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Review

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Soil biota and invasive plants

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Contents

Summary

Key words: mutualism, mycorrhiza, nonnative plants, pathogens, plant invasions, plant–soil feedbacks, soil biota.

Interactions between plants and soil biota resist invasion by some nonnative plants and facilitate others. In this review, we organize research and ideas about the role of soil biota as drivers of invasion by nonnative plants and how soil biota may fit into hypotheses proposed for invasive success. For example, some invasive species benefit from being introduced into regions of the world where they encounter fewer soil-borne enemies than in their native ranges. Other invasives encounter novel but strong soil mutualists which enhance their invasive success. Leaving below-ground natural enemies behind or encountering strong mutualists can enhance invasions, but indigenous enemies in soils or the absence of key soil mutualists can help native communities resist invasions. Furthermore, inhibitory and beneficial effects of soil biota on plants can accelerate or decelerate over time depending on the net effect of accumulating pathogenic and mutualistic soil organisms. These 'feedback' relationships may alter plant–soil biota interactions in ways that may facilitate invasion and inhibit re-establishment by native species. Although soil biota affect nonnative plant invasions in many different ways, research on the topic is broadening our understanding of why invasive plants can be so astoundingly successful and expanding our perspectives on the drivers of natural community organization.

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I. Introduction

Most naturalized nonnative species appear to behave ecologically more or less like resident species, and occur at low to mid frequencies (Huston, 1994; Williamson & Fitter, 1996; Davis *et al.*, 2000; Brown & Peet, 2003). However, a small proportion of introduced nonnative species become locally dominant (Levine *et al.*, 2003, and citations therein) and change relatively diverse communities into near monocultures. These species are generally referred to as 'invasive' (Colautti & MacIsaac, 2004). This transformation of communities indicates that very powerful, but poorly understood, ecological phenomena are at work. Interest in the causes and effects of invasions has prompted the development of a number of nonmutually exclusive hypotheses to explain invasions including: enemy release, the evolution of novel traits, disturbance, novel biochemical weapons, and empty niches in invaded communities (Mack *et al.*, 2000; Hierro *et al.*, 2005). Rapidly accumulating research has connected soil organisms to these hypotheses and indicates that they may have powerful effects on invasions. Here, we have organized research and ideas about the role of soil biota as drivers of invasion by nonnative plants and how the effects of soil biota on invasives may expand the general hypotheses that have been proposed for invasive success. In this context, we have organized this review into three sections: II, Soil community effects; III, Soil-borne antagonists; and IV, Soil-borne mutualists. Section II, Soil community effects, treats soil communities as a 'black box' while sections III, Soil-borne antagonists (i.e. nematodes and pathogens), and IV, Soil-borne mutualists (i.e. mycorrhizas and nitrogen fixers), attempt to dissect some components of the 'black box' and partition biological interactions into two distinct functional groups. Our groupings of organisms by their biotic interactions are broad generalizations used for organizational clarity (e.g. most mycorrhizas are classified as mutualists). However, it is important to clearly acknowledge that the effects of some individual species are counter to our classification (e.g. mycorrhizas can act as parasites instead of mutualists).

II. Soil community effects

1. Plant–soil biota feedbacks

Plant species alter soil biota in ways that lead to either positive or negative plant–soil biota feedback effects (Park, 1963; Bever *et al.*, 1997; Bever, 2002, 2003). In other words, plants affect organisms in their rhizospheres, and the rhizosphere biota in turn affects the plants. The direction of the feedback depends on the relative negative effects of accumulating soil-borne pathogens, herbivores and parasites (Park, 1963; Brown & Gange, 1989; van der Putten, 2001) vs the relative positive effects of accumulating mycorrhizal fungi, nitrogen fixing bacteria, and other beneficial soil organisms (Allen & Allen, 1984; Baker & Schwintzer, 1990; Garbaye, 1994) and the indirect effect of these plant–soil biota interactions on plant–plant interactions (Bever, 2003).

Plant–soil biota feedback experiments utilize a multistep process. In the first stage host-specific, or at least host-favoring, microbial communities are generated by growing a plant species in a common and nonsterile soil for several months or longer allowing the plant to interact with and alter the soil community. Next, the original plant is removed and a second plant is grown in the soil that was 'trained' or 'preconditioned' by the first plant (or soil aliquots). The purpose of the second step is to compare the effects of host-specific soil biota to non-host-specific biota. If the second plant grows larger in conspecific-conditioned soil (soil preconditioned by same species) than in heterospecific-conditioned soil (preconditioned by other species), the feedback is positive. If the second plant grows larger in heterospecific-conditioned soil than in conspecific-conditioned soil, the feedback is negative. However, feedbacks can be caused by factors other than soil biota. Plants can reduce nutrients or release allelopathic chemicals that cause negative feedbacks. Therefore, some studies have conducted parallel feedback experiments in nonsterile and sterilized soil to help distinguish the role of biota vs. nutrient availability or designed experiments to control for differences in nutrient availability. Another approach is to use soil solutions that have been filtered to contain specific portions of the microbial community (Klironomos, 2002).

Conceptually in accordance with the Janzen–Connell hypothesis on negative density dependence (Janzen, 1970; Connell, 1971), negative plant–soil biota feedbacks appear to be predominant in natural systems, and they provide frequency-dependent regulation of populations and help to maintain plant species diversity (Florence, 1965; Augspurger & Kelly, 1984; van der Putten *et al.*, 1993; Mills & Bever, 1998; Packer & Clay, 2000; Klironomos, 2002; Bever, 2003). Negative plant–soil biota feedbacks are driven by soil fungal pathogens (Mills & Bever, 1998), mycorrhizas (Bever, 2002), and bacteria (Westover & Bever, 2001).

