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RESEARCH ARTICLE

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Life in interstitial space: Biocrusts inhibit exotic but not native plant establishment in semi-arid grasslands

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Abstract

1. Exotic plant species commonly exploit disturbances more successfully than native plants. This outcome is widely attributed to the fact that disturbance reduces biotic resistance from native plant competitors. However, biocrusts, communities of mosses, lichens, and micro-organisms, are a prominent component of semi-arid grasslands occurring in the interstitial spaces between vascular plants. Biocrusts may provide an important source of biotic resistance to invaders, different from native plant competition, but poorly understood.
2. We established a large-scale field experiment to examine how intact versus disturbed biocrusts influenced the emergence and establishment of four native and four exotic plant species in intermountain bunchgrass systems over 2 years—one wet and one dry. We also conducted a complementary greenhouse experiment to explore how differences in moisture might influence biocrust effects on germination.
3. In the greenhouse, biocrusts inhibited the germination of both native and exotic plants in the high moisture treatment only. In field experiments, biocrusts inhibited the overall emergence of exotic seedlings in the wetter of the 2 years and inhibited the establishment of exotic seedlings in both years, but they had no overall effect on the emergence or establishment of native seedlings. We found that intact biocrusts in intermountain grasslands can suppress the establishment of some exotic plants, but have much weaker effects on natives. They also suggest that water availability may influence biocrust effects on seed germination.
4. *Synthesis*. Our results indicate that intact biocrusts may provide an important source of biotic resistance to exotic plant invasions in intermountain grasslands. Furthermore, precipitation inputs may mediate biocrust effects on plant establishment.

KEYWORDS
biological soil crusts, biotic resistance, disturbance, establishment, exotic plants, germination, grasslands, invasion

1 | INTRODUCTION

The success of exotic plant invaders has been linked to natural and anthropogenic disturbance, perhaps more than any other single causal factor (D'Antonio, Dudley, & Mack, 1999; Jauni, Gripenberg, & Ramula, 2015; MacDougall et al., 2014). Disturbances can alter many abiotic conditions that influence plant establishment like soil structure, hydrology, and nutrient content (White & Pickett, 1985). The biotic resistance hypothesis attributes the high success of exotic plant invaders following disturbance to reduced competition from native plants, which is linked to an increase in resource availability for invaders (Davis, Grime, & Thompson, 2000; Elton, 1958). But, in

semi-arid systems, disturbance affects not only vascular plants but also biological soil crusts (biocrusts hereafter) that occur in the interstitial spaces between vascular plants and may influence vascular plant establishment (Zhang, Aradottir, Serpe, & Boeken, 2016). Yet, disturbance-invasion experiments in biocrust-dominated systems generally have not distinguished the effects of vascular plants from those of biocrusts (e.g., Maron, Pearson, Potter, & Ortega, 2012; Pearson, Ortega, Villarreal, et al., 2018). Biocrusts may play an important but cryptic role in resisting exotic plant invasions that should be elucidated to fully understand the biotic resistance of arid and semi-arid systems.

Biocrusts are complex communities of lichen, moss, cyanobacteria, and other micro-organisms that inhabit soil surfaces among plants in arid and semi-arid systems, where they can cover large portions of the ground surface (Belnap, Büdel, & Lange, 2001; Daubenmire, 1942). Biocrusts can stabilize soil (Belnap & Gardner, 1993), regulate water, and nutrient cycling (Chamizo, Cantón, Lázaro, Solé-Benet, & Domingo, 2012; Harper & Pendleton, 1993; Pendleton, Pendleton, Howard, & Warren, 2003), buffer soil temperatures (Gornall, Woodin, Jonsdottir, & Van der Wal, 2009), and influence the establishment of vascular plants via physical and chemical effects on seed germination and seedling establishment (Zhang et al., 2016). In short, biocrusts provide many ecosystem services and may act as important filters to plant establishment in dryland systems.

Many studies examining the effects of biocrusts on vascular plant establishment are from systems where biocrusts are composed of cyanobacteria and/or lichen. In these systems, cyano-lichen biocrusts generally inhibit plant germination, with disturbance to biocrusts often improving the germination of both native and exotic plants (Deines, Rosentreter, Eldridge, & Serpe, 2007; Song, Li, & Hui, 2017; but see Havrilla & Barger, 2018). These inhibitory effects on germination have been primarily attributed to the negative impact of intact cyano-lichen biocrusts on seed water availability (Eldridge & Greene, 1994; Escudero, Martínez, de la Cruz, Otálora, & Maestre, 2007; Hawkes, 2004; Serpe, Zimmerman, Deines, & Rosentreter, 2008; Zhang, Wu, Zhang, & Zhang, 2010). In addition, seeds that do germinate on intact cyano-lichen biocrusts often do not survive because these biocrusts physically and chemically inhibit root penetration (Beyschlag, Wittland, Jentsch, & Steinlein, 2007; Eldridge, Semple, & Koen, 2000; Prasse & Bornkamm, 2000; Serpe et al., 2008; Song et al., 2017; Zaady, Gutterman, & Boeken, 1997).

