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ORIGINAL ARTICLE

Soil Microbial Community Associated with an Invasive Grass Differentially Impacts Native Plant Performance

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Abstract This study is one of the first to show that invasive plant-induced changes in the soil microbial community can negatively impact native plant performance. This greenhouse experiment tested whether soil microbial communities specific to the rhizospheres of an invasive grass (*Aegilops triuncialis*) and two native plants (*Lasthenia californica* and *Plantago erecta*) affected invasive and/or native plant performance. Each of these species were grown in separate pots for 2 months to prime the soils with plant-specific rhizosphere microbial communities. Each plant species was then planted in native- and invasive-primed soil, and effects on plant performance were monitored. At 5 months, differences in microbial biomarker fatty acids between invaded and native soils mirrored previous differences found in field-collected soil. *L. californica* performance was significantly reduced when grown in invaded soil compared to native soil (flowering date was delayed, aboveground biomass decreased, specific root length increased, and root mass ratio increased). In contrast, *P. erecta* and *A. triuncialis* performance were unaffected when grown in invaded vs native soil. These results suggest that in some cases, invasion-induced changes in the soil microbial community may contribute to a positive feedback loop, leading to the increased dominance of invasive species in an ecosystem.

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Introduction

Aboveground and belowground communities are inextricably linked. Plants influence rhizosphere community structure through root exudation and effects on soil nutrient availability [12, 37], whereas soil microorganisms, in turn, affect plant productivity, plant community composition, and ecosystem function [1, 29, 32, 35, 36].

Invasive plants have been shown to change the microbial community composition of soils they invade (e.g., 3, 13, 20, 21, 27). However, the effects of invasion-induced changes in the soil microbial community on native plant performance have been little explored [19, 39]. Research exploring more general effects of plant invasion on soil microbial communities are reviewed in Wardle [34], Wolfe and Klironomos [39] and Ehrenfeld et al. [10]. An invaded soil microbial community may contain organisms that are pathogenic to native plants or may lack beneficial organisms necessary for native plant establishment or fitness, potentially leading to increased invasion through suppression of native competitors.

A conceptual plant–soil organism feedback framework has been developed that examines how the soil community influences plant competition [4, 5]. Soil microorganisms can strongly influence plant community dynamics and may contribute to the coexistence of competing plant species (negative feedback) or to the competitive dominance of one plant species over another (positive feedback).

In a simple example derived from this framework, two plants (P_A and P_B) have different associated soil microbial communities (M_A and M_B) that may differentially impact the performance of P_A and P_B. In one scenario, M_A negatively impacts P_B and neutrally impacts P_A, whereas M_B negatively impacts P_A and neutrally impacts P_B. If the magnitude of these negative effects is roughly equivalent, this example of reciprocal negative feedback would lead to competitive coexistence of P_A and P_B. In an alternate example, M_A negatively impacts P_B and neutrally impacts P_A, whereas M_B neutrally impacts both P_A and P_B. This is an example of a positive feedback loop that could result in the loss of plant diversity and the competitive dominance of P_A via interactions with the microbial community. Many other scenarios are possible in this framework but are not discussed here for reasons of conciseness.

Many additional factors contribute to plant competition besides interactions with the soil microbial community, including competition for abiotic resources and herbivory [31]. However, isolating the effect of the soil microbial community can help in understanding whether interactions with the soil community contribute to the overall competitive ability of a plant.

In our previous work, we found that the invasive grass, *Aegilops triuncialis* (barbed goatgrass), changes the soil microbial community in invaded serpentine grasslands [3]. This study compared the soil microbial community of goatgrass with the soil communities of two native plants that appear to be negatively impacted by goatgrass in the field: *Lasthenia californica* and *Plantago erecta*. We performed a greenhouse experiment using these three species to (1) examine the effects of the invaded soil microbial community on native plant performance and (2) compare the invaded and native soil microbial communities established in the greenhouse to those observed in the field.

