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Biotic soil crust lichen diversity and conservation in shrub-steppe habitats of Oregon and Washington

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Abstract. Biological soil crusts are ecosystem engineers in arid and semi-arid habitats; they affect soil chemistry, stability, and vegetation. Their ecosystem functions may vary depending on species composition; however, lichen species diversity is poorly known in the Pacific Northwestern drylands of North America. We sampled 59 random and 20 intuitive plots throughout central and eastern Oregon identifying 99 lichen taxa, 33 of which occurred in only one plot and seven of which were new to Oregon (*Acarospora obpallens*, *A. terricola*, *Catapyrenium psoromoides, Placidium fingens, P. pilosellum, P. yoshimurae* and *Psora luridella*). We compile records from herbaria and other studies to evaluate the rarity of observed species and potentially rare species known from nearby locations. We conclude that 37 species are likely rare or uncommon in our study area. Many of these appear to be associated with calcareous substrates. We model occurrences in relation to climate and soil variables for four uncommon lichen species: *Acarospora schleicheri, Fuscopannaria cyanolepra, Rhizocarpon diploschistidina*, and *Texosporium sancti-jacobi.* Based on climate and soil variables, we map regions of Oregon that may support new populations of these species and overlay habitats unsuitable for biotic crusts due to development and agriculture. These species, except *Fuscopannaria cyanolepra*, are strongly associated with the fine soils along the Columbia and Treasure Valleys that are most intensively used for agriculture. We anticipate that our summaries will further the understanding of lichen component of biological soil crust communities in eastern Oregon and suggest focal species for future conservation efforts.

Keywords. *Acarospora*, biological soil crusts, climate models, *Fuscopannaria cyanolepra*, *Rhizocarpon diploschistidina*, sagebrush steppe, soil texture, *Texosporium.*

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The Columbia and Great Basins of central and eastern Oregon are home to rolling grasslands, juniper (*Juniperus occidentalis*) woodlands, and sagebrush (*Artemisia*) steppe. Among the vascular plants in these expansive rangelands, a textured carpet of colorful lichens, bryophytes, algae, bacteria and non-lichenized fungi stabilize the soil (Harper & Marble 1988; Leys & Eldridge 1998; Mazor et al. 1996). This soil surface community can be an important source of nitrogen and carbon in arid ecosystems (Belnap 2002; Beymer & Klopatek 1991; Rychert et al. 1979) and while also contributing plant-available micronutrients (Harper & Belnap 2001; Harper & Pentleton 1993). Biotic crusts can

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also structure and composition of vascular plant communities by favoring establishment of some native over invasive species (Belnap et al. 2001; Kaltenecker et al. 1999; Mitchell et al. 2006).

Sagebrush steppe vascular plant and biotic soil crust communities alike are imperiled by development, livestock grazing, changing fire regimes, and invasion by exotic grasses (USDA 1936; Noss et al. 1995; Pyke 1999; Ponzetti & McCune 2001; Ponzetti et al. 2007). Agricultural and developed lands managed for non-native vegetation have essentially no soil biotic soil crust lichen communities. In more wild areas, invasion by exotic grasses and mechanical soil disturbance caused by livestock trampling and human activities can substantially diminish biotic crust abundance (Belnap et al. 2001; Eldridge 1998; Ponzetti & McCune 2001). Because more than 90% of the native shrub-steppe in Oregon has been disturbed by grazing or other anthropogenic factors (Noss et al. 1995), some of these biotic crust species may be at risk.

Although subtle to the untrained eye, richly diverse soil lichen communities reflect patterns related to climate, vegetation, soil chemistry and texture (Root & McCune in press). Differences in species composition affect the degree to which biotic crust communities contribute to soil stability (Eldridge 1998) and nitrogen fixation (Beymer & Klopatek 1991). Soil crust organisms are not equally damaged by disturbance; in general, the more three-dimensional species seem to be most susceptible (Belnap et al. 2001) and lichens growing on sandier soils appear to be more easily disturbed.

Some studies have examined soil crust lichens in relatively small study areas (Link et al. 2000; Ponzetti & McCune 2001; Ponzetti et al. 2007; Miller et al. 2011), and one attempted to characterize biotic crust lichens throughout the Great Basin (St. Clair et al. 1993), but none have observed the diversity of soil lichens we report for central Oregon. Past efforts to explore biodiversity of soil crusts in the Columbia Basin have been limited compared to the variety and immensity of potential soil crust habitats in this area. Only two soil lichen species are listed by the Oregon Biodiversity Information Center (ORBIC 2010b); this reflects the scant information about soil crust communities in the dryland ecosystems typical of the Columbia Basin. The purpose of this study was to integrate our records from random and targeted surveys in Oregon with previous herbarium records from Oregon and Washington to: 1) Document species diversity in these habitats and report new species records; 2) Evaluate the relative frequencies of species to determine which species may be of conservation concern; and 3) Develop habitat models for species of interest, including *Acarospora schleicheri, Fuscopannaria cyanolepra, Rhizocarpon diploschistidina,* and *Texosporium sancti-jacobi* to map habitats that may support additional populations. For less common species that may be of concern, the paucity of records precludes statistical models; however, we report our field observations about habitat associations.

Methods

Study Area. To evaluate regional distributions, we focused on existing records from east of the Cascade crest in Oregon and Washington. Our new collections were limited to a smaller region including public lands (State of Oregon, USDA Forest Service and Bureau of Land Management) within the Bureau of Land Management's Prineville District in central Oregon. This study area included more than 667,700 ha scattered throughout central Oregon, from La Pine north to the Columbia River and from the high Cascades in the west to the town of John Day and the Harney County line.

Vascular plant communities within the study area include grasslands, sagebrush steppe, *Juniperus occidentalis, Quercus garryana* woodlands, and coniferous forests; however, we restricted our sampling to the non-forested ecoregions of the district. In our study plots, elevation, mean annual temperature and annual precipitation range from 170–1745 m, 6 to 12 °C and 22 to 45 cm/year, respectively (Daly et al. 2008). Soils vary from fine alluvial clays to volcanic sand and pumice.

Plot selection. We considered the nine non-forested, non-alpine USA-EPA Level IV Ecoregions (Clarke & Bryce 1997) to be potentially different biotic crust habitats. We selected sampling locations stratified by these ecoregions in two stages: In fall 2009, we planned to sample an equal number of sites in each ecoregion to best characterize the full range of diversity. In spring 2010, we focused on sampling ecoregions proportional to their abundance in the study area to characterize dominant patterns across the district. To optimize time spent searching for soil crust lichens, we restricted our sampling area to public lands within 3.22 km of a road known to be accessible by truck using ArcGIS v 9.3.1 (ESRI). Using Hawth's Tools (Beyer 2004), we selected randomly located plots within the constraints of the above criteria.