Unlike the negative feedbacks generally described for native plants, invasives often demonstrate positive feedbacks with soil biota in their new ranges. For example, when grown in native European soils in the absence of competitors, the soil biota that developed in association with *Centaurea maculosa* had increasingly negative effects on the plant's growth (Callaway *et al.*, 2004a). But in soils from North America (nonnative range), the soil biota that developed in association with *C. maculosa* had increasingly positive effects on itself, perhaps contributing to the development of near monocultures for which the species is famous in the northern Rocky Mountains. Furthermore, these plant–soil biota interactions translated into competitive effects, at least in pot experiments, which have not been reported before for invasive species (Figs 1 and 2). Competing with a French species (*Festuca ovina*) in European soils, *C. maculosa* grew much better in soils that had

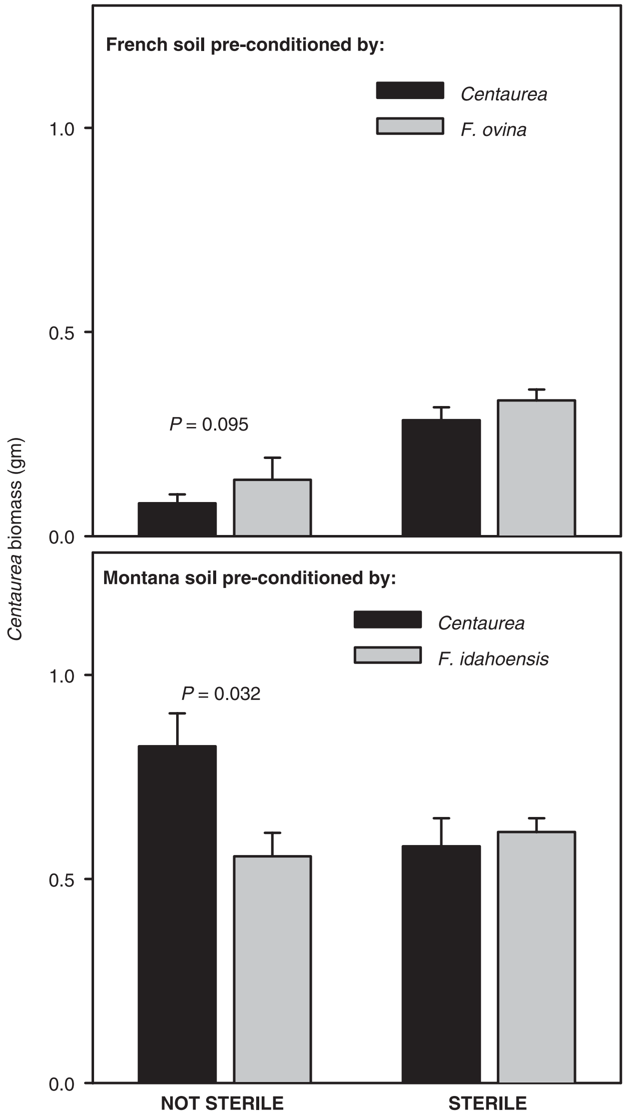

Fig. 1 Total biomass of *Centaurea maculosa* plants grown in competition in European soil (Central Massif population) and North American soil (Missoula population) that had been preconditioned by either *C. maculosa* or a *Festuca* species native to the place of soil origin. Plants were grown in soils either sterilized or not sterilized after preconditioning. In a three-way ANOVA (origin, species used for preconditioning and sterilization as main effects): $F_{\text{origin}} = 44.9$, df = 1,172, $P < 0.001$; $F_{\text{culture} \times \text{species}} = 0.77$, df = 2,172, $P = 0.288$; $F_{\text{origin} \times \text{culture} \times \text{species}} = 6.88$, df = 2,172, $P = 0.011$; $F_{\text{origin} \times \text{sterilization}} = 10.05$, df = 2,172, $P < 0.001$; $F_{\text{culture} \times \text{species} \times \text{sterilization}} = 4.11$, df = 2,179, $P = 0.020$. *P*-values shown above paired bars indicate a significant difference in preconditioning effects for those treatments. Reprinted from Callaway *et al*. (2004a).