We tested five hypotheses that affect plant coexistence via microbially mediated mechanisms. Compared to native soil, invaded soil has the following: H_0: no impact on either native or invasive plant performance, H_1: a negative impact on both native and invasive plant performance, H_2: a positive impact on both native and invasive plant performance, H_3: a negative impact on native plant performance and a positive/neutral impact on invasive plant performance, and H_4: a positive/neutral impact on native plant performance and a negative impact on invasive plant performance.

If the null hypothesis were true, then changing the soil microbial community would not contribute to goatgrass' invasive ability. If H_1 or H_2 were true, then depending on the strength of the negative or positive impacts, these scenarios could lead to either competitive coexistence (reciprocal negative feedback) or dominance of one species over another (positive feedback, either in the direction of invasive or native plant dominance). H_3 would contribute to the dominance of the invasive plant, whereas H_4 would contribute to the dominance of the native plant (both examples of positive feedback, leading to the competitive dominance of either the invasive or native species). Based on our field observations that *L. californica* and *P. erecta* are present in higher densities outside of goatgrass-invaded areas, we hypothesized we would find a result consistent with positive feedback leading to the dominance of goatgrass (i.e., H_1, H_2, or H_3).

Materials and Methods

Experimental Design

Seeds of all species were collected in spring 2002 from the University of California McLaughlin Reserve. Soil for this experiment was collected from the McLaughlin Reserve in October 2002 outside the goatgrass patches (native soil). Native soil was used in this experiment to simulate an invasion in the field; an invasive plant encounters native soil as it invades an area.

Soil was pounded, sieved, and mixed (1:1:1 mixture) with sand and Turface MVP soil amendment (Sierra Pacific Turf Supply, Rocklin, CA) before planting to improve soil structure and drainage after disturbance. Microbial community composition and soil chemistry were analyzed before the experiment. In February 2003, seeds of goatgrass, *L. californica*, and *P. erecta* were planted individually in pots (6.4 cm diameter, 25 cm depth) and grown for 2 months to "prime" the soil with the invaded or native soil microbial community associated with each plant [27]. Then, aboveground biomass was removed and a subset of pots was analyzed for soil microbial community composition and nutrients (C:N, P, K, and S). Seeds were planted back into these "primed soils" in the combinations shown in Fig. 1 (24 replicates per treatment) and grown for 3 months. Emergence and flowering dates were recorded. Plants were watered as needed; no additional nutrients were supplied. Pots were randomly placed and rotated weekly.

This method of priming the soil introduces a potentially confounding factor: the presence of the dead roots from the priming plant in the soil. We were unable to measure whether the presence of dead roots had an effect, allelopathic or otherwise, on the plants grown in this experiment. However, this method was chosen for two reasons: (1) Field-collected native and invaded soil contained significantly different nutrient concentrations, and differences in nutrient concentrations between treatments would likely be an even greater confounding factor than the presence of roots, and (2) the method has since been recommended as the standard for such experiments [27].

PLANT:	Goatgrass	*L. californica*	*P. erecta*
SOIL:			
Goatgrass-Primed	X	X	X
L. californica-Primed	X	X	
P. erecta-Primed	X		X

Figure 1 Plant–soil microbial community combinations. *X* indicates planted combinations

Plant Performance, Microbial Community, and Soil Chemistry Measurements

At 5 months, above-ground biomass was clipped at the soil surface, oven dried at 50°C, and weighed (24 replicates/treatment). Half of the soil samples were analyzed for root biomass and length (12 replicates/treatment); the other half were analyzed for soil microbial community composition and soil chemistry (12 replicates/treatment). Final numbers of replicates/treatment vary depending on plant mortality. Live roots were washed from the soil and analyzed for root length (Comair Root Length Scanner, Hawker de Havilland Victoria, Melbourne, Australia). After root length measurement, roots were oven dried at 50°C and weighed. Specific root length was calculated by dividing root length by root biomass. Root mass ratio was calculated by dividing root biomass by total plant biomass multiplied by 100.

