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Long-term changes in biological soil crust cover and composition

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Abstract

Introduction: Communities change over time due to disturbances, variations in climate, and species invasions. Biological soil crust communities are important because they contribute to erosion control and nutrient cycling. Crust types may respond differently to changes in environmental conditions: single-celled organisms and bryophytes quickly recover after a disturbance, while lichens are slow growing and dominate favorable sites. Community change in crusts has seldom been assessed using repeated measures. For this study, we hypothesized that changes in crust composition were related to disturbance, topographic position, and invasive vegetation.

Methods: We monitored permanent plots in the Columbia Basin in 1999 and 2010 and compared changes in crust composition, cover, richness, and turnover with predictor variables of herbivore exclusion, elevation, heat load index, time since fire, presence of an invasive grass, and change in cover of the invasive grass.

Results: Bryophytes were cosmopolitan with high cover. Dominant lichens did not change dramatically. Indicator taxa differed by monitoring year. Bryophyte and total crust cover declined, and there was lower turnover outside of herbivore exclusions. Lichen cover did not change significantly. Plots that burned recently had high turnover. Increase in taxon richness was correlated with presence of an invasive grass in 1999. Change in cover of the invasive grass was positively related to proportional loss and negatively related to gain.

Conclusions: Composition and turnover metrics differed significantly over 11 years, though cover was more stable between years. This study can be a baseline for assessing change in crust composition due to anthropogenic influences.

Keywords: Biological soil crust, Columbia basin, Composition change, Taxa turnover rate, Fire, *Bromus tectorum*, Livestock exclusion

Introduction

Biological communities change over time due to factors such as disturbance (Pickett et al. 2008; Platt and Connell 2003), changes in climate (Tylianakis et al. 2008), and species invasion (Mack et al. 2000). Understanding background rates of change is necessary when evaluating human impacts (Magurran et al. 2010). Arid lands are important ecosystems because they cover ~ 40% of Earth's land surface and are rapidly changing due to biophysical and social factors such as climate, cropland expansion, and overgrazing (Geist and Lambin 2004).

Biological soil crusts are communities of photosynthetic organisms that live on the soil surface of arid lands. Crusts

perform many roles in the ecosystem; the presence of mature crust is associated with reduced wind and water erosion and increased carbon and nitrogen fixation (Belnap and Lange 2001). The structure and composition of crust communities are related to precipitation levels, topographic position, soil type, and disturbance history (Belnap and Lange 2001; Ponzetti et al. 2007).

Changes in crust composition over time depend on site and vegetation characteristics, disturbance history, and characteristics of the crust taxa (Rosentreter et al. 2001). Sites with higher resource availability, such as moist microsites, can support more species (Garcia-Pichel and Belnap 2001) and can have higher productivity and more stability (Hooper et al. 2005). Invasive species such as the annual grass *Bromus tectorum* can decrease crust cover and species richness (Belnap et al. 2006). This grass may

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prevent crust from recovering (Dettweiler-Robinson et al. 2013) by competing for resources and/or reducing the fire return interval (Brooks et al. 2004). Disturbances such as fire, intense grazing, or drought can directly remove or damage crust. Disturbances can also indirectly affect crust by triggering abiotic changes, such as loss of soil stability (Bowker et al. 2004) or invasion by non-native plants (Chambers et al. 2007). The intensity, timing, recurrence, and type of disturbance can affect the rate of crust recovery even up to 30 years post disturbance (Bowker et al. 2004; Ford and Johnson 2006; Lalley and Viles 2008; Marble and Harper 1989; Zaady et al. 2007). For example, the first fire that burns through intact shrub cover following a long fire-free period would be of high intensity and therefore should have larger effects on the crust than subsequent fires that are less intense because of the reduced fuel loads. Crust taxa differ in susceptibility to damage and removal by different disturbances (Ponzetti et al. 2007). For example, organisms that live under plant canopies would be less likely to survive a high-severity fire than organisms that live in plant interspaces (Hilty et al. 2004). Succession may proceed differently based on timing and severity of disturbance, what portion of the community survived the disturbance, and the spatial arrangement of disturbed and undisturbed patches (White and Jentsch 2001).

Because some crust taxa are small, cryptic, and have slow growth rates, community change can be difficult to detect within short time scales. These changes reflect differences among taxa in growth rate and in response to environmental factors. Cyanobacteria and other single-celled components can colonize a site and expand rapidly in cover (Belnap 1993). In a scraping disturbance experiment, cyanobacterial cover quickly recovered to the level of the control treatment within 8 months and did not differ up to 32 months after treatment (Dojani et al. 2011). Bryophyte cover can increase rapidly in the absence of disturbance (Antos et al. 1983; Bates et al. 2009), and young mosses can grow more rapidly than older mosses (Barker et al. 2005). Lichens generally have slow growth rates that may decline with age (Armstrong and Bradwell 2010). Crustose lichens can invade soon after disturbance (Johansen et al. 1984) but may take a long time to increase in cover. Foliose and fruticose lichens may colonize later in succession because they require stable substrates (Belnap and Eldridge 2001). Dark cyanobacterial, moss, and lichen crusts responded more slowly and variably than light cyanobacteria in the scraping experiment (Dojani et al. 2011), suggesting that longer time scales are needed to identify cover and composition changes in lichen- and bryophyte-dominated crust communities following disturbance.

