limestone and dolomite outcrops. Here the species' individuals grow in several open grassland communities, dominated by *Sesleria rigida* Heuff. ex Rchb., *Festuca pallens* Host, *Carex humilis* Leyss. or *Stipa joannis* Čelak. It is a long-lived chamaephyte, with a characteristic branching rhizome below the soil surface. Clonal reproduction is limited to division of senescent ramets. Seed dispersal is mainly by gravity. According to Rabinowitz's classification of rarity forms (1986) and the National Red List (Oltean et al. 1994), *S. bellidifolia* is rare and locally abundant in the Romanian Carpathians.

### Site description

We conducted our field research on two limestone outcrops from the Romanian Carpathians (Pinet and Runc Gorges) (Fig. 1). The localities were ideal for this study because the habitats were heterogeneous, and *S. bellidifolia* was abundant and patchily distributed. The outcrop elevation is 1,215 m (Pinet) and 931 m (Runc Gorge), respectively. The south-oriented outcrop faces host three major habitat types: steep slopes with ledges and unbroken rocks dominated mainly by the endemic *Sesleria rigida*, scree cones resulting from weathering processes,

**Fig. 1** Distribution of *Saponaria bellidifolia* Sm. in Europe (literature and herbarium data). Study areas (Pinet and Runc Gorges) are shown within the square



dominated mainly by *Festuca pallens*, and less-steep, grassy habitats, dominated mainly by *Carex humilis* and locally by *Stipa joannis*.

### Sampling design and data collection

The extent of the sampled area was 4.3 km<sup>2</sup> in Pinet and 3.2 km<sup>2</sup> in Runc Gorge. As on these relatively small outcrops the shift between different habitat types happen at a approximately 10–20 m and the mean diameter of *S. bellidifolia* ramets is approximately 14 cm, a 10 × 10 m mesoscale and 0.5 × 0.5 m microscale sampling were designed for the study. The larger plots were picked from the meshes of a 10 × 10 m grid, following the horizontal transects along altitude contour lines. Only meshes with homogenous habitat conditions were sampled, while transitory ones were skipped. Within each plot all *S. bellidifolia* ramets were counted. The 10 × 10 m plots were then subsampled for measuring ecological parameters and recording floristic composition, by a phytosociological relevé (Central-European Phytosociological School, Braun-Blanquet 1964) performed on a 4 × 4 m quadrat placed randomly. Within each 4 × 4 m quadrat the following variables were recorded: species cover class, dominant habitat type (grassy, scree or rocky), total vascular vegetation cover, total moss cover, soil depth, aspect and slope. A total of 63 samples were thus collected and GPS referenced within the two outcrops (28 samples in Pinet and 35 in Runc Gorges). Subsequently, one 0.5 × 0.5 m fine-scale sample was taken within each 4 × 4 m quadrat for microhabitat parameters measurement. This microplot was centred on a *S. bellidifolia* individual whenever it was present or was taken randomly when the species was missing. The following variables were registered at this fine scale: presence–absence of the target species, main habitat type (as in the large sampling units), total vascular vegetation cover, total moss cover, vegetation height, soil depth, aspect, slope, pH and soil moisture.

Species cover classes (0–1, 1–10, 10–25, 25–50, 50–75, 75–100%) were visually estimated based on the scale as defined by Tüxen and Ellenberg (1937). Total vascular and moss species covers were estimated visually in percentages. The slope was measured with a clinometer, and was expressed in degrees. Average soil depth and vegetation height were based on four measurements placed in the

corners and one in the centre of the plot. Soil samples were collected from the top 15 cm of soil below the litter layer, at least 5 days after the last rain. pH samples were airdried, sieved and analysed with the pH-meter. Soil moisture samples were kept in a high-temperature dry closet at 105°C for 24 h until constant weight was reached. Soil moisture was expressed in percentages based on the difference between the initial and dry weights divided by the former.

### Data transformation

For data analysis purpose, species cover classes were converted into percentages, equating them with the class midpoint. Instead of standard aspect data, we used the folded aspect for heat load (FA-HL) at both scales, expressed in degrees and calculated following McCune and Keon (2002). Heat load (HL) and Potential Incident Solar Radiation (PISR) were also calculated at both scales, following the same authors.

### Exploratory data analyses

Analysis of variance (ANOVA) was used to determine whether significant differences existed between the main habitat types of *S. bellidifolia* (grassy, rocky and scree) with respect to continuous environmental and population variables at 10 × 10 m and 0.5 × 0.5 m scales. As not all data were normally distributed, the Kruskal–Wallis H-test based on rank transformation was employed for the analysis. The pairwise comparisons between habitat parameters were computed using the exact Mann-Whitney post hoc test based on Monte Carlo simulation with 100,000 permutations and sequential Bonferroni correction (Holm 1979) was applied.

