

Negative plant-soil feedbacks increase with plant abundance, and are unchanged by competition

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Abstract. Plant-soil feedbacks and interspecific competition are ubiquitous interactions that strongly influence the performance of plants. Yet few studies have examined whether the strength of these interactions corresponds with the abundance of plant species in the field, or whether feedbacks and competition interact in ways that either ameliorate or exacerbate their effects in isolation. We sampled soil from two intermountain grassland communities where we also measured the relative abundance of plant species. In greenhouse experiments, we quantified the direction and magnitude of plant-soil feedbacks for 10 target species that spanned a range of abundances in the field. In soil from both sites, plant-soil feedbacks were mostly negative, with more abundant species suffering greater negative feedbacks than rare species. In contrast, the average response to competition for each species was unrelated with its abundance in the field. We also determined how competitive response varied among our target species when plants competed in live vs. sterile soil. Interspecific competition reduced plant size, but the strength of this negative effect was unchanged by plant-soil feedbacks. Finally, when plants competed interspecifically, we asked how conspecific-trained, heterospecific-trained, and sterile soil influenced the competitive responses of our target species and how this varied depending on whether target species were abundant or rare in the field. Here, we found that both abundant and rare species were not as harmed by competition when they grew in heterospecific-trained soil compared to when they grew in conspecific-cultured soil. Abundant species were also not as harmed by competition when growing in sterile vs. conspecific-trained soil, but this was not the case for rare species. Our results suggest that abundant plants accrue species-specific soil pathogens to a greater extent than rare species. Thus, negative feedbacks may be critical for preventing abundant species from becoming even more abundant than rare species.

Key words: coexistence; interspecific competition; plant abundance; plant distribution; plant-soil feedbacks; species-specific effects.

INTRODUCTION

Plant-soil feedbacks (PSFs) occur when plant species over time culture microorganisms in soil that feed back to either help or harm conspecifics. Positive feedbacks are often due to accumulation of mutualistic arbuscular mycorrhizal fungi (AMF; Klironomos 2002); negative biotic feedbacks result from plants culturing pathogenic soil microorganisms (van der Putten et al. 1993). Our understanding of the ubiquity and strength of these feedbacks in natural systems has progressed substantially since the seminal work of Bever (1994). Yet one key issue that remains unresolved is the extent to which PSFs explain plant abundance in the field. Theory suggests that PSFs may maintain local diversity if negative feedbacks predominate and these negative feedbacks operate in a density-dependent fashion (Janzen 1970, Connell 1971,

Harms et al. 2000, Bell et al. 2006, Comita et al. 2010). There is substantial evidence for feedbacks being more negative than positive, although positive feedbacks are not uncommon (Bever 1994, Bever et al. 1997, Olff et al. 2000, Reinhart et al. 2003, Kardol et al. 2007, Kulmatiski et al. 2008). In terms of relationships between feedback strength and plant abundance, some evidence suggests that rare species are more negatively influenced by feedbacks than common species (Klironomos 2002, Mangan et al. 2010a), while other research suggests that dominant species can suffer strongly from negative feedbacks (van der Putten et al. 1993). More recently Reinhart (2012) found no relationship between species abundance and the strength of PSFs. However, single-species studies have found that PSFs can be more negative when individuals grow at high density than at low density (van de Voorde et al. 2012, Kos et al. 2013). These conflicting and limited results suggest that our understanding of the extent to which PSFs explain variation in plant abundance in the field remains poor.

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Another important but unresolved issue that has strong implications for the community-level consequences of PSFs is how interspecific competition and plant-soil feedbacks interact (Hodge and Fitter 2013). If PSFs are positive, for example in cases when plants have a positive growth response to mutualistic mycorrhizal fungi, they can gain competitive advantages over species that are less AMF responsive (Allen and Allen 1990, Hartnett and Wilson 1999, Scheublin et al. 2007). This interaction can promote competitive dominance and a loss of community diversity compared to when mycorrhizal fungi are suppressed (Hartnett and Wilson 1999, O'Connor et al. 2002, Karanika et al. 2008). However, the presence of AMF can also reduce competitive inequality (Wagg et al. 2011).

