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Ecology and functional roles of biological soil crusts in semi-arid ecosystems of Spain

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Abstract

Biological soil crusts (BSCs), composed of lichens, cyanobacteria, mosses, liverworts and microorganisms, are key biotic components of arid and semi-arid ecosystems worldwide. Despite they are widespread in Spain, these organisms have been historically understudied in this country. This trend is beginning to change as a recent wave of research has been identifying BSCs as a model ecological system. Many studies and research projects carried out in Spain have explored the role of BSCs on water, carbon and nitrogen fluxes, the interactions between BSCs and vascular plants, their dynamics after disturbances, and their response to global change, among other topics. In this article we review the growing body of research on BSCs available from semi-arid areas of Spain, highlighting its importance for increasing our knowledge on this group of organisms. We also discuss how it is breaking new ground in emerging research areas on the ecology of BSCs, and how it can be use to guide management and restoration efforts. Finally, we provide directions for future research on the ecology of BSCs in Spain and abroad.

Keywords

Semi-arid; Biotic interactions; Mediterranean; Nutrient cycling; Hydrological processes; Restoration

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Introduction

Biological soil crusts (BSCs), composed of eukaryotic algae, cyanobacteria, mosses, liverworts, fungi and lichens, cover the uppermost mm of the soil surface in most arid and semi-arid ecosystems throughout the globe, and are one of the most conspicuous and important biotic components of these areas (Belnap and Lange, 2003). They constitute a specialized biotic community that exert a strong influence on key ecosystem processes – including runoff and infiltration (Alexander and Calvo, 1990; Belnap, 2006), soil respiration (Maestre and Cortina, 2003) and nitrogen fixation and transformations (Belnap, 2002; Castillo-Monroy et al., 2010)–, influence the establishment and performance of vascular plants (DeFalco et al., 2001; Escudero et al., 2007), and act as habitats for a dependent foodweb of arthropods, fungi, bacteria, and other soil organisms (Belnap and Lange, 2003).

During the last two decades there has been an unprecedented upsurge in interest in BSCs worldwide, which has promoted important advances in our knowledge of the structure, composition, physiology and biogeography of these organisms (see Belnap and Lange, 2003 for a review). Much of this work, however, has been carried out in arid and semi-arid ecosystems of the United States, Australia, Israel and, particularly in recent years, China. Despite that semi-arid ecosystems comprise more than half of the extent of Spain (Ministerio de Medio Ambiente, Rural y Marino, 2008), and BSC communities there were described almost 40 years ago (Crespo, 1973; Llimona, 1974; Crespo and Barreno, 1975), their ecology was scarcely studied until the 1990's. This situation is being reversed, and nowadays several research groups in Spain are actively studying different aspects of the ecology and biogeography of BSCs, and their impact on ecosystem processes (Figs. 1A-1F). In this review we synthesize the literature on the ecology, biogeography, dynamics and ecosystem impacts of BSCs in semi-arid ecosystems of Spain. While the focus of this Special Issue is the Spanish southeast, we do not restrict this review to this region, as important studies have been carried out in areas such as the center of Spain, which hold similar BSC communities (e.g. Maestre et al. 2005; Martínez et al., 2006). With this review we aim to: i) synthesize the work on BSCs carried out to date in central and SE Spain; ii) illustrate how this research has provided new insights on the ecology of these organisms; and iii) discuss future research topics on BSCs, valid for Spain and other regions where these organisms are prevalent. Because of space limitations, this review does not discuss in detail all the relevant literature. However, we include in Appendices 1 and 2 a compilation of relevant references not explicitly discussed in the main text.

Composition of Spanish biological soil crusts

Macroscopic components of BSCs are well known in Spain from a floristic, phytosociological and taxonomical point of view (see Table S1 in Supplementary Material for a lichen species checklist). Among the BSC-forming lichens living in central and SE Spain that can be found in bare ground areas located between plant patches, we can find species such as *Aspicilia desertorum*, *A. fruticuloso-foliacea*, *A. hispida*, *A. fruticulosa*, *Cetraria steppae*, *Collema crispum*, *C. tenax*, *Diploschistes muscorum*, *Endocarpon pusillum*, *Fulgensia fulgida*, *F. fulgens*, *F. subbracteata*, *Gloeoheppia turgida*, *Heppia solorinoides*, *Heteroplacidium imbricatum*, *Leptogium schraderii*, *Peltula patellata*, *Placidium rufescens*, *P. squamulosum*, *Psora decipiens*, *P. vallesiaca*, *Squamarina cartilaginea*, *S. lentigera*, *Toninia albilabra*, *T. aromatica*, *T. diffracta*, *T. sedifolia*, and *T. tristis* subsp. *Pseudotabacina*. In gypsum soils, which cover large areas of SE Spain, we can found some of these species living together with gypsum specialists like *Acarospora nodulosa, A. nodulosa* var. *reagens*, *A. placodiiformis*, *Buellia almeriensis*, *B. zoharyi*, *Diploschistes diacapsis*, *Fulgensia desertorum*, *F. poeltii*, *Lecidea circinarioides*, *L. gypsicola*, *Lepraria crassissima*, *Placynthium nigrum*, *Psora decipiens*, *P. savizcii*, *Teloschistes lacunosus*, *Toninia coerulea* and *Xanthoparmelia pokornyi*. The species richness of BSC-forming lichens has been found to decrease from SE to central Spain (Casares-Porcel and Gutiérrez-Carretero, 1993; Maestre et al., 2009b).

The composition of the BSC community changes near higher plants such as *Stipa tenacissima* L. (Martínez-Sánchez et al,. 1994; Maestre et al., 2002, 2009b), which increases nutrient content and improves microclimate through shade (Martínez-Sánchez et al,. 1994; Maestre et al., 2001). In these microsites, the BSC community is enriched both in gypsum and calcareous soils by species requiring higher levels of humidity, such as *Cetraria aculeata*, *Cladonia convoluta*, *C. subrangiformis* or *Teloschistes lacunosus* and there is a clear increase in the number and cover of bryophytes, mainly mosses, such as *Syntrichia ruralis*, *S. papillosissima*, *Pleurochaete squarrosa*, *Tortula revolvens*, *Didymodon acutus* and *Weissia* sp. (Martínez-Sánchez et al., 1994; Maestre et al., 2002; Castillo-Monroy et al., 2010). The same phenomenon has been described in volcanic soils, where mosses like *Acaulon triquetum, Funaria pulchella* and *Phascum curvicolle*, and liverworts like *Riccia lamellosa*, *R. michelli* and *R. sorocarpa* can be found under the canopy of *Stipa* (Ros and Guerra, 1997).