Few studies have examined cover and composition dynamics within crusts (e.g., Anderson et al. 1982; Hilty

et al. 2004; Kaltenecker et al. 1999). In addition, these studies used a space-for-time approach, tended to focus on total crust cover rather than individual taxa, and occurred in sites dominated by cyanobacterial crust. In this study, we monitored permanent plots (Ponzetti et al. 2007) to document changes in a bryophyte- and lichen-dominated crust community 11 years apart. We assessed changes in crust taxa by comparing cover, frequency of occurrence, and indicator species between years. We quantified changes in community composition, total cover, covers of bryophytes and of lichens, and taxon richness, as well as proportional taxon loss, gain, and turnover. We examined the relationship between these variables and potential abiotic and biotic explanatory factors including exclosure from large herbivores, elevation, heat load index (HLI), time since fire (TSF), initial presence of *B. tectorum*, and change in *B. tectorum* cover. We expected (1) more change in cover and composition in recently burned quadrats because communities would be reassembling, (2) less change at higher elevation and cooler HLI as these areas have more moisture available to support high cover and diverse crust communities, and (3) more change in quadrats that initially contained *B. tectorum* or that had a large increase in *B. tectorum* cover.

Methods

Site description

The Horse Heaven Hills (HHH) complex (46.2°N, 119.5°W) in south-central Washington is managed by the Bureau of Land Management. The climate is semi-arid, with an average of 188 mm of precipitation per year, mostly falling between October and April. Heavy fog is common in the winter; we have noted that crusts can be active (green, indicating photosynthetic activity) on these foggy days. Mean daily temperatures are 0°C in January and 22°C in July (Western Region Climate Center 2012). Soil types include Ritzville silt loams and Kiona very stony silt loams (Soil Survey Staff and Natural Resources Conservation Service 2011). Plots are located on elevations from 250–550 m with generally northerly aspects.

The dominant disturbances in the area are fire and grazing. Fires occurred in the area in 1986, 1998, 2002, and 2007; fire history before 1980 is uncertain due to lack of spatially explicit data. Much of the area was grazed from the 1960s to the 1980s. There have been no active grazing leases since 1986, though there are scattered reports of trespass by cattle from nearby pastures.

Vegetation types are dominated by sagebrush (*Artemisia tridentata* ssp. *wyomingensis*, *A. tripartita*), bunchgrasses (*Pseudoroegneria spicata*, *Hesperostipa comata*, *Poa secunda*), or invasive annuals (*B. tectorum*) (NRCS and USDA 2012). *Artemisia* spp. are characteristic of mature

communities, but *A. tridentata* is removed by fire and does not recover quickly due to the low dispersal distance and short longevity of its seed (Young and Evans 1989). *Bromus tectorum* is able to colonize and expand in disturbed areas (Davies et al. 2012).

Previously, Ponzetti et al. (2007) surveyed 350 quadrats in this region and showed that crust diversity was highest on warm slopes and draws, crust richness and cover were inversely related to *Bromus tectorum*, and taxa differed in their tolerance of disturbance. The most abundant taxa were short mosses, *Syntrichia ruralis*, black cyanolichens, *Trapeliopsis bisorediata*, *Diploschistes muscorum*, and *Cladonia* spp. (Ponzetti et al. 2007).

Design

For this remeasurement, we focused on 48 permanently marked quadrats from Ponzetti et al. (2007), which are distributed across 12 plots spanning ~2,000 ha. A livestock enclosure (4.88 × 9.75 m) was erected on each plot in 1998. Two quadrats were located in diagonal corners of the enclosure, and two quadrats were diagonally adjacent to one another 50–100 m outside of the enclosure. Each quadrat was 0.5 × 4 m. Quadrats were monitored between October 1998 and May 1999 (hereafter “1999”) and again between November 2010 and March 2011 (hereafter “2010”). Live crust taxa were identified (Esslinger 2011; Flowers 1973; McCune and Rosentreter 2007) and cover recorded using five classes: 0, trace to 1%, >1–10%, >10–50%, and >50–100%. Taxa that were difficult to identify in the field or that had questionable identity across years were aggregated by genera or morphological group (see Additional file 1). Aggregating information to larger groups loses information about individual species but is a robust method for surveying small, cryptic organisms such as crusts (Eldridge and Rosentreter 1999) and preserves important trends in composition (McCune et al. 1997). This also ensured that we were conservative in assessing composition changes that may have occurred between the two monitoring periods. *Bromus tectorum* cover class was recorded on each quadrat.

Elevation, aspect, and slope were calculated from 10 m digital elevation models (DEMs; U.S. Geological Survey USGS 2011) to the scale of enclosures within plots. Heat load index (HLI) was calculated from latitude, aspect, and slope as per McCune and Keon (2002). Time since most recent fire (TSF) was calculated relative to 2010. Five plots burned prior to 1980 (TSF assigned a value of 30), two burned in 1986, two burned in 1998, two burned in 2002, and one burned in both 2002 and 2007.

