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Native congeners provide biotic resistance to invasive *Potentilla* through soil biota

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Abstract. Soil biota can facilitate exotic plant invasions and these effects can be influenced by specific phylogenetic relationships among plant taxa. We measured the effects of sterilizing soils from different native plant monocultures on the growth of *Potentilla recta*, an exotic invasive forb in North America, and conducted plant–soil feedback experiments with *P. recta*, two native congeners, a close confamilial, and *Festuca idahoensis*, a native grass species. We also reanalyzed data comparing the ability of *P. recta* to invade experimentally constructed congeneric monocultures vs. monocultures of a broad suite of non-congeners. We found that monocultures as a group, other than those of the native *P. arguta*, were highly invadable by *P. recta*. In contrast, this was not the case for monocultures of *P. arguta*. In our first experiment, the biomass of *P. recta* was 50% greater when grown in soil from *F. idahoensis* monocultures compared to when it was grown in soils from *P. arguta* or *P. recta* monocultures. Sterilizing soil from *F. idahoensis* rhizospheres had no effect on the biomass of *P. recta*, but sterilizing soil from *P. arguta* and *P. recta* rhizospheres increased the biomass of *P. recta* by 108% and 90%, respectively. In a second experiment, soil trained by *F. idahoensis* resulted in a positive feedback for *P. recta*. In contrast, soils trained independently by each of the two native *Potentilla* species, or the closely related *Dasiphora* (formerly *Potentilla*) resulted in decreases in the total biomass of the invasive *P. recta* indicating strong negative feedbacks. Soil trained by *P. recta* also resulted in intraspecific negative feedbacks. Our results demonstrate substantial negative feedbacks for an invader in its nonnative range under certain conditions, and that native congeners can mount strong biotic resistance to an invader through the accumulation of deleterious soil biota.

Key words: communities; exotic species; grasslands invasion; intermountain prairie; pathogens; plant–soil feedbacks.

INTRODUCTION

Soil biota have powerful effects on the distribution, abundance, and productivity of plants (van der Putten et al. 1988, Bever 1994, Packer and Clay 2000, Yamazaki et al. 2009, Maron et al. 2011, Schnitzer et al. 2011) and have considerable potential to affect exotic invasions (Callaway et al. 2004a, 2011, Kulmatiski et al. 2008, Mangla et al. 2008). For example, Klironomos (2002) compared the responses of “rare native plants” and “common exotic plants” in soil that had been previously cultured by conspecifics and found that five of five rare species experienced strong negative feedbacks that reduced plant growth whereas four of five invasive species experienced significant positive feedbacks, enhancing growth. This suggests that the exotics may have “escaped harmful pathogens by invading foreign territory.” Reinhart et al. (2003) compared the effects of soil pathogens from the native and nonnative ranges of

Prunus serotina. They reported dramatically higher densities of *P. serotina* in the nonnative range in the Netherlands that were correlated with much weaker negative feedbacks in soils from the Netherlands than in soil from the native range in Indiana. Their results indicate that host-specific soil biota have important density-dependent regulatory effects on *P. serotina* in its home range, but that this biotic constraint is escaped in Europe. In similar experiments Callaway et al. (2004b) found that in native European soil the invasive *Centaurea stoebe* cultivated strong negative feedbacks with soil biota either alone or in competition. However, in soils from North America, *C. stoebe* cultivated strong positive feedbacks. The same treatments in sterilized soil eliminated feedback effects in soils from both ranges. Studies such as these point to biogeographically delineated evolutionary relationships among pathogenic soil biota and plants (Knevel et al. 2004, Reinhart and Callaway 2004, van der Putten et al. 2005, 2007, Callaway and Rout 2011).