At 10 × 10 m scale, standard and partial Spearman correlations across all habitats were also calculated in order to explore the relationship between ramet density and environmental variables.

At 0.5 × 0.5 m scale, Fisher's exact test was computed to detect significant associations between habitat types and *S. bellidifolia* presence.

### Abundance data modelling at 10 × 10 m scale

Generalized Additive Models (GAM, Hastie and Tibshirani 1990; Yee and Mitchell 1991) and

Canonical Correspondence Analysis (CCA, ter Braak 1987; Palmer 1993) were computed to model the density of *S. bellidifolia* based on environmental variables. GAM allows a rather flexible specification of the response depending on the covariates. Continuous covariates were specified as smooth functions using thin plate regression splines (TPRS). As the response variable is a positive integer (count data) with non-constant variance, we assumed a Poisson distribution. Although there might be consistent departure from a Poisson distribution with the estimated  $\mu = 18$ , the dispersion was assessed as the Generalized Cross Validation (GCV) score, avoiding this way over- or under-smoothing. The flexibility and convenience of GAM comes with the prices of less exact inference. For the smoothed continuous variables the calculated *P*-values are approximate at best, so that we opted for graphical examination of the smoothed terms together with the associated confidence bands.

The CCA analysis was used to assess the separation of habitat types in the reduced ordination space, based on floristic and environmental matrices. Among variables previously used in the GAM analysis, habitat type was not involved into analysis, in order to emphasize the clear-out effect of the remainder variables. Rare species were downweighted. Significance of individual explanatory variables and of canonical ordination axes were assessed using 1,000 unrestricted Monte-Carlo permutation tests. Variables that were not significant at 0.05 alpha probability level in a model, initially including all variables, were dropped from the final data sets. *S. bellidifolia* abundance pattern was explored through contour plots based on a Generalized Additive Model (GAM), assuming a Poisson distribution of *S. bellidifolia* count data. Model selection was based on Akaike Information Criterion (AIC).

#### Occurrence data modelling at $0.5 \times 0.5$ m scale

Binomial Logistic Regression was used to model the probability of *S. bellidifolia* occurrence as a function of environmental variables. In the analysis, we opted for a stepwise variable selection strategy based on Akaike Information Criterion (AIC). We also tested whether there is evidence against the removal of variables by Likelihood Ratio Test. To assess the effect of the final covariates on the removed ones, the final multivariate

model was extended by adding one removed covariate and fitting a new extended multivariate model. The parameter estimates, the regression coefficients and associated statistics of dispersion were then compared with the parameter estimates of the univariate models. Genuine changes in magnitude or a change in sign indicate strong effect of the final variables on the removed ones, presumably due to multicollinearity (high correlation between the predictor variables). This implies that the regression coefficients of the variables are highly correlated as well, therefore the estimation is not consistent and coefficient estimates change erratically in response to changes in the model. As an external validating measure of the final model, Receiver Operating Characteristic (ROC) curve and the associated Area Under the ROC-curve (AUC) were used. Values close to 1 indicate a good classification accuracy of the model, whereas values close to 0.5 points towards a random classification.

GAM and logistic regression analyses were carried out using the R software v2.61 (R Development Core Team 2007) based on Faraway (2006) and Wood (2006). GAM was fitted using the *mgcv* 1.3–29 package of R. CCA analysis was performed in Canoco v4.5 (ter Braak 1987). All other analyses were computed in SAS v9.1.3 (SAS Institute 2005).

## Results

### Habitat type distinctness

All investigated parameters, except FA-HL and HL, were significantly different between the three main habitats of *S. bellidifolia* at both  $0.5 \times 0.5$  m and  $10 \times 10$  m scale. PISR values were also significantly different, but only at small scale. Grassy habitats had significantly higher values of vegetation and moss cover and soil depth at both scales. The high slope values registered in rocky habitats at both scales differed only from grassy habitats at large scale and from both grassy habitats and screes at small scale. The distinctness of the three habitat types was revealed also by the floristic composition of relevés, rather well separated in the CCA ordination space (Fig. 3). Among variables measured only at  $0.5 \times 0.5$  m scale, vegetation height and soil moisture were significantly higher in grassy habitats, while soil pH was significantly higher on screes (Table 1).



