



# The influence of environmental factors on biological soil crust: from a community perspective to a species level approach

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## Keywords

Diversity; Lichen; Moss; Precipitation; Richness; *Stipa tenacissima*; Semi-arid grassland; Shrub; Substrate

## Nomenclature

Nimis & Martellos (2004); Prieto et al. (2010a,b) for *Placidium*, *Catapyrenium* and *Placidopsis*; Hladun & Llimona (2002–2007), Prieto et al. (2010a,b) for lichens; Brugués & Cros (2012) for bryophytes

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## Introduction

Drylands worldwide hold rich and highly dynamic communities of biological soil crusts (BSC) (Rivera-Aguilar et al. 2006; Hernandez & Knudsen 2012). BSCs commonly dominate ground cover in such ecosystems, and strongly influence carbon and nitrogen cycles, enhance soil stability, participate in hydrological regime and provide habitat for other soil biota communities (Bamforth 2004; Bowker et al. 2008; Jiménez Aguilar et al. 2009; Chamizo et al. 2012; Elbert et al. 2012). They are mainly composed of cyanobacteria, lichens, liverworts and mosses growing on or within the soil surface, and constitute a unique ecosystem component, both from a functional and diversity perspective (Bowker et al. 2011; Miller et al. 2011).

## Abstract

**Questions:** Environmental factors have been identified as strong modulators of plant community distribution and diversity, especially in arid and semi-arid ecosystems. Despite recent advances in the ecology of biological soil crusts (BSC) from a community perspective, much remains unknown at the species level. Do environmental factors at different scales influence species richness, diversity and composition of BSC communities? At the species level, what are the main predictors for species occurrence and frequency?

**Location:** A geographic gradient from southeast to central Spain.

**Methods:** In a geographic gradient, we characterized BSC communities based on species richness and diversity, species composition and species frequency. Using generalized linear mixed models (GLMMs) and multivariate analyses we evaluated the effect of precipitation, type of soil substrate, presence of shrubs and presence of *Stipa tenacissima* on community attributes.

**Results:** Precipitation positively influenced species richness and diversity, but had little effect on BSC occurrence at the species level. Type of substrate was a strong predictor for species composition, occurrence and frequency, gypsiferous soils being those with higher species richness and diversity. At the local scale, *S. tenacissima* had more effect on species occurrence and frequency, while shrub presence was a poor predictor of community attributes.

**Conclusions:** Environmental factors influence BSC diversity predominantly at a large scale, while local-scale factors influence both community diversity and species distribution.

Under the emerging paradigm linking biodiversity with ecosystem functioning and resilience (Folke et al. 2004; Hooper et al. 2005), there is increasing interest in assessing BSC community contribution in this context (Bowker et al. 2010; Castillo-Monroy et al. 2011; Maestre et al. 2012). Unfortunately much about the environmental factors influencing BSC diversity structure and dynamics remains unknown, especially at the species level (but see Maestre 2003; Pintado et al. 2005; Zedda et al. 2011).

Diversity and composition of BSC communities depend on different factors operating at different spatial and temporal scales (García-Pichel & Belnap 2003; Ullmann & Büdel 2003; Bowker et al. 2006; Root & McCune 2012). For instance, the importance of microhabitat factors at local scales, such as some physico-chemical soil properties (Ponzetti & McCune 2001; Rivera-Aguilar et al. 2009) and the vascular

vegetation (Maestre et al. 2009) is well known, whereas at broader scales, macroclimate trends are by far the most relevant drivers (Eldridge & Tozer 1997; Zedda et al. 2011).

Small-scale soil physico-chemical properties influence BSC richness, composition and abundance of BSC communities. In particular, soil type has been related to differences in BSC diversity (Bowker & Belnap 2008), e.g. gypsiferous soils hold rich and diverse communities (Martínez-Sánchez et al. 1994; Martínez et al. 2006). Also, BSC composition varies depending on soil type, e.g. calcareous soils have been related to BSC communities dominated by mosses and liverworts (Downing & Selkirk 1993), whereas lichens generally dominate in gypsum soils (Büdel 2003).

In arid environments, the presence of vascular vegetation may favour particular groups of BSC organisms (such as mosses and liverworts), since it provide wetter soil microsites protected from direct solar radiation. On the other hand, plant cover may reduce potential habitat for BSC, since free soil interspaces diminish (Belnap et al. 2003). In particular, the importance of shrub cover remains controversial; some authors have found a negative relation between shrub cover and BSC lichen richness in disturbed sites (Root & McCune 2012), while others have not detected it (Maestre et al. 2009), although abrupt shifts in the dominant functional groups of the corresponding BSCs have been found.

One of the main limitations of previous works is related to the fact that they have considered BSCs as homogeneous entities (e.g. community level) or at best considered some functional or taxonomic groups (e.g. lichen and bryophyte taxa). However, the effect of these drivers may differ at the species level, as recently showed in other lichen-dominated cryptogram communities (Belinchon et al. 2007; Zedda et al. 2011).

In drylands, where perennial and annual plants along with BSC vegetation co-exist, the effect of large-scale environmental factors on ecosystem species richness and diversity is tightly related to vascular vegetation structure and dynamics (Maestre et al. 2009; Luzuriaga et al. 2012). BSCs represent a fundamental component in arid and semi-arid ecosystems and are critical for the ecosystem function and services these drylands provide (Bowker et al. 2010). Thus, there is a need to fully understand their response in diversity terms to environmental factors at several spatial scales, and also to know how the species effects are scaled up to the whole BSC. This is particularly relevant in the context of ecosystem management and conservation (Bowker et al. 2008), and to address global change impacts on BSC communities and ecosystem dynamics (Belnap et al. 2008).

The aim of the present study is to determine what are the drivers of the diversity and composition of lichen-dominated BSCs at several spatial scales, but simultaneously

taking into consideration the species responses to such factors. With this in mind, we surveyed an open grassland community (*espartales*, which are dominated by a tussock grass, *Stipa tenacissima*; Maestre et al. 2009) along a geographic gradient in the Iberian Peninsula, with different soil types scattered along the gradient, and explicitly considering several factors inducing heterogeneity at a local scale. This model ecosystem is especially suitable for our research since we have profound knowledge of the role played by its BSCs on ecosystem functionality (Maestre et al. 2011), and detailed studies on the flora and vegetation have been conducted in the region from the beginning of the 1970s (Crespo 1973; Llimona 1974; Crespo & Barreno 1975).

We addressed the following questions: (i) how do BSC species distribute along a geographic gradient; (ii) do environmental factors from regional to local scales (i.e. climate, type of substrate, vascular vegetation) influence species richness, diversity and composition of BSC communities; and (iii) at the species level, which are the main predictors for species occurrence and frequency?

## Methods

### Study area

We conducted our survey in 16 sites along a geographic gradient from the southeastern-most tip of the Iberian Peninsula (the driest conditions) to its centre, where more humid environments are found (Fig. 1, Table 1).