The taxonomical knowledge of other BSC components, such as cyanobacteria, is not well developed in Spain, as very few studies have targeted them. The diversity of these organisms can be, however, quite high. Maestre et al. (2006) found more than 15 taxa of cyanobacteria, including *Chroococcidiopsis* sp. *Microcoleus steentrupii*, *Leptolyngbya boryanum*, *L. foveolarum*, *Oscillatoria* sp., and *Phormidium* sp., associated to BSC-forming lichens from a *Stipa tenacissima* steppe in Alicante.

Ecophysiology of biological soil crust constituents

All BSC organisms are poikilohydric, meaning that they do not regulate water uptake or loss, but gain it from and lose it to the environment passively (Lange, 2003). In dry environments, poikylohydric organisms must be desiccation tolerant. When desiccated, all metabolic activity ceases. Thus, water relations and photosynthesis are largely coupled, as both photosynthesis and respiration are constrained by degree of hydration and length of hydration periods.

In order to maintain biomass and grow, BSC-forming organisms have developed ways of prolonging hydration events or increasing the number of hydration events. Soil crust cyanobacteria in Spain were the first microbial organisms observed to move in response to changes in soil surface drying fronts (García-Pichel and Pringault, 2001). These *Oscillatoria* colonies are composed of filaments of cells encapsulated in a polysaccharide sheath. Within the sheath, filaments are capable of gliding vertically, “greening” the surface upon wetting, then retreating into soil as drying occurred. The retreat may occur irrespective of light environment, and was demonstrated to be an active process requiring energy on the part of the cyanobacteria. This strategy assures that during hydration periods exposure to light is optimized, but during desiccation periods cyanobacteria can wait under the surface where they are better protected from other stressors such as UV light.

It has long been known that phycolichens (lichens with green-algal photobionts) are able to become active in the presence of water vapour, whereas contact with liquid water is necessary for metabolic activity in cyanolichens (Lange et al., 1986). The Spanish soil lichen flora is highly dominated by phycolichens. Working in the Tabernas desert (Almería, SE Spain), Del Prado and Sancho (2007) found that the BSC-forming lichen *Teloschistes lacunonus* did not become active under high relative humidity, but activated readily when exposed to dew, which may account for up to 12% of total rainfall in this region (Moro et al., 2007). The distribution of this species seems spatially linked to the commonness of dew depositions at a regional scale, and total amount of dew deposition at micro-scales. The erect, branching fruticose growth forms seems particularly effective in maximizing thallus contact with the atmosphere for dew harvest.

In the absence of regulation of water loss *via* stomata, ability to retain water is key to extending hydration periods. A study of 14 Spanish moss species from xeric, mesic and hydric environments revealed that two prevalent mosses of BSCs, *Syntrichia ruralis* and *Pleurochaete squarrosa*, had the longest and third longest water retention times during an experimentally imposed drying event (Deltoro et al., 1998). The authors did not comment upon an underlying mechanism, thus we can only speculate that this might be due to stem or colony morphological characteristics.

Carbon exchange rates vary widely across taxonomic groups of BSC organisms, and are strongly related to water. In Spain, and in general (Lange, 2003), net photosynthetic rates of lichens are more than double those of cyanobacterial crusts on an area basis; data on bryophytes are lacking (Table 1). BSC lichens have often been compared to “sun plants” because their photosynthetic rate tends to maximize at very high light levels (PPFD ≥1200 μmol m^{-2} s^{-1}; Lange, 2003). Further, photosynthetic rates increase as a function of temperature up to around 25°C, beyond which they fall again (Lange, 2003). These generalizations would suggest that warm, sunny locations would be ideal habitat, but this is often not the case. In a comparison of sun and shade populations of the lichen *Diploschistes diacapsis* at Tabernas, Pintado et al. (2005, 2010) found that this species was active only during the 20% of the year, an activity that mainly occurred during conditions of relatively low temperature and PAR radiation. Despite *D. diacapsis* exhibited photosynthetic saturation at high light, and a positive relation between photosynthetic rate and temperature, sun populations of this species occupied less area, and had less mass per area and thinner photobiont layers. These discrepancies suggest that this species is more likely to occupy shadier habitats and operate under suboptimal photosynthetic conditions, benefiting from longer hydration times, than to maximize photosynthesis during shorter activity periods. This would suggest that water availability and hydration times, are the most important in a hierarchy of environmental controls on field performance.

Sustaining a desiccation event and recovering photosynthetic efficiency upon rehydration is another hallmark of desiccation tolerators. To this end, xeric adapted mosses are able to maintain maximal levels of quantum efficiency when drying down to about 5% water content; in contrast, mosses from wetter environments start experiencing decreases between 20-40% water content (Deltoro et al., 1998). They also are much better at maintaining membrane integrity and avoiding cell leakage, and can regain similar levels of quantum efficiency upon rehydration (Deltoro et al., 1998).

Biotic interactions in biological soil crust communities

Interactions between BSC constituents

The study of plant-plant interactions in semi-arid areas has captivated ecologists since the early days of ecology (e.g., Shreve, 1910). Interestingly, and despite the prevalence of BSCs in semi-arid environments worldwide, our understanding of the interactions between the organisms forming them is quite limited (see Belnap and Lange, 2003 for a review). This is particularly true for aspects such as the interplay between facilitative and competitive interactions in BSC-forming organisms, which have been virtually neglected in the literature despite the renewed interest in this topic among plant ecologists (see Callaway, 2007 and Brooker et al., 2008 for recent reviews).

Although studies on biotic interactions between saxicolous and epiphytic lichens have been carried out since the early 1980’s (see Armstrong and Welch, 2007 for a review), similar studies using BSC-forming lichens and mosses were not initiated until 20 years later (Maestre, 2003a, 2003b; Maestre and Cortina, 2002). This work, carried out in *Stipa tenacissima* steppes from Alicante (SE Spain), studied the patterns of spatial co-variation between BSC-forming mosses and lichens (*Cladonia convoluta* and *Squamarina lentigera*), and the effects of *Stipa* on these patterns. These studies illustrate the tight relationships between mosses and lichens at different spatial scales, and show the occurrence of significant relationships between the two lichen species mentioned –particularly close to *Stipa* tussocks–, suggesting the presence of facilitative interactions between *Stipa* and *C. convoluta*.

This work has been recently expanded to study biotic interactions among BSC-forming lichens and mosses at the community level using null model analyses of co-occurrence patterns (see Gotelli, 2000 for a review of this methodology). Studies carried out at a single site in central Spain have shown that competition is more intense than facilitation in BSC communities (Maestre et al., 2008), and that the intensity of competition decreases and increases when water and nutrients are the main limiting resource, respectively (Maestre et al., 2009a). These findings represent the first empirical evidence of non-random species co-occurrence in lichen BSC communities. More recently, Bowker et al. (2010a) examined the intensity of biotic interactions at the community level and among species pairs along an environmental stress-gradient spanning about 112,400 km^2 over central, S, and SE Spain. These authors observed that negative species interactions were prevalent in the BSC communities studied, and that competition intensity increased with the enhancement of abiotic stress (the opposite trend has been predicted for vascular plant communities;

Callaway, 2007). They also found that competition was positively related to species richness at low abiotic stress, and negatively related to richness at high abiotic stress.