*Saponaria bellidifolia* abundance at the community scale (10 × 10 m)

According to the GAM model, habitat type significantly influenced the density of *S. bellidifolia* at the 10 × 10 m scale. Setting rocky habitat as a baseline habitat type, we recorded significant changes for both scree and grassy habitat types. Switching from rocky habitat to scree had a large positive influence on ramet density ( $\beta \pm 1SE$ :  $3.221 \pm 0.479$ ,  $t = 6.719$ ,  $P < 0.0001$ ). Grassy habitats also supported a higher number of individuals ( $\beta \pm 1SE$ :  $1.966 \pm 0.591$ ,  $t = 3.327$ ,  $P = 0.00157$ ). Indeed, *S. bellidifolia*

density varied largely between habitat types, but significant differences were registered only between screes and the other two habitats (Table 1). In addition to habitat type, two smoothed predictors (vegetation cover and slope) seemed to influence the abundance of *S. bellidifolia*. The species had the highest density at intermediate vegetation cover and slope values, which were registered on screes (Fig. 2a, b; Table 1). While the approximate *P*-value shows a genuine effect of vegetation cover ( $F = 3.286$ ,  $P = 0.0078$ ), the slope effect has only marginal significance ( $F = 1.993$ ,  $P = 0.0941$ ). This model explains 81.2% of the null deviance and 77%

**Table 1** Summary statistics (*M* = median, LCL/UCL = lower/upper confidence limits for the median, *N*-sample size) by habitat type, Kruskal–Wallis (*H<sub>c</sub>*) and Fisher statistics for

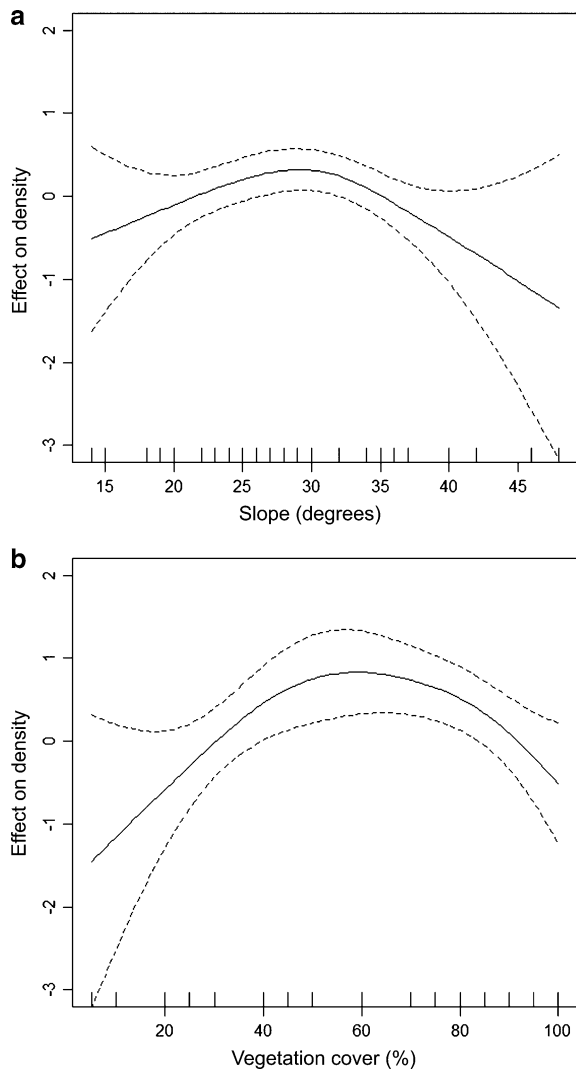
between-habitat comparison of environmental variables and population parameters in large (10 × 10 m) and small (0.5 × 0.5 m) plots, respectively

