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Applying community ecological theory to maximize productivity of cultivated biocrusts

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Abstract. Degraded rangelands around the world may benefit from the reestablishment of lost biological soil crusts (biocrusts, soil surface cryptogamic-microbial communities). Cultivation of biocrust organisms is the first step in this process, and may benefit from harnessing species interactions. Species interactions are a dominant force structuring ecological communities. One key element of community structure, species richness, is itself important because it can promote the productivity of the entire community. Here, we use biological soil crusts as a model to test the effects of species interactions on production of biocrust materials for use in ecosystem rehabilitation. We screened eight different moss and lichen species from semiarid rangelands of Montana, USA, for growth potential under two watering regimes. Mosses generally grew well, but we were unable to cultivate the selected lichen species. We produced a >400% increase in the biomass of one species (*Ceratodon purpureus*). We tested whether a parasite–host relationship between two lichens could be used to enhance productivity of the parasite species, but this also resulted in no net gain of lichen productivity. Finally, we constructed all possible community combinations from a pool of five moss species to test for overyielding (community productivity exceeding that expected from the growth of community members in monoculture), and to determine both if, and the mode in which, species richness increases productivity. Polycultures yielded more than would be expected based upon the production of community constituents in monoculture. Using structural equation models, we determined that there was a modest effect of species richness on community productivity (r = 0.24–0.25), which was independent of a stronger effect of the identity of species in the community (r = 0.41–0.50). These results will contribute to the optimization of biocrust cultivation, promoting the development of this emerging ecological rehabilitation technology.

Key words: biodiversity–productivity relationship; biological soil crust; ecological restoration; lichen; moss; species interactions.

Introduction

A fundamental process of community ecology is selection (Vellend 2010), whereby species in a community influence the persistence of other species via interactions (Tilman 1977, Bertness and Callaway 1994, Laird and Schamp 2008). Positive interactions, such as mutualisms and facilitation, may promote persistence of some species and possibly promote species richness by increasing niche space. They may also result in overyielding, which occurs when production of an entire community exceeds that expected based on the production of community members growing in monoculture (Schmid et al. 2008). Negative interactions, such as parasitism and competition, tend to reduce species richness, or induce underyielding. Species richness may in turn influence the productivity of the entire community (Tilman et al. 1996), along with other ecosystem functions (Zavaleta et al. 2010, Lefcheck et al. 2015). This pattern, commonly observed in plant communities, may arise due to complementarity of either response traits (differences in how species partition and use niche space [Tilman et al. 1996]) or effect traits (differences in how species affect their environment [Hector and Bagchi 2007]). These concepts have applications as well, for example the application of plant–plant facilitation in ecological restoration (Maestre et al. 2001, Padilla and Pugnaire 2006), or the practice of intercropping of multiple species in silviculture to boost productivity (Piotto 2008). These concepts can likely also be used in the context of an emerging ecological rehabilitation goal: the production of biological soil crusts (biocrusts) to rehabilitate degraded rangelands and other ecosystems.

Biocrusts include a variety of soil surface communities dominated by many different combinations of phototrophic and heterotrophic microbes, and cryptogams (broad sense; inclusive of mosses, liverworts, lichens), that are found throughout dry and cold regions where vascular plant production is limited (Weber et al. 2016*a*). Biocrusts are a model system in community ecology, for example allowing a useful array of economical manipulations to study species interactions and the outcomes of biodiversity (Bowker et al. 2014, Maestre et al.

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2016). Biocrusts are structured by species interactions that range from positive to negative (Bowker et al. 2010*b*, Baran et al. 2015). Among the most direct negative species interactions in biocrusts are parasite–host relationships among lichen species that may drive successional sequences (Root and Dodson 2016). Some lichens parasitize lichen thalli of other species, co-opting the photobiont of the host (Root and Dodson 2016). Suggestive of positive species interactions, biocrusts with higher levels of species richness have also been shown to exhibit higher cover (and presumably biomass), and be more highly functional with regards to ecosystem processes, and multifunctionality (Maestre et al. 2005, 2012, Bowker et al. 2013). The multifunctional nature of biocrusts makes them a desirable subject of ecological rehabilitation research (Bowker 2007, Wang et al. 2009, Chiquoine et al. 2015, Lan et al. 2014). Biocrusts function as primary producers, like plants, but also are exceptionally effective at stabilizing soil against erosion (Chaudhary et al. 2009), accumulating nutrient pools (Reynolds et al. 2001, Elbert et al. 2012), and influencing ecosystem water balance (Chamizo et al. 2016). An active line of research is the development of technology to artificially produce biocrusts ex situ, with the goal of reintroducing them to degraded ecosystems to elevate ecosystem function (Xu et al. 2008, Lan et al. 2014, Antoninka et al. 2016, Zhao et al. 2016).

Across the western United States, there are efforts underway to alter ecosystems by promoting native vegetation for ecological restoration, wildlife habitat enhancement, or invasive plant control purposes. These interventions may employ the use of herbicides for invasive plant control, removal of woody plants artificially favored by past management, and planting or seeding of native plant materials (Johnson et al. 2010, Pyke et al. 2017), but have not widely incorporated biocrusts. The MPG Ranch in the Bitterroot Valley of Montana, USA, provides an excellent microcosm in which to explore biocrusts as an ecological restoration material. The privately owned property harbors a mosaic of forest, semiarid grasslands and shrublands, and is representative of the western United States in that it was previously a cattle ranch, with considerable acreage devoted to wheat cropping or seeded range grasses. It is currently being managed for conservation goals, including provision of quality habitat for birds, ungulates, large carnivores and other fauna. A major component of this goal is restoration of native plant communities in the wake of past heavy grazing and tillage, which resulted in a shift towards domination by multiple exotic invasive plants. Restoration activities at MPG Ranch make heavy use of herbicides to eliminate unwanted dominant invasives, followed by soil-disturbing seeding activities such as drill seeding. Less disturbed native vegetation on the Ranch often supports substantial cover of biocrusts dominated by mosses and lichens, in contrast to degraded areas and treated restoration areas that may contain substantial bare ground. There is a need for a technology to recover lost biocrusts, in order to reduce bare ground, improve soil function and reduce erosion (Chaudhary et al. 2009, Condon and Pyke 2016), and possibly discourage reinvasion of some of the exotic plants (Serpe et al. 2006, Peterson 2013).

