Soil mutualists modify priority effects on plant productivity, diversity, and composition

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Abstract

Question: The importance of priority effects on community assembly is well recognized, as is, increasingly, the role of environmental context in shaping those priority effects. Distinguishing the effects of soil nutrients and soil mutualists may be critical in the context of restoration, but remains poorly understood. Additionally, we asked whether pioneer species and soil conditions influenced trade-offs or complementarities between vegetation production and species diversity.

Location: Plant Growth Center, Montana State University, Bozeman, MT, US.

Methods: Using experimental seed addition in mesocosms, we investigated how the priority effects of different plant species influenced productivity, diversity and composition of the resulting plant community. We also experimentally manipulated soil nutrients and mycorrhizae to determine how they modified those priority effects.

Results: We found that species-specific priority effects of pioneers strongly governed the productivity, diversity and species composition of the resulting community. Pioneer grasses, one native and one non-native species, both preempted light and space, prevented the colonization and growth of the subsequent community and restricted community dispersion (i.e. differences in species composition among mesocosms). By contrast, the pioneer forb species had little influence on the recruitment and establishment of the later colonizing species, and supported the assembly of divergent communities. We found evidence to suggest that amendments of soil mutualists, but not soil nutrients, modified the influence of one pioneer species on characteristics of the resulting community by enhancing community productivity and diversity in mesocosms with non-native grass pioneers. Across all treatments, species diversity declined as vegetation production increased, indicating an overall trade-off between productivity and diversity. However, relationships between productivity and diversity varied among pioneer treatments and mycorrhizal amendments.

Conclusions: Our results emphasize important interactions between priority effects and the use of soil mycorrhizal amendments in restoration, as well as highlight how pioneer species and mycorrhizae influence potential trade-offs between restoration objectives aimed at enhancing productivity vs species diversity.

Introduction

Restoration of ecosystems often involves intentionally assembling plant communities, sometimes beginning with bare mineral soil in cases such as mine reclamation or vegetation recovery following road decommissioning. The initial assembly order of ecological communities – either through active plantings or passive colonization of species – may partially govern successional trajectories of plant communities by influencing ecosystem function (e.g. productivity), species diversity and community composition. Pioneer species can strongly influence resulting succession.

These 'priority effects' of pioneer species determine community structure and function in both theoretical (e.g. Drake 1990) and applied (e.g. Almany 2003; Burger et al. 2005; Cifuentes et al. 2010; Fukami et al. 2010; Weslien et al. 2011) systems. For instance, a strongly competitive pioneer species may restrict local diversity and impact species composition, especially on productive sites (Huston 1979). In these cases, productivity could be maximized to the detriment of diversity (Grime 1973), resulting in a negative productivity–diversity relationship. Alternatively, a less competitively dominant pioneer species may result in positive productivity–diversity relationships by allowing, for example, the co-existence of more species or functional groups. In these cases, complementarities among co-existing species occupying different niches may allow for productivity and diversity to be simultaneously high (*sensu* Dukes 2001; Fridley 2001) on restored lands. Although trade-offs and complementarities between productivity and diversity have been observed in theoretical and experimental plant communities, rarely have these concepts been applied to determine whether target conditions represent conflicting or compatible values in a restoration context (but see Zedler 2009).

Relationships between productivity and species diversity in managed and natural ecosystems are the focus of many empirical and theoretical studies (Mittelbach et al. 2001), but the patterns and mechanisms producing these productivity–diversity relationships remain equivocal (Adler et al. 2011). In model microbial systems, Fukami & Morin (2003) found that varying assembly order could result in different shapes of productivity–diversity relationships. In other words, species diversity was either maximized or minimized with intermediate levels of productivity, or increased with increasing productivity, depending on the assembly order of communities. While few other studies have explicitly investigated the role of priority effects on productivity–diversity relationships (but see Chase 2010), numerous calls to investigate mechanisms explaining these varying patterns have been made (Grace et al. 2012), especially given their important management implications (*sensu* Belote et al. 2011).

While local diversity is typically monitored and used to statistically determine efficacy of restoration treatments, regional or among-site diversity and composition may be a more relevant management scale to consider (Martin & Wilsey 2012). Compositional differences among communities (i.e. community dispersion) in both theoretical and applied contexts have received growing attention in the last decade (Anderson et al. 2011; Kraft et al. 2011), with results emphasizing the importance of dispersion to sustain ecosystems (*sensu* Leibold et al. 2004). The influence of pioneer species on dispersion among assembling communities has received less attention, especially in a restoration

context. As with the priority effect of pioneer species on local diversity and productivity, community dispersion may also be driven by the competitive status of pioneers. Strong competitors may limit local diversity through resource preemption, which may ultimately constrain community dispersion. Alternatively, a less competitively dominant pioneer species could allow greater species co-existence at local scales, which may result in greater community dispersion.

