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Community composition influences ecosystem resistance and production more than species richness or intraspecific diversity

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Biodiversity describes the variety of life and may influence properties and processes of ecosystems, such as biomass production and resistance to disturbance. We investigated the effects of multiple facets of biodiversity – species richness and composition of the community, and intraspecific diversity in two key species – on both production and resistance of experimentally-assembled biological soil crusts (biocrusts). We found that productivity was most strongly influenced by community composition (variation in the presence and relative proportions of community members), and weakly positively influenced by species richness. Intraspecific diversity, encompassing both the richness and composition of clones, had a neutral effect on community productivity within one focal species (*Syntrichia caninervis*), but a moderately negative effect on productivity within the other focal species (*S. ruralis*). Resistance was also most strongly influenced by community composition, although different sets of species contributed most to resistance and production. Resistance was not affected by either species richness or intraspecific diversity in either focal species. Our findings supported our general expectation that community-level facets of biodiversity would be more influential than intraspecific diversity within a species because trait variability among species is usually greater than that within. These results also indicated that although species richness is often thought to strongly affect both productivity and resistance, the presence, absence and relative abundance of particular species may be more influential to both. Simultaneous manipulation of multiple facets of biodiversity in experiments may lead to a more complete understanding of the variety of ways in which biodiversity may regulate ecological systems.

Keywords: biocrust, biodiversity, biological soil crust, ecosystem function and services, ecosystem stability, intraspecific diversity, lichen, moss, species richness

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Introduction

Biodiversity is a many-faceted property of ecological systems, describing the variety of life and spanning multiple levels of organization including populations, communities, ecosystems, and landscapes (Whittaker 1960, Jarzyna and Jetz, 2016, Craven et al. 2018). A central inquiry in ecology has been: what are the outcomes of various types of biodiversity? One particularly well-documented outcome is the biodiversity-ecosystem function relationship; researchers commonly find positive, saturating relationships between community-level biodiversity measures such as species richness or trait diversity, and ecosystem functions such as productivity (Tilman and Downing, 1994, Cardinale 2011, O'Connor et al. 2017). In contrast, the hypothesis that greater biodiversity lends stability to ecological systems is less consistently supported (Jacquet et al. 2016, Pennekamp 2018). Resistance is one of the major components of stability, and refers to the ability of an ecological system to remain unchanged despite disturbance (Grimm and Wissel 1996). Recent literature documents conflicting diversity–resistance relationships when the disturbance is an aspect of climate change, e.g. finding that greater species richness decreases resistance to warming (Pennekamp 2018), but increases resistance to drought (Isbell et al. 2015). It is becoming increasingly important to better understand how and to what degree biodiversity increases or decreases resistance of ecological systems to disturbances, because climate change is increasingly perturbing communities and ecosystems globally (Middleton and Sternberg 2013, Prăvălie 2018).

Different facets of biodiversity, among and within species, may affect ecosystem function and stability. Positive species richness effects on various ecosystem functions have most often been attributed to two mechanisms: complementarity, and sampling or selection effects (Loreau and Hector 2001). The complementarity hypothesis holds that different species use space and resources differently, thus a richer community is more likely to more fully partition and use the available niche space resulting in lessened competition and greater productivity or ecosystem process rates (Hector 1998). The selection effect or sampling effect refers to the greater probability of a community containing a highly functional species (e.g. highly productive) when species richness is higher (Wardle 1999). Since the selection effect is brought about by the presence or relative abundances of a species present in a community, it also can be viewed as a specific outcome of community composition. Both complementarity and selection effects might be expected to also be outcomes of diversity within a population of clones of a single species, despite a narrower range of trait variation within one species compared to that across multiple species (Reusch et al. 2005, Hughes et al. 2008, Cook-Patton et al. 2011, Schöb et al. 2015). Simultaneous manipulation of both inter- and intraspecific diversity is still uncommon in the literature (Cook-Patton et al. 2011, Prieto et al. 2015, Zeng et al. 2017), and some studies demonstrate interaction between these facets (Fridley and Grime 2010, Crawford and Rudgers 2012). Partitioning these influences, and their interactions, in more study systems would broaden our understanding of biodiversity–function and biodiversity–stability relationships.

Biological soil crusts (biocrusts) are a set of global terrestrial community types dominated by primary producers such as mosses, lichens and cyanobacteria that aggregate and inhabit the uppermost millimeters of exposed soil surfaces (Belnap et al. 2003). Biocrusts contribute to many ecosystem functions in addition to primary production, including: resisting erosion (Chamizo et al. 2017), cycling and fixation of nutrients (Weber et al. 2015), and regulating hydrological processes (Eldridge et al. 2020). Although generally stress tolerant, biocrusts have a known sensitivity to certain growing conditions including frequent sub-optimal hydration periods and hydration during supra-optimal temperatures (Reed et al. 2012, Doherty et al. 2018). This property indicates sensitivity to disturbances that might be linked to climate change (Wuebbles et al. 2017). Like many other primary producer communities, the effects of species richness and composition on various ecosystem functions are well-documented in biocrusts (Maestre et al. 2012, Bowker et al. 2013). There are some indications that different biocrust dominant species may differentially affect stability of ecosystem multifunctionality (Liu et al. 2017), but overall there is a paucity of studies of the effects of different facets of biodiversity on stability in this study system.

