

# Climate and small scale factors determine functional diversity shifts of biological soil crusts in Iberian drylands

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Received: 15 November 2013 / Revised: 20 February 2014 / Accepted: 24 March 2014 /  
Published online: 3 April 2014  
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**Abstract** Understanding functional diversity is critical to manage and preserve biodiversity and ecosystem functioning in the face of global change. However, the efforts to characterize this functional component have been mostly directed to vascular vegetation. We sampled lichen-dominated biological soil crusts (BSCs) in semiarid grasslands along an environmental gradient in the Iberian Peninsula. We characterized five effect functional traits for 31 lichens species, and evaluated the influence of large scale (i.e. precipitation) and small scale factors (i.e. substrate type, shrub presence, *Stipa tenacissima* presence) on dominant trait values; i.e. community weighted means, and functional divergence; i.e. Rao quadratic entropy in 580 sampling quadrats. Across the gradient, we found multiple trait shifts and a general increase of functional divergence with increasing precipitation. We also observed that substrate type and small scale biotic factors determined shifts in all traits studied, while these factors affected less to functional divergence. Comparing functional diversity with taxonomic diversity, we found contrasting responses to both large and small scale factors. These findings suggest that BSC community trait composition is influenced by multi-scale abiotic and biotic factors with environmental filtering dominating at large spatial scales and limiting similarity at specific small scales. Also, our results emphasize the potential differences between taxonomic and functional diversity in response to environmental factors. We concluded that functional diversity of BSCs not only provides novel and critical knowledge of BSC community structure, but also it should be considered

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Communicated by Guest Editors of S.I.: Biocrust.

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as a critical tool in biodiversity conservation strategies, ecosystem services assessment and ecological modelling.

**Keywords** Biological soil crusts · Calcareous soils · Functional diversity · Gypsum soil · Lichen · Precipitation · Semiarid grassland · Shrub · *Stipa tenacissima* · Traits

## Introduction

Functional diversity, e.g. the distribution in functional trait space of the species presence and abundance in a given community (Mason et al. 2005), has emerged as a key concept in ecology to respond to a variety of critical questions. For example, functional diversity may allow us to disentangle the mechanisms of community assembly and local species coexistence, to predict the consequences of global change in terms of ecosystem functioning (Petchey and Gaston 2006), or to contribute in ecosystem services assessment (Díaz et al. 2007; Dias et al. 2012). Contrary to taxonomic diversity (e.g. number of species) that is a poor surrogate of ecosystem functioning, functional diversity is very efficient and provides information on ecosystem processes and services (Mokany et al. 2008). This critical use of the functional diversity is based on the fact that some traits which are characteristics of an organism or a group of organisms affect directly or indirectly organism performance and fitness (Violle et al. 2007).

Research on functional traits has been focused on terrestrial vascular plants fueled by detailed and standardized protocols (Cornelissen et al. 2003; Chave et al. 2009; Pérez-Harguindeguy et al. 2013). However, there is a necessity to extend the existing paradigms on plant functional diversity to ecosystems where vascular vegetation is scarce. This is especially demanding in the case of those ecosystems such as drylands or other stressful habitats dominated by biological soil crusts (hereafter BSCs), which are mainly formed by soil lichens, bryophytes, and other microbial organisms (i.e. cyanobacteria, algae and fungi) (Belnap and Lange 2003).

This complex biological structure has received increasing attention during the last two decades due to the key ecosystem functional roles it performs by (1) fixing carbon and nitrogen (Elbert et al. 2012), (2) participating in nutrient cycling (Harper and Belnap 2001; Austin et al. 2003), (3) protecting soil surface from erosion forces, and contributing to soil formation and stability (Bowker et al. 2008; Chaudhary et al. 2009), and finally, (4) taking part in biotic interactions with the vascular plant and soil fauna components (Escudero et al. 2007; Darby et al. 2010). BSCs also contribute to the ecosystem “insurance” in the face of environmental changes (Loreau et al. 2003) by enhancing the resilience of the ecosystem. Due to global change, drylands are expected to experience the greatest modification in biodiversity terms and ecosystem functioning (MA 2005); thus, it is crucial to ensure their resilience through functional diversity conservation.