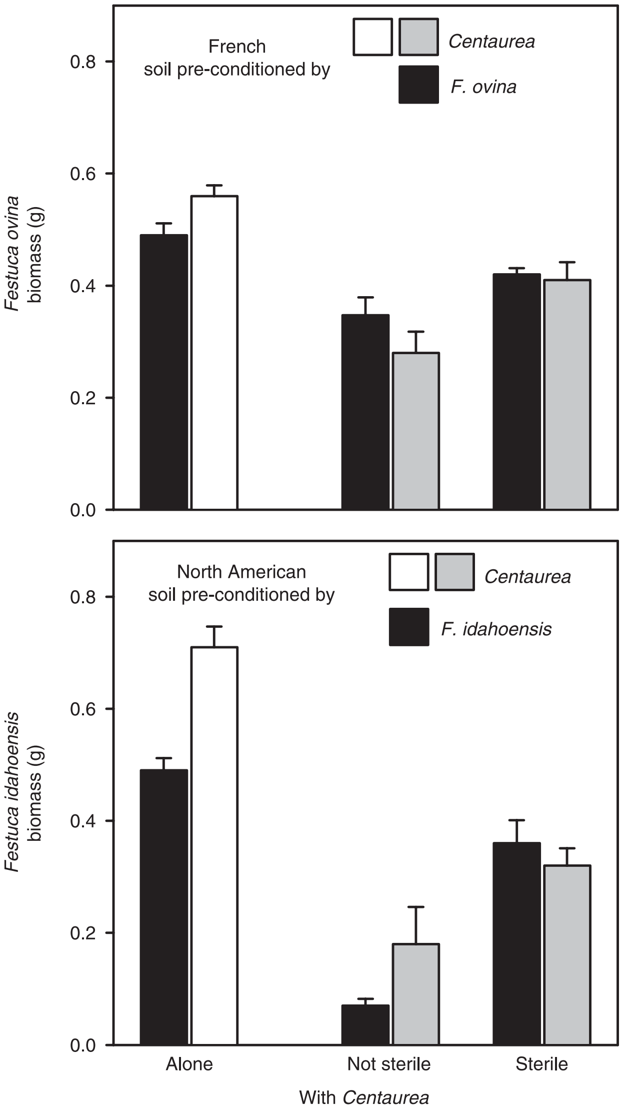

Fig. 2 Total biomass of *Festuca* species grown alone and in competition with *Centaurea maculosa* in soils from native and invaded regions that had been 'preconditioned' by either the Festuca species or *C. maculosa*. Error bars show 1 SE. The overall effect of *C. maculosa* on *Festuca* was competitive ($F_{Centaurea} = 11.33$, df = 1,170, $P < 0.001$), but *C. maculosa* had stronger competitive effects on *F. idahoensis* in North American soil ($F_{Centaurea \times \text{region}} = 8.83$, df = 2,170, $P < 0.001$) but *Festuca* species and soil region are confounded. More importantly, while sterilization of European soil slightly enhanced *Festuca ovina* biomass ($P = 0.037$), there was no significant preconditioning effect on *F. ovina*. Sterilization of North American soil strongly enhanced the biomass of *Festuca idahoensis* ($P < 0.001$), and preconditioning nonsterile North American soil with *C. maculosa* gave *F. idahoensis* a strong competitive disadvantage against *C. maculosa* competitors (in nonsterilized soil, $F_{\text{pre-culturing effect}} = 3.77$, df = 1,82, $P = 0.036$).

been previously conditioned by *F. ovina* than soils that had been conditioned by conspecifics (Fig. 1), indicating negative plant–soil biota feedbacks. By contrast, *C. maculosa* competing with an American species (*Festuca idahoensis*) in American soils tended to grow better in soils that had been conditioned by conspecifics than soils conditioned by *F. idahoensis*, indicating positive plant–soil biota feedbacks. Sterilization of the soil eliminated the feedback relationships in both cases. In summary, feedback effects on *C. maculosa* in competition were very similar to feedback effects of *C. maculosa* growing alone. Interestingly, these feedback-competition patterns were observed in the effects of *C. maculosa* on *F. idahoensis* (Fig. 2). In both North American and European soils, both Festuca species grown alone performed better in soils conditioned by *C. maculosa* than in soils conditioned by *Festuca*, indicating negative plant–soil biota feedback effects. However, in competition plant–soil biota feedback effects changed. When grown with a *C. maculosa* competitor, *F. ovina* performed better in European soils conditioned by *C. maculosa* than soils conditioned by conspecifics, probably because of negative feedback effects on *C. maculosa*. By contrast, *F. idahoensis* performed much better in soils conditioned by conspecifics than in soils conditioned by *C. maculosa*, perhaps because of the strong positive plant–soil biota feedbacks experienced by *C. maculosa* in American soil (but see Bais *et al.*, 2003 regarding the potential confounding effects of allelopathic root exudates).

Agrawal *et al.* (2005) tested the effect of soil microbial feedbacks of 10 congeneric pairs of native and nonnative herbaceous plant species in Ontario, Canada. Soil microbial feedbacks were twice as negative for native than nonnative species. These results differ from two other studies comparing the pathogens and pathogenic activity associated with congeneric pairs of native and nonnative species (Blaney & Kotanen, 2001; I. M. Parker & G. S. Gilbert, unpublished; see section III.2. Pathogens).

Klironomos (2002) found that the relative abundance of 61 grassland species was highly correlated with the strength and direction of soil feedbacks (rare species experienced strong negative feedbacks and common species experienced positive feedbacks), suggesting that community composition was strongly affected by plant–soil biota feedbacks. Although the effects of soil chemistry were not controlled in this large experiment, Klironomos later determined that the feedback effect of a subset of 10 species was driven by the varying effects of pathogenic/saprophytic fungi. Furthermore, this subset was divided into five rare native species and five dominant nonnative species. He found that four of five nonnative species experienced significant positive feedbacks while five of five rare native species experienced negative feedbacks. The negative feedbacks experienced by rare natives were driven by host-specific soil-borne pathogens, whereas the invasive nonnative species were not affected by soil-borne pathogens. In contrast to these results for five rare native and five highly abundant nonnative species, the relationship between soil feedback and species abundance for native (26 species) vs nonnative species (35 species) spanning a range of abundances was virtually identical (K. O. Reinhart & J. N. Klironomos, unpublished). In other words, abundant native and nonnative species experienced more neutral to positive feedbacks, whereas less abundant native and nonnative species experienced more negative feedbacks. However, this comparison did not separate invasives from the total pool of nonnative species.

2. Net effect of soil biota

Of the five experiments conducted on five species (Table 1) four show more negative effects of soil biota in the native ranges than in the nonnative ranges. Although the number of current studies is meager, they suggest that invasive success may be influenced by escape from the inhibitory effects of below-ground organisms.

Ammophila arenaria, a dune grass from Europe, has invaded coastal dunes in the western USA, South Africa, New Zealand, and Tasmania. Knowledge about *Ammophila* in its native and nonnative ranges is probably more detailed than for any other species; however, the results vary. Soil nematodes and pathogens inhibit the growth of *Ammophila* in its native European range (van der Putten *et al.*, 1988, 1990, 1993; De Rooij-van der Goes, 1995). Beckstead & Parker (2003) compared the effects of soil biota on *A. arenaria* in its introduced range (California) with those in its native range (The Netherlands). While not directly comparing European and North American soils in the same experiment, they found that North American soils also dramatically inhibited the growth of *Ammophila*. Seed germination was reduced by 12–16%, seedling survival was reduced by 7–13%, and root and shoot biomass decreased up to 80% in the nonsterilized soil treatments relative to the sterilized treatments. These strong inhibitory

Table 1 Summary of biogeographical comparisons of plant–soil biota interactions associated with invasive nonnative plant species in their native and nonnative ranges

Species	Effect of soil biota in native range	Effect of soil biota in nonnative range	Biogeographical effect	Reference
Acer negundo	—	–, =, +	yes	Reinhart & Callaway (2004)
Acer platanoides	—	–, =, +	yes	Reinhart & Callaway (2004)
Ammophila arenaria	—	—	no	Beckstead & Parker (2003)
Ammophila arenaria	—	–, =, +	yes	Knevel *et al*. (2004)
Centaurea maculosa	—	–	yes	Callaway *et al*. (2004a)
Prunus serotina	—	=, +	yes	Reinhart *et al*. (2003)

—, Strong negative effect; –, mild negative effect; = , no effect; +, positive effect.