Using dryland biocrusts as a model system (Bowker et al. 2014), we experimentally tested the relative importance of three distinct types of biodiversity: intraspecific diversity within the dominant species, species richness of the community, and variation in species composition, in regulating productivity and conferring resistance to disturbance. We first allowed rapid growth of assembled biocrust communities under favorable conditions, then observed the response to a disturbance that consisted of an abrupt transition to unfavorable growing conditions. The conditions of the disturbance simulated elements of the projected future climate, which is becoming warmer and thus more arid, especially at the soil surface (Wuebbles et al. 2017). We hypothesized that: 1) both interspecific and intraspecific diversity within the dominant species would exert measurable positive effects on production, both before and after disturbance; 2) At the community level, influences on production before and after disturbance would consist of both effects of richness, and community composition because species differ in their productivity; 3) Community diversity would more strongly influence productivity prior to disturbance than intraspecific richness because greater trait variability and niche complementarity are possible across species than within species (Schöb et al. 2015), and; 4) intraspecific richness of the dominant species would promote resistance to disturbance by decreasing the likelihood of a population decline in the dominant species. To our knowledge, our study is the first to simultaneously manipulate intraspecific and species-level facets of diversity in a study system not dominated by vascular plants and does so under an experimentally imposed disturbance. Biocrusts provide an interesting alternative model system to vascular plants for these questions, because they contain organisms from different kingdoms, growing side by side, with broad trait breadth.

Material and methods

Collection and culturing of biocrust materials

We created cultures of single clones of the dominant biocrust moss species *Syntrichia caninervis* and *Syntrichia ruralis*. These originated from multiple sites at least 5 km apart on the Colorado Plateau in the states of Utah and Colorado (Supporting information), each featuring 10 collections at least 5 m apart of *Syntrichia* patches, as part of a broader collection effort (Doherty et al. 2018, Massatti et al. 2018). For each site, we selected four stems from each of three or more discrete moss patches per site to clone, carrying forward successful cultures into our experiments. Although most clones failed to grow, we cultured useful quantities of eight *S. caninervis* clones sourced from six geographically separated sites (> 5 km), and 11 *S. ruralis* clones from eight geographically separated sites (Supporting information). Our strategy was aimed at maximizing probability that clones differed genotypically. Previous studies support that although these *Syntrichia* species are clonal in nature, individual genotypes are mostly confined to a few square meters within a site (Baughman et al. 2017), and are not known to be shared across geographically separated sites (Massatti et al. 2018).

We grew clones in a fog chamber, on a bed of autoclaved dune sand in 16 well plates and augmented with Knop solution to provide nutrients. The fog chamber was based on the system described in Doherty et al. (2020). The sand (93.9% sand, 5.5% silt, 0.6% clay, and pH 8.4) was sourced near Moab, Utah (Bowker and Antoninka 2016), and was shown to be a suitable substrate for biocrust growth in previous studies (Doherty et al. 2015, 2018, Antoninka et al. 2016). Some cultures were later transferred to a growth chamber to speed growth. Growth chamber conditions were as follows: daytime conditions of 20 per 12 h, and night-time conditions of 8 per 12 h. When growth was sufficient, we split cultures to continue increasing biomass.

We also field-collected biocrust community members commonly found in association with one or both *Syntrichia* species including: 1) *Gemmabryum caespiticium* (moss); 2) *Gemmabryum kunzei* (moss); 3) *Encalypta vulgaris* (moss); 4) *Enchylium* sp. (lichen; most specimens are visually consistent with *E. tenax* and usually distinguishable from *E. coccophorum* in this region, but we cannot ensure that no contamination occurred without microscopic sexual characters); 5) *Peltula* sp. (lichen; specimens visually consistent with *P. patellata*, but without microscopic sexual characters, firm identifications are difficult), and; 6) *Clavascidium lacinulatum* (lichen). All were sourced from southeast Utah, except for *Peltula* which was sourced from the Jornada Experimental Range in New Mexico due to its higher abundance there (Supporting information).

In preparation for our experiment, we cleaned all biocrust materials of adherent soil to the greatest degree possible by disaggregation and wet-sieving and allowed them to slowly air-dry over 2–3 days on the bench, while covered with paper towels.

Experimental design

We established two parallel greenhouse experiments, one featuring *S. caninervis* and one featuring *S. ruralis* as focal dominant biocrust species. In both experiments we grew biocrust communities with varying levels of species richness, and varying numbers of distinct clones within the focal *Syntrichia* species.

To create experimental units, we used 100 ml plastic specimen cups (76 mm tall, 64 mm wide at the mouth), backfilled with 60 g of autoclaved, sterile dune sand. We drilled five holes (2 mm diameter) in a circular pattern in the bottom of each cup to allow irrigation via capillary action. On each sand-filled cup we added a total cover of ~20% of biocrust materials; 13% cover was composed of species other than the focal *Syntrichia*, and 6–9% cover was composed of one of the *Syntrichia* spp. We added materials precisely by mass, using species-specific relationships of air-dried biomass to cover. To create a species richness gradient, we randomly selected 1–4 species from our species pool of five to add along with the focal *Syntrichia* (Fig. 1, Supporting information). We added the additional species such that they comprised an equal proportion of the cover to one another.

We created levels of intraspecific diversity within *Syntrichia ruralis*, by adding material of either two, five or eight of the clones drawn from our pool of 11 (Fig. 1). We did the same for *Syntrichia caninervis*, except that the highest intraspecific diversity level was 6–7 clones due to limitations of material, and our clone pool consisted of eight clones. Due to limitations in the amount of material available for some individuals in both species, a fully random draw approach was not possible, and some clones were always present in our mixes. Lower intraspecific diversity treatments were composed of subsets of the clones added to higher diversity treatments. Thus, we caution that our intraspecific diversity treatment simultaneously varies clonal richness (number of clones present) and clonal composition (identity and relative abundance of clones). In this paper we use the general term, ‘intraspecific diversity’, to refer to these two elements collectively, and the specific terms ‘clonal richness’ and ‘clonal composition’ to refer to the individual elements as defined above. To enhance interpretation of this gradient we developed post hoc analytical techniques to help us determine which of these components of intraspecific diversity was most influential to ecosystem properties . Furthermore, some clones were so scarce that we were forced to decrease the amount of material added, and partially compensate with more material of more abundant clones. This led to somewhat different starting abundances of *Syntrichia* being added to various treatments. We used a data standardization to minimize the effect of this source of variation.