In applied settings of vegetation restoration, the competitive strength of pioneer species is generated in part by the life form or functional status of plants (e.g. Jarchow & Liebman 2012), such as annual or perennial grasses or forbs arriving at sites first. Priority effects can often-times lead to undesirable plant communities, especially when non-native species are the first to be planted or colonize recently disturbed sites. Grasses can outcompete forbs and restrict their recruitment, biomass and diversity (Dickson & Busby 2009), especially in high nutrient environments (e.g. Shaver & Chapin 1986; Bowman et al. 1993; Burkle & Irwin 2010). Grasses as pioneer species could thus steer community assembly by preventing other species and functional groups from recruiting, ultimately influencing species diversity and composition. Later in succession, such grass-dominated communities may be highly productive in terms of biomass, but depauperate in terms of diversity (Collins & Wein 1998). Non-native grasses, in particular, are often used to seed land in need of rehabilitation, delineating them as pioneer species and strongly influencing the trajectory of community development (Holl 2002).

In addition, it is critical to recognize the importance of environmental context in community assembly. In microcosm model systems, resource availability influenced the outcomes of priority effects by altering the composition of predator–prey communities (Jiang et al. 2011), as well as relationships between productivity and diversity (Fukami & Morin 2003). In naturally colonizing communities, soil mutualists are known to strongly influence various ecosystem characteristics (Hoeksema et al. 2010), and have the potential to mediate plant community assembly by accentuating or ameliorating priority effects. Soil mutualists can influence the growth of individuals, including pioneer or invading species (Nuñez et al. 2009), and can alter the competitive interactions among species (Marler et al. 1999). Understanding the complex ways in which priority effects influence developmental trajectories of communities, the resulting emergent properties including relationships between species diversity and productivity, and how these effects may be mediated by soil conditions will provide a better foundation for applying community theory to restoration practice (*sensu* Lockwood 1997). Techniques for restoration that are successful in one location may fail

in others (Young et al. 2001), possibly because of differences in environmental context.

With these issues in mind, we conducted a mesocosm experiment to address the following questions: (i) how do pioneer species representing several plant functional groups influence community assembly and the resulting patterns in productivity, species diversity and community dispersion; (ii) how do pioneer species influence productivity–diversity relationships; and (iii) to what degree does the soil environment (i.e. soil nutrient addition and inoculation of the soil with a suite of mycorrhizal species) modify these patterns?

Methods

Greenhouse methods

We conducted a greenhouse mesocosm experiment using a completely randomized design with three fully crossed factors: (1) identity of a pioneer species (one of three possible species, or bare); (2) soil nutrients (enriched or not); and (3) soil mycorrhizae (added or not). We established 176 community mesocosms using pots (30 cm × 20 cm × 8 cm deep) filled with locally collected Montana topsoil (silty clay texture, pH = 7.5, cation exchange capacity = 30.7 meq 100 g^{-1}). Mesocosms were divided into four groups of 44, representing each of the four pioneer treatments: bare soil (no focal priority seed added; this treatment served as a control); a native forb, *Linum lewisii* (Ag Depot, Bozeman, MT, US); a native grass, *Bromus marginatus* (garnet variety, BBBSeed.com, Boulder, CO, US); or a non-native grass, *Dactylis glomerata* (Ag Depot, Bozeman, MT, US). Twenty seeds of focal priority plant species were planted in a grid arrangement across the soil surface of each mesocosm. We originally included a *Lupinus argenteus* pioneer treatment in order to test a native nitrogen fixer, but we excluded all mesocosms in this treatment because of germination failure. These pioneer species are known to be mycorrhizal (e.g. West 1996; Pendleton et al. 2004). This experiment took place at the Plant Growth Center on the campus of Montana State University between July and October 2011. Conditions maintained in the greenhouse include 22 °C day and 18 °C night temperatures and a 16-h photoperiod.

In nutrient enrichment mesocosms, 1.5 teaspoons (7.5 g) of Osmocote (Smart-Release Plant Food, Flower & Vegetable, 14-14-14) granules were used according to the manufacturer's instructions, and randomly added to half of the mesocosms. In the mycorrhizae treatment, two tablets of MycoTabs (Fungi Perfecti LLC, Olympia, WA, US), containing spore masses of arbuscular and ectomycorrhizal species (App. S1), were randomly added to half of the mesocosms, placed 10 horizontal cm from each other and from the sides of the pot. In a restoration context, MycoTabs are

readily available and an easy way to inoculate soils. In total, the experimental design included 11 replicates of each complete treatment combination (4 pioneer treatments × 2 mycorrhizal treatments × 2 nutrient treatments × 11 reps = 176 experimental units). All mesocosms were watered three times per week throughout the duration of the experiment. We randomly rotated the mesocosms every 4 wk to minimize any spatial effects. One replicate was excluded from the ANPP analyses below because of a labelling error.