Soil biota can also have phylogenetically delineated evolutionary relationships with plant taxa. For example, strong interactions between particular plant taxa and the

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effects of arbuscular mycorrhizal fungi (AMF) have been found among tropical tree species (Mangan et al. 2010) and California grasses (Brandt et al. 2009). Such phylogenetic relationships between plants and components of the soil biota provide a context for comparing native and invasive congeners to explore the effects of soil biota on invasion (Gerlach and Rice 2003, Reinhart and Callaway 2004, Burns and Winn 2006). For example, Skálová and Pyšek (2009) found that a suite of *Impatiens* species easily recruited into plots dominated by native *Impatiens* species; however, plots dominated by the invasive *I. glandulifera* resisted encroachment by all other congeners. Dostál and Palečková (2010) found that soil conditioned by the native *Epilobium hirsutum* reduced the performance of the invasive *E. ciliatum* more than that of other genera, but found no consistent effect of soil conditioning by two different congeneric pairs of natives and exotics. Agrawal et al. (2005) compared pathogen attack on 15 pairs of native and exotic (not all were invasive) congeners and found that native congeners experienced far more negative soil feedbacks than exotic congeners, indicating that even closely related exotic taxa might escape consumer regulation. These patterns correspond with other work that indicates that phylogenetic novelty correlates with some successful invasions in general (Strauss et al. 2007). For example, Diez et al. (2008) found that naturalization of exotic species was negatively related to native congener abundance, suggesting some form of phylogenetically based biotic resistance. Furthermore, once exotics had naturalized, exotic abundance within habitats was negatively related to the abundance of native congeners, which also indicated that phylogenetic biotic resistance occurred within habitats.

The apparent escape from inhibitory soil biota in home ranges, yet the potential for congeneric sharing of common soil pathogens and other soil biota in recipient communities, predicts that some invaders may be inhibited by shared soil biota when they grow near native congeners. To test this, we initiated two complementary experiments. First, we compared the effects of sterilizing soils sampled from experimentally constructed monocultures of either the native, *Potentilla arguta*, or other native species on the growth of *P. recta*. Second, we conducted plant–soil feedback experiments with *P. recta*, four native congeners, and a dominant native grass species. We also reanalyzed biomass data collected from these monocultures (as reported in Maron and Marler 2008) to ask whether *P. recta* had reduced invasion success and therefore had lower biomass within *P. arguta* monocultures compared to monocultures of nine other natives more distantly related to *P. recta*.

METHODS

Potentilla recta L. (sulfur cinquefoil) is native to Eurasia and can be a dominant invader in intermountain grasslands of the northern Rocky Mountains (Sheley

and Petroff 1999, Lesica and Martin 2003). *Potentilla recta* can have strong competitive effects on native North American species (Maron and Marler 2008) and is listed as a noxious weed in Colorado, Montana, Nevada, Oregon, and Washington.

Experimental monocultures

In April 2003, monocultures were planted consisting of 10 native perennial plant species that commonly co-occur in grasslands in the intermountain west (two grasses [*Festuca idahoensis* Elmer and *Koeleria macrantha* (Ledeb.) Schult.], three early-flowering forbs [*Geum triflorum* Pursh., *Antennaria rosea* Greene, and *Penstemon procerus* Douglas ex Graham], and five mid-season forbs [*Achillea millefolium* L., *Gaillardia aristata* Pursh., *Monarda fistulosa* L., *Penstemon wilcoxii*, Rydb., and *Potentilla arguta arguta* Pursh. (synonymous with *Drymocallis arguta*)]). Monocultures were created by transplanting greenhouse-grown seedlings of each species into separate 3 × 3 m plots. A total of six plots were planted for each native monoculture, half of which were randomly assigned to a water treatment. Each plot was divided into four 1.3 × 1.3 m subplots (separated by 0.2-m buffer strips) and each subplot was planted with the same species at the same initial density (32 individuals per subplot). Three subplots were randomly assigned to be invaded by one of three perennial exotics, one of which was *P. recta*. The fourth subplot was an uninvaded control. In September 2004, we invaded a randomly selected subplot within each plot with 0.85 g of *P. recta* seeds. In September 2005, half the number of seeds added in 2004 was again added to the same subplot. All monocultures were weeded continuously of species not assigned to the plot. (For more details of the experimental design, see Maron and Marler [2008]).

To determine whether invasion and subsequent growth of *P. recta* was inhibited to a greater degree in *P. arguta* monocultures compared to all others, we reanalyzed biomass data (from unwatered plots only; plants harvested for biomass in 2007) that were originally reported in Maron and Marler 2008. Here we used ANOVA (Systat 11; Systat, Chicago, Illinois, USA) to determine whether there was a difference in *P. recta* biomass (log-transformed) when it invaded *P. arguta* monocultures compared to its biomass when invading all other native monocultures combined. The biomass of *P. recta* across monocultures reflects both differences in the ability of *P. recta* to invade monocultures of different native species and then the subsequent growth of individual plants within those plots.