In contrast, if PSFs are negative, for example in interactions between plants and soil pathogens, PSFs can prevent competitive dominance (Bever 2003, Bonanomi et al. 2005). Negative PSFs could change competitive hierarchies in two ways. First, if strong enough to kill particular species, negative PSFs could completely eliminate competitive effects. Second, strong negative feedbacks could alter plant performance in ways that greatly exacerbate (Petermann et al. 2008) or attenuate competitive effects or responses. In other words, species that are dominant competitors (or very tolerant of competition) may turn into weak competitors or have poor competitive tolerance when they suffer from negative soil feedbacks (van der Putten and Peters 1997). But instead, rather than exacerbating effects of competition, if plant-soil feedbacks are driven by species-specific soil pathogens, there might be a "dilution effect" when two different plant species compete. That is, the presence of two species might decrease frequency-dependent attack on the focal species compared to if that species grew alone. This has been proposed as a mechanism that explains why productivity of species-poor assemblages is less than species-rich ones (Maron et al. 2011). If this occurs, then feedbacks should be weaker when plants compete interspecifically than intraspecifically. Surprisingly few studies have examined these crucial interactions (but see Pendergast et al. 2013).

Studies that have quantified how competition and plant-soil feedbacks interact to influence native plant performance have found mixed results. Bever (1994) found no effect of negative plant-soil feedbacks on competitive interactions, whereas other work has shown that the negative effects of competition can be stronger when plants suffer from strong negative PSFs compared to when PSFs are more neutral (van der Putten and Peters 1997, Kardol et al. 2007, Pendergast et al. 2013). In fact, the competitive replacement of species that suffer disproportionately more from negative feedbacks is thought to drive directional succession in some systems (van der Putten and Peters 1997, Kardol et al. 2006). Casper and Castelli (2007) found that the joint effects of negative plant-soil feedbacks and interspecific competition varied depending on the species examined, and Hendriks et al. (2015) found strong interactions between competition and negative

feedbacks that influenced root growth, but that did not translate to above ground performance. Finally, Reinhart and Callaway (2006) found that positive feedbacks can influence the outcome of interspecific competition.

Interactions between PSFs and competitive ability might be quite different for dominant vs. rare species. For example, negative PSFs have been shown to be more intense for uncommon species than for more abundant ones (Klironomos 2002, Mangan et al. 2010a). Conversely, dominant species are often superior competitors to rarer species (Weiner 1990, Pennings and Callaway 1992, Schwinning and Fox 1995, Facelli and Temby 2002, Gilbert et al. 2009). This predicts that dominant species would be more tolerant of competition than rarer species, and that the effects of soil biota (for example, whether plants compete in self-cultured or heterospecific-cultured soil) would not change their competitive response. In contrast, if rare species are particularly negatively affected by PSFs, then they should respond more negatively to competition when growing in self-trained soil, whereas their competitive response should improve when growing in heterospecific-trained soils. We know of no study that has tested these relationships for species within the same community, and examined how abundance in the field might predict interactions between plant-soil feedbacks and competition.

We took several different approaches to explore these issues. First, we examined how the strength of PSFs and plant competitive response correlated with the abundance of 10 native species that co-occur in two savanna communities in western Montana. Second, we grew the same 10 focal species in both conspecific-cultured and sterile soil, with species grown alone or in competition with each of the other focal species. This enabled us to compare the strength of competition and PSFs on plant growth. It also allowed us to ask whether PSFs significantly altered plant average competitive response and whether the presence of a heterospecific exacerbated or "diluted" any feedback effects that occurred in isolation of competition. Third, we competed plants in either conspecific-cultured, heterospecific-cultured or sterile soil. We hypothesized that plants that were either abundant or rare, common or rare in the field would respond differently when competing in self-cultured soil compared to the other two types. Specifically, we predicted that if PSFs correlated with plant abundance, those species suffering from strong negative PSFs would be affected more negatively when competing with heterospecifics in self-trained soil than in the other two soil types. In contrast, species at the other end of the PSF-abundance continuum would have the same response to competition regardless of soil type.

METHODS

Field sites

Our two field sites were located near Clinton, Montana, USA, at approximately 1,706 m (site 1) and 1,585 m

(site 2). Both sites were in open Ponderosa pine (*Pinus ponderosa*) and Douglas fir (*Pseudotsuga menziesii*) savanna. The plant community we sampled consisted of perennial grasses (*Festuca idahoensis*, *Poa secunda*, *Pseudoroegneria spicata* and *Koeleria macrantha*) and diverse perennial forbs. In this community, plants occur at moderate densities (average cover of all species combined was 50%, with native species richness averaging 12 species per m²; Pearson and Ortega, *unpublished data*) with bare interstitial space between plants.