Biological soil crust-forming lichens and mosses are fundamentally different from vascular plants in terms of their facilitative and competitive mechanisms, and thus the plant-centric mechanisms of competition and facilitation –which form the core of current paradigms (e.g. Grime, 2001; Tilman, 1988; Callaway, 2007)– may not apply. Because BSCs are primarily two-dimensional, microclimatic buffering and light competition are unlikely to be key forces structuring them. At high densities, competition for available living space between BSC-forming organisms is prevalent. But the absence of facilitation mechanisms common in vascular plants does not imply that facilitation does not occur among BSC constituents. Lichens and bryophytes exhibit a remarkable array of secondary chemicals, some of which have roles in nutrient uptake and defense against pathogens (e.g., Hauck et al., 2009); thus, species with complementary chemical arsenals may mutually benefit by association. Morphological differences may also influence the redistribution of water (discussed below), which could lead to facilitative species combinations (Spitale, 2009). Finally parasitism among lichens is common; a lichen mycobiont can steal the photobiont of other species and overtop the original lichen (Schaper and Ott, 2003); under this scenario, the host is facilitating the development of the parasite species.

Interactions between BSCs and other soil organisms

The only experiment available on this topic from Spain (Castillo-Monroy et al., in press) found that the presence or absence of species in the bacterial community of a gypsum steppe located in Central Spain (Belmonte de Tajo, Madrid) was insensitive to the BSC community structure; however, there were several sensitive bacterial species. Some lichens, including *Fulgensia subbracteata* and *Toninia* spp., exhibited apparent antibacterial activity, while *Diploschistes diacapsis* consistently affected sensitive bacterial species, sometimes positively. These results highlight the role of the composition and structure of BSC in modulating their effects on microbial communities. Given that most studies on this topic have evaluated the effects of broad types of BSC (e.g. crust dominated by lichens and mosses vs. crust dominated by cyanobacteria) on particular groups of microorganisms (e.g., Yeager et al., 2004; Soule et al., 2009), future studies should explicitly consider BSC attributes such as diversity and composition when evaluating BSC-microbial interactions.

Interactions between BSCs and vascular plants

It is well known that BSCs exert a strong influence on the establishment and performance of vascular plants (Belnap and Lange, 2003). Empirical evidences of the effects of BSC on these plants are numerous but contradictory, ranging from negative to positive (e.g., Hawkes and Menges, 2003; Anderson et al., 1982; DeFalco et al., 2001). However most of these studies have considered both the plant and BSC communities as a whole, without taking into consideration the species involved. As part of a more recent effort to unveil the relation between both plant and BSC diversity in these ecosystems, a small set of works have explored species-specific responses of vascular plants to BSCs (e.g., Hawkes and Menges, 2003; Zaady et al., 1997), sometimes considering some broad structural BSC classifications (Rivera-Aguilar et al., 2005). These studies have also found contradictory BSC effects on vascular plants but corroborated the importance of BSCs as a key modulator of seedling emergence and performance.

This controversy is probably a consequence of the fact that plant–BSC interactions are likely to be highly species specific, similarly to the situation found with plant-plant interactions (Callaway, 2007). If so, diverse responses are expected depending on the composition and structure of both BSC and plant communities. To test this hypothesis, Escudero et al. (2007) experimentally evaluated the effect of two dominant lichens (*S. lentigera* and *D. diacapsis*) on the emergence of three gypsophytes from central Spain. They found significant and different effects of *Squamarina lentigera* and *Diploschistes diacapsis* on the three plant species studied. In addition, Escudero and Martínez (unpublished data) have evaluated the effect of BSC-forming lichens on the emergence of annual gypsophytes during a six-year period on well conserved gypsum outcrops from central Spain. They found that the relationships between BSC and vascular plant species were extremely complex, with repulsions, attractions and neutral responses between components of both communities at the species level. The potential mechanisms underlying these interactions are also complex and involve plant traits related to seed morphology and dispersal, and BSC traits such as the existence of allelochemicals and the morphology of the thallus (foliose or crustose), which are highly related to their function (Bowker et al., 2010b). These results illustrate the importance of species-specific interactions between vascular plants and BSC-forming soil lichens to understand how BSCs affect plant composition and structure.

Most studies on the interaction between BSC and vascular plants have focused on seed germination and early phases of seedling establishment. Conversely, the effects of BSC on adult plants have scarcely been studied. In a recent work, Cortina et al. (2010) found that BSC disturbance had a weak effect on short-term performance of neighbor *Stipa tenacissima* tussocks in a semi-arid steppe from Alicante. Yet, killing the BSC with herbicide had a significant effect on the water use efficiency of this species.

Role of biological soil crusts on ecosystem functioning

Effects on nutrient cycling

Semi-arid ecosystems of Spain are characterized by a sparse vegetation cover, which is often arranged as a two-phase mosaic of vegetated and bare ground patches (Puigdefábregas et al., 1999; Maestre and Cortina, 2002). Distribution of soil nutrients in these areas is strongly linked to discrete plant patches, and the formation of "resource islands" has been reported under the canopy of widely distributed plant species, such as *Stipa tenacissima* and *Retama sphaerocarpa* (L.) Boiss. (Maestre et al., 2001; Pugnaire et al., 2004; Goberna et al., 2007). However, a large proportion of the soil in these ecosystems is unvegetated and covered by BSCs. Therefore, most nutrient inputs to and losses from semi-arid soils must pass through the soil boundary created by these organisms (Belnap et al., 2003). Indeed, the role of BSCs as a key modulator of the carbon (C) and nitrogen (N) cycles has long been acknowledged (e.g. Calder, 1959), and has been thoroughly studied during the last decades (see Belnap and Lange, 2003 for a review).