Microbial community composition was measured using phospholipid fatty acid (PLFA) analysis described previously [6]. Briefly, lipids were extracted from 8-g soil samples using a one-phase chloroform/methanol/phosphate buffer solvent. Roots were removed from the soil, and the soil was homogenized before analysis. Phospholipids were separated from nonpolar lipids and converted to fatty acid methyl esters (FAMEs) before analysis on a Hewlett Packard 6890 GC, using a 25-m Ultra 2 (5%-phenyl)-methylpolysiloxane column (J and W Scientific). Peaks were identified using bacterial FAME standards and the MIDI peak identification software (MIDI, Newark, DE). PLFA biomarkers of interest included total microbial biomass, number of fatty acids, i17:1ω5c (biomarker for *Thiobacillus*, a genera of sulfur-oxidizing bacteria), i17:1 (biomarker for *Desulfovibrio*, a genera of sulfate-reducing bacteria), and 16:1ω5c (biomarker for arbuscular mycorrhizal fungi [AMF], Gram (−) bacteria, and type-I methanotrophs) [9, 15, 18, 25, 26, 38]. With the exception of total microbial biomass, a previous study found that goatgrass-invaded field-collected soil contained higher amounts of these biomarkers compared to native soil [3]. Soil carbon and nitrogen were determined by high temperature combustion (Phoenix 8000, Fisons Instruments). Other soil chemistry measurements (P, K, Ca, S, and pH) were performed by A and L Western Agricultural Laboratories (Modesto, CA).

Statistics

Multivariate analysis of variance (MANOVA) was performed on PLFA biomarkers, soil chemistry, and plant performance measurements at 2 and 5 months using the JMP software (2000 SAS Institute, Cary, NC). When necessary, data were transformed to meet assumptions of homogeneity of variance and normality of residuals.

MANOVAs were performed to control for type-I experiment-wise error rate when performing multiple univariate comparisons [30]. When an overall MANOVA was significant, individual ANOVAs were then performed on the variables included in the MANOVA model, $\alpha=0.05$ according to the Hummel–Sligo procedure described in Barker and Barker [2]. At 2 months, a subset of soil samples was analyzed for PLFA biomarkers and soil chemistry data to examine the effect of soil priming using two separate MANOVAs. At 5 months, three more MANOVAs were performed on plant performance measures, PLFA biomarkers, and soil chemistry. More variables could be included in the PLFA MANOVAs at 5 months than at 2 months because more replicates were available. All plant performance MANOVAs included emergence date, aboveground biomass, specific root length, and root mass ratio. Additional ANOVAs were performed on flowering date for the *L. californica* and *P. erecta* comparisons; goatgrass did not flower during the experiment. Flowering date was not included in the overall MANOVAs because not all of the plants flowered during the course of the experiment and MANOVAs cannot be performed with missing data [30].

Results

Fatty Acid Biomarkers

Differences in biomarker fatty acid concentrations must be interpreted with caution: Different microbial species within

the same genera may contain different concentrations of biomarker fatty acids in their cell membranes, certain fatty acids can be biomarkers for more than one group of organisms, and biomarker fatty acids are occasionally not present in certain species of the genera they supposedly represent [3]. However, given these caveats, differences in biomarker fatty acids can provide interesting information and inform hypotheses that can be tested in future experiments.

Overall MANOVAs of biomarker fatty acids in invasive- and native-primed soils at 2 and 5 months showed significant differences (at 2 months, P=0.005, df=12, F=3.04; at 5 months, $P\leq$0.0001, df=10, F=10.43). At 2 months, total microbial biomass and number of fatty acids did not differ between the three primed soils; however, they were lower in the 2-month soils than in the initial soil (P=0.01, df=3, F=5.12 and P=0.02, df=3, F=4.18, respectively, individual analyses of variance [ANOVAs], Fig. 2a). In contrast, biomarkers for *Thiobacillus* (P=0.02, df=3, F=4.73) and *Desulfovibrio* (P=0.02, df=3, F=4.72) were significantly higher in the two native primed soils than in the initial or invaded soils (ANOVAs).