Public land parcels were often inaccessible because they required crossing private land, steep buttes, rivers, or impassible roads. When a plot was inaccessible, we proceeded down the list of selected potential plots to identify a replacement. In one ecoregion near Lonerock, Oregon, no pre-selected plots were accessible; we determined which parcels could be accessed and arbitrarily selected plots within them without reference to the biotic crust lichen community or vegetation. One plot was on land that was being cultivated for agricultural purposes; it contained no crust lichens and was excluded from analyses. In total, we visited 34 randomly selected plots in 2009 and 25 in 2010 (**Fig. 1**).

In addition to the randomly selected plots, we visited 20 target plots chosen because they had relatively pristine native vegetation, exposed caliche or were observed to contain crust lichens of potential concern (**Fig. 1**). In these target plots, we did not conduct full surveys of soil crust lichens but rather focused on collecting uncommon species to learn more about their habitats and distribution.

Field protocol. Lichen sampling was designed to characterize the lichen crust community by recording as many species as possible. Our protocol was modified from the Forest Health Monitoring Protocol (McCune et al. 1997) but adapted to terrestrial species rather than epiphytes. Plots were 34.7 m in radius and were searched for terricolous lichens for two hours or until no new species had been found for a half hour. Because soil crust lichens can be very small, the surveyor crawled on hands and knees with a hand lens or magnifying eyeglasses to improve detection of lichens. To focus more broadly on soil crust communities, we included lichens growing on cow pies and organic matter that was integrated into the soil matrix in our searches. We excluded, however, lichens growing on small pebbles, moss over rock or fallen twigs. Inclusion of lichen species on these substrates would have introduced saxicolous and epiphytic species.

Lab protocol. Species identifications were based primarily on McCune & Rosentreter (2007) along with reference to other pertinent taxonomic literature and specialists (noted in association with taxa in **Table 1**). We report primarily specimens that could be identified to species. Some collections were unidentifiable because they were sterile or in groups in need of further taxonomic study Again: were these included or not?. Thin layer chromatography (Culberson 1972) was necessary to identify some *Cladonia* and *Xanthoparmelia* species. Vouchers for all species are deposited at OSC. Lichen nomenclature follows Esslinger (2010) with a few exceptions noted in **Table 1;** vascular plants follow the USDA PLANTS database (NRCS 2011).

To determine which taxa required further investigation, we evaluated species frequencies in our random and target plots. For potentially uncommon or rare species in our dataset and those thought to be uncommon nearby, we assembled herbarium records to further evaluate species rarity and habitat associations. We tallied species records with unique geographic coordinates as occurrences; some were in very close proximity. Specimens with questionable identifications or without vouchers were excluded. Information regarding range and abundance of species was also assembled from the literature (McCune & Rosentreter 2007; Nash et al. 2002, 2004, 2008), herbarium records and authors' experiences. Herbarium records were from the Oregon State University Herbarium (OSC), the Consortium of North American Lichen Herbaria (2011), and the personal databases of Heather Root, Bruce McCune, Jeanne Ponzetti, Ann DeBolt, Rick Demmer, and Roger Rosentreter.

Analysis. We evaluated climate and soil habitat associations for *Acarospora schleicheri, Fuscopannaria cyanolepra, Texosporium sancti-jacobi* and *Rhizocarpon diploschistidina.* These species were selected because they were sufficiently common to provide well-supported statistical models but uncommon enough to be of potential conservation concern. We included records from our plots as well as those from herbaria with geographic coordinates

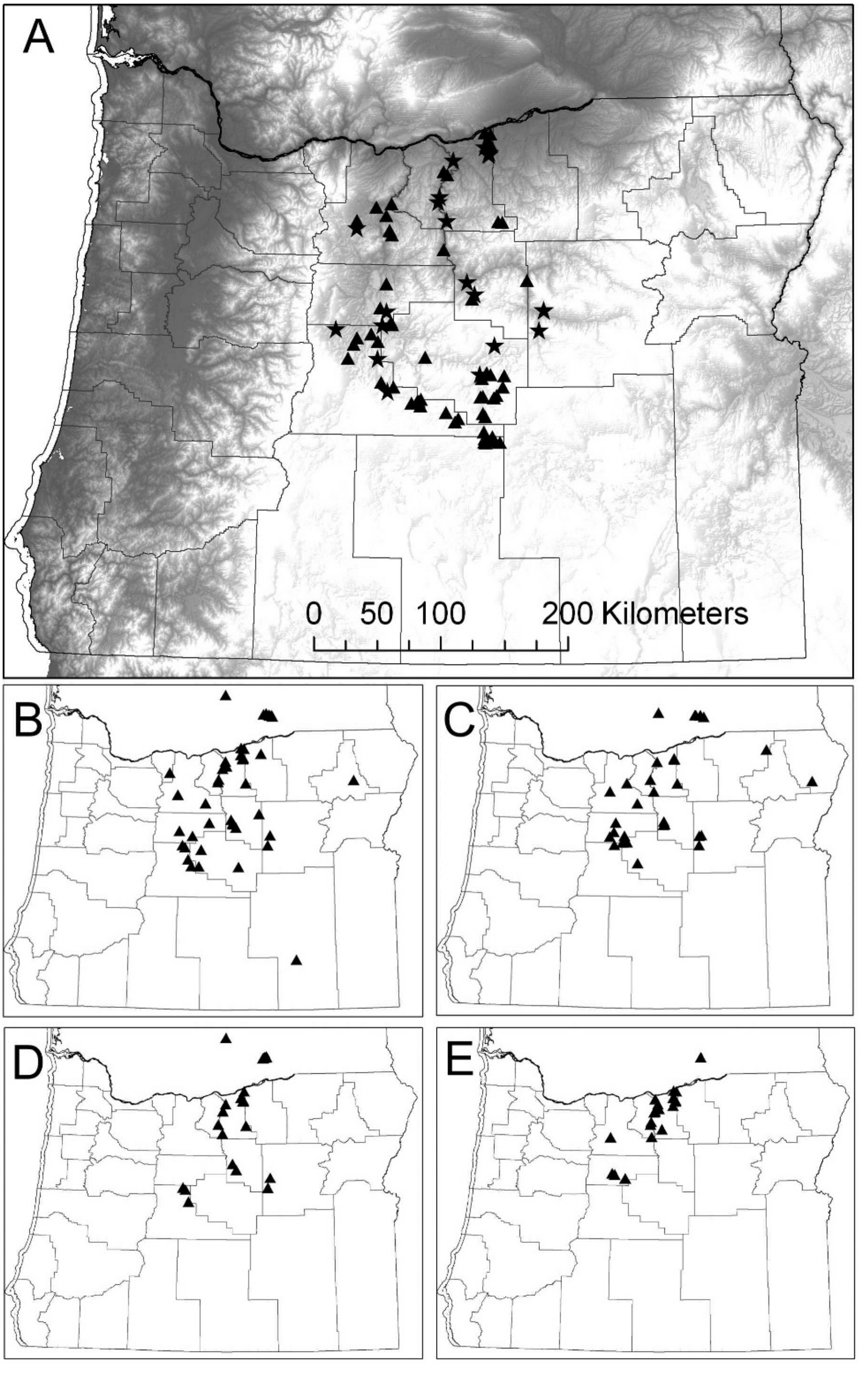

Figure 1. A. Study sites in Oregon, USA with county boundaries random; intuitive plots are symbolized with stars. Dark shading represents lower elevations. **B–E**: Occurrences of (**B**) *Acarospora schleicheri*, (**C**) *Fuscopannaria cyanolepra*, (**D**) *Rhizocarpon diploschistidina*, and (**E**) *Texosporium sancti-jacobi* known from our plots and herbarium records in steppe habitats of Oregon and Washington east of the Cascade crest.

