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Bryophyte-environment relationships in rock outcrops of North-western Portugal: the importance of micro and macro-scale variables

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Résumé – Les effets des variables micro et macro-échelle sur la composition des groupements de bryophytes saxicoles ont été étudiés dans le nord-ouest du Portugal. L'analyse des correspondances canoniques (CCA), utilisant toutes les variables, indiquent que la répartition des espèces de bryophytes est principalement influencée par une combinaison de variables micro-échelle liées à l'humidité locale et les variables macro-échelle (notamment les précipitations). L'approche de la partition de la variation, basée sur CCA, a été utilisée pour évaluer des effets uniques et communs des variables micro et macro-échelle sur la composition des groupements. Cette approche a montré que les effets des variables micro-échelle sur la variabilité des groupements recoupent des facteurs macro-échelle, expliquant 7,7 % contre 3,5 % de la variation de la composition des groupements, respectivement. La variation sur l'effet combiné des deux groupes de variables est marginale (0,8 %). Les patrons de micro-échelle dans la composition des communautés sont liés à la préférence des espèces de bryophytes pour l'humidité et la lumière. La richesse des espèces par échantillon augmente avec l'exposition au nord et les pentes abruptes. Les espèces xérophiles ont tendance à être associées à un recouvrement élevé de lichens crustacés et à des expositions sud et des pentes douces, tandis que des espèces hygrophiles sont plus fréquentes dans les sites d'échantillonnage avec un recouvrement élevé des lichens fruticuleux et aux expositions nord et pentes abruptes. L'analyse des patrons de macro-échelle sur la variation des groupements a montré que la latitude et les précipitations sont les principales macro-variables qui influent sur la structure des groupements.

Bryophytes / Lichens / Partition de la variation / CCA / Conservation

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Abstract – The effects of micro and macro-scale variables on the composition of saxicolous bryophyte communities have been studied in North-western Portugal. The canonical correspondence analysis (CCA), using all the variables, suggest that the distribution of bryophyte species is mainly influenced by a combination of micro-scale variables related to local humidity and macro-scale variables (especially precipitation). A variation partitioning approach, based on CCA, was used to assess common and unique effects of micro and macro-scale variables on species composition. This approach showed that the effects of micro-scale variables on the community variability superimpose to the macro-scale factors, explaining 7.7% against 3.5% of the variation in community composition, respectively. The variation related to the combined effects of both variable sets was marginal (0.8%). Micro-scale patterns in community composition seem to be related to different preferences of bryophyte species for humidity and light conditions and species richness per sample plot clearly increases with both northerly exposure and steepness of slope. Xerophytic species tend to be associated with a higher cover of crustose lichens and with southerly exposures and gentle slopes, while hygrophytic species are more frequent in sampling sites with a higher cover of fruticose lichens and with northerly exposures and steep slopes. Analysis of macro-scale patterns on community variation revealed that latitude and precipitation are the most important macro-variables that influence the community structure.

Bryophytes / Lichens / Variation partitioning / CCA / Conservation

INTRODUCTION

Bryophyte community ecology has played a central role in understanding how bryophyte species are arranged within plant communities (Vitt, 2006). Various multivariate methods allow testing specific hypotheses on relationships between communities and environmental gradients (Økland & Eilertsen, 1994). Analysis of the variation of a community composition, i.e. a measure of beta diversity, is a widely used approach in community ecology and fundamental for understanding the functioning of ecosystems. Variation partitioning methods are broadly used to investigate species-environment relationships and to isolate the amount of variation in community data explained by two or more sets of variables (Borcard *et al.*, 1992; Peres-Neto *et al.*, 2006; Legendre, 2008). Although variation partitioning results cannot be used to determine causal relationships, they are an important procedure to test hypotheses about the processes that may have generated the observed patterns (Borcard *et al.*, 1992; Anderson & Gribble, 1998; Cushman & McGarigal, 2002). Applications of this method cover a wide range of research fields including biogeography, ecology and vegetation (Legendre & Legendre, 1998). As examples, it has been used to investigate how environment and land-use relate to the compositional variation in grasslands (Vandvik & Birks, 2002); the relative amount of variation in epiphytic macrolichen communities attributable to human impact, macroclimate, spatial context and environmental differences (Werth *et al.*, 2005); the effects of vegetation cover, radiation, microhabitat variables and maritime influence on the floristic composition of a saxicolous lichen community (Bjelland, 2003); the fraction of variation in species abundance of boreal coniferous forest vegetation explained by environmental and spatial variables (Økland & Eilertsen, 1994).