In contrast, biocrusts composed of lichens and mosses appear to have different effects on plants than cyano-lichen biocrusts. Intact lichen-moss biocrusts vary in the direction of their effect on native plant germination from positive to negative, sometimes within the same system, and perhaps due to species-specific vascular plant responses (Deines et al., 2007; Godínez-Alvarez, Morín, & Rivera-Aguilar, 2012; Hernandez & Sandquist, 2011). Intact lichen-moss biocrusts also generally negatively influence exotic plant germination (Eldridge & Simpson, 2002; Hernandez & Sandquist, 2011; but see Deines et al., 2007). Importantly, most of these studies have taken place in artificial environments or incorporated only a few native or exotic species (Deines et al., 2007; Eldridge & Simpson, 2002; Godínez-Alvarez et al., 2012). In the only replicated field experiment that has evaluated the influence of lichen-moss biocrusts on the germination of multiple native and exotic species, exotics generally benefitted more from biocrust disturbance than did natives (Hernandez & Sandquist, 2011). These findings suggest that disturbing biocrusts reduces biotic resistance and facilitates invasion; however, this study did not control for seed inputs, a factor which can strongly influence invasion (Von Holle & Simberloff, 2005). A better understanding of how lichen-moss biocrusts influence invasion outcomes requires field experiments that manipulate biocrust disturbance while controlling for seed inputs across multiple native and exotic plant species. Moreover, given that interactions between some biocrusts and plants vary mechanistically with plant ontogeny (Godínez-Alvarez et al., 2012; Prasse & Bornkamm, 2000; Serpe et al., 2008; Song et al., 2017; Zhang et al., 2010), studies should evaluate the effects of biocrusts at different developmental stages.

In the semi-arid intermountain grasslands west of the Continental divide in the United States, lichen-moss biocrusts historically accounted for over 50% of the land cover unoccupied by vascular plants prior to the introduction of livestock (Mack & Thompson, 1982). However, widespread and long-term livestock grazing has caused extensive damage to biocrusts (Poulton, 1955; Daubenmire, 1942; Krannitz, 2008), coincident with the proliferation of exotic plants (Krannitz, 2008; Mack, 1981). Positive correlations between native plants and biocrust cover, and negative correlations between exotic plants and biocrust cover, suggest that intact biocrusts may contribute to biotic resistance in these systems (Lesica & Shelly, 1992; Peterson, 2013; Scott & Morgan, 2012; Stohlgren, Otsuki, Villa, Lee, & Belnap, 2001). While field experiments in intermountain grasslands show that disturbance strongly favours the establishment of exotic plant species over natives (Maron et al., 2012; Pearson, Ortega, Villarreal, et al., 2018), these studies have not considered the role of biocrusts.

We investigated the role of lichen-moss biocrusts on native and exotic plant establishment in intermountain grasslands of western Montana, USA. We conducted field experiments in which we added the seeds of four native and four exotic plant species to biocrusts that were intact, disturbed or removed to examine whether biocrusts differentially affected the germination and establishment of native and exotic plants in natural grasslands. We also mimicked this experimental design in a greenhouse setting to evaluate the effects of biocrusts on seedling germination and emergence under controlled conditions. Furthermore, we incorporated a high and low moisture treatment in the greenhouse experiment to evaluate how moisture levels influenced biocrust effects on germination and emergence since the field experiment suggested that inter-annual differences in precipitation inputs might alter biocrust effects. Our approach offers a unique examination of biocrust function by combining a large-scale field experiment that evaluates the responses of multiple native and exotic plant species to biocrust manipulations over 2 years with a complementary greenhouse experiment.

2 | MATERIALS AND METHODS

2.1 | Field experiment

Our field experiments were conducted at four locations within bluebunch wheatgrass (*Pseudoroegneria spicata*) habitats of west-central Montana (Mueggler & Stewart, 1980) from 2015 to 2017. Without invasion, these communities are comprised of scattered native perennial bunchgrasses, forbs, and shrubs with interstitial spaces dominated by lichen-moss biocrust communities. Biocrust cover in our study sites was predominately lichens from the genera *Peltigera* and *Cladonia* and mosses from the genus *Syntrichia* with a physical microtopography that could be characterized as "rolling" (Belnap, 2001). Annual rainfall in our study area averages 325 mm a year and occurs primarily in May and June, with low rainfall from July through mid-September (www.ncdc.noaa.gov). The 2 years of our experiments varied substantially in rainfall during the timeframe that is most likely to influence seedling germination and growth, with 78% more precipitation falling from January to June in 2017 than in 2016 (25.6 vs. 144 mm respectively).