The annual precipitation and temperature for the gradient ranged from 282 to 497 mm and from 13 to 17 °C, respectively. Soils were calcareous (*Lithic Calciorthid*) for 11 sites and gypsiferous (*Typic Gypsiorthid*) for five sites (Soil Survey Staff 1994), and in all sites the dominant vegetation was an open grassland dominated by tussocks of *S. tenacissima* L. interspersed in a bare ground matrix with well-developed BSCs. *Quercus coccifera* L., *Juniperus oxycedrus* L., *Rhamnus lycioides* L., *Rhamnus alaternus* L. and *Pistacia lentiscus* L., and occasionally *Quercus ilex* L., are the most common shrubs. Total cover values of perennial vegetation ranged from 31% to 67%.

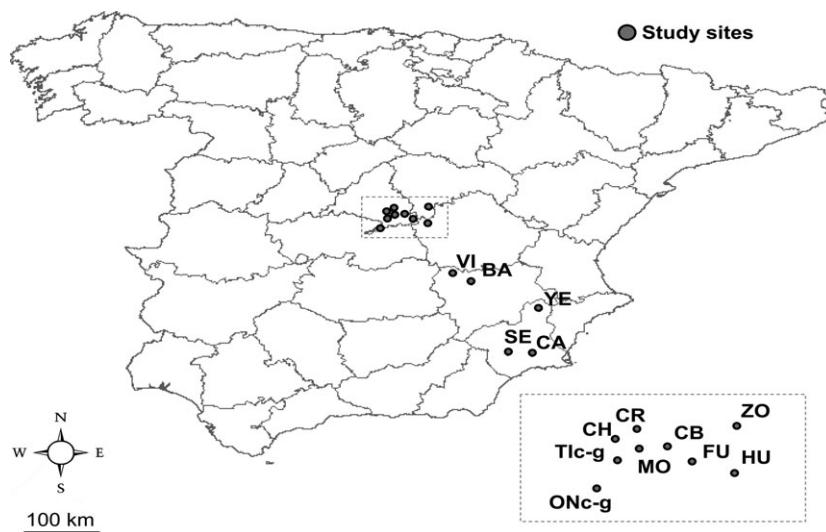
### Fieldwork

The BSC sampling was carried out between late summer and early autumn of 2006. We established two paired plots (30m × 30m) at each site along the geographic gradient. As we wanted to know the influence of both climatic variables and vascular vegetation on the richness, diversity and composition of BSC communities, we selected one of those plots in an area with shrubs and the other in areas without shrubs. In addition, we established at each plot ten sampling quadrats associated with *S. tenacissima*

**Table 1.** Site characteristics. Elevation, climatic variables, soil type and total number of species for each site along the environmental gradient.

| Site               | Ele (m a.s.l.) | P (mm) | T(°C) | Soil type          | No. of species | UTM N, UTM E       |
|--------------------|----------------|--------|-------|--------------------|----------------|--------------------|
| Carrascoy (CA)     | 406            | 282    | 17    | Lithic Calciorthid | 14             | 649 300, 4 185 217 |
| Yecla (YE)         | 819            | 336    | 14    | Lithic Calciorthid | 4              | 656 928, 4 272 868 |
| Sierra Espuña (SE) | 663            | 364    | 16    | Lithic Calciorthid | 16             | 616 839, 4 187 005 |
| Ontígola (ONG)     | 593            | 426    | 14    | Typic Gypsiorthid  | 19             | 446 915, 4 427 092 |
| Ontígola (ONc)     | 593            | 431    | 14    | Lithic Calciorthid | 17             | 447 271, 4 427 264 |
| Barrax (BA)        | 781            | 433    | 14    | Lithic Calciorthid | 20             | 566 691, 4 322 614 |
| Zorita (ZO)        | 632            | 434    | 14    | Lithic Calciorthid | 11             | 510 519, 4 467 352 |
| Titulcia (Tlg)     | 551            | 439    | 14    | Typic Gypsiorthid  | 23             | 456 397, 4 446 093 |
| Titulcia (Tlc)     | 628            | 440    | 14    | Lithic Calciorthid | 18             | 457 304, 4 448 724 |
| Villarobledo (VI)  | 748            | 446    | 14    | Lithic Calciorthid | 20             | 542 006, 4 340 126 |
| Chinchón (CH)      | 593            | 447    | 14    | Typic Gypsiorthid  | 21             | 456 433, 4 458 275 |
| Fuentidueña (FU)   | 603            | 452    | 14    | Typic Gypsiorthid  | 20             | 488 787, 4 443 880 |
| Morata (MO)        | 627            | 455    | 14    | Lithic Calciorthid | 15             | 464 440, 4 451 222 |
| Carabaña (CB)      | 630            | 462    | 14    | Typic Gypsiorthid  | 20             | 478 288, 4 455 557 |
| Campo Real (CR)    | 642            | 465    | 14    | Lithic Calciorthid | 15             | 463 842, 4 463 566 |
| Huelves (HU)       | 891            | 497    | 13    | Lithic Calciorthid | 17             | 508 577, 4 435 542 |

Ele = Elevation; P = Annual precipitation; T = mean annual temperature; UTM N, UTM E = UTM coordinates north and east, respectively. Sites are arranged in order of increases in precipitation. Site codes are given in parenthesis.



**Fig. 1.** Site locations along the geographic gradient from southeast to central Spain. Sites are described in Table 1.

tussocks, and ten quadrats in apparently bare soil ( $N = 20$  for each plot). A 'shrub plot' was located on land with well-developed adult individuals of sprouting shrubs (26.4% of total perennial cover, on average) and a 'no shrub plot' was located on land with no adult shrubs (0.4% of total perennial cover, on average; Table 1).

The two plots were located by <1000 m apart in order to ensure that shrub and no shrub plots shared the same climatic conditions. Each pair had very similar physiographic (slope, aspect) and geologic (parent material) characteristics. Although *S. tenacissima* grasslands are typically subjected to livestock production in the region, no grazing activity has been carried out in the study sites during the last decade (*in situ* observations and pers. com.). Inside

each 30m × 30m plot, we randomly placed ten quadrats (50m × 50m) associated with *S. tenacissima* tussocks (*Stipa* microsite) and ten quadrats in apparently bare soil (open microsite) in order to examine the probable influence of tussock nearness. The number of sampling quadrats at the microsite level ( $N = 10$ ) was sufficient to find 95% of species. Finally, a total of 580 quadrats were surveyed. Available surface for the BSC components was always around 100%.

### The BSC identification and sampling

The BSC communities were identified to genus and species level when possible, following Nimis & Martellos (2004)

and Prieto et al. (2010a,b) for *Placidium*, *Catapyrenium* and *Placidiopsis*. Nomenclature follows Hladun & Llimona (2002–2007) and Prieto et al. (2010a,b) for lichens, and Brugués & Cros (2012) for bryophytes.

We collected the upper soil layer of each quadrat, and all material was examined under a binocular microscope (Nikon SMZ800; Nikon, Kawasaki, Kanawaga, Japan) in order to detect the highest number of species. We recorded the occurrence of each species as 1 when the species was present in a quadrat and 0 when absent. In addition, we calculated the frequency of occurrence (frequency hereafter) for each species at the microsite level as the number of quadrats with the species ( $N = 10$ ).

Species richness was calculated as the total number of different species occurring in a quadrat. We estimated species diversity using the Shannon diversity index ( $H$ ) based on species frequency at the microsite level.