Measure	<i>N</i>	Grassy			<i>N</i>	Scree			<i>N</i>	Rocky			<i>H<sub>c</sub></i>
		LCL	M	UCL		LCL	M	UCL		LCL	M	UCL	
10 × 10 m													
Vegetation cover (%)	18	97.5	100 <sup>a</sup>	100	16	40	60 <sup>b</sup>	70	29	20	40 <sup>b</sup>	50	37.12***
Moss cover (%)	18	37.5	61.25 <sup>a</sup>	66.25	16	0.5	0.75 <sup>b</sup>	2	29	0.5	0.5 <sup>b</sup>	1	21.73***
FA-HL (degrees)	18	135	146.25	157.5	16	135	135	157.5	29	90	112.5	135	5.72 <sup>ns</sup>
Heat load (MJ cm <sup>-2</sup> year <sup>-1</sup> )	18	0.860	0.902	0.968	16	0.930	0.960	0.981	29	0.734	0.878	0.946	5.60 <sup>ns</sup>
PISR (MJ cm <sup>-2</sup> year <sup>-1</sup> )	18	0.873	0.924	0.948	16	0.881	0.916	0.937	29	0.877	0.948	1.000	2.05 <sup>ns</sup>
Slope (degrees)	18	21	25 <sup>a</sup>	28	16	25.5	30 <sup>ab</sup>	35	29	30	34 <sup>b</sup>	36	12.97**
Soil depth (cm)	18	14.9	20 <sup>b</sup>	24	16	13.1	16.6 <sup>b</sup>	20	29	3.3	6 <sup>a</sup>	7.5	33.23***
Density (ramets/100 m <sup>2</sup> )	18	0.0	5.5 <sup>b</sup>	10	16	34	48.5 <sup>a</sup>	86	29	0.0	0.0 <sup>b</sup>	0.0	37.77***
0.5 × 0.5 m													
Vegetation cover (%)	17	50	80 <sup>a</sup>	95	23	30	40 <sup>b</sup>	50	26	20	30 <sup>b</sup>	42.5	17.31***
Vegetation height (cm)	17	16	24.2 <sup>a</sup>	32.6	23	9	11.6 <sup>b</sup>	14	26	9.2	11.7 <sup>b</sup>	13.5	16.15***
Moss cover (%)	17	10	37.5 <sup>a</sup>	62.5	23	0.5	0.5 <sup>b</sup>	2	26	0.5	0.5 <sup>b</sup>	1	16.41***
FA-HL (degrees)	17	90	135	157.5	23	112.5	135	157.5	26	90	112.5	135	6.10 <sup>ns</sup>
Heat load (MJ cm <sup>-2</sup> year <sup>-1</sup> )	17	0.8082	0.859	0.908	23	0.824	0.857	0.877	26	0.7383	0.862	0.921	0.07 <sup>ns</sup>
PISR (MJ cm <sup>-2</sup> year <sup>-1</sup> )	17	0.7724	0.857 <sup>ab</sup>	0.906	23	0.809	0.833 <sup>b</sup>	0.857	26	0.8776	0.915 <sup>a</sup>	0.948	8.57*
Slope (degrees)	17	14	15 <sup>b</sup>	20	23	10	15 <sup>b</sup>	18	26	25	29 <sup>a</sup>	36	20.29***
Soil depth (cm)	17	14.2	16.6 <sup>b</sup>	18.6	23	11.4	15.6 <sup>b</sup>	16.6	26	1.5	2.5 <sup>a</sup>	5.3	40.67***
Soil moisture (%)	17	13.534	16.333 <sup>a</sup>	19.490	23	6.900	9.770 <sup>b</sup>	11.320	26	7.355	8.155 <sup>b</sup>	14.023	15.35***
Soil pH	17	7.67	7.76 <sup>b</sup>	7.82	23	7.86	7.92 <sup>a</sup>	7.96	26	7.69	7.75 <sup>b</sup>	7.81	19.03***
Ramets frequency (expected values under the null hypothesis are reported for reference)			Observed/expected			Observed/expected				Observed/expected			Fisher's table <i>P</i>
	17		9 <sup>a</sup> /9		23		22 <sup>b</sup> /12		26		4 <sup>c</sup> /14		1.3E–9***

Different superscript letters (a, b, c) indicate significant pairwise tests at 0.05 alpha probability level

\*\* *P* < 0.01; \*\*\* *P* < 0.001; ns, not significant

FA-HL folded aspect for heat load, PISR potential incident solar radiation

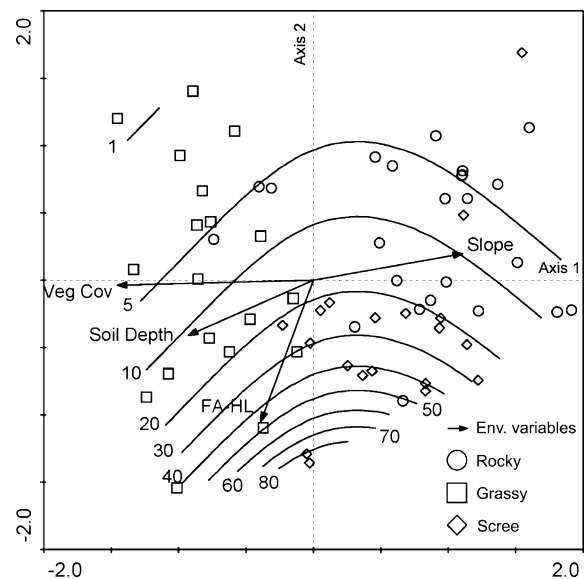


**Fig. 2** The variation of smoothed effects of slope (a) and vegetation cover (b) on *S. bellidifolia* abundance with approximate 95% pointwise confidence bands (10 × 10 m plots). Curves are based on non-parametric generalized additive model (GAM) fits

of the initial variation of *S. bellidifolia* abundance. Removing slope from the set of predictor variables worsens the model fit. The explained null deviance decreases to 78.3% which is not a considerable change, but the explained initial variation of *S. bellidifolia* abundance suffers more,  $\Delta_R^2 = -11\%$ . Also, there is strong evidence against the exclusion of slope from the predictors of the model ( $F = 4.5675$ ,  $P = 0.0158$ ).

In the CCA analysis, only moss cover was not significant in the multivariate test of the model.