Feedbacks and plant abundance in the field

To quantify relative plant abundance, at each site in 2005 we systematically distributed 52 0.7 × 0.7 m quadrats at 20-m intervals along four transects oriented perpendicular to the slope and 50 m apart. Within each quadrat, we estimated cover by species to the nearest 1% twice during the growing season: early during the wet period (May–June) and late during the dry period (July–August). To ensure accuracy and consistency, we marked plot frames to denote 1% cover increments, and cover estimation was conducted by the same two-person team at all sites. We took the maximum cover value obtained across the two sampling periods for each species in each quadrat, and averaged these values across all 52 quadrats for each site. Based on these values, we selected 10 target species that occurred at both sites, were similar in their relative abundance at each site, and represented both grasses and forbs (Table 1). We assigned each of our 10 target species to two broad abundance classes based on their relative cover: abundant and rare (Table 1). As another metric of relative abundance, we also calculated the percentage of quadrats (out of 52) containing each focal species.

In mid-May 2013, we collected a pooled soil sample from each site. Soil was collected in the top 12 cm of soil at a minimum of 30 points stratified across each site. Sampling points were away from plant rhizospheres in the interstitial space between plants. We sampled away from focal plants rather than in their rhizospheres because we

did not want variation in the history of plant occupancy between species to influence our results. Rather, we were interested in how species might differ in their ability to culture soil biota (and their susceptibility to pathogens) in soil from the two sites. Within a week of harvesting soil, we filled 720 500 mL pots (360 pots/site) with 200 mL of sterile sand (in the bottom of each pot), topped with a 1:1 mixture of field-collected soil and sterile sand. Seeds of each of the 10 target species were collected at each site, supplemented with seeds purchased from local seed companies. For each species, seed were sown directly on the soil surface of each of 36 pots. A few species did not germinate in the first week after sowing so we germinated them in petri dishes and transplanted the seedlings into pots. Plants were grown for approximately 29 weeks in a greenhouse. On sunny days, photosynthetically available radiation ranged from 300 to 1,500 μmol·m⁻²·s⁻¹ and temperatures ranged from 20°C to 30°C. Plants were harvested in mid-December 2013. Soil used to grow each species was kept separate by pot and used as inoculum for the second round of the feedback experiment.

In early January 2014, we started the second round of the feedback experiment. We designed this second round of soil culturing to address three questions. First, we wanted to determine how the strength of PSFs and plant competitive response correlated with plant abundance in the field. Second, we wanted to determine how plant-soil feedbacks interacted with interspecific competition to influence plant size. To answer these first two questions we factorially crossed a “live” vs. “sterile” soil treatment with a ± interspecific competition treatment for each species. “Live” soil consisted of 40 mL inoculum from conspecific-trained soil from the first round of plant growth. Inoculum for the “sterile” treatment was 40 mL of conspecific-trained soil that was triple autoclaved at 100–135°C for a total of 3 h in each round to kill soil biota. 200 mL pots were first filled with 150 mL of a 50:50 mixture of sterilized field soil from grassland in the Missoula Valley, Montana, USA, and sterilized silica sand. This substrate was topped with either live or sterile inoculum. The competition treatment

TABLE 1. Target species used in the feedback experiment, their functional type (FT) and their relative abundance (RA) expressed as mean percent cover at each site. Relative abundance was calculated as the maximum percent cover (from two sampling periods) averaged across 52 quadrats at each site. Based on these relative abundance values, each species was assigned to one of two abundance classes (A = abundant, R = rare).

Species	FT	RA (%) Site 1	RA (%) Site 2	Abundance class
<i>Festuca idahoensis</i>	Grass	10.05	6.49	A
<i>Achillea millefolium</i>	Forb	1.94	4.81	A
<i>Pseudoroegneria spicata</i>	Grass	2.04	3.05	A
<i>Danthonia unispicata</i>	Grass	2.60	2.43	A
<i>Poa secunda</i>	Grass	2.27	1.94	A
<i>Lupinus sericeus</i>	Forb	0.34	0.79	R
<i>Geum triflorum</i>	Forb	0.63	0.43	R
<i>Antennaria microphylla</i>	Forb	0.10	0.66	R
<i>Arabis holboellii</i>	Forb	0.16	0.08	R
<i>Koeleria macrantha</i>	Grass	0.06	0.14	R