Recent research is showing the important roles BSCs have in modulating C and N heterogeneity and cycling in semiarid ecosystems from Spain. Castillo-Monroy et al. (2010) found that, over a two-year period, *in situ* availability of NH_4^+-N under plant canopies (*Stipa* and *Retama*) did not differ from that found under adjacent bare soil and BSC-dominated microsites in a semi-arid steppe located in Aranjuez (central Spain). However, the rate of NO_3^--N produced in the field, as well as the potential nitrification rate, was reduced under BSC-dominated areas compared to bare ground microsites and soils located under plant canopies (Fig. 2). In the same study area and period, Delgado-Baquerizo et al. (2010) reported mean N availability values ranging between 51.2 mg N kg^{-1} soil and 25.5 mg N kg^{-1} soil (0-4 cm depth) for areas with high and low BSC cover, respectively. NO_3^--N was the dominant N form for bare soil microsites and low BSC cover areas, but dissolved organic N was the dominant N form when the BSC cover was high. By using experimental manipulations (surface soil cutting and herbiciding), Cortina et al. (2010) evaluated the effect of the physical structure and the biotic component of BSCs on soil N dynamics in a semi-arid steppe from Alicante. Herbicide application had a strong effect on N fixation activity, suggesting that the populations of N-fixing cyanobacteria and cyano-lichens may have been reduced for an extended period of time. In contrast to herbicide application, physical alteration of the surface soil did not affect BSC ability to fix atmospheric nitrogen. Maestre et al. (2006) evaluated the functioning of BSC-inoculated soils in a microcosm experiment, and found that this inoculation significantly increased the C and N fixation of the soil. Maestre and Cortina (2003) found a high degree of spatial variability in soil CO_2 flux in a semi-arid steppe from Alicante, largely attributable to corresponding heterogeneity in cyanobacteria- and lichen-dominated BSCs. In this study, BSC-dominated microsites had significantly higher soil respiration during spring than bare-ground areas. Similar responses have been observed after three years of *in situ* measurements in a gypsum *Stipa tenacissima* steppe located in Aranjuez (A. P. Castillo-Monroy & F. T. Maestre, unpublished data). At this site, and when compared to bare ground areas, soil respiration increased with increases in BSC cover. In the same direction, Maestre et al. (2005) also found a positive relationship between the total cover of BSCs and soil respiration (measured in the laboratory under optimal temperature and moisture conditions) in BSC-dominated ecosystems from Madrid and Alicante. However, ongoing research being carried out in two calcareous *Stipa* steppes from Almería (SE Spain) is showing that, over a three-year period, soil respiration in BSC-dominated areas does not differ from that found under the canopy of *Stipa* and bare ground areas (A. Rey, unpublished data). Future studies need to be done to explain these differences, which may be due to soil and climatic differences between study areas, and to fully understand under which conditions BSCs modulate soil respiration.

Other studies have attempted to partition the effects of particular attributes of BSC communities (cover, diversity and biotic interactions) on nutrient cycling indicators. At small spatial scales (a single site located in Belmonte de Tajo), attributes such as BSC cover and species richness explained a substantial part of the variation found in variables such as the activities of the β-glucosidase and urease enzymes (Bowker et al., 2010b). Increases in cover and richness promoted an increase on the activity of these enzymes, and thus on nutrient cycling. At this site, very little of the effects of BSC attributes on ecosystem function could be ascribed to changes within the bacterial community, suggesting a primary importance of the lichens themselves (Castillo-Monroy et al., in press). Maestre et al. (2005) found that the richness and evenness of BSC communities negatively influenced the amount of total soil N in two semi-arid ecosystems from Madrid and Alicante, suggesting that N inputs in the soil were related to the abundance of particular species. At regional spatial scales (a 112,400 km^2 area encompassing central, S, and SE Spain), climatic variables were the main driver of changes in the activities of the β-glucosidase and phosphatase enzymes (Maestre et al., 2010). Of secondary importance were the effects of community properties such as total cover, which in the case of phosphatase were moderately strong. At this spatial scale, increases in BSC cover led to increases in the activities of these enzymes. Species interactions also indirectly affected ecosystem functioning via their moderate effects on community properties such as cover.

These regulatory roles of BSCs in nutrient cycling are very likely subject to change under shifting climate regimes. Ongoing experimental manipulations of temperature and rainfall are also being carried out at Aranjuez (Fig. 1E). In this area, we are evaluating soil CO_2 flux and N responses to simulated climate change in plots with and without BSCs to explore the role of BSC communities as modulators of ecosystem responses to ongoing climate change. Preliminary results from the first year of this experiment show that average increases in temperature of 2.6 $°C \cdot year^{-1}$ promote a slight, but not significant, increase in soil CO_2 flux in the plots without BSC (Maestre et al., 2010). However, such an increase was clearly significant in plots with well developed BSCs. The amount of CO_2 respired over the study period per unit of BSC cover was higher in the elevated temperature plots. These results provide evidence of strong short-term effects of the increase of temperature on soil respiration, a response that was controlled by total BSC cover (i.e. areas of low BSC cover did not show any response to the warming treatment), but not by BSC richness, evenness or biotic interactions among BSC constituents. They also indicate that, if warming increases soil respiration particularly in areas of high BSC cover, BSC-forming organisms such as lichens and mosses may be at risk of C deficits if they do not increase their photosynthetic rate concomitantly.

Effects on water fluxes and erosion

In the arid and semi-arid ecosystems of SE Spain, BSCs have a large impact on infiltration and erosion processes. Several works have analyzed the influence of BSCs on runoff and erosion at small spatial scales in badlands systems, mostly developed on marls, under simulated (Alexander and Calvo, 1990; Calvo-Cases et al., 1991; Solé-Benet et al., 1997; Chamizo et al., 2009) and natural (Cantón et al., 2001) rainfall events (Fig. 1F). These studies reported a wide variation of runoff coefficients on BSC dominated surfaces, ranging between 11 and 72% under extreme simulated rainfalls (1 hour duration; 50-55 mm h^{-1} constant rainfall intensity and dry conditions), and between 0 and 71% for natural rains (Fig. 3). Erosion rates also vary substantially, both under natural rainfalls and simulated rain, with values between 5 and 150 g m^{-2} after extreme simulated rainfall events (Calvo-Cases et al., 1991). This variability is attributed to the interaction of factors like the characteristics of the underlying material (Calvo-Cases et al., 1991; Chamizo et al., 2009), the slope gradient (Solé-Benet et al., 1997; Chamizo et al., 2009) and the functional traits of the species forming the BSCs. The composition of the BSC community has been identified as a key factor to explain the differences in erosion. For example Chamizo et al. (2009), under the same environmental conditions, found reduced runoff coefficients on mosses (about 12%), while for crustose and squamulose lichens these coefficients were higher than 60%. Furthermore, BSCs are often associated with varying degrees of physical crusting and the variation in the proportions of physical crusts and different types of BSCs affects runoff and sediment yield. Other properties of BSCs, such as roughness (Chamizo et al., 2009), porosity (Alexander and Calvo, 1990) and hydrophobicity (Souza-Egipsy et al., 2002) have been identified as key factors controlling the variability in runoff response. Two common patterns are highlighted from these studies: infiltration is lower in BSCs than in plant covered patches and in many cases comparable to physically crusted soil (Fig. 3), and the presence of BSCs significantly reduce sediment yield at the patch scale (Calvo-Cases et al., 1991; Solé-Benet et al., 1997; Cantón et al., 2001). Nevertheless, the effect of that additional runoff from BSCs patches on erosion has to be evaluated at larger spatial scales, especially in ecosystems where BSCs cover complete landforms, because it can increase erosion risks downslope or favors water harvesting in vegetated areas.