Rock outcrops are relatively stable habitats and are good model systems to relate habitat and community structures (Alpert, 1991; Ódor & Standovár, 2002). Several studies have shown that micro-scale factors such as exposure, slope, water availability and the chemical nature of the rock and variables (e.g. temperature, precipitation) affect saxicolous bryophytes richness and communities (Jonsgard & Birks, 1993; Heegaard, 1997; Werner, 2000; Kuntz & Larson, 2006). Although there are several studies about the influence of environmental and micro-scale factors on the structure of bryophyte communities from rock outcrops, no investigations have focused specifically on rock outcrop communities in Portugal through a standardized sampling protocol. Additionally, no attempts have been made to use the method of variation partitioning to quantify the relative importance of environmental and micro-scale factors affecting the composition of saxicolous bryophyte communities. We chose to examine saxicolous bryophyte-environment relationships using two sets of variables at to different scales. We decide to analyze macro and micro-scale variables since different species potentially respond to the environmental cues operating at these two scales. The specific objectives of this study were: (1) to determine the relative contributions of micro and macro-scale variables to the bryophyte communities' variability (2) to analyse the effects of the studied explanatory variables on bryophyte species richness and composition.

MATERIALS AND METHODS

Bryophyte sampling

Fieldwork was carried out in 67 localities, in 7 protected mountain areas distributed in the North-western Portugal (Fig. 1). The study area, dominated by granitic bedrock and subject to strong oceanic influence, is located between latitudes 40° and 42° N and longitudes of 8.7° and 7.5° W. Mean annual precipitation in mainland Portugal is around 900 mm and the highest values are found in the highlands of North-western region. In addition, insolation decreases, in general, from south to north, with the altitude, and from east to west and the lowest values of insolation are found in North-western territory. Particularly, in the study area, the mean annual precipitation ranges between 1200 and 3800 mm, and insolation present average values from 1800 to 2600 hours per year. The average annual mean temperature in the research area ranges from a minimum of 8°C and a maximum of 14°C. Rock outcrops are well represented in the study area, being surrounded by mesophytic to xerophytic heaths on siliceous and podsolic soils. In each mountain area the number of sampling localities was variable and was selected taking into account the extent, lithology and altitudinal variation of each mountain. Then, sample plots that represented as well as possible the whole ecological and floristic variation within a given sampling locality, were selected. In each locality five sample plots were performed on granitic rock surfaces. Percentage cover was used to obtain an estimate of bryophyte species abundance in each sample plot (25×25 cm^2). Fieldwork was performed from March 2005 to November 2006 and in April 2007. The nomenclature follows Hill *et al.* (2006) for mosses and Ros *et al.* (2007) for liverworts. *Hedwigia striata* (Wilson) Bosw. is here recognized as a distinct species, based on recent morphological and molecular analyses (Buchbender *et al.*, 2010). The preferences of each individual species for humidity and light follow the classification of Dierβen (2001).

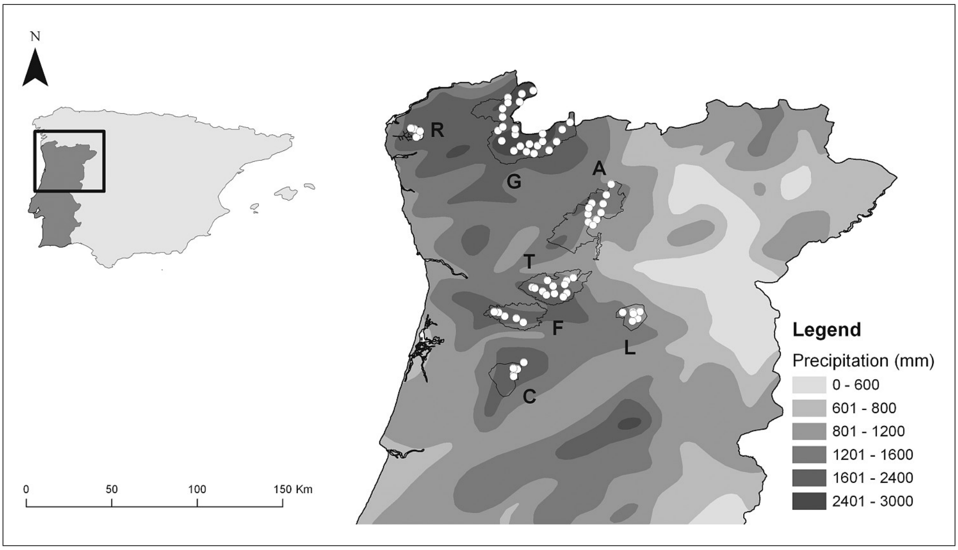


Fig. 1. Location of the sampling localities within each mountain area. R – Arga; G – Peneda/ Gerês; A – Alvão; T – Montemuro; F – Freita; L – Lapa; C – Caramulo.