was designed so each focal plant species would compete with each of the other nine species, with each unique species pair replicated 3–5 times. Sample sizes varied due to issues we had germinating particular species. Thus for each focal species, the “+” competition treatment consisted of pots containing each of the 9 other species \times 3 replicates/species = 27 pots/species containing conspecific-trained inocula and 27 pots/species containing sterile soil, resulting in 540 pots total (54 pots/species \times 10 focal species). The “- competition” treatment had 10 focal species \times 10 replicates/species \times conspecific-trained or sterile soil = 200 pots. In total we had 740 pots containing soil from Site 1 and 740 pots containing soil from Site 2 for a total of 1480 pots.

The third question of interest involved determining whether plants growing with competitors performed differently depending on the type of soil biota they experienced. Thus, in addition to growing plants in “live” conspecific-trained and sterile soil, we also competed plants (as described above) in “live” soil that had been trained by the heterospecific competitor that the focal species was planted with. This added an additional 10 species \times 27 pots/species \times heterospecific-trained soil = 270 pots containing soil from Site 1 and an equal number containing soil from Site 2.

Analysis

Plant-soil feedbacks, competitive response and plant abundance in the field.—We calculated the strength of plant-soil feedbacks and plant competitive ability using two different metrics. We calculated the strength of plant-soil feedbacks for each species based on the following formula: $(B_{\text{LiveX}} - B_{\text{SterileX}}) / B_{\text{SterileX}}$ where B_{LiveX} = the average biomass (above+below ground) of species \times grown in live soil inoculum and B_{SterileX} = the average biomass of species \times grown in sterile soil. For each site separately, we calculated this index for plants grown alone in sterile soil, and also for plants grown in competition in sterile soil. We calculated plant competitive response as: $(B_{\text{CompX}} - B_{\text{AloneX}}) / (B_{\text{AloneX}})$ where B_{CompX} = the average biomass of species by grown in competition in sterile soil, B_{AloneX} = the average biomass of species by grown alone in sterile soil. Thus, the competitive response for each species was its competitive response averaged over all species it competed with.

We determined whether the strength of PSFs (in the absence of competition) and competitive response (in the absence of live soil biota), respectively, varied with the relative abundance of our target species in the field. To do this, we performed two ANCOVAs, with site treated as a fixed factor, feedback (or competitive response) for each species treated as a covariate, and the site \times feedback (or site \times competitive response) interaction testing whether the relationship between feedback strength and abundance was the same at each site. We performed a similar ANCOVA with our second measure of relative abundance (the percentage of quadrats containing a focal species as opposed to average maximum cover per quadrat) to determine if feedback strength explained more of the

variation in this metric of relative abundance than our primary measure. We omitted from these analyses, and those below, data points representing plants that grew very poorly (final dry weight <0.05 g; $n = 23$ Site 1, $n = 6$ Site 2).

Effects of soil biota, competition and abundance class on plant size.—To examine how the effects of relative abundance of the target species, soil biota (sterile or cultured by the focal plant), competition (no competition or interspecific competition), and the interaction of these factors influenced plant size, we ran a generalized linear mixed effects model (GLMM) using the GLIMMIX module in SAS (version 9.4, Cary, North Carolina, USA). To account for positive skewness in the response (biomass), we used a normal distribution with a log link function, the latter of which substantially improved model fit over the default link function ($\Delta\text{AICC} = -215$). Based on their relative abundance in the field and natural break points in the data, we categorized each of our 10 target species as being either abundant or rare (Table 1). Abundance class, soil biota, competition, site, and their interactions were included as fixed factors in the initial model. Three-way and the four-way interactions involving site were not significant ($P > 0.05$), so we dropped them for simplicity to result in an improved model (ΔAICC final vs. full model = -14). Responses for each species and treatment combination (i.e. competition \times soil biota) were treated as repeated measures by specifying species and species \times competition \times soil biota as random factors.