Table 1. Biotic crust lichen species found in our samples from steppe in central Oregon or believed to be uncommon in similar habitats nearby. Number of records in 59 random (Rd) and 20 target (T) plots or in herbarium records from steppe habitats east of the Cascade crest in Oregon (OR) and Washington (WA); we do not report frequencies of common taxa in target plots or herbarium records (−). We scored species rarity (Sc) as common (C), poorly known (?), uncommon (U) or rare (R); for the latter three, we report ease of field identification as easy (E), moderate (M) or difficult (D) and note association with calcareous soils (*) and those endemic to western North America (+). Notes discuss other substrates, records, taxonomic issues, distribution in North America (NA) and rarity in nearby habitats. Collection numbers listed are for Heather Root (HTR), Bruce McCune (BM), Ann DeBolt (AD) or include full names where collectors have not assigned specimen numbers.

Lichen species	Rd	T	OR	WA	Sc	Notes
Acarospora obpallens	1	0	0	2	RM	Previously unknown from Oregon (HTR2474). U in southwest NA.
Acarospora schleicheri	5	15	14	8	UE	
Acarospora superfusa	0	0	1	0	?D	Collection by Rick Demmer; identified by Kerry Knudsen.
Acarospora terricola	1	0	0	3	?M	Previously unknown from OR (HTR2487). U in southwest NA.
Acarospora thamnina	1	-	-	-	C	C on rocks, U on soil
Acarospora nodulosa	0	0	0	0	RM*	U in western NA but not known from OR or WA.
Amandinea punctata	44	-	-	-	C	
Arthonia glebosa	41	-	-	-	C	
Aspicilia filiformis	24	-	-	-	C	
Aspicilia hispida	16	-	-	-	C	
Aspicilia cf. *mastrucata*	2	-	-	-	C	C on rock and moss, U on soil.
Aspicilia reptans	47	-	-	-	C	
Aspicilia rogeri	0	0	5	0	RE*	R in western NA; in OR only known east of study area. Follows Sohrabi et al. (2011).
Aspicilia spp.	14	-	-	-	?D	Includes several morphotypes of *Aspicilia*, possibly *Aspicilia desertorum* and *Aspicilia* cf. *aspera* (HTR2497, identified by Roger Rosentreter).
Bryonora pruinosa	0	0	1	0	RM	U in western NA; also U on alpine soil.
Buellia elegans	0	0	0	0	RE*	Unknown from OR, WA, but C further inland.
Buellia epigaea	3	3	2	0	UE	U but widespread in continental sites in western NA.
Caloplaca arenaria	1	-	-	-	?D	HTR2679 tentatively identified by Ulf Arup, however this species complex is being actively researched.
Caloplaca atroalba	1	-	-	-	C+	C and widespread on rock, U on soil.
Caloplaca jungermanii	5	-	-	-	C	C in western NA steppe, alpine.
Caloplaca stillicidiorum s. lat.	35	-	-	-	C	Species complex is being actively researched (Šoun et al. 2011).
Caloplaca tiroliensis	3	-	-	-	C	C on alpine moss, U on soil.
Caloplaca tominii	17	-	-	-	C	
Candelaria concolor	7	-	-	-	C	C on rock or bark, U on soil.
Candelariella aggregata	43	-	-	-	C	
Candelariella rosulans	4	-	-	-	C	C on rock and soil.
Candelariella vitellina	6	-	-	-	C	C on rock, wood, bark and soil.
Catapyrenium psoromoides	1	-	-	-	?D	Previously unknown from OR or WA. HTR2762 identified by Othmar Breuss. Usually on bark and organic debris further south.
Cladonia cariosa	7	-	-	-	C	Widespread temperate worldwide, but only occasional in steppe.
Cladonia fimbriata	27	-	-	-	C	

Table 1. Continued.

Lichen species	Rd	T	OR	WA	Sc	Notes
Cladonia imbricarica	5	1	7	1	RD	R in western NA; requires chromatography to identify.
Cladonia pulvinella	4	0	0	2	RD	R in OR, WA; requires chromatography to identify.
Cladonia pyxidata	3	-	-	-	C	C on organic substrates and in less arid sites.
Cladonia verruculosa	1	-	-	-	C	C on organic substrates and in less arid sites.
Collema coccophorum	2	-	-	-	?D	
Collema tenax	1	-	-	-	C	
Collema tenax group	24	-	-	-	C	
Dematocarpon cf. *bachmanii*	0	0	10	0	UE	Vagrant forms U; rock-dwelling form C.
Dermatocarpon reticulatum	0	0	1	0	UE	Vagrant forms U; rock-dwelling form C.
Diploschistes muscorum	33	-	-	-	C	
Endocarpon adsurgens	0	0	1	1	RM	U in arid WA and OR.
Endocarpon loscosii	3	0	0	3	UM	U WA south to Mexico.
Endocarpon pussillum	7	-	-	-	C	Also on rock, wood and bark.
Fulgensia bracteata	0	0	1	1	RE*	U on calcareous soil in western NA.
Fulgensia desertorum	0	0	0	0	RE*	Not known from OR or WA, but one specimen in nearby Idaho.
Fulgensia fulgens	0	0	0	0	RE*	Not known from OR or WA, but one specimen in nearby Idaho.
Fuscopannaria cyanolepra	5	12	11	7	UE+	U on soil in Pacific Northwest NA.
Gyalidea asteriscus	0	0	0	0	RM*	Dry calcareous sites in Alberta and British Columbia, Canada.
Gypsoplaca macrophylla	0	0	0	0	RM*	Rare on gypsum soils in southwest NA, Alaska, and British Columbia.
Heppia lutosa	1	2	1	0	RM	R in OR and WA but widespread further in southwest NA. HTR1696, 2566, 2567.
Heteroplacidium congestum	0	0	3	0	RD+	R in OR; also east of the continental divide and in southwest NA.
Involucropyrenium sp.	1	-	-	-	?D	Species unknown. HTR2604 identified by Othmar Breuss.
Lecanora crenulata	1	-	-	-	C	C on rock, U on soil.
Lecanora flowersiana	10	-	-	-	C	
Lecanora garovaglii	1	-	-	-	C	C on rock, U on soil.
Lecanora hagenii	12	-	-	-	C	
Lecanora laxa	1	-	-	-	C	C on bark, U on soil.
Lecanora muralis	4	-	-	-	C	C on rock, U on soil.
Lecanora phaedropthalma	1	-	-	-	C	C on rock, U on soil.
Lecanora sp. 4	24	-	-	-	C	Follows Sliwa & Wetmore (2000).
Lecanora zosterae	14	-	-	-	C	
Lecidea fuscoatra	1	-	-	-	C	C on rock, U on soil.
Lecidella stigmataea	1	-	-	-	C	C on rock, U on soil.
Lecidella wulfenii	1	-	-	-	C	C in alpine and on organic matter, U on steppe soils.
Lepraria caesioalba	14	-	-	-	C	C on rock or moss; determined by James Lendemer.
Lepraria eburnea	1	-	-	-	C	C on moist tree bases, but U in steppe habitats; HTR1784b determined by James Lendemer.
Leptochidium albociliatum	21	-	-	-	C	
Leptogium cf. *gelatinosum*	1	-	-	-	C	C in NA, but U in steppe habitats.