Explanatory variables

An initial set of 21 variables were used to characterize the sampling sites. They were grouped as macro and micro-scale variables (Table 1). Micro-scale variables were determined and registered at each sampling site. Exposure and slope were assessed for each rock surface using a compass with a clinometer. Exposure was then recoded into two components, north-south and east-west, according to the codes in Table 2. This coding allows treating separately the gradients north-south and east-west. Rock surface pH was determined in the field using a handheld pH meter (model 330i/SET, WTW) with a flat surface electrode (model Sentix Sur, WTW). The weathering index (Harnois, 1988) was calculated based on standard laboratory evaluations of the major chemical elements in the rock samples. The percentage cover of lichens, bryophytes, vascular plants and bare rock was visually estimated. Macro-scale variables related to topography (exposure and slope) were derived from Digital Elevation model (SRTM, 2009). Climatic data (annual average temperature, fog, frost, relative humidity and insolation) were supplied by Agência Portuguesa do Ambiente (APA, 2009); annual average precipitation was obtained from Sistema Nacional de Informação Geográfica (SNIG, 2009), and minimum temperature of coldest month, maximum temperature of warmest month, precipitation of driest month and precipitation of wettest month were available from WorldClim database (Hijmans *et al.*, 2005). Latitude and longitude were determined for each locality using a handheld global positioning system (GPS) device. Since some of the explanatory variables were semi-quantitative or ordinal and qualitative variables, all quantitative variables were transformed on semi-quantitative variables by grouping its values into classes of same frequency prior to analyses. This coding avoids extreme values like in a logarithmic transformation (Lepš & Šmilauer, 2003).

Table 1. Variables used in the analyses. Variables marked with an asterisk were the selected variables for each scale using the forward selection procedure outlined in Blanchet *et al.* (2008).

Variables (abbreviations)	*Description*
Micro scale variables	
*crus	% Crustose Lichens
*frut	% Fruticulose Lichens
*mslop	Slope
*ns	East-west component of exposure
*ew	North-south component of exposure
brock	% Bare Rock
bryo	% Bryophytes
exp/shad	Type of shading (exposed or rock shading)
fol	% Foliose Lichens
pH	Rock surface pH
vasc	% Vascular plants
Weath	Weathering Index
Macro scale variables	
*Fog	Fog
*Lat	Latitude
*Prec	Annual average precipitation
*Slop	Slope
*TminCM	Minimum temperature of coldest month
*TmaxWaM	Maximum temperature of warmest month
Fros	Frost
Hum	Relative humidity
Ins	Insolation
Long	Longitude
NS	North-south component of exposure
EW	East-west component of exposure
PDM	Precipitation of driest month
PWtM	Precipitation of wettest month
Temp	Annual average temperature

Table 2. Values assigned to the recoding of variable Exposure in two components.

Exposure	*North-south variable (NS)*	*East-west variable (EW)*
N	1	0
NE	0.5	0.5
E	0	1
SE	-0.5	0.5
S	-1	0
SW	-0.5	-0.5
W	0	-1
NW	0.5	-0.5

Data analyses

Species found in less than 5% of the sampling localities were excluded to avoid the influence of rare species on the analysis (ter Braak & Šmilauer, 2002). All multivariate analyses were performed in CANOCO version 4.5 (ter Braak & Šmilauer, 2002). Detrended correspondence analysis (DCA), an indirect technique where ecological gradients are inferred from species composition data alone, was used first. Subsequently, data were analyzed using canonical correspondence analysis (CCA), a direct ordination technique, based on preliminary DCA to evaluate species unimodal response patterns to the variables studied. The results of both direct and indirect ordination analyses were compared in order to investigate how successfully the measured variables capture the main variation in species data.

The amount of variation in community composition that could be accounted for the measured variables and the relative importance of each scale of variables were assessed by the variation partitioning approach, following the procedures outlined in Legendre (2008). This procedure is based on three canonical correspondence analyses; the first one uses both sets of variables; the second only the first set of variables; and the third one only the second set of variables. All remaining fractions, such as the common fraction of variance shared by both sets of variables and unexplained variation, can be obtained by simple subtractions (Legendre, 2008).