We report here on the initial stage of developing this biocrust restoration technology: creating and optimizing a cultivation strategy for the production of biocrust materials. In addition to addressing practical questions about biocrust cultivation, we tested whether prevailing theories in community ecology could be applied to enhance production of biocrust inoculum. We screened five moss and three lichen species for growth potential under two watering regimes in a greenhouse cultivation system. For most of these species, there is no literature on their potential for cultivation. Dryland lichen cultivation is still in its infancy (Bowker and Antoninka 2016) and might be enhanced by harnessing both negative and positive species interactions. We tested the hypothesis that a known parasitic relationship among two lichens, a negative species interaction, could be exploited such that the growth of the parasite species would be enhanced by the presence of its host. As a corollary, we also hypothesized that the host species would grow more poorly in the presence of its parasite. Finally, we tested whether greater richness of biocrust communities under cultivation would induce greater productivity or overyielding, due to positive species interactions. A positive diversity–productivity relationship has been demonstrated in multiple natural communities (Tilman et al. 1996, Zavaleta et al. 2010, Lefcheck et al. 2015); the present study attempts to apply this theory to the purpose of producing more biomass for use in rehabilitation.

Methods

Collection site

All biocrust materials were collected from a variety of sites with natural grassland (*Pseudoroegneria spicata*, *Festuca idahoensis*, *Poa secunda*), shrubland (*Artemisia tridentata*), or human-altered vegetation within MPG Ranch in the northern Sapphire Mountains of Montana, USA (Appendix S1: Fig. S1). Biocrusts at the study site are dominated by mosses and lichens. Cyanobacteria are likely present, but do not form visible biocrusts. Predominant soils are Haploxerolls, and to a lesser extent Argixerolls in the USDA Soil Taxonomy classification, with a loam to sandy loam texture and a gravel component. Soil pH ranges from near neutral to slightly acidic. Mean annual precipitation ranges from 325 to 454 mm in the sampled areas, with most precipitation falling in the cool season. Mean temperatures ranged from 14.0° to 17.7°C in the warmest quarter, and from −3.3° to −5.6°C in the coolest quarter. Long-term climate averages were sourced from WORLDCLIM (Hijmans et al. 2005).

Greenhouse-based cultivation system

We cultured biocrust organisms on sand in a modification of the automatically irrigated, greenhouse-based cultivation system initially described in Doherty et al. (2015). This system employs an irrigation-from-below method based on capillary action. Each experimental unit was a 739-mL plastic container backfilled with 400 mL of autoclaved fine sand sourced from a dune near Moab, Utah (93.9% sand, 5.5% silt, 0.6% clay; pH = 8.4). We used this sand because it rapidly hydrates and drains, and because we have a history of using it successfully to cultivate biocrust organisms from various locations (Antoninka et al. 2016, Doherty et al. 2015, Bowker and Antoninka 2016). Despite that the sand is not sourced from MPG Ranch, unpublished trials indicated that growth of MPG Ranch-sourced biocrust organisms is superior on the sand compared to both the native soil from MPG Ranch, and to a purchased organic soil (K. D. Doherty, *unpublished data*). During a hydration event, a temporary water film is gently created at the soil surface, fully hydrating biocrust organisms, after which the unit drains to field capacity. Our modification to the Doherty et al. (2015) system largely involved water purification and timer-based control of hydration. Hydration events were controlled by connection to a system of four solenoid valves and an OpenSprinkler timer. In each event, the system delivered water for 45 s three times daily at 07:00, 12:00, and 15:00, which kept units hydrated for at least 24 h. Hydration period length (in days) can be controlled by repeating hydration events on consecutive days, without allowing drying in between hydration events. We hydrated with municipal tap water treated with a sediment and carbon filter prior to use. Previous experiments have indicated that untreated tap water results in suppressed growth of target organisms and enhanced growth of contaminants (Bowker and Antoninka 2016). We applied 8 mL of Knop solution (a dilute nutrient solution; Reski and Abel 1985) to all units following a watering event once monthly, because past experiments indicated that faster growth rates of biocrusts can be obtained with supplemental fertilizer (Antoninka et al. 2015). Greenhouse temperature was maintained via thermostat at an average of 17.7° ± 5.6°C (mean ± Standard Deviation). Relative humidity was not controlled, but was monitored and averaged 45% ± 20.2%. Light was neither controlled nor monitored, and varied over the 6 month duration of the experiment; generally PPFD inside the greenhouse is about one-half that outside. Measurements in early March ranged from 321 to 628 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$.