Table 1. Continued.

Lichen species	Rd	T	OR	WA	Sc	Notes
Leptogium intermedium	35	-	-	-	C	
Leptogium lichenoides s. lat.	2	-	-	-	C	C on rock, U on soil.
Leptogium palmatum	3	-	-	-	C	C in moister habitats, U on steppe soil.
Leptogium schraderi	0	0	0	0	?D*	R in NA, known from British Columbia and one specimen in southwest OR.
Leptogium sp. 1	29	-	-	-	C	C; follows McCune & Rosentreter (2007).
Leptogium turgidum	0	0	0	1	RD*	One calcareous site in WA.
Massalongia carnosa	12	-	-	-	C	Includes one specimen that may be *M. microphylliza* but is sterile.
Megaspora verrucosa	23	-			C	
Ochrolechia turneri	1	7	1	0	UM	Previously unknown from steppe but epiphytic in western WA and Europe (pers. comm. Tor Tønsberg, 2011).
Ochrolechia upsaliensis	1	-	-	-	C	Locally C in western NA.
Peltigera didactyla	19	-	-	-	C	
Peltigera kristinssonii	3	-	-	-	C	Widespread in western NA more C at higher elevations.
Peltigera ponojensis	12	-	-	-	C	
Peltigera rufescens	5	-	-	-	C	
Peltula patellata	0	0	0	0	RM*	Unknown from OR or WA; nearest known populations are in Montana.
Phaeorrhiza nimbosa	0	0	0	2	UM	U in western NA and on alpine soil.
Phaeorrhiza sareptana	23	-	-	-	C	
Physconia enteroxantha	4	-	-	-	C	C on bark or mosses over rock.
Placidium fingens	1	-	0	0	?D	Previously unknown from OR, WA; HTR2765 identified by Othmar Breuss. In western NA mostly epiphytic but also on soil in southwestern NA.
Placidium imbecillum	6	-	0	1	?D	
Placidium pilosellum	2	-	-	-	?D	Previously unknown from OR and WA, but known from calcareous sites in southwestern NA. HTR2764 identified by Othmar Breuss.
Placidium rufescens	1	-	-	-	?D	U but widespread in western NA.
Placidium squamulosum	3	-	-	-	?D	Widespread and C in western NA. HTR 2754, 2770 identified by Othmar Breuss.
Placidium yoshimurae	3	-	-	-	?D	Previously not reported in NA; widespread in Eurasia, following Bruess (2010). HTR2755, 2767 identified by Othmar Breuss.
Placynthiella icmalea	11	-	-	-	C	C on soil, bark, wood, and rock.
Placynthiella oligotropha	3	-	-	-	C	
Placynthiella uliginosa	10	-	-	-	C	C on soil, bark and wood.
Polychidium muscicola	7	-	-	-	C	C on rock and soil.
Psora cerebriformis	12	-	-	-	C	
Psora decipiens	0	1	7	6	UE*	C on calcareous soils worldwide; WA records very close together. HTR1809.
Psora globifera	21	-	-	-	C	
Psora himalayana	1	-	-	-	C	C on rock, ? on soil.
Psora luridella	1	0	0	2	?D	Widespread in western NA. HTR1804 det. Einar Timdal.
Psora montana	14	-	-	-	C	Endemic to western US.

Table 1. Continued.

Lichen species	Rd	T	OR	WA	Sc	Notes
Psora nipponica	1	-	-	-	C	C on rock, ? on soil.
Psora tuckermanii	1	-	-	-	C	C in rock crevices.
Rhizocarpon diploschistidina	3	14	2	9	?E	Recently described; name follows Lumbsch et al. (2011).
Rhizoplaca melanopthalma	1	-	-	-	C	C on rock, ours not vagrant.
Rinodina conradii	1	-	-	-	C	C on dead wood, U on soil.
Rinodina pyrina	1	-			C	C on bark, U on soil.
Rinodina roscida	1	0	2	0	UD	U throughout western NA and on alpine soil. HTR2448.
Rinodina terrestris	13	-	-	-	C	
Squamarina lentigera	0	0	0	0	R	Widespread in NA and Eurasia; R west of the Continental Divide.
Tetramelas papillatus	1	0	10	2	UE	U in western NA and on alpine soil. HTR2530, 2531.
Tetramelas terricolus	4	6	8	3	UE	U in western NA and on alpine soil.
Texosporium sancti-jacobi	3	9	13	2	UE+	Listed federally as a Species of Concern (ORBIC 2010).
Thelenella muscorum var. *octospora*	0	0	4	0	?D	Circumboreal, few specimens from Idaho, Montana and British Columbia.
Thrombium epigaeum	1	-	-	-	?D	Very inconspicuous.
Toninia ruginosa	3	-	-	-	C	C on rock and moss, U on soil.
Trapeliopsis bisorediata	2	2	7	29	UM+	Endemic to OR, WA, CA; most specimens from WA close together.
Trapeliopsis glaucopholis	2	-	-	-	C	Endemic to western NA, more C on moss on rock west of Cascades and south to California.
Trapeliopsis granulosa	0	1	-	-	?	More C in boreal and montane areas.
Trapeliopsis steppica	0	1	6	12	UM+	Endemic to OR, WA, CA; many specimens from WA close together.
Xanthomendoza fulva	17	-	-	-	C	C as epiphyte and on dried cow dung.
Xanthoparmelia chlorochroa	0	0	0	2	RM	More C further east on soil and rock. BM17926 and Jessica Allen 1.
Xanthoparmelia neochlorochroa	0	0	1	0	RE*	U northwestern NA. AD2601.
Xanthoparmelia norchlorochroa	0	0	1	0	RE*	U northwestern NA. AD2693.
Xanthoparmelia wyomingica	3	0	1	0	UM	U in steppe and subalpine.