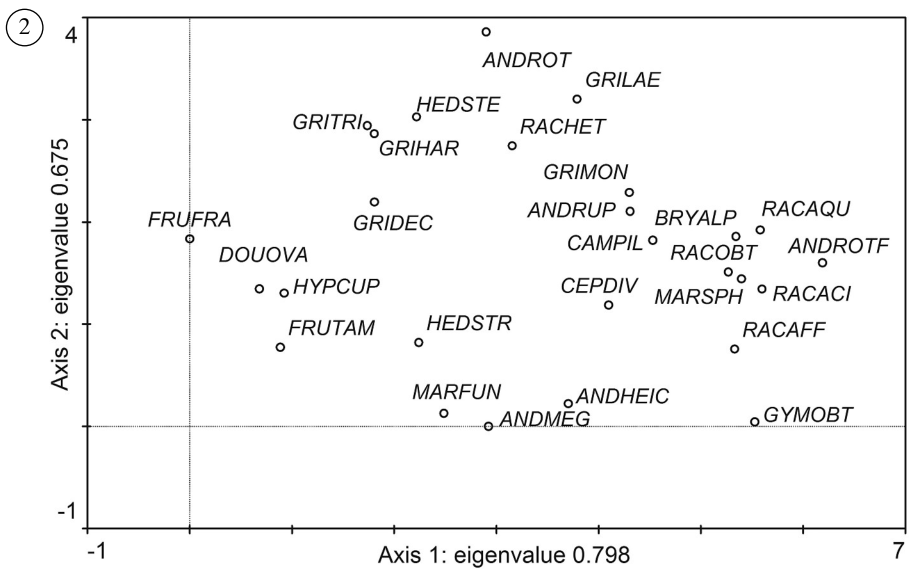
Previous to variation partitioning, Monte Carlo permutations tests with 499 unrestricted permutations, were used to test the statistical significance of the first canonical axis and of all canonical axes of each set of explanatory variables. Since these tests were significant ($p < 0.002$), each set of explanatory variables was analysed separately by the forward selection procedure in CANOCO, using Monte Carlo permutation tests, in order to retain only the most important variables. We ran a forward selection on each set of explanatory variables separately, following the approach of Blanchet *et al.* (2008). According to this new procedure, the forward selection has to be carried out with two stopping criteria, the usual alpha significance level ($p \leq 0.05$) and the adjusted coefficient of multiple determination calculated using all explanatory variables, since, very often, the R_a^2 calculated with all significant variables ($p \leq 0.05$) is higher than the R_a^2 calculated using all explanatory variables. Therefore, the use of R_a^2 as an additional stopping criterion, provide a selection of a set of variables that explain almost the same amount of variance as the total set and corrects for the overestimation of the proportion of explained variance (Borcard *et al.*, 1992). Only the selected variables for each scale (Table 1), using the previous method, were used in subsequent analyses.

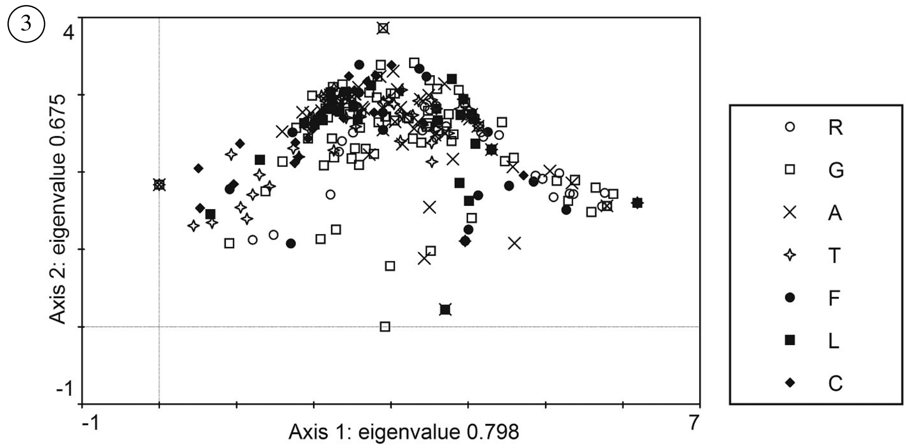
We adjusted the proportion of variation in species data explained by both sets and each set (the same as R^2) to account for the number of sampling sites and explanatory variables and report the adjusted values (R_a^2) throughout, since R_a^2 is an unbiased estimator of the real contribution of a set of explanatory variables to the explanation of a response variable. This adjustment was applied to canonical analyses, according to the formula [R_a^2 = 1- (1- R^2) (n-1/n-p-1), where *n* is the number of sampling units and *p* is the number of predictors] described in Peres-Neto *et al.* (2006).

RESULTS

Overall bryophyte-environment relationships

DCA eigenvalues of species ordination were high (Fig. 2) and a clustering of groups is evident when examining species location in DCA





Figs 2-3. Ordination diagrams produced by detrended correspondence analysis (abbreviations according to Table 1 and 3). **2.** Species scores; **3.** sample scores with classification of samples according to each mountain area (R – Arga; G – Peneda/Gerês; A – Alvão; T – Montemuro; F – Freita; L – Lapa; C – Caramulo).

ordination space (Fig. 2), which show the presence of strong patterns in bryophyte community composition. In addition, the analysis of sample plots distribution in DCA ordination space (Fig. 3) revealed that samples from the same mountain area are not positioned near each other, pointing out that the geographic location of sampling localities is not the strongest gradient. CCA species-variables biplot (Fig. 4), using all the variables, shows that the first and second axes are well correlated with variables data (axis 1: r = 0.772; axis 2: r = 0.636) and that both axes are associated with micro and macro-scale variables. The first axis is