We conducted seed addition experiments in 2015–2016 and 2016–2017 to evaluate how biocrust, biocrust disturbance, and biocrust removal affected emergence and establishment of eight common native and exotic plant species (Table 1). In October 2015, we selected four field sites separated by at least 70 km and all sites distributed over ~20,000 km^2 (Site 1: 47.3706° N, 114.2571° W; Site 2: 46°54′43.4″N 113°58′07.1″W; Site 3: 46°39′37.2″N 113°14′49.9″W; Site 4: 46°59′28.2″N 113°05′44.5″W). Grasslands at our sites were moderately disturbed, primarily by livestock, but contained intact lichen-moss biocrusts. Experiments were set up along four 20 m transects each separated by at least 20 m. Five (2015–2016) or eight (2016–2017; see below) 1 × 1 m quadrats were placed along each transect where biocrusts were abundant enough to establish treatments. New transects and quadrats were established in the second year. Each quadrat on each transect was assigned to one plant species, with all species represented on each transect once. Three 10 × 10 cm subplots with biocrusts were located in each quadrat. One subplot was disturbed by striking the ground with a mallet 20 times. This method effectively broke up the biocrust and roughly simulated trampling by cattle hooves under wet conditions. Biocrusts were removed from a second subplot by scraping, but with minimal disturbance to the underlying soil. Biocrusts were left intact in the third subplot. In October 2015 and 2016, we added 20 seeds of a single plant species to the surface of each subplot within each quadrat (seed collection discussed below). In 2015, we sowed seeds of three native species, *Achillea millefolium*, *Cerastium arvense*, and *Poa secunda*, and two exotic species, *Centaurea stoebe* and *Poa bulbosa* at each site. In 2016, we established new transects at each site and sowed seeds of the same five species but added the native *Pseudoroegneria spicata* and the exotics *Bromus tectorum* and *Potentilla recta*. We added *Pseudoroegneria* in 2016 to include a dominant bunchgrass. *Bromus* and *Potentilla* were added because they are the first and fourth highest impact invaders in this system, respectively, with *Centaurea* being the second highest impact invader (Pearson, Ortega, Runyon, & Butler, 2016). Additionally, *Bromus* provided an example of an annual exotic. For each species and each treatment at each of the four sites, in both years, there were four replicates. Because species varied substantially in the timing of their germination, we visited the plots two times each year in the spring to record emergence, defined as the maximum number of seedlings on either date. Thus, emergence was a rough estimate of true emergence since seeds may have emerged and died between our visits and surviving seeds may have emerged after early visits. We visited the plots a third time in each year to record establishment, defined as the number of surviving seedlings, at the beginning of the dry season. In 2016, we recorded emergence on 10 March and 14 April and establishment on 10 May, yet could only measure establishment at three of our four sites. In 2017, we recorded emergence on 7 April

TABLE 1 Vascular plant species included in field and greenhouse studies are categorized by plant origin, family, functional group, and life-history strategy. Number of seeds added for each plant species in the greenhouse (GH) and field experiments are included as are the years that each species was included in the field experiment (Field Years) and its' seed mass

Species	Origin	Family	Functional group	Life history	# Seeds GH/field	Field years	Seed mass (mg)
Achillea millefolium Common yarrow	Native	Asteraceae	Forb	Perennial[c]	20/20	2016, 2017	0.13
Cerastium arvense Field chickweed	Native	Caryophyllaceae	Forb	Annual[c]	20/20	2016, 2017	0.28
Poa secunda Sandberg bluegrass	Native	Poaceae	Grass	Perennial[c]	15/20	2016, 2017	0.43
Pseudoroegneria spicata Bluebunch wheatgrass	Native	Poaceae	Grass	Perennial[c]	15/20	—, 2017	1.52
Centaurea stoebe Spotted knapweed	Exotic[a]	Asteraceae	Forb	Perennial[b]	20/20	2016, 2017	2.55
Potentilla recta Sulphur cinquefoil	Exotic[a]	Rosaceae	Forb	Perennial[c]	20/20	—, 2017	0.21
Poa bulbosa Bulbous bluegrass	Exotic	Poaceae	Grass	Perennial[c]	15/20	2016, 2017	1.64
Bromus tectorum Cheatgrass	Exotic[a]	Poaceae	Grass	Annual[c]	15/20	—, 2017	3.04

[a]Species listed as a noxious weed or Priority 3 species by the Montana Noxious Weed List. [b]Boggs and Story (1987). [c]https://plants.usda.gov.

and 5 May and establishment on 1 July at all four sites. Emergence and establishment were measured later in 2017 because of a more persistent snowpack and rainy spring.

Seeds were collected annually from >30 individuals of each species in the Missoula Valley, MT (46.8787° N, 113.9966° W), which is centrally located among the experimental sites. Seeds from all plants for a species were combined and mixed before sowing. *Bromus tectorum* seeds were placed in a warm and dry location for 1 month to end dormancy prior to sowing (Serpe et al., 2008). All species exhibited ≥85% germination on filter paper in Petri dishes. A subset of seeds for each species was dried at 60°C for 48 hr and weighed individually (n = 8).

2.2 | Greenhouse experiment

The long distances between field sites prevented us from visiting sites frequently enough to measure germination repeatedly and precisely in the field. Therefore, we conducted a greenhouse experiment to examine the potential effects of lichen-moss biocrusts on the germination of our study species under high and low moisture conditions. Dry plugs of intact biocrusts were collected with a bulb planter (6.5 cm wide and 7.5 cm deep) from two of our field sites on 14 and 15 June, 2016 and placed into 6.5 × 6.5 cm square plastic Ziploc containers that allowed drainage. Containers were randomly assigned to treatments as follows: intact biocrusts, disturbed biocrusts (crumbled by hand) and bare soil (soil from below biocrusts that were removed). Initially, all containers were misted twice a day, 2 min per misting, for 10 days to allow settling from harvesting and promote the germination and removal of preexisting seeds and seedlings (Zhang & Belnap, 2015). On 25 June, seeds from the same eight study species (Table 1) used in our field trials in the second year were sown on the biocrust or soil surface (n = 16 for each species and each treatment). Because grass seeds were much larger than forb seeds and pots were small, we sowed 15 grass seeds versus 20 forb seeds in each pot (in all cases, seed number was later incorporated in our statistical models). Containers were randomly assigned to either a high water treatment or a low water treatment. High water treatment containers were misted for 1 min a day, which completely hydrated the biocrusts and soil but allowed them to dry out by the time they were watered the next day. Low water treatment containers were watered for 1 min every 3 days which meant that biocrusts and soils were very dry for 2 days (n = 8 per species per disturbance treatment by water treatment combination). Containers were rotated randomly on the tables within their respective watering treatments every 3 days. Seedlings first appeared on 29 June and were counted daily for 12 days, after which very few new seedlings emerged. We determined the total percentage of sown seeds that germinated for each species and the average first day of germination.