In semi-arid *Stipa tenacissima* steppes from SE Spain, water typically flows from the bare ground areas to the vegetated patches (Cerdá, 1997; Maestre et al., 2002), enhancing their productivity (Puigdefábregas et al., 1999). Maestre et al. (2002) found that differences in the composition of the BSC community contributed to the increased infiltration found under the canopy of tussocks, as cyanobacteria –that dominated the BSC community in bare ground areas– were negatively related with infiltration. Eldridge et al. (2010) evaluated the effects of *Stipa*, BSCs and rabbits (*Oryctolagus cunniculus*) on infiltration processes in Aranjuez. They found that at the landscape scale, both *Stipa* tussocks and BSCs promoted infiltration, whereas rabbits compromised the crust effect. This effect of BSC was initially unexpected, but was explainable by the relative prevalence of mosses, mostly infiltration promoters, versus lichens, runoff promoters. This study illustrates, for the first time, the relationships between crust species–level community structure and ecosystem function in the form of infiltration, and demonstrates one reason why BSCs behave differently at locations with different suites of components.

Very little is known about the influence of BSCs on other components of the water balance. Over a 43-month monitoring period, A. P. Castillo-Monroy & F. T. Maestre (unpublished data) have found important variations in soil moisture between bare soil and areas with medium (25-75%) and high (>75%) BSC cover in a gypsum area from central Spain (Appendix 3). These authors observed higher moisture under medium BSC cover, particularly after spring and autumn rainfalls. These results may be promoted by the reductions in infiltration promoted under high BSC-cover microsites, as many of these microsites are dominated by lichens such as *Diploschistes diacapsis*, which can seal the soil surface. In the Tabernas desert, Cantón et al. (2004) showed that soil lichens can preserve soil water in summer, an effect attributed to the reduction of evaporation promoted by the structure of lichens, which is effective in retaining water at the lichen–soil interface (Souza-Egipsy et al., 2004), and to the white color of some lichens (e.g. *Squamarina lentigera*, *Lepraria crassissima* and *Buellia zoharii*), which favors the reflectance of solar radiation and lowers temperatures. Lázaro et al. (2008) showed how different BSC communities living at Tabernas had contrasted microclimatic features. They found that PAR radiation and surface temperature were considerably lower in all the lichen-dominated communities than in cyanobacteria-dominated communities, whereas soil moisture and the duration of dew deposition (minutes during which lichen temperature was under the dew point temperature) were higher in the former communities. These results suggest that differences in BSC composition affect both evaporation and dew deposition.

Dynamics of biological soil crusts after disturbances

Ongoing studies being carried out at Tabernas are providing important insights regarding the colonization capacity and growth of different BSC species and communities after disturbances. In areas where BSCs have been removed, the dominant species of the surrounding BSC community are often the best colonizers (Lázaro et al., 2008). However, cyanobacteria and some lichen species, such as *Placynthium nigrum, Squamarina lentigera* and *Fulgensia* sp. have been found to be good colonizers in all sites. Early-successional BSC communities (dominated by cyanobacteria, fungi and algae) showed the largest recovery capacity at Tabernas (28.3% in average 1 year after experimental BSC removal), followed by those dominated by *Diploschistes diacapsis* (21.1%) and *S. lentigera* (14.6%); communities dominated by *Lepraria crasissima* had the smaller capacity of recovery after disturbances (4.7%; R. Lázaro, unpublished data). Different results have been reported from central Europe, where the removal of BSCs promoted the replacement of cyanobacteria/ algae by macro-cryptogams like lichens and mosses (Langhans et al., 2010). These authors did not find significant differences between BSC-removal treatments and controls after two years from treatment application, showing that succession and recovery processes depend on rainfall patterns, and are different and much faster in central Europe than in SE Spain.

Belnap and Eldridge (2003) provided data about recovery times ranging from decades to centuries (depending on crust type, soil type, severity of disturbance, and climate) from semi-arid North America and Australia. However, they stated that recovery time is much faster in soils with inherent aggregate stability, which are common in SE Spain (e.g. Rillig et al., 2003). Indeed, results from Tabernas show yearly increments in total BSC cover after disturbances as large as 30%, and decadal recovery times after BSC removal are expected in this area under low erosion levels (Lázaro et al., 2008). In this site, disturbed areas that were completely void of BSCs in 1990 show a 90% of cover of these organisms today (R. Lázaro, unpublished data). However, recovery rate at Tabernas has been found to be quite variable, and depends not only of BSC type but also on the microclimatic oscillations and on rainfall erosivity (Lázaro et al., 2008). Under low erosion conditions, maximum individual growth rates measured at this site after experimental BSC removal varied between 0.5 - 1.5 $cm^2 \cdot year^{-1}$, depending on the species considered and on overall climatic conditions (R. Lazaro, unpublished data).

Bevan (2009) studied the resistance of several dominant BSC-forming lichen species to drop impacts and their sensitivity to trampling at Tabernas. She found unexpected small inter-specific differences in such resistance, which was much larger than that found in soil aggregates immediately under the same crusts. This explains the strong positive effects of BSCs in protecting the soil against erosion and suggests positive feedback processes in BSC development, at least from a certain BSC cover threshold (Lázaro et al., 2008). In spite of their resistance to erosion, BSCs from Tabernas were mechanically fragile (as found in many other areas; Warren and Eldridge, 2003), especially when they were dry, being the BSC dominated by cyanobacteria more resistant to trampling than that dominated by lichens.

Restoration of biological soil crusts

Given the key roles they play in maintaining ecosystem structure and functioning, re-establishment of BSCs should be undertaken when they can contribute toward reestablishment of a more highly functional ecosystem. In general, restoration practitioners have barely considered BSCs in their work (Bowker, 2007). This is particularly true in SE Spain, as most restoration efforts carried out there have prioritized the increase in forest cover (Maestre and Cortina, 2004a). The lack of attention to BSC in restoration practices is not surprising, as awareness on the role of BSCs and their effects on ecosystem services is minimal, and most information available on the functional role of BSC in the region comes from small-scale experiments, whose relevance at the scale of management is unknown.

As illustrated in the preceding section, the rate of spontaneous BSC colonization of degraded areas, once the stress factor is released, may be faster than initially expected. Albeit the data available do not allow the establishment of generalizations, observations from SE Spain suggest that this rate is fast enough to start considering these organisms during restoration activities. There are two primary situations where BSCs may have a role to play in restoration in SE Spain: degraded *Stipa tenacissima* steppes, and roadside or quarry revegetation. Wooded *Stipa* steppes were probably impoverished for centuries by fuel wood harvesting and cropping of this grass (Cortina et al., 2009; Maestre et al., 2009b). Most *Stipa* steppes in SE Spain are currently at this somewhat degraded ecosystem state (Maestre and Cortina, 2004b). Further pressure leads to a state of reduced plant cover and local scale erosion. We clearly need research to determine if BSCs would improve ecosystem recovery at this stage. As discussed above, BSC colonization might increase soil stability and protect the soil against drop impacts, generate runoff that may be recaptured by impoverished *Stipa* cover, and increase C and N contents compared to bare soil, as found in steppes from central Spain (Castillo-Monroy et al., 2010). One the other hand if BSCs are partially composed of mosses, infiltration may be enhanced, as has been recently demonstrated in a *Stipa* steppe from central Spain (Eldridge et al., 2010). The restoration of roadsides and quarries may benefit from assisted recovery of BSCs, as promoting these organisms in these areas would help stabilize the soil surface, fix atmospheric nitrogen, and potentially create the heterogeneity needed to increase plant production in vegetated patches.