in Oregon east of the Cascade crest. We sought to include variables representing historical grazing pressure across the region. While we were able to discuss the grazing history of specific sites with land managers, a complete layer with such data across all sites was not available. Climate variables included average annual and monthly minimum and maximum temperatures and precipitation between 1971 and 2000 with a resolution of 800 m (PRISM, Daly et al. 2008). We reduced these 40 interrelated variables to six independent principal components using principal components analysis (PCA) in PC-ORD (McCune & Mefford 2011). To span the full range of climate variability in the ecoregions of interest as opposed to just those in our plots, PCA was performed on a grid of 1179 points in the nonforested ecoregions in eastern Oregon and Washington (**Supplementary Table S1**). PCA scores were then calculated for our plots using the linear combinations generated by the region-wide PCA grid. The Oregon soils data (NRCS 2011; **Table 2**) resolution varied as some counties have had more thorough surveys than others. For the few records without soil data, we used soil characteristics from the nearest mapped site (always less than 200 m from the record's GPS location). We also included a heatload index calculated from latitude, slope and aspect (30 m accuracy) using nonparametric

Table 2. Potential spatial climate and soil variables for uncommon biotic crust habitat models. Climate variables are synthetic linear combinations from a PCA of monthly means (Daly et al. 2008); arrows describe strongest positive (↑) and negative (↓) associations among axis scores and climate variables (monthly precipitation (precip) and minimum (min) and maximum (max) temperatures (temp)). Soils variables were compiled from NRCS spatial layers (NRCS 2010).

Variable	Name
Climate: ↑ temp, ↓ precipitation	PC1
Climate: ↓ min temp, ↑ max temp	PC2
Climate: ↑ winter max temp, ↑ winter precip	PC3
Climate: ↑ winter precip, ↓ summer max temp, ↓ summer precip	PC4
Climate: ↓ winter precip, ↑ summer precip	PC5
Climate: ↓ July & Aug min temp, ↑ July & Aug. precip	PC6
Heatload: index calculated from latitude, slope, and aspect	Heat
Soil: available water capacity (cm/cm)	AWC
Soil: bulk density (g/cm^3)	BD
Soil: depth (cm)	Depth
Soil: pH	pH
Soil: % sand in top 5 cm	Sand
Soil: % clay in top 5 cm	Clay
Soil: % silt in top 5 cm	Silt
Soil: % rock in top 5 cm	Rock

regression (McCune 2006) in HyperNiche v 2.10 (McCune & Mefford 2011).

We combined locality data for known sites with absences from random plots and regressed these against soil and synthetic PCA climate variables using nonparametric multiplicative regression (NPMR; McCune 2006) with a local mean estimator and Gaussian kernel function (Bowman & Azzalini 1997). We chose NPMR over logistic regression to accommodate a wide range of response surfaces and avoid making binomial distributional assumptions. The model-selection approach sought the best possible combination of predictors of occurrence for each species by maximizing the cross-validated log-likelihood ratio (LogB), which expresses model strength compared to a naïve model in which the likelihood of species occurrence is the species' frequency. We evaluated model fit using the area under curve (AUC) for the receiver operating characteristic, in which 0.5 = random expectation and 1 = perfect fit. Tolerances reflect how broadly an estimate is based on surrounding levels of the predictor variable and are optimized to maximize LogB, subject to overfitting constraints. We specified a minimum average neighborhood size of 10 plots and evaluated the significance of the model using a randomization test with 100 permutations of the response variable in relation to all potential predictors. We interpreted the effect size of predictors using sensitivity; when sensitivity is 1.0, a change in a predictor results in a response of equal magnitude, when expressed as proportions of the variable ranges (McCune 2006). The average neighborhood size, N*, is the average amount of data contributing to the estimate of the response variable at each point. We then mapped the predicted probability of occurrence of species of interest based on each NPMR model (McCune 2006) by calculating predicted probabilities of occurrence in each 800 m square map cell. To accommodate the need for raster data, we converted the necessary soils variables from feature classes to raster files with the same resolution as the climate variables (800 m) taking the soils values for the center of each raster cell. Where the neighborhood size for the set of predictor values was lower than 25% of the model's average neighborhood size, we map the predicted probability as missing because we lacked data for sites with similar habitats. For *Texosporium*, we overlaid an additional layer representing developed and agricultural areas (ORBIC 2010a).

Results

Diversity and new records. We report a total of 126 soil crust lichen taxa (**Table 1**), 99 of which we observed in our plots (the remaining ones are only known from herbarium records) and only 66 of which occurred in more than one plot. Species diversity on our random plots ranged from seven to 28 taxa with an average of 16.46 species per plot. We reported seven taxa previously not reported from Oregon, including *Acarospora obpallens*, *A. terricola*, *Catapyrenium psoromoides*, *Placidium fingens*, *P. pilosellum*, *P. yoshimurae* and *Psora luridella*. Five of these were squamulose pyrenolichens that are very difficult to identify and were brought to our attention through collaboration with Othmar Breuss (Wien, Austria). The other two were *Acarospora*

Table 3. NPMR models for presence of four uncommon lichen species in Oregon east of the Cascades. Climate variables were reduced to six independent synthetic variables (**Table 2, Supplementary Table S1**). Model fit was evaluated using the area under curve for receiver operating characteristic (AUC), which is 0.5 for a random expectation and 1.0 for a perfect fit. *N** is the average amount of data bearing on an estimate; the *p*-value results from randomizing the data with all potential predictors. Tolerances (Tol.) reflect how broadly an estimate is based on surrounding levels of the predictor variable and decreases with importance of the predictor. Sensitivity (Sens.) measures effect size; when it equals 1.0, a change in the predictor by 10% of its range results in a 10% change in the frequency of occurrence.

Species (presences, absences)	AUC	*N**	*p*	Predictors	Tol.	Sens.
Acarospora schleicheri (40, 54)	0.83	10.2	0.01	Sand	18.7	0.35
				PC1	1.53	1.80
				PC2	2.22	0.43
Fuscopannaria cyanolepra (28, 54)	0.86	10.1	0.01	Silt	14.4	0.37
				PC2	2.449	0.28
				PC3	0.54	1.14
Rhizocarpon diploschistidina (22, 55)	0.88	10.1	0.01	Sand	11.85	0.45
				PC1	1.77	0.86
Texosporium sancti-jacobi (28, 56)	0.95	14.7	0.01	Silt	9.66	0.49
				Rock	15.9	0.29
				PC1	3.95	0.27

obpallens and *A. terricola*, which had been reported from a site with similar habitats in south-central Washington.