2.3 | Statistical analyses

Except for percent germination, analyses were conducted in R version 3.5.1 (R Core Team, 2018) using the MASS (Venables & Ripley, 2002), lme4 (Bates, Maechler, Bolker, & Walker, 2015), and emmeans (Lenth, 2018) packages. To test the effects of plant origin (native vs. exotic) and biocrust treatment (intact biocrust, disturbed biocrust, or removed biocrust) on the number of seedlings, we used generalized linear mixed-effects models (one GLMM for emergence and one for establishment). Since we used different numbers of species in each of our two study years (2015–2016 or 2016–2017), we ran two separate GLMMs for each year (four GLMMs total). In these models, treatment was nested in species, transect, and site and treated as a random factor. We also analysed the number of emerged and established seedlings for each plant species individually (16 separate GLMMs). For those species with 2 years of data, both years of data were included. However, when factors had a significant effect on emergence or establishment of an individual species as determined by a χ^2-test ($p < 0.05$), we analysed the number of emerged or established seedlings for a single plant species in each year separately with one GLMM per year. Site (four sites) was included as a random factor for blocking with transect (four per site) and treatment nested within site for all models. For two species (*Pseudoroegneria* and *Bromus*), no seedlings survived on intact biocrusts. Mixed models for establishment in these cases were simplified by removing the random effects to reach convergence. We accounted for zero inflation with a negative binomial distribution in all models. We examined residuals with normality tests which in all cases were reasonable. When factors had a significant effect on a response variable, as determined by a χ^2-test ($p < 0.05$), we used least squares mean contrasts to evaluate those relationships. Data from experimental subplots that were disturbed in ways other than our removed/disturbed treatments were excluded from the final analyses (0 subplots affected in 2016; 9 subplots affected in 2017). There were only a few cases where results differed between disturbed and removed biocrust treatments for origin or species, so these two treatments were pooled in our final analyses. The estimation method used in GLMMs accounts for imbalances in sample size (Bolker et al., 2009). The negative binomial distribution accounts for heteroscedasticity among treatment groups by assuming that the variance increases with the mean. Because of this, our least squares means were adjusted for imbalances. Finally, to understand how seed mass relates to seedling establishment on intact or removed/disturbed biocrusts, we evaluated the relationship between seed mass and seedling establishment for all species with both years of establishment combined on intact or removed/disturbed biocrusts with regression analysis.

To assess the effect of plant origin, biocrust treatment, and water treatment on percentage seed germination (number of seeds germinated/number of seeds added), we ran a log-normal Type III ANOVA model using the GLIMMIX module (SAS, version 9.2) to account for the skewness of the data. Post hoc differences among treatment means were evaluated with multiple comparisons and adjusted for the number of comparisons. We used a GLMM to determine how plant origin (native or exotic), biocrust treatment (intact, disturbed, or bare soil), and water treatment (high or low water) influenced the average first day of seed germination in our

TABLE 2 Results from mixed models used to compare the effects of origin and biocrust treatment (Trtmt) by year on the number of seedlings in the early (*emergence*) and later part (*establishment*) of the growing season in our field experiment. Significant ($p \leq 0.05$) values are in bold

	Emergence			Establishment		
Effect	***Df***	χ^2	***p*-value**	***df***	χ^2	***p*-value**
2016						
Origin	1 (239)	23.9	**<0.001**	1 (179)	7.97	**0.005**
Treatment	1 (239)	0.92	0.338	1 (179)	0.73	0.393
Origin × Trtmt	1 (239)	1.01	0.314	1 (179)	7.76	**0.005**
2017						
Origin	1 (382)	0.33	0.563	1 (373)	7.73	**0.005**
Treatment	1 (382)	24.1	**<0.001**	1 (373)	9.87	**0.002**
Origin × Trtmt	1 (382)	2.46	0.117	1 (373)	7.84	**0.005**

greenhouse experiment. When factors had a significant effect on a response variable ($p < 0.05$), we used least squares mean contrasts to evaluate those relationships. Site where biocrusts were collected ($n = 2$) was included as a random variable in all greenhouse models. Germination patterns on disturbed and bare soil treatments were similar and thus, pooled as above. To understand how seed mass relates to seed germination on intact or removed/disturbed biocrusts, we evaluated the relationship between seed mass and seed germination for all species and water treatments combined on intact or removed/disturbed biocrusts with regression analysis.

3 | RESULTS

3.1 | Field experiment

3.1.1 | Emergence

In 2016, across all treatments, five times more exotic seedlings emerged than native seedlings (Table 2). In 2016, there was no difference in exotic seedling emergence on intact versus removed/disturbed biocrusts (LSMeans, $Z_{1,64} = -0.29$, $p = 0.99$), but in 2017, 41% fewer exotic seedlings emerged on intact biocrusts than on removed/disturbed biocrusts (LSMeans, $Z_{1,127} = -4.54$, $p < 0.001$; Figure 1). For natives, there was no difference in the number of seedlings that emerged on intact or removed/disturbed biocrusts in 2016 (LSMeans, $Z_{1,96} = -1.36$, $p = 0.52$) or in 2017 (LSMeans, $Z_{1,129} = -2.52$, $p = 0.06$; Figure 1). For individual species, there was lower seedling emergence on intact biocrusts than removed/disturbed biocrusts for the native forb *Cerastium* (both years), the exotic forb *Potentilla* (2017 only), and the exotic grass *Bromus* (2017 only; Table 3, Figure 2). However, *Cerastium* seedling emergence was only lower on intact versus removed/disturbed biocrusts in 2017 (GLMM, $df = 1(47)$, $\chi^2 = 11.25$, $p < 0.001$), and not in 2016 (GLMM, $df = 1(47)$, $\chi^2 = 0.09$, $p = 0.767$).