### Statistical analyses

To test the effect of climatic variables (annual precipitation and mean annual temperature) and variables at local scale (type of substrate, shrub presence and *S. tenacissima* presence) on BSC community attributes (species occurrence, frequency, richness and diversity), we applied generalized linear mixed models (GLMMs; McCullagh & Nelder 1989). We found that annual precipitation and mean annual temperature were highly and significantly correlated (Coef. Pearson =  $-0.849$ ,  $P < 0.0001$ ), thus temperature were not included in GLMM analysis. Since our data on BSC community attributes had a hierarchical structure, with quadrats nested within plots and plots nested within sites, we analysed the data using a multi-level approach, and considered the variables 'site' and 'plot' as random factors to take in account the intra-class correlation. We performed GLMMs for species richness, species diversity, and separate models for species occurrence and frequency for each species. For species richness, we fitted the mixed models using a Poisson distribution with a log link function. For species diversity, we fitted the models using a normal distribution with an identity link function, after exponential transformation of the data to achieve normality, and for species occurrence and frequency we used a binomial distribution with a logit link function. For all models, we included the annual precipitation, type of substrate (calcareous or gypsiferous), presence/absence of shrubs (shrub hereafter) and presence/absence of *S. tenacissima* (*Stipa* hereafter) as fixed factors. Moreover, we also included in our models the interactions between precipitation  $\times$  shrub, precipitation  $\times$  *Stipa* and shrub  $\times$  *Stipa*, when possible. For logistic reasons, rare species (i.e. species present in  $<1\%$  of

total sampling quadrats) were excluded from the analysis, and factor interactions were not evaluated for those variables calculated at the microsite level (frequency and diversity). Also, the variable type of substrate was not included in the models when the species were only found in calcareous or gypsiferous soil (reported as nd = no data in tables). We estimated the significance of each predictor by means of ANOVA (Guisan et al. 2002).

All GLMM computations were performed using SAS Macro program GLIMMIX, which iteratively calls SAS Procedure Mixed until convergence (GLIMMIX v. 8; SAS/STAT, [www.sas.com.techsup/download/stat/](http://www.sas.com.techsup/download/stat/)). To determine the degree of similarity in BSC composition along the geographic gradient, we conducted non-metric multi-dimensional scale analysis (NMDS) of the BSC community data (microsite level) with species frequency data using Bray–Curtis distance. To evaluate the potential effect of large-scale environmental factors on BSC community composition, we obtained Pearson correlations between BSC ordination axes and both precipitation and temperature. We previously rotated NMDS ordination axes to maximize correlation with horizontal axis (following Bowker et al. 2011). All multivariate analyses were performed with Primer v. 6 (Clarke & Gorley 2006).

### Results

#### The BSC distribution along the geographic gradient

We found a total of 41 taxa: one cyanobacterium identified at genus level (*Nostoc* sp.), 32 lichens, seven mosses and one liverwort. Lichen species included 17 genera and 13 families, whereas bryophytes species comprised six genera and three families. *Verrucariaceae* and *Pottiaceae* were the dominant lichen and moss families, respectively (Table 2). Gypsiferous sites had a higher number of species than calcareous sites. In particular, Titulcia (gypsiferous site) had 23 species, while Yecla (calcareous site) had only four species (Table 1).

*Nostoc* sp., nine lichens and the liverwort *Riccia* sp. were found only on calcareous soil (Table 2). Six lichens (*Acarospora nodulosa* var. *reagens*, *Buellia zoharyi*, *Diplo-tomma epipolium*, *Leproloma* sp., *Psora globifera* and *Lecidea lurida*) and three mosses (*Syntrichia caninervis*, *Syntrichia papillosissima* and *Tortula revolvens*) were exclusively found in sites with gypsiferous soils (Table 2), although *P. globifera* and *L. lurida* were extremely rare. We observed that 16 lichen and four moss species were substrate indifferent (Table 2). *Diploschistes muscorum* and *Didymodon acutus* were present only in the shrub plots of calcareous and gypsiferous soils, respectively, whereas *Leproloma* sp. was only found in no-shrub plots of gypsiferous soils (Table 2). *Collema crispum*, *C. tenax*, *Psora decipiens*, *Squamarina lentigera*