Statistical analysis

We averaged each taxon’s cover across the 48 quadrats and tallied the number of quadrats on which each taxon

occurred. We used these data to evaluate differences in cover and frequency between 1999 and 2010 for each taxon. We used Indicator Species Analysis to identify BSC taxon groups that were strongly associated with each sampling year. The Indicator Value (*IV*) is calculated independently for each taxon group *i* as the product of its relative abundance and relative frequency in each year *j* (1999 vs. 2010) (Bakker 2008). Indicator values range from 1 to 100. Significance was assessed by permuting group identities 99 times and recalculating *IV_{ij}*. *IVs* were calculated using the function given in Appendix S1 of Bakker (2008). Significant indicators were those with $P < 0.05$ and $IV_{ij} > 25$ (Dufrêne and Legendre 1997). Significant indicators were taxa that changed in abundance from 1999 to 2010.

Community change was assessed in several ways. Cover classes were converted to the mean percent cover in the class as follows: 0% = 0%, trace to 1 = 1%, >1–10% = 5%, >10–50% = 30%, and >50–100% = 75%. We calculated the Bray-Curtis dissimilarity between each quadrat in 1999 and in 2010. The covers of all bryophytes and lichens were summed for each quadrat in each year. We calculated the change in total, bryophyte, and lichen cover by subtracting the value in 1999 from the value in 2010.

Community change is also a result of taxa gains and losses. We calculated the change in taxon richness as $S_{2010} - S_{1999}$, where S_{1999} and S_{2010} are the taxon richness in 1999 and 2010, respectively. We also calculated the proportional taxa gain (G_p), proportional loss (L_p), and total proportional turnover (T_p) for each quadrat. All rates were expressed as proportions of the average number of taxa present during the measurement period: $G_p = G / (0.5 [S_{1999} + S_{2010}])$, $L_p = L / (0.5 [S_{1999} + S_{2010}])$, $T_p = (G + L) / (S_{1999} + S_{2010})$, where G is the number of taxa absent in 1999 but present in 2010, and L is the number of taxa present in 1999 but absent in 2010 (Anderson 2007).

The various change metrics were response variables in separate linear mixed models. Plot was included as a random block effect in all analyses to account for variability across the landscape. Enclosure was a fixed treatment nested within plots. Quadrats were nested within enclosure × plot combinations to account for microsite variability. Potential predictors included three discrete factors. Enclosure had two levels, “in” and “out.” Time since fire (TSF) was binned into two classes: quadrats that burned between the 1999 and 2010 measurements (“recent”), and quadrats that burned prior to the 1999 measurement (“late”). Although *B. tectorum* cover was recorded by cover class, we converted these data to presence/absence because they were strongly right-skewed, with over half of all quadrats containing no *B. tectorum* in 1999. We also included three continuous variables: elevation, HLI, and change in *B. tectorum* cover from 1999 to 2010.

Table 1 Biological soil crust taxa (see Additional file 1), functional type (McCune and Rosentreter 2007), percent cover (mean ± SD), frequency of occurrence (out of 48 quadrats), Indicator Value (IV), and P-value in 1999 and 2010