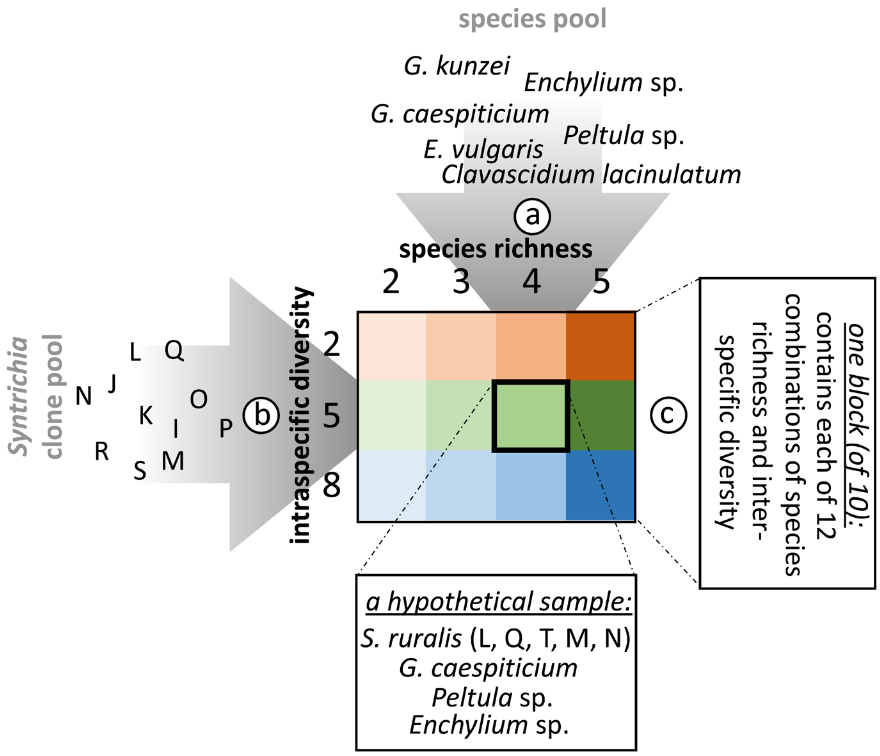

Figure 1. Diagrammatic summary of our experimental design (depicts S. *ruralis* experiment). We created communities, always containing one *Syntrichia* species, and 1–4 additional community members which were randomly drawn from a species pool of six, to create a species richness factor (A). Multiple clones of *Syntrichia* were added, drawn from a pool of 11, to create an intraspecific diversity gradient of two, five and eight clones (B). Each combination of species richness and intraspecific diversity, represented by cells in the grid below, was assembled into a block (C). There were 10 blocks. In the *S. caninervis* experiment, the highest level of clonal richness was 6–7, drawn from a pool of eight (clones A–H); otherwise it employs the same design.

We crossed the levels of intraspecific diversity with the levels of species richness to create 12 unique combinations for each of the focal *Syntrichia* species. One replicate of each of the twelve combinations of these factors were housed together in one 34 × 21 × 12 cm plastic box, creating an experimental block. We created ten replicate blocks for *S. ruralis* units, and another 10 blocks for *S. caninervis* units, bringing our total to 240 experimental biocrust units.

Experimental conditions: productivity phase

From early May to early July 2019 (10 weeks), we conducted the first phase of growth in the NAU Research Greenhouse, aimed at increasing biomass under favorable conditions and tracking productivity. We kept each block hydrated by manual addition of charcoal-filtered water to each plastic box, hydrating each cup and the growing biocrusts via capillary action. For the first two weeks, we watered daily, inducing continuous hydration after Doherty et al. (2015). After the first two weeks, we shifted to five consecutive days of hydration followed by two days without irrigation. All blocks were housed within a fog chamber, constructed as diagrammed by Doherty et al. (2020). The fog chamber sustained hydration periods by elevating relative humidity (~100% at night, and as low as 35% during midday). Over the course of the productivity phase, the greenhouse temperatures averaged 20 ± 6 overall, dropping as low as 11° overnight, and rising as high as 32 at midday. Day length ranged from ~13:40 – 14:32. Blocks were randomly relocated within the chamber every 2–3 days to account for potential differences in relative humidity, temperature, or watering within a block.

Experimental conditions: resistance phase

After the first phase of the experiment, nearly all experimental units had attained a high percentage of cover. In July 2020, all 20 blocks were moved out of the fog chamber into a portion of the greenhouse with no climate control. Biocrusts can be stressed by repeated, short-duration hydration events at supra-optimal temperatures (Reed et al. 2012, Doherty et al. 2018). Thus, we watered each unit daily with 5 ml of water (<3.5 mm rainfall equivalent) at 01:00 pm when greenhouse temperatures ranged from 30°–40°C, inducing only partial hydration and subsequent rapid desiccation (Barker et al. 2005). Due to cloud cover, two days were cooler than this range (28°), so we used a portable space heater to maintain 30°–40°C during the hydration period. Samples generally desiccated within 4 h. Day length was ~ 14:20 – 14:28 during this phase. We continued this climatic disturbance for 17 days, after which most units had suffered from visible senescence and death.

Monitoring

During both phases, we monitored cover based on the normalized difference vegetation index (NDVI; Doherty 2017, Fischer et al. 2012, Supporting information). To do so, we used a digital camera and an infrared filter to repeatedly obtain photos in the visible and near infrared region of the electromagnetic spectrum to later calculate NDVI. Indices were calculated using the crustCover package in R (Doherty 2017). We estimated total biocrust cover from NDVI values by setting a threshold value, and reclassifying pixels with an index value greater than the threshold as biocrust cover. This method does not distinguish among species or clones. We obtained these data five times during the productivity phase at day 10, 18, 27, 40 and 67, and about weekly during the resistance phase at day 69, 78 and 84. Over this time scale, biocrusts generally exhibit more horizontal than vertical growth, thus change in cover is expected to be a reasonable, practical surrogate for change in biomass (Antoninka et al. 2016). In between the two phases of the experiment, we visually estimated species richness in each unit, to provide an updated estimate prior to the onset of the disturbance.