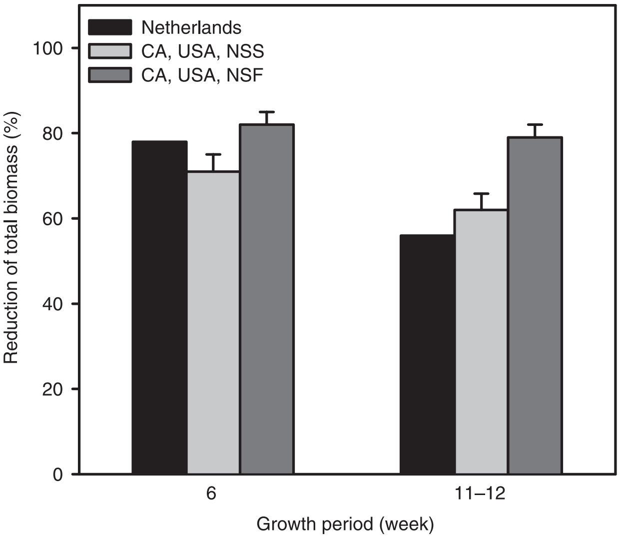

Fig. 3 Comparison of the percentage of reduction of total biomass for plants grown in soil from the European native range in the Netherlands and introduced range in California for two growth periods (van der Putten & Peters, 1997). Soil in California was either nonsterilized stored (NSS) or nonsterilized fresh (NSF); soil from The Netherlands was nonsterilized. Bars show bootstrapped means ± 1 SD; iterations = 1000. Redrawn from Beckstead & Parker (2003) with permission from the authors and from The Ecological Society of America.

effects from soil biota in the invaded region were as strong as, or stronger than, those found in the native region (Fig. 3). Ideally, comparative experiments would be performed in the same place and at the same time, but these results suggest that invasive *Ammophila* does not seem to have escaped the inhibitory effects of soil biota. In a separate experiment, Knevel *et al.* (2004) compared the effects of the soil biota from native (the Netherlands) vs nonnative ranges (South Africa) to one another and to a control (sterilization treatment). They report that in three of five sites in the native range, *Ammophila* produced less than half of the amount of biomass produced in sterilized soils. By contrast, a similar growth reduction was observed in only one of seven sites in the portion of the experiment using soil from the nonnative range, contrasting with Beckstead & Parker (2003), suggesting that *Ammophila* has escaped the suppressive effects of the soil biota in its homeland. However, five of seven sites in the nonnative range showed a lower growth response relative to the sterilization control indicating that *Ammophila* experienced negative effects of soil biota even in its nonnative range.

Plant–soil biota interactions have been found to differ in the native and nonnative ranges of three tree species. One of these tree species, *Prunus serotina*, is negatively affected by soil pathogens (*Pythium* spp.) in its native range (Packer & Clay, 2000; Reinhart *et al.*, 2005). Interestingly, *P. serotina* is an invasive in woodlands of north-western Europe (Starfinger *et al.*, 2003, and citations therein) where it reaches much higher local densities than in North America (Reinhart *et al.*, 2003; K. O. Reinhart, unpublished). Reinhart *et al.* (2003) found that soil sterilization increased the survival and growth of *P. serotina* seedlings in soil in its native range; however, sterilization had no effect on seedling survival and a negative effect on seedling growth in the nonnative range. The contrasting results for seedling survival in the native and nonnative ranges suggest that *P. serotina* experience greater soil-borne disease in their native than nonnative ranges (suggestive support of enemy release hypothesis, Fig. 4b) while the biomass data suggest that *P. serotina* may have escaped its below-ground enemies and/or acquired better below-ground mutualists in its nonnative ranges than its native ranges (suggestive support of enhanced mutualisms hypothesis, Fig. 4c). In another study, sterilization of soil from native ranges had a positive effect on the growth of *Acer platanoides* and *Acer negundo*. However, soil effects in invaded nonnative ranges were more complex. In the nonnative ranges, sterilization of soil collected near resident native species had a negative effect on the biomass of *A. platanoides* in one part of its nonnative range, and had a negative effect on the change in relative height of *A. negundo* and *A. platanoides* in their nonnative ranges (Reinhart & Callaway, 2004). These negative effects of soil sterilization in the nonnative vs native ranges of two *Acer* species and *P. serotina* provide support for both the enemy release and enhanced mutualisms hypotheses (Fig. 4).

Similar to the previous studies, soil microbes from the European home range of *C. maculosa* have stronger inhibitory effects on its growth than soil microbes from soils in North America (also see section II.1 Plant–soil biota feedbacks). Callaway *et al.* (2004a) found that sterilization of soils collected from four populations of *C. maculosa* in its native range (Europe) caused an average 166% increase in the total biomass. By contrast, sterilization of soils collected from six populations of *C. maculosa* in its nonnative range (north-western USA) only increased its growth by an average of 24% (Fig. 5). These studies have been repeated under different conditions and with different sources of soil, and like those for *Ammophila* recent results have not been consistent. For example, experiments with Romanian soil biota have not shown evidence suggestive of enemy release (R. M. Callaway, unpublished). We do not know why the results of sterilization experiments have varied so much but there are many possible causes. First, the variation between the studies may represent natural ecological variation in plant–soil biota interactions over space and time (Blaney & Kotanen, 2001; O'Hanlon-Manners & Kotanen, 2004). Thus, species with large ranges are likely to have varying plant–soil biota interactions throughout their range. This suggests that past sampling has not been conducted at large enough biogeographical scales. Replication of populations is important and should be representative of the entire range or targeted if justified by ecologically significant information (i.e. knowledge of the location of the founding population). Second, sterilization can cause nutrient flushes (Troelstra *et al.*, 2001); however, in the *C. maculosa* experiments

