Breaking New Ground: Soil Communities and Exotic Plant Invasion

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For several decades, ecologists have been characterizing the interactions of exotic plant species with components of native ecosystems. A major focus of this work is describing the effects that exotic species have on native plant communities as well as the attributes of native communities that make them susceptible to invasion (Rejmanek 1998). Invaded communities often differ from native communities in organismal composition and may have altered ecosystem functions compared with native communities, including the rates and dynamics of biogeochemical processes (Ehrenfeld 2003) and the suitability of habitat for other organisms (Levine et al. 2003).

Although soil organisms play important roles in regulating ecosystem-level processes (box 1; Wardle et al. 2004), and soils contain much of the biodiversity of terrestrial ecosystems (Torsvik et al. 1990, Vandenkoonhuyse et al. 2002), most of the work on effects of plant invasions has focused on aboveground flora and fauna (Levine et al. 2003). This disparity in knowledge is largely due to the greater immediacy of aboveground communities in our everyday lives. As many soil organisms can only be detected through the presence of signature biomolecules, scientists have only recently developed the tools to characterize the composition of soil communities at a resolution that can detect changes induced by plant invasions (box 2).

The composition and functioning of soil biota are closely linked with aboveground composition and functioning (Wardle et al. 2004), and exotic plants can directly or indirectly disrupt these links (figure 1). An exotic plant species may have limited direct effects on the soil community, but shifts in plant community composition caused by the invasion of the exotic species can indirectly alter soil community composition. These shifts in soil community composition may directly affect ecosystem processes. Alternatively, an exotic plant may have limited direct effects on plant community composition, but direct effects on the composition and function of soil communities may create a feedback with influences on the composition of aboveground communities. Interactions between aboveground and belowground communities might persist following invasion, but the direction or the magnitude of these interactions might shift as a result of an invader.

In this article, we review some of the recent advances made in understanding interactions between soil organisms and exotic plant species in the context of the links between aboveground and belowground communities. We first describe the mechanisms by which exotic plants affect the structure and function of soil communities, and highlight recent case studies that provide detailed information on the interactions between exotic plants and soil organisms. We then address the role that some soil organisms play in affecting the ability of exotic plants to establish and flourish in novel ranges. We also consider the emerging awareness of the need to incorporate...
Effects of exotic plant invasions on soil communities

Several mechanisms by which exotic plants affect soil communities have been identified by studying a variety of exotic plant invasions in different ecosystems. It is important to note that native plants can influence soil communities using the same mechanisms discussed below, but the effects of an invader may be more pronounced, or a particular mechanism may be novel to a native community. In addition, more than one mechanism may apply to the effects of a particular exotic plant species on soil communities.

How exotic plants alter soil communities. A main linkage between plant and soil communities is the provision of photosynthate belowground by plants. Plants supply resources for soil communities by providing organic matter through leaf-litter inputs, through the release of root exudates, or through other methods of deposition of organic compounds into the soil environment. Plants have diverse methods of supplying these resources to the soil, and as a result, unique soil communities form under different plant species (Bever et al. 1996, Westover et al. 1997) and under plant communities that differ in composition and abundance (Zak et al. 2003, Johnson et al. 2004). As an exotic plant species invades a community, it can alter links between native aboveground communities and belowground communities, including the timing, quality, quantity, and spatial structure of plant-derived soil inputs. For example, an invading exotic plant could alter the quantity, quality, and timing of litter production, which would alter nutrient inputs into the soil (figure 2). Some exotic plants cause increases in litter production that can lead to increases in fire intensity and frequency (D’Antonio and Vitousek 1992). Changes in fire regime could indirectly alter soil communities, as fire frequency and intensity are known to affect soil community structure and function (figure 2; Chen and Cairney 2002, Boerner and Brinkman 2003).