To simulate priority effects, pioneer plants were allowed to establish and grow for 5 wk before the rest of the community was added. To simulate a randomly establishing community of species, we added 1 g seed mix (Rocky Mountain Wildflower Mix, Rainier Seeds, Inc., Davenport, WA, US) homogeneously to the surface of each mesocosm (see App. S2 for species list). After 10 wk of development of the secondary colonizing community (hereafter referred to as colonists), plant communities had established in mesocosms, and crowding and competition for light appeared to be present. Thus, at this time we terminated the experiment, harvested the above-ground biomass (ANPP) from each mesocosm, sorted it to species, and dried and weighed it. To assess below-ground root biomass, we sampled a 6.5-cm diameter core from the centre of each mesocosm to avoid edge effects. We separated the roots from the soil, and dried and weighed them.

Statistical analyses

After 10 total weeks of colonist community development, we investigated treatment effects and their interactions on above-ground productivity (total and colonist community ANPP), on above-ground diversity (colonist community species richness and Pielou's evenness), and on below-ground root biomass (ln-transformed) using three-way MANOVAs. Interactions where $P > 0.1$ were removed from the models. Significant MANOVAs ($P < 0.05$ in all cases) were followed by three-way ANOVAs, and we focused on reporting these ANOVA results. Significant ANOVAs were followed by Tukey HSD tests to further determine differences among treatments. To investigate how the productivity of pioneers might influence the productivity of colonists (i.e. we expected strongly competitive pioneers to limit the growth of colonists), we tested how the ANPP of each pioneer species was related to the ANPP of the colonist community using separate correlations. We tested for treatment effects on species composition and variance in composition (i.e. estimate of community dispersion) using multivariate analysis of variance ('adonis' in vegan package in R, based on Bray-Curtis dissimilarity; R Foundation for Statistical Computing, Vienna, AT) and 'betadisper' in vegan

package in R, respectively. We investigated composition between treatments considering the entire community, which included the pioneer species, as well as composition for only the colonist community, excluding the pioneers. We conducted the analysis both ways in order to determine effects of pioneer species dominance on community composition, as well as to reveal potentially concealed patterns of composition among the colonist communities after removing pioneers from the analysis. To determine which species, if any, contributed most strongly to the compositional differences among treatments, we used similarity percentage analyses ('simper' in vegan package in R).

To investigate patterns between productivity and diversity across mesocosms, we investigated relationships between species richness and total ANPP among and within pioneer, mycorrhizae and nutrient treatments, as well as their interactions, in an analysis of covariance. We decided to fit both linear and quadratic forms of productivity to the data after noticing possible hump-shaped relationships (cf. Fukami & Morin 2003). We used Akaike information criterion (AIC) to determine whether to include quadratic forms of productivity in models (i.e. to test whether adding the extra squared term was worth the reduction in parsimony). The potential for *both* linear and quadratic forms of the covariate productivity may have precluded our ability to find a significant productivity × pioneer treatment interaction using *either* the linear or quadratic form of productivity in a full model (see Results). Thus, we analysed productivity–richness relationships for each pioneer treatment separately, and conducted *post-hoc* models of richness as a function of productivity and mycorrhizae treatment *within* pioneer treatments following results of the full model (see Results). With these analyses of patterns, we do not imply directionality or causality in the relationships between productivity and diversity. Data met all assumptions of statistical tests. All analyses were performed in R 2.15.1.

Results

Productivity

After 10 wk of community development, priority effects on the colonist communities were evident. Across all mesocosms, only pioneer treatment influenced total community ANPP (Fig. 1a, Table 1) and colonist community ANPP (Fig. 1b, Table 1). There were marginal negative relationships between pioneer and colonist community ANPP for *D. glomerata* ($r = -0.29$, $P = 0.055$) and *B. marginatus* ($r = -0.21$, $P = 0.067$) and no relationship for *L. lewisii* ($r = 0.14$, $P = 0.38$). However, there was a marginal interaction between pioneer and mycorrhizae treatments for colonist community ANPP (Table 1). For bare and *B. marginatus* pioneer treatments, there were no mycorrhizal treatment effects on pioneer or colonist community ANPP (bare: $P > 0.80$, MB: $P > 0.30$). In the *L. lewisii* pioneer treatment, there was a marginal negative effect of mycorrhizae on colonist community ANPP (25% decline, $F_{1,41} = 3.28$, $P = 0.078$). In the *D. glomerata* pioneer treatment, mycorrhizal addition doubled colonist community ANPP ($F_{1,42} = 5.03$, $P = 0.031$). This effect was driven by weak, joint responses of many colonist species; *Papaver rhoeas* and *Cosmos sulphureus* contributed most strongly to differences in community composition between inoculated and non-inoculated *D. glomerata* mesocosms at 7.4% and 6.6%, respectively (see community composition results below).