Although some works on lichen trait diversity have recently appeared, most of them has focused on (1) “response traits” rather than “effect traits”, and (2) epiphytic lichen communities in forests, rather than terricolous or saxicolous lichens (Ellis and Coppins 2006; Lakatos et al. 2006; Stofer et al. 2006; Pinho et al. 2011a, b; Giordani et al. 2012, but see Bowker et al. 2010a, Giordani et al. 2013). As a consequence, to extend this preliminary knowledge to lichen-forming communities in BSCs seems inappropriate and remains as a frontier in the understanding of ecosystem functioning particularly in

drylands. Since BSCs are one of the most abundant ecosystem components in drylands worldwide and perform key, diverse functional roles complementary to those of plants (Miller et al. 2011, Bowker et al. 2013), it is critical to examine their functional diversity and establish the connection with ecosystem functioning.

As a first step we want to know if coexistence of lichen forming BSCs responds to some ecological assembly rules based on the presence and abundance of some specific traits (Mouchet et al. 2010). Previous evidences suggested that large scale environmental factors act as abiotic filters for the establishment and abundance of BSCs as a whole in a given ecosystem (Eldridge and Tozer 1997, Zedda et al. 2011). They pointed out that low precipitation and high temperature exert a positive effect on BSCs probably due to an increase in the habitat availability (i.e. reduced vascular plant cover and competition) and their high resistance to harsh environmental conditions. However, BSCs are composed by numerous organisms which seem to be assembled by fine scale processes. For instance, local scale factors related to soil properties (e.g. soil pH, soil nitrogen, sand content) and plant cover influence the species composition of lichen dominated-BSCs; i.e. species occurrence, frequency and abundance (Ochoa-Hueso et al. 2011; Concostrina-Zubiri et al. 2013a), reflecting the particular microhabitat requirements of each lichen species (i.e. ecological niche). Obviously the functional diversity of such BSCs would be a direct response to local scale heterogeneity but to environmental factors operating at large scales too. In turn, BSCs promote shifts in soil properties, as such as total available N (Delgado-Baquerizo et al. 2013), surface stability (Chaudhary et al. 2009) and micronutrients concentration (Concostrina-Zubiri et al. 2013b) due to their physical-morphological attributes and chemical activity, contributing to small scale soil heterogeneity. We suggest that lichen species in these BSCs show a range of functional traits that leads for an assembly of them into realized BSCs in response to filtering processes. In vascular plant communities, the effect of multiple assembly processes (environmental filtering or limiting similarity) is reflected on particular functional diversity components and contribute to structure community (Spasojevic and Suding 2012). Recent works have detected shifts and patterns in functional diversity along environmental gradients varying at contrasting spatial and time scales (Garnier et al. 2007; Cornwell and Ackerly 2009; Mason et al. 2012; Spasojevic and Suding 2012; de Bello et al. 2013), suggesting that functional diversity is influenced by both large and local-scale factors in a hierarchical fashion. In particular, variations in large scale factors are likely to determine differences in the dominant trait value, while changes in local scale factors are likely to promote differences in the dissimilarity of functional traits (de Bello et al. 2013). The functional diversity within a community may be quantified through several metrics (Villéger et al. 2008). In this study, we specifically focused on two metrics of community functional structure: (1) community weighted means of trait values (CWMs), as summary of functional composition, which reflects the dominant trait in a given community (e.g. Garnier et al. 2004; Lavorel et al. 2008), and (2) Rao quadratic entropy, as a measure of functional divergence between communities, which express the sum of trait dissimilarities between species weighted by species relative abundance (Rao 1982; de Bello et al. 2010a, b). These two metrics have been identified as complementary measures to characterize community structure from a functional approach (Ricotta and Moreti 2011). Our working hypothesis are (1) large-scale environmental factors—climate—determine shifts in trait values in BSC communities, and (2) changes in small scale factors influence mostly functional divergence. In addition, we compare functional diversity (i.e. Rao quadratic entropy) with taxonomic diversity responses (i.e. species richness and Shannon Diversity Index) to biotic and abiotic factors along the surveyed environmental gradient.