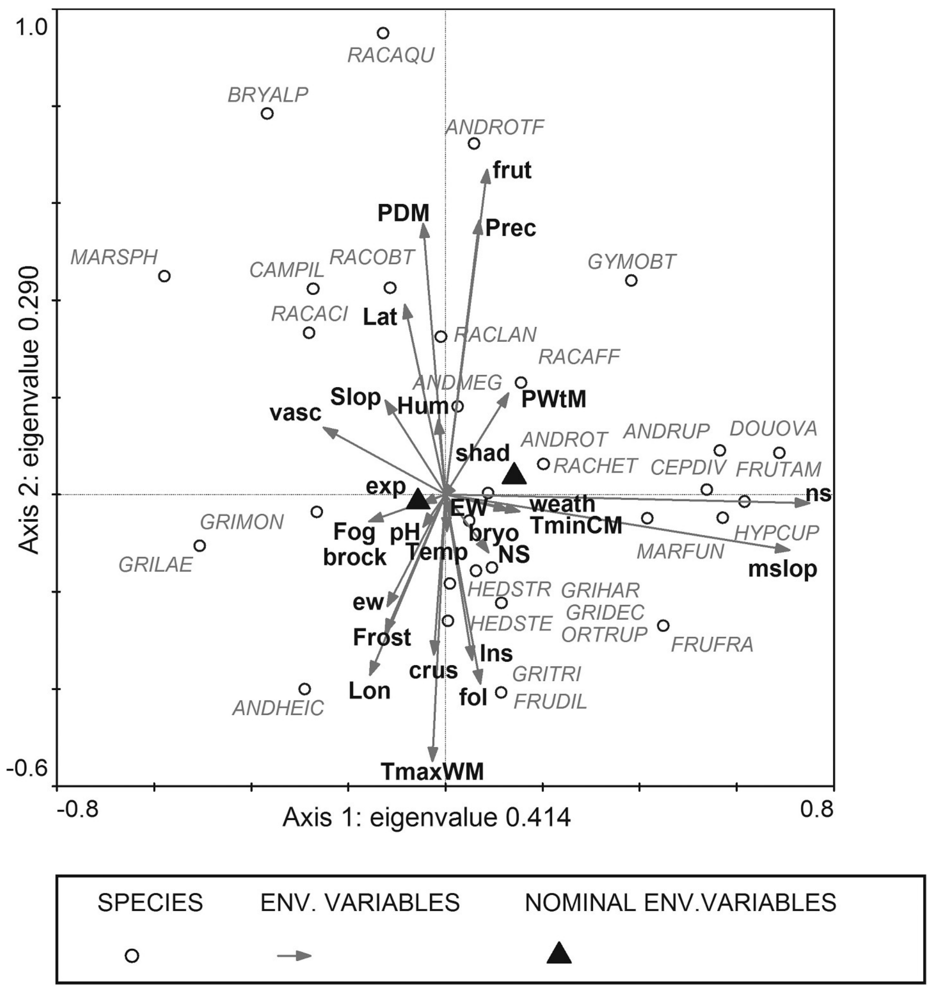


Fig. 4. CCA species-variables biplot using all the variables (abbreviations according to Table 1 and 3). Species-environment correlation for axis 1 and 2 are 0.772 and 0.636, respectively.

correlated mainly with the north-south component of exposure and slope of rock surfaces and, to a lesser extent, with the minimum temperature of the coldest month. The second ordination axis is more correlated with annual average precipitation and precipitation of driest month, maximum temperature of warmest month, latitude and cover of crustose and fruticose lichens. The eigenvalues for axes 1 and 2 decrease from the indirect to direct ordinations, indicating that a portion of the floristic variation is not accounted by the measured variables.

Variation partitioning

The full model explained 12% of the total variation in species data and the two groups of variables explained independently significant amounts of variation. The largest amount of variation was explained by the set of micro-scale variables (7.7%). Macro scale variables explained 3.5% of the community variation. The variation related to the combined effects of both variable sets was marginal (0.8%). A high percentage of residual variation (88%) was observed.

Micro and macro-scale patterns of community composition

Since the combined effects of both variable sets were marginal, CCA species-variables biplot were produced separately for each of two scales of variables, to show which variables within each set most influence the structure of bryophyte communities.