Statistical analysis

Because different treatments received slightly different *Syntrichia* cover initially, we standardized NDVI-estimated cover data (Cover_{st}) for each time point as a percentage increase over the calculated initial cover, as follows:

$$\mathrm{Cover}_{st} = \frac{\mathrm{Cover}_{\mathrm{time\,i}} - \mathrm{Cover}_{\mathrm{time\,0}}}{\mathrm{Cover}_{\mathrm{time\,0}}}$$

We analyzed the standardized data directly in the productivity phase as a measurement of productivity. In the resistance phase, we calculated a resistance value by subtracting the standardized cover at day 40, the period of peak cover in the productivity phase, from standardized cover of a timepoint within the resistance phase. This difference represents the degree to which a sample lost biomass, with more negative values representing greater loss and less resistance, and values closer to or exceeding zero indicating greater resistance.

$$\mathrm{Resistance} = \mathrm{Cover}_{\mathrm{st\,time\,i}} - \mathrm{Cover}_{\mathrm{st\,time\,40}}$$

We used multi-group structural equation models (SEM) as our primary analysis tool, adopting an approach used in Bowker et al. (2017) to partition species richness effects into those likely linked to complementarity and those likely linked to the presence or abundance of particular species or compositions. We invoked a blocking effect, main effects of species richness (number of species added) and intraspecific diversity (number of clones added) and their interaction, and a community composition (composite of the starting relative abundances of species) effect as predictors of Cover_{st} or resistance. We used the initial species richness treatment level in productivity phase models, and the measured species richness at the initiation of the resistance phase in the models for that phase. To model the interaction term, we z-transformed species richness and genotypic diversity, and cross multiplied them, an extension of the method of Kline and Dunn (2000). The blocking effect and community composition effects were modeled using composite variables (Grace 2006). A composite variable is an interpretational tool which can be used to pool the influences of multiple paths into one composite path (Grace 2006). In the case of block, binary dummy variables coding for the different blocks were created, and their effects were pooled (omitting one) using a composite variable to estimate the overall influence of the blocking factor. To create the community composition variable, we pooled effects of the proportional abundances of the different members of the species pool, omitting one (*Gemmabryum kunzei*). Composite variables are more fully explained in the Supporting information. Our model allowed for correlations among exogenous predictor variables, except where our experimental design ensured that these correlations should be zero.

Multi-group SEM is used when there are different groups of data, in our case time points, in which the same model structure is expected to apply, but the values of some parameters may differ (Grace 2003). In our case, there were not strong differences among time points based on the χ^2 goodness of fit test and Bollen–Stine bootstrap test (Bollen and Stine 1992) as absolute tests of fit. Thus, we present results of the 'constrained' model in which parameters do not differ among time points in our results. However, we also created a partially unconstrained version of each model using Akaike's information criterion (AIC) as a relative test of fit to determine if relaxing parameter constraints improved a model. Results of partially unconstrained models are summarized in the Supporting information. We also describe additional details of our modeling approach in the Supporting information. We built our SEMs in AMOS 26.0 (IBM SPSS).

To interpret whether intraspecific diversity effects detected in structural equation models were due to the number of clones present, or the prevalence of particular clones, we used conditional variable importance for a random forest model as a post hoc test (Strobl et al. 2008). This approach is useful when predictor variables may be highly collinear. To focus the analysis just on variation explained by intraspecific diversity, we fit the response data to all other model factors, saving the residuals to analyze further. We modeled residuals as a function of clonal richness and the starting relative abundances of the particular clones present in each sample. We also plotted a partial dependence plot in one case to determine the direction of a detected pattern (Freidman 2001). Random forest modeling was conducted in R ver. 3.6 (<www.r-project.org>) using the party (Strobl et al. 2008) and pdp packages (Greenwell 2017).