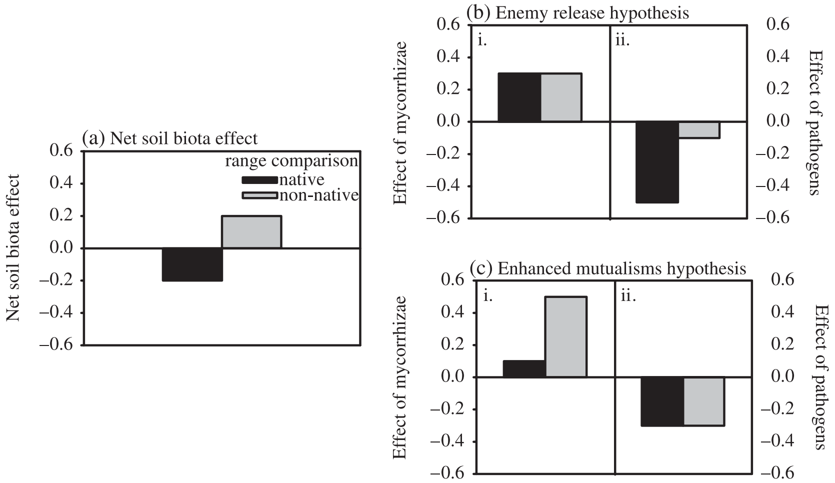

Fig. 4 Invasive plants often experience more negative net soil biota effects in their native ranges than in their nonnative ranges (a), refer to Table 1. This variation in interaction strength and/or direction can be explained by the varying impact of either antagonists (b) or mutualists (c). The enemy release hypothesis (b) predicts more negative impacts of antagonists (pathogens) in native than nonnative ranges and similar impacts of mutualists (mycorrhizas) between ranges. By contrast, the enhanced mutualisms hypothesis (c) predicts more positive effects of mutualists in nonnative than native ranges and similar impacts of antagonists between ranges. The *y*-axes represent hypothetical relative response indexes. Positive numbers indicate either a positive net soil biota (a) or a positive effect of mycorrhizas (i) or pathogens (ii), and negative numbers indicate negative interactions. The specific values depicted in (a) are hypothetical but consistent with biogeographical trends in Table 1. To highlight the differences between these two competing hypotheses, we have drawn (b) and (c) as if the effects of mycorrhizas and pathogens are additive and mutually exclusive; however, some combination of these hypotheses is most likely to exist and determine outcomes of invasions. Other groups of mutualists and antagonists can be substituted. The data in these are hypothetical but could be derived from glasshouse/field experiments including plantings in experimental soil treatments, pathogenicity trials, biocide experiments, etc. (e.g. net soil biota effect = (nonsterile soil − sterilized soil) × nonsterile soil^{-1}).

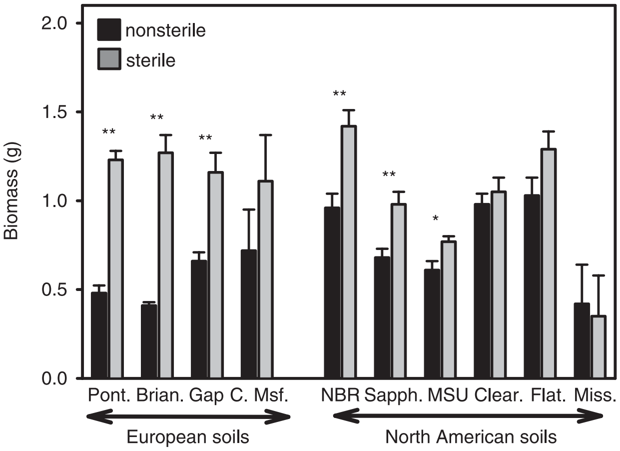

Fig. 5 Total biomass of *Centaurea maculosa* plants grown in nonsterilized and sterilized soil collected from European and North American populations. Soils were collected from the rhizospheres of grasses near *C. maculosa* individuals. In a four-way analysis of variance (ANOVA) (region of origin, rhizosphere and sterilization as main effects, and population nested within region of origin): $F_{\mathrm{origin}} = 40.18$, df = 1,297, $P < 0.001$; $F_{\mathrm{pop}} = 21.81$, df = 5,297, $P < 0.001$; $F_{\mathrm{rhizosphere}} = 21.12$, df = 1,297, $P < 0.001$; $F_{\mathrm{sterilization}} = 110.87$, df = 1,297, $P < 0.001$; $F_{\mathrm{origin \times sterilization}} = 29.35$, df = 1,297, $P < 0.001$; $F_{\mathrm{origin \times pop \times rhizosphere}} = 16.2$, df = 2,314, $P < 0.001$. Redrawn from Callaway *et al*. (2004a).

pots were well fertilized. Third, sterilization only sets initial conditions, and soils certainly do not remain sterile for the course of the experiment. In fact, total microbial biomass can be higher after a several-month experiment in initially sterilized soils than in nonsterilized soils (W. H. Holben and R. M. Callaway, unpublished). It is difficult to know if re-colonizing bacteria (or other microbes) are beneficial, neutral, or inhibitory and if microbial immigrants have different effects in nonsterile vs sterilized soils, or if different sterilization events or sterilization of different soils can drive recolonization in different directions. Clearly, sterilization experiments have the potential to yield insight, but this insight needs to be corroborated by other types of measurements and experiments.

Other types of measurements and experiments include the identification of microbial taxa in sterilization experiments, addition of selective biocides (but see Hood *et al*., 2004), experimental addition of particular microbial taxa to sterilized soils or plant–soil biota feedback experiments. However, soil taxa can be very difficult to identify, and choosing which taxa (or amount) to add or the particular conditions in which to test the effects of particular taxa is likely to be arbitrary since the choice may not be directly related to the highly diverse and variable interactions and conditions found in natural systems. Plant–microbe interactions also vary substantially in different abiotic environments. Biotic complexity may also muddy the results of experiments with soil microbes. Plant–soil biota feedback experiments are an ideal method of describing plant–soil biota interactions (see section II.1 Plant–soil biota feedbacks and Bever, 1994, 2002, 2003). However, it may prove difficult to expand these experimental designs beyond a single community and to include two or more plant communities, and to sufficiently describe interactions among multiple populations (i.e. adequate spatial sampling) interacting with a focal species in its native and nonnative ranges.