		1999			2010		
		Cover	Number	IV, P	Cover	Number	IV, P
Lichens							
Black crustose thalli lacking apothecia	Crustose	7.2 ± 8.9	48	58, 0.15	5.2 ± 9.6	45	39, 0.86
<i>Cladonia squamules</i>	Squamulose to fruticose	3.8 ± 5.8	47	45, 0.66	4.6 ± 7.0	45	51, 0.36
<i>Trapeliopsis steppica</i>	Squamulose	3.1 ± 6.0	32	46, 0.05	1.4 ± 4.4	23	15, 0.94
<i>Diploschistes muscorum</i>	Crustose	2.2 ± 1.9	46	52, 0.12	1.9 ± 2.0	38	36, 0.89
<i>Trapeliopsis glaucopholis</i>	Squamulose	1.4 ± 4.5	17	13, 0.81	2.4 ± 7.3	19	25, 0.22
White crustose thalli lacking apothecia	Crustose	1.0 ± 1.1	35	61, 0.01	0.2 ± 0.4	9	3, 1
<i>Massalongia carnosa</i>	Lobate	0.9 ± 1.2	30	37, 0.23	0.6 ± 0.5	29	25, 0.80
<i>Leptochidium albociliatum</i>	Lobate	0.9 ± 0.3	44	52, 0.01	0.7 ± 0.5	33	30, 1
Cf. <i>Buellia</i> spp.	Crustose	0.8 ± 1.0	32	27, 0.73	1.2 ± 1.4	27	34, 0.31
<i>Arthonia</i> sp.	Crustose to squamulose	0.6 ± 0.4	8	6, 1	0.5 ± 0.4	16	22, 0.05
<i>Aspicilia</i> spp.	Crustose to fruticose	0.6 ± 0.5	27	15, 0.99	1.6 ± 3.1	35	54, 0.02
Cf. <i>Trapeliopsis bisorediata</i>	Crustose	0.6 ± 0.5	27	13, 1	1.8 ± 4.3	41	65, 0.01
Cf. <i>Lecanora garovaglii</i>	Crustose	0.4 ± 0.8	15	14, 0.81	0.5 ± 1.0	16	19, 0.26
Cf. <i>Rhizocarpon diploschistidina</i>	Lobate	0.4 ± 0.5	17	21, 0.18	0.2 ± 0.4	12	10, 0.93
<i>Psora</i> spp.	Squamulose	0.4 ± 0.5	19	22, 0.42	0.3 ± 0.5	16	15, 0.75
<i>Aspicilia filiformis</i>	Lobate	0.2 ± 0.4	8	5, 0.99	0.4 ± 0.6	16	24, 0.03
<i>Acarospora schleicheri</i>	Crustose	0.2 ± 0.5	29	33, 0.22	0.3 ± 0.5	24	23, 0.88
Brown crustose thalli lacking apothecia	Crustose	0.1 ± 0.2	3	3, 0.62	0.1 ± 0.2	3	3, 0.7
<i>Candelariella citrina</i>	Crustose	0.1 ± 0.3	4	3, 0.85	0.1 ± 0.3	7	9, 0.35
<i>Cladonia fimbriata</i>	Fruticose	0.1 ± 0.3	4	3, 0.96	0.2 ± 0.3	9	13, 0.13
Cf. <i>Endocarpon</i> spp.	Squamulose	0.1 ± 0.3	4	1, 1	0.5 ± 0.5	24	43, 0.01
<i>Fuscopannaria cyanolepra</i>	Crustose	0.1 ± 0.3	4	8, 0.08	0	0	0, 1
<i>Physconia</i> spp.	Lobate to foliose	0.1 ± 0.3	5	5, 0.74	0.1 ± 0.3	6	7, 0.48
Cf. <i>Caloplaca jungermanniae</i>	Crustose	<0.1 ± 0.1	1	1, 0.78	<0.1 ± 0.1	1	1, 0.72
<i>Collema</i> spp.	Crustose	<0.1 ± 0.1	1	1, 0.71	<0.1 ± 0.1	1	1, 0.78
<i>Caloplaca tomenii</i>	Crustose	<0.1 ± 0.2	2	2, 0.81	0.1 ± 0.2	3	4, 0.49
<i>Caloplaca stillicidiorum</i>	Crustose	0	0	0, 1	<0.1 ± 0.1	1	2, 0.57
<i>Cladonia verruculosa</i>	Fruticose	0	0	0, 1	<0.1 ± 0.1	1	2, 0.42
Cf. <i>Lecanora zosteræ</i>	Crustose	0	0	0, 1	<0.1 ± 0.2	2	4, 0.28
<i>Texosporium sancti-jacobi</i>	Crustose	0	0	0, 1	<0.01 ± 0.2	2	4, 0.18
<i>Lecidea fuscoatra</i>	Crustose	0	0	0, 1	0.1 ± 0.2	3	6, 0.11
Green crustose thalli lacking apothecia	Crustose	0	0	0, 1	0.1 ± 0.3	4	8, 0.08
<i>Candelaria</i> sp.	Crustose	0	0	0, 1	0.1 ± 0.2	4	8, 0.06
Total lichen cover		25 ± 12			26 ± 16		
Bryophytes							
Small moss	Short moss	34.5 ± 23.2	48	61, 0.02	20.7 ± 20.8	48	38, 1
Cf. <i>Syntrichia</i> spp.	Tall moss	31.3 ± 14.7	47	69, 0.01	9.0 ± 11.1	44	27, 1
<i>Cephaloziella divaricata</i>	liverwort	0.4 ± 0.8	14	15, 0.65	0.3 ± 0.7	16	16, 0.48
Total bryophyte cover		56 ± 22			30 ± 23		
Total crust cover		82 ± 26			56 ± 30		

Data are organized in order of declining cover by lichens and bryophytes. Significant IV's are in bold font.

All analyses were run in R (version 2.14.0; R Core Team 2012) using the lme function in the package “nlme” using backwards stepwise regression. Significance was assessed by comparing *t*-values to a random normal distribution. Delta AIC values of the final model were compared to those of a model with only the plot random block effect. Delta AIC values >2 indicated that the models had some support, and values > 10 indicated that the models had considerable support.

Results

We recorded 34 lichen taxa and 3 bryophyte taxa, for a total of 37 taxa (Table 1). Black crusts, *Cladonia* squamules, *Trapeliopsis* spp., and *Diploschistes muscorum* were dominant and common lichen groups in both years. *Trapeliopsis steppica*, white crust, and *Leptochidium albociliatum* were significant lichen indicators in 1999, while *Aspicilia* spp., cf. *Trapeliopsis bisorediata*, and cf. *Endocarpon* spp. were indicators in 2010. Although two bryophyte taxa, *Syntrichia* spp. and small moss, consistently had higher cover than other taxa, they were significant indicators in 1999 because they declined in cover by 2010.