Restoration techniques explicitly based on BSCs have not yet been tested in Spain, but some research has addressed nutrient and water constraints that may limit BSC recovery under field conditions. Maestre et al. (2006) studied cyanobacterial colonization of bare unfertile soil by applying either BSC fragments or slurry, with and without organic amendments, and maintaining the soil in a growth chamber. Surface soils were watered twice and 5-times a week to 80% field capacity. Six months after inoculation, they found that cyanobacteria density was high enough to show a distinctive rate of C and N fixation, and aggregate the 2 mm surface soil. Watering frequency increased cyanobacterial activity by as much as 8 times, and organic amendments were also effective.

Thus we know that in combination with inoculation, elimination of moisture and nutrient constraints may result in rapid cyanobacteria establishment, although field trials are lacking. Provision of inoculation materials are the limiting factor at this time. Inoculation may be carried out by transplanting field-collected BSC materials (Maestre et al., 2006; Bowker, 2007). This technique has the advantage of using local organisms, but it is destructive and may only be applicable at small scales. In contrast, application of commercially-available inoculums, produced *ex-situ*, ensures a homogeneous, controlled and accessible source of cyanobacteria, and can be easily applied using standard hydroseeding systems. Disadvantages of this technique are the current lack of locally available products, and the lack of inoculum produced with local genotypes.

Conservation of biological soil crusts

A Spanish Red List of endangered BSC-forming organisms is currently lacking. However, some regional Red Lists have been developed in order to detect those lichen species with current conservation problems. Atienza & Segarra (2000) published a preliminary Red List of the lichens of the Valencian Community (eastern Spain). Some BSC-forming species from gypsum soils such as *Acarospora placodiiformis* (endangered), *A. nodulosa* var. *reagens* (vulnerable), *Diploschistes diacapsis* (lower risk), *Fulgensia desertorum* (vulnerable), *F. poeltii* (endangered), *Lecidea circinarioides* (endangered), *Psora saviczii* (endangered) are included in this list. Moreover, *Aspicilia fruticulosa* (endangered) and *Heppia gigantea* (vulnerable) are also included in this list. Guerra et al. (1995), in a study about the bryophyte and lichen flora of the gypsiferous outcrops of SE Spain, pointed out that 17 lichen taxa are rare or endemic, living exclusively or almost exclusively on gypsum soils.

Importance of biological soil crust research in Spain and future research directions

The semi-arid ecosystems from Spain are an excellent field laboratory to work with BSCs. Despite that these organisms have traditionally been ignored, research carried out in this country has been characterized by its originality, as topics poorly studied worldwide have been tackled by scientists working in this country. These include species-specificity of BSC effects on plant germination (Escudero et al., 2007), the study of biotic interactions among BSC organisms (Maestre et al., 2008, 2009; Bowker et al., 2010a) and the use of BSCs as model systems to explore ecosystem structure-functioning relationships (Bowker et al., 2010b; Maestre et al., 2010). Biological soil crusts are proving to be an excellent model system to foster new ways of thinking about key community and ecosystem ecology topics, and open new and highly promising research lines. As an example, the greater number of species interactions possible under low stress conditions may render intransitivity (*sensu* Laird and Schamp, 2008) dominant over niche segregation and expansion, potentially resulting in positive effects of competition on species richness in low stress situations (Bowker et al. 2010a). These results might not have been observed using a vascular plant study system and highlights the utility of BSCs as a model system for increasing our understanding of the mechanisms structuring biotic communities. In a similar direction, unlike other soil communities, BSCs tend to exhibit linear non-saturating dependencies of some ecosystem functions upon biodiversity (Maestre et al., 2010; Bowker et al., 2010b), illustrating the potential of BSCs as a model system to explore the diversity-function relationship between diversity and ecosystem functioning at several spatial scales.

Although the advance in our knowledge of the ecological role of BSCs in Spain has been enormous during the last ten years, much remains to be learned from these organisms. Below we identify some key research topics that deserve special research attention in the future:

i) *Roles of particular BSC species/traits on ecosystem functioning*. Future studies should explicitly consider which particular traits are underlying species-and site-specific effects of BSCs on nutrient cycling and soil water dynamics. The trait lists proposed for lichens, mosses and cyanobacteria/algae by Bowker et al. (2010b) provides an excellent starting point to tackle this issue.

ii) *Interactions between BSC and other soil organisms*. To date, no study has explored the effects of BSCs on key soil communities such as nematodes, protozoa and soil mesofauna in Spain. This is an important gap in our knowledge that must be urgently filled by future research. Similar research efforts must be carried out to study heterotrophic microbial populations associated to BSCs in Spain.

iii) *Hydrological effects of BSCs*. Information on the influence of BSCs on rainfall interception, soil moisture, evaporation or dew deposition hardly exist for SE Spain, despite results from other sites suggest their importance. Future studies should study in more detail the effects of BSCs on these components of the water balance at fine and coarser spatial scales.

iv) *Ecosystem-scale effects of BSCs on the C and N cycles*. As estimations at the ecosystem scale based only on vegetated and bare-ground areas can be rather conservative if the sampling effort is not high enough to capture the spatial variability in the C and N fluxes induced by BSCs, future studies should explicitly consider the effects of BSCs when modeling and estimating C and N budgets at the ecosystem scale.

v) *Restoration of BSCs*. Promoting the recovery of BSC components is far from being integrated in current restoration practitioner’s agenda. To fill this gap, pilot studies and demonstration projects are needed to evaluate the potential of current BSC restoration techniques.