## Methods

### Study area and environmental factors

A total of 580 quadrats of 50 × 50 cm on well developed BSCs were sampled in 16 sites along a geographic and climatic gradient; from the southeasternmost tip of Iberian Peninsula (the driest, warmest conditions) to its centre where more humid and cooler environments are found. In particular, the annual precipitation and temperature ranged from 282 to 497 mm and from 13 to 17 °C, respectively. All the sites were characterized by open grasslands dominated by tussocks of *Stipa tenacissima* interspersed in a bare ground matrix with well developed BSCs.

In order to record the influence of vascular vegetation on the functional structure and diversity of BSC communities, we selected two paired plots (30 × 30 m) at each site along the geographic gradient: (1) a “shrub plot”, that was located on land with well-developed adult individuals of sprouting shrubs (26.4 % of total perennial cover on average), and (2) a “no shrub plot”, that was located on land with no adult shrubs (0.4 % of total perennial cover on average). Shrub encroachment is a common phenomenon in semiarid drylands of Spain, affecting both community structure and ecosystem functioning (Maestre et al. 2009). In addition, we established at each plot ten sampling quadrats associated with *S. tenacissima* tussocks, and ten quadrats in apparent bare soil. The most common shrubs were *Quercus coccifera*, *Juniperus oxycedrus*, *Rhamnus lycioides*, *Rhamnus alaternus* and *Pistacia lentiscus*. Here, BSCs are dominated by lichens (Concostrina-Zubiri et al. 2013a). For this reason, this study is focused on the functional diversity of lichens only.

Sampling design includes all the variability in BSC diversity associated to small scale heterogeneity in the territory. Thus, quadrats were set up following a stratified design: (1) two different soil substrates: calcareous and gypsiferous (site level), (2) two different environments: with shrub presence (“shrub plot”) and with no shrubs (“no shrub plot”; plot level, nested within site), and (3) two different microsites within each plot: under *Stipa tenacissima* canopy (“*Stipa*” hereafter) and in apparent bare soil microsites (“open” hereafter). Detailed BSC sampling and identification methods are available in Concostrina-Zubiri et al. (2013a).

### Taxonomic diversity

We calculated species richness as the total number of different lichen species occurring in a quadrat. In addition, we estimated species diversity using the Shannon diversity index (H) based on species frequency at the microsite level ( $N = 57$ , since one of the microsites contained bryophyte species only). Quadrat size was large enough for accumulating 95 % all the lichen species in these BSCs (Maestre et al. 2008; Concostrina-Zubiri et al. 2013a).

### Lichen functional traits

Based on expert knowledge and previous work, we classified BSCs lichens according to five functional traits: (1) Morphology; (2) Thallus continuity; (3) Chemistry; (4) Attachment structures; and (5) Reflectance (Table 1). They are multinomial traits reflecting key functional roles performed by BSC in drylands. Specifically, lichen morphology is related to (1) soil surface protection by reducing water and wind erosion; e.g. squamulose thalli increase soil roughness, (2) soil–water relation by absorbing and retaining water; e.g. gel-

**Table 1** Functional trait categories and codes for chemistry, thallus continuity (“Continuity”), chemistry, attachment structures (“Attachment”) and reflectance