Plants release secondary compounds into the soil environment from their roots as exudates, and if the compounds released by an exotic plant are novel to a soil community, they may alter the composition and function of the soil community (figure 2). Allelochemicals released from plant roots have been widely used as an explanation of the success of exotic plants in the context of plant–plant interactions (Hierro and Callaway 2003), but evidence of allelochemicals altering the interactions between native plants and soil communities has only recently been established. Diffuse knapweed (Centaurea diffusa) is a Eurasian knapweed species that has invaded many natural ecosystems in western North America. This species releases the chemical 8-hydroxyquinoline from its roots, which has been demonstrated to be an antimicrobial agent (Vivanco et al. 2004). Diffuse knapweed can cause shifts in the composition of the soil microbial community (Callaway et al. 2004), possibly through the release of these allelochemicals. Garlic mustard (Alliaria petiolata; figure 3), another exotic species in North America that is native to Europe, is a member of the Brassicaceae, a family of plants in which many species produce glucosinolates. Vaughn and Berhow (1999) proposed that these compounds are deposited in the soil, through root exudation or litter production, where they may cause changes in soil microbial communities. The dominance of garlic mustard in North American forests has been shown to cause significant declines in the abundance (Roberts and Anderson 2001) and function (data available from J. N. K.) of arbuscular mycorrhizal fungi (AMF). These are symbiotic fungi that colonize plant roots and extend hyphae beyond the reach of host plant roots, which can lead to substantial increases in the nutrient uptake of host plants. Because AMF can have individual-, population-, and community-level effects on plants (Smith and Read 1997),

Native soil communities play fundamental roles in ecosystem properties and processes, which is why the potential alteration of these communities by exotic plant invasion is of concern. Some of these roles and a few examples of organisms involved include the following:

**Biogeochemical cycling**
- Mineralization of nutrients (bacteria and fungi)
- Decomposition of complex substrates (invertebrates and fungi)
- Nitrogen fixation (bacteria)

**Direct effects on plant growth**
- Deleterious effects of pathogens and herbivores (nematodes, fungi)
- Positive effects of mutualists (mycorrhizal fungi, nodulating nitrogen-fixing bacteria)

**Soil structure**
- Aeration and turnover of soils (earthworms)
- Aggregation of soils (fungi)

The composition of soil communities, both in terms of abundance and in terms of the presence or absence of certain species or functional groups, has been linked to functionally significant processes, both aboveground and belowground. For example, higher numbers of species of arbuscular mycorrhizal fungi led to higher plant biomass, plant nutrient uptake, and plant community diversity in an old-field ecosystem in southern Ontario (van der Heijden et al. 1998). If an exotic plant alters the composition of soil communities by changing the abundance of (or completely eliminating) certain taxonomic groups, these diversity–function relationships in the soil community may be altered.

Belowground communities in ecosystem management and restoration in the context of plant invasions.

**Box 1. The role of soil communities in ecosystems.**

<table>
<thead>
<tr>
<th>Role</th>
<th>Description</th>
</tr>
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</table>
| Biogeochemical cycling | - Mineralization of nutrients (bacteria and fungi)  
- Decomposition of complex substrates (invertebrates and fungi)  
- Nitrogen fixation (bacteria) |
| Direct effects on plant growth | - Deleterious effects of pathogens and herbivores (nematodes, fungi)  
- Positive effects of mutualists (mycorrhizal fungi, nodulating nitrogen-fixing bacteria) |
| Soil structure | - Aeration and turnover of soils (earthworms)  
- Aggregation of soils (fungi) |

Invasion of soil communities by exotic plant species can alter the composition and function of soil microbial communities. For example, the release of allelochemicals by exotic plants can affect soil microbial communities. Exotic plant species can alter the nutrient availability and soil structure, which can affect the composition and function of soil communities.
Box 2. Contemporary tools to assess the structural and functional diversity of soils.

Unlike species in aboveground communities, where it is relatively easy to measure biodiversity, many organisms that live in the soil cannot be easily observed and quantified. Soil ecologists employ a variety of techniques to detect the effects of exotic plant invasions on soil community composition and function. Here we present an overview of some of the techniques used to assess the structural and functional diversity of soil microbes.

Techniques for assessing structural diversity

Culture-dependent techniques. Traditional methods for assessing the diversity of soil communities involve incubating soil extracts on various sterile media that favor microbial growth. Organisms that grow on these media are identified using morphological or physiological traits. This approach only captures a small fraction of total soil diversity, and has largely been replaced by the methods discussed below.

Fatty acid analysis. Specific groups of soil microbes have “signature” fatty acids in their biomass that can be extracted from the soil and used to detect the presence and abundance of these groups. One commonly used fatty acid analysis, phospholipid fatty acid analysis, assesses changes in the production of phospholipids, which are components of cell membranes and are found only in living cells. This technique only detects changes in broad groups of soil organisms, such as specific bacterial and fungal groups, and generally cannot resolve changes in community composition at the species level. However, it has been used as a sensitive indicator of changes in microbial communities in numerous studies (Zelles 1999) and has been correlated with changes in microbial community structure in plant invasion studies (Kourtev et al. 2002, 2003).