Bray-Curtis dissimilarity was significantly different than 0 (mean = 22.4), indicating composition changed significantly from 1999 to 2010. However, none of the potential predictors were significantly related to Bray-Curtis dissimilarity (Table 2).

Total crust cover and bryophyte cover declined significantly outside the exclosures (Figure 1, Table 2). Lichen cover did not change significantly during this period, nor did total crust and bryophyte cover change significantly inside exclosures.

Change in taxa richness was significantly positively related to presence of *B. tectorum* in 1999 (Figure 2,

Table 2). Plots with no *B. tectorum* in 1999 did not significantly change in taxa richness.

There was significant proportional loss, gain, and turnover of taxa. Quadrats that burned between the two monitoring dates lost significantly more taxa and had higher proportional turnover than those that did not burn (Figure 3, Table 2). Quadrats inside exclosures gained significantly more taxa and had higher proportional turnover than those outside exclosures (Table 2, Figure 3C). Change in *B. tectorum* cover was significantly positively related to proportional loss and negatively related to proportional gain.

Elevation and HLI had no significant effect on any of the change metrics.

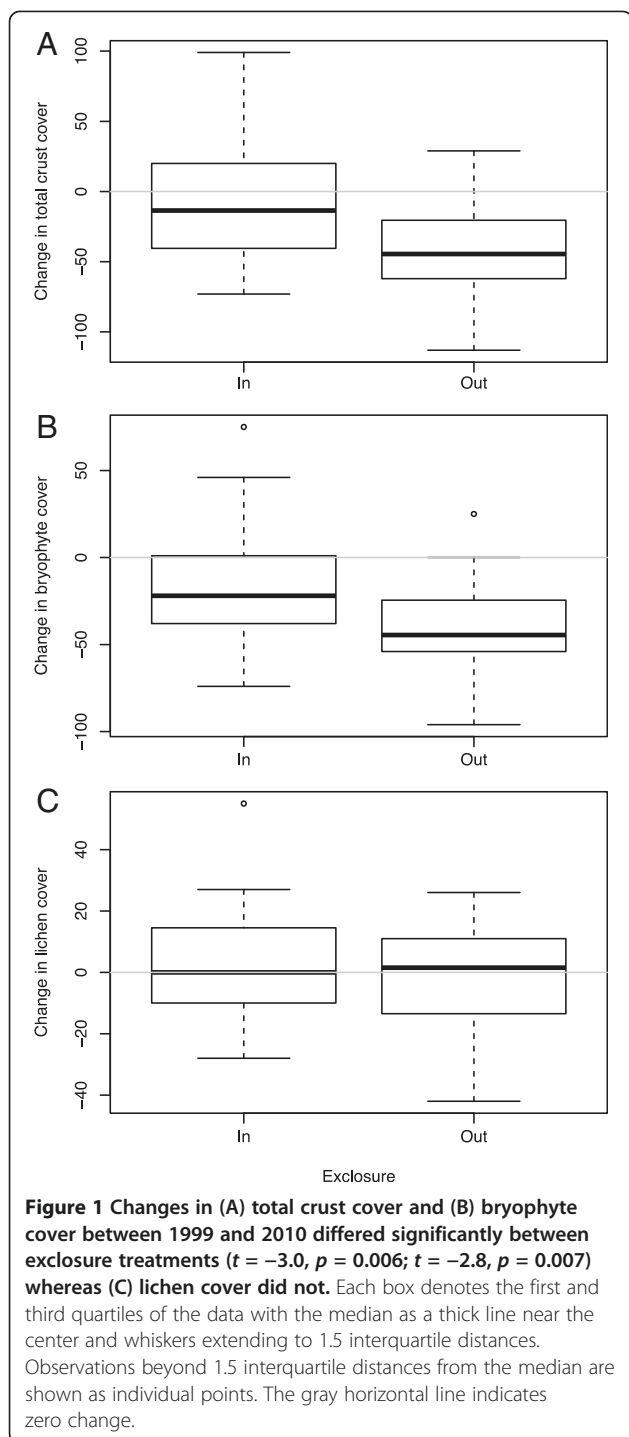
Discussion

This is one of the first studies using repeated sampling of permanent plots to assess change in lichen- and bryophyte-dominated crust communities and provides a baseline for assessing change in similar crust communities. The significant changes in indicator species, crust composition, and proportional turnover metrics support the finding that crust communities are more dynamic over short time scales than previously thought (Belnap et al. 2006). Even quadrats that did not burn within 11 years and that were protected inside exclosures could show high rates of change (Figures 1,2,3, Table 2). Changes in cover and taxa richness metrics responded to different abiotic and biotic factors, with cover responding more strongly to exclosure treatment, and taxa richness and turnover responding to disturbance and annual grass invasion. Changes in cover and taxon richness were less variable than proportional turnover metrics, indicating that dominant and common species have strong effects on total

Table 2 Significant predictors included in the final models for Bray-Curtis dissimilarity; change (Δ) in total covers of BSC, lichens, and bryophytes; change in species richness; and species gain, loss, and turnover between 1999 and 2010