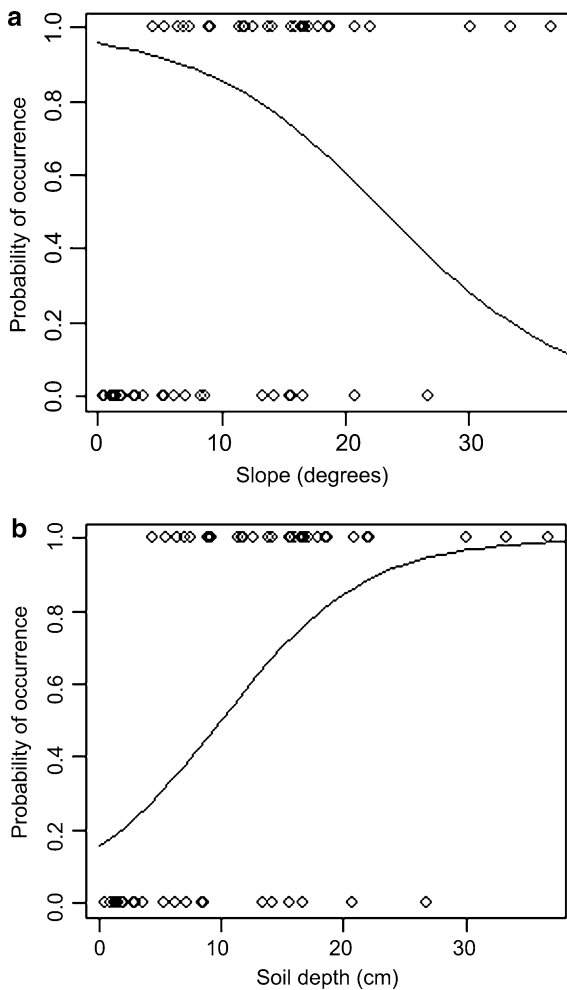
The first axis was primarily related to a vegetation cover gradient combined with soil depth, which separated the rocky habitats and the screes from the grassy habitats. The second axis was related to FA-HL, separating the screes mainly from the rocky habitats. The GAM contour plots of *S. bellidifolia* density ranked the higher values towards the lower part of the ordination space and the lowest values in the upper right and left side, suggesting a complex (nonlinear) gradient from rocky to grassy and finally, to scree habitats (Fig. 3). The shape of density isolines and their position with respect to environmental vectors confirmed the unimodal response of *S. bellidifolia* to vegetation cover and slope variables, both having the highest loadings on the first axis. On the other hand, ramet density showed a more or less monotonic increase with FA-HL, but with the tendency of levelling off towards higher values of this variable. A less obvious unimodal response was distinguishable with respect to soil depth. Otherwise a monotonic relationship between soil depth and ramet density was also indicated by both standard and partial Spearman correlations ( $\rho = 0.532$ ,  $P < 0.0001$  and  $\rho = 0.531$ ,  $P < 0.0001$  respectively).



**Fig. 3** Density contour lines of *S. bellidifolia* based on GAM curves fit ( $F = 51.73$ ,  $P < 0.0001$ ) overlapped on the CCA ordination plot of 10 × 10 m samples. The first two axes account for 46.1% and 31.9% of the total variance of species-environmental relation

*Saponaria bellidifolia* occurrence at a fine scale  
(0.5 × 0.5 m)

*S. bellidifolia* was present in 4 of the 26 rocky plots (15.3%), 22 of the 23 scree plots (95.6%) and 9 of the 17 grassy plots (52.9%) (Table 1). The logistic regression model evidenced strong effects of four predictors (scree, slope, soil depth and vegetation cover) on the occurrence of *S. bellidifolia* (Fig. 4a, b; Table 2). The model had high classification accuracy (AUC = 0.924), thus the assembly of the mentioned variables had genuine predictive power on the presence of *S. bellidifolia*. While one unit increase in slope slightly reduced the probability of species occurrence, scree variable had a high impact on its



**Fig. 4** Probability of *S. bellidifolia* occurrence with respect to slope and soil depth (0.5 × 0.5 m plots). The response curves are based on univariate binomial logistic regressions

**Table 2** Binomial logistic regression model of *S. bellidifolia* occurrence at 0.5 × 0.5 m scale ( $\beta$  = regression coefficient,  $z$  = Wald test statistic)

Variable	$\beta$	SE ( $\beta$ )	$z$	$P$
Intercept	2.211	1.553	1.424	0.154
Habitat type (scree)	3.672	1.394	2.634	0.008
Soil depth	0.225	0.091	2.463	0.014
Slope	-0.151	0.055	-2.776	0.005
Vegetation cover	-0.040	0.021	-1.899	0.058

presence (odds ratio = 57.53). Indeed, in the univariate model, the scree predictor had higher classification accuracy (AUC = 0.837) than slope (AUC = 0.798). Soil depth alone had satisfactory classification accuracy as well (AUC = 0.781), while vegetation cover offered no classification accuracy alone (AUC = 0.521). However, there was evidence against the removal of vegetation cover from the final model ( $\chi^2 = 4.99$ ,  $P = 0.0254$ ;  $\Delta_{AIC} = 2.99$ ).