3.1.2 | Establishment

In 2016, twice as many exotic seedlings established on removed/disturbed biocrusts than on intact biocrusts (LSMeans, $Z_{1,64} = -2.60$, $p = 0.05$). In 2017, over five times as many exotic seedlings established on removed/disturbed biocrusts than intact biocrusts (LSMeans, $Z_{1,124} = -4.05$, $p < 0.001$; Figure 1). There was no overall difference in the number of native seedlings that established on intact versus removed/disturbed biocrusts in either year (LSMeans, 2016: $Z_{1,72} = 1.33$, $p = 0.54$; 2017: $Z_{1,126} = -1.20$, $p = 0.62$). In 2016, over four times more exotic than native seedlings established on removed/disturbed biocrusts than on intact biocrusts (LSMeans,

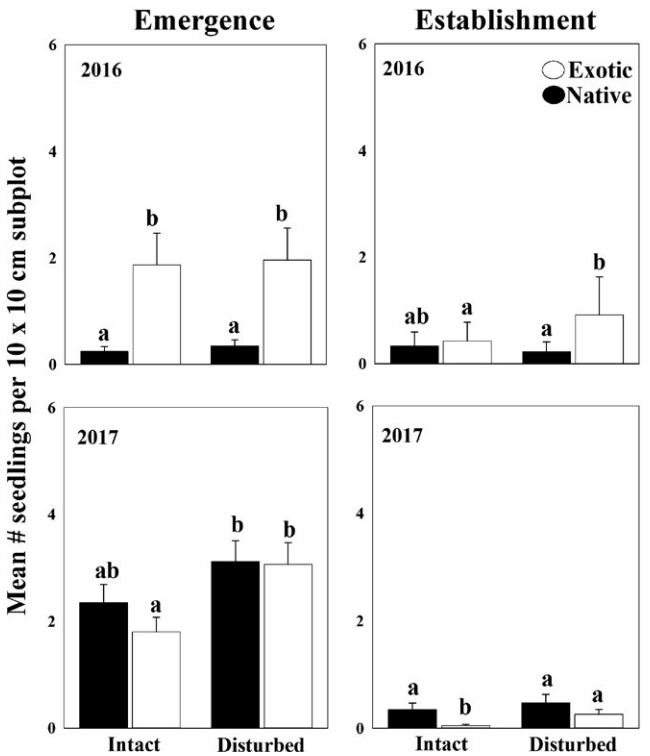

FIGURE 1 Seedling emergence and establishment for native and exotic plant species on intact or experimentally removed/disturbed biocrusts in northwestern Montana grasslands in 2016 and 2017. Seedling emergence is defined as the maximum number of seedlings present during either of our two spring surveys. Establishment is defined as the number of surviving seedlings at the beginning of the dry season. Bars represent least squared means + *SE*. Different letters indicate differences among treatments based on least squares mean contrasts

TABLE 3 Results from mixed models (16 separate models) used to compare the effect of biocrusts on seedling emergence and establishment for each study species in the field experiment. Data were pooled between years for all species except *Pseudoroegneria*, *Potentilla*, and *Bromus* which were used only in the second year (see Table 1). Significant ($p \leq 0.05$) effects of biocrusts are in bold

	Emergence			Establishment		
	df	χ^2	*p*-value	*df*	χ^2	*p*-value
Native species						
Cerastium	1 (90)	3.79	**0.051**	1 (81)	1.48	0.224
Achillea	1 (90)	2.68	0.101	1 (75)	0.46	0.497
P. secunda	1 (90)	0.61	0.433	1 (81)	1.50	0.221
Pseudoroegneria	1 (42)	0.11	0.744	1 (45)	1.19	0.275
Exotic species						
Potentilla	1 (42)	16.0	**<0.001**	1 (42)	5.88	**0.015**
Centaurea	1 (90)	2.20	0.138	1 (78)	8.49	**0.004**
Bromus	1 (41)	3.89	**0.048**	1 (41)	12.1	**<0.001**
P. bulbosa	1 (90)	2.44	0.118	1 (78)	3.49	0.061

$Z_{1,68} = 2.82$, $p = 0.005$), but there was no difference in the number of exotic and native seedlings that established on intact versus removed/disturbed biocrusts in 2017 (LSMeans, $Z_{1,126} = -1.71$, $p = 0.32$). Seven times more native than exotic seedlings established on intact biocrusts in 2017 (LSMeans, $Z_{1,126} = -3.94$, $p < 0.001$). For individual species, establishment of all exotic species except *P. bulbosa* was inhibited by intact biocrusts (Table 3, Figure 2). In contrast, intact biocrusts did not inhibit the establishment of any native species (Table 3). Seed mass did not explain seedling establishment patterns on intact or removed/disturbed biocrusts (Table S2).