III. Soil-borne antagonists

Soil biota can suppress the growth, fecundity, and survival of plants in natural communities (Augspurger & Kelly, 1984; van der Putten *et al.*, 1993; Mills & Bever, 1998; Klironomos, 2002; Hood *et al.*, 2004; Reinhart *et al.*, 2005; Thorpe & Callaway, 2006), and it is logical to assume that escape from harmful soil biota would allow many species to increase in abundance. The enemy release hypothesis predicts that invasive nonnative species escape frequency dependent control by host-specific natural enemies (e.g. herbivores and pathogens, Fig. 4b), resulting in a rapid increase in their abundance and distribution (Keane & Crawley, 2002). As much as native herbivores can inhibit nonnative invasives, the presence of strong indigenous below-ground antagonists may resist invasion by nonnative species. For example, attempts to grow several species of agricultural (e.g. apple, pear, cherry) and forestry significance (Douglas fir and pines) in new regions of the world have been hindered by the direct negative effect of indigenous pathogens (Scheffer, 2003). Unfortunately, little is known about the causes of failed invasions.

Biocontrol practitioners have long recognized that pathogens from an invasive plant's homeland, including pathogens in the soil, might suppress the invasives in their new habitats (Caesar, 2000; Charudattan & Dinoor, 2000). To our knowledge, the most thorough case study of biocontrol by a pathogen is that of the foliar rust, *Puccinia chondrillina* on *Chondrilla juncea*, a perennial weed of cereal crops native in Europe and introduced to Australia and North America (Burdon *et al.*, 1981; Panetta & Dodd, 1995). Bioherbicides have also been developed that utilize soil-borne pathogens (e.g. *Phytophthora palmivora*) (Charudattan & Dinoor, 2000).

1. Nematodes

As noted above, soil nematodes (and pathogens) inhibit the growth of *A. arenaria* in its native European range (van der Putten *et al.*, 1988, 1990, 1993; De Rooij-van der Goes, 1995). Van der Putten *et al.* (2005) compared the total number of taxa of root feeding nematodes and of specialist root feeding nematodes associated with *A. arenaria* in its native (Europe) and nonnative ranges (Pacific coast of USA, South Africa, New Zealand, and Tasmania). The average number of plant-feeding nematodes did not differ between the native and many of the nonnative ranges (i.e. USA, South Africa and Tasmania), and New Zealand was the only region where *A. arenaria* encountered fewer nematode species relative to in its native range. However, there were fewer taxa of root feeding specialist nematodes in three of the four surveyed nonnative ranges (South Africa, New Zealand and Tasmania) relative to observations in the native range. This decrease in specialist nematodes is similar to patterns recorded for above-ground herbivores of other invasive species (Jobin *et al.*, 1996; Wolfe, 2002; Wolfe *et al.*, 2004), but comparisons of the impact of nematodes in native and nonnative ranges are necessary to provide a complete picture of enemy release.

2. Pathogens

The enemy release hypothesis has been tested at the community-level by testing the prediction that native species will support more enemies than phylogenetically similar nonnative species. Blaney & Kotanen (2001) tested the effects of soil fungal pathogens on buried seeds of 15 congeneric pairs of native and nonnative herbaceous plant species in Ontario, Canada. Soil pathogens did not have a greater affect on native than nonnative species. Similarly, in a comparison of 18 native and nonnative clovers, no difference was found in pathogen diversity, infection, leaf damage, or fitness effects of foliar and damping-off fungi between native and nonnative species (I. M. Parker & G. S. Gilbert, unpublished). These studies do not support the enemy release hypothesis (but see Agrawal *et al.*, 2005). However, these studies have not separated invasives from the total pool of nonnative species and have not explored invasives that are phylogenetically distinct from natives. The probability of host shifts by pathogens from natives to nonnatives is expected to be greater if the nonnative plant species are phylogenetically similar to native species (Mack, 1996; Parker & Gilbert, 2004; but see Duncan & Williams, 2002), and comparisons of invasives to unrelated dominant native species may yield different results.

Evidence for enemy release requires comparative experiments using soil biota from the native region and the invaded region to determine whether the plant experiences less pathogenic activity in the nonnative than native ranges. Ideally, these effects must characterize interactions occurring in the field, incorporate variation within native and nonnative regions, and include appropriate replication in both the native and nonnative ranges. Plant pathologists have described the importance of the abiotic environment in driving the expression of disease symptoms and consider environment as one of the three components in the 'disease triangle' (i.e. pathogen, host, and environment) (Park, 1963; Agrios, 1997). Because of variability in environments and ecotypes, experiments across a range of environments and with multiple populations should be compared so that variation among populations within a region (native vs invaded) can be compared with variation among regions. Biogeographic comparisons of other traits of invasives illustrate the importance of using multiple populations

(Maron *et al.*, 2004). However, experiments with soil biota have practical limitations. For example, the importation of foreign microbes, especially pathogens, is constrained by ethical considerations, trade regulations, and quarantine policies because of the largely unknown environmental threat that nonnative microbes pose. To our knowledge, no study of plant invasions and soil biota have met the criteria that we outline above, except possibly the body of research on *A. arenaria* (Beckstead & Parker, 2003; Knevel *et al.*, 2004; van der Putten *et al.*, 2005). However, these criteria are very difficult to meet for even above-ground enemies (but see DeWalt *et al.*, 2004).

IV. Soil-borne mutualists

Mutualistic effects of soil biota clearly facilitate some invasions, and some invasives alter soil-borne mutualists in ways that alter recipient plant communities (Richardson *et al.*, 2000). Two of the strongest soil mutualisms involve mycorrhizal fungi and nitrogen-fixers, both of which improve the nutrient status of their host-plants. Therefore, interactions between these mutualists and invasives have the potential to alter soil chemistry, which in turn can affect native plant communities (Miki & Kondoh, 2002; Hawkes *et al.*, 2005). Recent progress with molecular techniques linking microbial identity and diversity to function should dramatically improve our understanding of invasive-driven changes in microbial communities and affects on nutrient cycling (Schadt *et al.*, 2005; Torsvik & Øvreås, 2004). Related to microbial effects, the effects of nonnative plant species on soil chemistry and ecosystem function have been described in detail by Ehrenfeld (2004) and Wolfe and Klironomos (2005).