We hope that this brief review will serve to illustrate the variety and importance of the research carried out on Spanish BSCs during the last decades, and that it will stimulate other research groups from Spain and abroad to start working with these key organisms.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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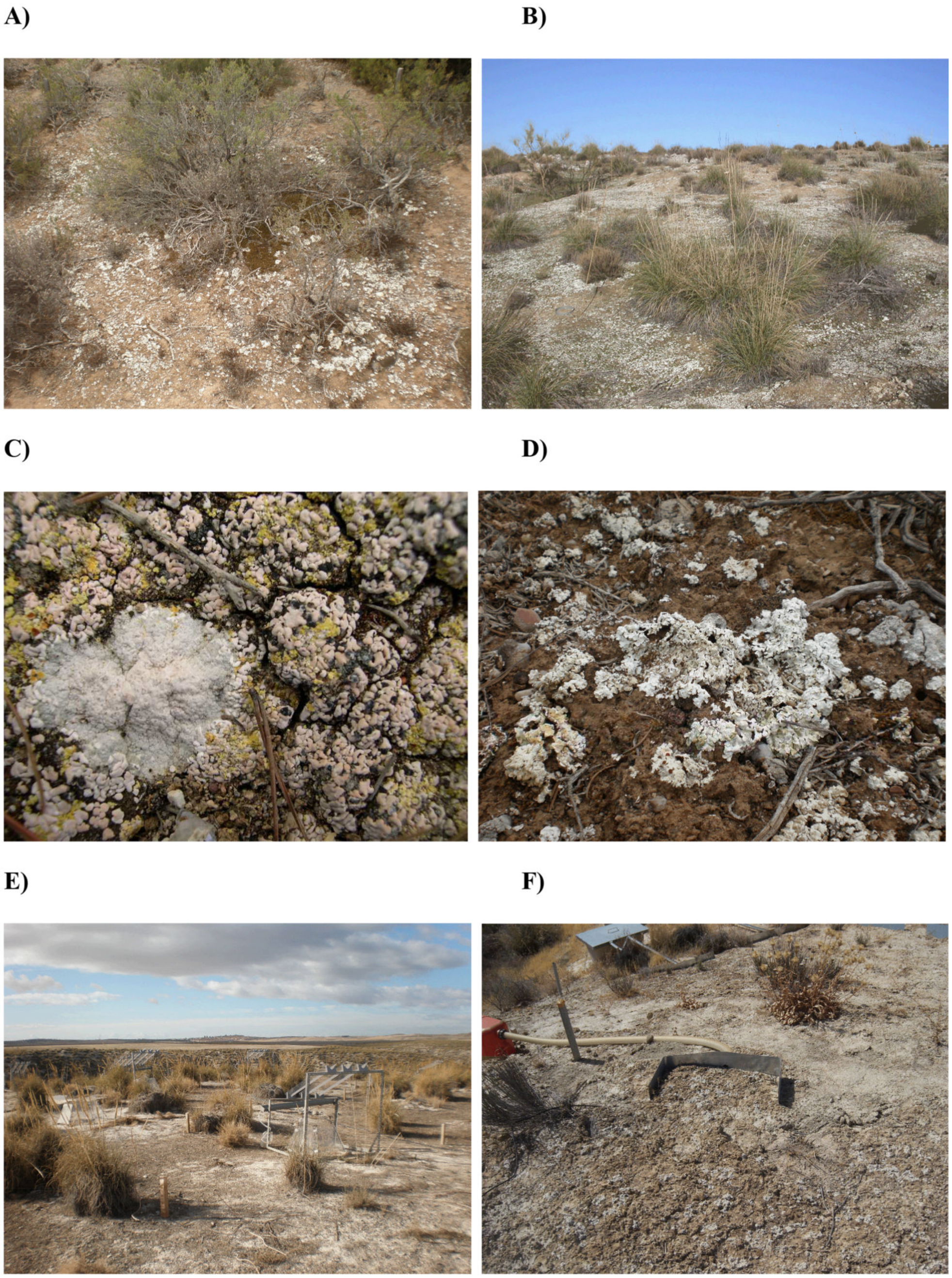

Figure 1.

Examples of Spanish semi-arid shrublands (A) and steppes (B), showing the dominance of biological soil crusts (BSCs) in plant interspaces. Close-up views of gypsum and calcareous BSC communities are shown in C) and D), respectively. Partial views of ongoing climate change (E) and erosion (F) experiments focusing on BSCs. Photo credits: F. T. Maestre (A-E) and Y. Cantón (F).

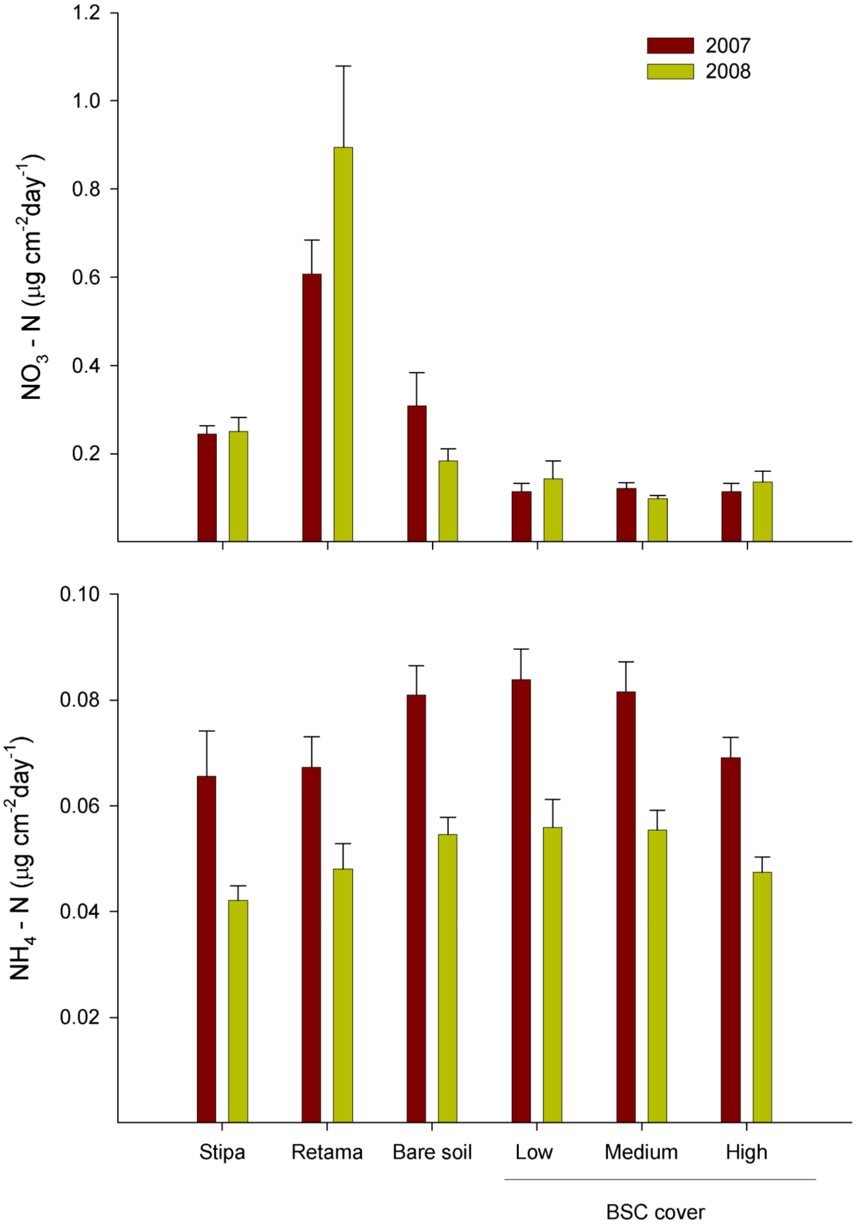

Figure 2.