Nucleic acid analysis. Analysis of nucleic acids is becoming one of the most informative and widely used methods in soil microbial ecology (Hill et al. 2000). Through the use of primers designed to target specific components of soil communities, the DNA of soil microbes from varying genomic locations is amplified through the polymerase chain reaction. Depending on the research question and the level of resolution needed, these nucleic acids are processed using different methods to produce “fingerprints” of soil community composition that can be compared between different samples. Such methods include denaturing gradient gel electrophoresis, or DGGE, and terminal restriction fragment length polymorphism, or t-RFLP. Alternatively, if more comprehensive knowledge of the composition of the community is desired, the nucleic acids of interest can be sequenced to determine the phylogenetic relationships among species present.

Techniques for assessing functional diversity

Measurements of nutrient cycling and soil enzyme activity. Since microbial communities play a major role in biogeochemical cycles, measurements of the rates and dynamics of these processes can indicate changes in microbial community function induced by exotic plant invasion. Soil ecologists measure amounts of nutrients available or rates of nutrient processing (mineralization, immobilization, etc.) to relate changes in soil community structure to changes in function.

Many soil microorganisms produce extracellular enzymes that can degrade complex substrates in the soil and alter the availability of nutrients (Sinsabaugh 1994). Measuring the activities of these enzymes using standardized protocols can serve as a useful indicator of the function of soil organisms in soils invaded by exotic plants compared with the same function in native areas (Kourtev et al. 2002).

Carbon substrate utilization techniques. To assess the metabolic diversity of soil microbial communities, soil ecologists measure the diversity of soil community responses to carbon substrates. With a technique known as substrate-induced respiration, different carbon compounds (amino acids, carbohydrates, polymers, etc.) are added to the soil, and the carbon dioxide produced by the soil community through respiration after the addition of these substrates is measured (Degens and Harris 1997). In an analogous method, known as community-level physiological profiling (CLPP; Garland and Mills 1991), a series of microwells on a plastic plate containing different types of carbon substrates is loaded with a soil suspension of the soil community being studied. As the microbial community utilizes the various carbon substrates through respiration, an indicator dye changes color to indicate the activity of the microbes on that particular substrate. Although this is a relatively rapid, sensitive, and inexpensive method used to detect changes in potential soil community function caused by exotic plant invasion, CLPPs are dependent on culturing microbial communities on specific carbon substrates and therefore do not capture the complete diversity of soil microbial communities.

Measurements of multitrophic function. Effects of shifts in soil organism abundance and diversity can also be assessed by measuring changes in the structure and function of other trophic groups. For example, soil communities that have been “cultured” by native plants versus exotic plants can be used as inoculum for growing individual plants or experimental communities to assess effects of these manipulated soil communities on aboveground communities.
alteration of AMF communities by garlic mustard may have long-term effects on the dynamics of understory and canopy plant species in these forests.

Other traits of exotic plants, such as novel nutrient acquisition strategies (figure 2), could also have implications for the structure and function of soil communities. A widely recognized example of an exotic plant altering the attributes of an ecosystem is the invasion of firetree (Myrica faya) in Hawaii, where this plant and its nitrogen-fixing root symbionts (Frankia spp.) have invaded nitrogen-limited communities, altering nitrogen cycling and plant community composition in these communities (Vitousek and Walker 1989).

Exotic plant species can directly alter physical properties of the soil environment, causing changes in environmental factors that may control soil community composition and function (figure 2). For example, saltlover (Halogeton glomeratus), a plant species that hyperaccumulates sodium derived from lower soil profiles in its biomass, has invaded rangelands of the western United States. In invaded soils, this species has caused increases in sodium concentrations, which may be causing concurrent changes in microbial community composition (Duda et al. 2003).

Current progress and future research needs. To date, it is difficult to make strong generalizations about the effects of exotic plants on soil communities, because only a handful of published studies have documented the effects of invasive plant species on the composition and functioning of these communities (as summarized in table 1). From these studies, it is apparent that belowground effects of exotic plant invasions can be highly variable. Studies have documented negative, neutral, or positive effects on soil composition and functioning, depending on the plant species considered, the community or ecosystem invaded, the methods used to assess changes in structure or function, and the temporal and spatial scales considered in the study.