Experimental design

We established three experiments in this system in September 2015. In each experimental unit, we added field-collected tissue of selected biocrust organisms over a bed of sand. Target species were removed from the soil surface in the field with knives and trowels in May 2014. We collected three lichen species based on their prevalence at the site: *Peltigera rufescens*, *Diploschistes muscorum*, and *Cladonia* spp. (a mixture mostly composed of *Cladonia pyxidata*, *Cladonia chlorophaea*, and *Cladonia fimbriata* lacking podetia, making species-level identification impossible). We also collected five prevalent moss species: *Ceratodon purpureus*, *Gemmabryum caespiticium*, *Homalothecium aureum*, *Polytrichum juniperinum*, and *Syntrichia ruralis.* Biocrusts primarily composed of cyanobacteria were not included because they were not observed at the study site. All collected materials were allowed to air dry, and were stored separately in an air-dry state at room temperature in the dark. We gently disaggregated the biocrust materials over a 2 mm mesh sieve, and cleaned them with water to remove the majority of soil particles. We repeatedly wet-sieved the tissues to remove additional soil. The materials were slowly air dried, then added by volume (2.5 mL total of material added) to the surface of each unit by sprinkling in a dispersed manner from a small measuring spoon. Each unit started at approximately 25% cover of added biocrust material, with a variable proportion of this being initially active. Active cover excludes senescent tissue: identified by abnormal coloration such as yellowing or reddening of moss tissue, graying or whitening in lichen tissue, or lack of greening upon hydration.

Using this material, we conducted three experiments in parallel from September 2015–March 2016. The first experiment was meant to screen all species for growth potential in our cultivation system and to determine optimal watering schedule. All eight mosses and lichens were added in monoculture to the soil surface and grown for 6 months under two water regimes. We tested 5 d of continuous hydration followed by a 2-d drying event every week (hereafter 5/2), and contrasted it to continuous hydration 7 d per week (hereafter 7/0). We replicated each combination of factors six times, a level of replication used successfully to detect treatment effects in past work (Bowker and Antoninka 2016).

In parallel, we conducted an experiment to grow the *Cladonia* spp. and their parasite *Diploschistes muscorum* both together and in monoculture (monocultures are also part of experiment 1). In all cases, we initially added the same total volume of lichen material, and in the species polycultures, equal volume of each species and cultivated them under both 5/2 and 7/0 hydration schedules. We replicated each combination of factors six times.

Finally, in a third experiment, using all of the mosses, we tested whether species richness can promote productivity in cultivated communities. For this experiment, we used only mosses because, based on our experience and that of others, we expected overall culturability of mosses to be greater than that of lichens (Bowker and Antoninka 2016). We created all possible polycultures with the same total volume of tissue added, and species always added in the same proportions, each replicated six times. All of these were grown only under the 5/2 watering regime. The moss monocultures from experiment 1 that were grown under the 5/2 watering regime were used here also.

Monitoring

We monitored percent coverage of active tissues at the start of the experiment and monthly thereafter, using a circular gridded quadrat (each grid cell = 2% cover) to aid in cover estimation. Active cover was monitored because it more accurately captures the portion of cover that is dynamic. Mosses and lichens were identified to species level where possible, otherwise to the generic level. We also tracked coverage of non-target organisms such as cyanobacteria, algae, and fungi and separated them by colony morphologies.

Calculating productivity and overyield

Since active cover differed by species at the start of our experiment, we adopted productivity as our primary response variable. Productivity was expressed as the percentage increase from initial conditions, and determined using the formula

$$(\text{Active cover time}_x - \text{Active cover time}_0)/\\ \text{Active cover time}_0 \times 100\%$$

where time_x refers to the time point of interest, and time_0 refers to initial conditions.

Overyield is the difference between expected and observed production of a polyculture, where the expected production is based on yield in monoculture. Yield was defined as active cover time_x − active cover time_0. To avoid bias in detection of overyield as a function of number of species in the polyculture, we used the average yield of monocultures of species contained within the mix being considered as the expected yield. This approach is justified when monocultures have strongly different growth rates (Schmid et al. 2008), which we confirmed in experiment 1. All of our calculations included target species only, excluding incidental contaminants. Incidental contaminants accounted for a low cover (median <2%), and never became dominant.

Statistical analysis

We analyzed experiments 1 and 2 using repeated-measures MANOVA, with the factors species (or species composition) and hydration schedule (5/2 vs. 7/0). In experiment 1, we compared monocultures of eight species, while in experiment 2, we compared 2 species growing in monoculture or together in polyculture. In both experiments, we analyzed the response variable production of target species. As part of our analysis of experiment 2, we also repeated a similar analyses focusing on the percentage increase of active *D. muscorum* and *Cladonia* spp. cover separately. The only substantive difference was that the community composition factor in these two tests had two levels (monocultures of each species compared to mixes containing both species).

We analyzed experiment 3 in two ways. (1) An explicit test of overyielding as a function of 26 different moss community compositions. This was accomplished using repeated measures MANOVA, with the factors species composition, time, and their interaction. In each time point, we also tested for an overall preponderance of over or underyield across all communities using one-sample *t* tests, verifying results with the nonparametric Wilcoxon signed-ranks test. (2) A structural equation model (SEM) partitioning the effects of species richness and sampling effects on percentage increase. There are two distinct mechanisms that may result in greater productivity as a function of species richness: complementarity (mentioned previously) and the greater probability of an increasing number of random draws from a species pool containing a highly productive species (the sampling effect; Wardle 1999, 2001).

SEM allows researchers to test networks of hypotheses regarding the influences of multiple variables on one another (Shipley 2000, Grace 2006). For our purposes it was useful to partition the effects of initial species richness and the initial proportional cover of individual species (our index of the sampling effect). Effect size of each factor is measurable with the path coefficient, related and analogous to a partial regression coefficient (Grace 2006); an R^2 reflects the proportion of variance explained in percentage increase of target species by factors in the model. As a means to capture sampling effects – attributable to individual species, rather than complementarity of multiple species – we calculated the initial proportional cover for each species (e.g., in a polyculture of *C. purpureus* and *S. ruralis*, each species was ascribed a value of 0.5), and pooled the effects of individual species' starting proportional cover using a composite variable. A composite variable is a construct employed in SEM that additively pools the unique effects of conceptually related predictors (Grace 2006). Briefly, the indicators of the composite are modeled as predictors of an unobserved variable with an error variance constrained to be 0. In turn, an effect of the unobserved variable is modeled on a response variable, and the associated path coefficient is interpreted as the joint, composite influence of all of the indicators on the response variable. Initial proportional covers of our species were allowed to intercorrelate, but the degree of correlation was fixed to be equal among all pairs. Initial richness and initial proportional cover values were uncorrelated in our model. Because special techniques are required to model nonlinear relationships, we confirmed that the relationships specified in our model were approximately linear before fitting our SEM.