Across all mesocosms, treatments influenced variability in total root biomass (Table 1). There was an effect of pioneer treatment (Table 1), with 25% lower root biomass in
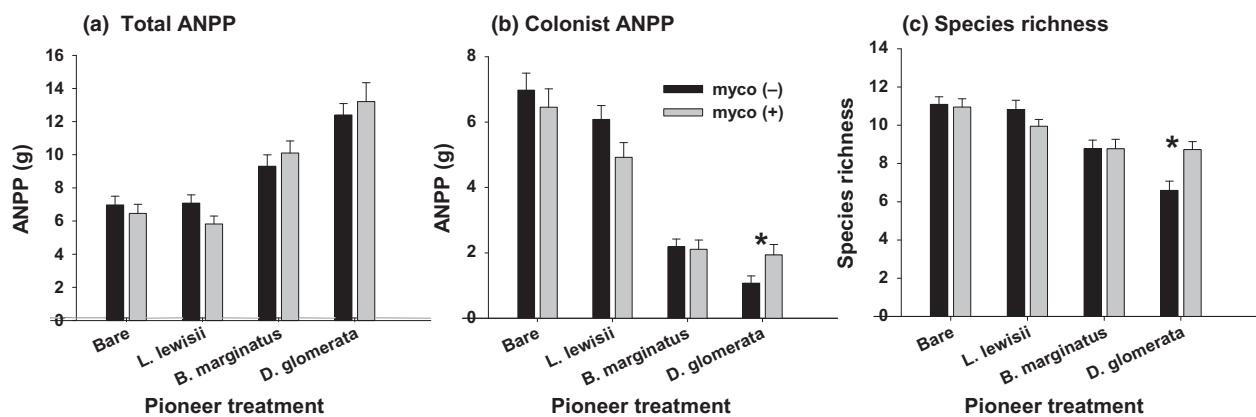

Fig. 1. Mean effects of pioneer species (bare, *Linum lewisii*, *Bromus marginatus* and *Dactylis glomerata*) on total ANPP (a), colonist community ANPP (b) and species richness (c). Error bars are ± 1 SE. For each pioneer species, significant differences (at α = 0.05) of mycorrhizal addition are illustrated with an asterisk.

Table 1. Productivity. The influence of pioneer species, mycorrhizal addition, fertilizer addition and their interactions on total ANPP (ANOVA model: $F_{8,166} = 21.87$, $P < 0.0001$), colonist community ANPP (ANOVA model: $F_{5,169} = 48.09$, $P < 0.0001$) and root biomass (ANOVA model: $F_{6,168} = 17.66$, $P < 0.0001$). Interactions where $P > 0.1$ were dropped from the models and run without them. Pioneer species treatment influenced total ANPP, colonist ANPP and root biomass. Additionally, mycorrhizae treatment affected root biomass.

Response	Treatment	df	F	P
Total ANPP	Pioneer	3,169	80.01	**<0.0001**
	Mycorrhizae	1,169	0.59	0.45
	Fertilizer	1,169	0.47	0.50
Colonist ANPP	Pioneer	3,166	35.53	**<0.0001**
	Mycorrhizae	1,166	0.008	0.92
	Fertilizer	1,166	0.28	0.59
	Pioneer × myc	3,166	2.22	0.088
Root Biomass	Pioneer	3,168	32.68	**<0.0001**
	Mycorrhizae	1,168	4.45	**0.037**
	Fertilizer	1,168	0.14	0.71
	Myc × fert	1,168	3.67	0.057

df refers to (treatment, error) degrees of freedom. Significant P-values at α < 0.05 are in bold.

Table 2. Diversity. The influence of pioneer species, mycorrhizal addition, fertilizer addition and their interactions on colonist community species richness (ANOVA model: $F_{8,166} = 11.52$, $P < 0.0001$) and evenness (ANOVA model: $F_{8,166} = 72.83$, $P < 0.0001$). Interactions where $P > 0.1$ were dropped from the models and run without them. Pioneer species treatment influenced colonist species richness and evenness, and pioneer species interacted with mycorrhizal treatment to affect colonist richness and evenness.

Response	Treatment	df	F	P
Colonist Species Richness	Pioneer	3,166	25.27	**<0.0001**
	Mycorrhizae	1,166	0.98	0.32
	Fertilizer	1,166	1.46	0.23
	Pioneer × myc	3,166	4.57	**0.0042**
Colonist Evenness	Pioneer	3,166	195.34	**<0.0001**
	Mycorrhizae	1,166	0.52	0.47
	Fertilizer	1,166	0.20	0.65
	Pioneer × myc	3,166	2.89	**0.037**

df refers to (treatment, error) degrees of freedom. Significant P-values at α < 0.05 are in bold.

bare and *L. lewisii* mesocosms than *B. marginatus* and *D. glomerata* mesocosms. Additionally, mycorrhizal addition decreased root biomass by 10%, especially in mesocosms that did not receive nutrient enrichment (i.e. marginal mycorrhizal by fertilization interaction; Table 1).