We found a few species that were unexpected as soil lichens in semi-arid habitats. *Ochrolechia turneri*, which contains variolaric acid (verified by Tør Tonsberg) is reported for the first time as a soil crust. It has been found in other parts of Oregon and Washington, but typically as an epiphyte in coastal hardwood forests. *Catapyrenium psoromoides* is known from further south but typically grows on bark and organic debris. Similarly, most *Placidium fingens* from further south are from organic matter. In many places we found several species that are typically associated with rock on soil, although always not far from rocks.

Rarity. Seventy one taxa were considered common either because they were frequent in our samples or because we know from other observations that they are more common in different habitats such as forests or have stronger associations with other substrates such as rock or wood (**Table 2**). We observed 15 poorly known taxa that were either newly discovered or in groups that are difficult to identify. Sixteen taxa were uncommon in the region, including four that are endemic to North America and one that is associated with calcareous sites. Twenty one taxa were rare. Ten of which are calciphiles and one is endemic to western North America.

Single-species models. Acarospora schleicheri was most likely to occur at warm, dry sites (PC1) with little monthly temperature variation (PC2) and low percent sand (**Table 3**, **Fig. 2**). In unfavorable climates, it was increasingly restricted to soils with lower percent sand. When climate was more favorable, it was, however, predicted to have a 50% probability of occurring on soils with up to 65% sand. In our study areas, it was predicted to occur most frequently along the Columbia, John Day and Deschutes Rivers and in some associated upland habitats. Outside of our study area, we predicted occurrences in Treasure Valley near Ontario and in south-central Oregon near Summer Lake and Plush (**Fig. 3**).

Fuscopannaria cyanolepra was most frequent in areas characterized by wet winters with warm monthly maximum temperatures (PC3), little monthly temperature variation (PC2) and silty soils (**Table 3, Fig. 2**). In favorable climates, the probability of occurrence was greater than 50% on soils with any percent silt. As climate became unfavorable it was, however, increasingly restricted to silty soils (**Fig. 2**). A slightly poorer model included the predictor heatload instead of PC3. *Fuscopannaria cyanolepra* was predicted to occur most frequently

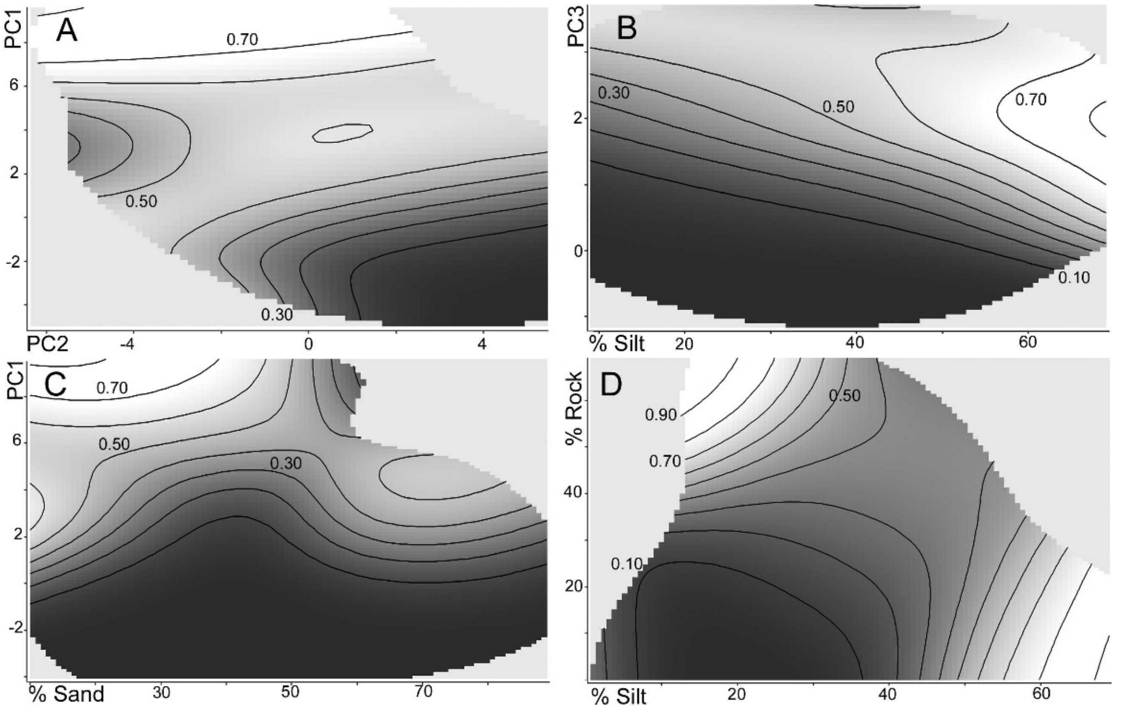

Figure 2. Relationships between presence of modeled species and soil or climate variables, showing the fitted surfaces from NPMR models (**Table 3**). **A.** *Acarospora schleicheri.* **B.** *Fuscopannaria cyanolepra.* **C.** *Rhizocarpon diploschistidina.* **D.** *Texosporium sancti-jacobi.* Shading and contours indicate the relative frequency of occurrence (0.0 = never, 1.0 = always); light gray areas had insufficient data to make estimates. The climatic axes are derived from PCA of monthly precipitation and minimum and maximum temperatures (**Supplementary Table S1**).

along the John Day and Columbia Rivers and on the Umatilla Plateau and near La Grande to the northeast of our plots. In south-central Oregon, soils and climate may support populations of *F. cyanolepra* in the higher elevation Siskiyous and near Summer Lake and Plush (**Fig. 3**).

Rhizocarpon diploschistidina occurred in warm, dry sites (PC1) with low percent sand (**Table 3**, **Fig. 2**). It was predicted to be most frequent along the Columbia and John Day Rivers and in the uplands between the John Day and Deschutes Rivers (**Fig. 3**). To the east of our study area, it is predicted in the lowlands near Hermiston, south of Walla Walla, Washington and La Grande. In eastern Oregon, it was predicted to have a higher frequency in Treasure Valley near Ontario and in southern Oregon at lower elevation sites near Fields, Paisley and Plush.

Texosporium sancti-jacobi was associated with warm, dry sites (PC1) with silty or rocky soil (**Table 3**, **Fig. 2**). It was predicted to have a high frequency of occurrence in lower-elevation sites in a broad band along the Columbia River and in Treasure Valley near Ontario in eastern Oregon (**Fig. 3**). Many of the sites where *Texosporium* was predicted to occur based on climate and soils are developed or agricultural lands (**Fig. 4**).