Functional trait	Categories
Morphology	G = Gelatinous; C = Crustose; S = Squamulose; F = Foliose; R = Fruticulose; P = Leprose
Continuity	C = Continuous; S = Semicontinuous; D = Discontinuous
Chemistry	U = Usnic acid; N = Norstictic acid; A = Antraquinones; O = Other compounds; Z = No compounds
Attachment	T = Thick (>3 $\mu\text{m}$ ); H = Thin (<3 $\mu\text{m}$ ); N = None
Reflectance	L = Low; M = Medium; H = High

like lichens absorb more water compared to crustose or squamulose lichens (Eldridge and Rosentreter 1999), and also to (3) seed germination; e.g. foliose lichens are more likely to trap plant seeds and create favourable microclimate conditions for germination (Escudero et al. 2007). Thallus continuity has been shown to influence soil stability; e.g. (Jiménez Aguilar et al. 2009). Secondary metabolites produced by lichens greatly contribute to ecosystem functioning due to their effects on (1) nutrient uptake; e.g. antraquinones (Hauck et al. 2009), (2) lichen-metal complex formation; e.g. norestictic acid (Hauck et al. 2009), and (3) microbial, herbivore and insect activity; e.g. usnic acid (Molnár and Farkas 2010). Lichen attachment structures, such as rhizines, generally enhance soil aggregation (Eldridge and Green 1994), and also promote soil porosity in soil surface, enhancing water infiltration (Warren 2003; Malam Issa et al. 2009). Finally, color of the thallus determines how much solar radiation is absorbed and how much is reflected, influencing (1) albedo, (2) soil temperature, and (3) evaporation rates (West 1990, Karnieli et al. 2003). Since the selected traits are species specific and lichens are perennial, long-life organisms (Nash 2008), these trait effects are likely to be maintained across seasons and long-term. Species classification was done following Nimis and Martellos (2004, 2008), and Prieto et al. (2010a, b).

### Functional structure evaluation

We evaluated the functional structure of BSC communities based on two metrics. First, to characterize the functional composition of BSC communities we estimated the community-level weighted means (i.e. CWMs) at the microsite level ( $N = 57$ ) (Garnier et al. 2004; Lavorel et al. 2008). The CWM of a community, considering a continuous trait, represents the sum of each species trait value weighted by its relative abundance in the community (Lavorel et al. 2008). For multinomial functional traits, the proportion of each individual trait-category was measured. Second, we calculated the functional diversity for each trait by Rao quadratic entropy index (RaoQ, hereafter) at the microsite level ( $N = 57$ ) (Petchey and Gaston 2002). Through this metric, we evaluated the species deviate from the mean distance to the trait centroid value weighted by the relative abundance (i.e. FDiv) (Rao 1982; Botta-Dukát 2005). This metric represents the sum of trait pairwise dissimilarities between species weighted by relative abundance. High levels of functional diversity (i.e. functional divergence) represent a niche differentiation and therefore low resources competition (Mason et al. 2005). We used frequency data instead of abundance data for the calculation of CWMs and RaoQ. To calculate CWMs and RaoQ metrics at the microsite