Effects of soil type and plant abundance class on competitive tolerance.—We used a parallel GLMM to determine how the abundance class of the target species (abundant or rare; Table 1), soil community type (sterile, conspecific-cultured soil, or heterospecific-cultured soil), and the interaction of these factors influenced plant size when individuals were competing with heterospecifics. The initial model included abundance class, soil community type, site, and their interactions as fixed factors. The three-way interaction involving site was not significant ($P > 0.2$), so we dropped it for simplicity to result in an improved model (ΔAICC final vs. full model = -7). Responses for each species and soil community type combination were treated as repeated measures by specifying species and species \times soil community type as random factors. To test for post-hoc differences among treatment means, we used multiple comparisons adjusted for the number of comparisons. Full fixed effects tables for both analyses are reported in Appendix S1: Tables S1 and S2.

RESULTS

Feedbacks, competitive response and plant abundance in the field

Abundant species suffered greater negative PSFs than did rare species (Fig. 1A; $R^2 = 0.40$, $F_{1,16} = 48.9$,

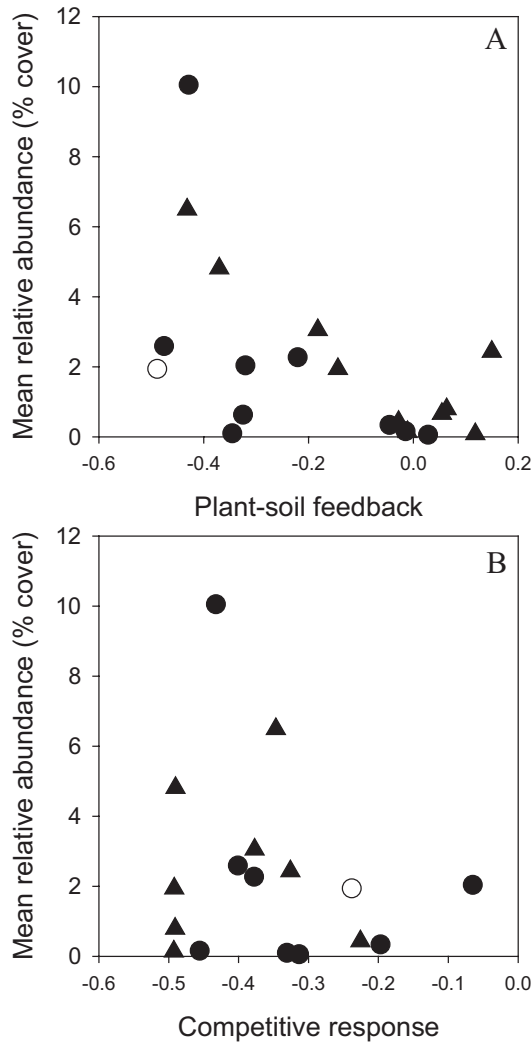


FIG. 1. Relationship between (A) plant-soil feedbacks or (B) plant competitive response and mean relative abundance of species at Site 1 (triangles) and Site 2 (circles). Each symbol represents the average plant-soil feedback intensity or average competitive response experienced by a given target species. More negative values mean that plants suffered more from soil biota or interspecific competition. See *Methods* for how feedback strength and competitive response were calculated.

$P < 0.006$). This relationship was stronger with another measure of plant abundance, the percentage of quadrats containing each focal species, or frequency ($R^2 = 0.49$, $F_{1,16} = 214$, $P < 0.0001$). The slope of the relationship between feedback strength and relative plant abundance was not different between sites (ANCOVA, $F_{1,16} = 0.15$, $P = 0.70$). In contrast to the relationship between feedbacks and relative abundance, average competitive response did not vary with plant abundance (Fig. 1B; $F_{1,16} = 4.9$, $P = 0.49$), or with site ($F_{1,16} = 0.60$, $P = 0.45$), and there was no competitive response \times site interaction ($F_{1,16} = 0.61$, $P = 0.45$).

Effects of soil biota, competition and plant abundance class on plant size.—Consistent with negative feedbacks, soil sterilization had a significant positive effect on plant biomass (Fig. 2A; $F_{1,24} = 12.69$, $P < 0.002$). As well, interspecific competition significantly reduced plant size (Fig. 2B; $F_{1,24} = 93.42$, $P < 0.0001$). Interestingly, competition did not alter the effect of soil biota on plant size (competition \times soil biota; $F_{1,24} = 0.03$, $P = 0.87$). Abundant species were larger than rare species ($F_{1,8} = 6.38$, $P < 0.04$) and soil sterilization had stronger effects on abundant than rare species (Fig. 2A; sterilization \times abundance interaction; $F_{1,24} = 12.35$, $P < 0.002$) but the impacts of competition did not vary between abundant and rare species (Fig. 2B; competition \times abundance interaction; $F_{1,24} = 1.76$, $P = 0.20$). In general plants grew larger in soil from Site 2 than Site 1 (site effect; $F_{1,911} = 660.6$, $P < 0.0001$) and feedbacks were generally of greater magnitude at Site 2 than Site 1 (sterilization \times site interaction, $F_{1,911} = 6.46$, $P < 0.02$).