3.2 | Greenhouse experiment

3.2.1 | Percentage germination

The germination percentage of native and exotic species was affected by biocrust and water treatments (Table 4). Seed germination percentages of native and exotic species were 17 and 11 times lower on intact biocrusts than on bare soil/disturbed biocrusts under high water conditions respectively (LS Means, native: $t_{1,98} = 5.71$, $p < 0.0001$; exotic: $t_{1,98} = 4.61$, $p < 0.0001$; Figure 3). Under low water conditions there was no difference in native or exotic seed germination percentages on intact versus bare soil/disturbed biocrusts (LS Means, native: $t_{1,97} = 0.25$, $p = 0.80$; exotic: $t_{1,98} = 0.64$, $p = 0.52$). When seeds were placed on bare soil/disturbed biocrusts, 2.7 times fewer exotic than native species germinated under high water conditions (LS Means, $t_{1,128} = -2.51$, $p = 0.01$). Seed mass did not explain seed germination patterns on intact or removed/disturbed biocrusts (Table S2).

3.2.2 | First day of germination

The average first day of germination was affected by plant origin, biocrust treatment, and water treatment (Table 4). There was no effect of water treatment on the timing of germination for native or exotic seeds on intact biocrusts (LS Means, native: $Z_{1,189} = -0.19$, $p = 0.998$; exotic: $Z_{1,190} = 1.92$, $p = 0.219$; Figure 3). However, native seeds germinated 3.7 days earlier on intact biocrusts than bare soil/disturbed biocrusts under high water conditions (LS Means, $Z_{1,189} = 2.43$, $p = 0.061$). The timing of germination for exotics did not differ between biocrust treatments under high water conditions (LS Means, $Z_{1,190} = 1.44$, $p = 0.476$) and there was no difference in the timing of native or exotic seed germination on intact or bare soil/disturbed biocrusts under low water conditions (Table 4).

4 | DISCUSSION

Disturbance in semi-arid grasslands is often followed by increases in exotic plant abundance. Such events can transform native perennial grasslands to stands of exotic forbs and annual grasses (Chambers et al., 2014; Knapp, 1996; Kulmatiski, 2006; Pearson, Ortega, Villarreal, et al., 2018). These widespread shifts in plant community composition are generally attributed to disturbance decreasing the strength of biotic resistance by reducing competitive resistance from native vascular plants (e.g., Besaw, Thelen, Sutherland, Metlen, & Callaway, 2011; Callaway et al., 2011; Jauni et al., 2015; Levine et al., 2003; Vilà et al., 2011). Interestingly, we found that the disturbance of biocrusts in the interstitial space between native vascular plants also increased the establishment of exotic species. These findings suggest that biocrusts may represent a unique source of biotic resistance in semi-arid grassland systems that should be considered in invasion theory.

Lichen-moss biocrusts provided a strong barrier to exotic plant invaders in our system. In fact, biocrusts suppressed establishment of three of the worst invaders in these grasslands: *Bromus*, *Centaurea*, and *Potentilla* (see Pearson et al., 2016). Across our field sites, intact biocrusts suppressed exotic plant establishment in both years (Figure 1), but native plant establishment was not affected by biocrusts in either year. In 2016, intact biocrusts held exotic establishment at levels comparable to the natives, but when biocrusts were disturbed exotic establishment increased to levels that were four times higher than that of the natives. In 2017, intact biocrusts suppressed exotic establishment seven times more than that of natives, and disturbance to biocrusts increased the establishment of