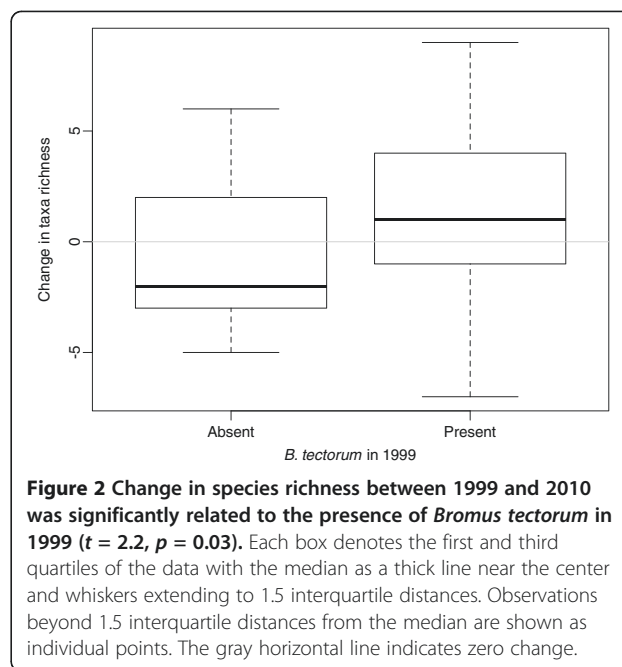
	Δ AIC	Fixed					Random	
		Intercept	Exclosure	Time since fire	<i>B. tectorum</i> cover 1999	Δ <i>B. tectorum</i>	Plot	Residual
		<i>t</i> , <i>P</i>	<i>t</i> , <i>P</i>	<i>t</i> , <i>P</i>	<i>t</i> , <i>P</i>	<i>t</i> , <i>P</i>	StdDev	StdDev
Bray-Curtis dissimilarity	NA	22.4, 0	-	-	-	-	<0.001	0.13
Δ Crust cover	12.8	-1.3, 0.19	-3.0, 0.006	-	-	-	0.004	37.01
Δ Bryophyte cover	NA	-1.9, 0.06	-2.8, 0.007	-	-	-	0.002	32.74
Δ Lichen cover	12.0	0.1, 0.91	-	-	-	-	3.641	18.03
Δ Species richness	4.4	-1.4, 0.17	-	-	2.2, 0.03	-	<0.001	3.45
Proportional loss	18.0	7.6, 0	-	6.6, <0.001	-	3.6, <0.001	<0.001	0.15
Proportional gain	5.8	10.1, 0	-2.5, 0.016	-	-	3.2, 0.002	0.069	0.13
Proportional turnover	11.7	14.0, 0	-3.0, 0.005	-6.1, <0.001	-	-	<0.001	0.09

Delta (Δ) AIC values indicate the difference in AIC between the final model and a model that includes only plot as a random effect. Fixed effects included exclosure, time since fire (relative to 2010 and binned into two classes: burned within the 11 years of the study and burned before the first measurement), the presence or absence of *Bromus tectorum* in 1999, and the change in cover of *B. tectorum*. For fixed effects, *t*-value and *P*-value are reported. Random effects included the blocking factor of plot and the residual. For random effects, the standard deviation is reported. Blanks indicate factors that were not significant and were not included in the final model.



production and do not change in cover or distribution as much as minor and uncommon species. Repeated, long-term sampling is desirable because one can detect the changes in rates of expansion and turnover (Magurran et al. 2010), but with two time points, we detected overall changes in the community in that interval.