Effects of soil type and plant abundance class on competitive tolerance.—When plants were competing, soil community type (i.e. sterile, conspecific-trained or heterospecific-trained soil) had a significant effect on plant size (Fig. 3; $F_{2,16} = 28.31$, $P < 0.0001$), with the magnitude of this effect varying between abundant and rare species (soil type \times abundance interaction; $F_{2,16} = 8.53$, $P < 0.004$). Competing abundant plants grew larger in conspecific-trained soil compared to both heterospecific-trained and sterile soil (post-hoc contrasts, $P < 0.0002$). There was no difference in the size of abundant plants when grown in sterile vs. heterospecific-trained soil (post-hoc contrast, $P > 0.05$). Competing rare plants were also larger in conspecific-trained soil than in heterospecific-trained soil (post-hoc contrast, $P < 0.002$). However, the size of rare plants did not differ when they grew in conspecific-trained vs. sterile soil (post-hoc contrast, $P > 0.05$). When competing, abundant plants were again larger than rare plants ($F_{1,8} = 6.89$, $P < 0.04$). Competing plants grew larger in Site 2 than Site 1 soils ($F_{1,905} = 422.33$, $P < 0.001$), and the difference in size between abundant and rare species was more exaggerated when growing in site 2 than Site 1 soils (site \times abundance interaction; $F_{1,905} = 17.25$, $P < 0.0001$).

DISCUSSION

Historically, interspecific competition has been considered a dominant force shaping patterns of plant abundance and community structure (Tilman 1982, Goldberg and Barton 1992, Howard and Goldberg 2001). Also, many plants suffer from negative PSFs (Kulmatiski et al. 2008), suggesting that PSFs may also play a strong role in affecting plant abundance and diversity in the field (Klironomos 2002, Mangan et al. 2010a). Yet few studies have attempted to jointly examine the relative strength of these two interactions and ask whether competition or PSFs better explain patterns of plant relative

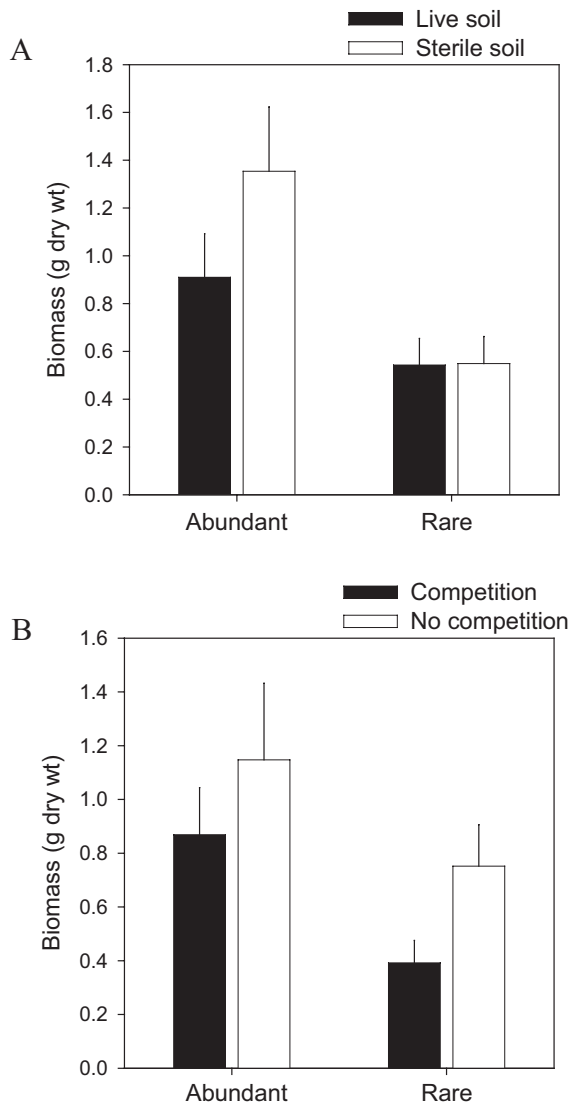


FIG. 2. Least square mean (+SEM) plant biomass (above +below ground) of abundant and rare species grown (A) in live conspecific-trained soil (black bars) or sterile soil (white bars) or (B) with an interspecific competitor (black bars) or alone (white bars). Least square means are from the abundance class \times sterilization and abundance class \times competition interactions, respectively (see *Methods* for the full statistical model).