In addition to variation in the effects of exotic invasion on soil communities across plant species and systems, it is also interesting to note that different taxonomic groups within a soil community may not respond similarly to the presence of an invasive exotic. For example, in arid grasslands in Utah, contrasting effects of invasion of cheatgrass (Bromus tectorum)
were observed for several components of a soil food web including bacteria-feeding nematodes, protozoa, and invertebrates (Belnap and Phillips 2001). Differences in the composition and function of preinvasion microbial communities, or variation in abiotic factors, may cause these dissimilar responses following invasion by a common exotic species. Understanding differential responses to invasion can provide important practical information about the impacts of exotic plant invasions as well as insight into the basic ecology of soil food webs and controls on soil diversity. Unfortunately, most studies have focused on only one or two taxonomic or functional groups, making it difficult to understand how entire dynamic soil communities respond to invasion.

One of the major methodological limitations of the current work in this area is that it does not attempt to link changes in the structure of belowground communities with changes in function. Although it is relatively easy to measure structure and function separately in both aboveground and belowground communities, it is difficult to understand and interpret the links between structure and function and to know what organisms are involved in specific processes. In one study that attempted to link structure and function, Peter Kourtev and colleagues (2002, 2003) documented the effects of two exotic understory species, Japanese barberry (Berberis thunbergii) and Japanese stilt grass (Microstegium vimineum), on soil biota in northeastern hardwood forests of North America. In the field, the composition of the microbial community, as determined by phospholipid fatty acid profiles (box 2), was different under these two invaders compared with the soil under native plant species. In barberry soils, there was an overall decrease in fungal abundance, indicating conversion to a community dominated by bacteria. In stilt grass soils, one of the most pronounced structural changes was an increase in the abundance of AMF. Using substrate-induced respiration and soil enzyme assays (box 2), functional differences that correlated with measures of soil community composition were noted between the soil communities associated with exotic and native plant species.

It is still unclear what temporal scale is most relevant when addressing the effects of exotic plants on soil communities. In the barberry and stilt grass system discussed above, plants were grown on previously uninvaded soils in the laboratory, and changes in soil community composition and function were detected within three months (Kourtev et al. 2003). Two years following the invasion of cheatgrass in an arid grassland in Utah (figure 4), significant changes in microbial community function occurred, as indicated by altered nitrogen cycling (Evans et al. 2001) and shifts in soil community composition (Belnap and Phillips 2001). Despite these rapid changes in structure and function, it is still unknown how long it takes for soil communities to recover.

Figure 3. Garlic mustard (Alliaria petiolata) and arbuscular mycorrhizal fungi (AMF). Garlic mustard, a European native, invades forests of North America, often decreasing the local plant diversity of these communities, and can also influence soil communities. The roots of this species (a) produce compounds (glucosinolates) that can decrease the abundance of propagules of AMF, such as spores (b), and internal root structures, such as vesicles (c), of native plant species. The crushed spore shown is approximately 150 micrometers (µm) in width, and the vesicles range from 20 to 50 µm in width. In a beech–hickory–maple forest in southern Ontario, sugar maple seedlings were not colonized by AMF in soil collected from areas dominated by garlic mustard, but were highly colonized by AMF in nearby uninvaded areas (data available from J. N. K.).
responses in the greenhouse and field, neither these studies nor other studies on exotic plants’ effects on soil communities have repeatedly sampled from communities over time after an invasion, a shortcoming that limits our understanding of the temporal dynamics of exotic effects on soil communities. Repeated sampling would indicate at what point there is detectable divergence in the composition and function of soil communities from those of native communities. Understanding these critical time points could assist in developing efficient management plans to minimize the effects of exotic plants on soil biota.

Other complexities limit researchers’ ability to predict the effects of exotic plant species invasions on soil microbial communities. Many plant communities are being invaded by multiple exotic species with different physiological traits or life histories (Kourtev et al. 2002). Interactive effects of multiple invaders may elicit different responses from soil communities from those predicted by studies focused on the effects of individual exotic plant species. Other global change phenomena, such as increases in atmospheric carbon dioxide concentrations and nutrient deposition, may interact with exotic plant species through their direct and indirect effects on the growth of invaders to mediate effects on soil biota. Future work addressing these effects will help to build a more complete, mechanistic understanding of exotic plant effects on soil communities.