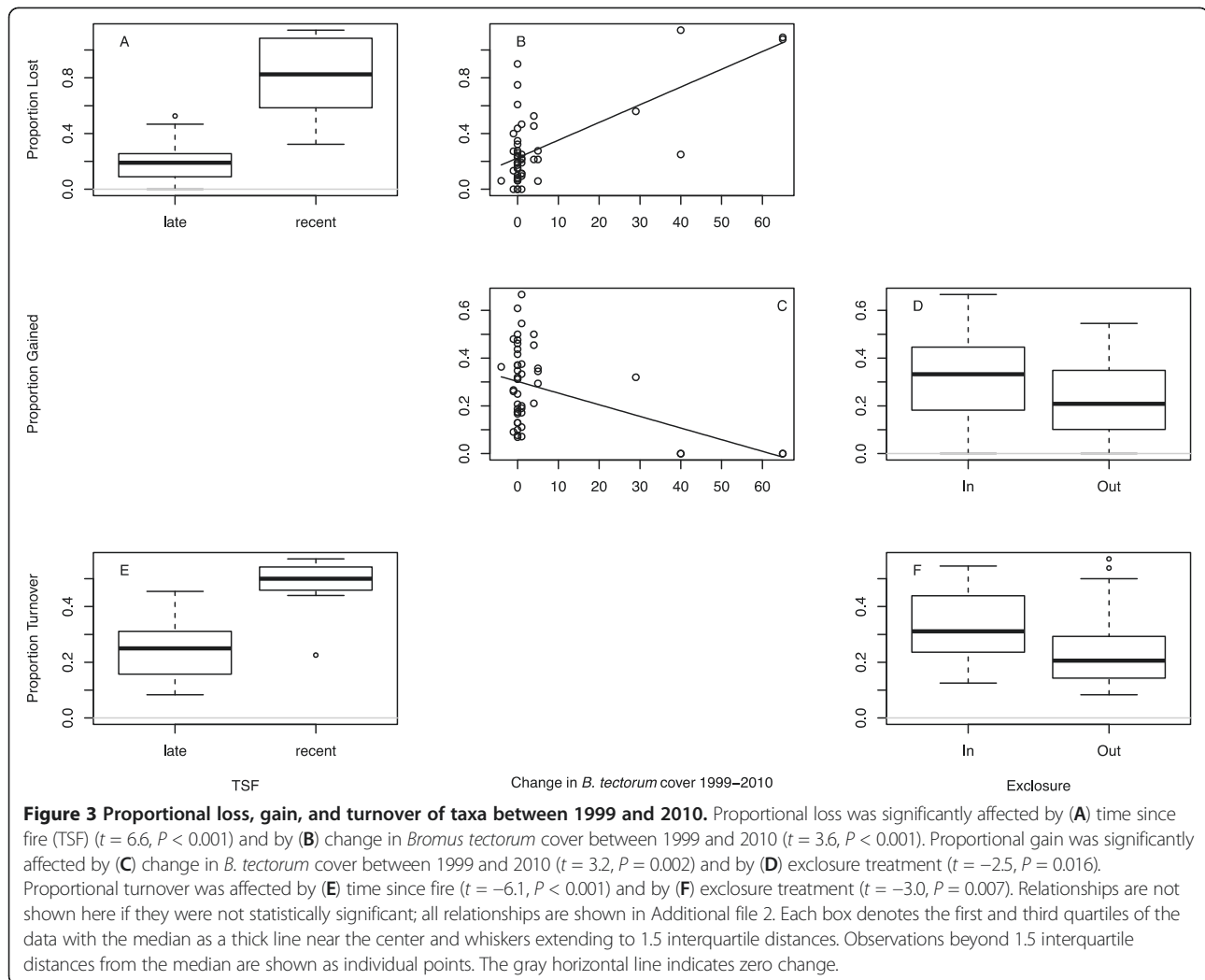
Though there were differences between years in each taxon's cover and distribution, the landscape generally



contained high-quality, diverse crust communities. We found fruticose-foliose morphological group lichens such as *Cladonia* spp., *Trapeliopsis* spp., *Diploschistes muscorum*, and *Aspicilia* spp. in most quadrats in both years (Table 1). These groups tend to be found in undisturbed areas (Hilty et al. 2004; Ponzetti et al. 2007; Dettweiler-Robinson et al. 2013). Lichens such as *Rhizocarpon diploschistidina*, which parasitizes *Diploschistes muscorum*, indicate even longer undisturbed time (Ponzetti, personal observation); this species occurred in at least a quarter of our quadrats (Table 1). In addition, *Texosporium sancti-jacobi*, a Washington state threatened species (Washington Natural Heritage Program 2010) was found on two quadrats in 2010 (Table 1). Either this species dispersed to and established on these quadrats between the two measurements, or it was present but not identifiable on these quadrats in 1999 and subsequently developed identifiable traits. Together, these taxa indicate that these quadrats currently have a relatively high-quality crust.

The changes documented here provide a baseline from which to assess future changes due to disturbance or invasion. However, with high-quality crust cover across this study site, recovery from small-scale disturbances such as individual fires, presence of invasive species, or mechanical disruption from mammals may have proceeded more rapidly than if a larger area was severely degraded; recovery rates of soil lichens are positively related to nearby undisturbed lichen cover (Lalley and Viles 2008).

Fragmenting, wind-dispersed taxa such as mosses and *Caloplaca* spp. were common on the landscape. Because these taxa are associated with disturbed sites (Kleiner



1983, Lalley and Viles 2008, Dettweiler-Robinson et al. 2013), their presence suggests that a mosaic of disturbance histories, including fire, burrowing animal activity, and trampling, maintains a species pool of both early- and late-successional species in the region.

Bryophyte cover and total crust cover declined outside the exclosures with no change inside, and proportional gain and turnover were higher inside exclosures. Similarly, Anderson et al. (1982) found an increase in crust from <5% cover to >15% cover with 14–18 years of protection from cattle grazing and found that moss had more dramatic increases than lichens. However, although the experimental exclosures were built in 1998 to test the effects of cattle grazing on crusts, no livestock grazing occurred between sampling dates. This suggests that the effects of exclosures on crusts are due to other factors, such as their effect on access or behavior of other animals. For example, in one exclosure, we found extensive small mammal burrows as well as signs of a coyote attempting to dig under the fence.

Deer were also present in the HHH. Areas inside exclosures would have been protected from trampling.