Diversity

There were treatment effects on colonist community species richness, with strong influence of the priority species and an interactive effect of mycorrhizae and priority species (Fig. 1c, Table 2). Colonist community richness was highest in bare and *L. lewisii* mesocosms, intermediate in *B. marginatus* and lowest in *D. glomerata* (Fig. 1c). For *D. glomerata* mesocosms, mycorrhizal addition enhanced colonist community richness by 40% ($F_{1,40} = 10.72$, $P = 0.0022$), allowing maintenance of similar community richness to that of *B. marginatus* mesocosms. Evenness of the colonist community showed similar patterns as richness in response to treatments. Bare and *L. lewisii* had 2.5-fold greater evenness than *B. marginatus* and *D. glomerata* ($F_{3,165} = 195.34$, $P < 0.0001$). There was also an interactive effect of mycorrhizal and pioneer treatments on evenness ($F_{3,165} = 2.89$, $P = 0.037$), with 50% greater evenness under mycorrhizal addition in *D. glomerata* mesocosms.

Composition and community dispersion

There were differences in total (Fig. 2a) and colonist community (Fig. 2b) species composition among pioneer treat-

ments (Table 3), with bare and *L. lewisii* having similar composition to one another but very different from either *B. marginatus* or *D. glomerata*. In particular, *Papaver rhoeas* (13.4–19.5% contribution), *Eschscholzia californica* (5.8–9.1%), *Cosmos sulphureus* (5.1–6.2%) and *Linum grandiflorum* (2.9–5.8%) contributed most strongly to compositional differences among pioneer treatments, each performing better in bare and *L. lewisii* mesocosms compared to *B. marginatus* and *D. glomerata* mesocosms. We also observed a significant interaction between pioneer and mycorrhizal treatments on colonist community composition, indicating that the effect of soil mutualist addition varied by pioneer species treatment, but there was no main effect of mycorrhizal treatment on colonist community composition across mesocosms (Table 3). Specifically, mycorrhizal addition marginally influenced colonist community composition in *B. marginatus* ($F_{1,42} = 2.04$, $P = 0.065$) and *D. glomerata* ($F_{1,42} = 1.82$, $P = 0.064$), but not bare ($F_{1,42} = 0.81$, $P = 0.57$) or *L. lewisii* mesocosms ($F_{1,41} = 0.75$, $P = 0.62$). Pioneer treatment also influenced the degree of variation dispersion in total community (Fig. 2c) and colonist community (Fig. 2d) species composition (Table 3). Specifically, bare and *L. lewisii* pioneer treatments supported more divergent species compositions than *B. marginatus* and *D. glomerata* pioneer treatments when the total community was considered (Fig. 2c). However, *D. glomerata* mesocosms supported greater community dispersion compared to the other pioneer treatments when only the colonist community was considered (Fig. 2d). There were no effects of fertilization treatment on either total or colonist community composition or dispersion, and there were no main effects of mycorrhizal
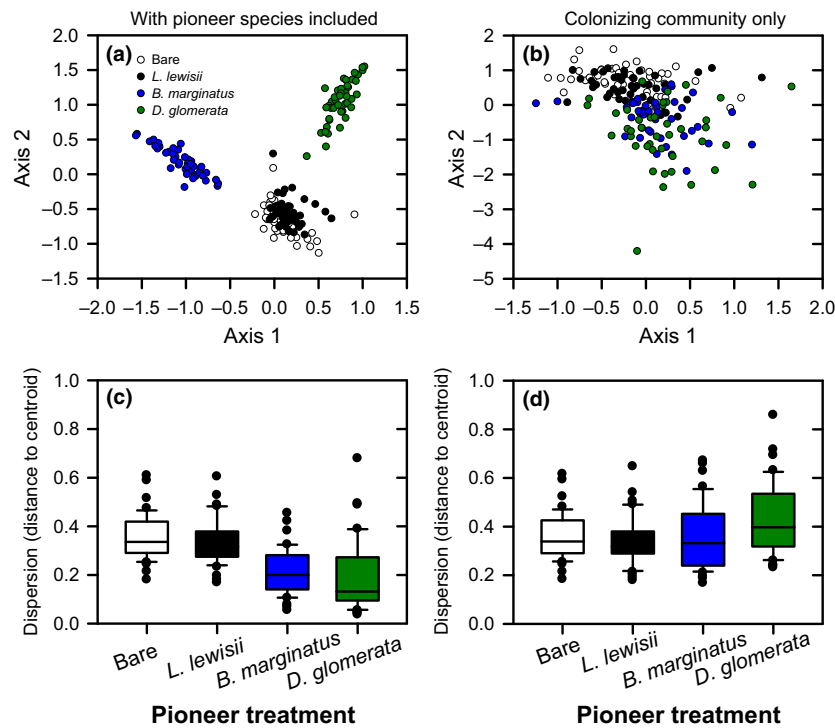
Fig. 2. Non-metric multidimensional scaling (NMDS) ordination of community composition for each pioneer species with all species included (a: total community) and with focal pioneer species removed from the analysis (b: colonizing community only). Community dispersion for each pioneer species with all species included (c: total community) and with focal pioneer species removed from the analysis (d: colonizing community only). NMDS stress values <15 in both cases. Box and whisker plots show the median dispersion value within pioneer treatments (line in box), the 25th and 75th percentile values (bottom and top of box, respectively), and 10th and 90th percentile values (bottom and top of whiskers, respectively). Outlying points are shown as black filled symbols.

