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Biological soil crust diversity and composition in southwest Idaho, U.S.A.

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Abstract. Biological soil crusts (BSCs) were sampled by habitat types within and adjacent to the Orchard Combat Training Center (OCTC) in southwest Idaho, U.S.A. Plots consisting of a 34.7 m radius circle, approximately equal to one acre or 0.38 hectares were sampled. We focused on five native vascular plant-dominated current habitat types within the OCTC, including: 1) Wyoming sagebrush, 2) saltbush, 3) rabbitbrush, 4) winterfat, and 5) Sandberg bluegrass. We describe how BSC cover and species richness varied with habitat types in the study area. We recorded the relative abundance of BSCs and vascular plant species and collected voucher specimens for each BSC. The biodiversity of each BSC in these arid habitat types was much greater than many ecologists have assumed. We found a total of 68 species of BSC across all 17 plots. BSC cover differed significantly across the different habitat types. BSC cover was significantly higher in sagebrush and saltbush as compared with *Poa*, rabbitbrush and winterfat habitat types. Overall, there was substantially more BSC richness (17–47 species) than vascular plant richness (4–13 species), and BSC richness was positively related to vascular plant richness (R^2=0.18, p=0.041). On average, each additional plant species was associated with 1.36 additional BSC species. BSC communities also varied across the habitat types with *Buellia punctata* as a significant indicator species for sagebrush, *Toninia sedifolia* for saltbush, and *Cladonia pocillum* for winterfat. Several BSC species were associated with 2 or 3 habitat types; for example, *Cladonia fimbriata, Diploschistes muscorum, Leptogium lichenoides, Massalongia carnosa, Riccia sorocarpa* and *Trapeliopsis steppica* were most common in the sagebrush, *Poa*, and rabbitbrush habitats. In contrast, *Caloplaca tominii, Endocarpon loscosii, Placidium squamulosum* and *Psora tuckermanii* were most common in winterfat and saltbush habitats.

Keywords. Biodiversity, biocrusts, Great Basin, lichens, bryophytes, military training area.

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Biological soil crusts (BSCs) are a close association between soil particles and cyanobacteria, microfungi, algae, lichens and bryophytes (mosses, liverworts) that live within or on top of the uppermost millimeters of soil (Belnap et al. 2001). They are found in all dryland regions of the world and in all habitat types within these lands, including the arid and semi-arid regions of North America (Rosentreter & Belnap 2001). Also known as microbiotic, cryptobiotic, biotic, and cryptogamic crusts, BSCs are often overlooked due to their tendency to blend in with the soil; thus, they are seldom collected. Due to the small size and fragility of the specimens, they are difficult to return to the lab intact and suitable for species determination. However, the importance of these organisms in performing many vital ecological functions such as providing habitat for microfauna, stabilising soils, producing nitrogen and carbon, and enhancing water flow through the soil, has been well documented (Belnap et al. 2001; Hilty et al. 2004; Ponzetti et al. 2007; Rosentreter & Eldridge 2004).

While many scientists acknowledge the close links between BSCs and the condition or health of dryland ecosystems (Klopatek 1993; Rosentreter & Eldridge 2002), BSCs and their component lichens and bryophytes are rarely recorded during field-

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based assessments (West 1990). In the mid to late 1980s, Australian rangeland scientists pioneered a range of techniques to determine the health of landscapes that placed more emphasis on soil and landscape function rather than relying, as previously, on the status and condition of the vascular plant community (Tongway & Smith 1989). The resulting Soil Surface Classification System used BSC cover as an important measure of the capacity of the soil to carry out two functions: resist deformation and cycle nutrients.

BSCs help to maintain critical ecosystem processes such as resistance of ecosystems to invasion. In the western U.S.A., lichen-dominated biocrust communities have been shown to reduce the invasibility of arid lands by large seeded Eurasian weeds such as *Bromus tectorum* (Deines et al. 2007; Serpe et al. 2008; Reisner et al. 2013). Before the introduction of European livestock, a combination of low levels of disturbance in dry seasons and the presence of a stable lichen-dominated biocrust, has kept invasive flammable grass species to low levels. With an increase in human- and livestock-induced soil disturbance, European annual grasses have proliferated, increasing the extent and intensity of wildfire in areas which had not co-evolved with frequent fire.

Some BSC lichen species appear more tolerant of trampling than others (Rogers & Lange 1971). This is probably due to differences in their morphologies, as foliose or fruticose forms seem to be more susceptible than crustose and squamulose forms (Eldridge & Rosentreter 1999). Morphological groups of biocrust lichens can also provide valuable insights into the health and recovery of ecosystems (Rosentreter et al. 2001). For example, in a study across more than 0.6 M km^2 of eastern Australia, Eldridge & Koen (1998) found that the presence of the 'yellow foliose' morphological group, which comprised foliose lichens of the genera *Heterodea, Xanthoparmelia* and *Chondropsis* spp., were consistently correlated with stable, productive landscapes with little evidence of accelerated erosion.

The Intermountain West of the U.S.A. supports a diversity of BSCs, with communities varying across a wide range of climates, soil types and habitats (Rosentreter & Belnap 2001). We focus on a poorly-known part of southwest Idaho, the Orchard Combat Training Center (OCTC). Set aside for military training, the OCTC is managed differently than many other public lands in the Intermountain West and a better understanding of BSC communities has the potential to inform land management decisions.