Soils from monocultures

Soil was collected from monocultures of the native grass *Festuca idahoensis* and the native forb *Potentilla arguta* that had been experimentally maintained for 7 years, and soils from very dense stands of the European exotic forb *Potentilla recta* (we refer to this as *P. recta*

monocultures) that had developed in invaded native monocultures plots over this 7-year period after experimental seed addition (see detailed description of the setup in Maron and Marler [2008]). This soil was subsequently used in feedback experiments. In summer 2010, we took five soil samples immediately below plants from each of the three vegetation types (*F. idahoensis*, *P. arguta*, and *P. recta*) in each of three plots in which the appropriate monocultures remained. Because this replication was small and therefore limited the amount of soil we could collect, we pooled all soil samples from the plots for each vegetation type. We emphasize that the lack of replication at the plot level strongly limits our scope of reference for this experiment. For each trained soil, we sterilized half of the soils by autoclaving them for 4 h. Then, we mixed each soil in a 50:50 mixture with sterile sand (560–940 μm) and filled 10 100-mL pots for each of the six experimental groups (three pre-trained soils \times 2 sterilization treatments). Finally, three *P. recta* seeds were planted in every pot. After germination, only one seedling was allowed to grow for up to 59 days, when plants were harvested, dried for 48 h at 60°C, and weighed to the nearest mg.

General linear models with a Tukey post hoc test were used to test for differences between soil pre-training and sterilization treatments.

Congeners and plant–soil feedbacks

On 30 June 2005, we collected small plants (<20 cm tall) of *Potentilla recta*, *P. gracilis* Douglas ex Hook., *P. arguta*, and *F. idahoensis* in intermountain grassland south of Missoula, Montana, USA (272201 easting, 5189747 northing). We also purchased small potted plants of *Dasiphora fruticosa* (L.) Rydb. from Bitterroot Restoration (Corvallis, Montana, USA), which were grown from locally collected seeds. Plant roots were cleaned of field soil and three individuals of each species were transplanted together in a 6-L pot. This was replicated five times for each of the five species. The pots contained a mix of 33% sand and 66% local field soil. Our intention was to use primarily field soil that contained natural soil biota and sand so that roots could be accurately harvested at the end of the two-phase experiment. These plants grew for 250 days, and then the plants were removed and discarded. The soils that had been trained by a particular species were combined and thoroughly mixed, which provided a total of 30 L of trained field soil per species.

In the second phase of this experiment, 15 L of each species-specific soil mixture were sterilized by autoclaving three separate times. Trained or sterilized soils were placed in 0.525-L pots containing synthetic batting on the bottom to prevent soil from leaking out, and 0.1 L of sterile 20/30 grit sand on top of the synthetic batting on pot bottom to facilitate drainage. A 0.4-L mixture of 1:3 ratio of sterile sand : trained soil was placed at the top of each pot. Seeds of each plant species were then planted into six pots containing sterile soil and six pots with non-

sterile soil that had been trained by conspecifics and into the same number of pots with sterilized and non-sterilized soil trained by each of the other five hetero-specific species. We grew plants for 100 days, harvested plants (shoots and roots) from each pot, dried them at 60°C for 72 hours, and then weighed each plant. We focused on two sets of statistical comparisons with this data set. First, we compared the effect of sterilization for each target species in each soil training treatment with independent-samples *t* tests (IBM SPSS 20, 2011). Second, we compared the biomass of each target species in non-sterilized soil trained by *F. idahoensis*, the three *Potentilla* species, and *Dasiphora* with a one-way ANOVA followed by a Tukey multiple comparisons test SPSS 20; IBM, Armonk, New York, USA).

RESULTS

Experimental monocultures

The mean aboveground biomass of *P. recta* invading all native monocultures other than those of the native *P. arguta* was $732 \pm 88.6 \text{ g/m}^2$ (mean \pm SE; Fig. 1). In contrast, the aboveground biomass of *P. recta* in monocultures of *P. arguta* was $69.5 \pm 27.6 \text{ g/m}^2$ (ANOVA, $F_{1,58} = 26.7$, $P < 0.012$; also see Maron and Marler [2008]). Only *Achillea millefolium* demonstrated similar resistance to *P. recta* as did *P. arguta*.