At 5 months, goatgrass and *L. californica* soils contained more total microbial biomass (P=0.02, df=2, F=4.70) and number of fatty acids (P=0.005, df=2, F=6.65) than *P. erecta* soil (ANOVAs, Fig. 2b). These soils had two "generations" of the same native or invasive species grown in them and, therefore, show the strongest single plant species effects on the soil microbial community (e.g., *L. californica* in *L. californica* soil). No differences in the *Thiobacillus* biomarker were observed; however, goatgrass soil contained more of the biomarkers for *Desulfovibrio* (P=0.01, df=2, F=5.60) and AMF/Gram (−) bacteria/type-I methanotrophs ($P\leq$0.0001, df=2, F=33.04) than either native soil (ANOVAs).

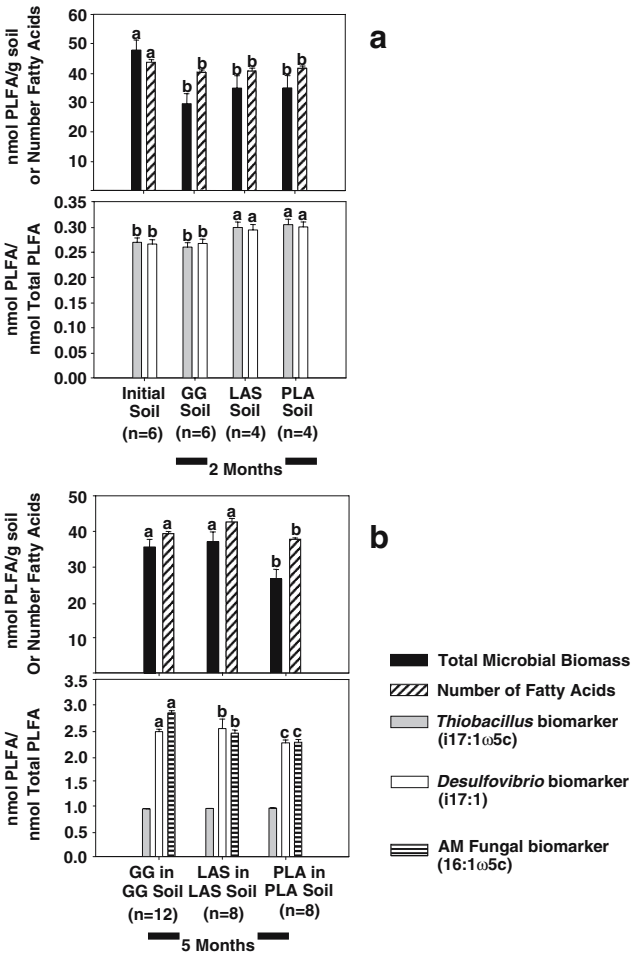

Figure 2 Fatty acid biomarkers in initial, 2-month, and 5-month primed soils. *GG* Goatgrass, *LAS L. californica*, *PLA P. erecta*. *Bars* are means with standard errors. *Bars sharing the same color and letter* are not significantly different at $\alpha\leq$0.05 (one-way ANOVAs). **a** Initial/2-month comparisons. i17:1 is presented as sine-transformed data. **b** Five-month comparisons. i17:1ω5c is presented as cosine-transformed data. i17:1 is presented as untransformed means; cosine transformed data was included in the model

Soil Chemistry

No significant differences in soil C:N, P, K, or SO_4^{2-} were found among 2-month primed soils at $\alpha\leq$0.05. K, however, had a statistically higher concentration in the initial soil than any of the 2-month primed soils (data not shown). At 5 months, soils grown with two "generations" of the same native or invasive species showed no differences in chemistry or pH (data not shown).

Plant Performance

The overall plant performance MANOVA for *L. californica* was significant (P=0.05, df=4, F=3.69). Individual ANOVAs revealed that in invaded soil, *L. californica* flowered significantly later (1 week later, P=0.02, df=1, F=6.78) and had significantly lower aboveground biomass (P=0.08, df=1, F=3.67), longer specific root length (P=0.03, df=1, F=6.03), and higher root mass ratio (P=0.008, df=1, F=9.90) than in native soil (Figs. 3 and 4a). Flower number was positively correlated with aboveground biomass for *L. californica* (R=0.75) and for this reason was not included in the overall MANOVA. However, in an unprotected ANOVA, there is a trend toward decreased flower number when *L. californica* was grown in invaded compared to native soil (P=0.09, df=1, F=3.29, data not shown).