In several tests, response data deviated from normality but were central tending. We adopted the following protocol to avoid problems associated with assumption violations. (1) We checked linearity among response variables visually, heterogeneity of variance using Levene's test, and multivariate normality using Mardia's test. If there were departures from multivariate normality, we also identified outliers using Mahalanobis distance. (2) When violations of assumptions occurred, we attempted log transformations to correct positive skew. This was successful in a few cases, but in general made distribution problems worse, so untransformed data were analyzed in other cases. (3) Although MANOVA in general is robust to deviations from multivariate normality, the Pillai's Trace statistic is the most robust to unequal variance (Johnson and Field 1993). Thus, where appropriate, we report Pillai's Trace results. (4) We repeated analyses of untransformed data with and without the most extreme outliers to ensure that major conclusions were not primarily driven by outliers. We used AMOS 24.0 (IBM Corporation, Armonk, New York, USA) for our SEM analysis, a web app of the R package MVN (Korkmaz et al. 2014) to test multivariate assumptions and identify outliers, and JMP Pro 12.2 (SAS Institute, Cary, North Carolina, USA) for all other statistics.

RESULTS

Experiment 1: Screening species for cultivation potential

The overarching result was that most treatments declined in productivity over time (Fig. 1; Appendix S1: Table S1), especially in the final 2 of 6 months ($F_{2,78}$ = 82.45, $P < 0.0001$). We attained high productivity early in the experiment for a few species, but most species were predominantly senescent or dead by 6 months (Fig. 1; Appendix S1: Table S1). Undesired molds were present throughout the experiment, but never became dominant and did not strongly increase through time. We found strong variability in growth rates under cultivation among the eight species tested ($F_{7,79}$ = 19.11; $P < 0.0001$). The moss *Ceratodon purpureus* consistently had a higher percentage of active cover than other species. Lichens were generally poor performers, losing active cover over time. The effect of species was also interactive with time ($F_{14,158}$ = 6.63, $P < 0.0001$) in that some species (especially *C. purpureus*) maintained higher cover than most species throughout the first 4 months, but the population crashed at some point before 6 months, decreasing the separation between species. The species factor also interacted with water ($F_{7,79}$ = 2.92; P = 0.009) and with both water and time ($F_{14,158}$ = 2.59; P = 0.002); these effects appeared partially driven by a positive influence of the 7/0 hydration schedule on *Ceratodon purpureus* at 4 months.

Experiment 2: Testing a role for parasite–host relationships

There was no evidence that co-cultivation of parasite and host could boost either total cover, or affect cover of either host or parasite (Fig. 2a; Appendix S1: Table S2). Overall, expressed as community productivity, lichens did not grow, and continued to lose cover through time ($F_{2,29}$ = 43.98, $P < 0.0001$; Fig. 2a). A negative influence of continuous hydration was the strongest experimental factor ($F_{1,30}$ = 8.95, P = 0.006). In contrast, productivity of target lichens was not clearly affected by the colocation or segregation of host and parasite ($F_{2,30}$ = 2.12, P = 0.14). It is worth noting that samples

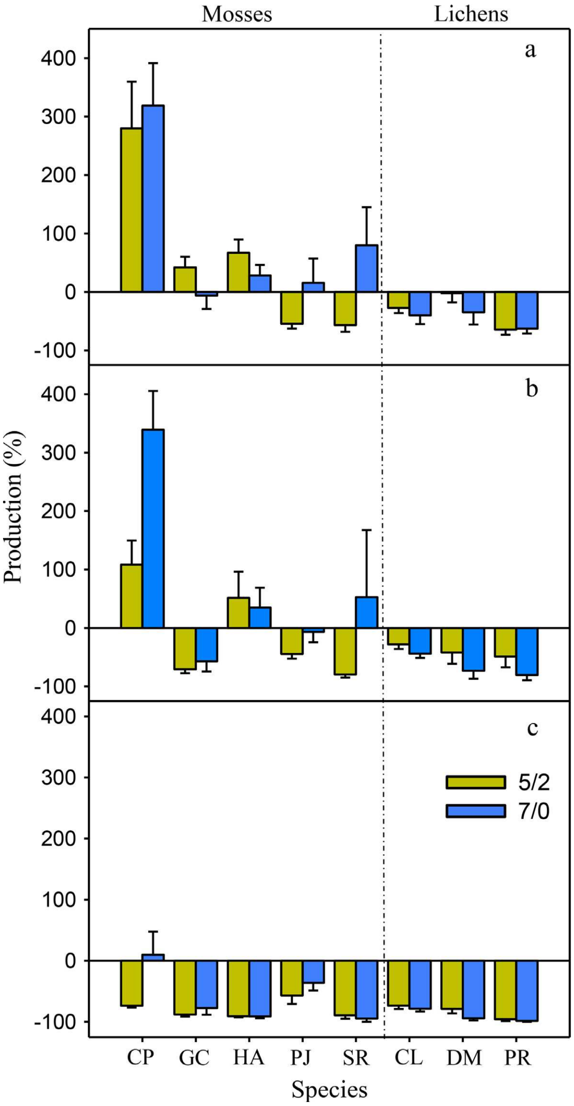

FIG. 1. Production of eight mosses and lichens through time as a function of hydration schedule: (a) November (time 1), (b) January (time 2), and (c) March (time 3). Abbreviations are 5/2, weekly hydration period of 5 d, followed by 2 d of drying; 7/0, weekly hydration period of 7 d (no drying period); CP, *Ceratodon purpureus*; GC, *Gemmabryum caespiticium*; HA, *Homalothecium aureum*; PJ, *Polytrichum juniperinum*; SR, *Syntrichia ruralis*; CL, *Cladonia* spp.; DM, *Diploschistes muscorum*; PR, *Peltigera rufesence*. Values are means and Standard error. [Color figure can be viewed at wileyonlinelibrary.com]