The first axis in CCA micro model reflects the north-south gradient and the increasing slope of rock surfaces (Fig. 5). Along this axis species more associated with southerly exposures and gentle slopes, with negative scores (e.g. *Bryum alpinum*, *Grimmia laevigata*, *G. montana*, *Marsupella sphacelata*) are separated from species more associated with northerly exposures and steep slopes, with high positive scores (e.g. *Andreaea rupestris*, *Douinia ovata*, *Frullania tamarisci*, *Hypnum cupressiforme* var. *cupressiforme*). The second axis is positively correlated with the cover of fruticose lichens and negatively correlated with the cover of crustose lichens and the east-west component of exposure. It separates those species with high positive scores which are more associated with increased cover of fruticose lichens and westerly exposures (e.g. *Andreaea rothii* subsp. *falcata*, *Campylopus pilifer*, *Racomitrium aquaticum*, *Racomitrium obtusum*) from species with negative scores associated with a higher cover of crustose lichens and easterly exposures (e.g. *Andreaea heinemannii* subsp. *crassifolia*, *Frullania fragilifolia*, *Grimmia trichophylla*, *Marsupella funckii*). Figure 6 clearly shows that species richness per sample plot increases with both northerly micro-scale exposures and steep slopes. Figure 7 illustrates that xerophytic species tend to be associated with a higher cover of crustose lichens and with southerly exposures and gentle slopes, while species more hygrophytic are more frequent in sampling sites with a higher cover of fruticose lichens and with northerly exposures and steep slopes. Figure 8 shows that sciophytic species and with wide amplitude with respect to the light conditions tend to be associated with northerly exposures and steep slopes; strictly photophytic species are regularly distributed along axis 1 and 2. It seems that axis 1 reflects a gradient of moisture and light availability and axis 2 probably also a moisture gradient.

The first axis in CCA macro model is positively correlated with precipitation and latitude and negatively correlated with maximum temperature of warmest month, while the second axis is somehow positively correlated with minimum temperature of coldest month and fog and negatively correlated with slope (Fig. 9). Results clearly show that axis 1 is the dominant gradient (Fig. 9), reflecting the geographic position of sampling localities that is highly correlated with precipitation. Species associated to more southern mountain areas, with low values of precipitation and latitude and high values of temperature of warmest month, have negative scores (e.g. *Andreaea heinemannii* subsp. *crassifolia*, *Grimmia decipiens*, *Grimmia tricophylla*) and species associated to more northern mountain areas with high values of precipitation and latitude and low values of maximum temperature of warmest month, have high positive scores (e.g. *Andreaea rothii* subsp. *falcata*, *Gymnomitrion obtusum*, *Racomitrium aquaticum*). No clear relationships were observed between macro-scale variables and species richness per sample plot and bryophyte preferences for humidity and light.

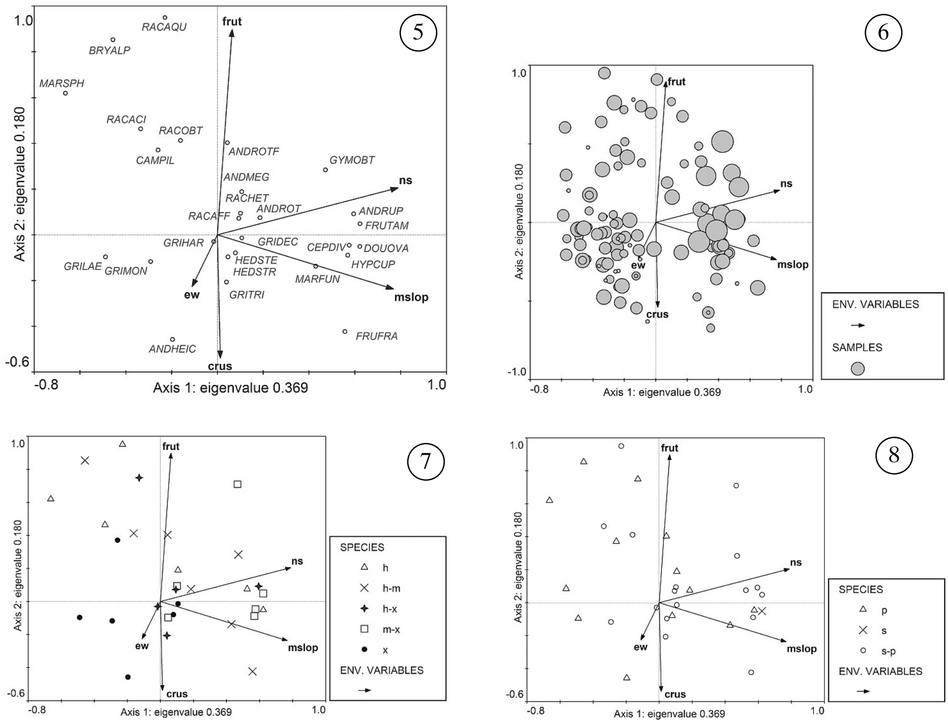


Fig. 5-8. CCA ordination diagrams based on micro-scale variables (abbreviations according to Table 1 and 3). Species-environment correlation for axis 1 and 2 are 0.731 and 0.526, respectively. **5.** Species-variables biplot; **6.** Sample-variables biplot with symbol size corresponding to the number of species in sample plots; **7.** Species-variables biplot with classification of bryophyte species according to their preferences for humidity (h- hygrophyte; h-m – hygrophyte to mesophyte; h-x – hygrophyte to xerophyte; m-x – mesophyte to xerophyte; x – xerophyte; **8.** Species-variables biplot with classification of bryophyte species according to their preferences for light (p- photophyte; s-p – sciophyte to photophyte; s- sciophyte).