Other studies in the region have reported ecological roles of BSCs (Eldridge et al. 2003) and their recovery following wildfire (Hilty et al. 2003, 2004). However, these publications evaluate biocrusts as a general group rather than at the species-specific level. Eastern Oregon is the nearest (**Fig. 1**) and most similar habitat where soil crust species composition has been well-studied. In north-central Oregon, the Boardman Research Natural Area, Mayfield and Kjelmyr (1984) identified 14 bryophyte and 7 lichen taxa. In the same region, the Lawrence Memorial Grassland, and ungrazed sagebrush steppe reserve, supported 45 BSC taxa (Miller et al. 2011). From nine sites in central and eastern Oregon, Ponzetti & McCune (2001) identified 48 taxa and several morphological groups. The nearest of these sites to the OCTC is 340 km to the northwest. In closer proximity to the OCTC, DeBolt (2008) identified 47 soil crust taxa in Birch Creek, 45 taxa near Rome (DeBolt 2010) and 56 biological soil crust taxa at Coal Mine Basin Area of Critical Environmental Concern (DeBolt 2011). These studies combined suggest that the region can host diverse BSC communities, but also when comparing species lists, it becomes clear that there is quite a bit of variability in composition between sites.

We aim to expand the regional knowledge of BSC communities with species-specific sampling in and near the OCTC. We focus on five common vascular plant habitat types in the region and compare the BSC communities that they support. Our specific objectives were to:

1. Describe how BSC cover and species richness varied with habitat types in the study area.
2. Describe BSC community composition in different habitats with detailed attention to lichen and bryophyte taxonomy.

Methods

Study area. The Orchard Combat Training Center (OCTC) is located south of Boise, Idaho in the Snake River Plain (**Fig. 1**). The area has mostly level ground and is covered by arid steppe

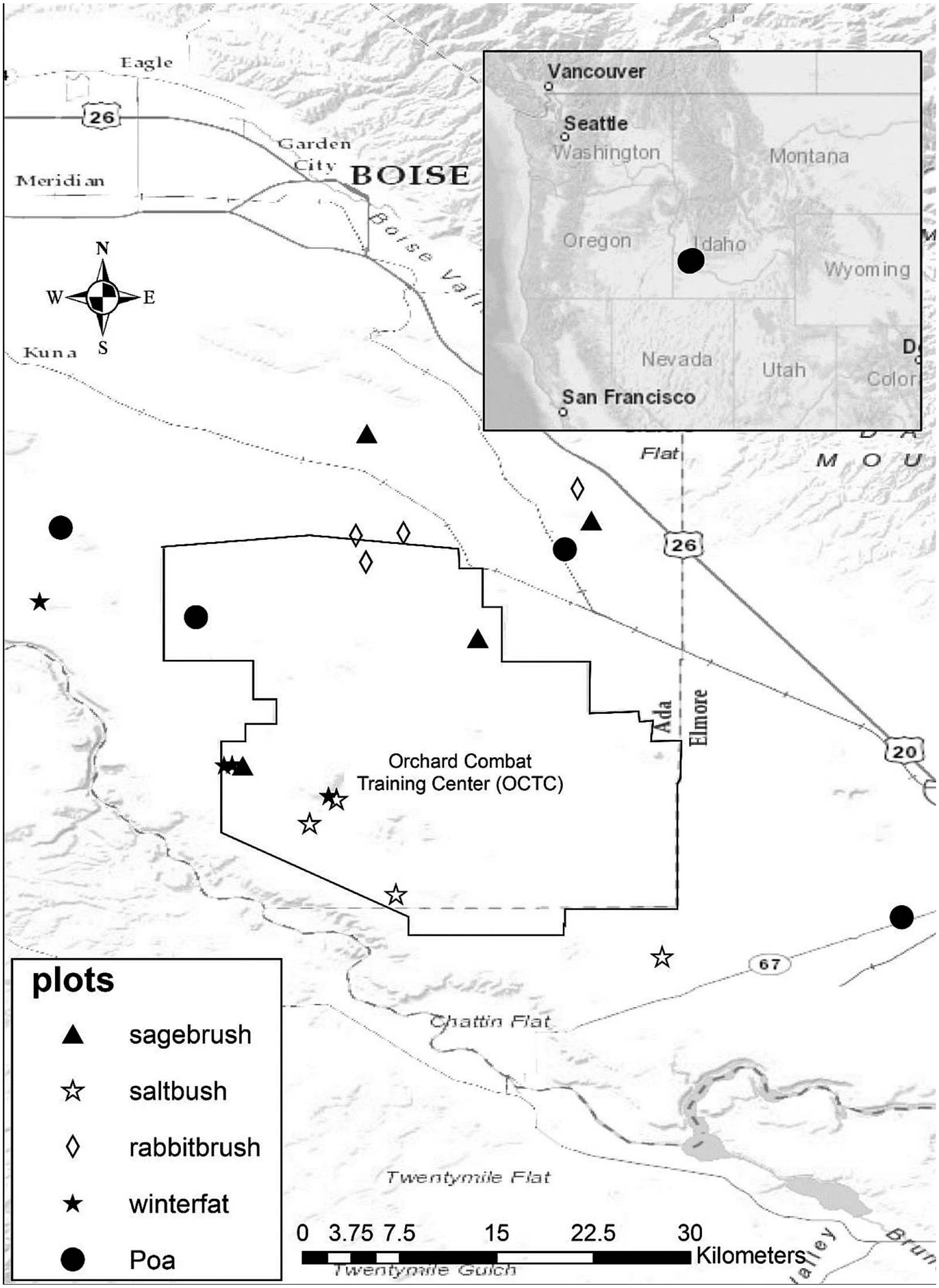

Figure 1. Map of BSC plots in the OCTC in southwestern Idaho, U.S.A. Symbols represent habitat types.

Table 1. Ecological characteristics of the habitat types sampled in Southwest Idaho. Soil classification based on the NRCS county soil survey (USDA 1991).