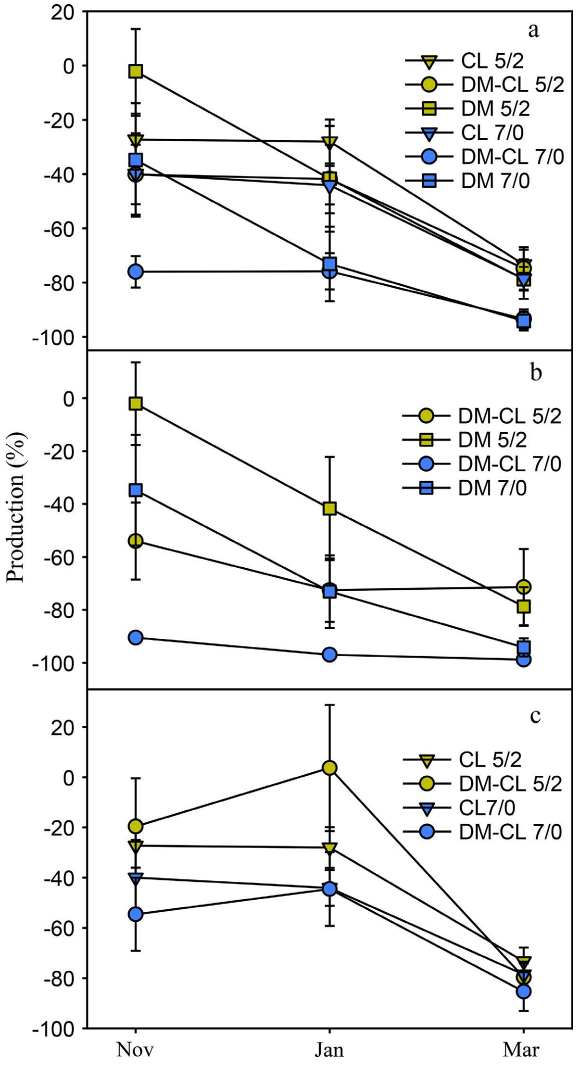

FIG. 2. Production of lichens in parasite–host pairings through time. (a) Total lichen production, (b) *Diploschistes muscorum* (DM; parasite) production, (c) *Cladonia* (CL; host) production. Values are means ± Standard error. [Color figure can be viewed at wileyonlinelibrary.com]

containing only *Diploschistes* declined in active cover more rapidly than those containing *Cladonia*, either alone or in combination with *Diploschistes* ($F_{4,60}$ = 4.54, P = 0.003).

Tests performed on the individual species largely confirmed the same results. Productivity of *D. muscorum* (parasite) was negative at all time points, indicating that it never attained positive growth (Fig. 2b; Appendix S1: Table S2). Time was the strongest overall effect, in that *Diploschistes muscorum* lost about half of its cover by the first monitoring period, and lost another ~25% of initial cover by the third ($F_{2,19}$ = 27.1, P < 0.0001). Productivity of *Diploschistes muscorum* (parasite) was lower when it was growing intermixed with *Cladonia* spp. (host) ($F_{1,20}$ = 6.2, P = 0.02). Time and species compositions interacted such that *Diploschistes* + *Cladonia* lost cover at a more gradual rate after time 1, although the apparent loss between time 0 and time 1 was greater ($F_{2,19}$ = 8.7, P = 0.002). *Diploschistes* lost more cover when hydrated 7 d per week ($F_{1,20}$ = 6.8, P = 0.02), though this effect was weaker when outliers were omitted.

Productivity of *Cladonia* (host) was also negative at all time points (Fig. 2c; Appendix S1: Table S2). Decline in active cover accelerated especially in the final 2 months of the experiment ($F_{2,19}$ = 19.86, P < 0.0001). Like *D. muscorum*, *Cladonia* lost more cover when hydrated 7 d per week, compared to 5 d per week ($F_{1,20}$ = 4.43, P = 0.05). *Cladonia* growth was essentially unaffected by the presence of *D. muscorum* ($F_{1,20}$ = 0.04, P = 0.85).

Experiment 3: Testing the biodiversity–productivity relationship

Overall, multispecies communities generated positive overyielding distinguishable from 0 (November mean = 1.2, t = 2.6, P = 0.0009; January mean = 1.2, t = 2.6, P = 0.01; March mean = 1.9, t = 6.4, P < 0.0001). Wilcoxon signed-ranks tests largely confirmed t test results, and are not reported here. Community compositions did not consistently differ from others across time points ($F_{25,129}$ = 1.2, P = 0.28). There was no clear directional change through time in the preponderance of over- or underyielding ($F_{2,128}$ = 2.2, P = 0.12; Fig. 3). Some species compositions did change through time more than others, indicating an interactive effect of species composition through time ($F_{50,258}$ = 2.0, P = 0.0002). This is perhaps best illustrated by two species communities, most of which initially underyield slightly in November, but switch to slightly overyielding by March (Fig. 3c). In absolute terms, all monocultures and communities declined in the final 2 months, however some of the two species communities were affected less than more complex communities.