Soils from monocultures

Soil training had a significant effect on *P. recta* growth ($F_{2,57} = 6.71$, $P = 0.002$; Fig. 2). The total biomass of *P. recta* grown in soil from *F. idahoensis* rhizospheres was 46–53% greater than the biomass of *P. recta* grown in either *P. arguta* rhizospheres (Tukey post hoc $P = 0.018$) or *P. recta* rhizospheres ($P = 0.004$).

Soil sterilization increased total plant biomass across all treatments ($F_{2,57} = 18.39$, $P < 0.001$), although the magnitude of the effect was different for each soil type. Sterilizing soil from *F. idahoensis* rhizospheres had no effect on the total biomass of *P. recta* ($F_{1,20} = 1.23$, $P = 0.281$), whereas sterilizing soils from *P. arguta* and *P. recta* increased the biomass of *P. recta* by 108% ($F_{1,19} = 14.5$, $P = 0.001$) and 90% ($F_{1,18} = 21.8$, $P < 0.001$), respectively.

Congeners and plant–soil feedbacks

In soil collected in the field but not near any *Potentilla* species, sterilization of soils trained independently by each of the two native *Potentilla* species or the closely related *Dasiphora* resulted in substantial and significant increases in the total biomass of the invasive *P. recta*, indicating strong negative feedbacks (–35% to –57%; Fig. 3). Soil trained by *P. recta* and sterilized also resulted in significantly larger *P. recta* than in soil but that was either trained by *P. recta* but not sterilized or not trained by *P. recta*, a congener, or the closely related *Dasiphora* (Fig. 3). In contrast, soil trained by *F. idahoensis* and then sterilized produced significantly smaller *P. recta* than trained but unsterilized soil,

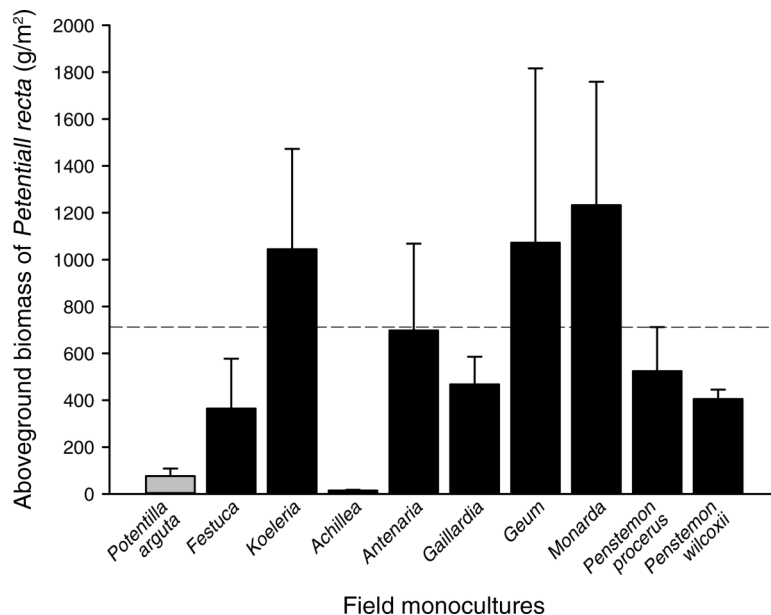


FIG. 1. Aboveground biomass of the invasive *Potentilla recta* when grown in monocultures of 10 different native North American species in the field. Error bars show +SE; the dashed line shows the mean of for all monocultures types other than *P. recta*.

indicating moderate positive (+17%) feedbacks. The feedback effects of native *Potentilla*, *Dasiphora*, and *P. recta* on native *Potentilla* species were usually nonsignificant or of weaker intensity than those experienced by *P. recta*. For example, only training with *P. recta* produced a significant negative feedback for *Dasiphora*, and no *Potentilla* congener or *Dasiphora* produced a negative feedback for *P. gracilis*. *Potentilla arguta* experienced negative feedbacks (−19% to −58%) when grown in soils trained by native congeners and *Dasiphora*, but a negative effect of sterilization when grown in soils trained by *P. recta*. For a separate comparison of the overall feedback intensities experienced by *P. recta* vs. *P. arguta* in soils trained by conspecifics, congeners, or *Dasiphora*, we conducted a three-way ANOVA with soil source for training (the three species that trained the soil), soil sterilization treatments (sterile vs. non-sterile), and *P. recta* vs. *P. arguta* as factors, and total plant biomass as the dependent variable. The invasive experienced a mean feedback inhibition of −50% across the three soil sources combined (2.20 ± 0.07 vs. 1.10 ± 0.05 g/plant in sterilized and non-sterilized soil, respectively; whereas the native *P. arguta* experienced a significantly lower mean feedback inhibition of −35% (1.52 ± 0.10 vs. 0.97 ± 0.06 g/plant in sterilized and non-sterilized soil, respectively; soil sterilization treatment \times target species $F = 15.61$; $df = 1, 70$; $P < 0.001$).