Table 3. Composition and community dispersion. The influence of pioneer species, mycorrhizal addition, fertilizer addition and their interactions on total and colonist community composition as well as their individual effects on total and colonist community dispersion. Interactions where $P > 0.1$ were dropped from the community composition models and run without them. Pioneer species treatment influenced total and colonist community composition and dispersion.

Response	Treatment	df	F	P
Total Community Composition	Pioneer	3,169	73.72	**0.001**
	Mycorrhizae	1,169	0.29	0.89
	Fertilizer	1,169	0.85	0.42
Colonist Composition	Pioneer	3,166	17.65	**0.001**
	Mycorrhizae	1,166	0.77	0.58
	Fertilizer	1,166	0.71	0.64
	Pioneer × myc	3,166	1.64	**0.036**
Total Community Dispersion	Pioneer	3,171	26.44	**<0.0001**
	Mycorrhizae	1,173	0.43	0.51
	Fertilizer	1,173	0.28	0.60
Colonist Dispersion	Pioneer	3,171	5.09	**0.002**
	Mycorrhizae	1,173	1.82	0.18
	Fertilizer	1,173	0.55	0.46

df refers to (treatment, error) degrees of freedom. Significant *P*-values at α < 0.05 are in bold.

treatment on total or colonist community dispersion (Table 3).

Productivity–diversity relationships

Across all mesocosms, there was a negative linear relationship between productivity and diversity (Table 4, Fig. 3a). There was also a significant interaction between the quadratic form of productivity and mycorrhizae treatment (Table 4, Fig. 3b). However, the magnitude and direction of the productivity–diversity relationship varied among pioneer treatments (Fig. 3c–f). There was a linear positive productivity–diversity relationship for bare mesocosms (Fig. 3c; $P = 0.04$, $n = 44$) and no relationship for either *L. lewisii* (Fig. 3e; $P = 0.69$, $n = 43$) or *D. glomerata* (Fig. 3f; $P = 0.86$, $n = 44$). The relationship between productivity and diversity in the *B. marginatus* pioneer treatments displayed a hump-shaped relationship (Fig. 3d; quadratic model $P = 0.03$, AIC = 195.3), which fit the data better than the linear form ($P = 0.24$, AIC = 198.2). No other quadratic forms of productivity–diversity

Table 4. Productivity–diversity relationships. The effects of experimental treatments (i.e. pioneer species and mycorrhizal addition), productivity (ANPP) and their interactions on total species richness. The main effect of fertilizer treatment and all interactions with fertilizer were not significant and removed from the model. Mycorrhizae influenced productivity–diversity relationships. The main effect of ANPP is shown in Fig. 3a and the ANPP^2 × mycorrhizae treatment interaction is shown in Fig. 3b.

	df	F	P
ANPP	1,158	16.95	**<0.0001**
ANPP^2	1,158	3.08	0.081
Mycorrhizae	1,158	1.71	0.19
Pioneer	3,158	22.53	**<0.0001**
ANPP^2 × Mycorrhizae	1,158	4.98	**0.027**
ANPP^2 × Pioneer	3,158	0.76	0.52
Mycorrhizae × Pioneer	3,158	4.06	**0.0082**
ANPP^2 × Mycorrhizae × Pioneer	3,158	0.93	0.43

df refers to (treatment, residual) degrees of freedom. Significant P-values at $\alpha < 0.05$ are in bold.

relationships within pioneer treatments fit the data better based on AIC.

Discussion

In our experimental mesocosms, species-specific priority effects of pioneers strongly governed the ANPP, diversity and species composition of the resulting community, as well as patterns of productivity–diversity relationships. The amendments of soil mutualists, but not soil nutrients, modified this influence of pioneer species on characteristics of the colonizing community. Combined, these results suggest that pioneer species interact with soil mutualists to govern diversity, community composition and ecosystem function. This is one of the first demonstrations that mycorrhizae modify priority effects on ecosystems.

Priority effects on plant productivity, diversity and composition

When grasses, either the native or the non-native species, were used as pioneers, their ANPP was negatively related to the ANPP and diversity of the colonizing community. This suggests that the quick establishment, fast growth and high productivity of the grasses competitively excluded other colonizing species through preemption of light and space. Both a native and a non-native grass restricted compositional differences among communities (i.e. community dispersion) by acting as a stronger community filter during the assembly process. By contrast, the pioneer forb species had little influence on the recruitment and establishment of the later colonizing species, and supported the assembly of divergent communities equivalent in composition to those without a pioneer species, containing many

unique species that were unable to establish in mesocosms with pioneer grasses.