Our SEMs were able to explain about one-quarter to one-third of the variation in productivity of our experimental communities (November R^2 = 0.31, January R^2 = 0.31, March R^2 = 0.23; Fig. 4). We detected both an effect of richness (r = 0.24 in November and March, r = 0.25 in January; Fig. 4a), and a stronger influence of the sampling effect (r = 0.5 in November and January, r = 0.41 in March). The primary difference between different time points was the identity of the species most responsible for driving the sampling effect (Fig. 4c). In November, the initial abundance of *C. purpureus* was the major positive driver of the sampling effect, while *S. ruralis* and *P. juniperum* were negative drivers. By January, *C. purpureus* was essentially the only (strongly positive) driver. By March, *P. juniperinum* and *S. ruralis* were strong negative drivers.

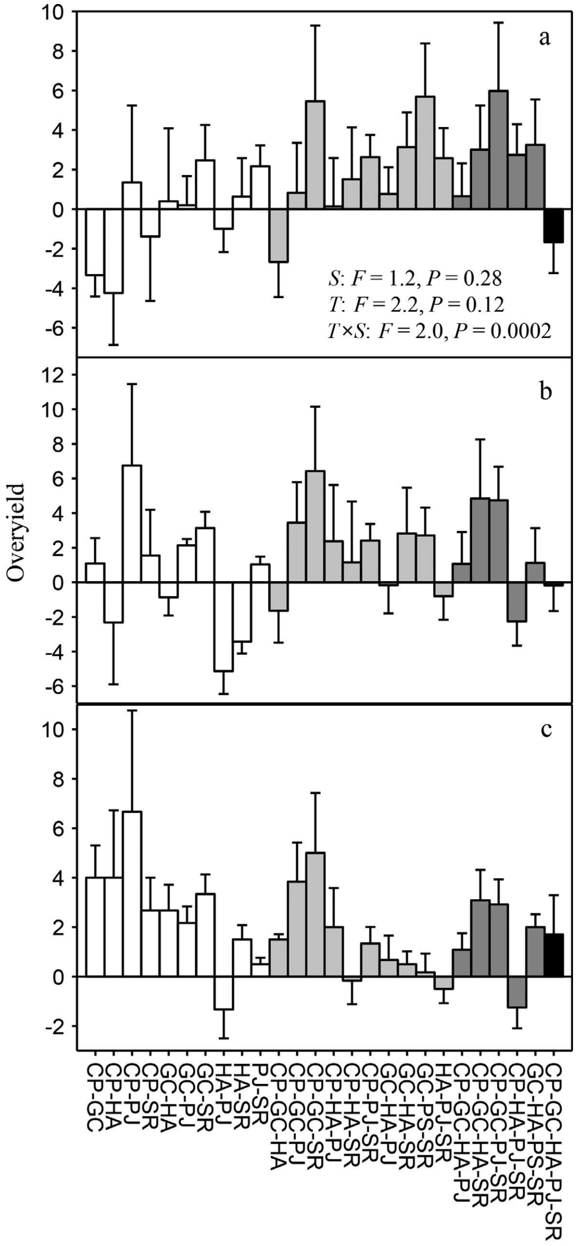

FIG. 3. Overyield as a function of 26 moss community compositions through time: (a) November (time 1), (b) January (time 2), and (c) March (time 3). Grayscale shading indicates number of species in each community (2–5). Values are means and Standard error. Species codes are explained in Fig. 1. MANOVA effect tests: *S*, species composition; *H*, hydration schedule; *T*, time.

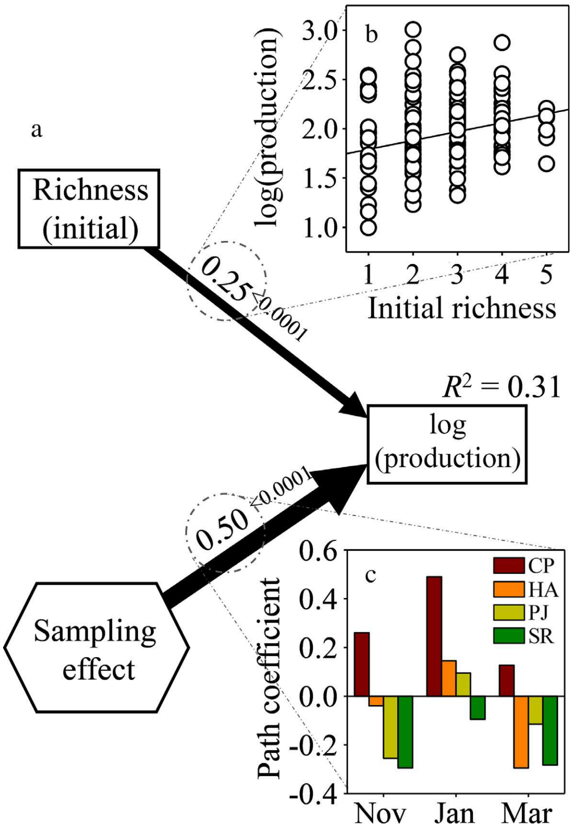

FIG. 4. Effects of initial richness (complementarity effect), and initial abundances of individual species (sampling effect) on production. (a) Structural equation model based on January data. Boxes represent measured variables, hexagon represents a composite of initial coverage values of four species (the fifth is omitted because it is statistically redundant). Arrows represent influences of one variable on another. Path coefficients appear adjacent to arrows, with *P* values in superscript; arrow widths are scaled proportionally to associated path coefficients. R^2 indicates variance explained in the response variable. Path coefficients and R^2 vary slightly among months (see *Results: Experiment 3: testing the biodiversity-productivity relationship*). (b) Scatterplot illustrating the relationship between initial richness and productivity in January data. (c) Bar graph illustrating the contribution of initial cover of individuals species of production across months, expressed as path coefficients; larger absolute values indicate that a species is a primary positive or negative driver of the sampling effect. Species codes are explained in Fig. 1. [Color figure can be viewed at wileyonlinelibrary.com]

DISCUSSION

Promising moss cultivation

Previous studies demonstrate the general culturability of biocrust mosses, achieving substantial growth over months or less in greenhouse systems (Bu et al. 2011, Doherty et al. 2015, Antoninka et al. 2016, Bowker and Antoninka 2016, Zhao et al. 2016). Here, we are able to explore a full range of responses of different species from extremely fast-growing ruderals to more slow-growing species. All five of our moss species attained positive growth at least initially under at least one of the hydration regimes. Some remained robust and attained high cover until populations of nearly all taxa rapidly declined in the final 2 months of the experiment, possibly in response to warm temperature (~25°C) experienced three times in February.