**Table 2** List of BSC species and functional trait categories

Species	Morphology	Continuity	Chemistry	Attachment	Reflectance
<i>Acarospora nodulosa</i> var. <i>reagens</i>	S	C	N	N	H
<i>Buellia zoharyi</i>	C	C	Z	N	H
<i>Cetraria aculeata</i>	R	D	O	N	L
<i>Cladonia convoluta</i>	F	S	U	N	H
<i>Cladonia rangiformis</i>	R	D	U	N	L
<i>Collema crispum</i>	G	S	Z	N	L
<i>Collema cristatum</i>	G	C	Z	N	L
<i>Collema tenax</i>	G	C	Z	N	L
<i>Diploschistes diacapsis</i>	C	C	O	N	H
<i>Diploschistes muscorum</i>	C	C	O	N	H
<i>Diplotoma alboatrum</i>	C	C	Z	N	H
<i>Endocarpon pusillum</i>	S	S	Z	H	L
<i>Fulgensia fulgens</i>	C	C	A	N	M
<i>Fulgensia subbracteata</i>	C	C	A	N	M
<i>Heteroplacidium imbricatum</i>	S	S	Z	T	L
<i>Leproloma</i> sp.	P	C	Z	N	H
<i>Leptogium schraderii</i>	G	D	Z	N	L
<i>Mycobilimbia lurida</i>	S	C	Z	N	M
<i>Placidiopsis cinerascens</i>	C	C	Z	T	L
<i>Placidiopsis custnani</i>	C	C	Z	T	L
<i>Placidium pilosellum</i>	C	S	Z	T	L
<i>Placidium squamulosum</i>	C	S	Z	T	L
<i>Placynthium nigrum</i>	C	S	Z	N	L
<i>Psora decipiens</i>	C	D	A <sup>a</sup>	N	M
<i>Psora globifera</i>	S	S	A	N	L
<i>Psora saviczii</i>	S	D	A	N	H
<i>Squamarina cartilaginea</i>	C	C	U	H	H
<i>Squamarina lentigera</i>	C	C	U	H	H
<i>Toninia albilabra</i>	S	S	Z	N	M
<i>Toninia sedifolia</i>	S	S	Z	N	M
<i>Toninia taurica</i>	S	S	Z	N	M

Codes for functional trait categories are described in Table 1

<sup>a</sup> Major concentration

level we used the dbDF function implemented in the FD package (Laliberté and Legendre 2010), converted each multinomial trait to a dummy variable and computed a distance matrix (Table 2).

### Statistical analyses

To test the effect of climatic variables and local scale factors (substrate type, shrub presence and microsite) on BSC taxonomic diversity (i.e. species richness and Shannon Diversity Index) and functional metrics (i.e. CWMs and RaoQ) of each trait we applied

Generalized Linear Mixed Models (GLMMs) (McCulloch and Searle 2001). For all models we included the annual precipitation, type of substrate (calcareous or gypsiferous), the presence/absence of shrubs, and the presence/absence of *Stipa* as fixed factors. Average annual temperature was not included in GLMM analysis because it was highly correlated with annual precipitation (Coef. Pearson =  $-0.849$ ,  $P$  value  $< 0.0001$ ). Since our data on lichen functional traits had a hierarchical structure with plots nested within sites, we analysed the data using a multilevel approach, and considered the variables site and plot as random factors to take in account the intra-class correlation.

All statistical analysis were carried out with R (R Development Core Team 2010). All GLMM computations were performed using `glmer` function of `lme4` package (Bates et al. 2012).

## Results

Functional diversity estimators were significantly influenced by environmental predictors at both large (i.e. climate) and local scales (i.e. microhabitat). First, we found multiple bidirectional and significant effects of precipitation, substrate type, shrub presence and *Stipa* influence on CWMs (Table 3). At the large scale, precipitation positively affected the dominance of lichens with discontinuous thallus; usnic acid; without attachment structures and high reflectance. In contrast, the dominance of crustose lichens; without secondary metabolites; presenting thick attachment structures and low reflectance increased with aridity. Gypsiferous soils presented a higher dominance of crustose and squamulose lichens; with “other compounds” and high reflectance, while in calcareous soils gelatinous and low reflectance lichens were dominant. At the local scale, shrub presence positively affected the dominance of lichens with atranorin and norestrictic acid, while it diminished the dominance gelatinous lichens, without secondary metabolites and low reflectance. In addition, *Stipa* presence increased the dominance of lichens with foliose morphology; continuous thallus; usnic acid; thin attachment structures and high reflectance. On the other hand *Stipa* decreased the dominance of crustose lichens; with semi and discontinuous thallus; with norestrictic acid and also lichens without secondary metabolites; thick attachment structures and low reflectance (Table 3).

