

***Interactions between invasive
plants and soil ecosystems:
positive feedbacks and their
potential to persist***

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INTRODUCTION

Plants indirectly affect their neighbors in many ways, but one of the most important is by altering the biotic, physical, and chemical characteristics of soils (Hobbie 1992; Angers and Caron 1998; Berendse 1998; Binkley and Giardina 1998; Northrup *et al.* 1998; Schlesinger and Pilmanis 1998; Van Breemen 1993; Wardle *et al.* 1998; Chen and Stark 2000; Eaton and Farrell 2004). These general effects have been understood for decades, but only recently have experiments demonstrated that complex interactions between plants and soil microbial communities can have strong effects on plant populations (Bever *et al.* 1997; Clay and Van der Putten 1999; Packer and Clay 2000), interactions among plant species (West 1996), and the organization of plant communities (Grime *et al.* 1987; Van der Putten *et al.* 1993; Bever 1994; Van der Putten 1997; van der Heijden *et al.* 1998; Hooper *et al.* 2000; Klironomos 2002). Soil communities alter competitive outcomes among plants through their pathogenic effects (Van der Putten and

Peters 1997), by favoring obligate mycorrhizal species over non-mycorrhizal or facultative mycorrhizal species (Hetrick *et al.* 1989; Hartnett *et al.* 1993), and by transferring resources and fixed carbon between species (Chiarello *et al.* 1982; Francis and Read 1984; Grime *et al.* 1987; Moora and Zobel 1996; Watkins *et al.* 1996; Simard *et al.* 1997; Marler *et al.* 1999; but see Robinson and Fitter 1999). By altering the biotic and abiotic characteristics of soils, plants can drive positive or negative feedbacks (Box 1), and these feedbacks can profoundly affect plant populations and communities.

Box 1

Positive feedbacks occur when plant species accumulate microbes that have beneficial effects on the plants that cultivate them, such as mycorrhizal fungi and nitrogen fixers. Positive feedbacks promote species dominance and are thought to lead to a loss of local community diversity (Bever *et al.* 1997, Bever 2002). Negative feedbacks occur when plant species accumulate pathogenic microbes in their rhizospheres and these interactions outweigh the benefits received from mutualistic interactions. Negative feedbacks create conditions that are increasingly hostile to the plants that cultivate the pathogens and are thought to promote community diversity (Van der Putten *et al.* 1993, Bever 1994, Klironomos 2002).

Jim Bever (1994; Bever *et al.* 1997) proposed the feedback model, in which a plant or population of plants alters the composition of the soil community. This change then feeds back to affect the growth and survival of the plant individual or population. This model describes how two different types of feedback could be established; positive feedback, which should occur when the negative effects of soil pathogens are outweighed by the beneficial effects of mutualistic mycorrhizae, and negative feedback, which is expected to occur either when the effects of pathogens outweigh the effects of mycorrhizae or when the soil community enhances the growth of competing plants more than that of the associated plant (Bever 1994; Bever *et al.* 1997). By favoring the local replacement of species, negative feedback is expected to maintain species diversity, whereas positive feedback is expected to lead to species dominance and a decrease in local species diversity (Bever 1994; Bever *et al.* 1997; Watkinson 1998). A growing body of research has demonstrated that plant-soil feedbacks can have important ecological consequences (Bever *et al.* 1996; Wardle and Nicholson 1996; Westover *et al.* 1997; Klironomos 2002). For example, in a study comparing feedback and relative abundance of 61 co-existing old field species from southern Ontario, Canada, Klironomos (2002) found a strong positive relationship between a plant's feedback with the soil community and its relative abundance (Fig. 1).

