

PRELIMINARY STUDY OF BIOLOGICAL SOIL CRUST ON
THE PALOS VERDES PENINSULA

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Master of Science

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Environmental Science

by

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This thesis is dedicated to my awesome and much loved family. Thank you for always
being there.

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ABSTRACT

Biological soil crusts (BSCs) are critical components of semi-arid and arid landscapes worldwide. In coastal sage scrub, studies looking at BSC are limited. The purpose of this study was to provide a preliminary look at BSC found on the Palos Verdes Peninsula (PVP), to see which environmental factors are significant predictors of percent cover of BSC and compose a species checklist for bryophytes on the PVP. A total of 240 quadrats were analyzed from three study sites in the Forrester Nature Reserve during the fall of 2016. An extensive survey was also conducted for BSC throughout the PVP to look at its distribution. Percent cover of organic litter on the soil surface, percent cover of loose rock on the soil surface, disturbance, and exposure were found to be significant predictors of percent cover of BSC on the PVP. In addition, 56 species of bryophytes were found on the PVP.

CHAPTER 1

INTRODUCTION

*When our soils are gone, we too, must go unless
we find some way to feed on raw rock*
Thomas C. Chamberlain

Advances in soil ecology have led to a greater understanding of how important soil and its biotic components are to human existence and natural communities (Doran and Zeiss 2000). Soil provides numerous ecosystem services and contains a large amount of biodiversity (Ritz and Putten 2012). Soil is a complex matrix that contains both horizontal and vertical heterogeneity (Berg 2012). Numerous terricolous organisms exploit this heterogeneous soil matrix to occupy different niches throughout and, in turn, ultimately affect the overall characteristics and health of soil (Doran and Zeiss 2000; Ritz and Putten 2012). Therefore, soil health, and the ecosystem services it provides, is intimately connected with the biota that dwells within it. Worldwide, the upper soil matrix is abundant in microorganisms and it is here that a large range of ecosystem functions and services are performed (Ritz and Putten 2012).

Occupying the soil surface between vegetation in semi-arid and arid lands worldwide is a microworld that is comprised of highly specialized and unrelated terricolous organisms (Belnap et al. 2001a; Belnap et al. 2001b; Rosentreter et al. 2007). These terricolous organisms interact with each other and the soil particles to create a complex community that ultimately consolidates and transforms the upper portions of the soil matrix into a living cover known as biological soil crust (BSC) (Belnap et al. 2001a;

Belnap et al. 2001b; Rosentreter et al. 2007). BSC contains diverse taxa and is usually composed, in varying proportions, of terricolous organisms such as cyanobacteria, algae, microfungi, lichens, and bryophytes (Belnap et al. 2001a; Belnap et al. 2001b). BSC is also home to other diverse microbes and microfauna such as microarthropods, diatoms, protists, and nematodes (Belnap et al. 2001a; Belnap et al. 2001e; Flechtner et al. 2008; Neher et al. 2009). The majority of these BSC organisms are extremely small in size and often overlooked (Belnap et al. 2001a).

There are two other types of crust that can form on the soil surface: physical crusts and chemical crusts (Belnap et al. 2001b). These two types of crusts are often found on degraded soils and lack the biological component that protects the soil (McIntyre 1958; Belnap et al. 2001b; Cheng et al. 2008). A physical crust is created by raindrop or trampling impacts to the surface of the soil and is especially common on soils that have been intensively cultivated or on soils that have been exposed to prolonged grazing (McIntyre 1958; Belnap et al. 2001b; Cheng et al. 2008). This physical crust can harden the surface of the soil, reduce the ability of the soil to absorb water, prevent plant establishment, and cause the soil to erode away rapidly when disrupted (McIntyre 1958; Belnap et al. 2001a; Cheng et al. 2008). A chemical crust develops on soils with high salt content where a layer of salt is precipitated out onto the surface of the soil (SQISC 2008). A chemical crust also reduces the soil's ability to absorb water and prevents plant establishment (Belnap et al. 2001a; SQISC 2008).

Colonization of the upper surfaces of the soil matrix by BSC-forming organisms happens at varying successional stages (Belnap et al. 2001a). Over time, if soil in semi-

arid to arid lands experiences minimal disturbances, a diverse assemblage of BSC-forming organisms can establish and create many morphological groups (Rosentreter et al. 2007). Filamentous cyanobacteria such as *Microcoleus sp.* are often the first to colonize and stabilize the upper parts of the soil matrix by creating bundles of sticky, negatively charged exopolysaccharide sheaths that weave throughout the upper portions of the soil matrix binding with the positively charged soil particles; this greatly stabilizes the soil surface (Li et al. 2001; Belnap 2003; Belnap et al. 2008). Along with filamentous cyanobacteria are microfungi that through their microfungal filaments (hyphae) also aid in binding soil particles together and stabilizing the soil surface (States et al. 2001). Saprotrophic microfungi appear to be the most common in BSCs and are represented by genera such as *Embellisia*, *Phoma*, and *Bipolaris* (States et al. 2001). Single-celled cyanobacteria that tend to be non-mobile, such as members of the genus *Nostoc*, and terrestrial free-living algae represented mainly by coccoid genera such as *Chlorococcum*, *Macrochloris*, and *Stichococcus*, can also occupy the soil surface at these early successional stages and aid in further stabilization (Falchini et al. 1996; Flechtner et al. 1998; Belnap et al. 2001a; Belnap et al. 2008).

Once the early colonizers have stabilized the surface of the soil matrix, the colonization by other organisms such as lichens and bryophytes can follow (Nash et al. 1977; Downing and Selkirk 1993; Eldridge and Tozer 1996; Belnap et al. 2001a; Belnap et al. 2001b; Martinez et al. 2006). Phycolichens and cyanolichens in all growth forms (crustose, foliose, fructose, and squamulose) are found to occur within BSCs and their rhizines help to further bind the soil surface particles together (Nash et al. 1977; Eldridge

and Tozer 1997; Belnap et al. 2001a; Rosentreter et al. 2007). Terricolous bryophyte components of BSCs are represented by mosses and liverworts and contain both annual and perennial species (Eldridge and Tozer 1996; Eldridge and Tozer 1997; Belnap et al. 2001a; Belnap et al. 2001b; Rosentreter et al. 2007). Moss species can form large turfs or can be individual plants where their rhizoids also help to bind soil surface particles together (Richardson 1981; Belnap et al. 2001c; Buck and Goffinet 2008).

The majority of organisms that occur within BSCs are poikilohydric and are only metabolically active when moisture is available (Proctor et al. 2007; Proctor 2008; Luttge et al. 2011). These organisms can remain in a desiccated state for long periods of time and can become active again within a matter of minutes after receiving moisture (Richardson 1981; Belnap et al. 2001a; Proctor et al. 2007; Proctor 2008; Luttge et al. 2011). They can also tolerate extreme temperatures, drought, and solar radiation when in the desiccated state (Luttge et al. 2011). Since these organisms are only metabolically active when moisture is available, growth of these organisms is slow and BSCs can be extremely old (> 200 yrs.) (Belnap et al. 2001a; Belnap et al. 2001b; Belnap et al. 2001f). It is possible that BSCs, and the organisms associated with them, might have played a critical role in creating suitable soil conditions that allowed for the initial colonization of terrestrial habitats on Earth by plants (Lipnicki and Ludwik 2015).

BSCs have now been recognized worldwide as having a major influence on terrestrial ecosystems, and they can be used as an indicator of habitat health (Downing and Selkirk 1993; Eldridge and Greene 1994; Eldridge and Koen 1998; Belnap et al. 2001a; Bowker et al. 2005). BSCs are found growing on many soil types. Soils

containing higher clay and silt content tend to have more bryophytes and lichens present, while soils that are more acidic and less salty tend to favor green algae (Downing and Selkirk 1993; Belnap et al. 2001a; Rosentreter and Belnap 2001; Martinez et al. 2006). Soils that are more alkaline or soils with a high salt content tend to favor cyanobacteria (Belnap et al. 2001a). BSCs also favor thin soil habitats, which are usually composed of thin soil over rock (Belnap et al. 2001a, Magney and Knudsen 2006). When BSCs experience different climates or disturbance regimes, or are composed of different organisms, the external morphology can take on different forms (Eldridge and Rosentreter 1999; Belnap et al. 2001b; Rosentreter et al. 2007). Four types of BSC have been recognized worldwide; smooth (flat), rugose, pinnacled, and rolling (Belnap et al. 2001b). All of these types can be dark in color due to high levels of cyanobacteria and cyanolichens present within them (Belnap et al. 2008). Certain moss species found in BSC, such as *Didymodon australiasae*, can also contribute to the dark color of BSC (personal observation). Each type of BSC may comprise one or more morphological groups (Eldridge and Rosentreter 1999). Belnap and colleagues (2001d) define these morphological groups as consisting of organisms that are similar in shape and general appearance. Some morphological groups that can be found in BSC worldwide are cyanobacterial crusts, green algal crusts, bryophyte crusts, and lichen crusts (Belnap et al. 2001b). There can also be BSC where more than one morphological group can be dominant such as in cyanobacteria lichen crusts and cyanobacteria lichen moss crusts (Belnap 1994).

Worldwide, BSCs provide a suite of ecosystem services and contain a high amount of biodiversity (Eldridge and Greene 1994; Eldridge and Tozer 1996; Belnap 1992; Belnap 2001a; Belnap 2001b; Belnap et al. 2001a; Evans and Lange 2001; Warren 2001a; Belnap 2003). BSCs prevent erosion by stabilizing the soil surface and protect the soil by acting as a living shield (Warren 2001b). BSCs influence soil fertility by trapping sediment and adding soil nutrients (Belnap et al. 2001a; Belnap 2003, Rosentreter et al. 2007), contributing organic matter to the soil surface (Belnap et al. 2001a), influencing carbon dynamics in the soil (Evans and Lange 2001; Yoshitake et al. 2010), and fixing atmospheric nitrogen into bio-available nitrogen (Belnap 1994; Eldridge and Greene 1994; Belnap 2001b; Belnap 2003; Belnap et al. 2008; Zhao et al. 2010). BSCs also influence hydrologic properties such as reducing water velocity across the surface of the soil and allowing for a greater rate of absorption and retention of water in the soil matrix (Belnap 1992; Eldridge and Greene 1994; Belnap et al. 2001b; Belnap 2003; Rosentreter et al. 2007; Chamizo et al. 2012). BSCs influence soil surface temperatures, soil surface albedo, and the soil micro-atmosphere (Allen 2005). BSCs act as inhibitors of non-native plant species, and they affect vascular plant germination and survival (Lesica and Shelly 1992; Serpe et al. 2006; Hernandez and Sandquist 2011).

BSC establishment, functionality, recolonization, and overall longevity are dependent upon intensity and frequency of disturbances (Anderson et al. 1982; Belnap and Eldridge 2001; Hilty et al. 2004; Barger et al. 2006; Liu et al 2009; Chamizo et al. 2012). Since the organisms that form BSCs are often minute, they can be easily smashed or disrupted by disturbances such as cattle grazing (Anderson et al. 1982; Beymer and

Klopatek 1992; Belnap et al. 2001b; Ponzetti and McCune 2001; Liu et al. 2009), foot traffic (Studlar 1980; Pietrasiak et al. 2011; Yan et al. 2014; Jagerbrand and Alatalo 2015), and mountain bikes or off-road vehicles (Belnap and Eldridge 2001; Belnap 2003). These types of disturbance can destroy BSC communities exceptionally quickly and allow for non-native plants to colonize the disturbed areas (Belnap and Eldridge 2001; Hernandez and Sandquist 2011). If disturbances are chronic they can hinder BSC recolonization and growth as well as arrest BSCs in an early successional stage where only cyanobacteria might be present (Belnap et al. 2001b; Belnap and Eldridge 2001). Many types of disturbance that threaten BSC worldwide have been identified, including certain anthropogenic land uses (Belnap et al. 2001d; Belnap and Eldridge 2001; Ponzetti and McCune 2001), non-native grasses and other invasive species (Belnap et al. 2001f; Hernandez and Sandquist 2011), altered fire regimes (Johansen 2001), and climate change (Evans et al. 2001).

BSCs have a worldwide distribution (Budel 2001d) and have been documented in Australia (Downing and Selkirk 1993; Eldridge and Tozer 1996; Eldridge and Tozer 1997; Eldridge 2001), Spain (Martinez-Sanchez et al. 1994; Budel 2001b; Martinez et al. 2006; Ochoa-Hueso et al. 2011; Concostrina-Zubiri et al. 2014), South America (Budel 2001a), Asia (Budel 2001c), the Middle East (Galun and Garty 2001), Africa (Ullman and Budel 2001), Antarctica (Green and Broady 2001), Arctic Greenland (Hansen 2001), the Alps (Turk and Gartner 2001), and North America (Rosentreter and Belnap 2001). The factors influencing this worldwide distribution and the species composition of BSC communities include elevation, soil type, topography, disturbance, timing of

precipitation, vascular plant community structure, ecological gradients, and microhabitats (Belnap et al. 2001f; Concostrina-Zubiri et al. 2014). BSCs are a major component of many habitats within the semi-arid and arid portions of western North America (Belnap et al. 2001f; Rosentreter and Belnap 2001). In North America, most BSC research has been focused in the western portions of the United States, primarily in the Great Basin Desert, the Mojave Desert, and the Sonoran Desert (Ponzetti and McCune 2001; Rosentreter and Belnap 2001; Serpe et al. 2006; Belnap et al. 2008; Neher et al. 2009; Hernandez and Sandquist 2011; Hernandez and Knudsen 2012; Antoninka et al. 2015). Throughout North America, factors influencing the distribution and composition of BSCs are elevation, precipitation, temperature, soils, and vascular plant community structure (Belnap et al. 2001f; Rosentreter and Belnap 2001). Studies conducted in the western United States have indicated that BSC cover decreases with an increase in vascular plant cover, elevation, loose rock on the soil surface, soil depth, and soil texture (Belnap et al. 2001f). However, more research on BSC is needed, especially from more regions and localities throughout the western portions of the United States to determine whether factors influencing the distribution and composition of BSCs are the same (Garcia-Pichel and Belnap 2001).

California is a known biological hotspot and contains an exceptionally high diversity of species, habitats, and endemic species (Ornduff 1974; Myers et al. 2000). Its unique geology, topography, climate, and soils together have produced many complex heterogeneous landscapes throughout the state (Munz 1974; Ornduff 1974; Rundel and Gustafson 2005; Baldwin and Goldman 2012). Much of the ecology of these landscapes

and the macro-organisms that inhabit them have been studied; however, soil ecology of California, especially in regards to BSCs, has not been adequately explored (Rosentreter and Belnap 2001; Hernandez and Sandquist 2011; Hernandez and Knudsen 2012). The valley foothills, woodland foothills, grasslands, coastal chaparral, coastal sage scrub, and the maritime channel islands of California are areas where BSCs have been documented (Belnap 1994; Rosentreter and Belnap 2001; Magney and Knudsen 2006; Flechtner et al. 2008; Hernandez and Sandquist 2011; Hernandez and Knudsen 2012). Many of these habitats are found within southern California, and the BSCs in these areas are often well developed, but inconspicuous and variable, across the landscape (Rosentreter and Belnap 2001; Hernandez and Sandquist 2011; Hernandez and Knudsen 2012). Belnap and colleagues (2001c) state that further research on BSCs should be focused in habitats throughout the world that are under-studied and especially areas where anthropogenic impacts are destroying habitat at an alarming rate. Coastal sage scrub (CSS) is a plant community that is disappearing rapidly due to urban sprawl and little is known about BSC in this habitat (Davis et al. 1994; Riordan and Rundel 2009; Hernandez and Sandquist 2011; Hernandez and Knudsen 2012). CSS is composed primarily of drought deciduous, low-growing, soft, aromatic shrubs, and it extends along the coastal portions and some inland valleys of California from Ventura County to San Diego County (Ornduff 1974; Gray and Schlesinger 1981; Rundel and Gustafson 2005; Riordan and Rundel 2009). CSS can be subdivided further into a more northern form known as Venturan sage scrub and a more southern form known as Diegan sage scrub (Rundel and Gustafson 2005). In CSS and chaparral areas, late-successional rugose cyanobacteria-

lichen-dominated crusts and late-successional rugose bryophyte crusts have been observed (Rosentreter and Belnap 2001; Magney and Knudsen 2006; Hernandez and Sandquist 2011; Hernandez and Knudsen 2012). However, research on BSC in CSS is limited and further research is needed (Hernandez and Sandquist 2011; Hernandez and Knudsen 2012). Hernandez & Sandquist (2011) examined late-successional rugose BSCs in CSS of Orange County and their response to disturbance. They suggested that BSCs act as an inhibitor of certain non-native plant species and could possibly facilitate the emergence of certain native plant species in CSS of Orange and Riverside counties. Hernandez & Knudsen (2012) found that BSCs in Orange and Riverside counties are extremely biodiverse and act as a critical refugium for BSC-forming lichens and mosses, describing five distinct late-successional BSC communities in CSS and chaparral. These include riversidian, spike moss, casperian, alisian, and lagunian. However, their study only examined BSCs of Diegan sage scrub. There is limited information on BSCs from Venturan sage scrub.

The Palos Verdes Peninsula (PVP), which is located in the South Bay area of southern California, is known for its scenic coastline, island feel, and remnant patches of CSS. These CSS patches dot the landscape and provide some of the last remaining CSS between Orange County and the Santa Monica Mountains. The PVP's remnant patches of CSS are also considered the southernmost distribution of Venturan sage scrub and a transition zone from Venturan to Diegan sage scrub (Westman 1981; Brylski et al. 1994). The remaining open spaces on the PVP also contain a suite of other native vegetation

types (Brylski et al. 1994; Verdone and Evens 2010). BSC can be found on the soil surfaces of the PVP in the spaces between and under shrubs (Fig. 1 and 2).

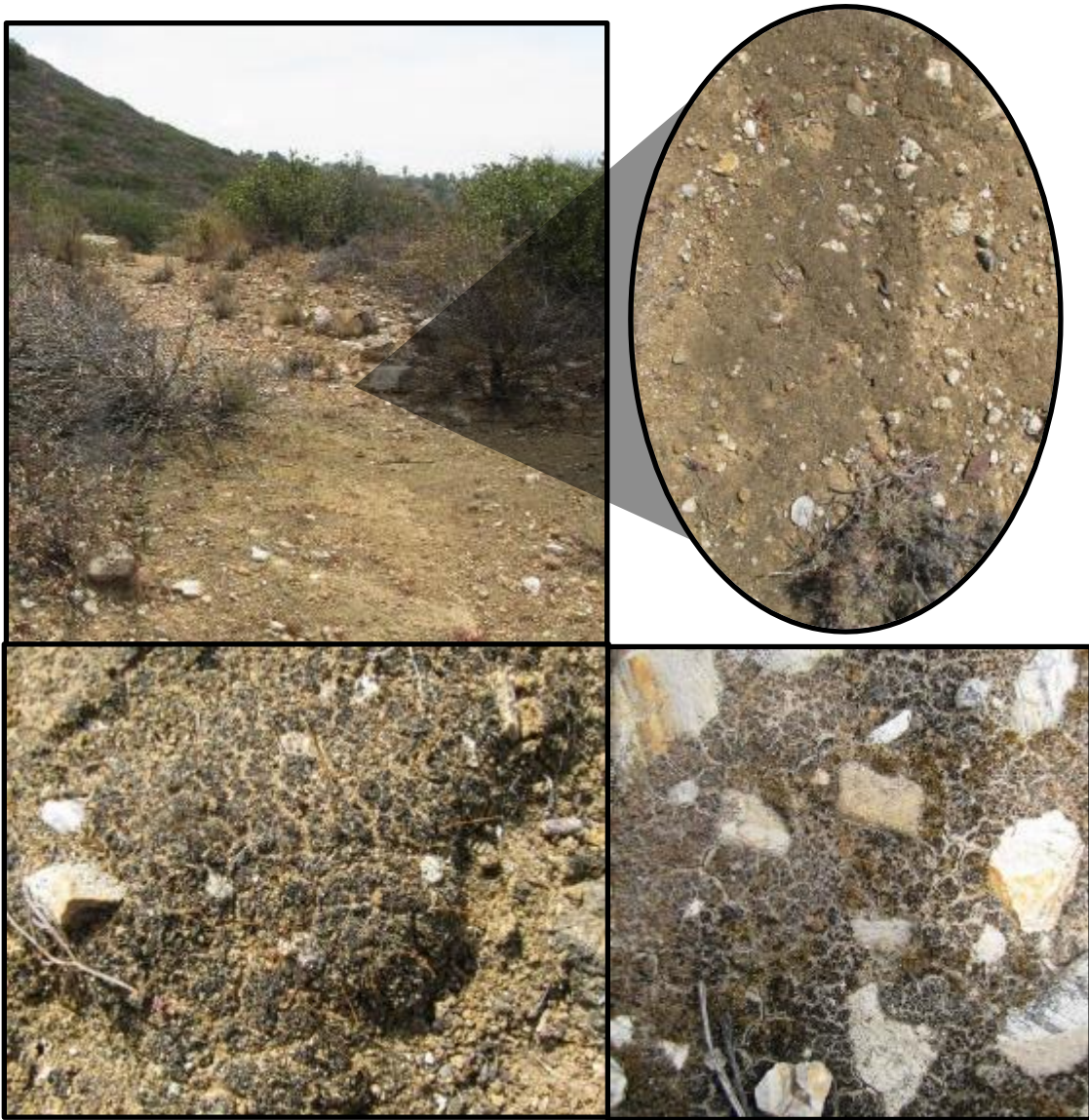


Figure 1. BSC on the PVP with close-ups of what it can look like on the soil surface. Note: original material collected by the author of this thesis.



Figure 2. BSC on the PVP. Note: original material collected by the author of this thesis.

To my knowledge, there has been no effort to date to document and study BSC on the PVP and its presence is only mentioned in two sources. Lipman et al. (1999) briefly mention BSC occurring on the PVP and that research on it is needed. In the RPESBB (1998), BSC is again briefly mentioned as occurring on the Airport Dunes in El Segundo, north of the PVP.

The purpose of this research is to provide a preliminary look at BSC found on the PVP as well as to see which environmental factors are significant predictors of percent cover of BSC. In addition, the bryophytes of the PVP were examined and a checklist was produced. It is hoped that this information will bring awareness to these unique biological resource and aid land managers in their protection.