Functional divergence, measured as RaoQ, increased with precipitation for morphology, continuity, chemistry and reflectance traits. Similarly, functional divergence was higher in gypsiferous soils for chemistry and reflectance. In addition, shrub presence increased functional divergence for chemistry, while *Stipa* has no effect on functional divergence for the studied traits (Table 4).

Finally, we found that species richness and Shannon Diversity Index were neither influenced by precipitation nor *Stipa* presence. However, both taxonomic components were higher in gypsiferous soils than in calcareous soils. In addition, Shannon Diversity Index diminished with shrub presence (Table 5).

## Discussion

This study shows that BSC lichen functional diversity in drylands varies with changing environmental conditions. Our results suggest that lichen-dominated BSCs are subjected to environmental filtering on trait selection, promoting coexistence among species with successful strategies (Weiher and Keddy 2001; Cornwell et al. 2006). Specifically, we

**Table 3** Summary of the Generalised Linear Mixed Models examining the effects of environmental factors on CWMi for each functional trait, written as  $CWMi \sim PPT + \text{Substrate} + \text{Shrub} + \text{Microsite} + (1|\text{Site}/\text{Plot})$ 

Trait	Category	Precipitation	Substrate	Shrub	<i>Stipa</i>
<i>Morphology</i>	Crustose	-0.0074*	1.0979**		-0.1357*
	Foliose				0.2709*
	Gelatinous		-1.8191***	-0.5079*	
	Leprose				
	Fruticulose				
	Squamulose		1.0735*		
<i>Continuity</i>	Continuous				0.4952***
	Semicontinuous				-0.2705***
	Discontinuous	0.0123*			-0.4855***
<i>Chemistry</i>	Atranorin			0.4974**	
	Norestrictic acid			0.7241*	-0.7138**
	Usnic acid	0.0121*			0.5205***
	Other compounds		5.5059***		
	None	-0.0134*		-0.5063*	-0.2983***
<i>Attachment</i>	Thin				0.5981***
	Thick	-0.0132***			-0.7391***
	None	0.0090**			
<i>Reflectance</i>	Low	-0.0134*	-1.9474**	-0.4903*	-0.2730***
	Medium				
	High	0.0118*	1.5032**		0.2561***

Precipitation, annual precipitation; Substrate, gypsiferous soil; Shrub, Shrub presence; *Stipa*, *Stipa tenacisima* presence. Coefficients of significant variables in the model are indicated. Significant values are shown as: \*\*\*  $P < 0.0001$ , \*\*  $P < 0.005$ , \*  $P < 0.05$

**Table 4** Summary of the Generalised Linear Mixed Models examining the effects of environmental factors on functional divergence (RaoQ), written as  $RaoQi \sim PPT + \text{Substrate} + \text{Shrub} + \text{Microsite} + (1|\text{Site}/\text{Plot})$ 

	Morphology	Continuity	Chemistry	Attachment	Reflectance
Precipitation	0.0003*	0.0004**	0.0003***		0.0005***
Substrate			0.0406***		0.0295*
Shrub			0.0165*		
<i>Stipa</i>					

Precipitation, annual precipitation; Substrate, gypsiferous soil; Shrub, Shrub presence; *Stipa*, *Stipa tenacisima* presence. Coefficients of significant variables in the model are indicated. Significant values are shown as: \*\*\*  $P < 0.0001$ , \*\*  $P < 0.005$ , \*  $P < 0.05$

document that environmental filtering involves changes in trait dominance and functional divergence along climate and simultaneously at local scale, due to changes related to plant community structure (encroachment and tussock canopy) and soil substratum (gypsiferous vs. calcareous soils). However, large scale factors affected functional divergence for a larger number of traits than small scale factors; i.e. precipitation increased functional



**Table 5** Summary of the Generalised Linear Mixed Models examining the effects of environmental factors on taxonomic diversity (species richness and diversity), written as Metric ~ PPT + Substrate + Shrub + Microsite + (1|Site/Plot)