abundance in nature. We found that both competition and PSFs had negative effects on plant size in a greenhouse experiment, but across 10 focal species and two sites, only PSFs correlated with plant abundance in the field. PSFs were generally more detrimental to the performance of abundant than rare species (Fig. 1A). In contrast, we found no relationship between a species' competitive response and its relative abundance in the field, either when plants grew in sterile soil (Fig. 1B) or conspecific trained soil (Maron et al., *unpublished data*). As such, our results suggest that PSFs may limit the abundance of dominant plant species in this system.

To our knowledge, only three prior studies have examined relationships between the strength of PSFs and plant relative abundance in field communities. Two of these found that feedbacks were more negative for rare than abundant species (Klironomos 2002, Mangan et al. 2010a) and one study found no relationship between PSF and plant abundance (Reinhart 2012). There have been several explanations put forth for why rare species might suffer from greater negative feedbacks than abundant species. First, rare species may accumulate soil pathogens faster than abundant species (Klironomos 2002). Second, rare species may be more susceptible to soil pathogens than abundant species (Mangan et al. 2010). Finally, in the case of old field plants, Klironomos (2002) speculated that density-dependent pathogen attack would drive abundant species to rarity, ultimately reducing the abundance of species and producing the observed pattern of stronger feedbacks on rare than abundant species. The implication of this is that plant abundance in old fields is dynamic. Soil pathogens build up around abundant species and drive them to lower abundance whereas species less vulnerable to these enemies are able to become common.

In our system, an open Ponderosa pine-Douglas fir savanna, the herbaceous community is composed of longer-lived perennials and in the absence of fire, relative plant abundance does not change much through time (Ortega and Pearson 2011). Thus PSFs are unlikely to drive dynamic changes in plant abundance as hypothesized for old fields. Rather, negative PSFs may simply

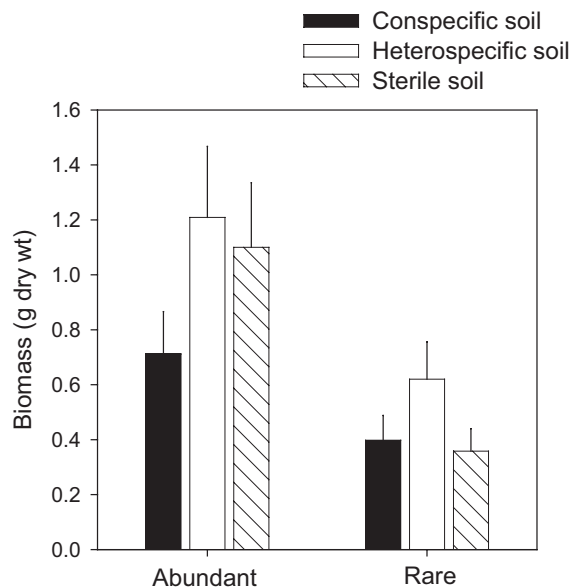


FIG. 3. Least square mean (+SEM) plant biomass (above + below ground) of abundant and rare species competing in conspecific-trained (black bars), heterospecific-trained (white bars) or sterile soil (hashed bars). Least square means are from the soil type \times abundance class interaction (see *Methods* for full statistical model).

help to keep relatively abundant plants in check, preventing them from attaining higher densities than they might otherwise. In a more limited sampling of species, Pendergast et al. (2013) demonstrated that *Solidago* species that grow at very high density can often experience greater negative soil feedbacks than other co-occurring species that grow at lower densities. Since we did not sample rhizosphere soil, our results do not suggest legacy effects. Rather, our results suggest that abundant species either promote the growth of pathogenic soil biota more than rarer species and/or are more susceptible to these pathogenic agents.