Priority effects of the different pioneer species were the only aspect of community assembly tested in this study that strongly affected the compositional dispersion among mesocosms. In agreement with our predictions, we found that dominant pioneer species (i.e. grasses) restricted community dispersion compared to the effects of a less-dominant forb pioneer species when the entire plant community was considered. These patterns indicate that strongly competitive pioneers may not only limit local diversity but also constrain compositional differences among sites, thus potentially homogenizing outcomes of community assembly. However, when dispersion of the colonizing communities alone was considered, dominant and non-native *D. glomerata* promoted the highest dispersion compared to the other pioneer species. This effect was primarily due to a few colonizing individuals of distinct species with low biomass contributions that recruited to each *D. glomerata* understorey, yet the composition of these colonists was variable among mesocosms. Thus, despite the appearance of enhanced colonizing community dispersion by dominant *D. glomerata* pioneers, we argue that maximization of both local diversity and dispersion of the total community may be best achieved by non-dominant pioneer species such as *L. lewisii*.

Soil mycorrhizae modified priority effects

While the priority effects of pioneer species on ANPP and composition of the colonizing community were clear, soil mycorrhizae modified the effect of pioneer species on species richness and composition. For instance, negative effects of the non-native pioneer grass species on the species diversity of the colonizing community were ameliorated by providing supplemental soil mutualists. In treatments where mycorrhizae were added, colonizing community richness established in mesocosms following the non-native grass pioneer treatment equalled colonizing community richness in mesocosms with the native grass treatment. This pattern occurred through modest productivity enhancement of many colonist species, and not responses of a select few. If these results are general, non-native grasses may have a more suppressive influence on species diversity of colonizing communities when soil mutualists are in low abundance, or soil mutualists temper the suppressive effect of non-native pioneer grasses. This important finding may suggest that soil mutualists provide mechanisms for maintaining species diversity in natural systems (Van der Heijden et al. 1998; Klironomos 2002), and that commercial soil mycorrhizal amendments could enhance diversity of degraded sites in plant community restoration projects. However, additional studies involving
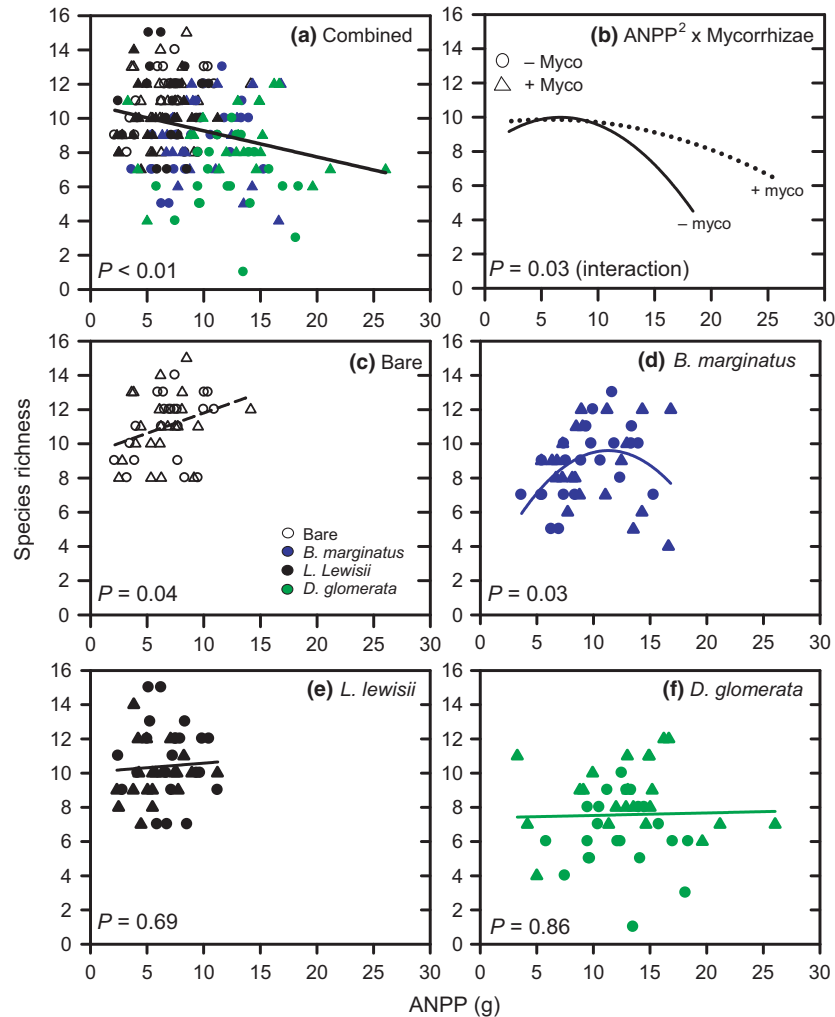
Fig. 3. Relationships between species richness and ANPP (total biomass) for all pioneer species combined (a), best-fit models for each mycorrhizal treatment (b) and for each pioneer treatment: bare (c), *Bromus marginatus* (d), *Linum lewisii* (e) and *Dactylis glomerata* (f).