Influence of soil organisms on exotic plant invasions

In discussing exotic plant invasions in the context of aboveground–belowground links, it is crucial to consider not only...
how exotic plants can affect soil organisms but, conversely, how the structure and function of soil communities may play a role in exotic plant invasions. Studies that have examined the role of soil organisms in exotic plant invasions have focused on how specific components of the soil community affect the plant invasion process or have considered how properties of whole soil communities may facilitate or inhibit the invasion of exotic plants.

Effects of specific components of the soil community on exotic plants. A main mechanism by which soil biota influence the invasion of plants into existing plant communities is through direct effects (either positive or negative) of specific soil organisms on plant growth. A dramatic example of how soil organisms can play a major role in the establishment and dominance of an invading plant is the facilitation of the invasion of pine (Pinus spp.) by ectomycorrhizal fungi in parts of the Southern Hemisphere. Most members of the genus Pinus grow symbiotically with ectomycorrhizal fungi, which can improve nutrient uptake and provide host plants with other benefits (Smith and Read 1997). There were no or few ectomycorrhizal fungal symbionts of pine native to many regions of the Southern Hemisphere, but with the introduction of suitable fungal symbionts with introduced trees, pines have been able to invade many plant communities in these regions (Richardson et al. 1994).

Although the role of soil biota in the invasion of Pinus was mainly elucidated through field observations as the invasion occurred, other work has experimentally examined how specific components of the soil community, such as mycorrhizal fungi or soil pathogens, can influence the growth and invasion dynamics of exotic species. At the level of individual plants, different soil community components have been shown to have varying effects on the growth, fecundity, and biotic interactions of exotic plant species (Marler et al. 1999, Callaway et al. 2001, Bray et al. 2003). For example, vegetative and reproductive traits of purple loosestrife (Lythrum salicaria), a major exotic plant species in wetlands throughout North America, are altered by the presence of AMF in the roots of these plants (Philip et al. 2001). At a community level, these symbiotic fungi have also been shown to affect the process of plant invasion. Invasion of hairy beggarticks (Bidens pilosa) into experimental plant communities in Hawaii (Stampe and Daehler 2003) was affected significantly by the species of fungi associated with the communities.

Feedbacks between exotic plants and soil biota. Although it is useful to understand the effects of specific soil biota to make predictions about the relative importance of different soil organisms in the invasion process, knowledge of the net effect of the soil community is more useful for understanding the role of the soil community in the invasion process in the
field. A second experimental approach to understanding the role of soil organisms in the invasion of exotic plants is through the soil feedback approach popularized by James Bever and colleagues (1997). As opposed to focusing on specific components within the soil community, plant–soil biota feedback studies use a whole-community approach to interactions between exotic plants and soil communities. As a plant grows in a local soil community, it can change the composition of the soil organisms within that community by altering abiotic or biotic components of the soil environment. These changes in the soil community can translate into changes in the effects of the soil community on plant growth (either positive, negative, or neutral), leading to feedbacks between plants and soil biota (Bever et al. 1997).

Within a plant community, the feedback between plants and the soil community can explain the relative abundance of plant species, with the most abundant species having positive or neutral feedbacks with the soil and the least abundant species having negative feedbacks (Klironomos 2002). When five of North America’s most notorious exotic invaders, including purple loosestrife, garlic mustard, and leafy spurge (Euphorbia esula), were grown in soil that had been cultured by each of the five species, a positive growth effect was observed compared with growth in soil that had been cultured by a different species. This suggested that changes in the soil community as a result of the presence of these plants would not result in negative growth effects on the same plant. When five rare native species were treated in the same way, a negative growth effect was observed when growing in their own soil compared with the growth of these plants in the soil of other species, suggesting that the plants accumulated pathogens in their local soil community. These preliminary studies suggest that exotic plants, and in some cases widespread native plants, can be abundant within native communities because they do not experience the same negative feedback with soil biota as do rare native species (figure 5; Klironomos 2002).