**Table 2.** List of biological soil crusts species and their frequency.

| Species   | <i>Lithic Calciorthid</i> |       |              |       | <i>Typic Gypsiorthid</i> |      |              |      | Tot. f. | Tot. q. |
|---|---------------------------|-------|--------------|-------|--------------------------|------|--------------|------|---------|---------|
|   | Shrub                     |       | No shrub     |       | Shrub                    |      | No shrub     |      |         |         |
|   | <i>Stipa</i>              | Open  | <i>Stipa</i> | Open  | <i>Stipa</i>             | Open | <i>Stipa</i> | Open |         |         |
| Cyanobacterium  |                           |       |              |       |                          |      |              |      |         |         |
| <i>Nostoc</i> sp.   | 5.34                      | 3.79  | 5            | 2.41  | 0                        | 0    | 0            | 0    | 16.55   | 96      |
| Lichen  |                           |       |              |       |                          |      |              |      |         |         |
| <i>Acarospora nodulosa</i> var. <i>reagens</i> (Dufour) Hue | 0                         | 0     | 0            | 0     | 0.34                     | 1.55 | 2.76         | 7.24 | 11.9    | 69      |
| <i>Buellia zoharyi</i> Galun                                | 0                         | 0     | 0            | 0     | 1.38                     | 2.93 | 2.07         | 5.34 | 11.72   | 68      |
| <i>Cetraria aculeata</i> (Schreb. Fz.)                      | 0.52                      | 0     | 0.17         | 0.17  | 0                        | 0    | 0            | 0    | 0.86    | 5       |
| <i>Cladonia convoluta</i> (Lam. Cout.)                      | 2.93                      | 2.07  | 3.97         | 4.14  | 1.9                      | 1.38 | 4.83         | 5.86 | 27.07   | 157     |
| <i>Cladonia rangiformis</i> Hoffm.                          | 1.72                      | 1.55  | 1.21         | 1.72  | 0                        | 0    | 0            | 0    | 6.21    | 36      |
| <i>Collema crispum</i> (Huds.) Weber ex F.H. Wigg           | 4.83                      | 8.1   | 8.45         | 6.21  | 2.41                     | 2.93 | 6.38         | 7.93 | 47.24   | 274     |
| <i>Collema cristatum</i> (L.) F.H. Wigg                     | 0.34                      | 0.34  | 0.52         | 0.17  | 0                        | 0    | 0            | 0    | 1.38    | 8       |
| <i>Collema tenax</i> (Sw.) Ach. Em. Degel                   | 10.69                     | 10.34 | 7.76         | 11.72 | 0                        | 0.34 | 1.03         | 0    | 41.9    | 243     |
| <i>Diploschistes diacapsis</i> (Ach.) Lumbsch.              | 0.34                      | 0.34  | 0.69         | 1.21  | 2.41                     | 2.76 | 7.41         | 8.45 | 23.62   | 137     |
| <i>Diploschistes muscorum</i> (Scop) R. Santi               | 0.52                      | 0.34  | 0            | 0     | 0                        | 0    | 0            | 0    | 0.86    | 5       |
| <i>Diplotomma epipolium</i> (Ach.) Arnold                   | 0                         | 0     | 0            | 0     | 0.52                     | 1.21 | 1.21         | 3.1  | 6.03    | 35      |
| <i>Endocarpon pusillum</i> Hedw.                            | 0.17                      | 1.03  | 0.69         | 0.17  | 0                        | 0    | 0            | 0    | 2.07    | 12      |
| <i>Fulgensia fulgens</i> (Sw.) Elenkin                      | 2.93                      | 2.59  | 5            | 3.97  | 0                        | 0    | 0.17         | 0.17 | 14.83   | 86      |
| <i>Fulgensia subbracteata</i> (Nyl.) Poelt                  | 0.17                      | 0     | 0.34         | 0.34  | 3.45                     | 3.45 | 7.24         | 8.28 | 23.28   | 135     |
| <i>Heteroplacidium imbricatum</i> (Nyl.) Breuss             | 0.34                      | 0.17  | 0            | 0.17  | 0                        | 0    | 0            | 0    | 0.69    | 4       |
| <i>Lecidea lurida</i> (Ach.)                                | 0                         | 0     | 0            | 0     | 0                        | 0    | 0            | 0.86 | 0.86    | 5       |
| <i>Leproloma</i> sp.  | 0                         | 0     | 0            | 0     | 0                        | 0    | 0.17         | 1.38 | 1.55    | 9       |
| <i>Leptogium schraderii</i> (Ach.) Nyl.                     | 3.28                      | 4.66  | 1.21         | 3.62  | 0                        | 0.17 | 0.17         | 0.17 | 13.28   | 77      |
| <i>Placidopsis cinerascens</i> (Nyl.) Breuss                | 0.52                      | 0.34  | 0.17         | 0.17  | 0                        | 0    | 0            | 0    | 1.21    | 7       |
| <i>Placidopsis custnani</i> (A. Massal.) Körb               | 0                         | 0     | 0            | 0.17  | 0                        | 0    | 0            | 0    | 0.17    | 1       |
| <i>Placidium pilosellum</i> (Breuss) Breuss                 | 0.86                      | 1.72  | 2.24         | 2.07  | 0.17                     | 0.34 | 1.21         | 1.72 | 10.34   | 60      |
| <i>Placidium squamulosum</i> (Ach.) Breuss                  | 1.55                      | 4.14  | 4.14         | 5.86  | 1.38                     | 2.93 | 2.93         | 5.52 | 28.45   | 165     |
| <i>Placynthium nigrum</i> (Huds.) Gray                      | 0                         | 0.17  | 0            | 0     | 0                        | 0    | 0            | 0    | 0.17    | 1       |
| <i>Psora decipiens</i> (Hedw.) Hoffm.                       | 2.59                      | 4.48  | 5            | 6.9   | 1.38                     | 3.45 | 8.1          | 8.45 | 40.34   | 234     |
| <i>Psora globifera</i> (Ach.) A. Massal                     | 0                         | 0     | 0            | 0     | 0                        | 0    | 0            | 1.03 | 1.03    | 6       |
| <i>Psora saviczii</i> (Tomin) Follmann et A. Crespo         | 0                         | 1     | 0            | 0.17  | 0.17                     | 0.86 | 1.55         | 4.83 | 8.45    | 49      |
| <i>Squamarina cartilaginea</i> (With.) P. James)            | 6.03                      | 2.07  | 4.83         | 2.59  | 0.34                     | 0.34 | 1.03         | 0.34 | 17.59   | 102     |
| <i>Squamarina lentigera</i> (Weber) Poelt                   | 1.38                      | 2.07  | 3.1          | 3.62  | 3.45                     | 3.45 | 8.1          | 8.45 | 33.62   | 195     |
| <i>Toninia albilabra</i> (Dufour) H. Olivier                | 0.69                      | 0.86  | 0.34         | 0.17  | 0                        | 0    | 0.34         | 0    | 2.41    | 14      |
| <i>Toninia sedifolia</i> (Scop.) Timdal                     | 0.69                      | 1.9   | 2.76         | 2.59  | 2.41                     | 3.45 | 4.83         | 8.28 | 26.9    | 156     |
| <i>Toninia taurica</i> (Szatala) Oxner                      | 0                         | 0     | 0            | 0     | 0.52                     | 0.34 | 0.86         | 0.34 | 2.07    | 12      |
| Moss  |                           |       |              |       |                          |      |              |      |         |         |
| <i>Barbula</i> sp.  | 0.69                      | 0.86  | 0.52         | 1.21  | 0.17                     | 0.34 | 3.28         | 2.24 | 9.31    | 54      |
| <i>Didymodon acutus</i> (Brid) K. Saito                     | 0                         | 0     | 0            | 0     | 1.55                     | 1.38 | 0            | 0    | 2.93    | 17      |
| <i>Pleurochaete squarrosa</i> (Brid) Lindb.                 | 8.1                       | 1.21  | 10.52        | 1.38  | 2.41                     | 2.41 | 0.86         | 1.21 | 28.1    | 163     |
| <i>Syntrichia caninervis</i> Mitt                           | 0                         | 0     | 0            | 0     | 0                        | 2.24 | 0.86         | 1.03 | 4.14    | 24      |
| <i>Syntrichia papillosum</i> (Copp.) Loeske                 | 0                         | 0     | 0            | 0     | 1.55                     | 1.38 | 0.86         | 0.17 | 3.97    | 23      |
| <i>Tortula revolvens</i> (Schimp.) G. Roth                  | 9.48                      | 5.69  | 7.76         | 4.83  | 3.28                     | 3.1  | 7.24         | 7.59 | 48.97   | 284     |
| <i>Weissia</i> sp.  | 3.79                      | 6.55  | 6.55         | 8.28  | 0                        | 1.38 | 1.03         | 1.21 | 28.79   | 167     |
| Liverwort   |                           |       |              |       |                          |      |              |      |         |         |
| <i>Riccia</i> sp.   | 0.17                      | 0     | 0            | 0     | 0                        | 0    | 0            | 0    | 0.17    | 1       |

Frequency is expressed as a percentage of 580 (total number of sampling quadrats) in each of the different conditions considered in the study. Tot. f. = total frequency of each species; Tot. q. = total number of quadrats where a species was found.

and *Tortula revolvens* were the most frequent species, present in more than a third of the quadrats. However, their relative frequencies differed depending on the type of substrate, e.g. total frequency of *Collema tenax* was 40.5% in calcareous soils and 1.4% in gypsiferous soils (Table 2).