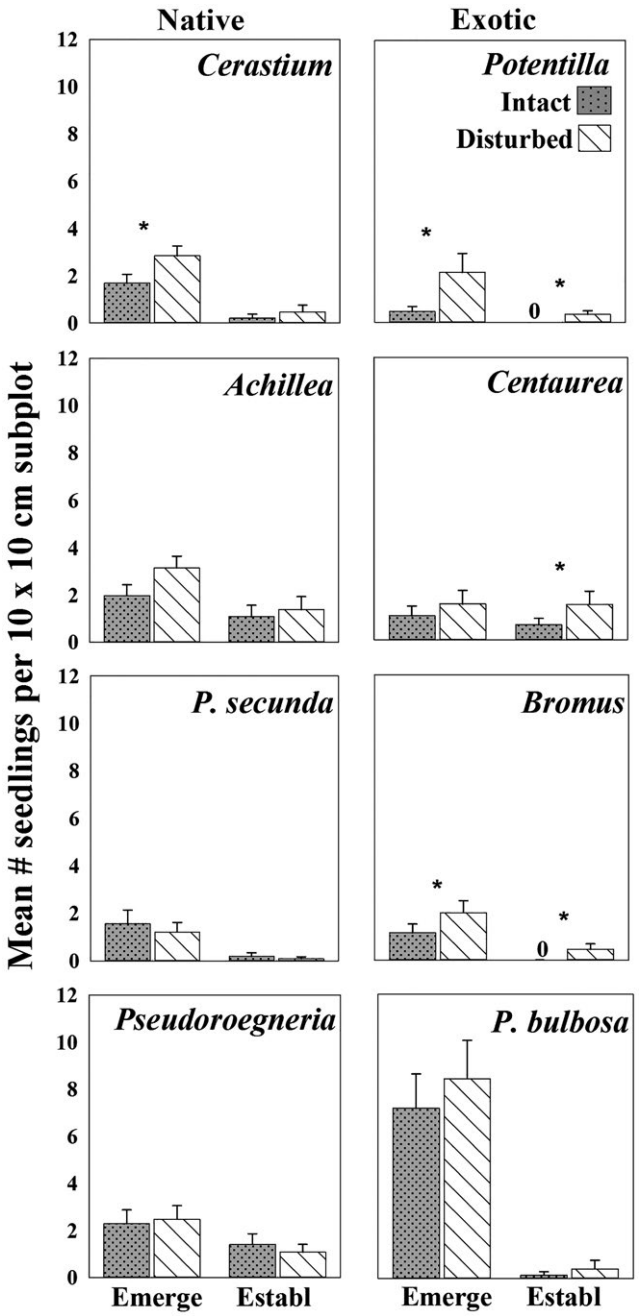

FIGURE 2 Seedling emergence and establishment for individual native and exotic plant species on intact or experimentally removed/disturbed biocrusts in northwestern Montana grasslands. Data are 2 years averages for all species but *Pseudoroegneria*, *Bromus*, and *Potentilla* which were only included in the 2017 study. Biocrust effects on *Cerastium* emergence were driven by emergence effects during the wet study year (2017). Bars represent least squared means + *SE*. Asterisks indicate differences between treatments based on least squares mean contrasts

exotics to levels comparable to that of natives. These patterns were generally consistent across species with three of four exotics showing increased establishment on disturbed biocrusts and no natives exhibiting this pattern (Figure 2). In sum, biocrusts suppressed exotic but not native plant establishment in our field experiments. An important question then is how do biocrusts suppress plant establishment and why might this differ by species' origin?

Interactions between lichen-moss biocrusts and vascular plants can vary at different stages in plant ontogeny (Deines et al., 2007; Godínez-Alvarez et al., 2012). Mechanistically, lichen-moss biocrusts can inhibit seed germination and seedling emergence through competition for water, exudation of secondary compounds (Favero-Longo & Piervittori, 2010; Michel, Burritt, & Lee, 2011; Serpe et al., 2008), or by creating a physical barrier that prevents roots from contacting the soil (Deines et al., 2007), but these processes are poorly understood. Few studies have compared the effects of biocrusts on native versus exotic plants from germination to establishment and, to our knowledge, none have considered the influence of water availability on these effects.

Our results suggest that moisture inputs may mediate lichen-moss biocrust effects on vascular plants in intermountain grasslands. In the greenhouse, we found that intact biocrusts inhibited the germination of both native and exotic species under high but not low water conditions (Figure 3). In the field experiments, this pattern was mirrored to some extent, with biocrusts inhibiting germination of one native and two exotics only in the wetter year. Notably, the two exotic species, *Potentilla* and *Bromus*, were only added in the wetter year, so it remains unclear whether these species would have shown germination inhibition in the field in the dry year. Overall, biocrust suppression of native and exotic plant germination appeared to be mediated by higher moisture conditions—a result that could arise from direct competition for water (Serpe et al., 2008) or from inhibitory biocrust exudates (Favero-Longo & Piervittori, 2010; Michel et al., 2011). However, it remains unclear to what extent these processes influenced final plant establishment in the field since native establishment was not affected by biocrusts in either year and exotic establishment was suppressed by biocrusts in both the wet and dry years. Hence, water inputs may influence biocrust effects on plant germination but other factors are also important in determining final plant establishment in the field—the ultimate measure of how biocrusts influence plant populations and communities.

Community assembly theory (Keddy, 1992) suggests that plant traits should determine their responses to ecological filters like biocrusts, and recent work suggests that traits can also explain provenance effects in this context (Pearson, Ortega, Eren, & Hierro, 2018; Pearson, Ortega, Villarreal, et al., 2018). As such, life-history strategy, functional group, or quantitative traits like seed size or seed morphology might explain vascular plant interactions with lichen-moss biocrusts, but few studies to date have explored these patterns. In Californian coastal sage scrub, the native ruderal perennial, *Lotus scoparius*, was inhibited by intact biocrusts, whereas the native late successional perennial, *Artemisia californica*, was facilitated by biocrusts (Hernandez & Sandquist, 2011). In our study, even with eight species, we saw no clear linkages between biocrust effects on establishment and life-history or functional traits for our species (see Table 1). Biocrust microtopography can interact with traits like seed size and seed external morphology to influence germination in systems where biocrusts have a thick

Effect	Germination percentage			Germination day		
	df	*F*	*p*-value	*df*	*F*	*p*-value
Origin	1 (373)	6.27	**0.013**	1 (373)	5.50	**0.019**
Biocrust treatment	1 (373)	31.3	**<0.001**	1 (373)	4.54	**0.033**
Water treatment	1 (373)	47.2	**<0.001**	1 (373)	22.3	**<0.001**
Biocrust × Origin	1 (373)	0.12	0.725	1 (373)	0.01	0.942
Water × Origin	1 (373)	0.24	0.623	1 (373)	0.99	0.318
Water × Biocrust	1 (373)	22.1	**<0.001**	1 (373)	3.20	0.073
Water × Biocrust × Origin	1 (373)	0.54	0.462	1 (373)	1.35	0.246

TABLE 4 Results from type III tests (germination percentage) or mixed models (germination day) used to compare the fixed effects of plant origin, biocrust treatments, and water treatments on seed germination percentage and first day of germination in the greenhouse experiment. Significant ($p \leq 0.05$) values are in bold