The predicted distribution maps of *S. bellidifolia* (Figs. 5 and 6) based on probabilities of occurrence indicated that the chance of finding the species was 0.60 or higher in 48.28% of the plots in Pinet and 48.65% in Runc Gorges. By comparison, the species was observed in 58.62% of the plots in Pinet and 48.65% in Runc Gorges.

## Discussion

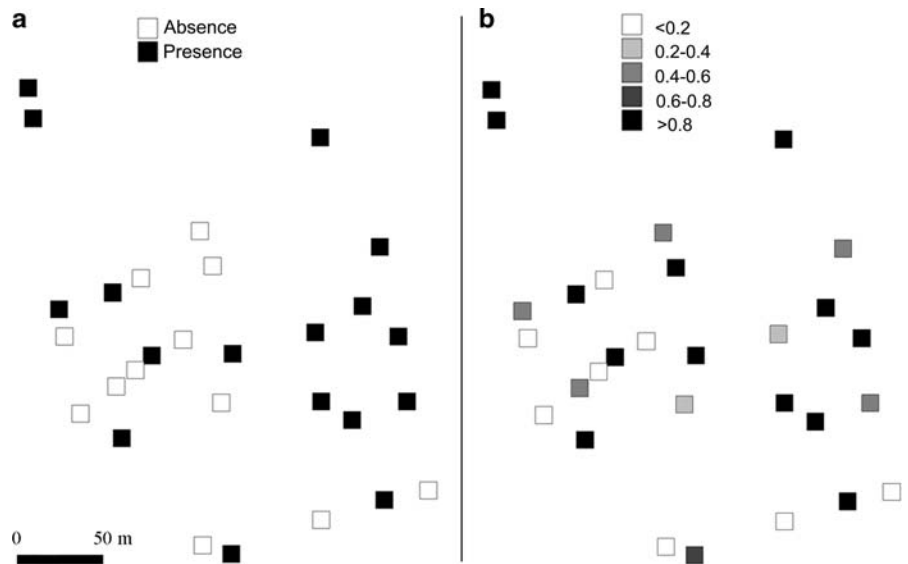
### *S. bellidifolia* abundance pattern at a 10 × 10 m scale

We have found significant spatial substructuring of the studied *S. bellidifolia* populations, determined mainly by the patchiness of habitat attributes. Also, ecologically and physiognomically the three habitat types identified were clearly distinguishable in terms of the variables taken into account. We have also revealed a moderate floristic distinctness of the three habitat types.

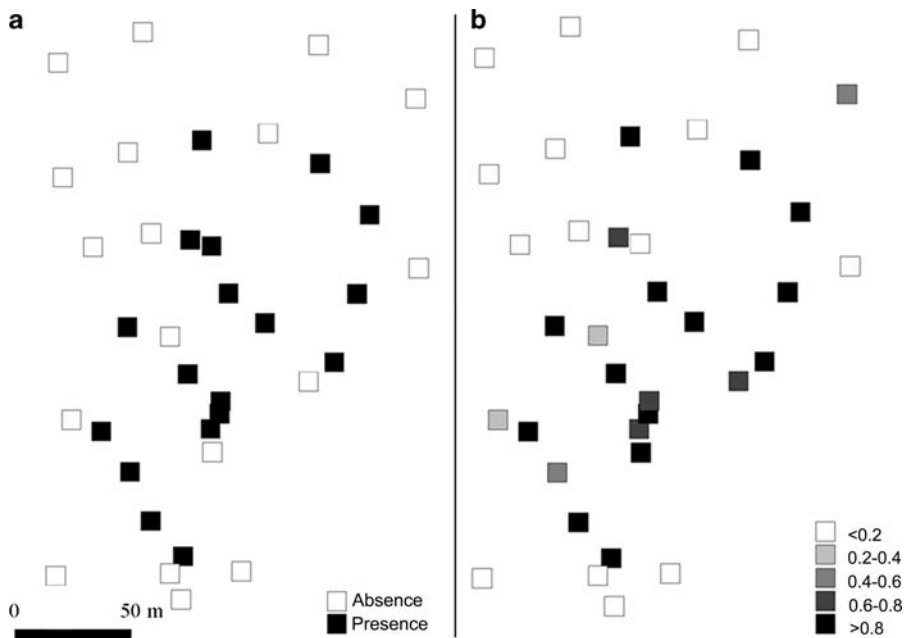
At larger scale (10 × 10 m), the screes are the most suitable to *S. bellidifolia*, followed by grassy and rocky habitats. Under their specific disturbance regime, scree communities may never reach successional maturity and thus, the survival of weaker competitors is facilitated (Rejmánek et al. 2004). This could also be the case of *S. bellidifolia*