Ceratodon purpureus was the best performing species, and its biomass can be increased four- to fivefold in only

2 months. This species is known to be a widespread habitat generalist, and disturbance increaser, e.g., after fire, but frequently persists in late successional communities at low abundances (Clément and Touffet 1981, Jules and Shaw 1994). Given ruderal tendencies, the quick growth of this species was unsurprising, and has been achieved by others (Jones and Rosentreter 2006, Gross 2009).

Some later successional species also demonstrated some promise. For example, *H. aureum* sustained modest positive growth in the first 4 months. It is widespread across the study area, tending to occupy mesic and shady microsites, so could have high value as one of several species to use in restoration. The most frequent dominant species, *S. ruralis*, sustained growth similarly to *H. aureum* under the 7/0 hydration regime, but failed to grow under a 5/2 regime. The modest performance of *S. ruralis* is puzzling, especially given that much better results have been generated for the same species in the past, including under 5/2 hydration regimes (Jones and Rosentreter 2006, Antoninka et al. 2015, Doherty et al. 2015, Bowker and Antoninka 2016). This may suggest differing growing condition preferences among populations, which has been observed before (Doherty 2014), and that cultivation practices may need to be optimized for particular populations.

Polytrichum juniperinum, which is widespread but attains dominance at higher elevations, was our least successful moss, never sustaining positive growth. Others have also found relatively poor growth of this species using greenhouse-based growth techniques (Gross 2009), suggesting that this species may simply be more difficult to develop as a restoration material. However, recent developments using liquid culture practices appear promising for this species, but have yet to be applied toward growing gametophytes (Ruiz-Molina et al. 2016).

Elusive lichen cultivation

Although lichen mycobionts can be isolated and kept alive in culture (Honegger et al. 1992), greenhouse cultivation of the whole lichen may be difficult or impossible for most, but not all species. Lichens fall into multiple groups based on photobiont type (cyanolichens, chlorolichens, multiple photobionts; Friedl and Büdel 1996). Lichens may also be grouped into two broad classes based on structural complexity (Büdel and Scheidegger 1996): (1) stratified lichens are organized in layers, with a distinct photobiont layer between distinct fungal layers; (2) gelatinous lichens have photobiont cells well distributed through an unlayered matrix of fungal tissue. Bowker and Antoninka (2016) successfully cultivated gelatinous cyanolichens of the genus *Collema*, but failed to grow four other stratified chlorolichens. In the present study, we attempted to grow three stratified chlorolichens and one stratified cyanolichen. No attempts to our knowledge have attempted to grow gelatinous chlorolichens, such as *Placynthiella* spp. Thus, to date, we have failed to grow 89% of taxa that have been tested. Bowker and Antoninka (2016) conjectured that *Collema* grew better than four chlorolichens because this genus attains higher photosynthetic rates in warm environments than the other species (Lange et al. 1998), and the greenhouse used may have attained relatively high temperatures. In the present study, a cooler greenhouse with improved climate control was used, better matching optimal temperatures (~18°C) of many stratified chlorolichens (Lange et al. 1997). Nevertheless, sustained growth of lichens did not occur. Thus, although it is very plausible that *Collema* benefits from warmer growing temperatures, the failure of other lichens to grow was not likely due *only* to excessive heat.

With only one successful trial among two studies (*Collema*) we cannot determine what factor is most likely to determine success or failure of lichen cultivation efforts, but we can advance two working hypotheses:

1) Chlorolichens are limited by availability of their photobiont in soils. About 89% of lichens associate with green algae, most in the genus *Trebouxia* (Honegger 2012), which is only rarely detected free-living (and then, controversially; Ahmadjian 1988). Hypothetically, free-living potential photobionts could encourage expansion of a lichen at low cost to the mycobiont because there would be no need for current symbiotic photobiont cells to retain C for cell division. In contrast, common cyanobacterial photobiont genera (e.g., *Nostoc*) may grow to abundance independently of a lichen thallus both in cultivated (Antoninka et al. 2016) and in natural biocrusts (Büdel et al. 2016). Thus, there may be a greater limitation of photobiont availability for chlorolichens, restricting their growth. Photobiont limitation has been proposed to be the driving factor underlying the parasitism of lichens by other lichens (Honegger 2012). One outcome of the parasitism is to co-opt the photobiont of the host, a phenomenon largely associated with chlorolichens (Root and Dodson 2016). While photobiont limitation of chlorolichens could plausibly be a factor in culturability of some lichens, it is not a complete explanation, since the stratified cyanolichen *Peltigera rufescens* also failed to grow in the current experiment despite that *Nostoc* cyanobacteria (the same genus as its photobiont) were common on soil surfaces of our experimental units.
2) Stratified lichens are less culturable using our approach than gelatinous ones, due to physical or biological properties. One physical property of some stratified lichens was their propensity to float during hydration events. This is consistent with hydrophobicity, common in stratified lichens and contrasting with the relative hydrophily of gelatinous lichens (Büdel and Scheidegger 1996, Honegger 2012). Other hydration techniques, e.g., misting from above, may be needed for stratified lichen cultivation. We cannot rule out the possibility that there is a role for the newly discovered third partner in lichens (basidiomycete yeasts; Spribille et al. 2016). These fungi are

associated with the cortex, which is a feature of stratified lichens, and it is possible that their growth is disfavored in our cultivation system.