### Effects of environmental factors on BSC community attributes

Results of the mixed models showed mainly the primary influence of large-scale drivers such as climatic variables and type of substrate on BSC diversity attributes. Species

**Table 3.** Summary of the generalized linear mixed models examining the effects of environmental factors on species richness and diversity.

|           | Effect               | Estimate ± SE           | F-value      | P-value       |
|-----------|----------------------|-------------------------|--------------|---------------|
| Richness  | P                    | <b>0.0089 ± 0.0026</b>  | <b>6.77</b>  | <b>0.022</b>  |
|           | Substrate            | <b>-0.9410 ± 0.2799</b> | <b>11.3</b>  | <b>0.0052</b> |
|           | Shrub                | 0.5563 ± 0.7104         | 0.6          | 0.4482        |
|           | <i>Stipa</i>         | <b>1.3363 ± 0.3702</b>  | <b>13.13</b> | <b>0.0003</b> |
|           | P * Shrub            | -0.0014 ± 0.0016        | 0.75         | 0.3997        |
|           | P * <i>Stipa</i>     | <b>-0.0033 ± 0.0008</b> | <b>15.33</b> | <b>0.0001</b> |
|           | Shrub * <i>Stipa</i> | -0.0106 ± 0.05953       | 0.03         | 0.8586        |
| Diversity | P                    | <b>0.0293 ± 0.01142</b> | <b>6.58</b>  | <b>0.0231</b> |
|           | Substrate            | <b>-5.2964 ± 1.3028</b> | <b>16.53</b> | <b>0.0011</b> |
|           | Shrub                | <b>-1.1260 ± 0.4314</b> | <b>6.81</b>  | <b>0.0221</b> |
|           | <i>Stipa</i>         | -0.5166 ± 0.3104        | 2.77         | 0.1073        |

P = annual precipitation, Substrate = calcareous soil, Shrub = shrub presence, *Stipa* = *Stipa tenacissima* presence. Significance at 0.05 level are shown in bold.

richness and diversity were significantly higher in sites with higher precipitation and on gypsiferous substrate (Table 3). The presence of *S. tenacissima* had a positive

effect on species richness but this effect varied with precipitation, as shown by the interaction precipitation × *Stipa* (Table 3). The presence of shrubs was negatively related to species diversity (Table 3).

A total of 30 species were used for occurrence and frequency models. The most relevant predictors for species occurrence and frequency were the type of substrate and the presence of *S. tenacissima* (Table 4), with large differences between species. There was a group of species whose occurrence was tightly linked to gypsiferous soils, e.g. *Diploschistes diacapsis*, *Fulgensia subbracteata*, *Placidium squamulosum*, *Psora decipiens*, *P. saviczii*, *Squamarina lentigera*, *Toninia sedifolia* and *Tortula revolvens*, whereas *Collema tenax* and *Fulgensia fulgens* preferred calcareous soils. Regarding frequency, the majority of lichen species were more frequent on gypsiferous soils, except *Collema tenax*, *Fulgensia fulgens*, *Leptogium schraderi* and the moss *Weissia* sp. (Table 5).

Shrub presence-absence had no effect on occurrence of other BSC species (Table 4). However, some species such as *Syntrichia papillosissima* was more frequent in relation to

**Table 4.** Summary of the generalized linear mixed models examining the effects of environmental predictors on occurrence of the 30 species considered.