DISCUSSION

Our results suggest several interrelated interpretations. First, the invasive *P. recta* experienced far stronger negative feedbacks in soil trained by conspe-

cifics or congeners compared to soil trained by the native bunchgrass, *F. idahoensis*. This suggests that invading communities containing congeners should be less favorable to *P. recta* than communities containing more phylogenetically distant species (see Strauss et al. 2007). However, it should be noted that we only used one species that was not phylogenetically related to *P. recta*.

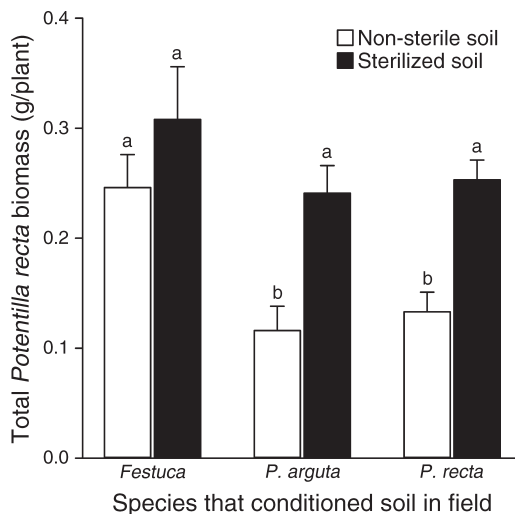


FIG. 2. Total biomass of the invasive *Potentilla recta* when grown in soil collected from the rhizospheres of the native grass *Festuca idahoensis*, the native forb *Potentilla arguta*, and *P. recta*. Soil was collected from experimental field monocultures (see Fig. 1) and used in a greenhouse experiment. Soil was either sterilized by triple autoclaving or not. Error bars show +SE. Bars with the same lowercase letters show values that are not significantly different ($P > 0.05$).