Annual changes in NO_3^--N (upper graph) and NH_4^+-N (lower graph) availability between five microsites in a semi-arid *Stipa tenacissima* steppe from central Spain. Stipa = *Stipa tenacissima* tussocks; Retama = *Retama sphaerocarpa* shrubs; Bare soil, Low, Medium and High indicate areas with very low (< 5% cover), low (5-25% cover) medium (25-75%) and high (> 75%) biological soil crust (BSC) cover. Note the differences in scale in the y-axis. Data represent means ± SE (n = 4 surveys). Data adapted from Castillo-Monroy et al. (2010).

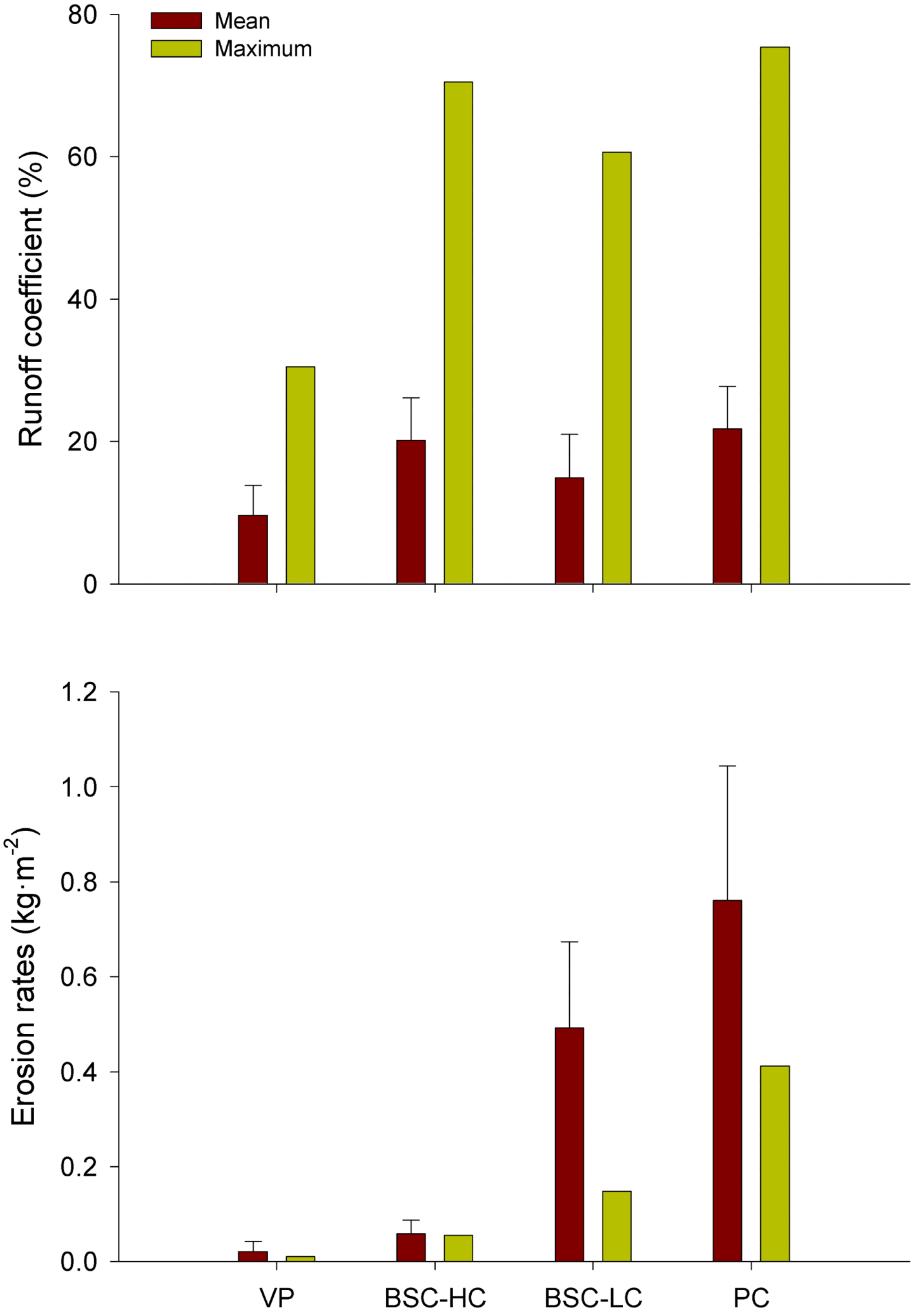

Figure 3.

Mean annual runoff coefficient (ratio between runoff rate and rainfall) and erosion rates, and maximum runoff coefficient and erosion rates registered in a single rainfall event in different microsites during three hydrological years in the Tabernas Desert (Almería, SE Spain). Data were recorded after natural rainfalls in circular micro-plots (0.24 m^2) with different types of soil cover. Micro-plots with biological soil crusts (BSCs) consist in a mix of lichens and cyanobacteria. VP = vascular plants, BSC-HC = high cover (> 90%) of BSCs, BSC-LC = low cover (< 50%) of BSCs, and PC = physical soil crust. Error bars indicate SD (*n* = 3).

Table 1

A summary of measurements relevant to biological soil crust photosynthesis from Spanish studies. See the original articles for details on the experimental treatments/populations studied in each case.

Study	Material	Treatments	Chl a (mg m^{-2})	Chl a+ b (mg m^{-2})	Net CO$_2$ exchange (μmol m^{-2} s^{-1})	Quantum efficiency PSII
Maestre et al. (2006)	Synthetic cyanobacterial and lichen crusts	Fragment inoculation, without fertilization, watering	27	37	1.9[a]	
		Fragment inoculation, without fertilization, no watering	19	30	0.6[a]	
		Fragment inoculation, fertilization, watering	70	81	2.2[a]	
		Fragment inoculation, fertilization, no watering	45	58	0.8[a]	
		Slurry inoculation, without fertilization, watering	45	55	2.5[a]	
		Slurry inoculation, without fertilization, no watering	33	45	1.7[a]	
		Slurry inoculation, fertilization, watering	69	80	3.2[a]	
		Slurry inoculation, fertilization, no watering	42	47	2.3[a]	
Pintado et al. (2005)	*Diploschistes diacapsis*	Sun population		1350	5[b]	0.28[c]
		Shade population		1780	4.13[b]	0.25[c]
Del Prado & Sancho (2007)	*Teleoschistes lacunosus*	Two habitat types				0.6-0.7
Deltoro et al. (1998)	*Pleurochaete squarrosa and Syntrichia rurales, field conditions*	*P. squarrosa*				0.53-0.56
		S. ruralis				0.53-0.57

[a] values reflect treatment means,

[b] values reflect maximal rates, and

[c] coarse estimate converted from quantum yield.