In contrast, invaded soil had no effect on either *P. erecta* or goatgrass performance (Fig. 4b and c; MANOVAs P=0.13 and P=0.19, respectively). An additional nonparametric test was performed on flowering date for *P. erecta* and was also nonsignificant (P=0.53, Kruskal–Wallis test; Fig. 3). This nonparametric test was performed because

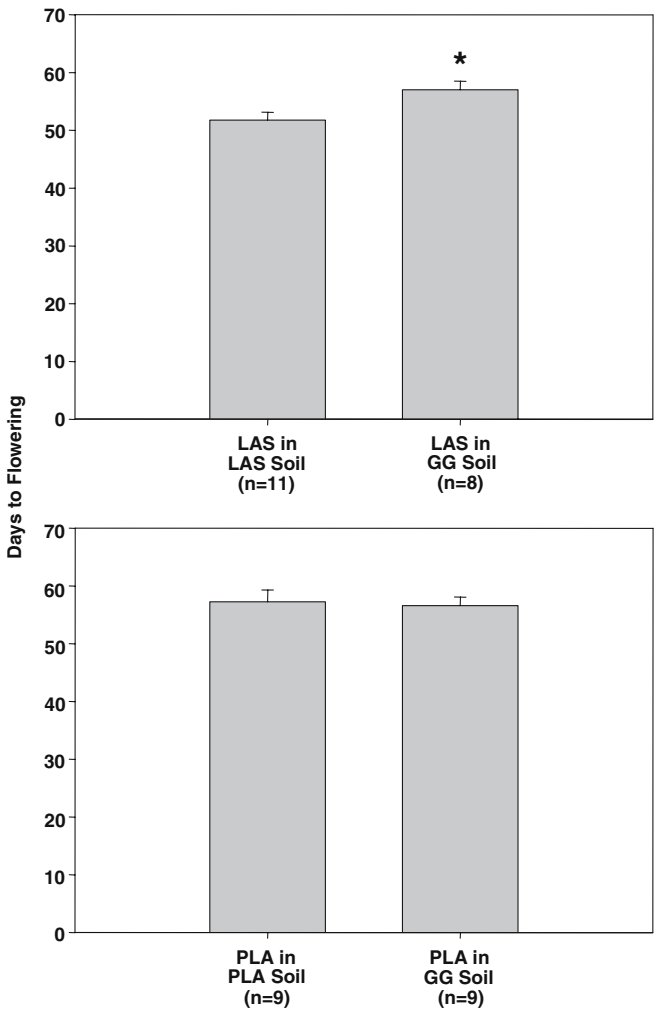

Figure 3 Flowering date in native and invaded soils. *GG* Goatgrass, *LAS L. californica*, *PLA P. erecta*. *Bars* are means with standard errors. *Asterisks* indicate significantly greater means at $\alpha \leq 0.05$

the data could not be transformed to achieve homogeneity of variance.

Discussion

Plant-induced Changes in the Soil Microbial Community

After 2 months, native-primed soils contained higher amounts of the biomarkers for *Thiobacillus* and *Desulfovibrio* than either the invaded or initial soils. This result contrasted with previous findings from field-collected soil. However, this result revealed that the priming treatment had a significant effect on the soils: Native and invaded soil microbial communities were measurably different. Field and greenhouse environments differ considerably, and plant-associated soil microbial communities in the greenhouse may differ from those associated with the same plants grown in the field [16]. By the end of the experiment, however, soil communities exposed to two "generations" of the same plant species resembled those in field-collected soils. Goatgrass soil contained higher total microbial biomass and number of fatty acids compared to *P. erecta* soil and higher levels of the biomarkers for *Desulfovibrio* and AMF/Gram (−) bacteria/type-I methanotrophs than either native soil.