Habitat type	Soil type and classification	Elevation (m)	Associated plant species
Wyoming Sagebrush *Artemisia tridentata* ssp. *wyomingensis*	Silt-loam Catchell-Chilcott-Banbury	980–630	*Poa secunda, Elymus elymoides, Vulpia* spp.
Saltbush *Atriplex confertifolia*	Shallow silt-loam Tadpole-Corder	630–790	*Picrothamnus desertorum, Poa secunda*
Rabbitbrush *Ericameria nauseosa* ssp. *consimilis*	Silt-loam Chilcott-Cachell-Chardonton	980–630	*Poa secunda, Elymus elymoides, Lithophragma bulbifera*
Winterfat *Krascheninnikovia lanata*	Deep silt-loam Corder-Tadpole	630–790	*Picrothamnus desertorum, Poa secunda*
Poa *Poa secunda*	Silt-loam Doman-Minverno-Power	980–630	*Elymus elymoides, Lithophragma bulbifera*

vegetation. The climate is characterized by hot dry summers and cold, moist winters. Average annual precipitation is 20 to 25 cm. Elevation ranges from 671 to 975 m. Soils are derived from ash and basalts, both of volcanic origin. The lower elevation areas receive less precipitation and the soils are generally more silty (USDA 1991; **Table 1**). The saltbush and winterfat habitat sites are restricted to those lower elevation areas and are not as widely sampled geographically due to the limited distribution (**Table 1**; **Fig. 1**). Disturbances include past, historic and current livestock grazing, roads, military training and recreational trails.

Field and laboratory protocols. We focused on five native-dominated habitat types within southwest Idaho (**Table 1**; **Fig. 1**), including: 1) Wyoming sagebrush (*Artemisia tridentata* ssp. *wyomingensis*), 2) saltbush (*Atriplex confertifolia*), 3) rabbitbrush, (*Ericameria nauseosa* ssp. *consimilis*), 4) winterfat, (*Krascheninnikovia lanata*) and 5) Sandberg bluegrass (*Poa secunda*). Within each habitat type, as best as could be determined in the field, each soil-dwelling species encountered within a plot was carefully collected and numbered.

All plots were randomly established within and adjacent to the OCTC using the criteria: no roads (including two-tracks) going through the plot, no salt blocks within 1/4 mile of the plot, >1/4 mile from livestock water, and no plow and seeded sites. To assess biological soil crust diversity at the study site, we used a modified Forest Health Monitoring sampling protocol (McCune et al. 1997). A minimum of 30 minutes and a maximum of 2 hours were spent examining each of the plots consisting of a 34.7 m radius, approximately equal to one acre or 0.38 hectares. This modified method has been applied to other treeless ecosystems (DeBolt 2008, 2010, 2011; McCune et al. 2009; Root & McCune 2012; Root et al. 2011).

Each BSC sample was lightly moistened with a water spray bottle, wrapped in tissue for padding and protection, and placed in a small paper bag or a mini-petri dish. Additional data recorded at each plot included GPS coordinates, elevation, aspect, and associated vascular plant species. Before leaving the field site, the relative abundance of each collected species was ranked. A species was considered "rare" if 5 or fewer individuals or colonies of the species were present within the plot. "Infrequent" taxa were those with 5–10 individuals or colonies present, and species were "common" if more than 10 individuals or colonies were present within the plot.

Specimens were returned to the lab and curated using standard bryological and lichenological techniques (Brodo et al. 2001; McCune & Rosentreter 2007; Rosentreter et al. 2007). Voucher specimens were deposited into the Snake River Plain herbarium at Boise State University or with the Idaho Army National Guard. Each BSC was assigned to a functional group based on McCune (1994) and based on the primary ecological function it contributes to the ecosystem (**Table 2**).

Analysis. We used an analysis of variance (ANOVA) in the software R (R development core team 2017) to determine whether BSC richness or cover differed across the habitat types. Normality and equal variance assumptions were tested and met. Where habitat types were found to differ significantly, we followed the overall test with pairwise comparisons using the Tukey correction for multiple tests. To relate BSC richness to vascular plant richness, we used simple linear regression in the software R after checking assumptions.

To explore differences in community composition across habitat types, we used ordination and indicator species analysis using the relative abundance ratings recorded in the field. Indicator species analysis (ISA, Dufrene & Legendre 1997), also using the software PC-Ord, allowed detection of species most consistent and faithful to a habitat type. Indicator values (IVs) range from 0 to 100 with 100 being the strongest and indicating that a species is always found only in a particular habitat type. Unconstrained ordination was performed using using non-metric multidimensional scaling (NMS, Kruskal 1964) with Sorensen distance in the software PC-Ord (McCune & Mefford 2011).

Results

The biodiversity of biocrusts in these relatively arid habitat types is much greater than many ecologists have reported. On the OCTC, we collected 68 BSC species from sampling 17 one-acre plots (**Table 2**). These 68 species were composed of 50 lichens, 18 bryophytes and one cyanobacteria. Soils differed only slightly among plots, ranging from shallow silt loam to deep silty-loam.

There was no evidence that BSC species richness differed between habitat types ($p=0.165$; **Fig. 2**); however, BSC cover differed significantly across the different habitat types ($p=0.011$). BSC cover was significantly higher in saltbush as compared with winterfat habitat ($p=0.027$; **Fig. 2**) and with *Poa* habitat ($p=0.0068$; **Fig. 2**).

There was suggestive evidence that plant species richness was positively correlated with BSC species richness ($R^2=0.18$, $p=0.041$; **Fig. 3**). Overall, there was substantially more BSC richness (17–47 species) than vascular plant richness (4–13 species). On average, each additional plant species was associated with 1.36 additional BSC species (this is the estimated slope for the regression, $p=0.041$).

Indicator species analysis identified three species associated with particular habitat types. The sagebrush habitat type had *Buellia punctata* (IV=49, $p=0.02$), while the saltbush type had *Toninia sedifolia* (IV=56, $p=0.04$), and the winterfat type had *Cladonia pocillum* (IV=44, $p=0.03$).

NMS ordination suggested that the different habitat types hosted fairly distinct BSC communities (**Fig. 4**). The method successfully reduced dimensionality to 3, with a final stress of 10.2 and instability <0.000001. The axes were all orthogonal and described 49.8, 26.0 and 11.6 percent of the variation for a total of 87.4% of the total community variation. In particular, saltbush and winterfat habitats had communities that were quite distinct from the others (**Fig. 4**).