These initial feedback studies suggested that exotic plants may escape the negative effects of soil pathogens in their novel ranges, supporting the enemy-release hypothesis that has been demonstrated for some exotic plants with above-ground antagonists, such as herbivores (Maron and Vila 2001) and fungal and viral pathogens (Mitchell and Power 2003). Several recent studies have followed up this work by comparing the soil feedbacks of exotic plants in their native and exotic ranges. Spotted knapweed (Centaurea maculosa), a major exotic plant that dominates many grasslands of western North America, is native to Europe. In soils collected from several populations in its native range, spotted knapweed causes changes in the soil community that detrimentally affect its growth. When grown in soils in North America, this plant alters the soil community in a way that is beneficial to its own growth, possibly from the positive effects of mutualistic AMF (Callaway et al. 2004). Spotted knapweed can even exploit resources of neighboring plants via AMF hyphal connections between plants (figure 5; Marler et al. 1999). Similar work with black cherry (Prunus serotina) showed positive feedback responses to soil communities in its introduced range (Europe) and negative responses to soil communities in its home range (North America) (figure 6; Reinhardt et al. 2003).

Conflicting studies on the release of exotic plants from negative soil feedbacks in invasive ranges make it difficult to generalize how important this mechanism may be in explaining the success of invasive plants. For example, European beachgrass (Ammophila arenaria) was introduced into California in the 1800s and has had many negative effects on dune ecosystems of western North America. In its native range (Europe), this plant is an early-successional dune species that is replaced by other species as it accumulates soil organisms that negatively affect its growth (van der Putten et al. 1993). In California, the soil community was found to have similar negative effects of antagonistic soil organisms and may receive benefits from mutualistic soil organisms such as arbuscular mycorrhizal fungi, leading to positive feedbacks between exotic plant and soil biota. (3) Exotic plants may also exploit resources of neighboring plants via hyphal connections among plants. Soil organisms that are not directly associated with roots, such as those involved with detrital food webs, are not represented in this diagram because their role in observed plant feedbacks is currently unknown.

**Figure 5.** Conceptual diagram illustrating three potential pathways by which soil organisms can differentially affect native plants (on the left) and exotic plants (on the right). (1) Antagonistic soil organisms such as pathogenic fungi and root herbivores can accumulate in the rhizosphere of native plants, leading to negative feedbacks of these species with soil biota. (2) Some exotic plants appear to escape the negative effects of antagonistic soil organisms and may receive benefits from mutualistic soil organisms such as arbuscular mycorrhizal fungi, leading to positive feedbacks between exotic plant and soil biota. (3) Exotic plants may also exploit resources of neighboring plants via hyphal connections among plants. Soil organisms that are not directly associated with roots, such as those involved with detrital food webs, are not represented in this diagram because their role in observed plant feedbacks is currently unknown.

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effects on this species (Beckstead and Parker 2003), suggesting that European beachgrass does not escape the negative effects of soil biota in its invasive range. However, escape from the negative feedback from soil biota was observed in populations in South Africa, another region where European beachgrass has invaded plant communities (Knevel et al. 2004). Surprisingly, European beachgrass is considered more aggressive in California and other parts of North America, where there was very limited escape from the negative soil biota observed in its native soil. These discrepancies suggest that soil communities will not have the same magnitude or direction (positive versus negative) of effect on the invasion of all exotic species in all novel ranges, as is highlighted by a recent meta-analysis by Levine and colleagues (2004).

Current progress and future research needs. Taken collectively, this work suggests that soil organisms can influence the growth of exotic plant species, and that these effects might be different from those observed with native plant species. However, it is too early to know how the effect of soil biota compares with other factors that can influence the invasion process, such as dispersal, propagule production, competition with resident plant species, and interactions with other biota (Levine et al. 2004). It will be important for future experiments to test simultaneously the effect of soil biota and these other mechanisms on exotic plants.

It is also important to consider that the importance of soil biota in the invasion process may depend on the stage in the process at which it exerts its influence. Exotic plant invasion consists of the introduction of exotic plant propagules, the establishment of the exotic species, the spread of the species within a community, and the impacts of the invader once it has spread through native communities (Levine et al. 2004). It is not yet clear at which stage or stages in the invasion process soil communities are most important. Some work suggests that in the introduction stage, the effect of soil organisms such as pathogenic fungi on propagule survival does not differ between native and exotic plant species (Blaney and Kotanen 2001). This finding contrasts with the strong differences in the effects of soil communities between exotic and native plants observed at the establishment stage of invasion (Klironomos 2002). To date, a comprehensive test of the role of soil biota throughout all stages of the invasion process for one or more exotic plant species has yet to be conducted.