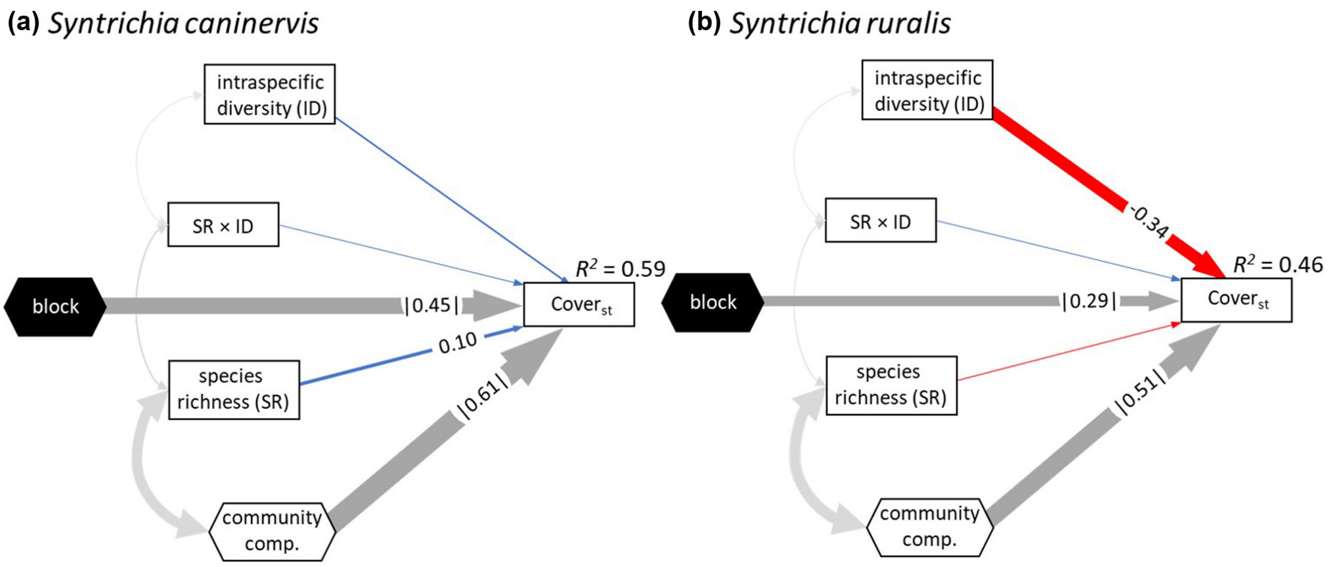

Figure 2. Community composition more strongly influences productivity of biocrusts than other facets of biodiversity. The figure depicts fitted structural equation models. Rectangles represent measured variables, and hexagons represent composite variables, with black fill indicating a categorical variable. Directional arrows represent hypothesized causal influences in the models. Width of arrows is scaled to the standardized path coefficient and weaker path coefficients are not shown for simplicity. Red arrows signify negative path coefficients, blue arrows signify positive path coefficients, and gray arrows signify relationships for which a sign is uninterpretable. Bi-directional arrows specify undirected correlation among variables.

Results

Effects of three facets of biodiversity on productivity

Our constrained model of the *Syntrichia caninervis* experimental system was able to explain 59% of the variation in Cover$_{st}$, our index of productivity (Fig. 2A). The most influential facet of biodiversity, and most influential factor overall, was community composition (r=|0.61|; $p < 0.001$; Table 1). This effect seemed to be driven primarily by negative influences of some lichens, and a positive influence of the moss *Gemmabryum caespiticium.* Species richness also exerted a minor but detectable positive effect on productivity (r=0.10; $p < 0.001$; Table 1). Intraspecific diversity and its interaction with species richness had no detectable influence on productivity. Finally, the block effect was a strong influence (r=|0.45|; p=0.03; Table 1).

Table 1. Facets of biodiversity influence productivity and resistance. Path coefficients are standardized. Bootstrap probability values are based on 95% confidence intervals.

Focal species	Phase	Model effect	Path coefficient	Bootstrap (p)
S. caninervis	Productivity	Species richness (SR)	0.1	0.004
		Intraspecific diversity (ID)	0.04	0.16
		SR × ID	0.003	0.91
		Community Comp.	|0.61|	0.01
		Block	|0.45|	0.03
S. ruralis	Productivity	Species richness (SR)	−0.01	0.59
		Intraspecific diversity (ID)	−0.34	0.007
		SR × ID	−0.02	0.55
		Community Comp.	|0.51|	0.01
		Block	|0.29|	0.11
S. caninervis	Resistance	Species richness (SR)	−0.04	0.29
		Intraspecific diversity (ID)	−0.01	0.70
		SR × ID	0.06	0.14
		Community Comp.	|0.28|	0.02
		Block	|0.61|	0.02
S. ruralis	Resistance	Species richness (SR)	0.04	0.42
		Intraspecific diversity (ID)	0.09	0.04
		SR × ID	0.007	0.73
		Community Comp.	|0.45|	0.02
		Block	|0.41|	0.08

Our constrained model of the *S. ruralis* experimental system explained less variation in Cover$_{st}$ overall ($R^2 = 0.46$; Fig. 2B). Again, the most influential facet of biodiversity, and most influential factor overall, was community composition ($r = |0.51|$; $p < 0.001$; Table 1), and again, this effect was associated with negative influences of lichens on productivity, and neutral to positive influences of mosses (Table 2). In the *S. ruralis* experiment, it was intraspecific diversity which exerted a moderate and negative effect on productivity ($r = -0.34$; $p < 0.001$), whereas species richness ($r = -0.01$; $p = 0.69$) and the interaction between intraspecific diversity and species richness ($r = -0.02$; $p = 0.57$) had no effect (Table 1). The intraspecific diversity effect appeared to be driven by both the clonal richness, and the prevalence of particular clones (Fig. 3A). Both the structural equation model and post hoc conditional random forest analyses supported a negative effect of clonal richness on *S. ruralis* productivity (Fig. 2B, Supporting information). As in the *S. caninervis* experiment, the block effect was influential, but less strong ($r = |0.29|$; $p < 0.001$).

Effects of three facets of biodiversity on resistance

Our constrained model of the *S. caninervis* experimental system explained 46% of the variation in resistance (Fig. 4A). As with productivity, the most influential facet of biodiversity was community composition ($r = |0.28|$; $p < 0.001$); species richness, intraspecific diversity and their interaction did not have detectable effects on resistance ($r \leq |0.06|$; $p \geq 0.15$) (Table 1). A different set of influences appear to drive the community composition effect: lichens, especially *Enchylium* and *Peltula* were positively related to resistance. The block effect was more pronounced than in our analysis of productivity, and was the strongest predictor by far, overall ($r = |0.61|$; $p < 0.001$; Table 1).

Our constrained model of the *S. ruralis* experimental system explained 39% of the variation overall in resistance (Fig. 4B). As in our other models, the most influential facet of biodiversity was community composition ($r = |0.45|$; $p < 0.001$; Table 1). This effect appeared to be driven by positive effects of lichens, especially *Enchylium* and *Clavascidium lacinulatum* (Table 2). The negative effect of intraspecific diversity on productivity was replaced by a weaker positive effect in the resistance phase ($r = 0.09$; $p = 0.03$; Table 1). This effect was not driven by clonal richness, but rather was mostly attributable to the prevalence of specific clones (Fig. 3B). There were no detectable effects of species richness or the interaction of species richness and intraspecific diversity ($r \leq 0.04$; $p \geq 0.31$). The block effect was similar in magnitude to the productivity phase ($r = |0.45|$; $p = 0.08$).