**Fig. 5** Observed (a) and predicted (b) distribution of *S. bellidifolia* within 0.5 × 0.5 sampled plots in the Pinet Gorges, based on binomial logistic regression. Predictions are given based on probability classes with a range of 0.2 units



**Fig. 6** Observed (a) and predicted (b) distribution of *S. bellidifolia* within 0.5 × 0.5 sampled plots in the Runc Gorges, based on binomial logistic regression. Predictions are given based on probability classes with a range of 0.2 units



individuals, which seem to prefer conditions of lower competition and, on the other hand, tolerate higher levels of mechanical stress. The great ability of *S. bellidifolia* to exploit open habitats has been repeatedly noticed after incidental fires in Runc Gorges and other neighbouring limestone outcrops (Csergő, personal observation). This shows its good colonization capacity and explains its high local abundance in disturbed, competition-relaxed habitats. Similarly, microsite availability and local disturbance regimes

are important for successful regeneration of other rare species in rocky grasslands (Kephart and Paladino 1997; Moretti et al. 2008), on eskers (Kalliovirta et al. 2006) or other types of grasslands (McIntyre and Lavorel 1994). However, as stated by Rejmánek et al. (2004), on screens only species with sufficient belowground resources can tolerate high levels of disturbance. As a rhizomatous chamaephyte, *S. bellidifolia* might have a high degree of resilience, which could play an important role in survival within

mobile scree communities. Moreover, screes offer seeds the highest chances to be buried in relatively short time. As seed germination of *S. bellidifolia* is strongly inhibited by light (Şuteu and Mocan 1998), this habitat appears favourable for successful seedling recruitment.

It is a long-standing recognition that at geographic range limits, species' competitive ability decreases (Case and Taper 2000 and references therein). We did not study the core populations, but based on literature data *S. bellidifolia* seems to generally prefer open habitats (Ritter-Studnicka 1967), and therefore we hypothesize that its competitive abilities could be weak across its entire distribution range. In this perspective, our results would mirror the behaviour of a rare species more than that of marginal, environmentally constrained populations. Nevertheless, our findings are consistent with other outcomes on marginal populations. For instance, Baack et al. (2006) suggest that frequent disturbance could relax competition and expand the local range of the rare *Gilia tricolor* from California grasslands. Similarly, Moretti et al. (2008) found that fire and open, stressful habitats drive the occurrence of the northern peripheral *Cistus salvifolius*.

The unimodal response of *S. bellidifolia* density to vegetation cover at 10 × 10 m scale suggests that both the too open (rocky) and the too closed (grassy) habitats are unsuitable for this species at community scale. In rocky habitats, *S. bellidifolia* might be excluded because of strong competition for water and soil resources. Rocky habitats from the two localities are either unbroken rocks with widely spaced crevices, or ledges with soil pockets of different sizes. Scarcity of soil makes these open rocky habitats "biotically closed" (Davis 1951) and prone to water deficit, where a few, strong competitors occupy most of the available space. In our study site, the tussock-forming grass *Sesleria rigida* was the dominant species, and the rare *S. bellidifolia* individuals were noticed only on the more open ledges. There is empirical evidence that ledge area and soil volume have significant effects on the assembly of rock communities (Kuntz and Larson 2006a). For certain plants, like *Silene douglasii* var. *oraria*, rocky habitats can provide favourable conditions on outcrops (Kephart and Paladino 1997), although population dynamics are unstable compared with grassy habitats. On the other hand, within the grassy

habitats, the intermediate to low density of *S. bellidifolia* could be associated with shade avoidance (high vegetation of grassy habitats seems to hinder ramets' growth of *S. bellidifolia*) or litter accumulation (which influence the establishment, growth and survival of seedlings) (Kephart and Paladino 1997; Baack et al. 2006; Moretti et al. 2008). Indeed, *S. bellidifolia* individuals were recorded only in sites where vegetation cover did not reach high values (total species cover was below 90%) and thus microgaps were available.

It should be mentioned that, despite lower densities, individuals from apparently inhospitable habitats may be an important source of seeds for other microsites and their role played in interpatch dynamics should not be underestimated (Kephart and Paladino 1997).

The hunchback-shaped response curve of species density to slope suggests the same ecological background, namely that *S. bellidifolia* avoids both the inhospitable steep rocky habitats and the mild slopes with high vegetation cover. In addition, it is likely that the screes receive the highest heat load on south facing mountain sides, as they develop on intermediate slopes (Frank and Lee 1966).