CHAPTER 2

METHODOLOGY

Study Region

The study was conducted on the Palos Verdes Peninsula (PVP) (Fig. 3), which is located at the southwest tip of Los Angeles County. It falls within the South Coast geographic subdivision of California as defined in the second edition of the Jepson Manual (Baldwin and Goldman 2012).

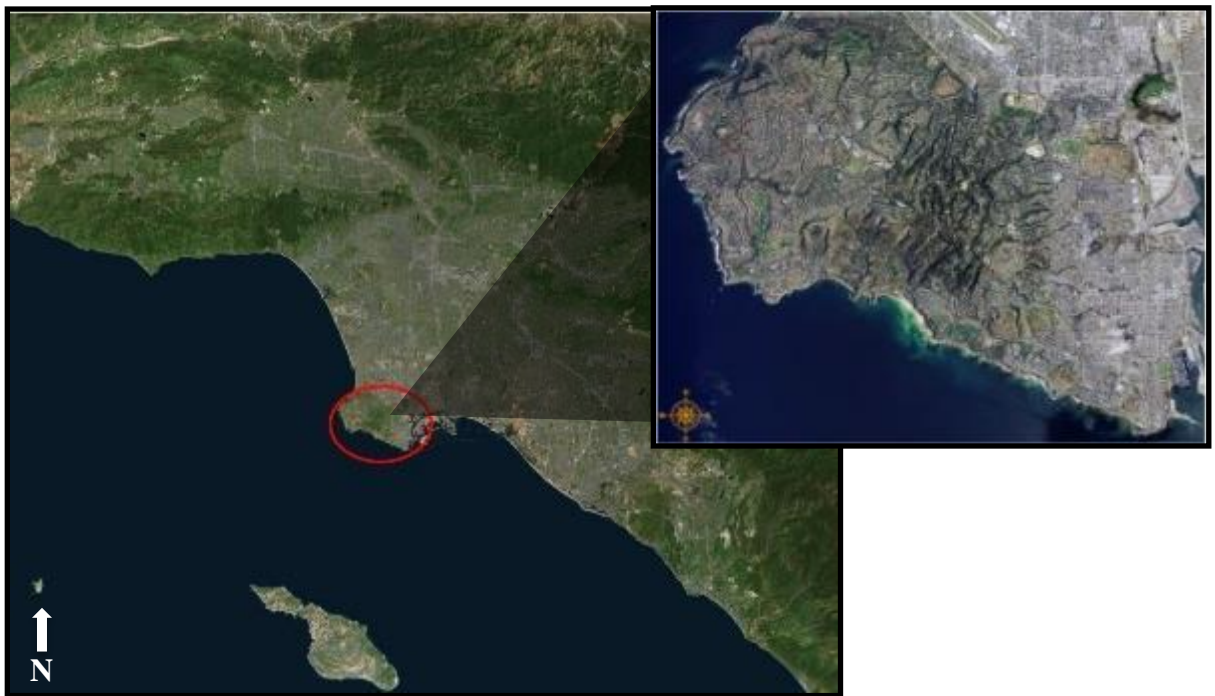


Figure 3. The Palos Verdes Peninsula, CA, USA (N33° 46' 15'' W118° 22' 40''). Maps created using ArcGIS® and ArcMap™ by Esri.

The PVP projects out from the Los Angeles County mainland into the Pacific Ocean and is about 14.5 kilometers long and 8 kilometers wide (Ehlig 1982). Surrounding the boundaries of the PVP is the Pacific Ocean on the south and west, the Los Angeles Harbor and parts of the South Bay area on the east, and the greater South Bay and Los Angeles metropolitan area to the north (Ehlig 1982). The climate is classified as semi-arid (Kauffman 2003). Rainfall and cooler temperatures are winter and spring dominant, while summer and fall are usually drier and warmer (Gale 1974). Due to its close proximity to the Pacific Ocean, the PVP also experiences thick marine layers throughout the year and has relatively cooler temperatures than the surrounding greater Los Angeles area (Gale 1974). The PVP is also unique in that it was an island during the early Pliocene and was connected to the mainland during the late Pleistocene to early Holocene (Dibblee 2000; Dibblee and Ehrenspeck 2000). Thus, much of the terrain of the PVP is island-like and reminiscent of nearby Catalina Island. The dominant plant community on the PVP is coastal sage scrub (CSS) (Brylski et al. 1994). However, due to the PVP's diverse topography, soils, and climate it hosts a wide diversity of plant communities and vegetation types (Verdone and Evens 2010). The soil of the PVP is composed mostly of clay loam or gravelly clay soils (Woodring et al. 1946).

Study Site

The study was conducted in the Forrestal Nature Reserve on the PVP. The Forrestal Nature Reserve is a 115-acre nature reserve within the Palos Verdes Nature Preserve system and is managed by the Palos Verdes Peninsula Land Conservancy (PVPLC). This reserve contains some of the most intact portions of the native vegetation

in the area and is mostly dominated by CSS (FNPMP 2005). In addition, a vegetation mapping project conducted by the California Native Plant Society (CNPS) in 2010 revealed that several other vegetation alliances and associations also exist within the Forrestal Nature Reserve (Verdone and Evens 2010).

The Forrestal Parcel experienced mining operations that began in the 1920s and ceased in 1956, which altered portions of the native habitat; however, much of it remained undisturbed (FNPMP 2005). The geological strata that are found near the surface of the Forrestal Parcel are characterized by basalt volcanics and Altamira shale (Woodring et al. 1946; Dibblee and Ehrenspeck 2000; FNPMP 2005). The Altamira shale component is composed of interbedded tuff, bentonite, clayey siltstone, shale, silicious shale, fine grained dolomite, and minimal amounts of sandstone (Woodring et al. 1946; Dibblee and Ehrenspeck 2000; FNPMP 2005). The majority of the soil type in the Forrestal Parcel is a moderately fine clay loam that contains crystalline materials such as quartz, barite, and dolomite (FNPMP 2005). Many thin-soil areas are also present throughout the reserve (personal observation).

Methods

In September 2015, I conducted a survey for BSC throughout the Forrestal Nature Reserve. From visual assessment of the reserve, multiple locations were found containing BSC and three study sites were established (Fig. 4). These sites were selected based on the criterion that the ground contained significant cover of BSC (> 60%) on the soil surface (Beymer and Klopatek 1992; Hernandez and Sandquist 2011). The study sites are referred to as sites 1-3 (Fig. 4).

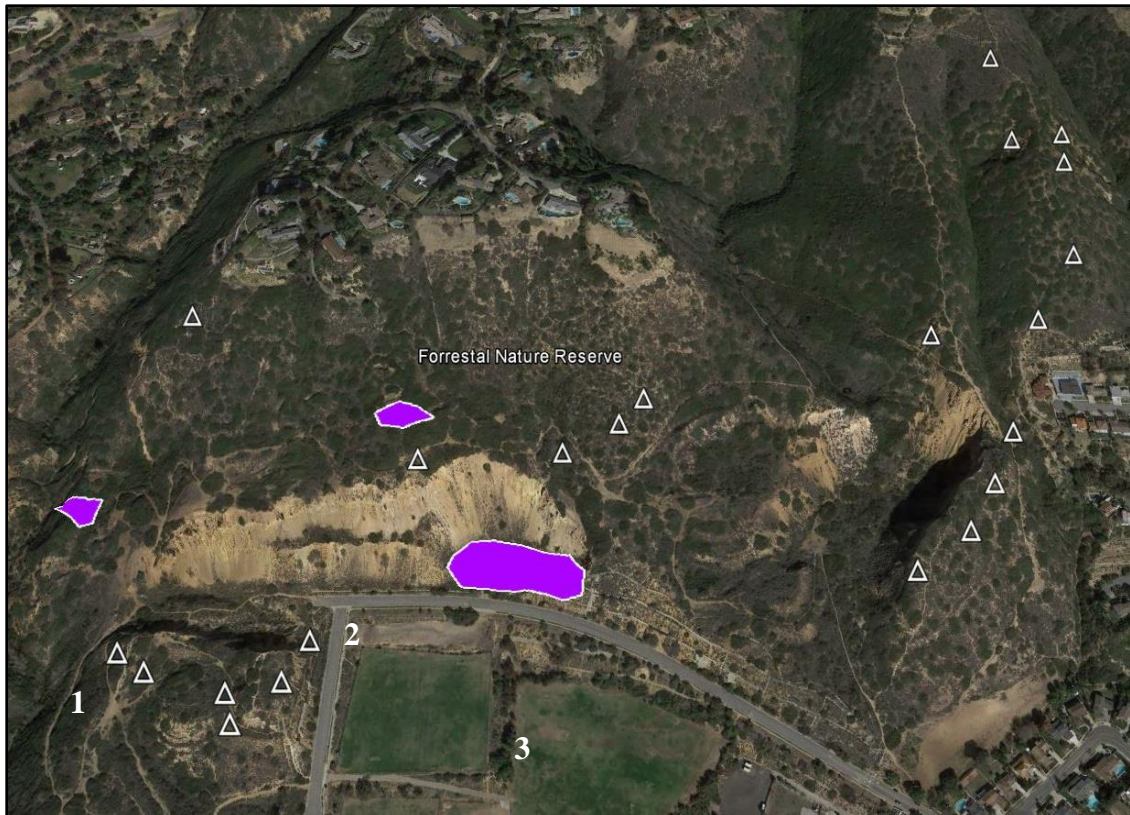


Figure 4. Forrestal Nature Reserve – study sites 1, 2, 3 (purple polygons) and other BSC locations (white triangles). *Source:* “Forrestal Nature Reserve.” 33°44′25.80″ N and 118°21′00.19″ W. Google Earth. February 2, 2016. October 31, 2016.

In addition, within each study site multiple study areas were chosen: these are referred to as 1A, 1E, 2B, 3C, and 3D. Study areas were selected to capture as much heterogeneity in microtopography, disturbances, and vascular plant cover as possible. Within each study area a 240 cm long primary transect was set out to capture the longest transect across BSC. Points along the primary transect were generated using a random number generator. At the primary transect points, secondary transects of varying lengths, based on topographic barriers were then established perpendicular to the primary transect (Table 1). Using a random number generator, points were generated along the secondary

transects and those points were sampled. Following Belnap et al.'s (2001b) recommendations for quadrat size, a small quadrat (5 cm x 5 cm) was used to sample. A total of 240 quadrats were sampled among the three study sites. While sampling, organic litter and loose rock on the soil surface, if present, were moved to see if BSC was present underneath. For each quadrat, data on environmental variables, as described below, were collected in the field.

Exposure – Exposure was determined as the amount of sun exposure that the BSC within the quadrat would receive. Exposure was classified as either direct sunlight (for at least part of the day) or no direct sunlight.

Disturbance – All visible signs of disturbances to the BSC were recorded. If the source of disturbance was known (i.e. trail, water erosion, etc.) this was also recorded.

Slope – If the surface of the soil had any change in microtopography (i.e. flat, mounded, hill) it was recorded.

Vascular plants providing shade – If BSC within the quadrat was in the shade of any vascular plant, then the species of vascular plant was recorded.

Vascular plants within quadrat – If any vascular plants (or seedlings) were found growing in the quadrat, then the species of vascular plant was recorded.

Table 1. Primary and secondary transect lengths. Note: table developed by the author of this thesis.

Study Site	Study area	Primary	Secondary
1	A	240 cm	500 cm
1	E	240 cm	160 cm
2	B	240 cm	170 cm
3	C	240 cm	730 cm
3	D	240 cm	160 cm

In addition to the data on the variables described above, a photograph was taken of the quadrat at the time of sampling. Visual measurements of the following were made from the photographs captured in the field: % cover of crust, % cover of loose rock on the soil surface, and % cover of organic litter on the soil surface.

BSC samples (4cm x 4cm) from the study sites, as well as at other locations within the Forrestal Nature Reserve, were collected. Samples were hydrated with distilled water to allow for identification of the organisms within them. Moss species present within the samples were identified down to the species level when possible, using Sharp et al. (1994) and FNA (2007; 2014). Lichens were identified to the genus level when possible using Nash et al. (2002). If cyanobacteria were encountered, they were identified down to the genus level using Belnap et al. (2001a) and Rosentreter and Belnap (2001). If any other BSC-forming organisms were encountered, then the type of organism was recorded and described.

An extensive survey was conducted from spring 2015 to spring 2016 throughout the PVP for BSC as well as bryophytes. Overall, 283 samples of bryophytes were collected and identified down to species using Sharp et al. (1994) and FNA (2007; 2014).

In order to determine which environmental factors are significant predictors of percent cover of BSC, a generalized linear model (GLM) was performed in JMP 12.1.0 (SAS Institute, Cary NC).

CHAPTER 3

RESULTS

In total, 65% of the 240 quadrats that were analyzed contained BSC. The mean percent cover of BSC encountered at each study site ranged from 30.9% to 43.6 % (Table 2). However, the high standard deviations indicate heterogeneity within the study sites. BSC was found in multiple locations throughout the Forresteral Nature Reserve and often on thin soil habitats (Fig. 4). The most commonly encountered type of BSC at all three study sites and throughout the PVP was late-successional rugose BSC. Early-successional BSC was also observed.

Twelve of the 240 quadrats had a vascular plant within them. Seven of those 12 quadrats contained *Stipa lepidota* (California native) and the remaining five contained stunted *Melilotus indicus* (non-native). Of the five quadrats containing *M. indicus*, four had evidence of disturbance. The three most commonly encountered shrubs in the area of the study sites were *Artemisia californica*, *Salvia mellifera*, and *Rhus integrifolia*. All are California natives. Seedlings of *A. californica*, *S. mellifera*, and *Stipa lepidota* were also observed growing within the BSC in the Forresteral Nature Reserve.

Disturbance and exposure were categorical variables. Disturbance was found to be a significant predictor of percent cover of BSC ($p = 0.0001$). Overall, disturbance was in 28 % of the quadrats. Exposure was also found to be a significant predictor of percent cover of BSC ($p = 0.04$). Overall, 58 % of the quadrats were exposed to direct sunlight for at least part of the day. Site 3 had the highest rate of disturbance, while site 1 had the lowest (Table 3).

Percent organic litter on soil surface and percent loose rock on soil surface were numerical variables. Percent loose rock on soil surface was also found to be a significant

negative predictor of percent cover of BSC ($R^2 = 0.15$; $p = 0.0001$) (Fig. 6). Percent organic litter on soil surface was found to be a significant negative predictor of percent cover of BSC ($R^2 = 0.26$; $p = 0.0001$) (Fig. 7). BSC was not observed growing either under or on top of the organic litter or the loose rock on the soil surface.

Cyanobacteria, mosses, and lichens were commonly encountered in the BSC on the PVP. Thirteen terricolous moss species were found within the BSC and all were acrocarpous mosses (Table 4). These 13 terricolous moss species represented three families, with 10 of the 13 mosses belonging to the family Pottiaceae. Of the 13 species of mosses, seven appeared to be restricted to BSC on the PVP (Table 4). Seven of the 13 moss species also possessed an awn-like projection at the apex of the leaf. No liverwort species were observed in the BSC.

Crustose, squamulose, and gelatinous lichen growth forms were commonly encountered in the BSC. Three genera of lichens were present representing three families (Table 4). The gelatinous lichen genera *Collema* and *Endocarpon* were most commonly encountered, while the genus *Toninia* was uncommon and was only found occurring in the late-successional rugose BSC of the Forrestal Nature Reserve. Three unknown crustose lichens, found on rock embedded within the BSC, were also observed within the BSC of the study sites.

Cyanobacteria were commonly encountered in the BSC, representing two genera (*Microcoleus* and *Nostoc*) (Table 4). Following early rains, cyanobacteria were abundant on the soil surface.

BSC was found throughout the PVP in 40 different locations (Fig. 5). Canyon walls and coastal bluffs contained BSC. Hillside scrubland of intact CSS contained BSC in the spaces between vascular plants. Sandy soil sites such as Linden H. Chandler Nature Preserve and the Defense Fuel Supply Point also contained BSC.

Prior to this study there had been no survey of the bryophytes of the PVP. The survey resulted in a checklist of 66 species, all of which have been previously reported in California. From the 283 samples collected, 58 species of mosses and eight species of liverworts were found (Table 5). Overall, 57 of the 58 species of mosses, and seven of the eight species of liverworts, are native to California. *Gemmabryum demaretianum* was the only non-native species of moss and *Lunlaria cruciata* was the only non-native species of liverwort encountered. No hornworts were encountered during the survey. Mosses occurred throughout the PVP, while liverworts were only encountered on the northeast side of the PVP in mesic areas. Thallose liverworts and leafy liverworts were found, but were locally uncommon. One species of moss, *Tortula californica*, is a CNPS 1B.2 species (rare, threatened, or endangered in California and elsewhere; California Native Plant Society rare plant program) and occurred in BSC at one location in the Forrestal Nature Reserve. The finding of the liverwort *Sphaerocarpos michelli*, which occurs in northern California, is a large range extension for this species and this is the first record of it occurring in southern California.

Commonly encountered bryophyte families were Pottiaceae, Bryaceae, Fissidentaceae, Funariaceae, and Brachytheciaceae. Commonly encountered bryophyte genera were *Didymodon*, *Tortula*, *Bryum*, *Rosulabryum*, *Scleropodium*, and *Targionia*. Mosses were found growing on soil, rock, brick, and bark. Liverworts were found growing on soil, rock, and bark. Overall, the bryoflora of the PVP appears very similar to the bryoflora of the Channel Islands (Carter 2015) and the Santa Monica Mountains (Sagar and Wilson 2007).

Table 2. Mean percent cover for scored cover classes at the three study sites at Forrestal Nature Reserve (mean \pm 1 sd). Note: table developed by the author of this thesis.

	Site 1	Site 2	Site 3
% Cover of crust	31.4 \pm 31.1	43.6 \pm 38.1	30.9 \pm 35.1
% Cover of organic litter	25.5 \pm 32.8	14.1 \pm 29.5	20.4 \pm 30.6
% Cover of rock on soil surface	35.0 \pm 23.7	23.6 \pm 26.1	32.8 \pm 26.7

Table 3. Percentage of quadrats with disturbance and exposure at the three study sites at Forrestal Nature Reserve. Note: table developed by the author of this thesis.

	Site 1	Site 2	Site 3
% with disturbance present	10	24	45
% with exposure to direct sunlight	59	70	67

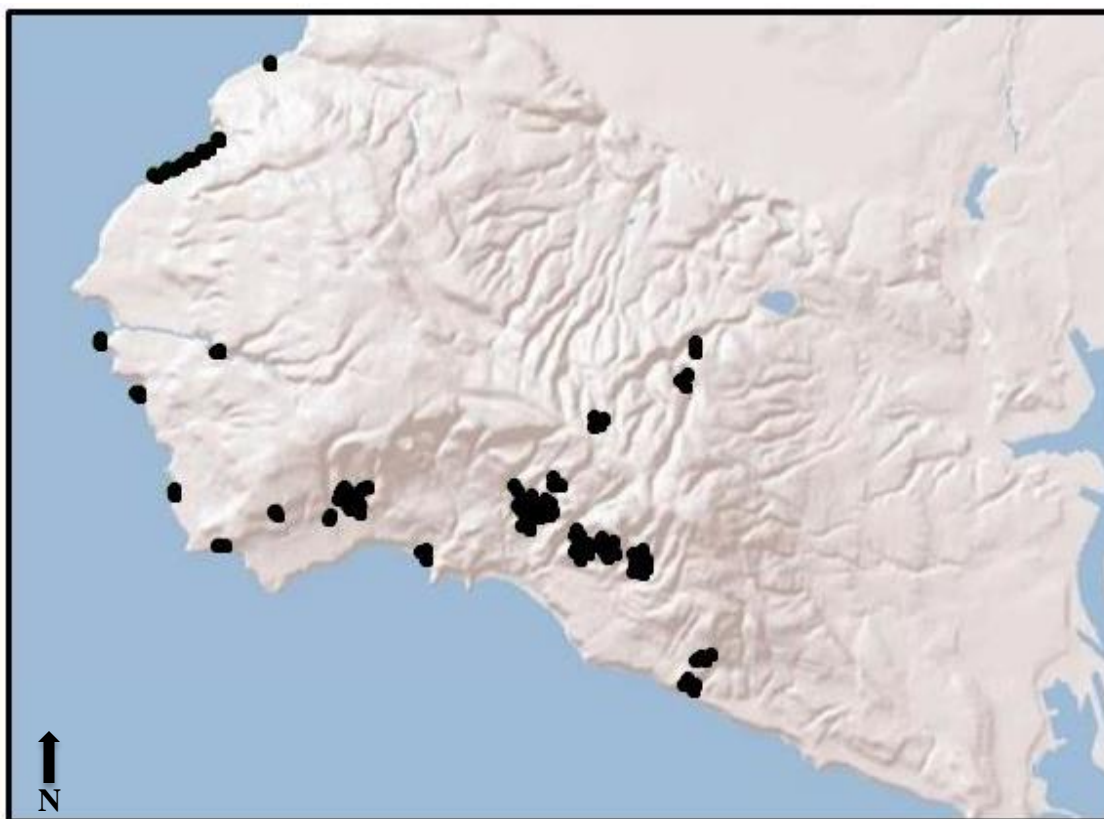


Figure 5. Locations where BSC was found throughout the PVP. Map created using ArcGIS® and ArcMap™ by Esri.