Discussion

Overall, we found stronger influences of community composition on both productivity and resistance in experimentally assembled biocrust communities than any other investigated facet of biodiversity, but different species appeared to promote productivity and resistance to differing degrees. This supported our hypotheses 2 and 3. Contrary to our hypotheses 1 and 4, we found that we could not attribute strong or consistent positive effects on productivity and resistance to either species richness or intraspecific diversity. Positive effects were minor and inconsistent. In one of our experiments, intraspecific diversity had a clear negative effect on productivity, perhaps indicating that some of the clones were less adapted to the experimental conditions than others, which if true could be important for predicting evolutionary responses to climate change. In both phases of both experiments, we observed a strong block effect. As a check of robustness of our results, we also ran our models without the block effect and obtained very similar path coefficients for the other factors; thus, the block effect did not affect our assessment of whether our hypotheses were supported. The block effect may capture: 1) residual differences in microclimate among our blocks; 2) a block-level selection effect brought about by variation in the combinations of clones and species among blocks or; 3) both.

Partitioning community-level influences, and associated mechanisms, on production and resistance

We had expected to observe clear effects of both species richness and initial community composition both on production and resistance. What we found instead is that variation in community composition among samples was the most influential facet of biodiversity in determining production and resistance. This means that particular species, or particular combinations of species, were more productive and maintained productivity better than others when perturbed by a climatic disturbance. By comparison, species richness effects on production were small and they dwindled to near zero

Table 2. Individual species account for community composition effects on productivity and resistance. Values are standardized direct effects (calculated from standardized path coefficients generated in our structural equation models) of individual species on Cover$_{st}$ in the productivity phase, and on resistance in the stress phase.

Taxon	*S. caninervis*		*S. ruralis*	
	Production	Resistance	Production	Resistance
Gemmabryum caespiticium	0.21	0.07	0.06	0.04
Enchylium sp.	−0.38	0.21	−0.34	0.39
Clavascidium lacinulatum	−0.35	0.11	−0.43	0.28
Peltula sp.	−0.38	0.22	−0.32	0.11
Encalypta vulgaris	−0.02	−0.06	−0.10	−0.10

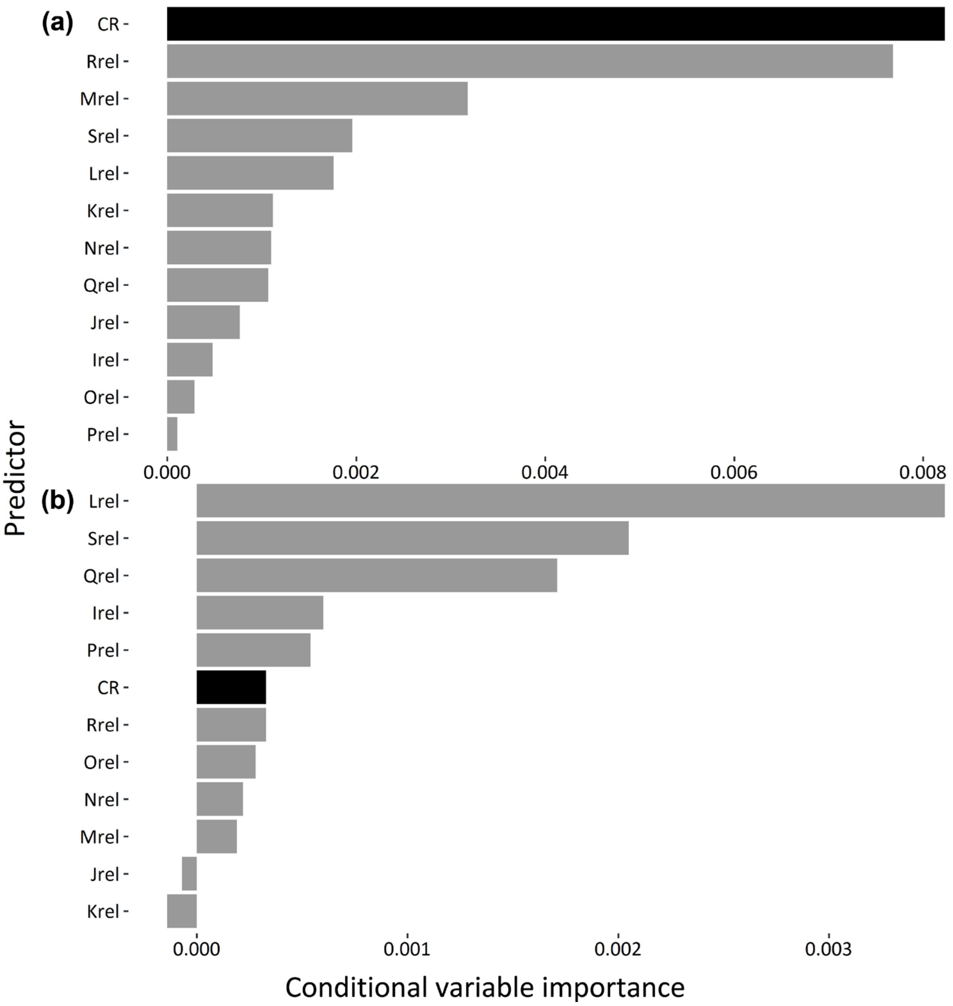

Figure 3. Intraspecific diversity effects on productivity (A) and resistance (B) of *Syntrichia ruralis* are partially to strongly explained by the abundances of individual clones. The data are conditional importance values obtained using random forests. CR, clonal richness; the number of clones present in a sample. Additional codes indicate the relative abundance of different clones; e.g. Irel is the relative abundance of clone 'I', Jrel is the relative abundance of clone 'J', and so on.

for resistance. Better understanding of these results requires an examination of the possible mechanisms that we are partitioning.