Only a few exotic plant species in one or two community types or geographic regions have been investigated so far. Therefore, a priority of future research should be to examine additional exotic plant species across different community or ecosystem types. Perhaps interactions with soil biota are important only for a small subset of exotic plant species or particular ecosystem types. If this is the case, it is essential to understand what traits of these plants or what characteristics of these ecosystems contribute to soil biota playing a role in the invasion process.

Although experimental tests of soil feedback have been a productive approach for understanding the role of soil biota in the invasion process, this approach can be improved to become more comprehensive and realistic. One major component lacking in most soil feedback studies is an understanding of the specific differences in soil communities between native and foreign ranges that may lead to the observed differences in feedback. Further exploration of the specific organisms or groups of organisms involved with these feedbacks using contemporary techniques (box 2) will help us better understand how soil communities may inhibit or facilitate plant invasion. Most feedback studies are also lacking rigorous field studies to demonstrate that observed feedbacks with short-term greenhouse experiments represent potential feedbacks.
in the field (but see Callaway et al. 2004). Finally, the current feedback approach only measures responses of plants to soil biota in terms of biomass. Although biomass may serve as an indicator of plant establishment within a community, it is not likely to be a good predictor of fitness effects on the plants, making it difficult to predict how plant feedbacks with soil biota can affect the long-term spread and persistence of exotic plant species within communities.

**Soil communities and restoration following invasion**

After an invasive species establishes and begins to dominate in an area, land managers often try to stop the spread of the invading plant, to remove plants that have established, and to restore attributes of the preinvasion community. Traditionally, these restoration approaches have been “aboveground-centric,” only considering the organisms in the community that can be easily seen and monitored over time as the restoration progresses. In some cases, the physical properties of the soils at a site being restored have been considered, but soil biota has generally been ignored.

One approach for incorporating soil biota in the restoration process could involve monitoring the structure and function of the soil community in relation to a benchmark community, such as the community that existed before exotic plant invasion or nearby communities where invasion has not occurred (Smith et al. 2003). Specific management regimes could be used to favor the development of target soil communities that are also compatible with the development of desired aboveground communities. This approach will probably not become practical until the technical challenges and costs of current soil microbial community analyses are reduced and until we obtain a better understanding of what measures of microbial community structure and function can serve as reliable and meaningful indicators (Harris 2003).

In addition to monitoring soil organisms during the restoration process to detect progress toward the target community, managers may need to reestablish the belowground community at a site by reintroducing certain soil organisms. This will only be necessary if important soil organisms have been eliminated from much of the site during the restoration process or if the existing soil communities are functionally dissimilar from the target native communities. In the garlic mustard example above, it might be necessary to introduce propagules of AMF back into a site that was heavily invaded by garlic mustard, because the fungi might be eliminated from the soil.

With our current understanding of the role of soil biota in exotic plant invasions, we suggest the following questions be considered in the restoration and management of invaded natural areas:

- Do invasive exotic plants at the restoration site have any particular traits, such as those outlined above, that differ from those of the native plant species in the community and may lead to functionally significant changes in the soil community?
- Are there any unique attributes of the soil community, such as high abundance of key functional groups, that could be altered during the invasion process?
- Are any of the plants within the target community somewhat or completely dependent on soil biota? For example, some orchids are dependent on soil fungi for establishment and growth (Smith and Read 1997). If dominance by a nonhost exotic plant species has eliminated these fungi from a site, it may be necessary to introduce propagules of the fungus as well as the orchid.

As soil ecologists, plant ecologists, and specialists in the field of ecological restoration collaborate to obtain answers to these and similar questions in different restoration settings, the importance of soil biota in restoration of invaded habitats will become more apparent.

**Conclusions**

As a result of human activity, plant species continue to be introduced into new ranges, where they often flourish and significantly change the properties of native ecosystems. Recent studies have demonstrated that soil organisms play an important role in the invasion of exotic plant species. Soil communities differentially respond to the presence of exotic plant species and can have strong effects on the process of plant invasion. Our ability to generalize about interactions between soil biota and exotic plants is currently weak, as a result of the limited amount of work in this area and the variability in the outcomes of these interactions across exotic plant species and invaded communities. However, as exotic plant invasions continue, an integrated aboveground–belowground understanding of ecosystems is necessary for elucidating basic principles of community ecology and for the successful management and restoration of invaded communities.

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**References cited**


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