Significant exclosure treatment effects may also indicate spatial autocorrelation. We did not account for smaller-scale variation in soil characteristics and topography, such as texture, pH, calcium carbonate concentration, or water availability, which are strongly related to crust composition (Eldridge and Tozer 1997). These characteristics may have been similar between adjacent quadrats in one exclosure treatment but may differ from others.

Although recent fire had no effect on crust cover nor change in taxa richness, it resulted in higher proportional loss and turnover. Previous work showed that the number of moss and lichen species was lower in burned plots but that there was no difference in total moss or total lichen cover (Bowker et al. 2004). Presumably, species that are more sensitive to fire are removed while surviving species can expand in cover, leading to overall similar cover.

The metrics of change in taxa richness and proportional turnover metrics differ in that proportional turnover uses an average of taxa richness between the two years, so if there was low species richness in both years and one species was lost, it would be a high percent turnover but the absolute change in species richness would not be dramatically different.

Contrary to our initial hypothesis that *B. tectorum* would decrease cover and species richness, sites with *B. tectorum* present showed an increase in species richness. Because this site had low *B. tectorum* cover (average $6 \pm 12\%$), the presence of *B. tectorum* cover may have indicated a previous disturbance that affected both *B. tectorum* and crust (see Additional file 2). For example, following disturbance such as fire or burrowing mammal disturbance, there would be an initial increase in crust taxa richness as they colonize, and *B. tectorum* could also invade in the disturbed site. This is further reflected by the significant effect of change in *B. tectorum* on proportional gain and loss (Table 2).

Based on a larger survey of quadrats throughout the region, Ponzetti et al. (2007) determined that crust composition was related to topographic position. We found no significant relationships between elevation or HLI and composition change. We sampled a much smaller range of topographic positions (see Additional file 3), and the 10 m DEMs did not account for microtopography in the quadrats.

Crust dynamics can be related to climate because Belnap et al. (2006) found that the aboveground biomass of crust organisms responded to seasonal differences in temperature and moisture. There was little seasonal difference in composition detected at these sites (Ponzetti et al. 2007). However, the trend of decreased bryophyte cover from 1999 to 2010 (Table 2) may relate in part to variation in annual precipitation, because annual precipitation in the 2 years prior to the 1999 sampling period was well above average (> 225 mm per year) but was below average (< 180 mm per year) in the 2 years prior to the 2010 sampling (Western Region Climate Center 2012). However, we had limited spatial and temporal extent and did not test this.

Changes in crust composition may affect ecosystem functioning by, for example, reducing soil stability (Lalley and Viles 2008), nitrogenase activity (Yeager et al. 2004), and chlorophyll content (Belnap 1993; Rychert 2002). The full recovery of visual cover of cyanobacteria did not correspond with recovery of chlorophyll content, lichen species number, and bryophyte and lichen cover up to 5 years following disturbance in Utah (Belnap 1993), indicating that ecosystem structure and function do not recover as rapidly as visual cover.

Conclusions

With increased anthropogenic disturbances, the diversity and function of crust communities may be at risk. Repeated

disturbances may degrade crust communities so that late-successional species are lost from the community or cover declines. We have shown that crust communities are dynamic through time in terms of composition and proportional turnover, and disturbance and invasive species have major effects on crust composition.

Additional files

Additional file 1: Crust taxon codes with species or groups included during monitoring in 1999 and 2010. In 1999, monitoring occurred on 350 quadrats (Ponzetti et al. 2007) and thus some of the taxa included in a given species group were not necessarily present on the 48 quadrats monitored in 2010.

Additional file 2: Bivariate relationships between all predictor variables. The continuous variables include elevation, heat load index (HLI), time since fire relative to 2010 (TSF 2010), cover of *Bromus tectorum* in 1999, and difference in cover of *B. tectorum* between 1999 and 2010. The discrete factors include plot, enclosure, TSF 2010 binned to <11 years, between the two monitoring periods ("recent"), and >11 years, prior to first monitoring period ("late"), and *B. tectorum* cover in 1999 binned to absent and present.

Additional file 3: Bivariate relationships between the potential predictor variables and change metrics. Predictors include plot, enclosure treatment, elevation, heat load index, time since fire relative to 2010 as a continuous variable, time since fire binned to recent (<11 years; within the two measuring periods) and late (>11 years; prior to first measuring period) as used in the analysis, *Bromus tectorum* cover in 1999 as a continuous variable, *B. tectorum* cover in 1999 binned to present and absent as used in the analysis, and change in cover of *B. tectorum* from 1999 to 2010. The response variables include change from 1999 to 2010 in total cover of biological soil crust, cover of bryophytes, cover of lichens, taxa richness, proportional gain, proportional loss, proportional turnover, and Bray-Curtis dissimilarity. A gray horizontal line indicates zero change.

Competing interests

The authors declare that they have no competing interests.

Authors' contributions

EDR carried out the sampling, conducted the analysis, and prepared the manuscript. JMP was involved in the conception and design, carried out the sampling, and helped revise the manuscript. JDB contributed to the acquisition of funds, analysis and interpretation of the data, and helped revise the manuscript. All authors read and approved the final manuscript.

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