The ordination results suggested that although habitat types differed in their BSC communities, each habitat overlapped somewhat with at least one other. This pattern makes it less likely to detect indicator species because species were often associated with two or three habitat types. Species positively associated with the first ordination axis were uncommon in winterfat and saltbush habitats and more common in sagebrush, *Poa* and rabbitbrush habitat; these included *Cladonia fimbriata, Diploschistes muscorum, Leptogium lichenoides, Massalongia carnosa, Riccia sorocarpa* and *Trapeliopsis steppica* (**Fig. 5**). Species negatively associated with the first ordination axis were most common in winterfat and saltbush habitat types and included *Caloplaca tominii, Endocarpon loscosii, Placidium squamulosum* and *Psora tuckermanii*. Species positively associated with the second ordination axis were generally found in more diverse plots with sagebrush or winterfat and included *Arthonia glebosa* and *Psora montana*. Species that were positively associated with both ordination axes were found in the more diverse sagebrush and rabbitbrush plots. These included *Leptochidium albociliatum* and *Placynthiella icmalea*.

Other observations were: 1) *Aloina bifrons*, a small moss, occurred in all the habitat types but only on microsites that were subsoil, particularly in mounds produced by badger diggings; 2) the ungrazed (>50 years) winterfat habitat supported the tall moss, *Syntrichia ruralis* 2–4 times taller than this same species in other habitats and in the grazed winterfat habitat.

Discussion

This study is one of the few species-level, voucher-based, ecological studies of BSCs in the sagebrush steppe of the Intermountain West, U.S.A. Collecting vouchers is a valuable piece of BSC ecological fieldwork because it allows improved quality of species identification and the ability to revisit vouchers or study sites even if there are nomenclatural or taxonomic changes. Furthermore,

Table 2. Biocrusts found in 17 plots at the Orchard Combat Training Center (OCTC) and their life forms: lichen (l), bryophyte (b), cyanobacteria (c), ecological functional group (McCune 1994), morphological type. Nomenclature is based on: Consortium of North American Lichen Herbaria [Accessed 2018] http://symbiota.org/nalichens/ and Consortium of North American Bryophyte Herbaria [Accessed 2018]. Functional groups are modified from McCune (1994) and morphological types are from Eldridge & Rosentreter (1999).

Species and authorities	Life form	Ecological functional group	Morphological type
Acarospora schleicheri (Ach.) A.Massal.	l	old growth steppe soil crust	crustose
Acarospora terricola H.Magn.	l	old growth steppe soil crust	crustose
Aloina bifrons (De Not.) Delg.	b	pioneer soil stabilizer	short moss
Arthonia glebosa Tuck.	l	steppe soil crust	crustose
Aspicilia aspera (Mereschk.) Tomin	l	steppe soil crust	crustose
Aspicilia filiformis Rosentreter	l	steppe soil crust	fruticose
Aspicilia masourii Sohrabi	l	steppe soil crust	crustose
Aspicilia reptans Looman	l	steppe soil crust	crustose
Athalamia hyalina (Sommerf.) S.Hatt.	b	pioneer soil stabilizer	liverwort
Bryum argenteum Hedw.	b	pioneer soil stabilizer	short moss
Bryum lanatum (P.Beauv.) Hampe	b	pioneer soil stabilizer	short moss
Bryoerythrophyllum columbianum (F.J.Herm.& E.Lawton) R.H.Zander	b	Soil binder	Short moss
Buellia punctata (Hoffm.) Coppins & Scheid. (=*Amandinea punctata*)	l	detritus binder	crustose
Caloplaca atroalba (Tuck.) Zahlbr.	l	detritus binder	crustose
Caloplaca jungermanniae (Vahl) Th.Fr.	l	detritus binder	crustose
Caloplaca lactea (A.Massal.) Zahlbr	l	detritus binder	crustose
Caloplaca tominii Savicz.	l	pioneer soil stabilizer	sorediate crustose
Candelariella aggregata M.Westb.	l	detritus binder	crustose
Candelariella rosulans (Müll.Arg.) Zahlbr.	l	soil binder	crustose
Candelariella vitellina (Hoffm.) Müll.Arg.	l	soil binder	crustose
Cephaloziella divaricata (Roth) Warnst.	b	soil binder	short moss
Ceratodon purpureus (Hedw.) Brid.	b	pioneer soil stabilizer	short moss
Cladonia fimbriata (L.) Fr.	l	pioneer soil stabilizer	fruticose
Cladonia pocillum (Ach.) Grognot	l	pioneer soil stabilizer	foliose
Cladonia pyxidata (L.) Hoffm.	l	pioneer soil stabilizer	foliose
Collema coccophorum Tuck.	l	N-fixing	foliose
Collema tenax (Sw.) Ach.	l	N-fixing	gelatinous
Collema sp. (very small one)	l	N-fixing	crustose
Didymodon australasiae Zander	b	soil binder	short moss
Didymodon brachyphyllus (Sull.) R.H.Zander	b	soil binder	short moss
Didymodon vinealis (Brid.) R.H.Zander	b	soil binder	short moss
Diploschistes muscorum (Scop.) R.Sant.	l	old growth steppe soil crust	crustose
Encalypta vulgaris Hedw.	b	soil binder	short moss
Endocarpon loscosii Mull.Arg.	l	steppe soil crust	scale
Endocarpon pallidum Ach.	l	Steppe soil crust	scale
Endocarpon pusillum Hedwig	l	steppe soil crust	scale
Funaria hygrometrica Hedw.	b	pioneer soil stabilizer	short moss
Grimmia tenerrima Renauld & Cardot	b	soil binder	short moss
Heteroplacidium congestum (Breuss & McCune) Breuss	l	old growth steppe soil crust	crustose
Lecanora epibryon (Ach.) Ach.	l	soil binder	crustose
Lecanora flowersiana H.Magn.	l	detritus binder	crustose
Lecanora muralis (Schreber) Rabenh.	l	rock lichen “on soil"	crustose
Lecidea laboriosa Mull.Arg.	l	steppe soil crust	crustose
Leptochidium albociliatum (Desm.) M.Choisy	l	N-fixing	gelatinous
Leptogium lichenoides (L.) Zahlbr.	l	N-fixing	gelatinous
Massalongia carnosa (Dickson) Körber	l	N-fixing & old growth steppe soil crust	foliose
Microcoleus sp.	c	N-fixing & pioneer soil stabilizer	filamentous cyanobacteria

Table 2. Continued.