1. Mycorrhizas

One of the most ubiquitous mutualisms on earth is that between mycorrhizal fungi and plants. As mentioned earlier, the affect of individual mycorrhizal species can range from parasitic to mutualistic. Thus, the potential exists for new combinations of nonnative species and resident mycorrhizas to yield either strong parasitic or strong mutualistic interactions. Invasives might possibly encounter soil biota that facilitate establishment, but the potential for stronger facilitation by soil microbes in new habitats (nonnative) than in old habitats (native) does not fit into any of the current hypotheses for invasion. Here we refer to this concept as the enhanced mutualisms hypothesis (see Fig. 4c). Relative to the enemy release hypothesis (see III. Soil-borne antagonists), we know much less about how enhanced mutualisms affect invasions (Fig. 4b vs c). Furthermore, the evolutionary and ecological processes by which invading species might encounter novel yet stronger mutualists than those in the invasive's home community are not yet clear. It is not surprising for a nonnative plant to find a new mutualist partner that allows its existence in new regions of the world (Richardson *et al.*, 2000); however, for a nonnative species to find a new mutualistic partner that drives the transformation of a species from low to super abundance does not have a clear theoretical underpinning. For haphazard encounters with mutualists from the nonnative range to drive far more beneficial relationships than mutualisms in the invasive's native range, mutualisms must be general, weakly specialized, or tend to evolve away from intense interaction strengths. Alternatively, it is important to consider that interactions between plants and mycorrhizas are not always simple two-way mutualisms where both partners benefit. For example, nonnative plants may exploit mycorrhizal associations because individual mycorrhizas form symbioses with multiple plants at one time forming a mycelial network. The nonnative species may be able to exploit the benefits of the symbiosis while escaping the mutual cost of maintaining the network. This sort of parasitism may be unstable but may help the invasive species establish and displace native species as the system reaches a new stable equilibrium (Schlaepfer *et al.*, 2005). So far, we know little about mutualisms and invasives and to our knowledge there is no evidence for nonnative plants establishing new mutualisms that specifically lead to dominance and competitive exclusion of native species. However, there is a great deal of evidence that mutualistic interactions among soil biota and plants contribute to plant invasions.

Ectomycorrhizal fungal species tend to be more host-specific than arbuscular mycorrhizal fungi (Borowicz & Juliano, 1991), and the absence of ectomycorrhizas initially limited the introduction of many *Pinus* species to new regions of the world (Brisco, 1959; Poynton, 1979). However, this barrier has been overcome and appropriate ectomycorrhizas for *Pinus* species have been transported around the world and are now common throughout the southern and northern hemispheres (Richardson *et al.*, 1994). There is also evidence that the invasive success of some plant species has been enhanced by the presence of native ericoid mycorrhizas (Wardle, 1991; Lazarides *et al.*, 1997). Unlike ectomycorrhizas and ericoid mycorrhizas, arbuscular mycorrhizal (AM) fungi have been thought to neither limit nor facilitate invasion because of their cosmopolitan distribution and general lack of host-specificity (Richardson *et al.*, 2000). Therefore, the presence of appropriate AM fungal mutualists may only allow invasion.

Mycorrhizal plants associate with large numbers of species of AM fungi (Borowicz & Juliano, 1991; Molina *et al.*, 1992; Eom *et al.*, 2000; Streitwolf-Engel *et al.*, 2001). Therefore, we might not expect powerful new alliances among invasives and AM fungi that cause invasive dominance. Conversely, different partner pairings can result in highly variable ecological effects (Johnson *et al.*, 1997; van der Heijden *et al.*, 1998; Klironomos, 2003), creating the potential for unusual relationships and pairings in plant invasions. In the only direct experimental test of potential biogeographic effects of AM fungi, Klironomos (2002) found that the AM fungal fraction of a North American soil had only slightly more beneficial effects on rare native North American (four of five species) than invasive nonnative species (two of five species). Furthermore, these positive effects were only realized when the negative effects of soil-borne pathogens were excluded.

Despite the general lack of host-specificity in AM fungi associations, specificity in the growth responses of infected plants exist. The extreme variability in the growth responses of plants to different species of AM fungi can be a major determinant of local plant species diversity in natural systems (Johnson *et al.*, 1997; Bever, 2002; van der Heijden *et al.*, 2003). Klironomos (2003) tested the effect of multiple AM fungi isolates from native and nonnative sources on the mycorrhizal plant-growth responses for a number of grassland species. He found that plant growth associated with AM fungi that naturally co-occurred with a species (native AM fungi treatment) ranged from highly parasitic to highly mutualistic, depending on the combination of plant and fungal species (Johnson *et al.*, 1997; Klironomos, 2003). Although the magnitude of responses was greater when using combinations of local plants and fungi, plant–mycorrhizal interactions varied from parasitic to mutualistic regardless of whether the source of AM fungi was native or nonnative (Klironomos, 2003). However, the nonnative AM fungi used were not necessarily associated with the tested invasive plants in their nonnative ranges. Incorporating AM fungi that are actually associated with species that either fail to establish in nonnative ranges or become problematic invasives may reveal important trends that correspond with invasive success. For example, AM fungi which have highly parasitic associations with nonnative species may repel invasives while highly mutualistic associations may facilitate invasion.

Arbuscular mycorrhizas are important mediators of competitive interactions between nonnative and native plants. Several studies have found that competitive effects of the invasive *C. maculosa* on the native grass *F. idahoensis* are mediated by AM fungi (Marler *et al.*, 1999; Zabinski *et al.*, 2002; Callaway *et al.*, 2004b; Carey *et al.*, 2004). When competing with *C. maculosa*, *F. idahoensis* plants were 171% larger when grown in field soil that was sterilized and provided with a microbial wash than when grown in field soil that was not sterilized (Marler *et al.*, 1999). By contrast, *C. maculosa* grown with larger *F. idahoensis* were 66% larger in untreated field soil than field soil drenched with a fungicide that reduced AM fungi colonization (Marler *et al.*, 1999). Other studies have reported similar interactions between this invasive and native grasses (Zabinski *et al.*, 2002; Callaway *et al.*, 2004b; Carey *et al.*, 2004), suggesting that mycorrhizal networks mediate this interaction either through carbon transfer from *Festuca* to *Centaurea* via a shared mycorrhizal network (Carey *et al.*, 2004) or increased phosphorus uptake (Zabinski *et al.*, 2002). Similar general effects of soil fungi have also been shown for the annual invasive, *C. melitensis* (Callaway *et al.*, 2001, 2003).