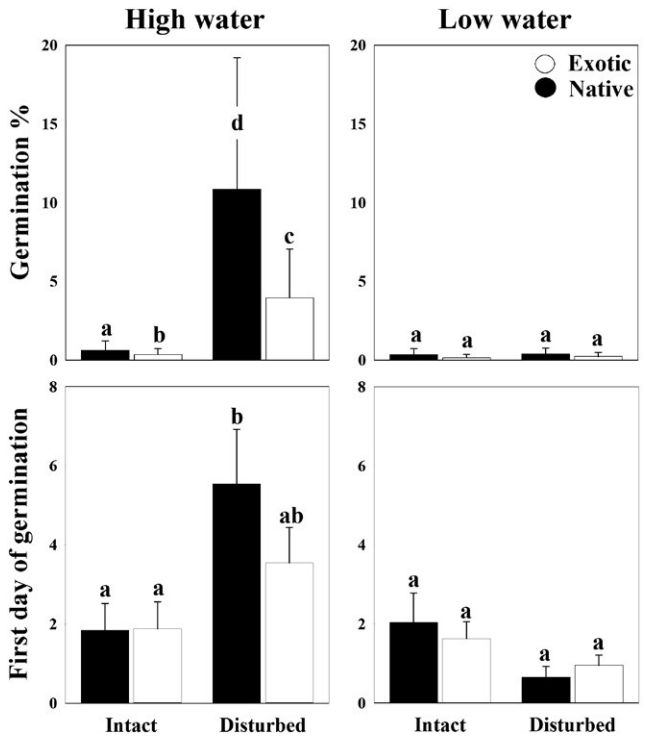

FIGURE 3 Seed germination percentage (upper panels) and first day of germination (lower panels) for native and exotic species on intact or removed/disturbed biocrusts in a greenhouse experiment. Seeds were watered daily (high) or every 3 days (low). Bars represent least squared means + *SE*. Different letters indicate differences in least squares mean contrasts

rolling microtopography and are dominated by mosses (Morgan, 2006) or when biocrusts have a pinnacled or rugose microtopography and are dominated by lichen and cyanobacteria (Havrilla & Barger, 2018; Zhang & Belnap, 2015). Smaller seeds may slip through cracks commonly found on biocrust surfaces to encounter soil, whereas larger seeds or seeds with appendages like awns may fail to contact soil through biocrust cracks and have less access to moisture (Eldridge & Greene, 1994). We found that seed mass did not explain germination or establishment patterns on intact or disturbed biocrusts (Table S2). Awns were present on two grasses in our study, the exotic *Bromus* and the native *Pseudoroegneria*, but only the exotic was inhibited by biocrusts.

Differences in the timing of germination, and plasticity in germination timing, can benefit plant establishment by providing additional time for resource acquisition prior to the onset of dry conditions (Gioria, Pyšek, & Osborne, 2018) or by enabling seedling establishment prior to pathogen attacks (e.g., Beckstead, Meyer, Connolly, Huck, & Street, 2010). Exotic species often differ from native species in their germination phenology (Gioria et al., 2018; Pyšek & Richardson, 2007) and annual exotics, in particular, may find success in perennial grasslands by germinating earlier than native species (Abraham, Corbin, & D'Antonio, 2009; Wainwright & Cleland, 2013). In contrast, we found that germination timing was only altered for native species and only in the high water treatment where native species germinated earlier than exotic species on intact biocrusts (see Table S1 for species-specific patterns). Overall, we found no clear linkages between the plant traits that we evaluated and plant germination or establishment responses to biocrusts in intermountain grasslands.

It is possible that the provenance difference we observed was due to increases in nutrient availability associated with biocrust removal and disturbance. While we did not quantify the effects of disturbance on nutrient availability, prior work indicates that biocrusts can increase nutrient availability following disturbance (Barger, Weber, Garcia-Pichel, Zaady, & Belnap, 2016; Ferrenberg, Faist, Howell, & Reed, 2017). Exotics are known to exploit such nutrient increases more effectively than native species (Besaw et al., 2011; Ferrenberg, Tucker, & Reed, 2017; Jauni et al., 2015; MacDougall et al., 2014), but the reason for this provenance bias is unresolved. Mechanistically, recent work in intermountain grasslands demonstrated that experimental disturbances increased nitrogen availability which favored exotic over native plant establishment—a result linked to the fact that exotics in local species pools were more strongly represented by ruderal species than were the more stress-tolerant natives (Pearson, Ortega, Villarreal, et al., 2018). The exotics that responded most strongly to biocrust disturbance in our study were among the more ruderal species that we examined, but we did not have enough species to rigorously evaluate this question. A better understanding of how ecological filters like biocrusts affect biological invasions will require studies that examine multiple traits for many native and exotic species.

Our finding that lichen-moss biocrusts are important ecological filters which may interact with precipitation inputs to affect plant establishment has important implications for understanding intermountain grasslands. Although establishment was low in this study, as were the absolute differences between native and exotic responses to biocrusts, prior work demonstrates that factors affecting early plant establishment in these systems have lasting effects on plant populations and community structure (Bricker, Pearson, & Maron, 2010; J.L. Maron & D.E. Pearson, *unpublished data*). Moreover, while recruitment is low in most years (Maron et al., 2012; Pearson & Callaway, 2008), wetter weather in spring greatly increases plant recruitment (Maron, Hajek, Hahn, & Pearson, 2018; Pearson, Valliant, Carlson, et al., 2019). Therefore, understanding these and possibly other semi-arid grassland systems requires knowledge of the roles that biocrusts and precipitation play as independent and interacting ecological filters in vascular plant establishment.

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AUTHORS' CONTRIBUTIONS

M.L.S., R.M.C., and D.E.P. designed the study. M.L.S. performed the research and analysed the data; and all authors contributed to writing.

DATA ACCESSIBILITY

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.08dn485 (Slate, Callaway, & Pearson, 2018).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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