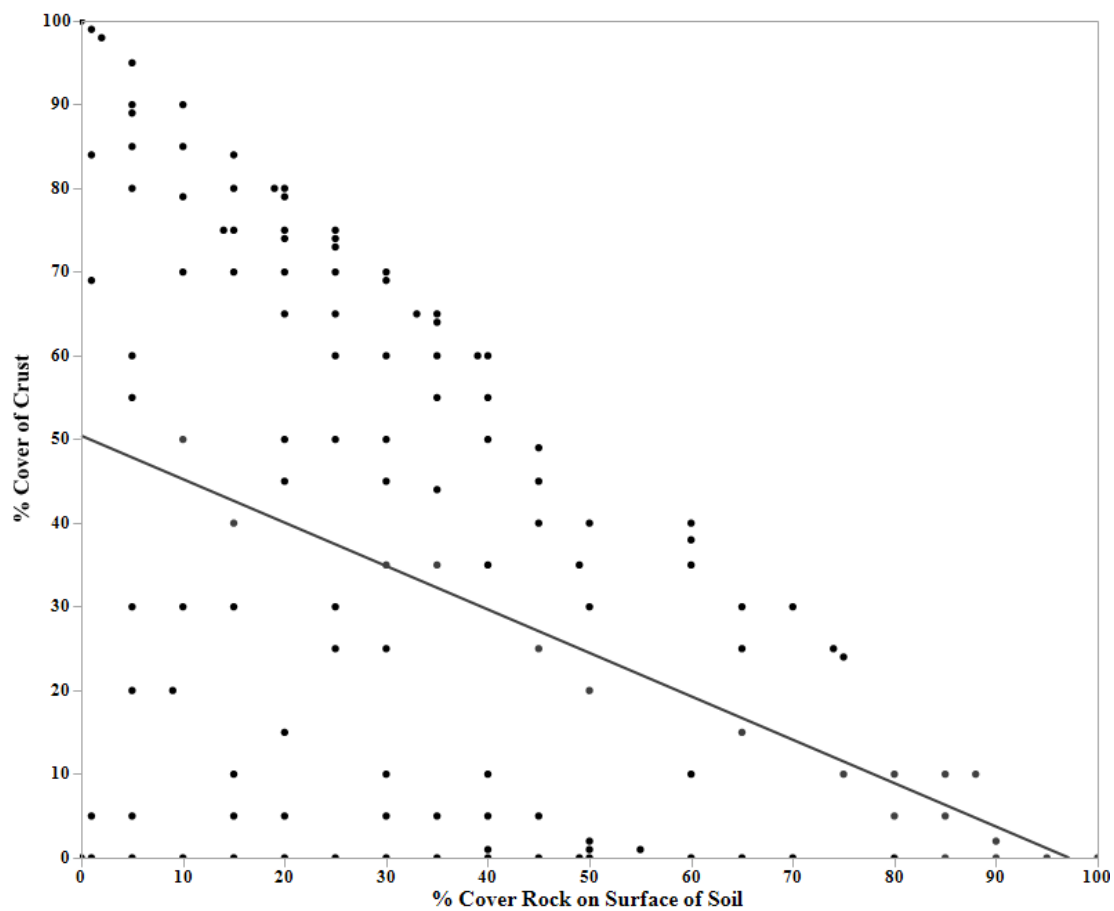


Figure 6. Relationship between total crust cover and surface rock cover at the three study sites at Forrestal Nature Reserve. Note: figure developed by author of this thesis.

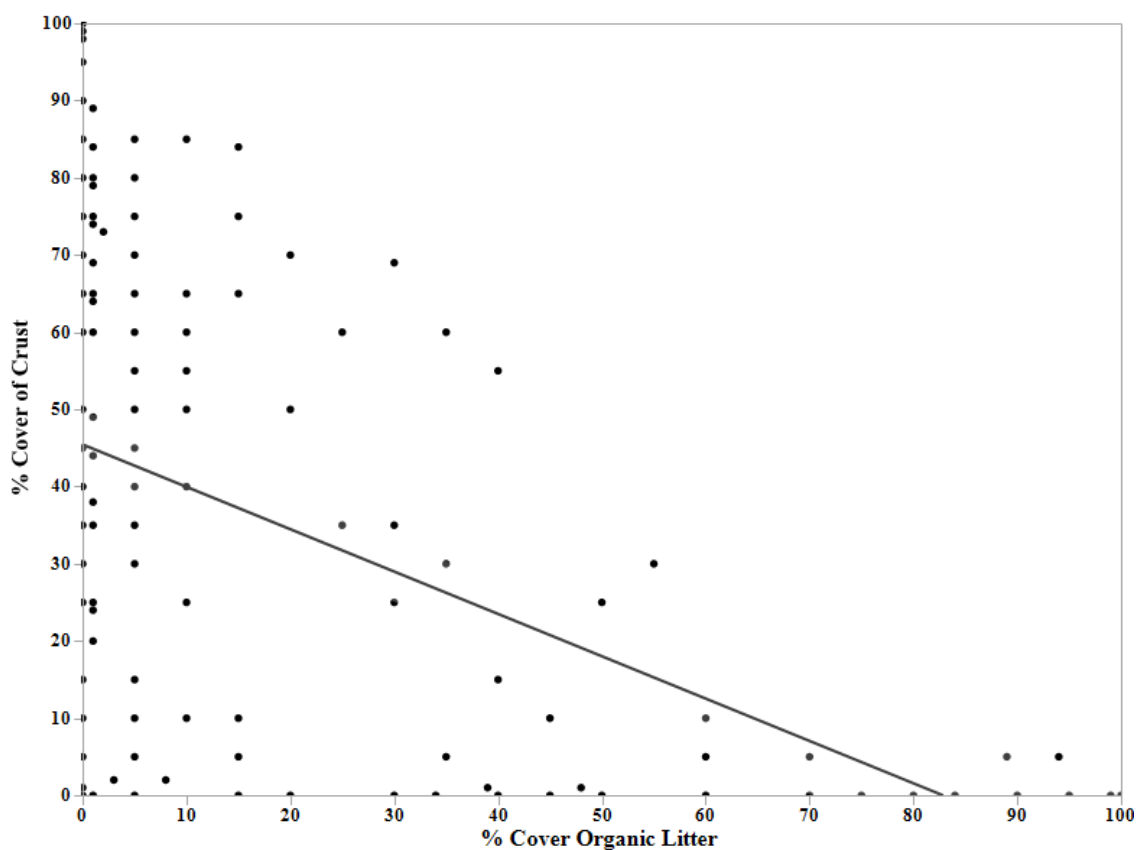


Figure 7. Relationship between total crust cover and organic litter cover at the three study sites at Forrester Nature Reserve. Note: figure created by the author of this thesis

Table 4. Mosses, lichens, and cyanobacteria encountered in late-successional BSC on the PVP. Note: table created by author of this thesis.

Mosses	Lichens	Cyanobacteria
POTTIACEAE	VERRUCARIACEAE	MICROCOLEACEAE
<i>Alonina bifrons</i> [°]	<i>Endocarpon sp.</i>	<i>Microcoleus sp.</i>
<i>Alonia aloides var. ambigua</i> [°]	COLLEMATACEAE	NOSTOCACEAE
<i>Didymodon vinealis</i>	<i>Collema sp.</i>	<i>Nostoc sp.</i>
<i>Didymodon australasiae</i> [°]	BACIDIACEAE	
<i>Didymodon brachyphyllus</i>	<i>Toninia sp.</i> [°]	
<i>Tortula brevipes</i>	Crustose lichens x3	
<i>Tortula inermis</i>	(genera unknown – on	
<i>Tortula californica (CNPS 1B.2)</i> ^{°*}	rocks that are	
<i>Crossidium squamiferum</i> [°]	embedded in BSC)	
<i>Crossidium seriatum</i> [°]		
BRYACEAE		
<i>Bryum lanatum</i> [°]		
<i>Bryum argenteum</i>		
FUNARUACEAE		
<i>Funaria hygrometrica</i>		

[°]Appears to be restricted to late-successional BSC.

^{*}(CNPS 1B.2) indicates rare, threatened, or endangered in California and elsewhere.

Table 5. Checklist of the bryophytes of the PVP. Note: table created by author of this thesis

DIVISION	FAMILY	Species
<u>BRYOPHYTA</u>		
<u>(MOSES)</u>		
	AMBLYSTEGIACEAE	<i>Amblystegium serpens</i> <i>Leptodictyum riparium</i>
	BRACHYTHECIACEAE	<i>Brachythecium bolanderi</i> <i>Brachytheciastrum velutinum</i> <i>Homalothecium arenarium</i> <i>Scleropodium californicum</i> <i>Scleropodium cespitans</i> <i>Scleropodium touretti</i>
	BRYACEAE	<i>Bryum argenteum</i> <i>Bryum lanatum</i> <i>Gemmabryum caespiticium</i> <i>Gemmabryum demaretianum*</i> <i>Gemmabryum gemmiferum</i> <i>Gemmabryum gemmilucens</i> <i>Gemmabryum kunzei</i> <i>Gemmabryum radiculosum</i> <i>Gemmabryum ruderae</i> <i>Gemmabryum valparaisense</i> <i>Gemmabryum vinosum</i> <i>Gemmabryum violaceum</i> <i>Rosulabryum gemmascens</i> <i>Rosulabryum torquescens</i>
	DITRICHACEAE	<i>Ditrichum schimperi</i>
	FISSIDENTACEAE	<i>Pleuridium subulatum</i> <i>Fissidens crispus</i> <i>Fissidens curvatus</i> <i>Fissidens sublimbatus</i>

FUNARIACEAE*Funaria hygrometrica**Funaria muhlenbergii***GRIMMIACEAE***Grimmia lisae***HEDWIGIACEAE***Hedwigia dentonsa***LEUCODONTACEAE***Nogopterium gracile***LESKEACEAE***Claopodium whippleanum***MNIACEAE***Pohlia atropurpurea***ORTHOTRICHACEAE***Orthotrichum franciscanum***POTTIACEAE***Aloina aloides* var. *ambigua**Aloina bifrons**Crossidium seriatum**Crossidium squamiferum**Didymodon australasiae**Didymodon brachyphyllus**Didymodon eckeliae**Didymodon rigidulus**Didymodon tophaceus**Didymodon vinealis**Hennediella stanfordensis**Stegonia hyalinotricha**Syntrichia princeps**Syntrichia ruralis**Timmiella anomala**Tortula brevipes**Tortula californica* (CNPS 1B.2)***Tortula guepinii**Tortula inermis**Tortula muralis**Tortula obtusifolia**Tortula plinthobia**Weissia controversa*

MARCHANTIOPHYTA
(LIVERWORTS)

AYTONIACEAE

Asterella californica

CEPHALOZIELLACEAE

Cephaloziella hampeana

FOSSOMBRONIACEAE

Fossombronia longiseta

LUNULARIACEAE

*Lunularia cruciata**

PORELLACEAE

Porella bolanderi

RICCIACEAE

Riccia sorocarpa

SPHAEROCARPACEAE

Sphaerocarpos michelli

TARGIONIACEAE

Targionia hypophylla

*Introduced to California

**(CNPS 1B.2) indicates rare, threatened, or endangered in California and elsewhere.

CHAPTER 4

DISCUSSION

The results of this study provide a preliminary look at BSC on the PVP concerning its distribution, morphology, and species composition. The study also provides future research topics that could be explored.

Organic Litter on the Soil Surface

Results from the study showed that percent cover of organic litter is negatively correlated with percent cover of BSC in the Forrestal Nature Reserve (Fig. 7). If a large amount of organic litter was present on the soil surface in the study sites (Fig. 8), then the percent cover of BSC was greatly reduced or absent. Spaces between shrubs that had minimal organic leaf accumulation often had BSC present in the Forrestal Nature Reserve. A survey of BSC in other locations throughout the PVP produced similar observations. Slopes and steep bluffs along the coastline often had minimal accumulation of organic litter and frequently had BSC present.



Figure 8. Organic litter on soil surface. Note: original material collected by the author of this thesis.

Peintinger and Bergamini (2006) also found that the amount of organic litter present on the soil surface can greatly influence the species composition occupying that portion of the soil matrix. Smaller non-mobile organisms such as bryophytes and lichens that occupy the soil surface cannot compete with large amounts of organic litter accumulating, and they eventually become shaded or buried (Peintinger and Bergamini 2006). Research on BSC in parts of western North America has shown that BSC decreases with an increase in organic litter on the soil surface (Belnap et al. 2001a; Belnap et al. 2001b). However, the effects of organic litter on BSC in CSS had not been examined previously. Organic leaf litter accumulation in CSS predominantly occurs around the bases of vascular perennial plants and the amount of organic litter produced varies depending upon what species of vascular plant it is (Gray and Schlesinger 1981).

The soil surface in the spaces between shrubs in CSS tends to have a low accumulation of organic litter and this is often where BSC is observed occurring in CSS (Magney and Knudsen 2006; Hernandez and Sandquist 2011; Hernandez and Knudsen 2012), consistent with the results of this study.

Loose Rock on Soil Surface

The effects of loose rock cover on BSC in CSS had not been examined prior to this study. At the Forrestal Nature Reserve study sites, high accumulation of loose rock was negatively correlated with percent cover of BSC (Fig. 6), as it was at other locations throughout the PVP (Fig. 9).



Figure 9. Loose rock on soil surface. Note: original material collected by the author of this thesis.

These results agree with findings from shrublands of western North America (Belnap et al. 2001a; Belnap 2001d). Another observation from the study sites was that where loose rock was embedded in the soil surface, the percent cover of BSC was higher (Fig. 10). This concurs with other research that has found that embedded rock near the surface of BSC allows for an increase in the percent cover of BSC (Belnap 2001d). Embedded rock creates even more microtopography on the soil surface that traps more water, and it acts like armor that protects BSC from certain physical disturbances (Belnap 2001d). In areas where BSC occurred on the Palos Verdes Peninsula, embedded rock was commonly encountered on the soil surface.

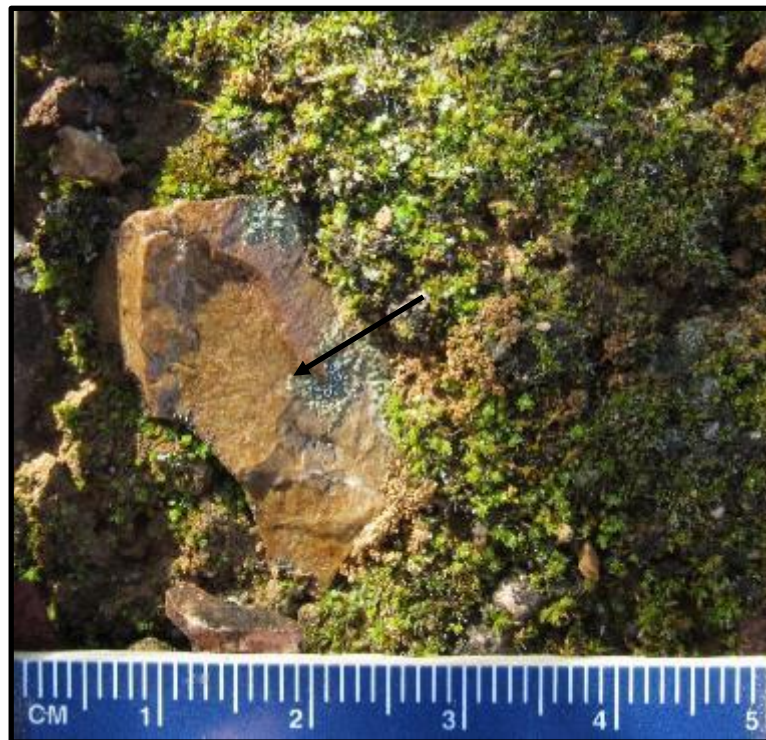


Figure 10. Rock embedded in soil surface (black arrow).
Note: original material collected by the author of this thesis.

Disturbance to the BSC

Research on disturbance and BSC has shown that both anthropogenic and naturally occurring disturbances can greatly effect BSC cover (Belnap 1995; Belnap et al. 2001b). Duration and intensity of disturbance can influence the composition of BSC as well as its recovery rate (Belnap 1993; Belnap and Eldridge 2001). If disturbances are chronic and intense, then BSC will be replaced by bare soil or it will only stay in an early-successional stage composed mostly of cyanobacteria (Belnap 1995; Belnap and Eldridge 2001). However, if disturbances are of a less intense nature and short lived, then BSC can recover (Belnap and Eldridge 2001). Recovery of BSC from most disturbances can be extremely slow, especially in semi-arid to arid lands (Belnap and Eldridge 2001). Only one study had previously looked at the effects of disturbance on BSC in CSS (Hernandez and Sandquist 2011).

Disturbance was found to be a significant predictor of percent cover of BSC. Within all the study sites, there were disturbances of either natural or anthropogenic origin. Some disturbances appeared to have a large impact on the BSC, while others had a minimal impact. In spots where certain disturbances occurred, BSC was greatly reduced or completely absent. Spur trails and boulder strikes created the largest impact to the BSC seen in the study sites. These types of disturbances smashed and fragmented the BSC. In study site 3, the upper cliff face experiences periodic erosion of large boulders that tumble down to the lower areas (personal observation). These boulders punch large holes in the BSC and pulverize the BSC in the impact spots (Fig. 11).



Figure 11. Boulder impact site to BSC. Impact site contains *M. indicus*. Note: original material collected by the author of this thesis

The loss of BSC in the impact spots allowed for *Melilotus indicus*, a non-native vascular plant, to establish in some of them. This concurs with Hernandez and Sandquist's (2011) study where disturbance to BSC allows for the colonization of non-native species. Since boulder strikes did not repeatedly occur in the same location, recolonization of BSC within some of the holes was observed. Spur trails were another type of disturbance observed in the study sites; these appeared to be caused by off-trail hikers and mountain bikers. The soil found within these spur trails was very loose and completely void of BSC (Fig 12). No recolonization of BSC on the surface of the soil of the spur trails was observed in the study sites.



Figure 12. Bike spur trail through area with BSC and soil within spur trail devoid of BSC. Note: original material collected by the author of this thesis.

However, an interesting observation was made during the survey conducted in the Portuguese Bend Nature Reserve. An old spur trail bisecting a portion of remnant intact habitat near the Ailor Cliff area, that had been closed by the Palos Verdes Peninsula Land Conservancy, had early successional BSC starting to form on the soil of the spur trail (Fig. 13). Cessation of the disturbance appears to have allowed the soil within the spur trail to consolidate and allow for BSC to recolonize. Since the PVP has a strong maritime influence and experiences fog banks throughout the year, this source of moisture coupled with removal of a disturbance might be playing a crucial role in BSC

on the PVP, allowing BSC to recolonize disturbed areas more quickly than in more arid locations.



Figure 13. Closed spur trail has allowed for early successional BSC to appear on the soil (black arrow). Note: original material collected by the author of this thesis.

Disturbance via water erosion was also observed in some of the study sites, but this type of disturbance appeared to be less intense and appeared to facilitate the movement of fragmented chunks of BSC to other locations (Fig. 14). Water erosion could possibly be acting as an incidental means of dispersal of BSC to other locations where it could then recolonize the soil surface. It has been shown in a greenhouse experiment that transplants of BSC from the field can be cultivated, and that inoculation of the soil

surface with crushed BSC can enhance recovery of BSCs on disturbed soils (Belnap 1993; Bowker 2007; Antoninka et al. 2015).



Figure 14. Loose chunks of BSC on soil surface. Note: original material collected by the author of this thesis.

The PVP during the early to mid 19th century experienced long-term anthropogenic disturbances that altered the landscape and greatly impacted the soil surface (Gale 1974). These included dryland farming, cattle ranching, military activities, mining, landslides, and housing development (Gale 1974; FNPMP 2005). These disturbances reduced native habitat and destroyed or augmented native soils, which probably resulted in large losses of BSC throughout the landscape.

Exposure and BSC

Exposure was found to be a significant predictor of percent cover of BSC. BSC was found occurring in full sun, partial shade, and full shade (Fig. 15). However, the percent cover of BSC was greater in full sun conditions than in full shade. Based on observations made of BSC in sites with full shade, BSC appears to have a slight shift in species composition. In full shade *Didymodon sp.* formed larger turfs that appeared to occur more often (Fig. 15). In addition, other moss species (*Aloina bifrons*, *Aloina aloides var. ambigua*, *Tortula brevipes*, *Tortula inermis*, *Didymodon australasiae*, *Crossidium squamiferum*, *Crossidium seriatum*, and *Bryum lanatum*) which tended to be more abundant in full sun and partial sun appeared to be far less abundant in full shade. BSC in full sun appeared to have less extensive coverings of *Didymodon sp.* turfs and more moss species that are annuals and do not form turfs. Lichens also appeared to be less abundant in partial shade with the more gelatinous and squamulose lichens being more abundant in full sun. Further research is needed to confirm this change in species composition within BSC on the PVP with different types of exposure.

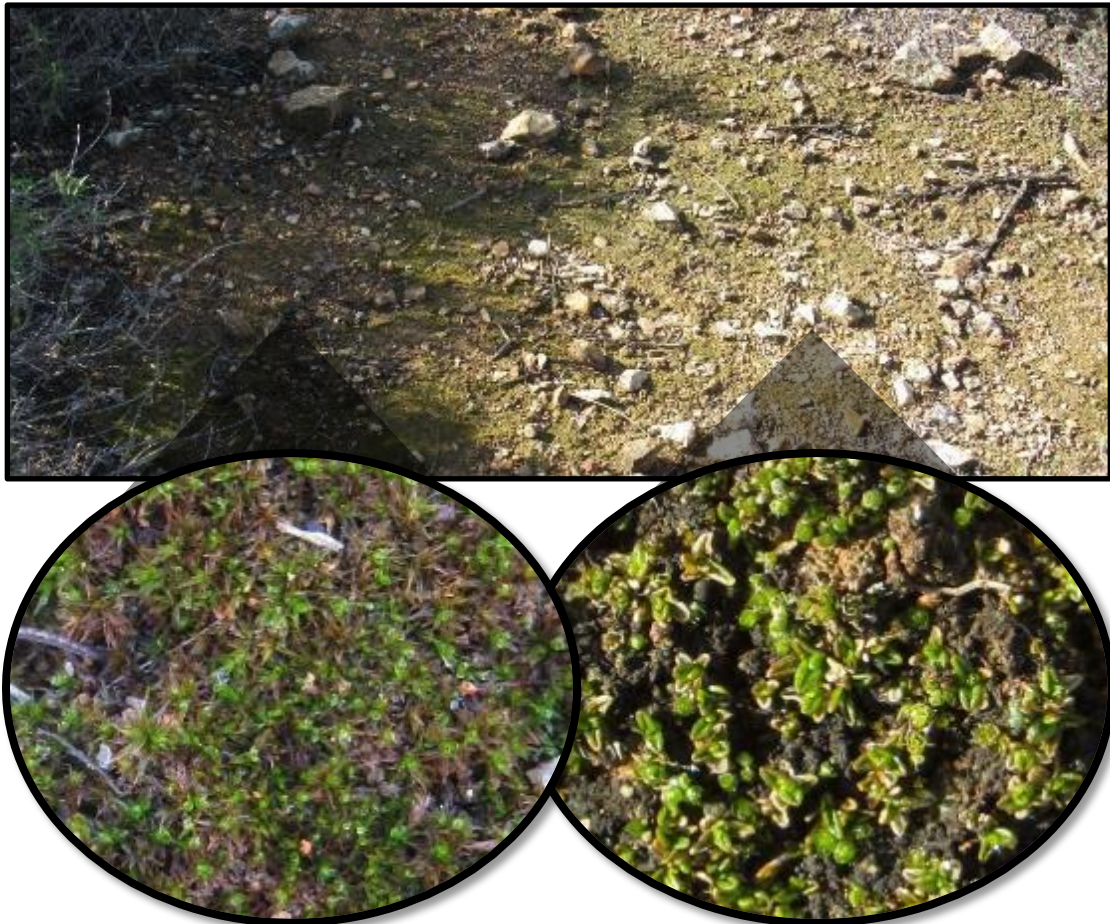


Figure 15. BSC in partial shade (A) with *Didymodon vinealis* turf and in full sun (B) with *Aloina aloides* var. *ambigua* and *Bryum argenteum*. Note: original material collected by the author of this thesis.