	Richness	Diversity
Precipitation		
Substrate	6.0329**	4.9960**
Shrub		−1.2211**
<i>Stipa</i>		

Precipitation, annual precipitation; Substrate, gypsiferous soil; Shrub, Shrub presence; *Stipa*, *Stipa tenacissima* presence. Coefficients of significant variables in the model are indicated. Significant values are shown as: \*\*\*  $P < 0.0001$ , \*\*  $P < 0.005$ , \*  $P < 0.05$

divergence for four of five traits, while gypsiferous soils and shrub presence increased functional divergence for only two or one, respectively. This partially agrees with findings on plant functional diversity patterns in which shifts in dominant traits are determined by large scale factors, while functional divergence is affected by environmental factors at multiple but smaller scales (de Bello et al. 2013).

First, we want to highlight that our results revealed a significant functional turnover along the climate gradient and depending on substrate type and plant influence. Thus we observed that higher precipitation and lower solar radiation incidence (i.e. under *Stipa* canopies), lead to a decrease in the dominance of crustose morphology. Crustose lichens are known to tolerate harsh environmental conditions since they have a low nutrient demand and high stress tolerance (Lalley and Viles 2005; Giordani et al. 2013). However, more humid conditions may lead to higher competition for space and light with other BSC components, where crustose lichens perform worst (Ellis and Coppins 2006). In addition, we found that the dominance of lichens without secondary metabolites diminished with increasing precipitation and shrub and *Stipa* presence, which are factors previously related to enhanced fertility in semiarid Iberian grasslands (Maestre et al. 2009). More favourable conditions may increase competition within lichen assemblages where only the more competitive species success (i.e. those species with chemical defences-allelopathies-). Finally, we observed a clear shift in thallus reflectance along the climate gradient and to plant influence. Low reflectance lichens dominated BSC communities in presence of shrubs and/or *Stipa*, while open microsites were dominated by high reflectance lichens. This shift may be related to pigment production in response to solar radiation incidence including photoprotection or photobiont adaptive strategies for light-harvesting in shade environments (Palmqvist and Sundberg 2000; Paoli et al. 2010). It is worth to note that in our study area, the most common low reflectance lichens are cyanolichens, which have previously shown a positive correlation with precipitation in Iberian drylands (Concostrina-Zubiri et al. 2013a). In epiphytic communities, changes in lichen functional traits such as morphology type, reproductive strategy and photobiont partner are generally determined by variations in humidity and solar radiation, but also related to differences in tree age, bark type and land-use intensity (Ellis and Coppins 2006; Stofer et al. 2006; Pinho et al. 2011a, Giordani et al. 2012). Similarly, it is known that BSCs are highly affected by some soil properties and microhabitat characteristics, in addition to climate, at the species level (Ochoa-Hueso et al. 2011; Concostrina-Zubiri et al. 2013b), due to their particular strategies for competition and resource acquisition under specific environmental conditions.

Moreover, these changes in dominant traits are relevant to ecosystem processes (Mokany et al. 2008). For instance we found that the dominance of more compact thallus morphology (i.e. crustose) and the presence of thick attachment structures decreased with higher precipitation and *Stipa* presence, while thalli become more discontinuous. This shift in dominant morphological attributes will be reflected in the capacity of BSCs to retain water and protect soil surface, likely influencing local erosion rates and hydrological cycles in drylands (Eldridge and Rosentreter 1999; Belnap 2006). In addition, substrate type is related to changes in lichen reflectance, which may affect several processes at the soil surface. For example, BSC reflectance may influence heat exchange processes and microbial activity (e.g. nitrogen fixation) due to albedo modification and variations in soil surface temperature (West 1990; Karnieli et al. 2003). Furthermore, changes in dominant traits may in turn determine the nature and strength of species interaction along stress gradients (Bowker et al. 2010b); e.g. the increase in the dominance of species producing secondary metabolites with shrub and *Stipa* presence is likely to promote facilitation (e.g. due to complementary combination of chemical activity from different compounds) or competition (e.g. due to allelopathic activity) between lichens, depending on the composition of secondary metabolites (Bowker et al. 2010a).