Discussion

Diversity and new records. Only a few studies have reported soil crust lichens for Oregon and Washington. Fifty one species were found in a single 2279 ha grazing allotment in southern Washington (Ponzetti et al. 2007) and 37 in nine small sites scattered throughout central and eastern Oregon (Ponzetti & McCune 2001). A preserve in central Oregon was home to 44 soil crust lichens (Miller et al. 2011). Ann DeBolt (pers. comm. Dec. 2010) reported 34 and 42 soil crust lichens from two sites in eastern Oregon. McCune & Rosentreter (2007) listed 144 biotic crust lichens that may be in the region based on herbarium records, although several have

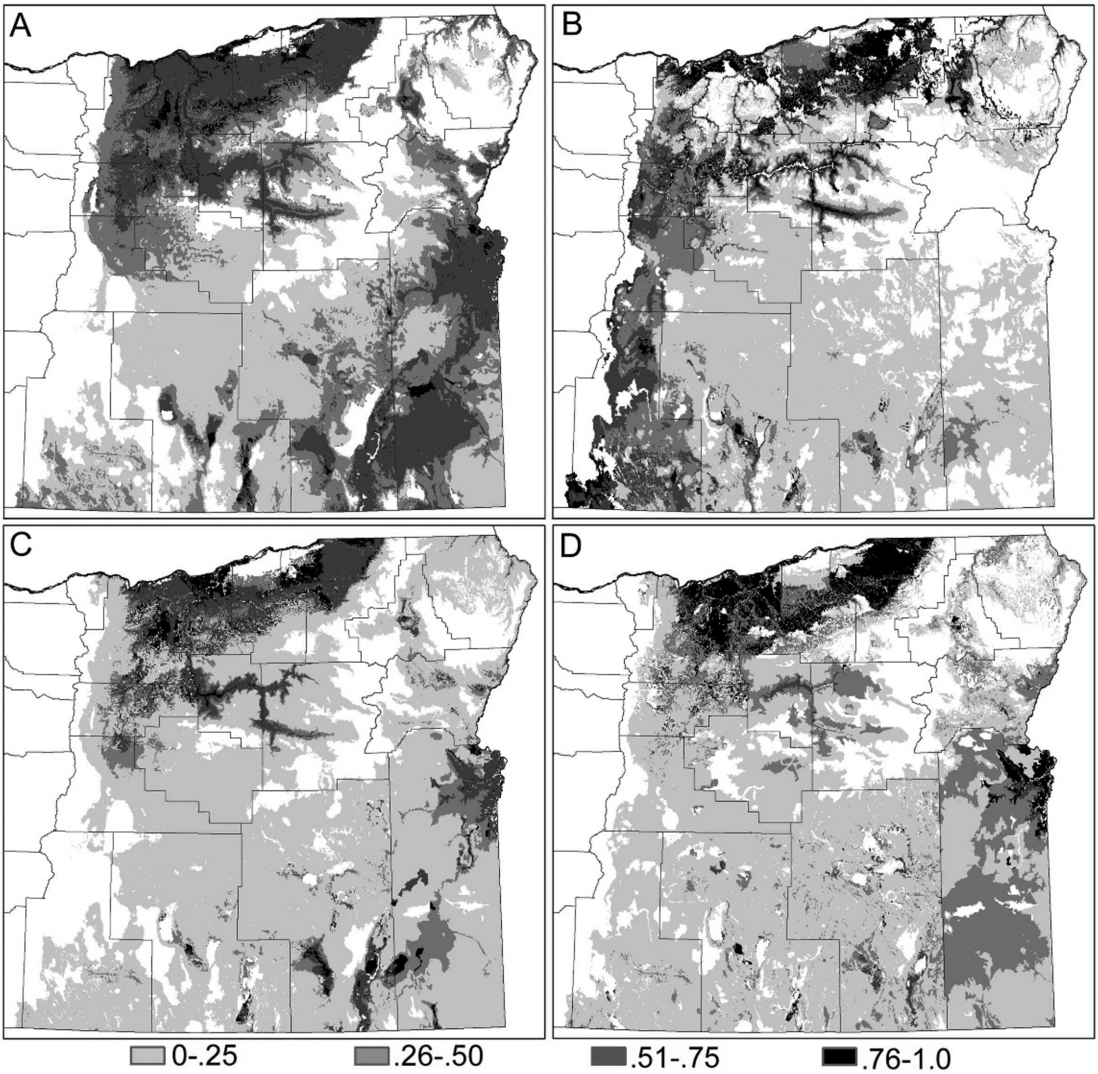

Figure 3. Predicted occurrence for modeled species in eastern Oregon; shading illustrates relative probability of occurrence. **A.** *Acarospora schleicheri*. **B.** *Fuscopannaria cyanolepra*. **C.** *Rhizocarpon diploschistidina*. **D.** *Texosporium sancti-jacobi*.

not yet been reported. Of our 99 species, five were not included in McCune and Rosentreter's (2007) list. Since each soil lichen study in the region continues to report a few new species and many of those that we found were only observed once, it seems likely that more studies are necessary to fully catalog the diversity and characterize habitat associations. It is also likely that, like vascular plants of some arid regions, many species truly are rare and demonstrate a patchy distribution on the landscape (Stohlgren et al. 2005). We did not map or analyze patterns of species that only occurred a few times because we may have overlooked them in other plots. Several were non-target collections or in groups that were frequently sterile but can only be distinguished when fertile.

We suspect that much of the remaining diversity is within taxonomically challenging groups such as *Acarospora, Aspicilia* and catapyrenioid lichens. Herein, we report five species of *Acarospora* that are uncommon, poorly known, or rare in the region. Except *A. schleicheri*, these species are easily overlooked in the field and revisions of the taxonomy are ongoing (Knudsen & Morse 2009; Lendemer & Knudsen 2011). Unidentifiable *Aspicilia* specimens were quite variable but typically infertile. Ongoing

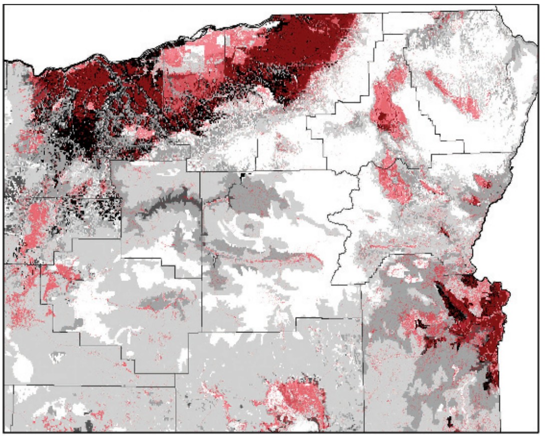

Figure 4. Regions of northeastern Oregon with predicted probabilities of *Texosporium sancti-jacobi* at a smaller scale than **Fig. 3** with agricultural and developed lands shaded in red. Land that is grazed but not plowed or used as intensive pasture is not colored red.

revisions of this genus (Sohrabi et al. 2010) may resolve many of the mysterious specimens that we observed. Several new records of *Placidium* were identifiable due to recent work on the group (Breuss 2010). We expect future surveys will help clarify this difficult group, particularly the species of *Involucropyrenium* and possibly more records of *Catapyrenium*. Habitats associations within this group were difficult to determine because poorly developed specimens typically cannot be identified.