Distribution of BSC on the PVP

In addition to the study sites, BSC was also surveyed in other locations throughout the PVP (Fig. 5). In total, BSC was found in 40 locations throughout the PVP. BSC was commonly encountered on thin soil habitats, which matches other observations made of BSC in other parts of southern California (Magney and Knudsen 2006). These thin soil habitats were found along coastal bluffs, canyon walls, historical road cuts, and in many of the nature reserves (Three Sisters, Portuguese Bend, Forrestal, George F

Canyon, and Alta Vicente) (Fig. 16). Portions of the coastal bluffs contained large coverings of BSC, especially on more north-facing bluffs.

The BSC of these coastal bluffs gives the soil surface a brownish black and gray color in the summer and a greenish black color in the wet season. The coastal bluffs of Bluff Cove, Christmas Cove, Abalone Cove, Sacred Cove, Lunada Bay, and Malaga Cove were found to contain extensive coverings of BSC.

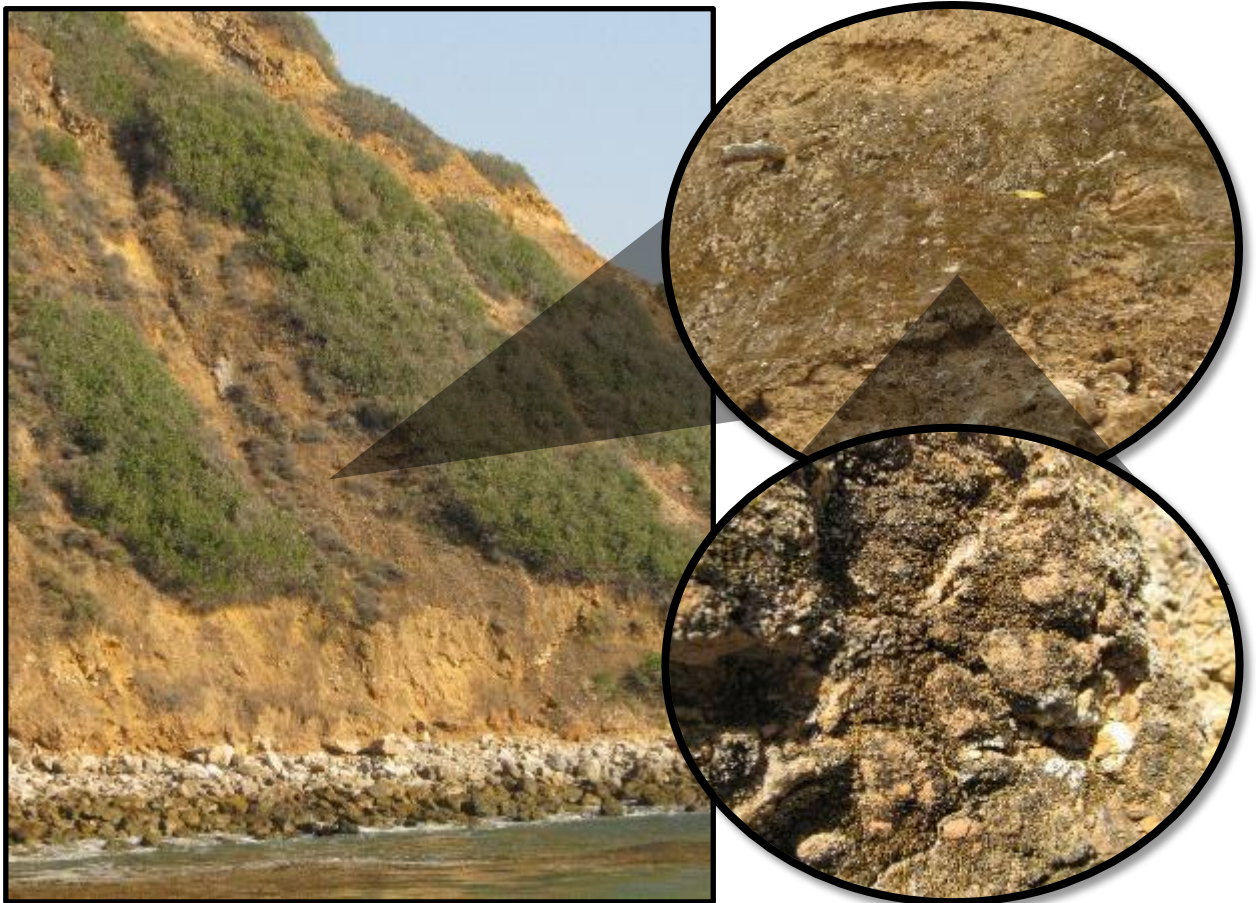


Figure 16. BSC of PVP coastal bluffs. Note: original material collected by the author of this thesis.

Surveys conducted in areas off trail in remnant intact CSS throughout the Palos Verdes Peninsula Nature Preserve often contained BSC on the soil surface between the shrubs. Canyon walls throughout the PVP also contained BSC. Lunada Canyon contained extensive coverings of BSC along portions of its walls (Fig. 17). Biological soil crust was also observed on the sandy soils of Linden H. Chandler Nature Preserve and on the sandy soils of the Defense Fuel Supply Point in San Pedro (Fig. 19). Another interesting location for BSC was in areas where the landscape has been shaped into a bench cut, which create pocket areas where BSC accumulates (Fig. 18). These bench cuts were observed in the Forrestal, Portuguese Bend, and Three Sisters Nature Reserves.

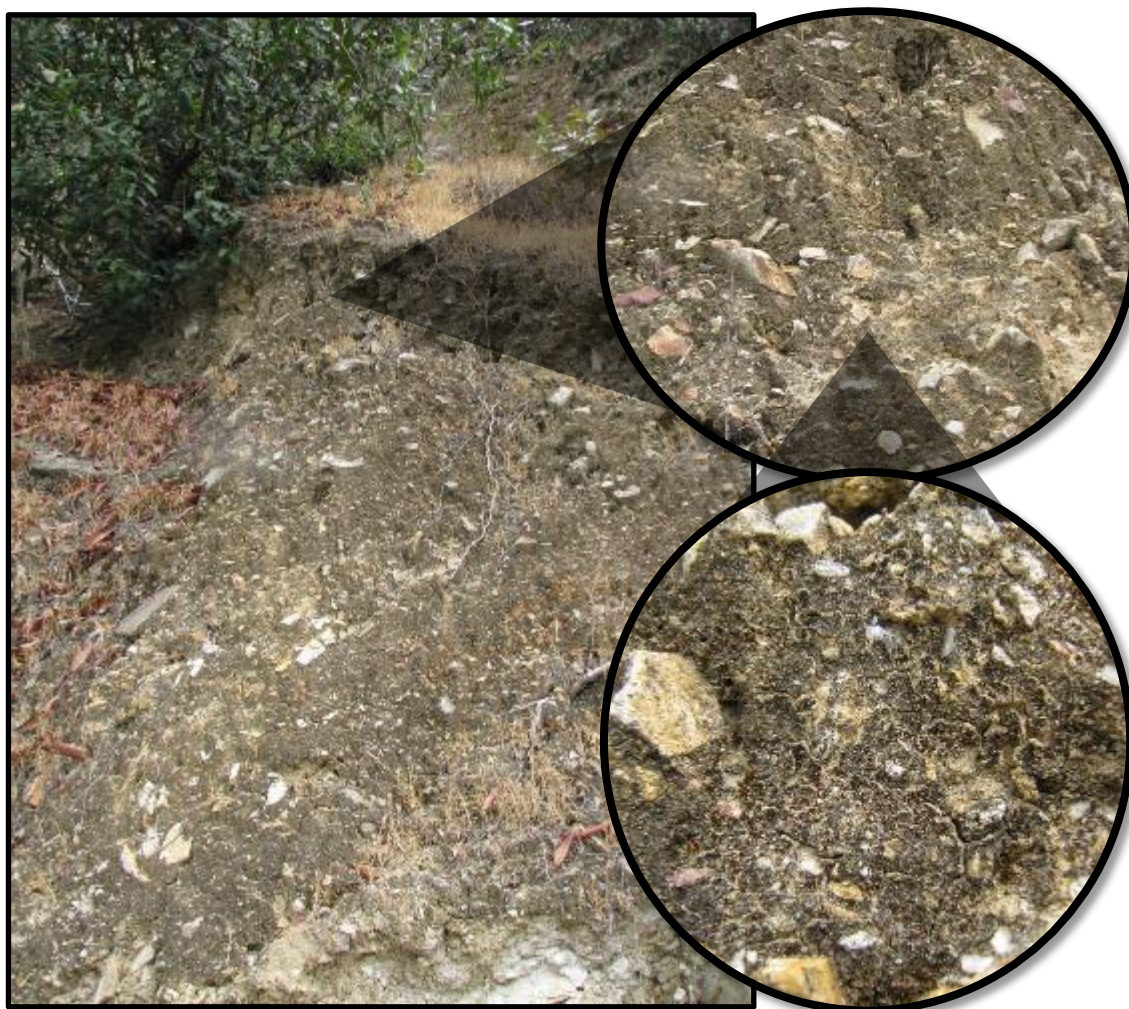


Figure 17. BSC along canyon walls. Note: original material collected by the author of this thesis.

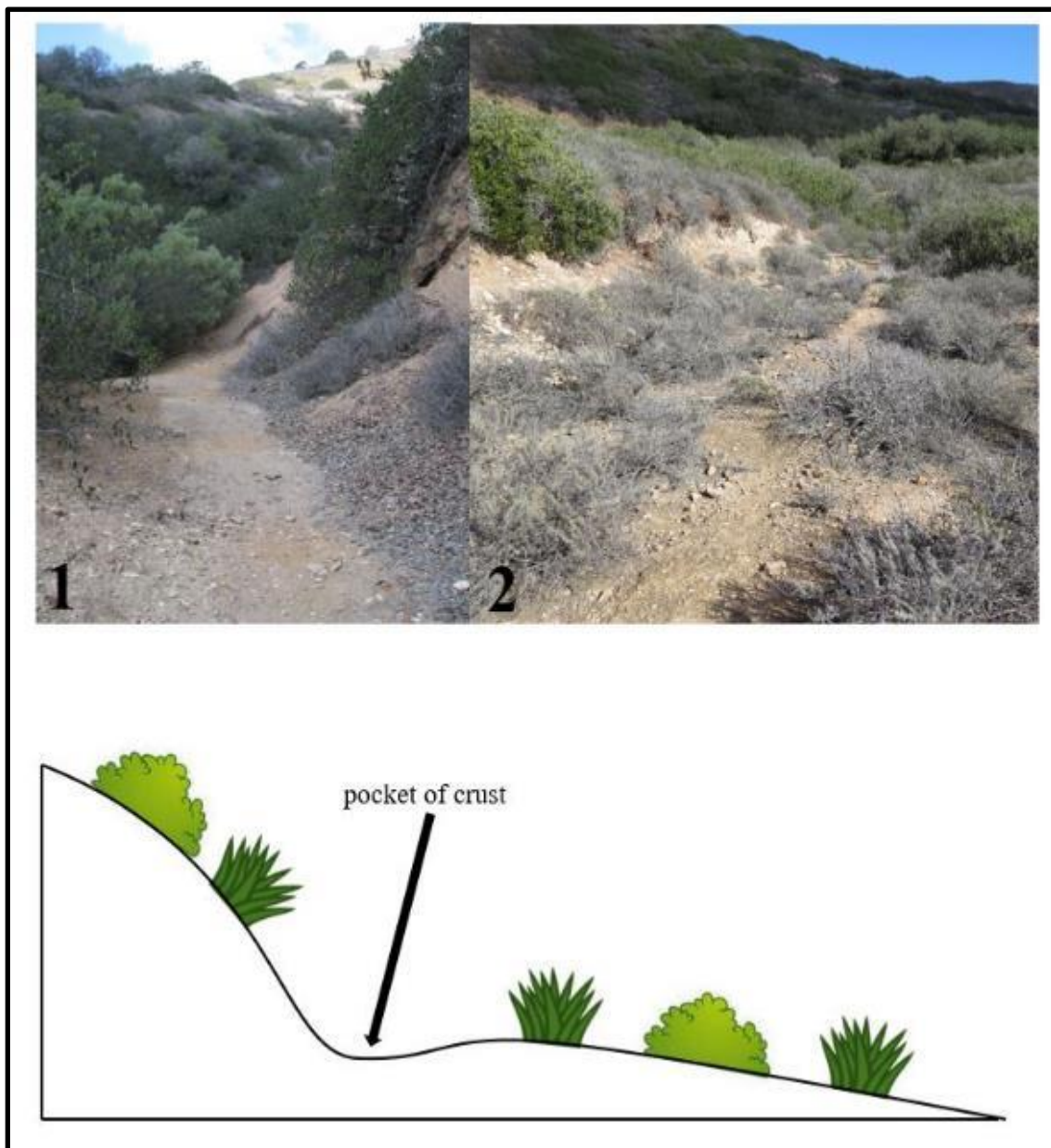


Figure 18. Bench cuts – pockets contain crust (1) and (2) showing pockets or low areas. Note: original material collected by the author of this thesis.

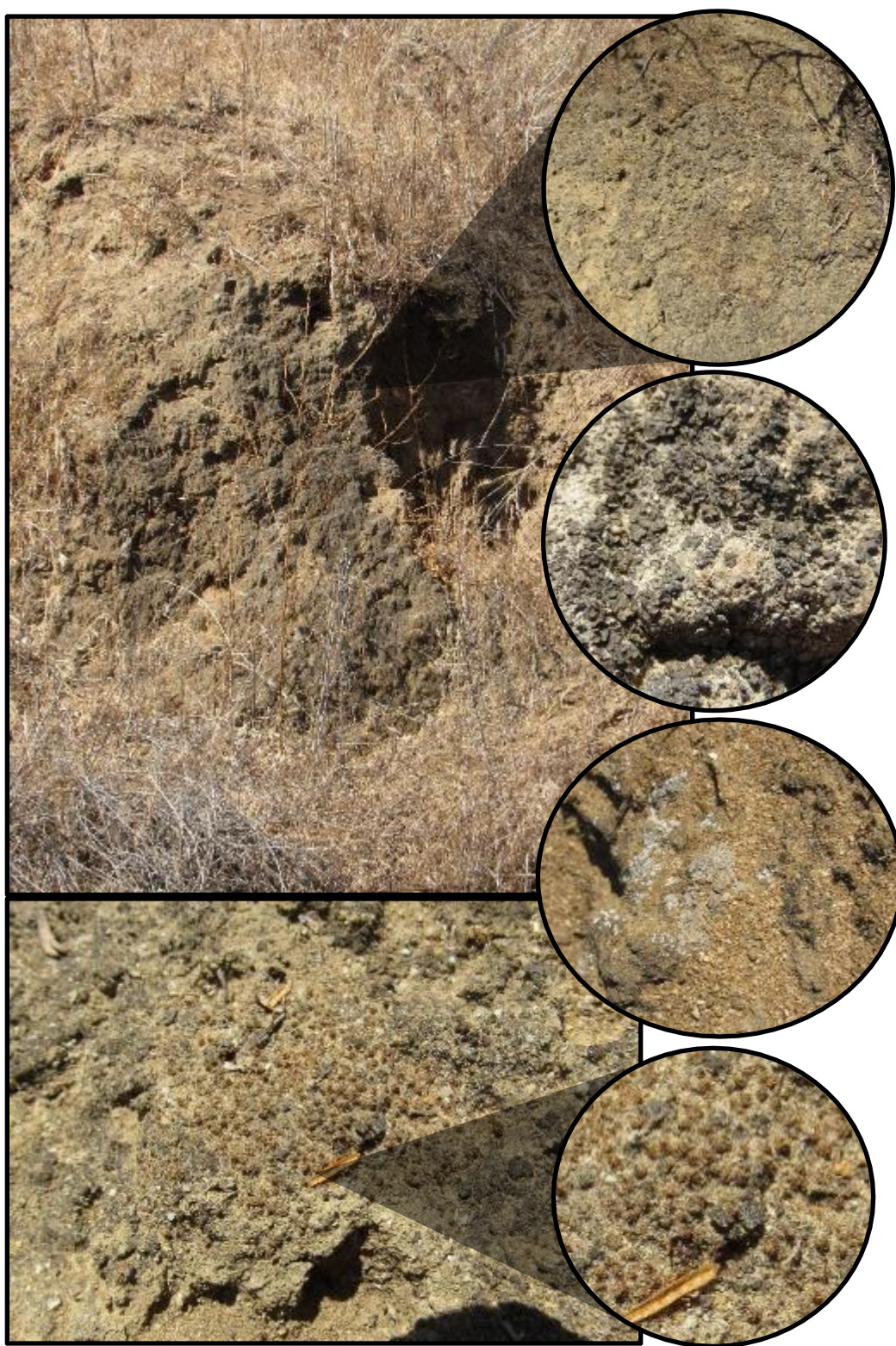


Figure 19. BSC of the Defense Fuel Supply Point in San Pedro. Note: original material collected by the author of this thesis.

Overall, BSC was found throughout the PVP in coastal bluff scrub, CSS, canyon riparian, and sandy soil sites. However, in these areas it had a sporadic distribution. This sporadic nature of the PVP BSC concurs with studies of BSC in CSS from Orange County (Hernandez and Sandquist 2011; Hernandez and Knudsen 2012). The distribution of BSC on the PVP has probably been greatly reduced due to the loss of habitat, invasion of non-native plants, altered fire regimes, and massive soil surface disturbance from historical land uses (for example, agriculture, and cattle grazing). Interestingly, the locations where BSC was found on the PVP appear to correlate with relict habitat seen in 1952 aerial imagery of the PVP.

Morphology of the PVP BSCs

In all three study sites, and throughout the Forrester Nature Reserve, the overall form of the BSC was late-successional rugose. The surface of the BSC was predominantly comprised of cyanobacteria, mosses, and lichens, which matches BSC from Orange County and Riverside County (Hernandez & Sandquist 2010; Hernandez & Knudsen 2011). In the dormant state, the late-successional rugose BSC in the study sites gave the soil surface a blackish gray and brown color (Fig. 20). It also has a fuzzy appearance and rough look due to slight changes in the soil surface topography.



Figure 20. Ground view of late-successional rugose BSC on the PVP demonstrating the fuzzy appearance due to leaf awns of certain moss species (black arrow). Note: original material collected by the author of this thesis.

The fuzzy look is the result of a large presence of moss species (*Aloina bifrons*, *Aloina aloides* var. *ambigua*, *Crossidium serreatum*, *Crossidium squamiferum*, *Bryum argenteum*, *Bryum lanatum*, *Didymodon vinealis*, and *Tortula brevipes*) on the surface of the BSC, which possess leaf awns or awn-like extensions (Fig. 20). The thalli of various lichens and the sporophytes of various mosses present in the late-successional rugose BSC contribute to its roughened appearance. The blackish-gray color of the late-successional rugose BSC in the study sites is a result of a large amount of cyanobacteria

and cyanolichens present within it (Fig. 23). Another contributing factor to the overall blackish-gray and brown color of the late-successional rugose BSC in the study sites is the blackish and grayish colors that certain mosses and lichens take on in their desiccated state (Fig. 21).

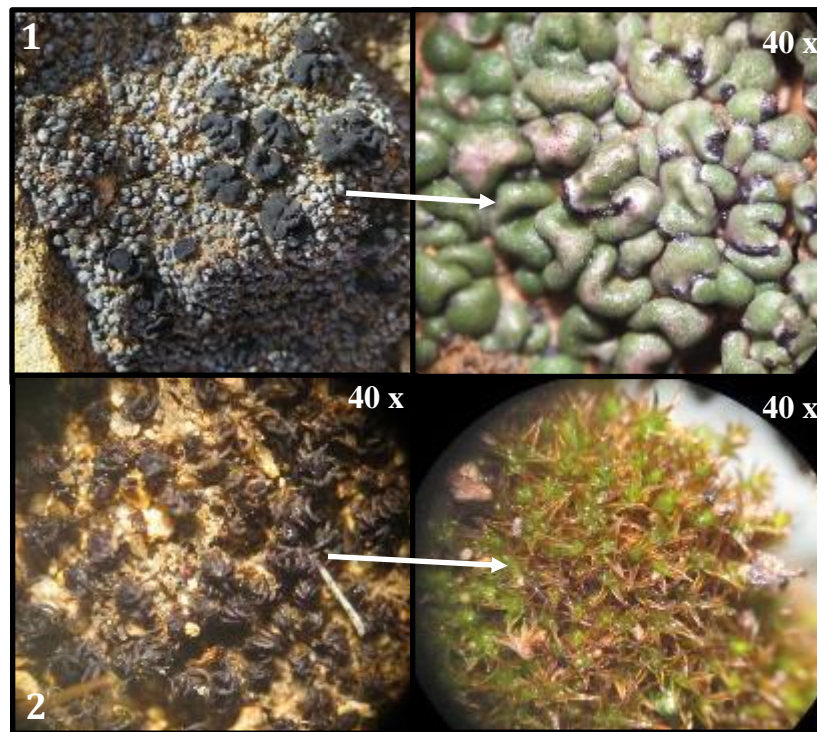


Figure 21. Color change of *Toninia sp.* (1) and *Didymodon australasiae* (2) from the desiccated state to hydrated state. Note: original material collected by the author of this thesis.