Previous work indicates that variation in the strength of PSFs can drive variation in plant relative abundance in the field. However, it seems equally likely that relative plant abundance might determine the strength of PSFs, particularly if negative feedbacks operate in a density-dependent fashion (Bell et al. 2006, Bagchi et al. 2010). In fact, it seems reasonable to assume that there might be a dynamic interplay between plant abundance and the negative effects of soil biota whereby any effect of PSFs on plant abundance can ultimately feedback to influence PSFs. Thus relationships between PSFs and relative abundance might depend on when in this temporal cycle the pattern is tested.

In addition to temporal variation in the strength of PSFs, it is likely that PSFs also vary spatially. For example, we found that PSFs were generally more negative at Site 2 than at Site 1 soils. We also found that plants growing in Site 2 soil generally grew larger (in both live and sterile soil) than they did in Site 1 soil (Fig. 1), suggesting Site 2 soil might be more nutrient rich than Site 1 soil. We do not know the nutrient status of soils from our two sites, but there is some evidence that N addition can outweigh the effects of feedbacks or modify the strength of feedbacks (Manning et al. 2008). In contrast, others have found that negative feedbacks can be independent of soil fertility (Harrison and Bardgett 2010).

One unique aspect of our study was that we were able to explicitly compare the strength of standardized effect sizes for PSFs and interspecific competition, and explore how these effect sizes varied depending on whether target species were abundant or rare in the field. In Site 1 soils, we found that effects sizes for PSFs and competitive response were roughly equal for all species except rare ones. Rare plants were less affected by PSFs than more abundant and common species, and therefore suffered more from competition than they did from PSFs. In Site 2 soils, plants generally suffered more from competition than from PSFs, and rare species were again less negatively affected by PSFs than were abundant species.

We expected interspecific competition to strongly interact with plant-soil feedbacks in ways found in previous studies. For example, Pendergast et al. (2013) found that competitive hierarchies among species were fundamentally altered by plant-soil feedbacks. Petermann et al. (2008) found that negative plant-soil feedbacks were

greatly exacerbated with plants grew in competition compared when they grew alone. Contrary to this, we found no significant interaction between the response to competition and plant-soil feedbacks. In other words, although feedbacks for plants growing in conspecific-trained soil were generally negative, this did not substantially increase the detrimental impacts of competition on plant size. It may be that plants are not “doubly penalized” for both competing and suffering from soil pathogens in conspecific-cultured soil because the addition of a heterospecific “dilutes” the negative effects of species-specific soil pathogens that may operate in a frequency dependent manner.

Although competitive response did not interact with PSFs, soil biota mediated the competitive response of plants based on their relative abundance class (Fig. 3). Abundant species performed more poorly when competing in conspecific-trained soil than in soil trained by their heterospecific competitor. This suggests that these species amplify species-specific pathogenic components of soil biota from which they escape when competing in heterospecific-trained soil. However, rare species were not more negatively influenced by conspecific- vs. heterospecific-trained soils. More generally, caution should be applied in generalizing our results pertaining to how plant abundance class influences performance in different soil types because the number of species belonging to each abundance class was small. However, our results do show that there are species-specific differences in how soil biota influences the impacts of competition on plants. More generally it shows that the response to competition can be influenced not only by the plant species involved, but also by soil biota.

Calculating PSFs based on the difference in plant size between cultured and sterile soil can be problematic if sterilization of soil releases nutrients. In such cases, plants might be larger in sterile vs. cultured soil, which could be falsely interpreted as evidence for negative PSFs. In our case, we think such effects are unlikely since competing plants generally grew as large, or larger, in heterospecific-trained soil than they did in sterile soil (Fig. 3).

Taken together, our results suggest that plant-soil feedbacks might facilitate coexistence in the following ways. First, local recruitment or performance may be more inhibited for abundant than rare species as a result of these species suffering greater negative PSFs. Thus, negative plant-soil feedbacks may operate similarly to Janzen-Connell effects (Janzen 1970, Connell 1971), whereby adults harbor host-specific enemies that reduce the success of progeny that recruit locally. Second, the propensity for abundant species to attain even greater dominance in the field might be kept in check due to the way in which feedbacks influence competitive response. Since abundant species were more harmed by competition in conspecific-cultured soil than were rarer species, over time less abundant species might more easily colonize sites around abundant species than the abundant species themselves.

Our results contribute to a growing body of evidence that that PSFs directly influence the distribution and abundance of plant species directly, but also indirectly by altering the outcomes of interspecific interactions.

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