Rarity. Assessing the conservation status of individual soil crust species across the landscape is challenging because the distribution of the species is poorly known due to a lack of studies, and many species are difficult to identify. In many cases it is unclear whether species with few records are simply under-collected or truly rare. At this time it seems appropriate to focus conservation efforts on rare species that are more readily identifiable. These rarely-reported but easily-identified species are more likely to be truly rare than the more cryptic rarely-reported species.

Calcareous and gypsiferous sites often support unique biotic crust communities (DeBolt pers. comm.; Rogers 1972; Ponzetti & McCune 2001). Many of the apparently uncommon species in our region may be fairly widespread and common elsewhere, particularly where more calcareous and gypsum soils are available. *Psora decipiens* is common on calcareous soils on all continents except South America and Antarctica but only eight populations are known from our study area. Similarly, *Acarospora nodulosa, Aspicilia fruticulosa, Buellia elegans, Fulgensia* spp., *Heppia lutosa* and *Peltula patellata* are more common south or east of our study areas on calcareous sites. Other species, such as *Gyalidea asteriscus* and *Gypsoplaca macrophylla* may be truly rare calciphiles throughout their ranges. The diversity and abundance of regionally uncommon lichens in these habitats suggest that future survey efforts specifically target calcareous and gypsiferous hotspots of diversity.

Single-species Models. Our model predicted *Acarospora schleicheri* to be relatively likely to occur in much of north-central and south-eastern Oregon. This species is considered an indicator of "old-growth" lichen communities (Rosentreter et al. 2007) because it often establishes on thalli of the crustose lichen *Diploschistes*, which often establishes on *Cladonia* squamules. In our study, *A. schleicheri* was a good indicator of sites with well-developed soil crust communities. However, the absence of this species did not necessarily indicate poor crust development. *Acarospora schleicheri* could be useful as an indicator for some hotspots for crust development and diversity because it can be easily observed from a standing position, unlike most soil crust lichens, due to its bright yellow coloration and relatively large size.

The other three species, *Fuscopannaria cyanolepra, Rhizocarpon diploschistidina* and *Texosporium sancti-jacobi* were predicted to occur in more restricted geographic ranges in eastern Oregon. *Fuscopannaria cyanolepra*, a Pacific North American endemic, also occurs west of the Cascades where it may be more common, especially on the banks of old road-cuts. On the east side of the Cascades, it is more common at sites with low heatloads; usually we observed populations on steep north-facing slopes on somewhat stable organic matter. Similarly, at Horse Heaven Hills in southern Washington, it occurred more frequently at shadier sites (Ponzetti et al. 2007). Its predicted occurrence on the eastern slopes of the Cascades likely reflects its association with wetter habitats.

Rhizocarpon diploschistidina had the lowest frequency of the four species modeled, perhaps because it has only recently been brought to the attention of lichenologists (Lumbsch et al. 2011). It appears to be an obligate epiphyte on thalli of *Diploschistes muscorum*. Like *Acarospora schleicheri*, this association with a second-generation soil crust lichen may limit it to well-developed sites with minimal disturbance. While it appears to require well-developed thalli of *Diploschistes*, we observed several sites with abundant *D. muscorum* that did not support *R. diploschistidina*.

Texosporium sancti-jacobi is the only crust lichen federally listed by the US Fish and Wildlife Service as a Species of Concern (ORBIC 2010b); it is also ranked in each state where it occurs (Oregon, Washington, Idaho, and California). Populations of *T. sancti-jacobi* in southern California may be ephemeral at very dry sites (Knudsen 2007); further understanding of the habitats and population dynamics of this species should include careful monitoring of permanent plots over time. We were surprised to find 12 new populations of this species, three of which were on randomly selected plots. In other parts of its range, *T. sancti-jacobi* is most common on organic matter such as dead bunchgrass stumps and old rabbit droppings (Riefner & Rosentreter 2004). In addition to those substrates, we also found populations growing on bare soil. In our study area, these habitats were in bunchgrass habitats with silty or rocky soil, often on slopes above or near rivers. At apparently degraded plots within the range of *T. sancti-jacobi*, we found small populations nestled in crevices between basalt outcrops, suggesting that these areas may provide refugia from trampling by domestic grazers. Had the random placement of our plots not forced further inspection, we would not have intuitively selected those sites because they did not appear to support well-developed soil crust communities.

The strong association of all four modeled species with fine-textured or rocky soils may reflect increased moisture retention or stability in fine soils compared with sandier sites. We observed that the surface of sandy and pumice soils, particularly near Bend and along Highway 20, dried quickly following rain; our footprints in the soil were substantially more evident at these sites as compared to those with finer soils. Both *Acarospora schleicheri* and *Fuscopannaria cyanolepra* were increasingly restricted to fine soils when climate conditions were less favorable. This could be because finer soils compensate for more variable temperatures or lower precipitation by retaining moisture longer. The stability of fine or rocky soils may also provide refugia from trampling by domestic livestock. It is difficult to disentangle these potentially synergistic mechanisms. If the latter is more important, perhaps we would not have observed such a strong association with fine and rocky soils in the absence of livestock grazing.

With the exception of *Fuscopannaria cyanolepra*, the crust species that we modeled were associated with fine sediments of riverine or lacustrine systems. These sites, particularly in the Treasure Valley of eastern Oregon and along the Columbia River in north-central Oregon, are also the most productive agricultural areas in the region. *Texosporium sancti-jacobi*, which was predicted to occur across a fairly large area, is probably uncommon partially because most suitable habitat has been developed or converted to agriculture. Although we do not show similar maps for *Acarospora schleicheri* and *Rhizocarpon diploschistidina*, a similar pattern was observed. We are not aware of any lichen surveys in the Treasure Valley area of eastern Oregon. Our models predict, however, that public lands in that area are likely to support unusual lichen soil crust communities.

Conservation Implications. Management practices to ensure the persistence of rare lichens have been undertaken across large areas west of the Cascades in the Pacific Northwest since the introduction of the Northwest Forest Plan in 1994 (FEMAT 1993); however, little attention has been given to soil crust lichen species east of the Cascades. Our species list for this region along with relative abundance values for each species should provide a starting point for conservation efforts. We found that many of the biotic crust lichen species were uncommon or rare; however, a solid effort to characterize their habitat associations will require more extensive and detailed sampling. We recommend that future surveys focus on sites with fine soils, especially near rivers, calcareous substrates, and unusual vegetation types to continue developing our understanding of the lichen soil crust communities of this region. Monitoring the diversity and abundance of these important ecosystem components is the only way to effectively protect the essential ecological roles they play in the Oregon's steppe in the face of increasing disturbances by livestock grazing, fires, construction of wind-energy facilities, or invasion by exotic annual grasses.

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Supplementary documents on-line

Table S1: Coefficients for the first six axes (Ax1-6) of a Principal Component Analysis of climate means in 1179 plots in eastern Oregon and Washington, USA.