In this study, community composition effects on productivity or resistance may arise due to presence or abundance of one or more species. That the presence or abundance of particular species can influence productivity is widely known (Wardle 1999, Loreau and Hector 2001). This is often called the sampling effect or selection effect, and it is known to be one of the mechanisms by which species richness can influence productivity (Loreau and Hector 2001). As the number of species drawn from a random species pool increases, the probability of including a highly productive species increases. In our study, however, any strong effect of an individual species, either on production or resistance would be accounted for as part of the community composition effect, because community composition is the joint influence of the abundances of individual species. It is also true that different combinations of species may be more productive or resistant than others (Maestre et al. 2012), potentially due to facilitation. Facilitation has been proposed to potentially increase with diversity due to multiple mechanisms such as dilution of species-specific pathogen loads, increasing likelihood of intransitive species interactions, or greater probability of the presence of species that increase resources or ameliorate microclimate (Wright et al. 2017). For example, in another study using an experimental biocrust study system, two moss species growing together both exhibited slight inhibition of growth compared to their growth in monoculture, suggesting a competitive interaction (Bowker and Antoninka 2016). However, the addition of a third species, an N-fixing lichen, led to greater growth of all three species compared to their growth in monoculture, suggesting facilitation (Bowker and Antoninka 2016). This example illustrates an effect of richness on production that can only be explained by facilitation. In contrast, in this study, effects of facilitation attributable to single species would be captured in our community composition variable, rather than as an effect of species richness.

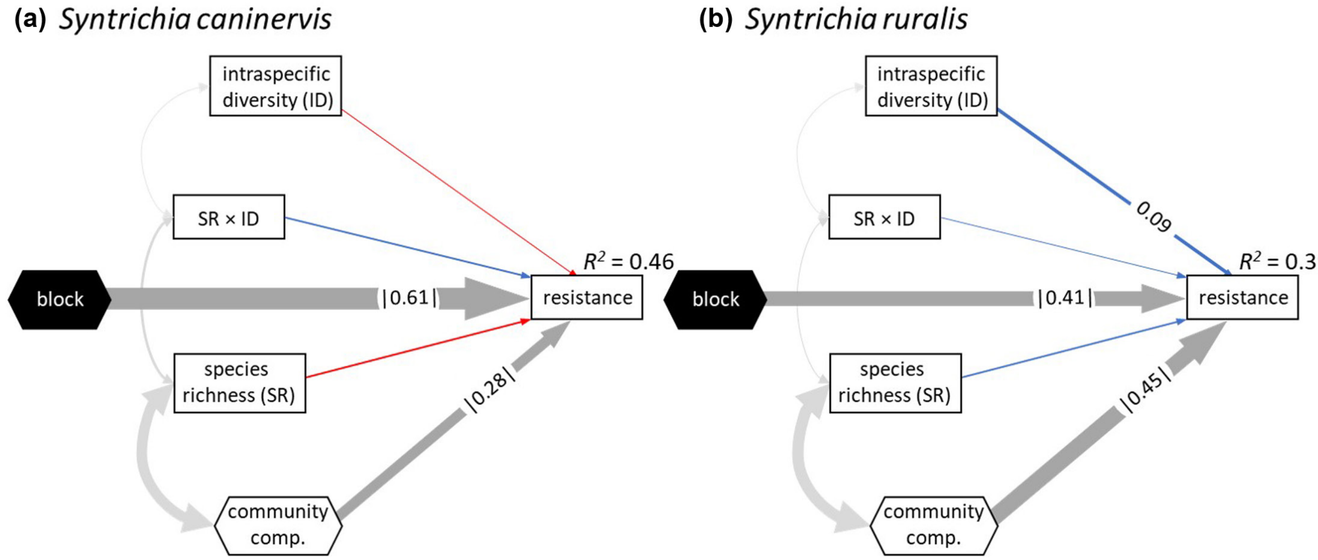

Figure 4. Community composition more strongly influences resistance of biocrusts than other facets of biodiversity. The figure depicts fitted structural equation models. Rectangles represent measured variables, and hexagons represent composite variables, with black fill indicating a categorical variable. Directional arrows represent hypothesized causal influences in the models. Width of arrows is scaled to the standardized path coefficient and weaker path coefficients are not shown for simplicity. Red arrows signify negative path coefficients, blue arrows signify positive path coefficients, and gray arrows signify relationships for which a sign is uninterpretable. Bi-directional arrows specify undirected correlation among variables.

Given that both productivity and resistance were most strongly influenced by community composition, an intriguing result was that different species conferred productivity and resistance to their communities. Mosses were more likely to have neutral to positive effects on productivity under favorable conditions but did not strongly increase resistance under disturbance (Table 2). Lichens were the opposite, dampening productivity under favorable conditions but conferring resistance under disturbance (Table 2). Although mosses and lichens grow together in many of the same habitats, they do have strong trait differences (Concostrina-Zubiri et al. 2016, Mallen-Cooper and Eldridge 2016). Biocrust mosses and lichens do not differ strongly either in maximal net photosynthetic or dark respiration rates, but they do differ in that mosses have greater optimal water contents, making them more productive in wetter conditions (Raggio et al. 2018). Perhaps related, mosses have more negative $\delta^{13}C$ values than lichens, a difference that could arise due to lichen preference for open microenvironments (and thus chronic exposure to and tolerance of hydric stress) and moss preference for sheltered microenvironments (Concostrina-Zubiri et al. 2018). One possible reason for greater drought tolerance in lichens relative to mosses may be longer water retention (Concostrina-Zubiri et al. 2016). As a general principle, few species would be expected to be able to simultaneously be among the most productive and among the most resistant, because of tradeoffs inherent among life history strategies (Grime 1977), or tradeoffs between specific traits aligning with productivity and stress resistance (Adler et al. 2014). Therefore, it is unlikely that a community can simultaneously maximize productivity and resistance, but an optimal balance might be possible with particular combinations of species, especially involving both mosses and lichens.

By estimating these community compositional effects separately from those of species richness, we constrain the possible mechanisms by which species richness can influence production or resistance. Niche complementarity, or differing usage of space or resources among species, should increase with species richness and lead to an overall reduction in competitive interactions among species and more efficient use of available niche space (Hector 1998). Variation in morphology among community members – which might be interpreted as a type of complementarity – has also been proposed to modify the environment in such a way that productivity of the community is favored (Rixen and Mulder 2005). We did observe a minor positive effect of species richness on production, in the *S. caninervis* experiment only, but , its magnitude was only a fraction of that of community composition effects. While we do not claim that sampling or compositional effects will generally be greater than richness effects on production, a recent study using different sets of experimentally assembled biocrust mosses from a different ecosystem arrived at a similar conclusion (Bowker et al. 2017). Another hypothesized effect of species richness, relevant specifically to resistance, is an insurance effect: if more species are present, the probability is greater that there are species present which can tolerate new conditions (Naeem and Li 1997). This specific mechanism is not supported here due to the lack of effect of species richness on resistance.