Soil chemistry did not differ among the 2-month primed soils or among the 5-month soils planted with two generations of the same plant species. The soil chemical measurements performed in this study provide static information and do not capture dynamic processes such as mineralization or immobilization. Therefore, these soil chemistry measurements do not reveal any potential differences in temporal nutrient dynamics during the 2- and 5-month periods. Nonetheless, the observed differences in PLFA biomarkers among treatments are not associated with differences in the measured soil chemistry variables and are likely to be plant induced. Because differences in PLFA biomarkers observed at the end of the experiment mirrored those found in the field, this provides additional support for the conclusion that goatgrass invasion changes soil microbial community composition.

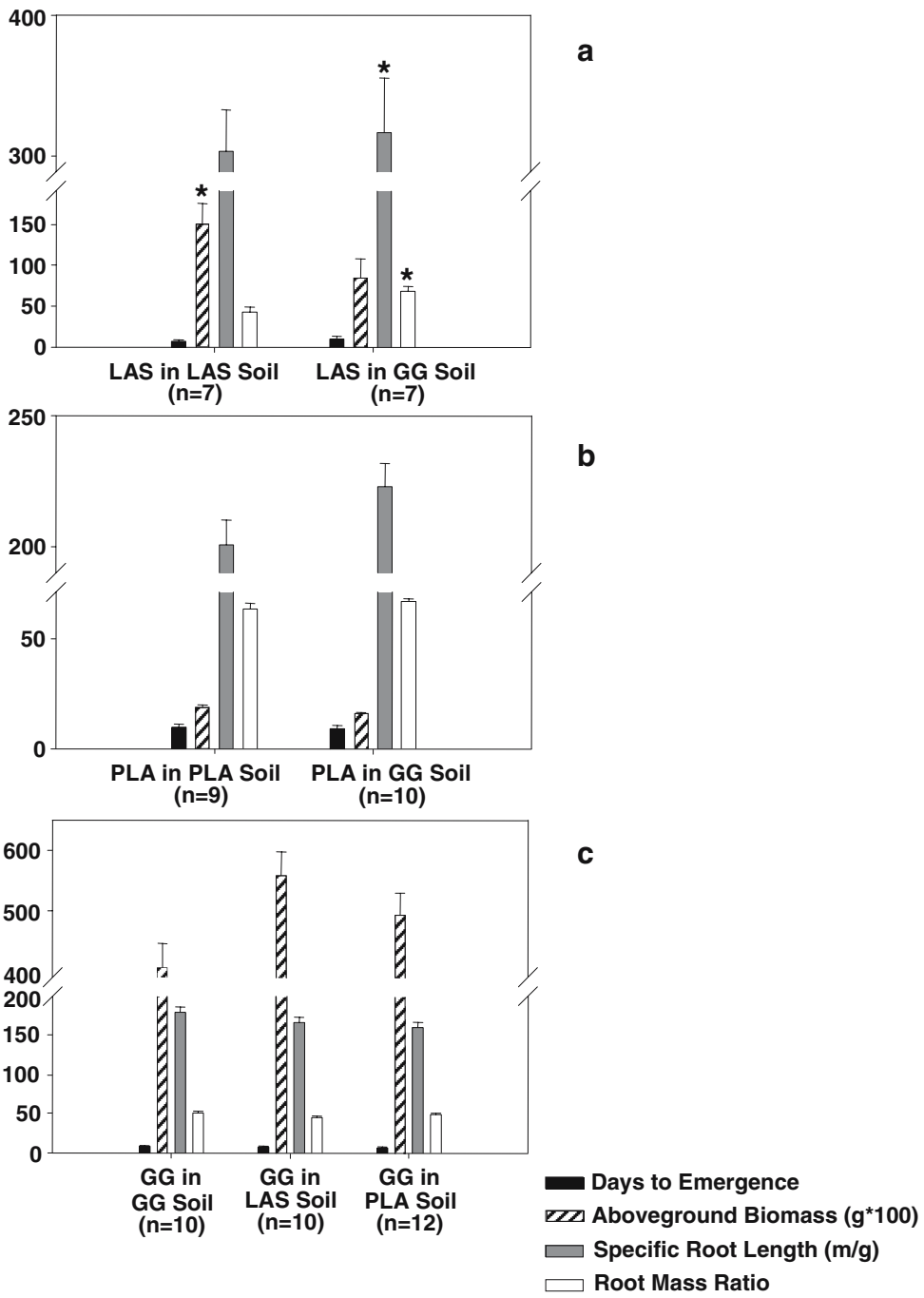

Figure 4 Plant performance in native and invaded soils. *GG* Goatgrass, *LAS L. californica*, *PLA P. erecta*. *Bars* are means with standard errors. *Asterisks* indicate significantly greater means at $\alpha \leq 0.05$ (one-way ANOVAs). **a** *L. californica* comparisons. Date of emergence and specific root length data are presented as untransformed means; cosine- and sine-transformed data were included in the model, respectively. **b** *P. erecta* comparisons. Date of emergence data are presented as untransformed means; sine-transformed data were included in the model. **c** Goatgrass comparisons

Effects of Invaded Soil Community on Plant Performance

Of the three plant species studied, only *L. californica* exhibited changes in growth and performance when grown in invaded vs native soil. These data suggest that the microbial community associated with goatgrass contributes to a positive feedback loop in competitive interactions with *L. californica*, facilitating the competitive dominance of goatgrass.

When grown in invaded soil, *L. californica* flowered approximately 1 week later and had lower aboveground biomass, longer specific root length, higher root mass ratio, and fewer flowers. Aboveground biomass and flower number are fitness-related traits [14, 28]; smaller aboveground biomass and fewer flowers suggest that *L. californica* has reduced fitness when grown in invaded soil. In addition, at our field sites, *L. californica* tends to flower in early April (one to two flowers per plant) and sets seed by May before the summer drought. A delay in flowering date during this relatively short reproductive period may reduce fitness by (1) isolating populations growing on invaded soils, preventing gene flow among populations, and (2) exposing populations to a higher likelihood of drought in

this Mediterranean climate, increasing the risk of seed abortion because of low water availability.