DISCUSSION

Analyses of species-environment relationships are critically needed for the management of species conservation programs. We were able to explain up to 12% of saxicolous bryophyte community variation. Although the amount of total variation explained by all the variables seem proportionally low, both micro and macro-scale variables play a significant role ($p < 0.001$) in the structuring of these communities, as indicated by DCA and CCA analyses. In addition, the first and second axes of the CCA analysis, using all the variables, are well correlated with micro and macro-variables (Fig. 4), suggesting that the distribution of bryophyte species is mainly influenced by a combination of micro-scale variables related to local humidity and macro-scale variables (especially precipitation). On the other hand, according to the variation partitioning approach, the largest amount of variation was explained by the set of micro-scale variables (7.7%) and macro scale

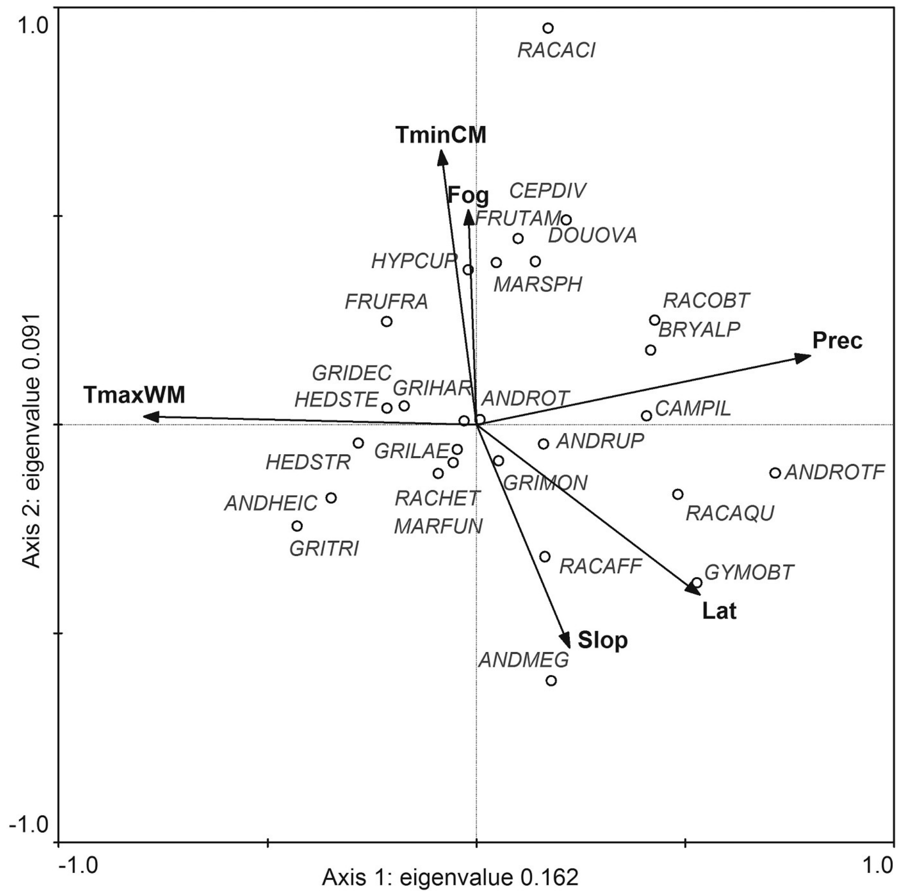


Fig. 9. Ordination diagram based on a CCA with macro scale variables (abbreviations according to Table 1 and 3). Species-environment correlation for axis 1 and 2 are 0.481 and 0.381, respectively.

variables explained 3.5% of the community composition variation. One possible explanation for these results is that the environmental parameters at a small-scale exert a strong influence on the bryophyte community, causing its patchiness with high variability at low scale ranges. Furthermore, mountain areas sampled in the current study probably do not span enough of a geographic range to detect a higher amount of variation explained by macro-scale variables that could superimpose to the micro-scale variability. Nevertheless, results from the variation partitioning approach should be confirmed, using a bigger sampling basis, since there are some differences in the sampling effort of the different areas in our study that can influence these results. Probably, more samples in a more widely geographic range, as well as a higher sampling effort in each sampling locality could give more insights to this theme of investigation and allow a lower unexplained variation.