| Species  | P                     | Substrate              | Shrub                   | <i>Stipa</i>            | P * Shrub             | P * <i>Stipa</i>      | Shrub * <i>Stipa</i>   |
|--|-----------------------|------------------------|-------------------------|-------------------------|-----------------------|-----------------------|------------------------|
| <i>Nostoc</i> sp.                              | 0.0090 <sup>ns</sup>  | nd                     | 6.9299 <sup>ns</sup>    | 1.6381 <sup>ns</sup>    | -0.0132 <sup>ns</sup> | -0.0011 <sup>ns</sup> | -0.6434 <sup>ns</sup>  |
| <i>Acarospora nodulosa</i> var. <i>reagens</i> | 0.0791 <sup>ns</sup>  | nd                     | 7.6332 <sup>ns</sup>    | <b>28.7086**</b>        | -0.0203 <sup>ns</sup> | <b>-0.0713**</b>      | 0.3277 <sup>ns</sup>   |
| <i>Buellia zoharyi</i>                         | 0.0989 <sup>ns</sup>  | nd                     | 0.5310 <sup>ns</sup>    | <b>43.5949***</b>       | 0.0015 <sup>ns</sup>  | <b>-0.1027***</b>     | -0.5083 <sup>ns</sup>  |
| <i>Cladonia convoluta</i>                      | 0.0621 <sup>ns</sup>  | -2.4031 <sup>ns</sup>  | 12.5987 <sup>ns</sup>   | 3.8301 <sup>ns</sup>    | -0.0322 <sup>ns</sup> | -0.0095 <sup>ns</sup> | <b>1.2081*</b>         |
| <i>Collema crispum</i>                         | 0.0084 <sup>ns</sup>  | -2.2618 <sup>ns</sup>  | -5.0850 <sup>ns</sup>   | -2.0753 <sup>ns</sup>   | 0.0126 <sup>ns</sup>  | 0.0051 <sup>ns</sup>  | <b>-1.4131**</b>       |
| <i>Collema cristatum</i>                       | -0.0411 <sup>ns</sup> | nd                     | -12.9886 <sup>ns</sup>  | <b>-76.1813**</b>       | 0.0366 <sup>ns</sup>  | <b>0.1780**</b>       | <b>-3.0985**</b>       |
| <i>Collema tenax</i>                           | <b>0.0210*</b>        | <b>3.4605**</b>        | -0.1684 <sup>ns</sup>   | <b>5.1649**</b>         | 0.0005 <sup>ns</sup>  | <b>-0.0137**</b>      | 0.5492 <sup>ns</sup>   |
| <i>Diplotomma epipolium</i>                    | 0.0675 <sup>ns</sup>  | nd                     | 16.4779 <sup>ns</sup>   | 5.5639 <sup>ns</sup>    | -0.0357 <sup>ns</sup> | -0.0159 <sup>ns</sup> | -0.2433 <sup>ns</sup>  |
| <i>Diploschistes diacapsis</i>                 | 0.0108 <sup>ns</sup>  | <b>-9.2661***</b>      | 7.2463 <sup>ns</sup>    | -1.1491 <sup>ns</sup>   | -0.0221 <sup>ns</sup> | -0.0011 <sup>ns</sup> | <b>1.2303*</b>         |
| <i>Endocarpon pusillum</i>                     | 0.4911 <sup>ns</sup>  | nd                     | 231.8700 <sup>err</sup> | 1.7928 <sup>ns</sup>    | -0.4773 <sup>ns</sup> | 0.0000 <sup>ns</sup>  | -4.3824 <sup>ns</sup>  |
| <i>Fulgensia fulgens</i>                       | -0.0003 <sup>ns</sup> | <b>3.2719*</b>         | -5.0391 <sup>ns</sup>   | -2.8496 <sup>ns</sup>   | 0.0102 <sup>ns</sup>  | 0.0076 <sup>ns</sup>  | -0.2512 <sup>ns</sup>  |
| <i>Fulgensia subbracteata</i>                  | 0.0030 <sup>ns</sup>  | <b>-10.7450***</b>     | -10.8513 <sup>ns</sup>  | 4.1122 <sup>ns</sup>    | 0.0236 <sup>ns</sup>  | -0.0118 <sup>ns</sup> | <b>3.2675*</b>         |
| <i>Leptogium schraderi</i>                     | 0.0168 <sup>ns</sup>  | 2.7279 <sup>ns</sup>   | 2.6461 <sup>ns</sup>    | 0.6045 <sup>ns</sup>    | -0.0055 <sup>ns</sup> | -0.0046 <sup>ns</sup> | 0.4292 <sup>ns</sup>   |
| <i>Placidopsis cinerascens</i>                 | 0.0017 <sup>ns</sup>  | nd                     | 4.9424 <sup>ns</sup>    | <b>8.4284*</b>          | -0.0095 <sup>ns</sup> | <b>-0.0207*</b>       | 0.0401 <sup>ns</sup>   |
| <i>Placidium pilosellum</i>                    | 0.0153 <sup>ns</sup>  | -2.3290 <sup>ns</sup>  | -5.9696 <sup>ns</sup>   | <b>14.6344*</b>         | 0.0124 <sup>ns</sup>  | <b>-0.0340*</b>       | <b>-1.0525*</b>        |
| <i>Placidium squamulosum</i>                   | 0.0054 <sup>ns</sup>  | <b>-1.5418*</b>        | 3.1048 <sup>ns</sup>    | -4.2290 <sup>ns</sup>   | -0.0079 <sup>ns</sup> | 0.0077 <sup>ns</sup>  | -0.4409 <sup>ns</sup>  |
| <i>Psora decipiens</i>                         | 0.0201 <sup>ns</sup>  | <b>-4.4258**</b>       | 4.8174 <sup>ns</sup>    | -0.1848 <sup>ns</sup>   | -0.0135 <sup>ns</sup> | -0.0014 <sup>ns</sup> | <b>-1.1302*</b>        |
| <i>Psora saviczii</i>                          | 0.0113 <sup>ns</sup>  | <b>-4.0402**</b>       | 1.6789 <sup>ns</sup>    | -2.3724 <sup>ns</sup>   | -0.0027 <sup>ns</sup> | 0.0009 <sup>ns</sup>  | -0.6583 <sup>ns</sup>  |
| <i>Squamarina cartilaginea</i>                 | 0.0114 <sup>ns</sup>  | 1.2454 <sup>ns</sup>   | -6.1155 <sup>ns</sup>   | 4.7044 <sup>ns</sup>    | 0.0142 <sup>ns</sup>  | -0.0083 <sup>ns</sup> | 0.5752 <sup>ns</sup>   |
| <i>Squamarina lentigera</i>                    | 0.0054 <sup>ns</sup>  | <b>-5.6813***</b>      | -1.4304 <sup>ns</sup>   | 0.6811 <sup>ns</sup>    | 0.0017 <sup>ns</sup>  | -0.0024 <sup>ns</sup> | -0.1080 <sup>ns</sup>  |
| <i>Toninia albilabra</i>                       | 0.5068 <sup>ns</sup>  | -11.3410 <sup>ns</sup> | -23.5948 <sup>ns</sup>  | 321.6600 <sup>***</sup> | 0.0597 <sup>ns</sup>  | <b>-0.7476***</b>     | 1.1950 <sup>ns</sup>   |
| <i>Toninia sedifolia</i>                       | 0.0089 <sup>ns</sup>  | <b>-3.9634***</b>      | -2.2963 <sup>ns</sup>   | -5.8115 <sup>ns</sup>   | 0.0044 <sup>ns</sup>  | 0.0108 <sup>ns</sup>  | -0.5549 <sup>ns</sup>  |
| <i>Toninia taurica</i>                         | -0.0048 <sup>ns</sup> | nd                     | -3.8453 <sup>ns</sup>   | <b>-29.8084*</b>        | 0.0119 <sup>ns</sup>  | <b>0.0703*</b>        | -0.9735 <sup>ns</sup>  |
| <i>Barbula</i> sp.                             | 0.0422 <sup>ns</sup>  | -2.6621 <sup>ns</sup>  | 0.8552 <sup>ns</sup>    | <b>16.0051*</b>         | -0.0020 <sup>ns</sup> | <b>-0.0356*</b>       | -0.6868 <sup>ns</sup>  |
| <i>Pleurochaete squarrosa</i>                  | <b>0.0170*</b>        | 1.4971 <sup>ns</sup>   | 3.3075 <sup>ns</sup>    | <b>-10.1316*</b>        | -0.0060 <sup>ns</sup> | <b>0.0292*</b>        | -0.4957 <sup>ns</sup>  |
| <i>Syntrichia caninervis</i>                   | 0.0424 <sup>ns</sup>  | nd                     | 12.7606 <sup>ns</sup>   | -0.4050 <sup>ns</sup>   | -0.0224 <sup>ns</sup> | 0.0000 <sup>ns</sup>  | -20.7590 <sup>ns</sup> |
| <i>Syntrichia papillosissima</i>               | 0.0204 <sup>ns</sup>  | nd                     | 1.3944 <sup>ns</sup>    | 2.1955 <sup>ns</sup>    | 0.0048 <sup>ns</sup>  | 0.0000 <sup>ns</sup>  | <b>-1.4023**</b>       |
| <i>Tortula revolvens</i>                       | 0.0188 <sup>ns</sup>  | <b>-3.3103*</b>        | 2.7501 <sup>ns</sup>    | <b>8.5199***</b>        | -0.0057 <sup>ns</sup> | <b>-0.0181***</b>     | 0.3859 <sup>ns</sup>   |
| <i>Weissia</i> sp.                             | 0.0092 <sup>ns</sup>  | 3.4842 <sup>ns</sup>   | 0.9159 <sup>ns</sup>    | <b>9.3556***</b>        | -0.0029 <sup>ns</sup> | <b>-0.0239***</b>     | <b>-1.4871**</b>       |

Coefficients of variables in the model are indicated. P = annual precipitation, Substrate = calcareous soil, Shrub = shrub presence, *Stipa* = *Stipa tenacissima* presence.

Asterisks denote interactions between variables. Significant values are shown in bold as: \*\*\*P < 0.0001, \*\*P < 0.005, \*P < 0.05, ns = not significant, nd = no data.

**Table 5.** Summary of the generalized linear mixed models of microsite-level predictors on the frequency of the 30 species considered.