Invasive plants also affect AM fungal communities in ways that may create a plant–soil biota feedback facilitating invasion and altering native communities. In California grasslands, native species are more dependent on AM fungi than nonnative species (Vogelsang *et al.*, 2005). The average growth response to a commercially available AM fungi species was *c.* 82% greater in seven native species than 10 nonnative species. This corresponded with a greater proportion of nonnative species than native species in this system occurring in families described as nonmycorrhizal. In three different experiments, they found that invaded grasslands vs neighboring areas without invasion were associated with 33%, *c.* 43%, and *c.* 83% reductions in per cent root colonization by AM fungi (Vogelsang *et al.*, 2005) and similar findings have been reported for areas invaded by garlic mustard (*Alliaria petiolata*) (Roberts & Anderson, 2001; Stinson *et al.*, 2006). In summary, it appears that invasion by nonmycorrhizal species can reduce the abundance of AM fungi, which negatively affects native plant species with strong dependencies on AM fungi. These altered soil microbial communities then facilitate additional invasion by nonmycorrhizal nonnative species, thus maintaining nonnative plant dominance and inhibiting the re-establishment of native species ('the degraded mutualisms hypothesis'; Vogelsang *et al.*, 2005). Others have reported that nonnative species are often less dependent on arbuscular mycorrhizal fungi (Reeves *et al.*, 1979; Allen & Allen, 1980; Pendleton & Smith, 1983; but see Marler *et al.*, 1999; Richardson *et al.*, 2000; Callaway *et al.*, 2004b). It is not clear whether the invasives inhibit mycorrhizas or preferentially invade areas inherently depauperate of mycorrhizas.

2. Nitrogen fixers

Invasive plants commonly increase levels of soil nitrogen, perhaps because many successful invasives take advantage of mutualisms with native nitrogen-fixing bacteria (*Rhizobium* spp. and *Frankia* spp.) (Allen & Allen, 1981; De Faria *et al.*, 1989; Clawson *et al.*, 1997; Ehrenfeld, 2003). Alternatively, invasive nonnative species may bring their symbionts with them, rather than enter into new associations with resident *Rhizobium* spp. (Weir *et al.*, 2004; Chen *et al.*, 2005). Regardless, symbioses between invasives and nitrogen-fixers are common even in areas without native flora that form these associations (Richardson *et al.*, 2000; Weir *et al.*, 2004). By contrast, the absence of *Rhizobium* inoculum or low inoculum densities can limit the invasive success of nonnative species (Parker, 2001). Parker (2001) reported that a threshold density of nitrogen-fixing bacteria is often necessary for nodule development on invading legumes. Indigenous legumes may provide necessary threshold densities (M. A. Parker, pers. comm.). Similar inoculum limitations may exist for species forming symbioses with *Frankia* spp. (Simonet *et al.*, 1999).

The absence of appropriate nitrogen-fixing bacteria may limit some invasions, but *Myrica faya* invasion in Hawaii appears to have been highly successful because of a symbiosis with the nitrogen-fixing actinomycete *Frankia* (Vitousek *et al.*, 1987; Burleigh & Dawson, 1994). We do not know if *Myrica* arrived with its own *Frankia* or if *Frankia* was already present in the system. Regardless, this mutualism has dramatically altered nitrogen cycling in Hawaiian ecosystems and contributed to highly altered native plant communities (Vitousek *et al.*, 1987). Invasion by nonnative plants with nitrogen-fixing symbionts may also enhance secondary invasions by nitrophilous weedy species (Yelenik *et al.*, 2004).

Non-nitrogen fixing invasives may take advantage of the soil legacies left by native plants and their nitrogen-fixing mutualists. Maron & Connors (1996) found that seedlings of the nonnative grass *Bromus diandrus* accumulated 48% more root biomass and 93% more shoot biomass when grown in soil collected under experimentally killed native nitrogen-fixing shrubs (i.e. lupines), compared with *B. diandrus* seedlings grown in soil collected at least 1 m away from lupines. Invasive nonnative plant species may also negatively affect the nodulation of resident plants and have direct negative effects on resident nitrogen-fixing microbes (and nitrifying bacteria) (Rice, 1964). Thus, interactions between plants and nitrogen-fixing symbionts may affect the establishment of nonnative species and their impact on resident native species.

Other microbes in the nitrogen cycle can be affected by invasives (Rice, 1964; Hawkes *et al.*, 2005). For example, Hawkes *et al.* (2005) determined that invasive nonnative grasses doubled gross nitrification rates, in part by increasing the abundance and altering the composition of ammonia-oxidizing bacteria in the soil. These plant-driven changes in soil microbial communities are likely to disrupt ecosystem function and leave an invisible legacy of invasion.

V. Conclusion

There are many direct and indirect mechanisms by which plant–soil biota interactions can affect the invasion of nonnative plant species. Although some ideas presented in this paper have more empirical and theoretical support than others, even the best understood processes are supported by no more than a handful of studies. Additional research with other species in other systems, and preferably with an explicit biogeographical context (Hierro *et al.*, 2005); will be crucial for developing reliable generalizations about the role of soil biota in promoting or repelling invasives. Focusing on specific soil-borne taxa and their direct effects may be necessary to test rigorously the enemy release hypothesis and enhanced mutualisms hypothesis (Fig. 4). However, elucidating the effects of single species of soil biota outside of the context of the entire soil community may not accurately describe interactions occurring in nature. For example, the powerful effects of a particular nitrifying bacterial species may be irrelevant in the absence of nematodes (Horiuchi *et al.*, 2005). However, a distinct advantage to studying soil communities is that the net effect of the entire community can be described relatively easily via plant–soil biota feedback or net soil biota effect experiments. The development of hypotheses that focus on the synergistic effects of the entire below-ground community may be particularly useful in determining the effects of soil biota on plants in their native and nonnative ranges. Importantly, attention to the effects of native soil biota on nonnative plants that do not successfully invade (Simberloff & Gibbons, 2004; Clay *et al.*, 2006) will be crucial if we are to assess the relative importance of soil biota in invasions.

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