more species of all functional groups tested here (i.e. native grasses, non-native grasses and forbs) are needed to confirm these patterns. Additionally, our study treated mycorrhizae additions as a fixed effect (i.e. experimental units were treated or not), but measuring inoculation rates among units was beyond the scope of our study. Interestingly, across pioneer treatments, mycorrhizal amendments reduced plant root biomass, especially when supplemental soil nutrients were not supplied, indicating that mycorrhizae alleviate the need for plant allocation to roots and may aid in plant restoration on nutrient-poor sites.

Soil nutrient addition did not influence plant community assembly

Other research has shown that resource availability is important in community assembly, but we did not observe

those effects. In an aquatic mesocosm experiment, Chase (2010) showed that processes of community assembly differed with nutrient availability. Highly productive environments experienced stronger priority effects, leading to greater community dispersion compared to low nutrient environments (Chase 2010). In a similar manner, but using a different model system, we did not find effects of soil resources on plant community dispersion. In our terrestrial system, soil resources were not as important as priority effects, which constrained community assembly irrespective of resources. In a different terrestrial system, Kardol et al. (2013) found that the magnitude of priority effects was modified by soil fertility, suggesting that the levels of nutrients present in our soil were adequate even in the absence of supplemental fertilizer. In our study, the lack of responses to added soil nutrients could be due to the fact that soil resource status was already high and the

relationships between soil resource availability and plant biomass responses may have been saturated, especially with the duration of our experiment and one-time application of slow-release fertilizer.

Productivity–diversity relationships

Priority effects as well as mycorrhizal treatments influenced relationships between productivity and diversity. Interestingly, species diversity was maximized at intermediate levels of productivity when *B. marginatus* were added as pioneer to mesocosms. This hump-shaped relationship was also frequently observed in the microcosm study of Fukami & Morin (2003), and also depended on assembly order of communities in their study. The dependence of productivity–diversity relationships on environmental context has been widely recognized (Waide et al. 1999; Fukami & Morin 2003; Adler et al. 2011; Belote et al. 2011; Fridley et al. 2012). Our results suggest that priority effects may at least partially govern productivity–diversity relationships. To varying degrees, each pioneer species preempted resources and prevented biodiversity establishment, shifting the productivity–diversity relationship into a negative one across mesocosms. More novel is our finding that mycorrhizae may also contribute to productivity–diversity relationships. Across mesocosms, mycorrhizal inoculation prevented declines in species richness with increasing ANPP across a greater range of productivity compared to mesocoms that were not inoculated, indicating that mycorrhizae may be able to ameliorate the trade-off between productivity and diversity.

Implications for restoration

Understanding how properties of plant communities depend on pioneer species and mycorrhizal composition and abundance may provide important consideration in restoration planning. There may be initial trade-offs between community productivity and species diversity, at least in situations where community assembly has strong priority effects involving a functional group with clear dominance over other species. Although productivity may be maximized with resultant positive effects on soil erosion (through greater root biomass and plant cover; Renard et al. 1991), in cases where grasses colonize or are planted first, species diversity may be reduced. If initial establishment or maintenance of high regional species diversity is a goal of conservation and restoration, then direct seeding of a diverse mix of forb species may be ideal. Because such seed mixes are often prohibitively expensive for restoration, planting readily available and inexpensive native forbs (such as *L. lewisii*) as pioneer species may help stabilize

the soil while simultaneously allowing the recruitment of diverse secondary communities from the local species pool (cf. Grant et al. 2011). If grasses are planted to meet vegetation production and cover goals, soil inoculation with mycorrhizae may temper this trade-off between productivity and diversity.

Conclusions

Our results confirm other studies that indicate the strong influence that priority effects and pioneer species identity have on community assembly and resulting trajectories of community productivity, diversity and composition, as well as patterns of productivity–diversity relationships. Our results expand on these widely-observed patterns by illustrating how enrichment of soil mycorrhizae can modify the influence of pioneer species and their priority effects on species diversity of emerging plant communities. We recognize that we observed the short-term effects of our treatments, and we encourage longer-term studies to investigate whether these trends in community assembly reverse, grow stronger or dissipate over time. More research should focus on how priority affects and community assembly are governed by their environmental context and the application of this understanding to active planting programmes conducted during ecological restoration.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. MycoTabs species list.
Appendix S2. Components of Rocky Mountain Wildflower mix.