On the whole, in the analysis of micro-scale patterns on community variation, bryophyte preferences for humidity and light (Figs 7, 8), according to

Table 3. Species code.

Species	*Code*
Andreaea heinemannii Hampe *et* Müll. Hal. subsp. crassifolia (Luisier) Sérgio	ANDHEIC
Andreaea megistospora B.M. Murray	ANDMEG
Andreaea rothii F. Weber *et* D. Mohr subsp. *rothii*	ANDROT
Andreaea rothii F. Weber *et* D. Mohr subsp. *falcata* (Schimp.) Lindb.	ANDROTF
Andreaea rupestris Hedw.	ANDRUP
Bryum alpinum Huds. *ex* With.	BRYALP
Campylopus pilifer Brid.	CAMPIL
Cephaloziella divaricata (Sm.) Schiffn.	CEPDIV
Douinia ovata (Dicks.) H. Buch	DOUOVA
Frullania fragilifolia (Taylor) Gottsche *et al.*	FRUFRA
Frullania tamarisci (L.) Dumort.	FRUTAM
Grimmia decipiens (Schultz) Lindb.	GRIDEC
Grimmia hartmanii Schimp.	GRIHAR
Grimmia laevigata (Brid.) Brid.	GRILAE
Grimmia montana Bruch *et* Schimp.	GRIMON
Grimmia trichophylla Grev.	GRITRI
Gymnomitrion obtusum Lindb.	GYMOBT
Hedwigia stellata Hedenäs	HEDSTE
Hedwigia striata (Wilson) Bosw.	HEDSTR
Hypnum cupressiforme Hedw. var. *cupressiforme*	HYPCUP
Marsupella funckii (F. Weber *et* D. Mohr) Dumort.	MARFUN
Marsupella sphacelata (Gieseke *ex* Lindenb.) Dumort.	MARSPH
Racomitrium aciculare (Hedw.) Brid.	RACACI
Racomitrium affine (F. Weber *et* D. Mohr) Lindb.	RACAFF
Racomitrium aquaticum (Brid. *ex* Schrad.) Brid.	RACAQU
Racomitrium heterostichum (Hedw.) Brid.	RACHET
Racomitrium obtusum (Brid.) Brid.	RACOBT

Dierβen (2001), allowed an explanation of the observed patterns and proved to be useful in interpretation of ecological differences between communities. This is in agreement with other studies (Alpert, 1985, 1991; Fransson, 2003). Therefore, we found that granitic rock outcrops support distinct assemblages of species with contrasting ecological requirements and micro-scale variables such as measured can be used as filters to assemble a list of species that are potentially able to coexist in a small scale. In addition, it was observed that bryophyte richness per sample plot seems to be related with micro-scale variables. It increases with higher moisture and lower light supply than often occur on northerly exposures and steep slopes (Fig. 6). Likewise, bryophyte species richness was only found to be correlated with micro-scale factors in a study performed in cliff faces (Kuntz & Larson, 2006). Analysis of macro scale patterns on community variation revealed that the geographic position of sampling localities within each mountain area, clearly related with precipitation, influence the community structure (Fig. 9), suggesting that these communities could be used to predict changes in its future distribution, given likely environmental changes (Birks *et al.*, 1998). These results are in agreement with similar investigations (Cox & Larson, 1993; Matthes *et al.*, 2000). Other studies have also indicated an important large-scale influence of precipitation on bryophyte community structure (Hill & Dominguez Lozano, 1994; Gignac, 2001; Callaghan & Ashton, 2008).

The residual variation of species assemblages is quite high (88%) and can be attributed to unmeasured variables, sampling method problems and to the stochastic fluctuations of the communities (Legendre & Legendre, 1998). Unmeasured variables could be related with nutrient availability that can vary greatly over periods of time, population or community processes such as random spore dispersal and cyclic succession (Jonsgard & Birks, 1993; Bates, 2000). Nevertheless, it is impossible to discriminate between the fraction of currently unexplained variation that could potentially be explained by additional variables and the real stochasticity in that unexplained variation, since it may not be feasible to measure all the variables that are relevant in an ecological study (Borcard *et al.*, 1992). Additionally, the fairly low percentage of explained variation is not uncommon in ecological studies (Økland, 1999) since species data are often very noisy (Gauch, 1982; Palmer, 1993; ter Braak & Šmilauer, 2002). In a study about the influence of environmental factors on the spatial distribution of saxicolous lichens in a Norwegian coastal community (Bjelland, 2003), 91% of unexplained floristic variation was found and it was shown that vegetation cover explained more of the floristic variation than microhabitat variables and other variables like radiation and maritime influence. This is not in accordance with our results that showed a high amount of variation in community structure explained by micro-scale variables.

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