Species and authorities	Life form	Ecological functional group	Morphological type
Physconia enteroxantha (Nyl.) Poelt	l	leaf lichen "on soil"	foliose
Physconia muscigena (Nyl.) Poelt	l	soil binder	foliose
Placidium lachneum (Ach.) B. de Lesd.	l	pioneer soil stabilizer	scale
Placidium lacinulatum (Ach.) Breuss	L	pioneer soil stabilizer	scale
Placidium squamulosum (Ach.) Breuss	l	pioneer soil stabilizer	scale
Placynthiella icmalea (Ach.) Coppins & P.James	l	detritus binder	crustose
Psora decipiens (Hedw.) Hoffm.	l	steppe soil crust	scale
Psora montana Timdal	l	steppe soil crust	scale
Psora tuckermanii R.A.Anderson ex Timdal	l	steppe soil crust	scale
Pterygoneurum ovatum (Hedw.) Dix.	b	pioneer soil stabilizer	short moss
Pterygoneurum subsessile (Brid.) Jur.	b	pioneer soil stabilizer	short moss
Riccia sorocarpa Bisch.	b	pioneer soil stabilizer	liverwort
Sarcogyne mitziae K.Knudsen, Kocourek & McCune	l	detritus binder	crustose
Synthrichia caninervis Mitten	b	Soil binder	Short moss
Syntrichia ruralis (Hedwig) F.Weber & D.Mohr	b	soil binder	tall moss
Texosporium sancti-jacobi (Tuck.) Nadv.	l	old growth steppe soil crust	crustose
Thelenella muscorum var. *octospora* (Nyl.) Coppins & Fryday	l	old growth steppe soil crust	crustose
Thrombium epigaeum (Pers.) Wallr.	l	pioneer soil stabilizer	crustose
Toninia ruginosa (Tuck.) Herre	l	detritus binder	crustose
Toninia sedifolia (Scop.) Timdal	l	detritus binder	crustose
Tortula brevipes (Lesq.) Broth.	b	pioneer soil stabilizer	short moss
Trapeliopsis bisorediata McCune & Camacho	l	old growth steppe soil crust	scale
Trapeliopsis steppica McCune & Camacho	l	old growth steppe soil crust	scale

our attention to taxonomic detail may have allowed us to more thoroughly describe the BSC diversity as compared with other studies. Indeed, our study found a greater diversity than others in the region, even those that did include voucher collection. Compared with other ecological studies in the region, where BSC species richness ranged from 21 to 56 species (DeBolt 2011; Mayfield & Kjelmyr 1984), we observed 68. This difference may be due to more careful attention to taxonomic detail or to our sampling design that intentionally brought us to several distinct habitat types.

Functional groups and growth forms inform us about ecosystem services that may vary across habitat types. As most BSC communities in the Intermountain West have been disturbed (Rosentreter & Belnap 2001), restoration efforts must target the functional groups and BSC species that can be supported, and which differ across habitats. Simply targeting functional groups for restoration may be an incomplete approach as the ecosystem services provided by BSCs may vary within a functional group, or even within a genus. For example, *Caloplaca tominii* is a soil stabilizer while *C. aggregata* is a detritus binder (McCune 1994). Within the genus *Psora,* we found that *P. tuckermanii* and *P. montana* occur in very different habitats. Within functional groups, we observed considerable variability in association with habitat types, suggesting that focusing at that level may miss important ecological patterns.

We found that soil stabilizers (16) and soil binders (11) were the most abundant functional groups across all habitat types (**Table 2**). These functional groups help provide the stability that is so critical to erosion prevention in arid systems (Eldridge & Rosentreter 1999). Greater diversity of soil stabilizers and binder species may increase site stability and resistance to exotic species invasion (Prieur-Richard et al. 2001). Loss of these BSCs can lead to soil erosion and creation of a seed bed for invasive annual species, leading to the unravelling of the ecosystem (Eldridge & Koen 1998). Biocrust species are foundational species that hold the soil, litter and the arid ecosystems together.