Increased specific root length may result in better competitive ability, allowing a plant to exploit a greater soil surface area for nutrients [22]. However, in the case of *L. californica*, an increase in specific root length was also accompanied by an increase in root mass ratio. An increased root mass ratio indicates that a plant is allocating more resources below-ground and is characteristic of plants in low nutrient environments [11, 22]. The combination of increased specific root length and root mass ratio in *L. californica* grown in goatgrass soil may indicate that *L. californica* experiences greater competition for nutrients with the soil microbial community in invaded soil vs native soil.

In contrast, neither *P. erecta* nor goatgrass exhibited any performance effects grown in invaded compared to native soil. These data do not provide evidence for either positive or negative feedbacks via the soil microbial community that contribute to competitive interactions between *P. erecta* and goatgrass.

Our results suggest that invaded soil microbial communities may contribute to the invasiveness and competitive ability of invasive species on a species-specific basis. Our data show that the microbial community associated with goatgrass may aid in its competitive dominance in interactions with *L. californica* (H_3). However, the influences of invaded soil on *P. erecta* and goatgrass performance are negligible (H_0). Thus, it is likely that biological factors, such as the difference in size between the two species, are more important determinants of goatgrass competitive success in interactions with *P. erecta* than are changes in the soil microbial community.

Linking Plant Invasion, Soil Microorganisms, and Shifts in Plant Community Composition

Accumulation of plant pathogens in the soil helps drive plant community succession [33]. Plant invasion is a different type of community shift that also is linked to changes in the soil microbial community; two other studies examined links between soil pathogens and invasive plant success. Klironomos [19] primed North American soil with different plant-associated microbial communities and found that five invasive plants from Eurasia were strongly positively affected when grown in their own (invaded) soil, whereas five rare plants native to North America were strongly negatively affected when grown in their own (native) soil. This difference in invasive and native plant performance was attributed to a slower accumulation of plant pathogens in invaded vs native soils. Callaway et al. [7] found that the biomass of *Centaurea maculosa* (a forb native to Europe and invasive in North America) decreased when grown in soil collected from Europe compared to US soil, and increased in US soil primed with its own soil microbial community compared to native primed soil. These results suggest that *C. maculosa* is suppressed by pathogens in European soil and may have escaped these pathogens in the US soil.