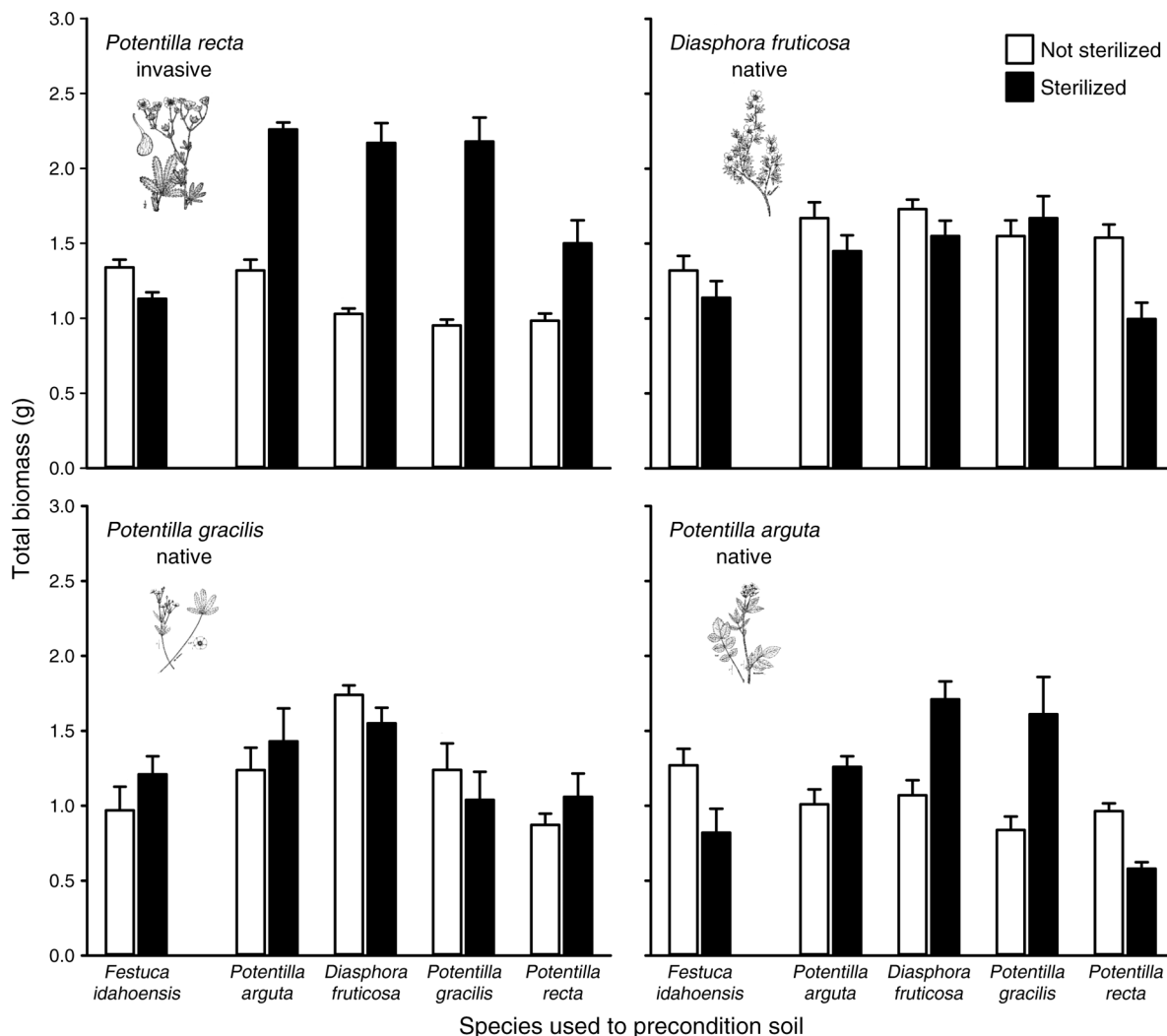


FIG. 3. Total biomass of three *Potentilla* congeners and the closely related *Dasiphora fruticosa* (formerly *Potentilla*) when grown in soils trained by each of these four species or the native grass *Festuca idahoensis*. After training, soil was either sterilized by triple autoclaving or not sterilized. Error bars show +SE. Asterisks denote a significant effect of sterilization (t test for each pair). Within a species, shared letters represent no significant difference ($P > 0.05$) for biomass of the target species in non-sterilized soil as determined with one-way ANOVA followed by Tukey multiple comparisons tests.

* $P < 0.05$; ** $P < 0.01$.

Considering the variability we measured among *Potentilla* congeners, we would expect even more variability among phylogenetically distant species, and thus we caution against extrapolating from the effect of *F. idahoensis* in this experiment to all other native species in general. However, in the long-term field experiment *P. recta* invaded all other monocultures of phylogenetically distant species (except *A. millefolium*) much more than those of *P. arguta*, suggesting that the importance of phylogenetic distance may extend beyond *F. idahoensis*. Interestingly, *P. recta* was highly invasive in monocultures of *Geum triflorum*, which is also in the Rosaceae. These results also suggest that there are *Potentilla*-specific soil pathogens or parasites that accumulate in the rhizospheres of all of the *Potentilla* species, as well as

Dasiphora fruticosa. Second, the negative feedback response of the invasive *P. recta* was far stronger in soil trained by all test species than were responses of the test species to the same training regimes. This exotic-native pattern is not common in the literature (Kulmatiski et al. 2008) and suggests that the North American natives have developed some degree of resistance to the *Potentilla*-specific pathogens that occur in the grassland soil we tested, but that *P. recta* has not developed such resistance.