#### *S. bellidifolia* abundance pattern at 0.5 × 0.5 m scale

At 0.5 × 0.5 m scale, *S. bellidifolia* ramets occur similarly on screes rather than in rocky or grassy habitats, on lower slopes and at low vegetation cover. In addition, *S. bellidifolia* displays a negative response to shallow-soiled rocky habitats and positive response to the deep-soiled scree cones and grassy habitats. Therefore, the extent of rock fracturing, strongly correlated with soil availability, is an important factor that drives the occurrence of *S. bellidifolia* on the studied limestone outcrops. This finding is in agreement with several habitat predictions of rare rock specialists (Davis 1951; Baskin and Baskin 1988; Wisser et al. 1996; Kuntz and Larson 2006a). That soil moisture was not predictive may reflect correlation with soil depth, to which it is usually related. However, with few exceptions, soil moisture was similarly a bad predictor for the rocky grassland endemic *Silene douglasii* var. *oraria* (Kephart and Paladino 1997).

One of the most appealing outcomes at this scale are the predicted probability plots of *S. bellidifolia*, which can be regarded as potential distribution maps of this rare species. The absence of ramets within these sites may be due not only to unsuitable habitats, but also to historical factors, e.g. seed dispersal dynamics in rocky sites (Pulliam 2000) or high levels of disturbance in scree sites (Rejmánek et al. 2004). These areas are potentially important for the conservation of the species and should be monitored in the future.

#### Abundance patterns across scales

*S. bellidifolia* density response to environmental parameters is generally consistent across  $10 \times 10$  m and  $0.5 \times 0.5$  m scales. All models selected the habitat type, vegetation cover and slope variables, but habitat type was undoubtedly the strongest parameter influencing the species abundance pattern, probably because of its complex nature. Vegetation cover had a more dominant effect at  $10 \times 10$  m scale, whereas slope had a stronger importance at  $0.5 \times 0.5$  m scale. The difference between the two models was given by soil depth, which has a fine-scale spatial variation, not detectable at larger scale. However, vegetation cover strongly correlated with soil depth at  $10 \times 10$  m scale, suggesting an overlapping effect of these two variables. Still, vegetation cover was a better predictor of *S. bellidifolia* density, probably because it bore the additional effect of competition. *S. bellidifolia*'s preference for warmer sites (FA-HL variable) was revealed only when habitat type was not involved in the model, suggesting a weaker effect of this topoclimatic parameter. The shape of responses to all continuous variables was unimodal at  $10 \times 10$  m and linear at  $0.5 \times 0.5$  m scale, suggesting a more straightforward effect at smaller extents. However, this differentiation does not reflect necessarily a scaling relationship because of the bias related to comparing different models in terms of algorithm (non-parametric GAM versus parametric logistic regression) and response variable (abundance versus occurrence).

#### Conclusions and perspectives

We have demonstrated a sensitive response of *S. bellidifolia* to outcrop heterogeneity and a strong

affinity to the open, disturbed environment of screes within the studied sites. We could not attest its strict confinement to the warmest microenvironments of limestone outcrops and we conclude that it is the microhabitat heterogeneity that has a more dominant effect on its distribution pattern. In a similar way, Norton et al. (2005) suggested that species' northern boundaries are probably not closely delimited by climate alone, and factors such as dispersal and microhabitat availability are extremely important for their distribution.

Given the distinct abundance pattern driven by the heterogeneous environmental conditions and based on evidences brought by Moretti et al. (2008) on northern peripheral populations, we suggest the existence of ontogenetic niche segregation in *S. bellidifolia*. Regeneration is expected to be more successful on screes, because of the increased availability of a regeneration niche (Grubb 1977). In turn, the more stable grassy habitats would represent its persistence niche (Bond and Midley 2001), where we hypothesize that seedling emergence is limited, but individuals' persistence is promoted through a longer life span. Within peripheral populations, this niche segregation may carry important evolutionary backgrounds, ensuring adaptation to changing environment. From a conservation perspective, the preservation of screes and periodic reformation of open habitats (through occasional fires or mechanical clearing) is probably beneficial to *S. bellidifolia* survival, as it is to the peripheral *Cistus salvifolius* populations (Moretti et al. 2008).

Because of the clumped spatial distribution pattern of *S. bellidifolia*, gene flow intensity (especially seed dispersal) could vary substantially within and between different habitat types and this could give rise to mechanisms of genetic divergence within the studied populations. Small-scale evolutionary events were observed repeatedly in rare plant species (Zangerl and Bazzaz 1984; Loveless and Hamrick 1984; Prentice and Cramer 1990; Travis and Ezard 2006; Gaudeul and Till-Bottraud 2008). Within peripheral and isolated populations, spatially constrained by scarcity of suitable habitats, such patterns and mechanisms that maintain genetic variability could be vital for species persistence.

By revealing patterns and processes that lay behind limestone outcrops heterogeneity, we can understand better the great evolutionary and

conservational significance of these particular habitats. We have shown once more that screes play an important role in rare species survival and they should receive a special attention from conservationists.

Over the long-term, under the global change scenarios (Alcamo et al. 1998), these northern isolated *S. bellidifolia* populations could represent vanguards of species range shift and in this perspective our results support the need for its conservation within the Southeastern Carpathians.

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