Our results differ from the above-mentioned greenhouse studies. In our study, goatgrass performance is not affected when grown in invaded soil, and native plants are differentially affected by invaded soil (a negative effect [*L. californica*] and a neutral effect [*P. erecta*]). Perhaps in our field site, certain native plant pathogens are facilitated by goatgrass invasion instead of primarily being accumulated in native plant soil as in Klironomos [19], or goatgrass has not escaped its pathogens as in Callaway et al. [7]. The PLFA method does not directly measure plant pathogens, so further study is required to address these hypotheses.

However, plant pathogens are not the only microbial organisms that interact with plants and that can help drive positive or negative feedbacks. Our study found differences in biomarkers for sulfate-reducing bacteria (*Desulfovibrio*) and AMF, both of which increased in goatgrass-invaded compared to native soil in the greenhouse and field.

The *Desulfovibrio* genera is not known to be pathogenic to plants; most likely, the plant fitness effects of *Desulfovibrio* are indirect via changes in the sulfur cycle. Sulfate-reducing bacteria, once believed to be obligate anaerobes, have been detected in highly oxic and microaerophillic habitats, and some can use oxygen as an electron acceptor [17, 24]. In serpentine soils, sulfate-reducing bacteria may act as facultative aerobes in oxic regions and may be reducing sulfate in anoxic microsites. Sulfur is an important plant nutrient, used in the production of amino acids, proteins, coenzymes, and secondary plant products [23]. Previous work revealed significantly less sulfate in field-collected goatgrass-invaded soil than native soil and that sulfate may be limiting in goatgrass-invaded field soils [3]. Thus, goatgrass invasion may affect the sulfur cycle by increasing numbers of sulfate-reducing bacteria and depleting soil sulfate; these changes could affect native and invasive plant fitness and alter plant community composition.

Alterations of AMF diversity or community composition potentially could enhance goatgrass dominance in interactions with some native plants; goatgrass has been shown to form mycorrhizal associations in the field [3], as has *P. erecta* [8]. PLFA biomarkers do not provide information on the diversity of organisms possessing these fatty acids. Thus, higher levels of 16:1ω5c accompanying goatgrass invasion may reflect increased numbers of one species of AMF or changes in diversity and population sizes of several species. Increased AMF diversity increases plant biodiversity and productivity [32]; therefore, if plant invasions decrease AMF diversity, this change could contribute to decreased native plant diversity and promote exotic-dominated communities with low species richness.

Recent work found slight decreases in the number of AMF species colonizing native plant roots in areas invaded by *Bromus tectorum* in Utah and slight increases in number of AMF species with *Avena barbata* and *Bromus hordeaceus* invasion in California [13]. Whether goatgrass alters the diversity of the AMF community remains to be explored. In addition to diversity, shifts in AMF species composition accompanying invasion are likely important; invasions in Utah and California were both associated with large shifts in AMF community composition in native roots [13]. Changes in AMF community composition may result in shifts in plant competition dynamics via plant–microbe feedback loops [5] and requires further study.

Measurable effects of goatgrass invasion on the soil microbial community and *L. californica* performance were observed in soils primed with plant-specific microbial communities for only 2 months. Thus, changes in the rhizosphere that influence plant performance can occur extremely quickly. Our study likely underestimates the effects of the invaded soil community on native plant performance over time; multiple years of growth of these species in the field likely lead to larger effects on the soil community [3], which may translate into larger effects on plant performance. Nonetheless, our study provides evidence of species-specific impacts of invaded soil microbial communities on native and invasive plant performance and suggests that in some cases, invasion-induced changes in the soil community may create a positive feedback loop that contributes to plant invasiveness.

Different invasive plants likely interact with and change the soil microbial community in different ways with varying effects on native plant performance. The same may also be true of the same invasive plant species across different soil types and/or environments. More research is needed to explore how plant invasion is linked with the soil microbial community and subsequent changes in plant community composition.

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