When the BSC of the study sites received moisture in late winter of 2016, the soil surface color changed from a blackish-gray and brown color to a greenish-black color (Fig 21, 22).



Figure 22. BSC desiccated state (1) to hydrated state (2) following rains. Note: original material collected by the author of this thesis.

The green color comes primarily from the rehydration of the mosses and from the phycolichens (*Placidium sp.*, *Toninia sp.*) dwelling in the BSC in the study sites. Further, the BSC also took on a gelatinous shiny look when in the hydrated state because of the cyanolichens and cyanobacteria in it (Fig. 23). Late-successional rugose BSC was also observed at other locations throughout the PVP.



Figure 23. Gelatinous shiny look of the cyanobacteria and cyanolichens in PVP BSC. Note: original material collected by the author of this thesis.

BSC containing lichens, mosses, or both indicate a more successional mature BSC, while the lack of one or more of these organisms can indicate an earlier

successional stage (Belnap et al. 2001b). Early successional stages of BSC were also observed on the PVP primarily occurring in recently disturbed areas (Fig. 24). The overall form of the early-stage BSC is flat (Belnap et al. 2001b) and fuzzy in appearance. The early successional stages of the BSC on the PVP consisted primarily of cyanobacteria (*Microcoleus sp.*) and only a few ruderal moss species (*Didymodon vinealis*, *Bryum argenteum*, *Funaria hygrometrica*), which give the BSC its fuzzy appearance. The BSC of this early successional stage gives the soil surface a reddish tan color, which is also a result of the moss component (Fig. 24). Early successional stages of the BSC were commonly seen along trail margins and in disturbed areas throughout the PVP.



Figure 24. Early successional stage BSC on the PVP. Note: original material collected by the author of this thesis.

Preliminary observations of the late-successional rugose BSC on the PVP showed that it contained a high taxon diversity. Numerous moss species and lichen genera were observed as well as two cyanobacteria genera (Table 4). Late-successional rugose BSC on the PVP appears to be acting as a refugium for these minute soil-surface dwellers. With further examination of the BSC of the PVP, no doubt additional species of mosses, lichens, cyanobacteria and other microorganisms (for example, diatoms, algae, fungi, and microarthropods) within the BSC will be discovered.

Cyanobacteria of PVP BSC

Cyanobacteria are a crucial component to the formation of BSC (Belnap 1992; Belnap 1994; Belnap 2003). Cyanobacteria are often the pioneer species that, through biological activities, stabilize the soil surface which ultimately allows for the colonization of other BSC-associated organisms and greatly reduces surface soil erosion (Belnap 1994; Li et al. 2001; Belnap 2003). Cyanobacteria can be found in BSC worldwide and prefer soils that are more alkaline in composition (Belnap 2003). Cyanobacteria in BSC act as carbon sinks while at the same time fixing atmospheric nitrogen into bio-available nitrogen, which can enhance soil fertility in nutrient-poor soils (Belnap 1994; Li et al. 2001; Belnap 2003; Zhao et al. 2010). BSC contains a high diversity of cyanobacteria (Belnap 1994; Flechtner et al. 1998; Flechtner et al. 2008). Flechtner et al. (2008) found that BSCs of San Nicholas Island off of the southern California coast contained 19 genera of cyanobacteria and discovered several new species. Flechtner et al. (1998) found that BSC of the Central Desert of Baja California contained 18 different species of cyanobacteria.

Southern California shares similar cyanobacteria species composition with the Channel Islands, southern Arizona, and Baja California (Belnap 1994; Flechtner et al. 1998; Flechtner et al. 2008). During the course of this study, two cyanobacteria were encountered in the BSC on the PVP, and these were only identified to the genus level. There was a filamentous cyanobacterium, which appeared to belong to the genus *Microcoleus*, that created gelatinous sheaths on and within the first few millimeters of the soil surface (Fig. 25). The sheaths of this filamentous cyanobacterium would appear on the soil surface following rehydration of the BSC from a rain event (personal observation). Review of the literature shows that the genus *Microcoleus* is one of the most abundant and commonly encountered cyanobacterium found in BSC of the western half of North America and within BSC of California's Channel Islands and Baja California (Belnap 1994; Flechtner et al. 1998; Flechtner et al. 2008). The *Microcoleus* species observed on the PVP could possibly be *Microcoleus vaginatus*, which is a common filamentous cyanobacterium of BSC on California's Channel Islands and Baja California (Belnap 1994; Flechtner et al. 1998; Flechtner et al. 2008).

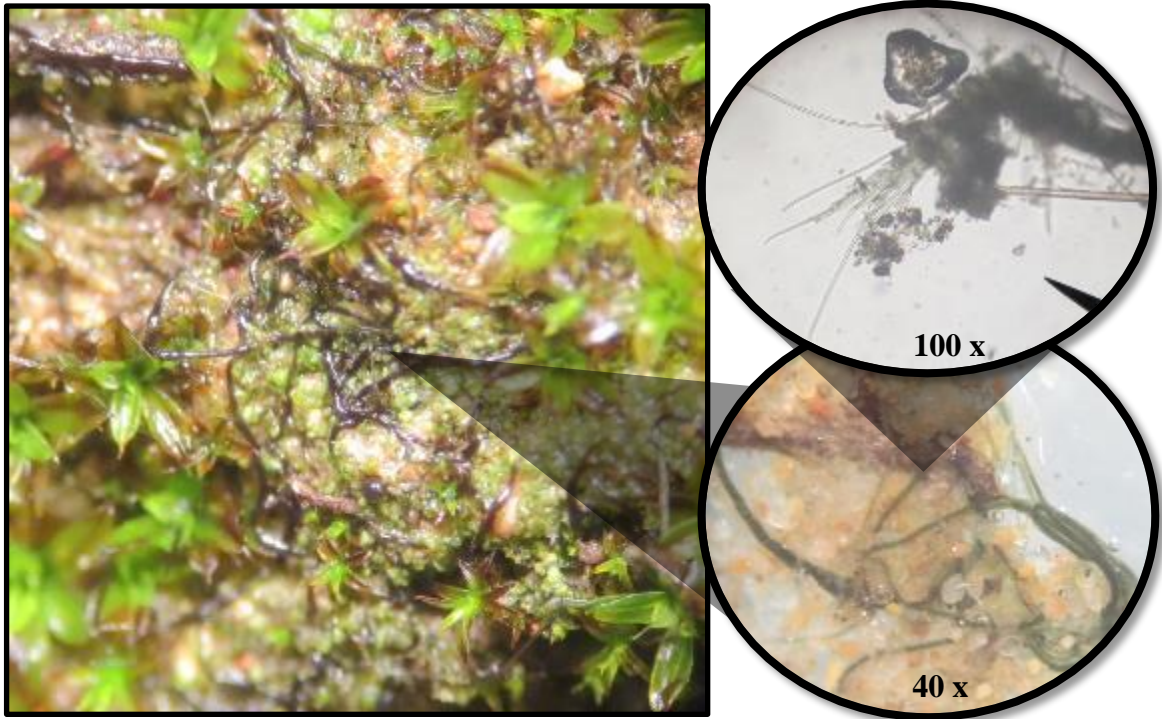


Figure 25. *Microcoleus* sp. observed in PVP BSC. Note: original material collected by the author of this thesis.

The second cyanobacterium encountered was of the genus *Nostoc*, and it was present throughout the PVP. It would form minute mucilaginous spheres (< 2 mm) on the surface of the BSC following a rain event. Dissection of the gelatinous spheres revealed a community of filaments of moniliform cells (Fig. 26). The genus *Nostoc* contains single celled cyanobacteria that often group together to form mucilaginous rounded colonies composed of filaments of moniliform cells that will appear on the soil surface following hydration of the soil (Rosentreter et al. 2007; Flechtner et al. 2008). Based on the description in Rosentreter et al. (2007) of *Nostoc punctiforme*, it appears that the second cyanobacterium observed might be this species. *Nostoc punctiforme* is another species of

cyanobacteria in BSC (especially of later successional BSC) that is widespread and abundant (Belnap 2003; Flechtner et al. 2008).

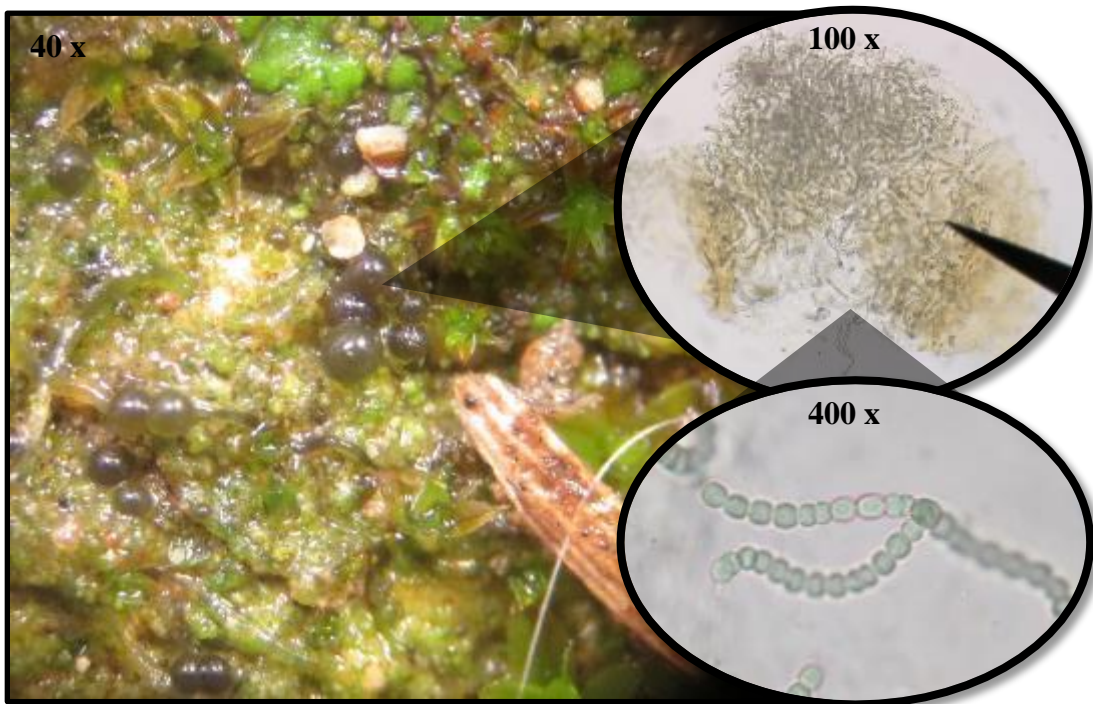


Figure 26. *Nostoc* sp. observed in PVP BSC. Note: original material collected by the author of this thesis.

Belnap et al. (2008) developed a non-destructive visual technique that incorporated a system of classes (1-10) to assess soil surface stability and different levels of cyanobacterial development (LOD) such as cyanobacteria biomass/number and polysaccharide content of BSC. Based on this classification system and factoring in BSCs with greater lichen and/or moss cover as mentioned, it appears that the late-successional rugose BSC within the study sites ranged from LOD classes 7 to 10. This indicates that within the study sites there is a high level of cyanobacterial development, the soil surface

is very stable, and lichen and moss cover is high. Coastal bluff BSC appeared to range from LOD classes 6 to 8, which also indicates a high cyanobacterial development and soil surface stability, and a moderate covering of mosses and lichens. It seems probable that, further research on the cyanobacteria of BSC on the PVP will uncover many more species.

Lichens of PVP BSC

Lichens are composite organisms that can grow in harsh environments where most other organisms are unable to survive (Beckett et al. 2008; Galloway 2008). They are often restricted to stable or sheltered microsites and play a crucial role in many environments (Seaward 2008). BSCs of arid to semi-arid lands worldwide have been shown to contain an abundant lichen diversity (Nash et al. 1977; Martinez-Sanchez et al. 1994; Eldridge and Tozer 1997; Martinez et al. 2006; Rosentreter et al. 2007; Ochoa-Hueso et al. 2011; Hernandez and Knudsen 2012). Terricolous lichens of BSC play a large role in increasing soil microtopography, influencing soil hydrological properties, contributing nutrients to the soil, acting as carbon and nitrogen sinks, and preventing soil erosion (Nash et al. 1977; West 1990; Belnap et al. 2001b; Belnap 2003). All lichen growth forms (crustose, foliose, fruticose, squamulose) have been found to occur within BSCs; however, crustose, squamulose, and foliose growth forms are the most common (Belnap et al. 2001a). Gelatinous lichens, which are lichens that have homoiomerous thalli and are most commonly formed with cyanobacteria, are also common in BSC worldwide (Nash et al. 2002). Since BSCs occur in arid to semi-arid environments, the lichen flora of these BSCs are able to withstand extreme temperatures and are

poikilohydric (Belnap 2003; Beckett et al. 2008). In the western United States, numerous studies have shown that the BSC of this geographic region contains an abundant lichen flora (Nash et al. 1977; Ponzetti and McCune 2001; Nash et al. 2002; Belnap 2003; Knudsen 2005; Rosentreter et al. 2007).

Southern California possesses a rich lichen flora from its coastline to its deserts (Hasse 1913; Nash et al. 2002; Knudsen 2005; Magney and Knudsen 2006; Knudsen et al. 2013; Tucker 2012). Maritime habitats of California, especially along southern California's coastline, contain a high lichen diversity due to the strong influence of fog from the Pacific Ocean (Magney and Knudsen 2006; Sharnoff 2014). As a result of habitat loss throughout southern California, numerous lichen species have become rare, and it has been estimated that as many as 94 lichenicolous fungi species have been extirpated from Los Angeles and Ventura Counties since 1915 (Knudsen 2010). Many of these southern California lichen species that are now rare are mostly terricolous lichens (Knudsen 2010). Terricolous lichen habitat was abundant during the early stages of the 20th century (Hasse 1913; Knudsen 2010), but it is now rare or greatly reduced in southern California due to anthropogenic disturbances such as historical ranching, development, introduction of non-native species, altered fire regimes, recreation use, and grazing (Knudsen 2010). BSC is a terricolous lichen habitat in southern California (Magney and Knudsen 2006; Hernandez and Sandquist 2011; Hernandez and Knudsen 2012). From a 41 km east-west environmental gradient conducted through Orange and Riverside Counties, looking at the biodiversity of BSC-forming lichens and mosses, a total of 31 species of lichens were observed representing 22 genera and 17 families

(Hernandez and Knudsen 2012). Hernandez and Knudsen (2012) also found that BSC in shrublands of southern California are more species-rich for lichens than North America's hot and cold deserts.

Work done by lichenologists in Santa Barbara and Ventura Counties has shown that both these areas have extremely diverse lichen flora (Knudsen 2005; Magney and Knudsen 2006; Tucker 2012). Geographically, these counties are quite close to the PVP. The Channel Islands, also close to the PVP, have also been shown to have a high diversity and abundance of lichens (Belnap 1994). The PVP lies in a unique location in southern California where its flora and fauna have connections to the mainland as well as to the Channel Islands. However, the PVP lichen flora is poorly understood. Hollinger (2012) performed the only preliminary survey for lichens on the PVP, consisting of four coastal bluff areas (Bluff Cove, Arroyo top of Paseo Lunado, Cliff tops north of Point Vicente, and Sacred Cove), and this survey resulted in a list of 64 lichen species. No BSC-dwelling lichens were mentioned in that preliminary survey.

Lichens were found to be abundant components of the BSC from the study sites at the Forrestal Nature Reserve as well as throughout the PVP. Lichen genera observed in the BSC of the study sites are listed in Table 4. Numerous crustose lichens were often present on embedded rock in the BSC (Fig. 28), but these were not identified. In addition, other terricolous lichens, also unidentified, were observed in the BSC throughout the PVP (Fig. 28). Cyanolichens appeared to be the most abundant type of lichen in the BSC of the PVP (Fig. 27).



Figure 27. *Collema* sp., a blackish gray gelatinous cyanolichen of PVP BSC (white arrow). Note: original material collected by the author of this thesis.

The most commonly encountered lichen genera in the BSC of the study sites and throughout the PVP were *Endocarpon* and *Collema* (Fig. 29). The genus *Toninia* was uncommon in the BSC on the PVP and was only found in the Forrestral Nature Reserve (Fig 29).

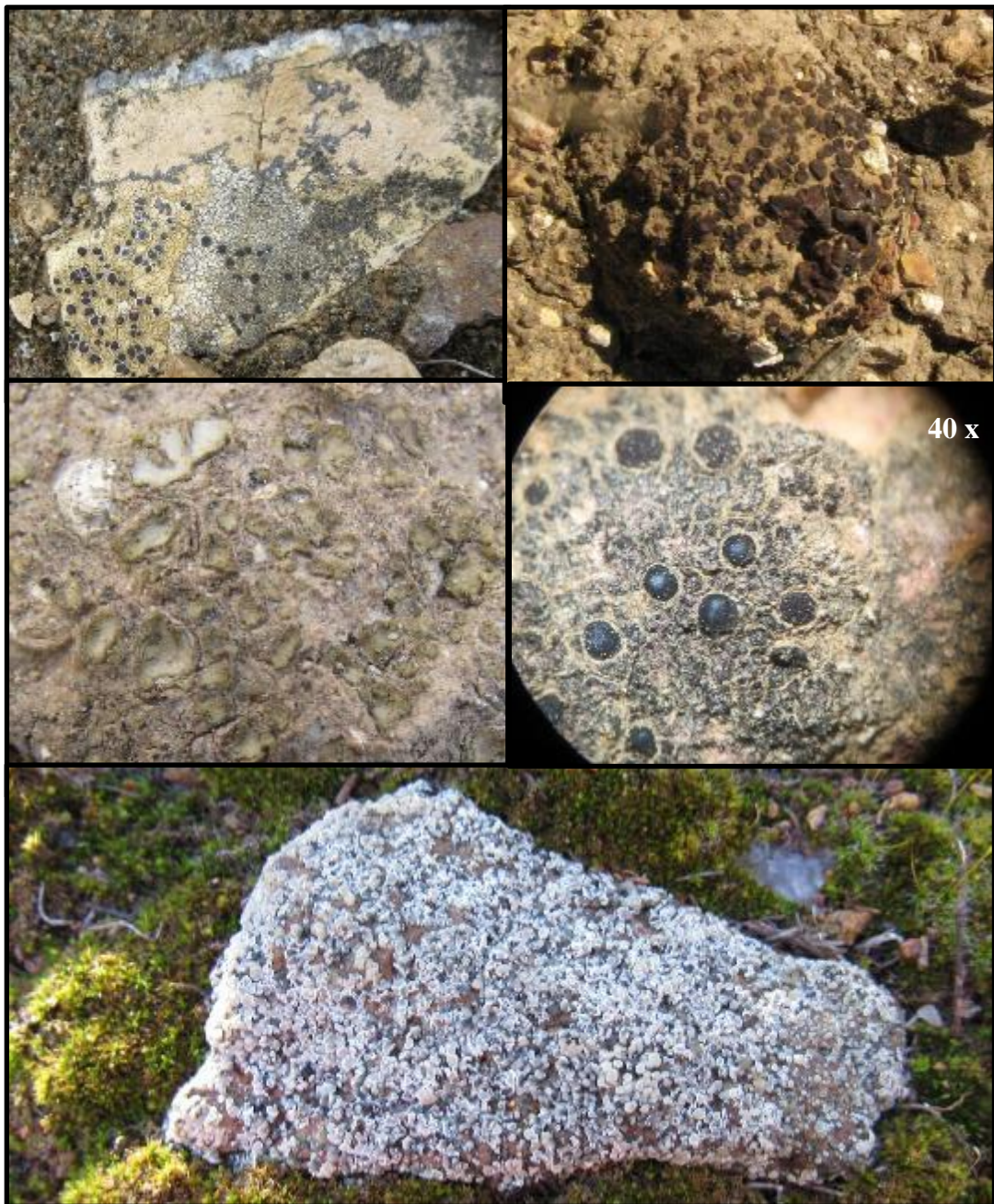


Figure 28. Examples of some lichens observed in the BSC of the study areas. Note: original material collected by the author of this thesis.

Surrounding the study sites and throughout the PVP a very high diversity of crustose, foliose, squamulose, and fruticose lichens were observed. These types of lichens

were found on shrubs (*Salvia leucophylla*, *Salvia mellifera*, *Rhus integrifolia*, *Artemisia californica*, and *Heteromeles arbutifolia*), and on various rock and soil types (Fig # 30, 31). Further research is needed on the species composition of lichens on the PVP and within its BSC.

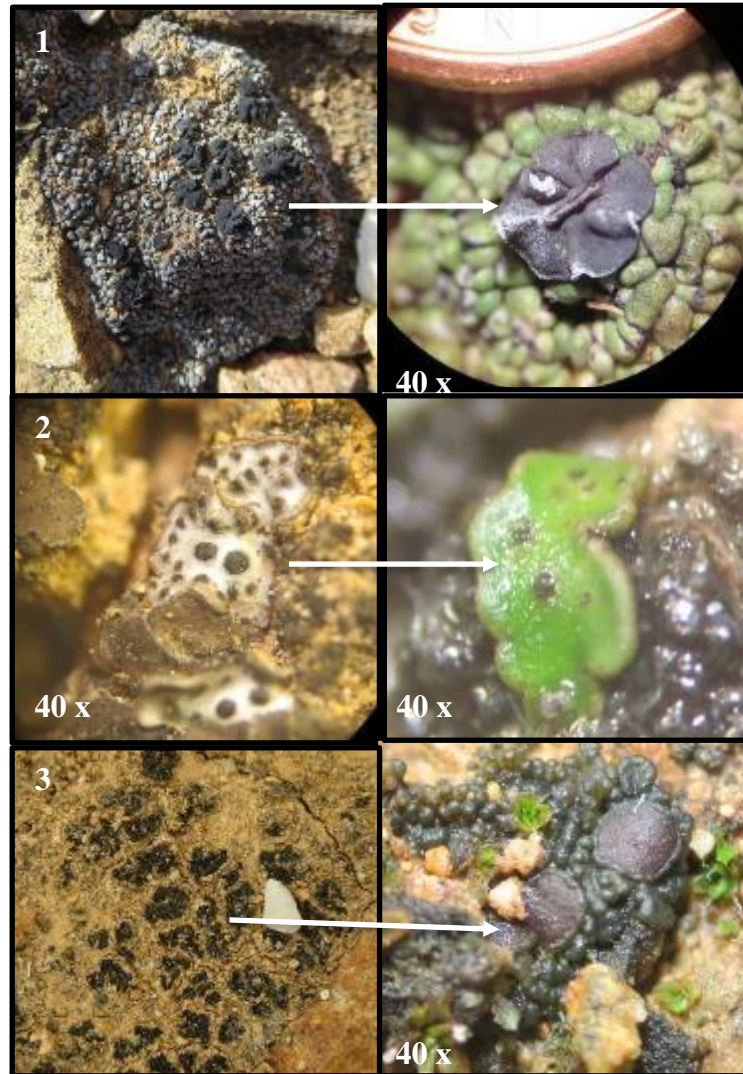


Figure 29. Lichens in BSC going from desiccated to hydrated: *Toninia* sp. (1), *Endocarpon* sp. (2), and *Collema* sp. (3). Note: original material collected by the author of this thesis.