Intraspecific diversity affects productivity and resistance inconsistently

We found a mixture of neutral, weak positive and moderate negative effects of intraspecific diversity across the phases of our experiments. Further, all non-zero intraspecific diversity effects on both productivity and resistance were found in *S. ruralis*, none in *S. caninervis*. We had expected generally positive effects of intraspecific diversity based on the reasoning that: 1) more clones would a) increase the breadth of traits present within the focal species, improving its niche utilization and reducing intraspecific competition (Cook-Patton et al. 2011, Schöb et al. 2015), or b) increase the likelihood that a highly productive clone was present, boosting community productivity (Fridley and Grime 2010), and that; 2) more clones would provide an insurance effect by boosting the probability that stress-tolerant traits occurred in the populations.

Contrary to our hypothesis, the clearest intraspecific diversity effect was a moderate negative effect of intraspecific diversity on productivity in *S. ruralis*-dominated communities. Our post hoc analyses suggested that although clonal richness does appear to be the single most important component of this intraspecific diversity effect, the relative abundance of one of the clones is nearly as strong of a predictor, and the summed influence of all of the clones is greater than the influence of clonal richness. Both positive and negative selection effects could contribute to explaining the influence of individual clones. This finding suggests a role for clonal composition (a within-species analog to community composition) in regulating productivity. Even after statistically accounting for the influence of individual clones, the bivariate relationship between clonal richness and productivity appears negative, albeit only slightly (Supporting information). We cannot definitively advance a mechanistic reason why the number of clones per se would decrease productivity. Possibly, our statistical approach failed to completely partition the influence of individual clones, and the apparent effects of clonal richness are simply effects of individual clones whose abundances correlate with clonal richness. A recent experimental study demonstrates nearly four-fold variation in productivity and about a two-fold variation in stress tolerance among different *S. ruralis* populations (Doherty 2017); we might expect even more variation across clones. The clones that were available in greater supply were used in more samples and had relative abundances that decreased as the number of clones increased. Clones that were available in a lesser supply were used primarily in more clonally rich treatments. If supply is indicative of general productivity of clones, then the effect of the productive clones might be diluted by effects of less productive clones in more clonally rich treatments. We also cannot rule out the possibility of inter-clonal growth inhibition.

The only case in which we encountered the expected positive effect of intraspecific diversity, albeit a weak one, was also in the *S. ruralis* experiment in the resistance phase. This effect was almost entirely accounted for by the abundances of just two of the clones and was negligibly affected by clonal richness. This finding suggests a role for clonal composition in regulating resistance and may suggest that some clones were better adapted for the experimental conditions than others. If that is the case, it could demonstrate evolutionary potential within *S. ruralis* to adapt to climate change. It also indicates the importance of considering intraspecific variation in climate change studies.

We anticipated and observed lesser effects of intraspecific diversity than community-level diversity because different species tend to harbor greater trait breadth than that found within a single species, especially across phylogenetically distant groups of species such as mosses and lichens (Concostrina-Zubiri et al. 2018), and widely-differing morphologies (Mallen-Cooper and Eldridge 2016). In another of only a few simultaneous manipulations of taxonomic and genotypic diversity, Prieto et al. (2015) found that taxonomic but not genotypic richness promoted productivity of agroecosystems, whereas genotypic but not taxonomic richness promoted stability. However, our community members (mosses and lichens of two kingdoms and several orders) spanned a greater trait breadth than those used by Prieto et al. (2015) (grasses and leguminous forbs of two angiosperm families) possibly leading to different results.

Implications for ecological restoration now and in the future

Our experimental disturbance simulated an abrupt change in growing conditions, shifting quickly to highly stressful. Although this was not designed to mimic a specific climate change scenario, it did induce some of the same stresses that we might expect under a climate change-induced heat wave (Wuebbles et al. 2017), such as high temperatures and reduced hydration event length. We produced no evidence that greater species richness or intraspecific clonal richness would provide resistance to such an event. Our results do imply that if species composition is spatially heterogeneous, we should expect resistance to spatially auto-correlate with particular species compositions or the presence of particular species. In our study system, the clonal composition of one of the key species also mattered, but much less so than species composition. A plausible application of our results is in climate-smart ecological restoration, or 'pre-storation' (Young et al. 2016, Butterfield et al. 2017). Pre-storation seeks to select genotypes or species (at least regionally native) for use in ecological restoration that can persist under both present conditions and expected future conditions. In the past decade, a rapid expansion of research has occurred focused on ecological restoration of biological soil crusts (Antoninka et al. 2020, Zhou et al. 2020). Despite the fact that substantial trait variation, e.g. in productivity and stress tolerance, may exist within a species (Doherty et al. 2018), maximization of intraspecific richness may not be the most viable strategy to improve climate-smart restoration outcomes, at least in our study system. Instead, selection of clones most adapted or resistant to emerging stresses could be beneficial. This strategy is somewhat related to the selection of locally adapted genetic material summarized by Kettenring et al. (2014), except that we must consider plausible environments of the future. Our results suggest that the biocrust species mixes used in restoration matter more than the clones used, in two distinct ways that could conflict to some degree. Some species may be more productive under favorable growing periods, a desirable attribute for faster results. However, sole reliance on such species might be an error because a different set of species may be better able to resist loss of productivity under the more stressful conditions expected with climate change. Our work suggests that species that resist disturbance and tolerate stress have a place in species mixes used for ecological pre-storation, alongside their more productive counterparts, even if they are relatively slow growing.

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Data availability statement

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.sf7m0cg6f>.

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