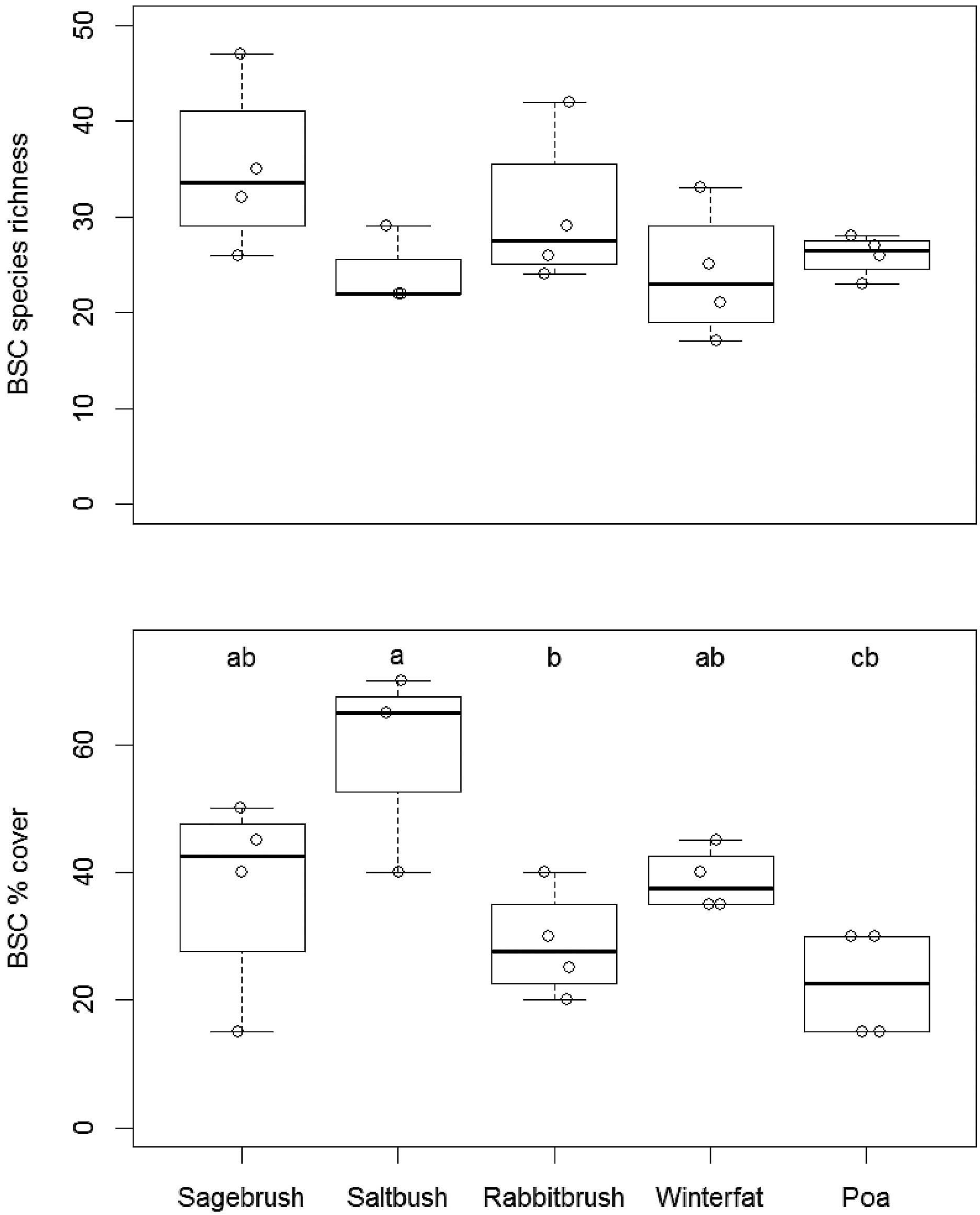

Figure 2. BSC richness and cover across five habitat types at the Orchard Combat Training Center, Idaho. Letters in the bottom panel indicate groups with BSC cover that differ significantly.

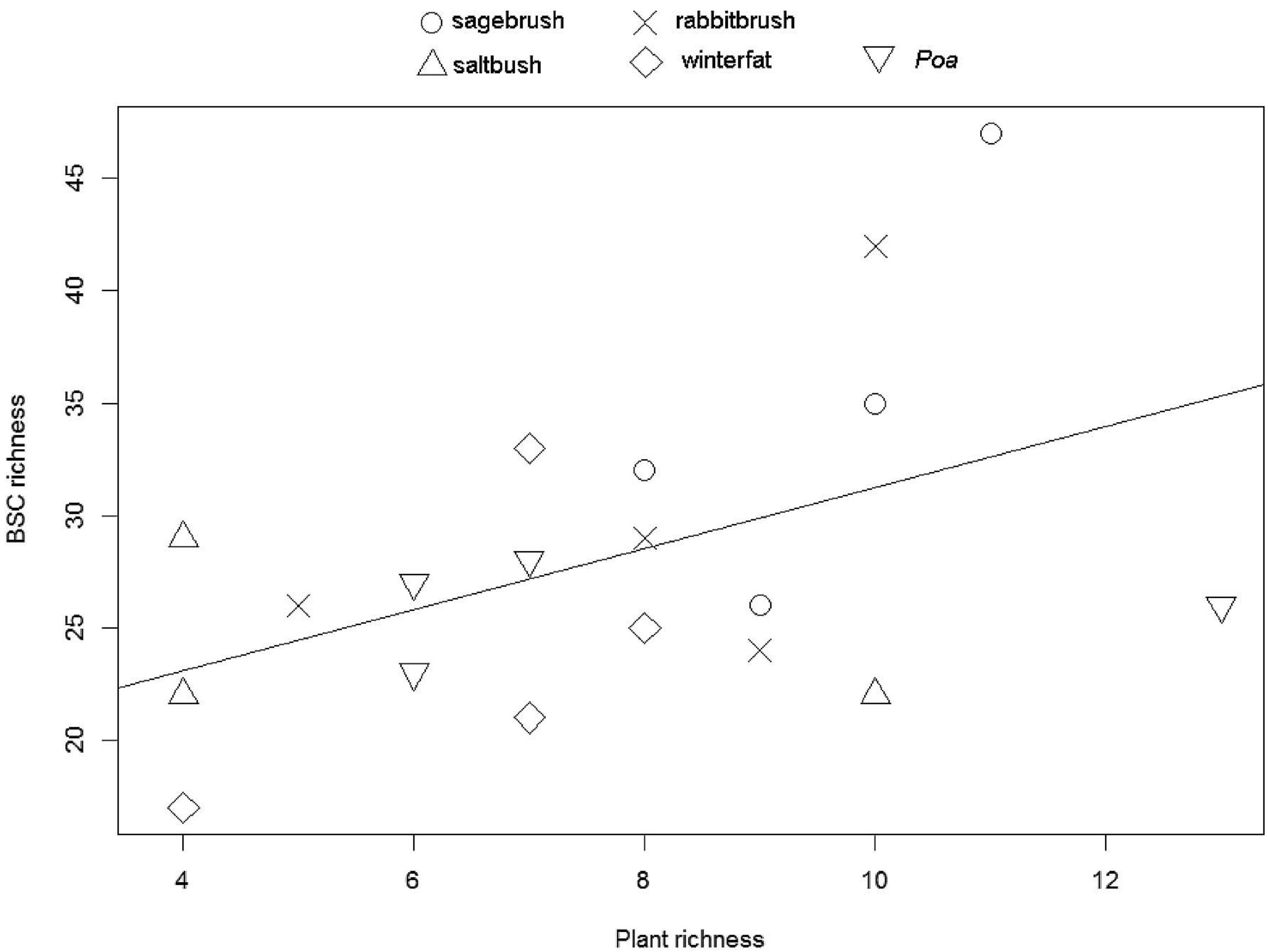

Figure 3. Comparison of BSC richness and vascular plant richness across five habitat types at the Orchard Combat Training Center, Idaho.