Figure 30. Examples of lichens observed throughout the PVP and around study sites.
Note: original material collected by the author of this thesis.



Figure 31. Examples of lichens observed throughout the PVP and around study sites. Note: original material collected by the author of this thesis.

Bryophytes of PVP BSC

Bryophytes are nonvascular spore-producing herbaceous plants made up of mosses, liverworts, and hornworts that have a worldwide distribution and can be found in almost all terrestrial and semi-aquatic environments (Raven 2005; Tan and Pocs 2008). Bryophytes of these terrestrial and aquatic environments are extremely important and greatly influence many ecosystem functions (Richardson 1981; Smith 1982; Raven 2005; Turetsky 2003). Bryophytes produce organic matter, trap sediment, alter hydrological processes, stabilize soil and debris, contribute and alter nutrients, act as nurseries, influence carbon/nitrogen cycling, provide food, and act as habitat for a wide diversity of micro and macro organisms (Richardson 1981; Smith 1982; Belnap et al. 2001b; Raven 2005; O'Neill 2008; Turetsky 2003). Bryophytes are often thought of as only occurring in non-hostile environments that have relatively high moisture levels; however, bryophytes can be found in many semi-arid to arid environments worldwide (Flowers 1973; Richardson 1981; Scott 1982; Downing and Selkirk 1993; Eldridge and Tozer 1997; Rosentreter and Belnap 2001; Belnap 2003; Ingerpuu et al. 2005; Sagar and Wilson 2009; Ochoa-Hueso et al. 2011). Bryophytes are able to occur in semi-arid to arid environments because of a diverse array of strategies such as being pokilohydric and desiccation-tolerant (Richardson 1981; Scott 1982; Rosentreter and Belnap 2001; Belnap 2003; Proctor et al. 2007; Proctor 2008; Luttge et al. 2011). In addition, bryophytes have also evolved a whole suite of morphological structures that aid them in surviving in semi-arid and arid environments (Scott 1982; Rosentreter and Belnap 2001; Buck and Goffinet 2008). Some morphological features of bryophytes in semi-arid and arid environments

are concave leaves, leaf lobules, hairs, papillae, lamellae, semi-hyaline to hyaline leaves, pigmentation, and thallus scales (Scott 1982; Rosentreter and Belnap 2001; Glime 2015) (Fig. 32).



Figure 32. *Aloina bifrons* of PVP BSC using leaf hair points to condense moisture from the marine layer (white arrow). Note: original material collected by author of this thesis.

Movement of the gametophyte also greatly aids bryophytes in surviving in semi-arid to arid environments. Leaves of mosses can shrink, fold, or twist when drying out (Scott 1982; Rosentreter and Belnap 2001; Glime 2015). These movements help to protect the photosynthetic tissues of the leaves as well as the overall gametophyte from solar radiation and other harsh environmental conditions when in the desiccated state

(Scott 1982; Rosentreter and Belnap 2001; Glime 2015). These changes in leaf shape can give the gametophyte a twisted look, which is commonly seen in desiccated mosses in semi-arid and arid environments (Scott 1982; Rosentreter and Belnap 2001) (Fig. 33). Some thallose liverworts when drying out roll up into a tubular form and the dorsal side of the thalli tubes are covered in dark pigmented scales (Fig. 33). These dark pigmented scales protect the gametophyte in the desiccated state from solar radiation (Belnap 2001). Bryophytes of semi-arid to arid environments can be perennial or annual, and mosses of these environments are usually acrocarpous mosses (Richardson 1981; Scott 1982).



Figure 33. Twisted form of desiccated moss (1) and rolled up thallus of desiccated liverwort (2) from the PVP. Note: original material collected by the author of this thesis.

Dominant moss families in semi-arid and arid environments as well as in BSC worldwide are Pottiaceae, Bryaceae, Funariaceae, Dittriciaceae, and Gigaspermaceae

(Rosentreter and Belnap 2001). For liverworts, the dominant family is Ricciaceae (Rosentreter and Belnap 2001). Research has shown 62 moss and liverwort genera are found to occur within BSC worldwide (Budel 2001b). Typical moss genera of BSC worldwide are *Bryum*, *Crossidium*, *Didymodon*, and *Tortula*, while for liverworts it is the genus *Riccia* (Budel 2001d). BSCs, especially late-successional BSCs, are habitat for numerous bryophyte species of semi-arid and arid environments (Nash et al. 1977; Richardson 1981; Scott 1982; Downing and Selkirk 1993; Martinez-Sanchez et al. 1994; Eldridge and Tozer 1997; Rosentreter and Belnap 2001; Belnap 2003; Ingerpuu et al. 2005; Martinez et al. 2006; Sagar and Wilson 2009; Ochoa-Hueso et al. 2011). However, research on bryophytes of BSC is still limited (Budel 2001d).

Much is known about the taxonomy, ecology, and geography of vascular plants of California but the bryoflora, especially regarding ecology and biogeography, is still largely unknown (Koch 1954; Thiers and Emory 1992; Shevock 2015). Preliminary work has shown that California contains a high diversity of bryophytes (Koch and Ikenberry 1949; Koch 1954; Koch and Ikenberry 1954; Harthill et al. 1979; Stark and Whittemore 1992; Thiers and Emory 1992). However, much of this preliminary work has been focused on bryophytes from northern California. However, southern California has received some attention regarding its bryoflora (Koch 1954; Harthill et al. 1979; Stark and Whittemore 1992; Thiers and Emory 1992; Sagar and Wilson 2007; Sagar and Wilson 2009; Carter 2015). Recently, work in southern California on bryophytes has focused around the Santa Monica Mountains, Channel Islands, Orange County, and

Riverside County (Sagar and Wilson 2007; Sagar and Wilson 2009; Hernandez and Sandquist 2011; Hernandez and Knudsen 2012; Carter 2015).

Research has shown that bryophytes in North America are commonly associated with BSC (Rosentreter and Belnap 2001). However, research on bryophytes of BSC in California and especially in southern California is limited (Rosentreter and Belnap 2001; Hernandez and Sandquist 2011; Hernandez and Knudsen 2012). Work by Hernandez and Knudsen (2012) has provided preliminary information on what species of bryophytes are associated with BSC in Orange and Riverside Counties. North of Orange County, this information is lacking. BSC dominated by bryophytes are a common crust component of chaparral and CSS in southern California, more than in the inland deserts because of the strong maritime influence along the coast (Rosentreter and Belnap 2001).

Mosses were found to be abundant components of the BSC within the study sites and throughout the PVP (Fig. 34, 35). A list of species encountered in the BSC is provided in Table 4. No liverwort species were observed in the BSC during the course of this study. The moss flora of the BSC on the PVP was composed entirely of acrocarpous mosses. Of the 13 moss species found within the PVP BSC, six appeared to be restricted to it.

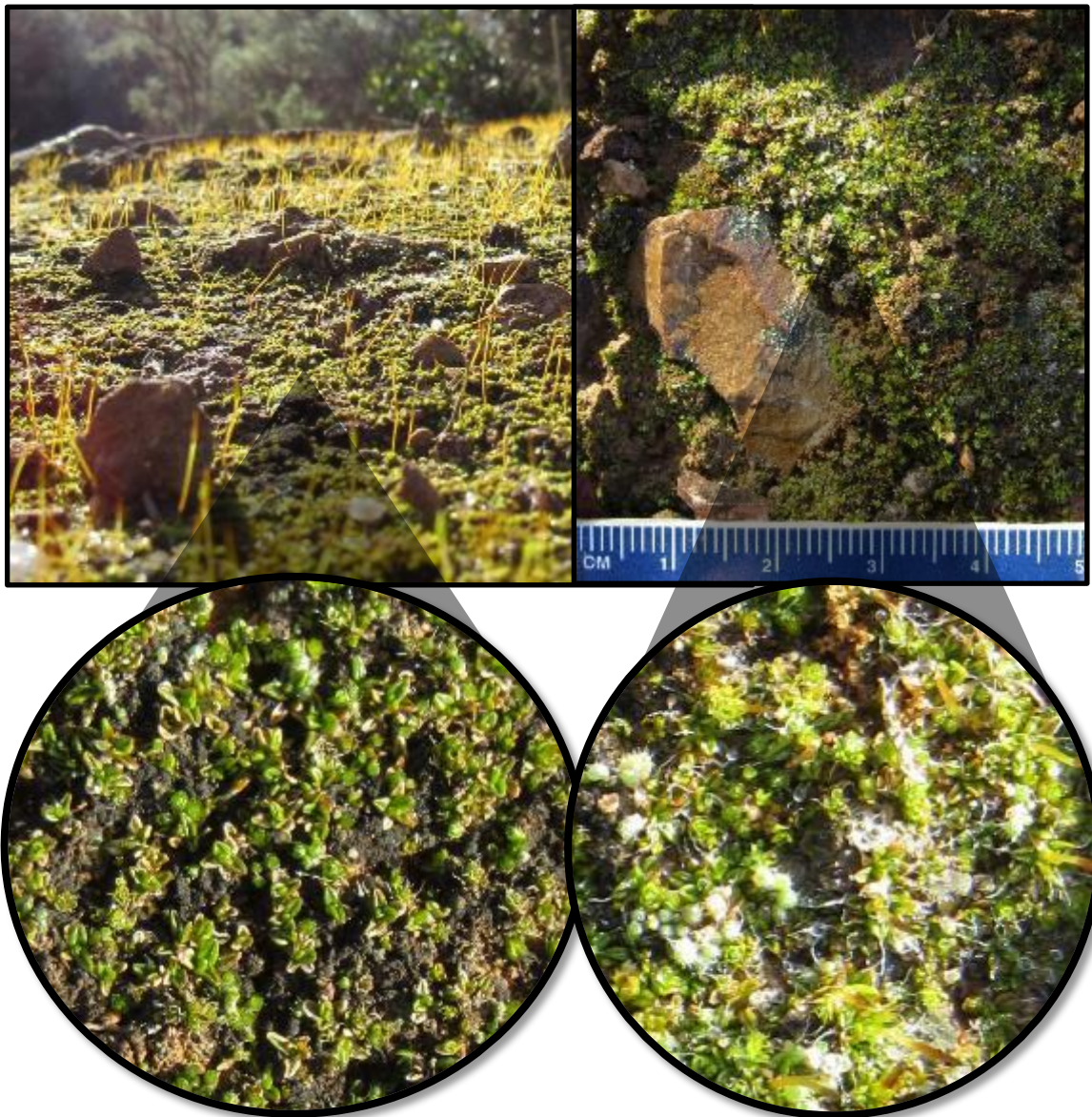


Figure 34. Moss component of BSC on the PVP. Note: original material collected by the author of this thesis.

The two dominant moss families encountered in the BSC of the PVP were Pottiaceae and Bryaceae. The most common species encountered in the BSC on the PVP were *Didymodon vinealis*, *Didymodon australiase*, *Tortula brevipes*, *Aloina aloides* var. *ambigua*, and *Bryum argenteum*.



Figure 35. Examples of mosses observed in BSC on the PVP. Note: original material collected by the author of this thesis.

Outside of the BSC, bryophytes were also found to be common on the PVP. The survey resulted in 66 species being found (Table 5). Of the three kinds of bryophytes (hornworts, liverworts, and mosses), only mosses and liverworts were found (Fig. 36). The survey was conducted during years where the peninsula received minimal rainfall (2014-2016), and this may explain the lack of hornworts. Bryophytes were found in scrubland, hillside mesic areas, canyons, streams, coastal bluffs, and sandy soil areas. Bryophytes were found on soil, sand, rock, brick, bark, and rotting hardwood (Fig. 37, 38). Bryophytes were most commonly encountered on soil and rock, and only a few were found growing on rotting hardwood (of various plant species), sand, or brick. The only vascular plant that was found to have bryophytes growing on its trunk and branches was old growth *Sambucus nigra* subsp. *caerulea* (Blue Elderberry) (Fig. 39). The bryoflora of the PVP is predominantly composed of mosses with most of the moss species being acrocarpous. Only a few pleurocarpous moss species were found. The moss families Pottiaceae, Bryaceae, and Brachytheciaceae were the dominant moss families on the PVP

(Fig. 40). These three families contained numerous species from different genera (Table 5). The most commonly encountered genera on the PVP were *Didymodon*, *Tortula*, *Bryum*, *Gemmabryum*, *Rosulabryum*, *Fissidens*, *Homaltheicum*, and *Scleropodium*. Both thallose and leafy liverworts were found. Thallose liverworts appeared to be more common than leafy liverworts and were found growing on soil. Leafy liverworts were very uncommon and were found growing in cracks of rock and on bark (Fig 41). The PVP bryoflora shares similarities in species composition with the Santa Monica Mountains (Sagar & Wilson 2007) and the Channel Islands (Carter 2015).



Figure 36. Examples of bryophytes on the PVP. Note: original material collected by the author of this thesis.

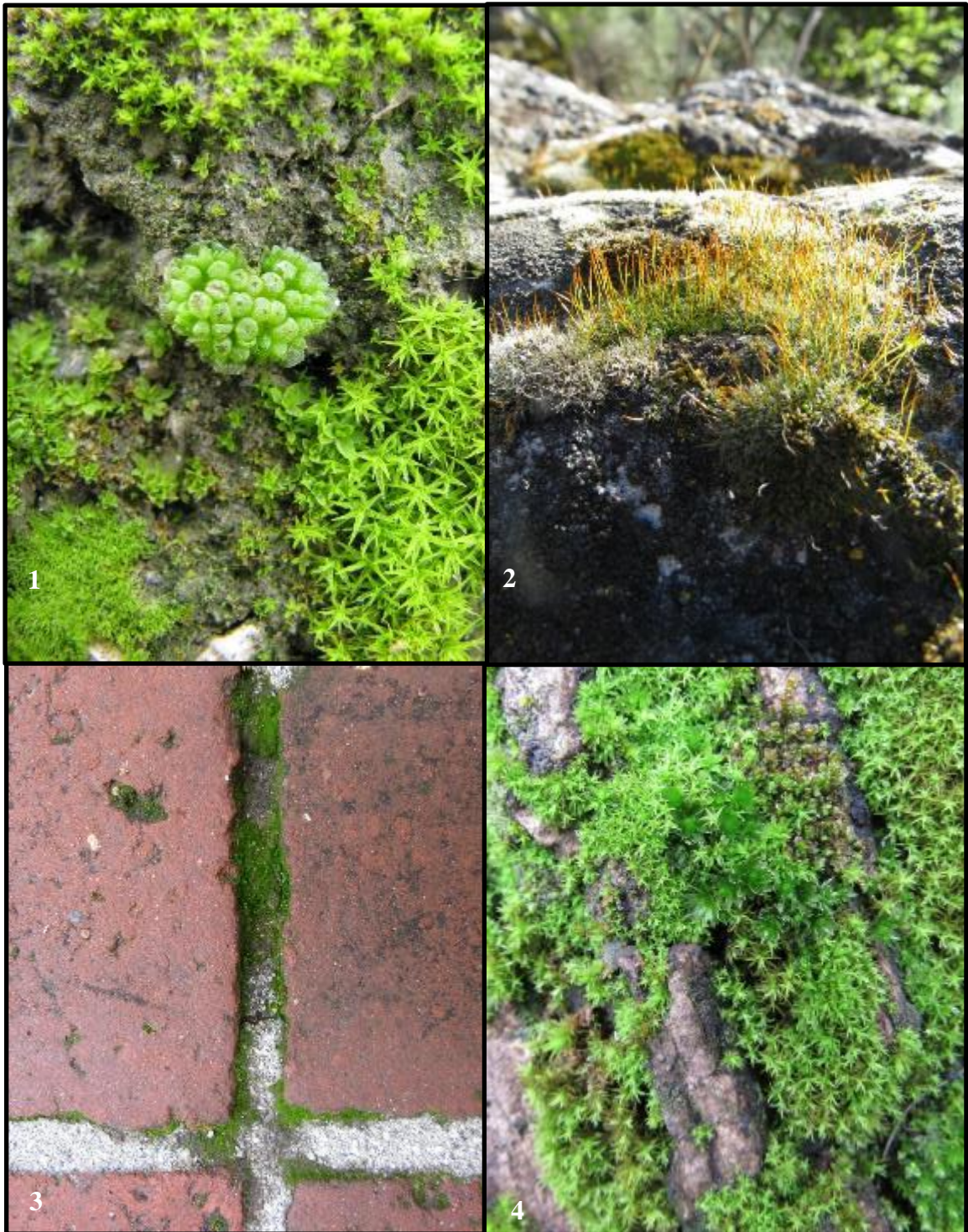


Figure 37. Substrates that bryophytes are found growing on throughout the PVP: soil (1), rock (2), brick (3), and bark (4). Note: original material collected by the author of this thesis.



Figure 38. Sandy soils on the PVP also contain bryophytes: Malaga Dunes (1), Defense Fuel Supply Point (2). Note: original material collected by the author of this thesis.



Figure 39. Bryophytes growing on bark of old growth *Sambucus nigra subsp. caerulea*.
Note: original material collected by the author of this thesis.



Figure 40. Pottiaceae (1); Bryaceae (2); Brachytheciaceae (3). Note: original material collected by the author of this thesis.



Figure 41. Thallose liverworts found growing on soil (1) and leafy liverworts found growing in cracks of rock (2) and on bark (3). Note: original material collected by the author of this thesis.

Non-native Plants and PVP BSC

Only one non-native plant, *Melilotus indicus*, was observed growing in the BSC of the study sites. Throughout the PVP, the BSC appeared to have very few non-native plants present within in it (Fig. 42). Disturbed BSC often contained non-native plants, but at a low density. Another observation was that cracks could sometimes form in the BSC when it was fully dry (Fig. 43). These cracks would occasionally contain non-native vascular plants growing out of them. In addition, non-native grass spikelets and florets were observed on top of the BSC in locations throughout the PVP. However, the florets of these non-native grasses spikelets never appeared to germinate (Fig. 44). It would be interesting to conduct further research to test whether the dark color of the BSC could be increasing soil surface temperatures to a high enough degree, during the summer months, to result in mortality of the grass florets.

Hernandez and Sandquist's (2011) study found that intact late-successional rugose BSC of CSS in Orange County can inhibit the establishment of certain non-native plants. From the survey of BSC on the PVP, it appears that the BSC is acting like a barrier and preventing the establishment of non-natives in areas where it occurs. Further research looking at the potential of BSC to inhibit the establishment of non-native plants on the PVP is needed.



Figure 42. BSC of PVP with minimal non-native plants present in the intact portions of it. Note: original material collected by the author of this thesis.



Figure 43. Cracks that can form in dry BSC of the PVP (white arrow). Note: original material collected by the author of this thesis.



Figure 44. Grass (*Bromus sp.*) florets found within the BSC on the PVP. Note: original material collected by the author of this thesis.

Native Vascular Plant Seedlings and PVP BSC

BSCs have been shown to facilitate or hinder the establishment of vascular native plant species (Belnap et al 2001b; Serpe et al. 2006; Su et al. 2007). BSC in the study sites and throughout the PVP was observed with seedlings of *Artemisia californica*, *Salvia mellifera*, and *Stipa lepida* present within it (Fig. 45). However, the seedlings were few and greatly spaced out. Interestingly, these particular vascular native plant species have minute seeds (*S. mellifera*, *A. californica*) or a mechanism for drilling into the soil (*S. lepida*). Further research looking at how BSC could influence the establishment of PVP native plants should be explored.



Figure 45. *Salvia mellifera* (1), *A. californica* (2), and *S. lepida* (3) seedlings found in BSC of the PVP. Note: original material collected by the author of this thesis.

Future Studies

Since this study is the first to look at BSC on the PVP, it provides information and questions that will ideally spark interest in the research, conservation, restoration, monitoring, and long-term study of this biologically diverse and critical component of the PVP wildlands. Listed below are some additional future research avenues to explore.

Algae

Research on BSC has shown that it contains a large diversity of both single-celled and filamentous algae (Flechtner et al. 1998; Hawkes and Flechtner 2002; Smith et al. 2004; Flechtner et al. 2008; Wu et al. 2011). Information on algae associated with BSC in CSS and on the PVP is lacking. During the course of this study, free-living algae on the

soil surface in mesic areas of the PVP were observed. One alga was determined to be of the genus *Vaucheria* (Fig. 46). The PVP probably contains a diverse composition of algae within its soils, waterways, and BSC. Further research is needed on the algae of the PVP as well as on the composition of algae within its BSC.

BSCs of the Channel Islands and Baja California have been shown to contain a large diatom diversity, with 10 and eight species of diatoms, respectively (Flehtner et al. 1998; Flehtner et al. 2008). In this study, one diatom was observed while preparing a moss leaf mount from a BSC sample from study site 1. Further research is needed on diatom composition of BSC on the PVP.