| Species  | P                     | Substrate             | Shrub                 | <i>Stipa</i>          |
|--|-----------------------|-----------------------|-----------------------|-----------------------|
| <i>Nostoc</i> sp.                              | 0.0004 <sup>ns</sup>  | nd                    | 0.6034 <sup>ns</sup>  | <b>0.5108*</b>        |
| <i>Acarospora nodulosa</i> var. <i>reagens</i> | 0.0271 <sup>ns</sup>  | nd                    | −0.7042 <sup>ns</sup> | − <b>1.0415***</b>    |
| <i>Buellia zoharyi</i>                         | 0.0246 <sup>ns</sup>  | nd                    | 0.2961 <sup>ns</sup>  | − <b>0.8755***</b>    |
| <i>Cladonia convoluta</i>                      | 0.0271 <sup>ns</sup>  | −1.8266 <sup>ns</sup> | −0.5725 <sup>ns</sup> | 0.0127 <sup>ns</sup>  |
| <i>Collema crispum</i>                         | <b>0.0075*</b>        | − <b>0.7618*</b>      | −0.0678 <sup>ns</sup> | −0.1316 <sup>ns</sup> |
| <i>Collema cristatum</i>                       | 0.0162 <sup>ns</sup>  | nd                    | 0.8393 <sup>ns</sup>  | <b>0.5108*</b>        |
| <i>Collema tenax</i>                           | <b>0.0066*</b>        | <b>2.3166***</b>      | 0.0604 <sup>ns</sup>  | −0.1401 <sup>ns</sup> |
| <i>Diplolepta epipolium</i>                    | 0.0500 <sup>ns</sup>  | nd                    | <b>0.3566***</b>      | − <b>0.9163***</b>    |
| <i>Diploschistes diacapsis</i>                 | <b>0.0914***</b>      | − <b>9.4653**</b>     | − <b>0.2634***</b>    | − <b>0.1609***</b>    |
| <i>Endocarpon pusillum</i>                     | 0.0659 <sup>ns</sup>  | nd                    | 0.9956 <sup>ns</sup>  | −0.3365 <sup>ns</sup> |
| <i>Fulgensia fulgens</i>                       | 0.0054 <sup>ns</sup>  | <b>2.9142*</b>        | −0.5997 <sup>ns</sup> | 0.1866 <sup>ns</sup>  |
| <i>Fulgensia subbracteata</i>                  | 0.0092 <sup>ns</sup>  | − <b>7.7003***</b>    | −0.1477 <sup>ns</sup> | − <b>0.0741*</b>      |
| <i>Leptogium schraderii</i>                    | 0.0097 <sup>ns</sup>  | <b>2.2558*</b>        | 0.1685 <sup>ns</sup>  | − <b>0.6162**</b>     |
| <i>Placidopsis cinerascens</i>                 | −0.0187 <sup>ns</sup> | nd                    | 1.3306 <sup>ns</sup>  | 0.2877 <sup>ns</sup>  |
| <i>Placidium pilosellum</i>                    | −0.0053 <sup>ns</sup> | −2.126 <sup>ns</sup>  | −1.1564 <sup>ns</sup> | −0.2683 <sup>ns</sup> |
| <i>Placidium squamulosum</i>                   | 0.0026 <sup>ns</sup>  | − <b>1.0338*</b>      | −0.3385 <sup>ns</sup> | − <b>0.6124***</b>    |
| <i>Psora decipiens</i>                         | 0.0121 <sup>ns</sup>  | − <b>1.5538*</b>      | − <b>0.6659*</b>      | − <b>0.3102*</b>      |
| <i>Psora saviczii</i>                          | 0.0105 <sup>ns</sup>  | − <b>4.4194**</b>     | 0.9592 <sup>ns</sup>  | − <b>1.3610***</b>    |
| <i>Squamarina cartilaginea</i>                 | 0.0089 <sup>ns</sup>  | 1.0189 <sup>ns</sup>  | 0.3297 <sup>ns</sup>  | <b>0.8287***</b>      |
| <i>Squamarina lentigera</i>                    | 0.0053 <sup>ns</sup>  | − <b>2.1964*</b>      | − <b>0.5000*</b>      | −0.0924 <sup>ns</sup> |
| <i>Toninia albilabra</i>                       | −0.0121 <sup>ns</sup> | −0.8464 <sup>ns</sup> | 0.4406 <sup>ns</sup>  | 0.2877 <sup>ns</sup>  |
| <i>Toninia sedifolia</i>                       | <b>0.0112*</b>        | − <b>2.0368**</b>     | −0.5013 <sup>ns</sup> | − <b>0.4162**</b>     |
| <i>Toninia taurica</i>                         | 0.0223 <sup>ns</sup>  | nd                    | 0.5664 <sup>ns</sup>  | <b>0.6931*</b>        |
| <i>Barbula</i> sp.                             | 0.0140 <sup>ns</sup>  | −2.0719 <sup>ns</sup> | −0.2656 <sup>ns</sup> | 0 <sup>ns</sup>       |
| <i>Pleurochaete squarrosa</i>                  | <b>0.0208*</b>        | 0.4702 <sup>ns</sup>  | 0.1140 <sup>ns</sup>  | <b>1.2607**</b>       |
| <i>Syntrichia caninervis</i>                   | 0.0189 <sup>ns</sup>  | nd                    | 1.4749 <sup>ns</sup>  | − <b>1.3350***</b>    |
| <i>Syntrichia papillosum</i>                   | 0.0221 <sup>ns</sup>  | nd                    | <b>1.0198***</b>      | <b>0.4418***</b>      |
| <i>Tortula revolvens</i>                       | 0.0021 <sup>ns</sup>  | − <b>1.2405*</b>      | 0.1754 <sup>ns</sup>  | <b>0.2692*</b>        |
| <i>Weissia</i> sp.                             | −0.0013 <sup>ns</sup> | <b>1.6004*</b>        | −0.4295 <sup>ns</sup> | − <b>0.4255*</b>      |

Coefficients of variables in the model are indicated. P = annual precipitation, Substrate = calcareous soil, Shrub = shrub presence, *Stipa* = *Stipa tenacissima* presence.

Asterisks denote interactions between variables. Significant values are shown in bold as: \*\*\* $P < 0.0001$ , \*\* $P < 0.005$ , \* $P < 0.05$ , ns = not significant, nd = no data.

shrubs presence, while *Diploschistes diacapsis*, *Psora decipiens* and *Squamarina lentigera* frequency were negatively associated with shrub presence (Table 5). *S. tenacissima* presence had a significant and strong positive effect on the occurrence of nine species (e.g. *Toninia albilabra*, *Buellia zoharyi*), while it had a strong negative effect on occurrence of *Collema cristatum*, *Pleurochaete squarrosa* and *Toninia taurica* (Table 4). The interaction of *S. tenacissima* presence with both precipitation and shrub presence had significant effects in BSC species of different magnitude and nature depending on species identity (Table 4).

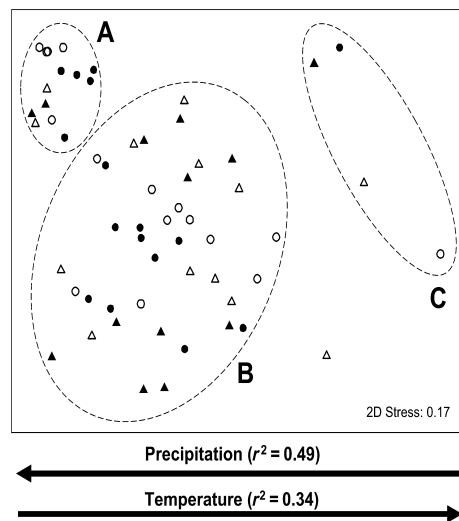
*Stipa tenacissima* presence had a significant, predominantly negative effect on most species frequencies (Table 5). Also, precipitation had a positive effect on the frequency of five species, including two cyanolichens, two chlorolichens and one moss species (Table 5). The *Leprolo-ma* sp. model did not reach convergence criteria and results for this species are not presented.