Can lichen-lichen parasitism be applied to mass cultivation?

We cannot conclude with certainty whether maintaining parasite–host interactions can be used to enhance lichen cultivation because in our test, neither host (*Cladonia* spp.) nor parasite (*D. muscorum*) ever attained positive growth. A different result will likely depend on a breakthrough in successful growth of a host that may then be used to promote growth of a parasite. Another factor worth investigating is the propagule type of the parasite. In nature, it is thought that spores of a parasitic lichen mycobiont species germinate on the thallus of a host lichen and co-opt the photobiont to form a new lichen (Honegger 2012). We added thallus fragments of the parasite and host together. It is possible that since thallus fragments already contain photobiont cells, the parasitic behavior was not necessary to obtain photobionts and therefore not induced. We can be reasonably confident that spores were also added because the thallus fragments of the parasite often bore apothecia, fungal fruiting bodies. Nevertheless, we did not attempt to isolate or regulate spore rain over host thalli; this type of manipulation is plausible and may be viable, because lichens can be induced to disperse spores. If and when a host is successfully cultured, this may be an intriguing experiment to perform. Other host–parasite symbioses exist to explore in the study area and elsewhere, for example, the parasite *D. muscorum* is commonly parasitized by *Acarospora schleicheri* (Root and Dodson 2016).

Diversity exerts a minor effect on productivity

Overall, two lines of evidence support that richness does enhance productivity via complementarity in biocrusts. First, considering all samples of multi-species communities regardless of community type, overyielding was greater than zero at all three sampling times, implying that their production was greater than what we might expect given the production of their components in monoculture. Detection of overyielding suggests that at least one species in the community is benefiting from the presence of at least one other species in the community, resulting in overall greater productivity. Another scenario that would result in overyielding is mutual facilitation of two or more species with complementary traits (Bowker and Antoninka 2016). There was no clear evidence that polycultures differed from each other in their degree of overyielding, a result that probably results from high variability in the overyielding observed within each group.

The second line of evidence supporting an effect of complementarity is the detection of a positive effect of initial richness of our cultivated bryophyte communities on production *that was independent of sampling effects* (Fig. 4). Richness can promote productivity through two distinct mechanisms: complementarity (Tilman et al.1996, Hector 1998) and the sampling effect (Wardle 1999, Loreau and Hector 2001). Our SEM approach allowed us to estimate both separately, so that they were not confounded. Several studies have demonstrated a link between natural biocrust richness and various ecosystem functions such as nutrient cycling, soil respiration, and multifunctionality (Bowker et al. 2010*a*, *b*, 2014, Castillo-Monroy et al. 2011). Experimental mosaics of biocrusts have also been used to demonstrate the existence of this phenomenon (Maestre et al. 2012). Using a culturing approach very similar to the one used here, a three species combination of a lichen and two congeneric mosses generated substantial overyielding due to complementarity (Bowker and Antoninka 2016). Thus, we are confirming the existence of a phenomenon that is common in biocrust communities whether they naturally occur, are assembled mosaics, from field collected fragments, or are grown from propagules.

Despite the evidence for the existence of complementarity in our cultivated biocrusts, and widespread support for the concept, the effect was relatively weak compared to the sampling effect. This may be because species richness is only an indirect indicator of the true underlying driver of complementarity: functional diversity based on traits (Cadotte et al. 2011). One reason why our complementarity effect may have been weaker than some other cases is that we used mosses only, while other experiments have mixed mosses and lichens (Bowker and Antoninka 2016). There was substantial variation in traits of the species we used, as we included both upward-growing (most species) and laterally growing species (*H. aureum*), partially vascular (*P. juniperinum*) and non-vascular species (most species), and purported disturbance tolerators (*G. caespiticium*, *C. purpureus*) and purported late-successional species, in addition to varying environmental preferences and tolerances. Nevertheless, the inclusion of other groups of organisms into constructed biocrust communities, such as lichens or liverworts, may greatly increase the functional diversity in the community, possibly leading to a greater potential for enhanced complementarity. For example, in a previous study, we hypothesized that the inclusion of the lichen *Collema*, and its key trait of N-fixation, was what catalyzed a shift from negative to positive complementarity in two-species to three-species communities (Bowker and Antoninka 2016). As methods to measure functional traits of biocrust species are developed (Mallen-Cooper and Eldridge 2016) and paired with functional diversity indices (Cadotte et al. 2011), estimates of complementarity will be improved and species richness and functional diversity may be experimentally varied independently.

Implications for practice

We learned several valuable lessons that can be applied to the production of biocrusts as ecological restoration materials. First, mosses are generally cultivable, whereas lichens will require more research effort to determine if most taxa can be grown at all. We have learned from this and other experiments that maximum moss yields are produced within 2–4 months, and longer growth periods do not result in greater production time period (Antoninka et al. 2015, Bowker and Antoninka 2016). Our attempt to synthesize a parasite–host relationship between a lichen pair failed to conclusively contribute toward a cultivation protocol for either biont. There are, however, other benefits to cultivating multiple species in communities. First, we can produce an inoculum for field use containing more than one species, potentially increasing the probability that at least one will be suited to the environment into which it is later introduced. This hypothesis has not yet been field tested. Second, we may enhance the productivity of our cultivated biocrusts, and decrease the amount of time needed to produce a sufficient quantity of inoculum. That said, in application, one could produce a larger quantity of biocrust material simply by ensuring that the best producing species (if known), e.g., *C. purpureus*, is a component of the cultivated community. If the best producing species is not known, or if species compositions specifically containing other species are desired, then increasing richness of cultures remains a promising strategy.

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DATA AVAILABILITY

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.4jp16