The BSC cover was lowest in the *Poa* and rabbitbrush habitats, which are likely to have burned and either lost all shrub cover (*Poa* habitat) or experienced low-intensity burns that allowed the rabbitbrush to resprout and dominate the site. Many of these rabbitbrush sites have remained rabbitbrush for the 38 years that one of us (RR) has been observing this local habitat type (Rosentreter 1986). The relatively high BSC richness found in these two habitat types helps abate the invasion of exotic annual grasses (Rosentreter et al. 2014; Serpe et al. 2008), and may be particularly important in these burned habitat types. Sagebrush habitats are less likely to have experienced wildfire; these habitats had variable but generally higher BSC cover, while the saltbush and winterfat habitats contained abundant calcareous biocrust indicator species such as *Psora decipiens, P. tuckermanii* and *Caloplaca tominii* (McCune & Rosentreter 2007). Soils in these other two salt desert habitats were slightly siltier and drier than the other habitat types that have the potential to support sagebrush (**Table 1**).

This study clearly documents that BSCs comprise a greater fraction of the biodiversity of these systems than do vascular plants, implying that efforts to maintain or restore biodiversity in steppe ecosystems must include an assessment of BSCs. The positive relationship between vascular plant richness and soil crust richness has not been studied since most BSC studies do not document BSC richness. However, the general ecological principle of greater species richness creating a more stable plant community resistant to invasion by exotics (Prieur-Richard et al. 2001) may hold true in arid habitats where the species considered are BSCs rather than vascular plants. Physical disturbances

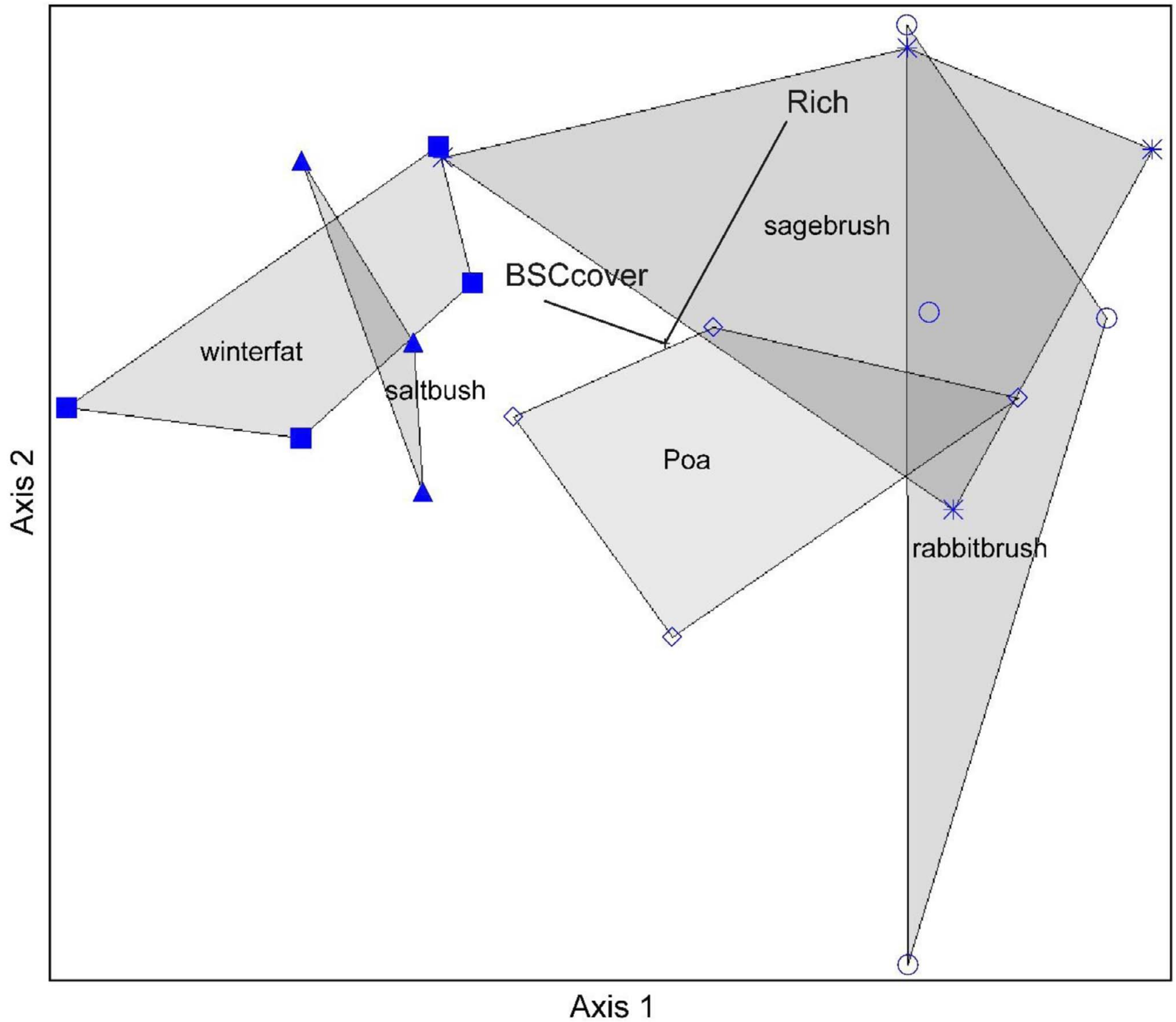

Figure 4. NMS ordination of plots and BSC species in five habitat types at and adjacent to the Orchard Combat Training Center, Idaho. Plots are represented by symbols according to vegetation type. Vectors show correlations between BSC cover (BSCcover) and BSC richness (Rich) with ordination scores.

were found to increase invasibility potential in warm low elevation habitats more than cool higher elevation habitats (Forcella & Harvey 1983; Lavin et al. 2013). Potential BSC cover and species richness relative to the type of vascular habitat type is not well documented and is dependent on many other biotic and historical factors, namely precipitation, soil texture, surface rock cover and disturbance history (Rosentreter et al. 2014).