Biota in *Potentilla*-free Montana soils appear to promote *P. recta*, as well as the native North American *P. arguta*. However, once cultured by native *Potentilla* species or *Dasiphora*, North American soil biota became far more hostile to *P. recta* than to North American

congeners. To our knowledge, this form of soil-feedback-based biotic resistance has not been reported in the literature. For example, in a meta-analysis of plant–soil feedbacks, Kulmatiski et al. (2008) found that feedback effects for native plant species are roughly twice as negative as those experienced by nonnative plants. Thus, invasive species appear to quite commonly escape more-or-less species-specific soil biota present in their native ranges. Our congeneric comparisons appear to differ than those described for most exotic vs. native congeners (Agrawal et al. 2005, Reinhart and Callaway 2004). There were relatively weak plant–soil feedbacks created by native *Potentilla* species and the closely related *Dasiphora fruticosa* for themselves, but these natives created much stronger negative feedbacks for their invasive congener.

The potential for strong biotic resistance from the effects of native *Potentilla* species on soil biota corresponded well with results from field monocultures. Invasion by *P. recta* into monocultures of the native *P. arguta* was roughly an order of magnitude lower than in plots with other genera combined. When soil from *P. arguta* or *P. recta* rhizospheres was sterilized the biomass of *P. recta* doubled, but when soil from *Festuca* rhizospheres was sterilized there was no difference in *P. recta* biomass. However, since we pooled soils collected from rhizospheres of the same plant species (following Reinhart et al. 2003, van der Putten et al. 2007, Van Grunsven et al. 2007), our ability to generalize these results is limited. Importantly however, despite the limitations of mixing soils, the results from the two experiments correspond well with each other and suggest that soil conditioned by native congeners strongly reduce *P. recta* performance compared to soil from a non-congeneric species (*F. idahoensis*).

Like other invasives, *P. recta* varies in the extent to which it invades North American grasslands, and the effects of soil biota may vary concomitantly. For example, Klironomos (2002) measured weak feedback effects (an approximately 15% reduction in size) for *P. recta* in soils collected from an old-field grassland in eastern Canada. However, these weak feedbacks corresponded to a low abundance of *P. recta* in this old field. Agrawal et al. (2005) compared plant–soil feedback strengths for 15 congeneric pairs of exotics and natives in the northeast United States and found that feedbacks were over twice as negative for exotics, even though not all exotics were invaders and invaders generally experience more negative feedbacks than noninvasive exotic species (Kulmatiski et al. 2008). One of Agrawal et al.'s congeneric comparisons was *P. recta* vs. *P. arguta* and for these congeners the native *P. arguta* showed stronger negative feedbacks than any other native. In contrast to our results in which *P. recta* showed very strong feedback response to soil training by all congeners and itself, the plant–soil feedback experienced by the invasive *P. recta* was roughly three times less than that of the native *P. arguta*. Of course soil biota from

different parts of North America might elicit quite different feedback effects, and considered together these results suggest substantial context dependency in plant–soil feedback interactions that vary among different combinations of soil sources and plant species.

The whole-soil sterilization approach we used has limitations. Primarily, heat sterilization of soils not only kills soil biota but it also commonly increases nutrient availability, which has the potential to confound the effects of suppressing biota. Furthermore, autoclaving some soils can cause manganese toxicity (Boyd 1971). The fact that all our test species experienced the same sterilization treatment mitigates some of these problems, but this does not eliminate the possibility that some species, and particularly the invasive species, responded differently to available soil nutrient levels or toxicity. Also, we diluted field soil with sand so that we could easily harvest roots. This dilution would have reduced nutrient availability and might affected relative performance across treatments.

Despite the fact that our results suggest inhibitory effects of native soil biota on *Potentilla recta*, there are a variety of other factors that clearly facilitate *P. recta* invasion. For example, human disturbance is highly associated with *P. recta* abundance (Endress et al. 2007) and *P. recta* can be competitively superior to a number of North American native species (Maron and Marler 2008). Our results suggest that one other factor that could contribute to invasion by *P. recta* and create variation in its performance is the presence of genus-specific soil biota.

Biotic resistance can come in many forms, apparently from almost any type of biological interaction identified by ecologists (Levine et al. 2004). Our results are not the first to show that the soil biota in a nonnative range might retard invasion (see Reinhart and Callaway 2004), but to our knowledge they are the first to indicate that native congeners can establish soil feedbacks for an invader that are disproportionately stronger to those created for themselves, and that suppress the growth of an invasive species. In another context, our results suggest that escape from strong inhibition from the broad suite of soil biota in a native range may contribute to invasive success, but that complex, community-scale interactions among soil biota and interacting native and nonnative plant species can have far more complex interactions that are affected by, among other things, close phylogenetic relationships.

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