We observed that BSC species ordination (2-D stress = 0.17) resulted in three distinct groups (Fig. 2). On

the left, sites corresponding to gypsiferous (A) and calcareous soils (B) separated into two different groups (Fig. 2). On the right, a calcareous site (C) with a specific species combination separated clearly from the previous two groups (Fig. 2). There was no clear separation of points related to shrub–no-shrub plots or *Stipa*–open microsites. However, shrub and no-shrub plots were less similar in the gypsiferous soils group (A, Fig. 2). Pearson correlation indicated that BSC composition gradients were related to precipitation ( $r^2 = 0.49$ ) and slightly related to temperature ( $r^2 = 0.34$ ; Fig. 2).

## Discussion

We found that BSC diversity was influenced both by large-scale variables (i.e. precipitation) and local-scale variables (i.e. type of substrate, shrub presence or encroachment and *S. tenacissima* presence) along the considered geographic gradient with comparable habitat types. Species richness and diversity was positively related to gypsiferous



**Fig. 2.** NMDS ordination plot. Each point represents BSC community composition at the microsite level ( $N = 10$ ). Correlations between community composition and gradient factors (precipitation and temperature) are shown. Ordination is rotated to maximize the correlation with gradient factors on the horizontal axis. (▲) Shrub – *Stipa*, (Δ) shrub – open, (●) no shrub – *Stipa*, (○) no shrub – open.

soils and higher precipitation. Type of substrate and microsite characteristics (related to indirect influence on incident solar radiation, temperature and water availability) were the main predictors for species occurrence and frequency.

#### Effects of large-scale environmental factors on BSC communities

Annual precipitation had a clear influence on BSC richness and diversity, and also on species composition. In general, BSC crusts dominated by lichens and mosses are moisture-limited across a wide range of scales (Bowker et al. 2006). This agrees with our results, as we found a positive relation between precipitation and BSC richness and diversity. In contrast, species richness and diversity of BSCs was similar along a precipitation gradient in a semi-arid shrubland region of California (Hernandez & Knudsen 2012), where elevation and distance to coast were the most influential variables. In this study, proximity to the coast may compensate for lower precipitation along the geographic gradient. Moreover, changes in altitude are generally related to variations in precipitation. In our study region, changes in species composition were more related to substrate characteristics than to variations in precipitation. This agrees with Ponzetti & McCune (2001), who found that among a wide variety of environmental variables (including precipitation) in shrub steppes of Oregon, soil properties (e.g. pH, EC and CIV scores) had most influence on BSC composition.

In terms of species occurrence and frequency, precipitation has a positive effect on only a few species. For example, that the frequency of *Toninia sedifolia* and *Diploschistes diacapsis* was positively related to precipitation, while previous studies found a negative influence of precipitation on other species of both *Toninia* (Zedda et al. 2011) and *Diploschistes* (Ponzetti & McCune 2001) genera. It is well known that lichens are poikilohydric organisms that have a high humidity requirement. This characteristic is particularly determinant of species establishment in arid and semi-arid habitats, where water availability is limited. Thus, the different responses of lichens and bryophytes to precipitation may be related to the existence of more shady and humid microsites that allow better tolerance to water limitation.

#### Effects of soil substrate on BSC communities

Both species richness and diversity were positively related to gypsisols. Also, community composition differed clearly between gypsiferous and calcareous soils. Furthermore, the type of substrate was the variable that better explained occurrence and frequency of the majority of BSC species, together with *S. tenacissima* presence. Soil chemistry has been identified as one of the main determinants in BSC distribution and composition, strongly related to soil pH (Hauck et al. 2009; Rivera-Aguilar et al. 2009). Overall, gypsiferous soils contain rich and diverse communities (Martínez-Sánchez et al. 1994; Martínez et al. 2006), especially when compared to other soil types (Bowker & Belnap 2008). Calcareous soils have been related to moss and liverwort-dominated BSC communities (Downing & Selkirk 1993). Lichens generally dominate BSC communities in gypsum environments (Büdel 2003), although affinity for gypsiferous or calcareous soil varies at the species level. For example, *Leptogium* spp. have been related to non-calcareous soils, while more calcareous soils were positively related to *Collema* spp. in central and eastern Oregon, US (Ponzetti & McCune 2001). In contrast, in our study region, both *Leptogium schraderei* and *Collema* spp. were generally more frequent on calcareous soils.

#### Effects of vascular vegetation on BSC communities

We found that shrub presence negatively affected BSC diversity, but had no effect on species richness or occurrence. Only the frequency of five lichen species was influenced by shrub presence, three of them negatively (i.e. *Diploschistes diacapsis*, *Psora decipiens* and *Squamarina lentigera*) and the other two positively (i.e. *Cladonia rangiformis* and *Diplozomma epipolium*). In contrast, a recent study in a semi-arid kermes oak ecosystem found that BSC occurrence and abundance were positively related to shrub presence, but only in north-facing microsites (Ochoa-Hu-



eso et al. 2011). In addition, the results of that study suggested that shrub cover induced competitive relationships between moss and lichen species, where mosses performed better. From a BSC morphological perspective, Maestre et al. (2009) evaluated the effect of shrubs on BSC diversity in grassland ecosystems along a similar geographic gradient. These authors found that BSC morphological groups with a higher requirement for soil moisture (e.g. mosses, gelatinous lichens and cyanobacteria) were more abundant in sites with shrub presence, while squamulose and crustose lichen abundance was not, thus differing somewhat from our results.

The positive effect of *S. tenacissima* on BSC species occurrence may be related to the higher maintenance of moisture through a shading effect from tussocks, allowing more species to co-exist. Previous works have demonstrated that areas under the influence of *S. tenacissima* tussocks have higher humidity and nutrient availability, which enhance the presence of BSC species with more stringent ecological requirements (Martínez-Sánchez et al. 1994; Maestre et al. 2009). In contrast, a negative effect of *S. tenacissima* on species richness and diversity of annual plants has been recently observed in a similar semi-arid gypsum steppe, under water-restricted conditions (Luzuriaga et al. 2012).

Eleven BSC species were more frequent in open areas where light availability is higher, whereas seven species mostly occurred in areas near *S. tenacissima* tussocks. Perennial vegetation promotes bryophyte cover, likely due to an increase in humidity (Martínez-Sánchez et al. 1994). Moreover, we found a significant interaction between precipitation and the presence of *S. tenacissima* on BSC species richness and occurrence. Increasing precipitation may result in a facilitation effect from *S. tenacissima* to annual communities, with consequent increased water uptake, while open microsites result in higher soil water availability for lichens and mosses. Competition for water resource between BSC and vascular vegetation may result in lower water availability for BSC species. Although lichens and bryophytes are desiccation-tolerant, water availability has been critically related to their establishment and development, as well as efficient physiological activity in these poikilohydric organisms (Pintado et al. 1997; Gignac 2001; Hauck 2011).

## Conclusions

In this study, we showed that environmental factors shape BSC community composition and highly influence diversity in semi-arid grassland ecosystems of Spain. Local factors, such as substrate type and vascular vegetation, determine the distribution and frequency patterns of BSC at the species level. However, we also found generalist species with higher tolerance to variations in local environmental factors. Our results highlight the relevance of combining

community and species approaches, where such interesting relations between environmental factors and BSC ecology are often ignored. In order to face potential changes in arid and semi-arid ecosystems related to global change, more multi-approach studies should be conducted to assure effective management and conservation of BSC diversity and associated functional roles.

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