This study explores the floristic richness of BSC species, describes how BSC communities differ across vascular plant habitat types, and finds that BSCs are diverse and positively related to vascular plant communities. Because habitats support different functional groups and BSC communities, conservation of this rich biodiversity will require attention to a wide variety of habitats. Often restoration work in steppe habitats targets the establishment of native or forage plants (Hilty et al. 2004); this approach is insufficient for the maintenance of a full complement of BSC species across a landscape. A baseline of the BSC species suited to different habitats as described in our study may aid in selecting species for BSC restoration efforts. The

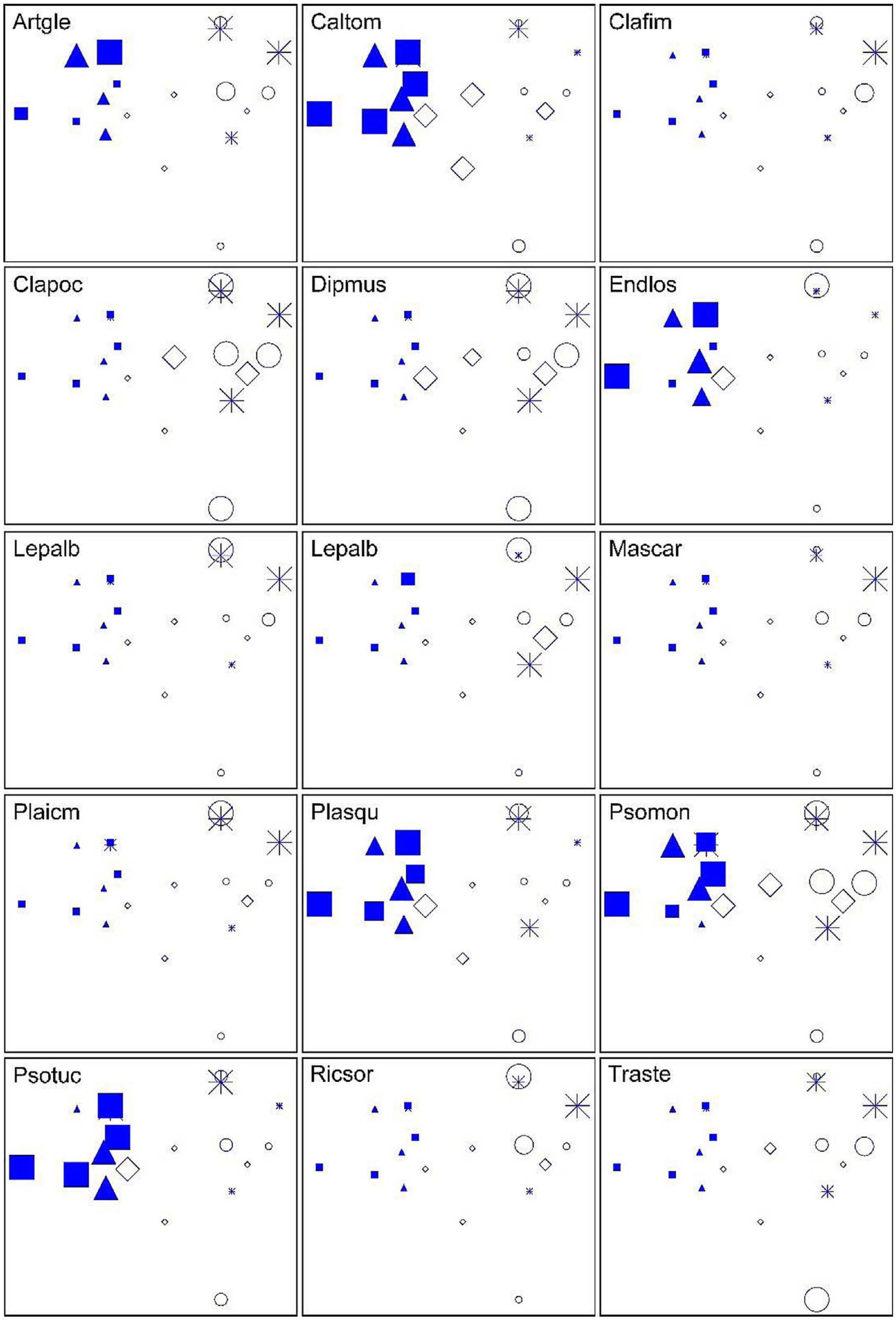

Figure 5. Individual species overlaid on the ordination shown in Fig. 4 such that symbol size is positively correlated with abundance. Species were selected to have the absolute value of $R>0.55$ with either ordination axis. Acronyms are *Arthonia glebosa* (Artgle), *Caloplaca tominii* (Caltom), *Cladonia fimbriata* (Clafim), *Cladonia pocillum* (Clapoc), *Diploschistes muscorum* (Dipmus), *Endocarpon loscosii* (Endlos), *Leptochidium albociliatum* (Lepalb), *Leptogium lichenoides* (Leplic), *Massalongia carnosa* (Mascar), *Placynthiella icmalea* (Plaicm), *Psora montana* (Psomon), *Psora tuckermanii* (Psotuc), *Riccia sorocarpa* (Ricsor) and *Trapeliopsis steppica* (Traste).

biodiversity of biocrusts in these arid habitat types is much greater than ecologists have assumed.

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