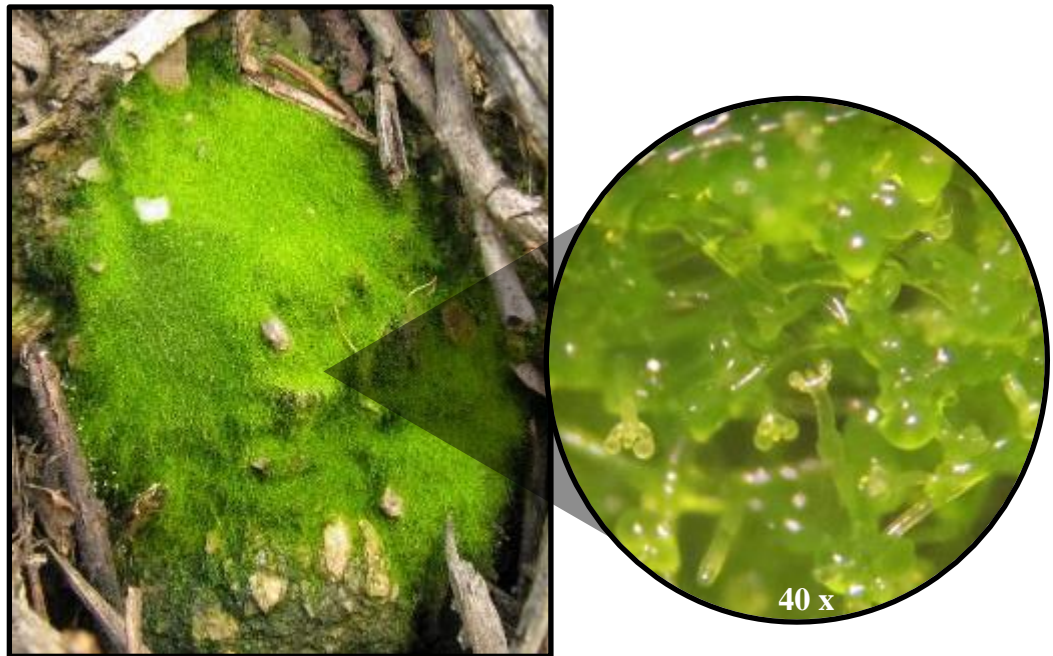


Figure 46. *Vaucheria sp.* growing on clay soil of the PVP. Note: original material collected by the author of this thesis.

Mircoarthropods

BSC contains a large diversity of microarthropods (Belnap 2001c; Neher et al. 2009). The microarthropod component of BSC in CSS and on the PVP has not been examined. Two microarthropods were observed from BSC samples from the Forrestal Nature Reserve, mites and a psuedoscorpion (Fig. 47). Further research is needed looking at the microarthropod composition of BSC on the PVP.



Figure 47. Mite (1) and psuedoscorpion (2) observed in BSC samples. Note: original material collected by the author of this thesis.

Microfungi

Fungi play a large role in the formation of BSCs worldwide; however, their composition and functional roles in BSC are still largely unstudied (States et al. 2001). BSC contains a diverse assemblage of fungi and these fungi have many functional roles

(States and Christensen 2001; States et al. 2001; Hawkes 2003; Bates et al. 2012). There has been no research on the fungal component of BSC in CSS or on the PVP as a whole, and this would be a good topic for future research.

BSC in Select Preserves

BSC occurs on many soil types (Belnap et al. 2001a). On sand, BSC is primarily composed of algae, mosses, cyanobacteria and diatoms (Belnap et al. 2001a.; Hawkes and Flechtner 2002; Smith et al. 2004; Wu et al. 2011). During the winter of 2016, what appeared to be an early stage of BSC comprising mosses, cyanobacteria, and possibly an alga was observed on sandy soil in the spaces between shrubs in the Linden H. Chandler Nature Preserve restoration areas (Fig. 48).

During a visit to the Defense Fuel Supply Point (DFSP) in San Pedro, BSC was observed on the sandy soils (Fig. 49). Another interesting observation made was in an area adjacent to the PVPLC nursery. A large portion of this site has an extensive covering of BSC, and where the BSC is present, a large amount of *Acmispon glaber* var. *glaber* is present. It appears that there may be greater recruitment of *Acmispon glaber* var. *glaber* in the areas where the BSC occurs and a minimal amount in adjacent areas. The BSC of the sandy soil of Linden H. Chandler Nature Preserve and the DFSP should be explored further.

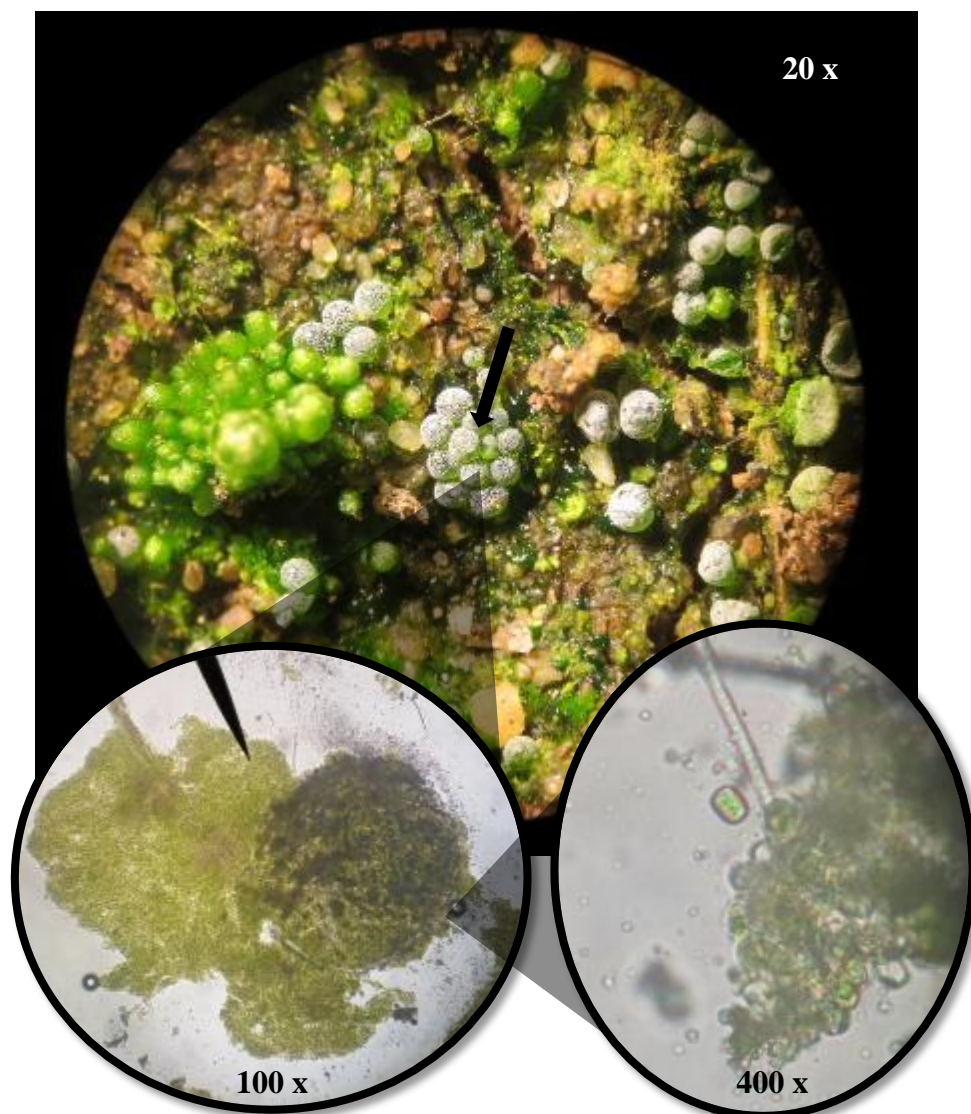


Figure 48. Linden H. Chandler Preserve – Early stage BSC on sand with a possible algae (black arrow). Note: original material collected by the author of this thesis.

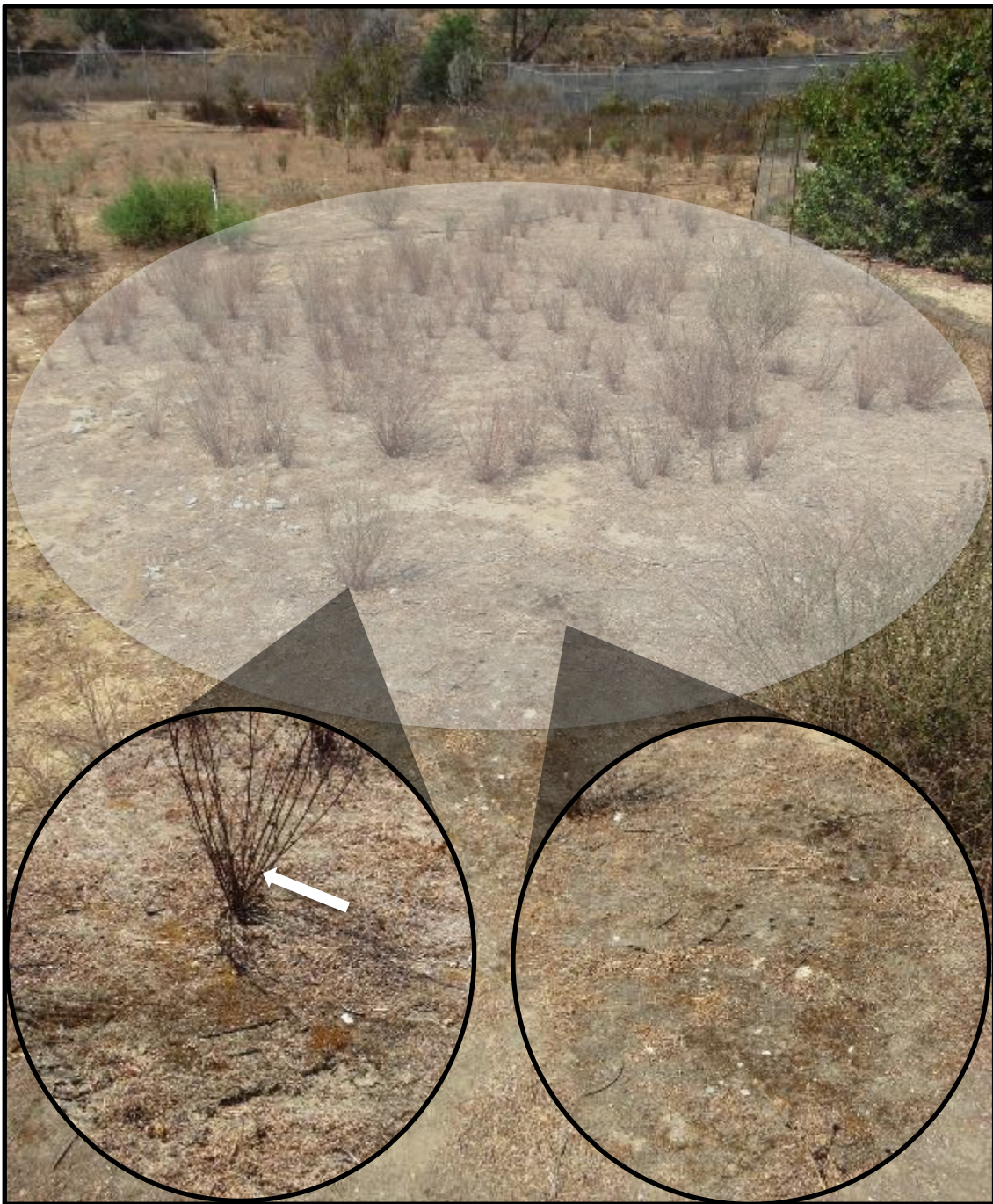


Figure 49. Palos Verdes Blue Butterfly area adjacent to PVPLC nursery within the DFSP. Area within it that contains large covering of BSC (red circle) with a large amount of *Acmispon glaber* var. *glaber* (white arrow) within. Note: original material collected by the author of this thesis.

Catalina Island and Venturan Sage Scrub BSC Comparison

Since the PVP was once a Channel Island and shares many similarities (flora and geology) with Catalina Island, a comparison of BSC between the PVP and Catalina Island in regards to its community composition and distribution would be interesting. During a visit to Catalina Island in the spring of 2016, large coverings of late-successional rugose BSC were observed throughout portions of its open spaces. The Catalina Island BSC appeared to contain a large moss and lichen diversity as well. In addition, since the PVP is believed to be closely associated with Venturan sage scrub (Westman 1981; Brylski et al. 1994) it would be interesting to compare the community composition of BSC on the PVP with BSC from other Venturan sage scrub locations.

Soil Chemistry

BSC cover and species composition has been shown to be influenced by soil chemistry in parts of North America and other parts of the world (Belnap et al. 2001b; Ochoa-Hueso et al. 2011). Soils that are composed of gypsum or soils that are calcareous have been shown to have a higher cover of BSC as well as a greater diversity of species within it (Belnap et al. 2001b; Ponzetti & McCune 2001). Detailed data on soil chemistry is lacking for the PVP, and further research on the soil chemistry of the PVP and how it might influence the cover of BSC should be explored.

Restoration

Biological soil crusts provide numerous ecosystem services and are important refugia for biodiversity (Belnap et al. 2001b). As a result, research on restoration of BSC

is increasing (Bowker 2007). Cultivation of BSC in greenhouse experiments is showing promising signs (Antoninka et al. 2015), as is establishment by way of slurry inoculants (Maestre et al. 2006). Since BSC appears to be a prevalent component of the wildlands of the PVP, restoration of BSC on the PVP should be explored.

REFERENCES

REFERENCES

- Allen CD. 2005. Micrometeorology of a smooth and rugose biological soil crust near Coon Bluff, Arizona. *Journal of the Arizona-Nevada Academy of Science*. 38(1):21-28.
- Anderson DC, Harper KTH, Rushforth SR. 1982. Recovery of cryptogamic soil crusts from grazing on Utah winter ranges. *Journal of Range Management*. 35(3):355-359.
- Antoninka A, Bowker MA, Reed SC, Doherty K. 2015. Production of greenhouse-grown biocrust mosses and associated cyanobacteria to rehabilitate dryland soil function. *Restoration Ecology*. 1-10.
- Baldwin BG, Goldman DH. 2012. *The Jepson manual: vascular plants of California*. Berkley and Los Angeles (CA): University of California Press 1568 p.
- Bates ST, Nash TH III, Garcia-Pichel F. 2012. Patterns of diversity for fungal assemblages of biological soil crusts from the southwestern United States. *Mycologia*. 104(2):353-361.
- Barger NN, Herrick JE, Zee JV, Belnap J. 2006. Impacts of biological soil crust disturbance and composition on C and N loss from water erosion. *Biogeochemistry*. 77(2):247-263.
- Beckett RP, Kranner I, Minibayeva FV. 2008. Stress physiology and the symbiosis. In: Nash TH III, editor. *Lichen Biology*. New York: Cambridge University Press. p. 315-335.

- Belnap J. 1992. Potential role of cryptobiotic soil crusts in semiarid rangelands. Paper presented at: Symposium on Ecology, Management, and Restoration of Intermountain Annual Rangelands; Boise, ID.
- Belnap J. 1993. Recovery rates of cryptobiotic crusts: inoculant use and assessment methods. *Great Basin Naturalist*. 53(1):89-95.
- Belnap J. 1994. Caynobacterial-lichen soil crusts of San Nicolas Island. Paper presented at: The Fourth California Islands Symposium: Update on the Status of Resources; Santa Barbara, CA.
- Belnap J. 1995. Surface disturbances: their role in accelerating desertification. *Environmental Monitoring and Assessment*. 37(1):39-57.
- Belnap J. 2001a. Biological soil crusts and wind erosion. In: Belnap J, Lange OL, Baldwin IT, Caldwell MM, Heldmaier G, Mooney HA, Schulze ED, Sommer U, editors. *Biological soil crust: structure, function, and management*. Berlin (DE): Springer-Verlag Press. p. 339-348.
- Belnap J. 2001b. Factors influencing nitrogen fixation and nitrogen release in biological soil crusts. In: Belnap J, Lange OL, Baldwin IT, Caldwell MM, Heldmaier G, Mooney HA, Schulze ED, Sommer U, editors. *Biological soil crust: structure, function, and management*. Berlin (DE): Springer-Verlag Press. p. 241-262.
- Belnap J. 2001c. Microbes and Microfauna associated with biological soil crusts. In: Belnap J, Lange OL, Baldwin IT, Caldwell MM, Heldmaier G, Mooney HA, Schulze ED, Sommer U, editors. *Biological soil crust: structure, function, and management*. Berlin (DE): Springer-Verlag Press. p. 167-176.

- Belnap J. 2003. The world at your feet: desert biological soil crusts. *Frontiers in Ecology and the Environment*. 1(4):181-189.
- Belnap J, Budel B, Lange OL. 2001a. Biological soil crusts: characteristics and distribution. In: Belnap J, Lange OL, Baldwin IT, Caldwell MM, Heldmaier G, Mooney HA, Schulze ED, Sommer U, editors. *Biological soil crust: structure, function, and management*. Berlin (DE): Springer-Verlag Press. p. 3-50.
- Belnap J, Rosentreter R, Leonard S, Kaltenecker JH, Williams J, Eldridge D. 2001b. *Biological soil crusts: ecology and management*. U.S. Department of the Interior Bureau of Land Management. p. 1-84.
- Belnap J, Eldridge DJ. 2001. Disturbance and recovery of biological soil crusts. In: Belnap J, Lange OL, Baldwin IT, Caldwell MM, Heldmaier G, Mooney HA, Schulze ED, Sommer U, editors. *Biological soil crust: structure, function, and management*. Berlin (DE): Springer-Verlag Press. p. 363-384.
- Belnap J, Phillips SL, Witwicki DL, Miller ME. 2008. Visually assessing the level of development and soil surface stability of cyanobacterially dominated biological soil crusts. *Journal of Arid Environments*. 72:1257-1264.
- Berg, MP. 2012. Patterns of biodiversity at fine and small spatial scales. In: Wall DH, Bardgett RD, Behan-Pelletier V, Herrick JE, Jones TH, Ritz K, Six J, Strong DR, Putten WH, editors. *Soil ecology and ecosystem services*. Oxford (UK): Oxford University Press. p. 136-152.

- Beymer RJ, Klopatek JM. 1992. Effects of grazing on cryptogamic crusts in pinyon-juniper woodlands in Grand Canyon National Park. *The American Midland Naturalist*. 127(1):139-148.
- Bowker MA, Belnap J, Davidson DW, Phillips SL. 2005. Evidence for micronutrient limitation of biological soil crusts: importance to arid-lands restoration. *Ecological Applications*. 15(6):1941-1951.
- Bowker MA. 2007. Biological soil crust rehabilitation in theory and practice: an underexploited opportunity. *Restoration Ecology*. 15(1):13-23.
- Brylski P, Brinkmann-Busi A, Atwood J, Mattoni R. 1994. Biological assessment Rancho Palos Verdes redevelopment area [Internet]. Rancho Palos Verdes (CA): City of Rancho Palos Verdes Planning Department; [cited 2016 May 5]. Available from <http://www.palosverdes.com/rpv/planning/pointvieweir/issues/Appendix%20C-1.pdf>
- Buck WR, Goffinet B. 2008. Morphology and classification of mosses. In: Shaw AJ, Goffinet B, editors. *Bryophyte Biology*. New York (NY): Cambridge University Press. p. 71-123.
- Budel B. 2001a. Biological soil crusts of South America. In: Belnap J, Lange OL, Baldwin IT, Caldwell MM, Heldmaier G, Mooney HA, Schulze ED, Sommer U, editors. *Biological soil crust: structure, function, and management*. Berlin (DE): Springer-Verlag Press. p. 51-56.
- Budel B. 2001b. Biological soil crusts of European temperate and Mediterranean regions. In: Belnap J, Lange OL, Baldwin IT, Caldwell MM, Heldmaier G, Mooney HA,

- Schulze ED, Sommer U, editors. Biological soil crust: structure, function, and management. Berlin (DE): Springer-Verlag Press. p. 75-86.
- Budel B. 2001c. Biological soil crusts of Asia including the Don and Volga region. In: Belnap J, Lange OL, Baldwin IT, Caldwell MM, Heldmaier G, Mooney HA, Schulze ED, Sommer U, editors. Biological soil crust: structure, function, and management. Berlin (DE): Springer-Verlag Press. p. 87-94.
- Budel B. 2001d. Synopsis: comparative biogeography and ecology of soil-crust biota. In: Belnap J, Lange OL, Baldwin IT, Caldwell MM, Heldmaier G, Mooney HA, Schulze ED, Sommer U, editors. Biological soil crust: structure, function, and management. Berlin (DE): Springer-Verlag Press. p. 141-154.
- Carter BE. 2015. A checklist of the bryophytes of the California Channel Islands. *Madrono*. 62(4):186-186-207.
- Chamizo S, Canton Y, Lazaro R, Sole-Benet A, Domingo F. 2012. Crust Composition and disturbance drive infiltration through biological soil crusts in semiarid ecosystems. *Ecosystems*. 15(1):148-161.
- Cheng Q, Ma W, Cai Q. 2008. The relative importance of soil crust and slope angle in runoff and soil loss: a case study in the hilly areas of the Loess Plateau, North China. *GeoJournal*. 71(2-3):117-125.
- Concostrina-Zubiri L, Martinez I, Rabasa SG, Escudero A. 2014. The influence of environmental factors on biological soil crust: from a community perspective to a species level approach. *Journal of Vegetation Science*. 25(2):503-513.

- Davis FW, Stine PA, Stoms DM. 1994. Distribution and conservation status of coastal sage scrub in southwestern California. *Journal of Vegetation Science*. 5(5):743-756.
- Downing AJ, Selkirk PM. 1993. Bryophytes on the calcareous soils of Mungo National Park, an arid area of southern central Australia. *Great Basin Naturalist*. 53(1):13-23.
- Doran JW, Zeiss MR. 2000. Soil health and sustainability managing the biotic component of soil quality. *Applied soil ecology*. 15(1):3-11.
- Dibblee TW. 2000. Geologic History Outline of the Palos Verdes Hills, California. In: Brown AR, Ehlert KW, editors. *A day in the field with Tom Dibblee in the Palos Verdes Hills, California*. Santa Barbara (CA): Thomas Wilson Dibblee, Jr. Geological Foundation. p. 16-17.
- Dibblee TW, Ehrenspeck HE. 2000. Geology of the Palos Verdes Hills, California. In: Brown AR, Ehlert KW, editors. *A day in the field with Tom Dibblee in the Palos Verdes Hills, California*. Santa Barbara (CA): Thomas Wilson Dibblee, Jr. Geological Foundation. p. 15.
- Ehlig PL. 1982. The Palos Verdes Peninsula: its physiography, land use and geologic setting. In: Brown AR, Ehlert KW, editors. *A day in the field with Tom Dibblee in the Palos Verdes Hills, California*. Santa Barbara (CA): Thomas Wilson Dibblee, Jr. Geological Foundation. p. 18-23.
- Eldridge DJ. 2001. Biological soil crusts of Australia. In: Belnap J, Lange OL, Baldwin IT, Caldwell MM, Heldmaier G, Mooney HA, Schulze ED, Sommer U, editors.