Second, we observed that functional divergence was generally higher when precipitation increased. In addition, functional divergence was also higher for chemistry and reflectance traits in gypsiferous soils, where rich and diverse communities are usually found (Martínez-Sánchez et al. 1994; Martínez et al. 2006). Thus, BSCs are likely to be experiencing a “limiting similarity” process in gypsiferous soils with more humid conditions, where functionally dissimilar species increase in abundance due to strong competition between functional similar species (Stubbs and Wilson 2004; Spasojevic and Suding 2012). This suggests that in a hierarchical fashion these assemblages are affected firstly by environmental filtering at large scales and secondarily by a limiting similarity process at small spatial scales under very specific conditions such as gypsum soils and relatively humid conditions.

On the other hand, we found that lichen taxonomic diversity (i.e. species richness and diversity) was insensitive to large scale climate variation. This is a surprising finding since in taxonomic diversity of complex BSCs (i.e. lichens, bryophytes and cyanobacteria) has been found to increase along the same climate gradient (Concostrina-Zubiri et al. 2013b). In contrast, we observed that functional diversity (i.e. functional divergence) showed a clear, positive response with increasing precipitation. In lichen-dominated BSCs, the relation between competition and taxonomic diversity has been found to be positive under low abiotic stress in Iberian drylands (Bowker et al. 2010b). These results support the idea that the correlation between taxonomic and functional diversity is dependent on the studied ecosystem and the environmental factors that operate on a given community (de Bello et al. 2013), and as we show here, on the type of organisms studied. This is particularly relevant in a context of global change, where changes in climate and plant community structure may lead to critical variations in BSCs functional structure and diversity with the consequent impacts on ecosystem functioning. For instance, decreases in precipitation and increases in temperature resulted in reduced BSC richness and diversity, and affected negatively to lichen abundance (Escolar et al. 2012). Similarly, shrub encroachment has been related to differences in BSC composition and morphological group abundance in semi-arid Mediterranean grasslands, likely due to changes in soil fertility and microclimatic conditions (Maestre et al. 2009).

## Conclusions

Despite BSCs have already been identified as a good model system to investigate the relation between taxonomic diversity and ecosystem functioning (Bowker et al. 2010a), quantitative measures of their functional diversity are lacking (Rao 1982; Cornelissen et al. 2007; de Bello et al. 2010a, b). Our results firstly report functional diversity metrics (i.e. CWMs and RaoQ) in BSC communities based on five traits. Overall, this study shows that both dominant traits and functional divergence of BSCs are highly influenced by biotic and abiotic factors at multiple spatial scales. Particularly, we showed a clear turnover of functional traits and hypothesize that first an environmental filtering and secondly a limiting similarity process at small spatial scales may be occurring in lichen dominated BSCs. Our findings regarding the turnover of functional classes suggest that future studies should also include quantitative traits in order to measure the impact of these changes in ecosystem functioning (e.g. measures of usnic acid concentration). Natural resource management and conservation strategies have been traditionally driven by taxonomic diversity indicators though it is known this is not a good measure of ecosystem functioning, since species may have redundancy in their functions (e.g. all the species present have the same functional role or all the species present have different functional roles). Integrating the functional component of biodiversity is of critical relevance in fields such as biodiversity conservation, ecosystem services assessment and ecological modelling in the face of global change.

**Acknowledgments** This work was partially supported by the Spanish Ministry of Economy and Competitiveness (Mountains: CGL2012-38427), the Ministry of Science and Innovation (project EPICON: CGL2010-22049/BOS) and the Government of Autonomous Region of Madrid (REMEDINAL2).

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