- Biological soil crust: structure, function, and management. Berlin (DE): Springer-Verlag Press. p. 119-132.
- Eldridge DJ, Greene RSB. 1994. Microbiotic soil crusts: a review of their roles in soil and ecological processes in the rangelands of Australia. *Soil Research*. 32(3):389-415.
- Eldridge DJ, Koen TB. 1998. Cover and floristics of microphytic soil crusts in relation to indices of landscape health. *Plant Ecology*. 137(1):101-114.
- Eldridge DJ, Tozer ME. 1996. Distribution and floristics of bryophytes in soil crusts in semi-arid and arid eastern Australia. *Australian Journal of Botany*. 44(2):223-247.
- Eldridge DJ, Tozer ME. 1997. Environmental factors relating to the distribution of terricolous bryophytes and lichens in semi-arid eastern Australia. *The Bryologist*. 100(1):28-39.
- Eldridge DJ, Rosentreter R. 1999. Morphological groups: a framework for monitoring microphytic crusts in arid landscapes. *Journal of Arid Environments*. 41(1):11-25.
- Evans RD, Lange OL. 2001. Biological soil crusts and ecosystem nitrogen and carbon dynamics. In: Belnap J, Lange OL, Baldwin IT, Caldwell MM, Heldmaier G, Mooney HA, Schulze ED, Sommer U, editors. *Biological soil crust: structure, function, and management*. Berlin (DE): Springer-Verlag Press. p. 263-280.
- Evans RD, Belnap J, Garcia-Pichel, Phillips SL. 2001. In: Belnap J, Lange OL, Baldwin IT, Caldwell MM, Heldmaier G, Mooney HA, Schulze ED, Sommer U, editors. *Biological soil crust: structure, function, and management*. Berlin (DE): Springer-Verlag Press. p. 417-430.

- Falchini L, Sparvoli E, Tomaselli L. 1996. Effect of *Nostoc* (cyanobacteria) inoculation on the structure and stability of clay soils. *Biology and Fertility of Soils*. 23(3):346-352.
- Flehtner VR, Johansen JR, Clark WH. 1998. Algal composition of microbiotic crusts from the central desert of Baja California, Mexico. *Great Basin Naturalist*. 58(4):295-311.
- Flehtner VR, Johansen JR, Belnap J. 2008. The biological soil crusts of the San Nicolas Island: enigmatic algae from a geographically isolated ecosystem. *Western North American Naturalist*. 68(4):405-436.
- Flowers S. 1973. *Mosses: Utah and the west*. Caldwell (NJ): The Blackburn Press 567 p.
- FNA (Flora of North America). Volumes 27 bryophytes: moss part 1. 2007. New York (NY): Oxford University Press 713 p.
- FNA (Flora of North America). Volumes 28 bryophytes: moss part 2. 2014. New York (NY): Oxford University Press 702 p.
- FNPMP (Forrestal Nature Preserve Management Plan), City of Rancho Palos Verdes. 2005. [Internet]. [Cited 10 May 2016.] Available from <http://www.rpvca.gov/documentcenter/view/5088>
- Gale DM. 1974. *Handbook of wildflowers, weeds, wildlife, and weather of the Palos Verdes Peninsula*. San Pedro (CA): Caligraphics Printing & Publishing. 214 p.
- Galloway D. 2008. Lichen biogeography. In: Nash TH III, editor. *Lichen Biology*. New York: Cambridge University Press. p. 315-335.

- Galun M, Garty J. 2001. Biological soil crusts of the Middle East. In: Belnap J, Lange OL, Baldwin IT, Caldwell MM, Heldmaier G, Mooney HA, Schulze ED, Sommer U, editors. Biological soil crust: structure, function, and management. Berlin (DE): Springer-Verlag Press. p. 95-106.
- Garcia-Pichel F, Belnap J. 2001. Small-scale environments and distribution of biological soil crusts. In: Belnap J, Lange OL, Baldwin IT, Caldwell MM, Heldmaier G, Mooney HA, Schulze ED, Sommer U, editors. Biological soil crust: structure, function, and management. Berlin (DE): Springer-Verlag Press. p. 193-202.
- Glime JM. 2015. Water relations: leaf strategies-structural [Internet]. Houghton (MI): Michigan Technological University; [cited 2016 Apr 27].
Available from <http://www.bryoecol.mtu.edu/>
- Gray JT, Schlesinger WH. 1981. Biomass, production and litterfall in the coastal sage scrub of southern California. *American Journal of Botany*. 68(1):24-33.
- Green TGA, Broady PA. 2001. Biological soil crusts of Antarctica. In: Belnap J, Lange OL, Baldwin IT, Caldwell MM, Heldmaier G, Mooney HA, Schulze ED, Sommer U, editors. Biological soil crust: structure, function, and management. Berlin (DE): Springer-Verlag Press. p. 133-140.
- Hansen ES. 2001. Lichen-rich soil crusts of Arctic Greenland. In: Belnap J, Lange OL, Baldwin IT, Caldwell MM, Heldmaier G, Mooney HA, Schulze ED, Sommer U, editors. Biological soil crust: structure, function, and management. Berlin (DE): Springer-Verlag Press. p. 57-66.

- Harthill MP, Long DM, Mishler BD. 1979. Preliminary list of southern California mosses. *The Bryologist*. 82(2): 260-267.
- Hasse H. 1913. The lichen flora of southern California. *Contributions from the United States National Herbarium*. 17(1):1-132.
- Hawkes CV. 2003. Nitrogen cycling mediated by biological soil crusts and arbuscular mycorrhizal fungi. *Ecology*. 84(6):1553-1562.
- Hawkes CV, Flechtner VR. 2002. Biological soil crusts in a xeric Florida shrubland: composition, abundance, and spatial heterogeneity of crusts with different disturbance histories. *Microbial Ecology*. 43(1):1-12.
- Hernandez RR, Sandquist DR. 2011. Disturbance of biological soil crust increases emergence of exotic vascular plants in California sage scrub. *Plant Ecology*. 212(10):1709-1721.
- Hernandez RR, Knudsen K. 2012. Late-successional biological soil crusts in a biodiversity hotspot: an example of congruency in species richness. *Biodiversity and Conservation*. 21(4):1015-1031.
- Hilty JH, Eldridge DJ, Rosentreter R, Wicklow-Howard MC, Pellant M. 2004. Recovery of biological soil crusts following wildfire in Idaho. *Journal of Range Management*. 57(1):89-96.
- Hollinger J. 2012. Survey of the lichen flora of Palos Verdes, southern California. *Bulletin of the California Lichen Society*. 19(2):71-84.
- Ingerpuu N, Liira J, Partel M. 2005. Vascular plants facilitated bryophytes in a grassland experiment. *Plant Ecology*. 180(1):69-75.

- Jagerbrand AK, Alatalo JM. 2015. Effects of human trampling on abundance and diversity of vascular plants, bryophytes and lichens in alpine heath vegetation, Northern Sweden. *SpringerPlus*. 4(1):95.
- Johansen JR. 2001. Impacts of fire on biological soil crusts. In: Belnap J, Lange OL, Baldwin IT, Caldwell MM, Heldmaier G, Mooney HA, Schulze ED, Sommer U, editors. *Biological soil crust: structure, function, and management*. Berlin (DE): Springer-Verlag Press. p. 385-400.
- Kauffman E. 2003. *Climate and topography: atlas of the biodiversity of California* [Internet]. CA: California Department of Fish and Wildlife; [cited 2016 May 10]. Available from <https://nrm.dfg.ca.gov/FileHandler.ashx?DocumentID=116547>
- Knudsen K. 2005. Lichens of the Santa Monica Mountains, part one. *Opuscula Philolichenum*. 2:27-36.
- Knudsen K. 2010. *Acarospora orcuttii* (Acarosporaceae), a rare terricolous lichen from southern California. *The Bryologist*. 113(4):713-716.
- Knudsen K, Harding M, Hoines J. 2013. The lichen flora of Joshua Tree National Park: An annotated checklist [Internet]. Fort Collins (CO): U.S. Department of the Interior National Park Service; [cited 2016 May 5]. Available from https://www.nps.gov/jotr/learn/nature/upload/lichen_report.pdf
- Koch LF. 1954. Distribution of California mosses. *The American Midland Naturalist*. 51(2):515-538.
- Koch LF, Ikenberry GJ. 1949. Preliminary studies of California mosses. I. The *Bryologist*. 52(2):84-89.

- Koch LF, Ikenberry GJ. 1954. Preliminary studies of California mosses. II. The Bryologist. 57(4):291-300.
- Lesica P, Shelly JS. 1992. Effects of cryptogamic soil crust on the population dynamics of *Arabis fecunda* (Brassicaceae).
- Li P, Harding SE, Liu Z. 2001. Cyanobacterial exopolysaccharides: their nature and potential biotechnological applications. Biotechnology and Genetic Engineering Reviews. 18(1):375-404.
- Lipman A, Longcore TR, Mattoni R, Zhang Y. 1999. Habitat evaluation and reintroduction planning for the endangered Palos Verdes blue butterfly [Internet]. Los Angeles (CA): University of California, Los Angeles-Geography Department; [cited 2016 May 5]. Available from <http://www.urbanwildlands.org/Resources/pvb.pdf>
- Lipnicki, Ludwik I. 2015. The role of symbiosis in the transition of some eukaryotes from aquatic to terrestrial environments. Symbiosis. 65(2):39-53.
- Liu H, Han X, Li L, Huang J, Liu H, Li X. 2009. Grazing density effects on cover, species composition, and nitrogen fixation of biological soil crust in an inner Mongolia Steppe. Rangeland Ecology & Management. 62(4):321-327.
- Luttge U, Beck E, Bartels D. 2011. Plant desiccation tolerance. New York (NY). Springer-Verlag Berlin Heidelberg Press 386 p.
- Maestre FT, Martin N, Diez B, Lopez-Poma R, Santos F, Luque I, Cortina J. 2006. Watering, fertilization, and slurry inoculation promote recovery of biological crust function in degraded soils. Microbial Ecology. 52(3):365-377.

- Magney D, Knudsen K. 2006. Rare lichen habitats and rare lichen species of Ventura County, California. *Opuscula Philolichenum*. 3:49-52.
- Martinez-Sanchez JJ, Casares-Porcel M, Gutierrez-Carretero L, Ros RM, Hernandez-Bastida J, Cano MJ. 1994. A special habitat for bryophytes and lichens in the arid zones of Spain. *Lindbergia*. 19(2/3):116-121.
- Martinez I, Escudero A, Maestre FT, Cruz A de la, Guerrero C, Rubio A. 2006. Small-scale patterns of abundance of mosses and lichens forming biological soil crusts in two semi-arid gypsum environments. *Australian Journal of Botany*. 54(4):339-348.
- McIntyre DS. 1958. Permeability measurements of soil crusts formed by raindrop impact. *Soil Science*. 85(4):185-189.
- Munz P. 1974. A flora of southern California. Berkley and Los Angeles (CA): University of California Press 1086 p.
- Myers N, Mittermeier RA, Mittermeier CG, Da Fonseca GAB, Kent J. 2000. Biodiversity hotspots for conservation priorities. *Nature*. 403(6772):853-858.
- Nash TH III, White SL, Marsh JE. 1977. Lichen and moss distribution and biomass in hot desert ecosystems. *Bryologist*. 80(3):470-479.
- Nash TH III, Ryan BD, Gries C, Bungartz F. 2002. Lichen Flora of the Greater Sonoran Desert Region. Volume 1, 2, 3. Tempe (AZ): Lichens Unlimited 532 p.
- Neher DA, Lewins SA, Weicht TR, Darby BJ. 2009. Microarthropod communities associated with biological soil crusts in the Colorado Plateau and Chihuahuan deserts. *Journal of Arid Environments*. 73(6):672-677.

- Ochoa-Hueso R, Hernandez RR, Pueyo JJ, Manrique E. 2011. Spatial distribution and physiology of biological soil crusts from semi-arid central Spain are related to soil chemistry and shrub cover. *Soil Biology & Biochemistry*. 43(9):1894-1901.
- O'Neill KP. 2008. Role of bryophyte-dominated ecosystems in the global carbon budget. In: Shaw AJ, Goffinet B, editors. *Bryophyte Biology*. New York (NY): Cambridge University Press. p. 344-368.
- Ornduff R. 1974. *Introduction to California plant life*. Berkley and Los Angeles (CA): University of California Press 152 p.
- Peintinger M, Bergamini. 2006. Community structure and diversity of bryophytes and vascular plants in abandoned fen meadows. *Plant Ecology*. 185(1):1-17.
- Pietrasiak N, Johansen JR, LaDoux T, Graham RC. 2011. Comparison of disturbance impacts to and spatial distribution of biological soil crusts in the Little San Bernardino Mountains of Joshua Tree National Park, California. *Western North American Naturalist*. 74(4):539-552.
- Ponzetti JM, McCune BP. 2001. Biotic soil crusts of Oregon's shrub steppe: community composition in relation to soil chemistry, climate, and livestock activity. *The Bryologist*. 104(2):212-225.
- Proctor MCF, Oliver MJ, Wood AJ, Alpert P, Stark LR, Cleavitt NL, Mishler BD. 2007. Dessication-tolerance in bryophytes: a review. *The Bryologist*. 110(4):595-621.
- Proctor MCF. 2008. Physiological ecology. In: Shaw AJ, Goffinet B, editors. *Bryophyte Biology*. New York (NY): Cambridge University Press. p. 225-247.

- Raven PH. 2005. Bryophytes. In: Raven PH, Evert RF, Eichhorn SE, editors. Biology of plants. New York (NY): W.H. Freeman and Company. P. 345-367.
- Richardson DHS. 1981. The biology of mosses. New York (NY): John Wiley & Sons Inc. 220 p.
- Riordan EC, Rundel PW. 2009. Modelling the distribution of a threatened habitat: the California sage scrub. *Journal of Biogeography*. 36(11):2176-2188.
- Ritz K, Putten WH. 2012. The living soil and ecosystem services. In: Wall DH, Bardgett RD, Behan-Pelletier V, Herrick JE, Jones TH, Ritz K, Six J, Strong DR, Putten WH, editors. Soil ecology and ecosystem services. Oxford (UK): Oxford University Press. p. 5-60.
- Rosentreter R, Belnap J. 2001. Biological Soil Crusts of North America. In: Belnap J, Lange OL, Baldwin IT, Caldwell MM, Heldmaier G, Mooney HA, Schulze ED, Sommer U, editors. Biological soil crusts: structure, function, and management. Berlin (DE): Springer-Verlag Press. p. 31-50.
- Rosentreter R, Bowker M, Belnap J. 2007. A field guide to biological soil crusts of western U.S. drylands: common lichens and bryophytes [Internet]. Denver (CO): U.S. Government Printing Office; [cited 2016 May 5]. Available from http://sbsc.wr.usgs.gov/products/pdfs/Field_Guide_Book_25.pdf
- RPESBB (Recovery Plan for the El Segundo Blue Butterfly (*Euphilotes battoides allyni*)), USFWS. 1998. [Internet]. [Cited 5 May 2016.] Available from https://www.fws.gov/carlsbad/SpeciesStatusList/RP/19980928_RP_ESB.pdf

- Rundel PW, Gustafson R. 2005. Introduction to the plant life of southern California. Berkley and Los Angeles (CA): University of California Press 316 p.
- Sagar T, Wilson P. 2007. Bryophytes of the Santa Monica Mountains [Internet]. Northridge (CA): California State University Northridge; [cited 2016 Apr 27]. Available from <https://www.csun.edu/~hcbio028/pubs/Sagar&Wilson%20SMM.pdf>
- Sagar T, Wilson P. 2009. Niches of common bryophytes in a semi-arid landscape. The Bryologist. 112(1):30-41.
- Scott GAM. 1982. Desert Bryophytes. In: Smith, A.J.E, editor. Bryophyte Ecology: New York (NY): Chapman and Hall. p. 105-122.
- Seaward, MRD. 2008. Lichen biogeography. In: Nash TH III, editor. Lichen Biology. New York (NY): Cambridge University Press. p. 274-298.
- Serpe MD, Orm JM, Barkes T, Rosentreter R. 2006. Germination and seed water status of four grasses on moss-dominated biological soil crusts from arid lands. Plant Ecology. 185(1):163-178.
- Sharnoff S. 2014. A field guide to California Lichens. New Haven (CT): Yale University Press 405 p.
- Sharp AJ, Crum H, Eckel PM. 1994. The Moss Flora of Mexico. Bronx (NY): The New York Botanical Garden 591 p.
- Shevock JR. 2015. Introduction to contributions toward a bryoflora of California, part IV. Madrono. 62(4):185.
- Smith, AJE. 1982. Bryophyte Ecology. New York (NY): Chapman and Hall 511 p.

- Smith SM, Abed RMM, Garcia-Pichel F. 2004. Biological soil crusts of sand dunes in Cape Cod National Seashore, Massachusetts, USA. *Microbial Ecology*. 48(2):200-208.
- SQISC (Soil Quality Indicators Soil Crusts), USDA Natural Resources Conservation Service. 2008. [Internet]. [Cited 24 October 2016.] Available from http://www.nrcs.usda.gov/Internet/FSE_DOCUMENTS/nrcs142p2_053281.pdf
- Stark LR, Whittemore AT. 1992. Additions to the bryoflora of southern California. *The Bryologist*. 95(1):65-67.
- States JS, Christensen M, Kinter CL. 2001. Soil fungi as components of biological soil crusts. In: Belnap J, Lange OL, Baldwin IT, Caldwell MM, Heldmaier G, Mooney HA, Schulze ED, Sommer U, editors. *Biological soil crusts: structure, function, and management*. Berlin (DE): Springer-Verlag Press. p. 155-166.
- States JS, Christensen M. 2001. Fungi associated with biological soil crusts in desert grasslands of Utah and Wyoming. *Mycologia*. 93(3):432-439.
- Studlar SM. 1980. Trampling effects on bryophytes: trail surveys and experiments. *The Bryologist*. 83(3):301-313.
- Su Y, Li X, Cheng Y, Tan H, Jia R. 2007. Effects of biological soil crusts on emergence of desert vascular plants in North China. *Plant Ecology*. 191(1):11-19.
- Tan BC, Pocs T. 2008. Bryogeography and conservation of bryophytes. In: Shaw AJ, Goffinet B, editors. *Bryophyte Biology*. New York (NY): Cambridge University Press. p. 403-448.

- Thiers BM, Emory KSG. 1992. The history of bryology in California. *The Bryologist*. 95(1):68-78.
- Tucker S. 2012. Lichens of Sedgwick Natural Reserve, Santa Barbara County, California. *Bulletin of the California Lichen Society*. 19(2):94-97.
- Turetsky MR. 2003. The role of bryophytes in carbon and nitrogen cycling. *The Bryologist*. 106(3):395-409.
- Turk R, Gartner G. 2001. Biological soil crusts of the subalpine, alpine, and Nival areas in the Alps. In: Belnap J, Lange OL, Baldwin IT, Caldwell MM, Heldmaier G, Mooney HA, Schulze ED, Sommer U, editors. *Biological soil crust: structure, function, and management*. Berlin (DE): Springer-Verlag Press. p. 67-74.
- Ullman I, Budel B. 2001. Biological soil crusts of Africa. In: Belnap J, Lange OL, Baldwin IT, Caldwell MM, Heldmaier G, Mooney HA, Schulze ED, Sommer U, editors. *Biological soil crust: structure, function, and management*. Berlin (DE): Springer-Verlag Press. p. 107-118.
- Verdone L, Evens J. 2010. Vegetation mapping of the Rancho Palos Verdes NCCP preserve: vegetation map and classification report [Internet]. Rancho Palos Verdes (CA): California Native Plant Society; [cited 2016 May 5]. Available from <http://www.cnps.org/cnps/vegetation/pdf/rancho-palos-verdes-nccp.pdf>
- Warren SD. 2001a. Synopsis: influence of biological soil crusts on arid land hydrology and soil stability. In: Belnap J, Lange OL, Baldwin IT, Caldwell MM, Heldmaier G, Mooney HA, Schulze ED, Sommer U, editors. *Biological soil crust: structure, function, and management*. Berlin (DE): Springer-Verlag Press. p. 349-362.

- Warren SD. 2001b. Biological soil crusts and hydrology. In: Belnap J, Lange OL, Baldwin IT, Caldwell MM, Heldmaier G, Mooney HA, Schulze ED, Sommer U, editors. *Biological soil crust: structure, function, and management*. Berlin (DE): Springer-Verlag Press. p. 327-338.
- Westman WE. 1981. Factors influencing the distribution of species of Californian coastal sage scrub. *Ecology*. 62(2):439-455.
- West NE. 1990. Structure and function of microphytic soil crusts in wildland ecosystems of arid and semi-arid regions. *Advances in Ecological Research*. 20:179-223.
- Woodring WP, Bramlette MN, Kew WSW. 1946. *Geology and paleontology of Palos Verdes Hills, California* [Internet]. Washington D.C.: United States Department of the Interior; [cited 2016 May 10] Available from <http://pubs.usgs.gov/pp/0207/report.pdf>
- Wu L, Lan S, Zhang D, Hu Chunxiang. 2011. Small-scale vertical distribution of algae and structure of lichen soil crusts. *Microbial Ecology*. 62(3):715-724.
- Yan X, Bao W, Pang X. 2014. Indirect effects of hiking trails on the community structure and diversity of trunk epiphytic bryophytes in an old-growth fir forest. *Journal of Bryology*. 36(1):44-55.
- Yoshitake S, Uchida M, Koizumi H, Kanda H, Nakatsubo T. 2010. Production of biological soil crusts in the early stage of primary succession on a high Arctic glacier foreland. *The New Phytologist*. 186(2):451-460.

Zhao Y, Xu M, Belnap J. 2010. Potential nitrogen fixation activity of different aged biological soil crusts from rehabilitated grasslands of the hilly Loess Plateau, China. *Journal of Arid Environments*. 74(10):1186-1191.