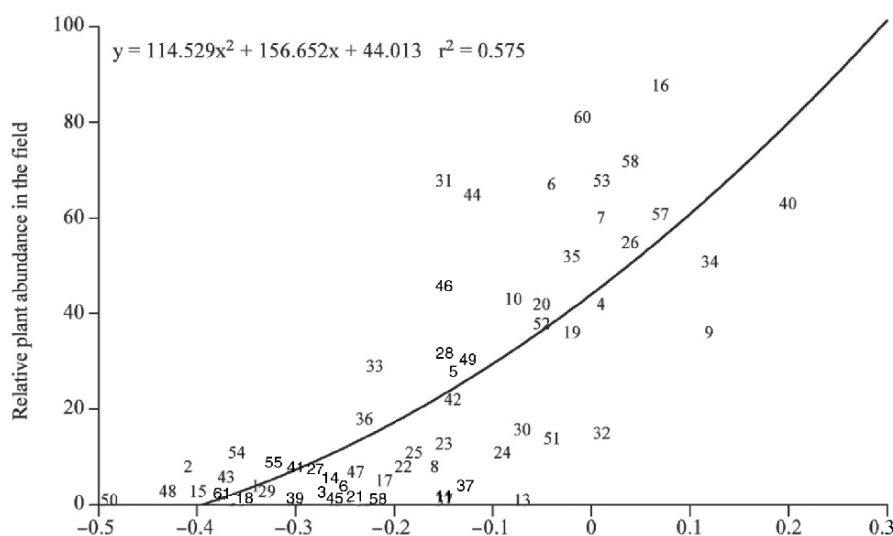


Fig. 1 The relationship between relative plant abundance in an old-field site and soil feedback response. Squares represent means. $y = 114.529x^2 + 156.652x + 44.013$, $r^2 = 0.575$, $P = 0.0001$. Numbers represent different plant species. 1, *Carex garberi*; 2, *Carex aurea*; 3, *Carex granularis*; 4, *Daucus carota*; 5, *Agrostis gigantea*; 6, *Solidago graminifolia*; 7, *Solidago nemoralis*; 8, *Aster simplex*; 9, *Aster vimineus*; 10, *Aster novaeangliae*; 11, *Cirsium vulgare*; 12, *Chenopodium ambrosioides*; 13, *Oenothera biennis*; 14, *Carex flava*; 15, *Juncus dudleyi*; 16, *Solidago canadensis*; 17, *Linaria vulgaris*; 18, *Cichorium intybus*; 19, *Cirsium arvense*; 20, *Solidago rugosa*; 21, *Geum aleppicum*; 22, *Satureja vulgaris*; 23, *Potentilla recta*; 24, *Coronilla varia*; 25, *Asclepias syriaca*; 26, *Achillea millefolium*; 27, *Apocynum cannabinum*; 28, *Hypericum perforatum*; 29, *Agrostis scabra*; 30, *Phleum pratense*; 31, *Poa compressa*; 32, *Echium vulgare*; 33, *Centaurea jacea*; 34, *Rudbeckia serotina*; 35, *Poa pratensis*; 36, *Dactylis glomerata*; 37, *Cerastium vulgatum*; 38, *Galium palustre*; 39, *Oenothera perennis*; 40, *Prunella vulgaris*; 41, *Trifolium pratense*; 42, *Convolvulus arvensis*; 43, *Silene cucubalus*; 44, *Erigeron strigosus*; 45, *Asparagus officinalis*; 46, *Hieracium auranticum*; 47, *Erigeron philadelphicus*; 48, *Veronica officinalis*; 49, *Plantagolanceolata*; 50, *Galium mollugo*; 51, *Hieracium pilosella*; 52, *Vicia cracca*; 53, *Hieracium pratense*; 54, *Medicago lupulina*; 55, *Ranunculus acris*; 56, *Taraxacum officinale*; 57, *Fragaria virginiana*; 58, *Chrysanthemum leucanthemum*; 59, *Tragopogon pratensis*; 60, *Bromus inermis*; 61, *Panicum lanuginosum*. Reprinted from Klironomos 2002.

Plant species that were found in low abundance in the field consistently displayed negative feedback interactions, whereas plants with high abundance either had low negative or positive feedback interactions (Klironomos 2002).

Plant invasions provide an exceptional opportunity for understanding how plants affect soils and drive feedback processes. Numerous studies have documented the effects of invasive species on the composition of soil biota (Belnap and Phillips 2001; Kourtev *et al.* 2002) and soil microbial function (Kourtev *et al.* 2002; Ehrenfeld 2003). However, much less is known about the role of feedbacks in the success of exotic plants. Feedbacks may also affect evolution — potentially most apparent in the rapid evolutionary changes that can accompany exotic invasion (Rice and Emory 2003).

If plant-soil feedbacks drive variation in fitness differences among individuals, then ultimately feedback interactions may be under selective pressure (Van der Putten 1997; Van Breeman and Finzi 1998). Based on theory developed by Bever *et al.* (1997) and Klironomos (2002), we hypothesize that positive feedbacks in general are likely to lead the plant community to shift towards a monoculture of the invasive species. However, we propose that the longevity of positive feedback interactions in evolutionary time may depend on whether the invasive plant is having its strongest effects on the pathogenic or the nutrient-cycling components of the soil ecosystem (Fig. 2). Microbes have a short generation time and thus can respond to evolutionary pressures quickly. Therefore pathogens may respond relatively rapidly to the invasion of non-native plants. This may ultimately lead to greater coexistence among species, where, although the invasive may still be present, it will not be the over-whelming community dominant. In contrast, feedbacks between invasive plants and nutrient cycles may be much more likely to persist. When the biotic component of the soil nutrient cycles is involved, it is expected that there would be a shift in the microbial community to populations that are better adapted to the new nutrient status of the ecosystem (Fig. 2; Atlas and Bartha 1998; Schimel and Bennett, 2004). In the case of alterations to abiotic components of the soil ecosystem, there is no direct selective pressure to stimulate adaptation (Fig. 2).

Here we discuss interactions between invasive species and the soil ecosystem (pathogenic and nutrient-cycling components), the mechanisms for these interactions, and evidence that these interactions have very different effects on the survival of invasive versus native species.

INVASIVE PLANTS AND SOIL PATHOGENS

One of the leading hypotheses for the remarkable success of some exotic species is that they have escaped the specialist enemies that control them in their native ranges (Keane and Crawley 2002). Embedded within this hypothesis is the idea that if microbial pathogens limit the growth of invasive plants in their native range, there will be negative feedbacks between the soil microbial community and the plant in the native range due to the accumulation of species-specific soil pathogens (Klironomos 2002; Mitchell and Power 2003; Callaway *et al.* 2004). In contrast, positive feedbacks may occur in the invaded range where exotic

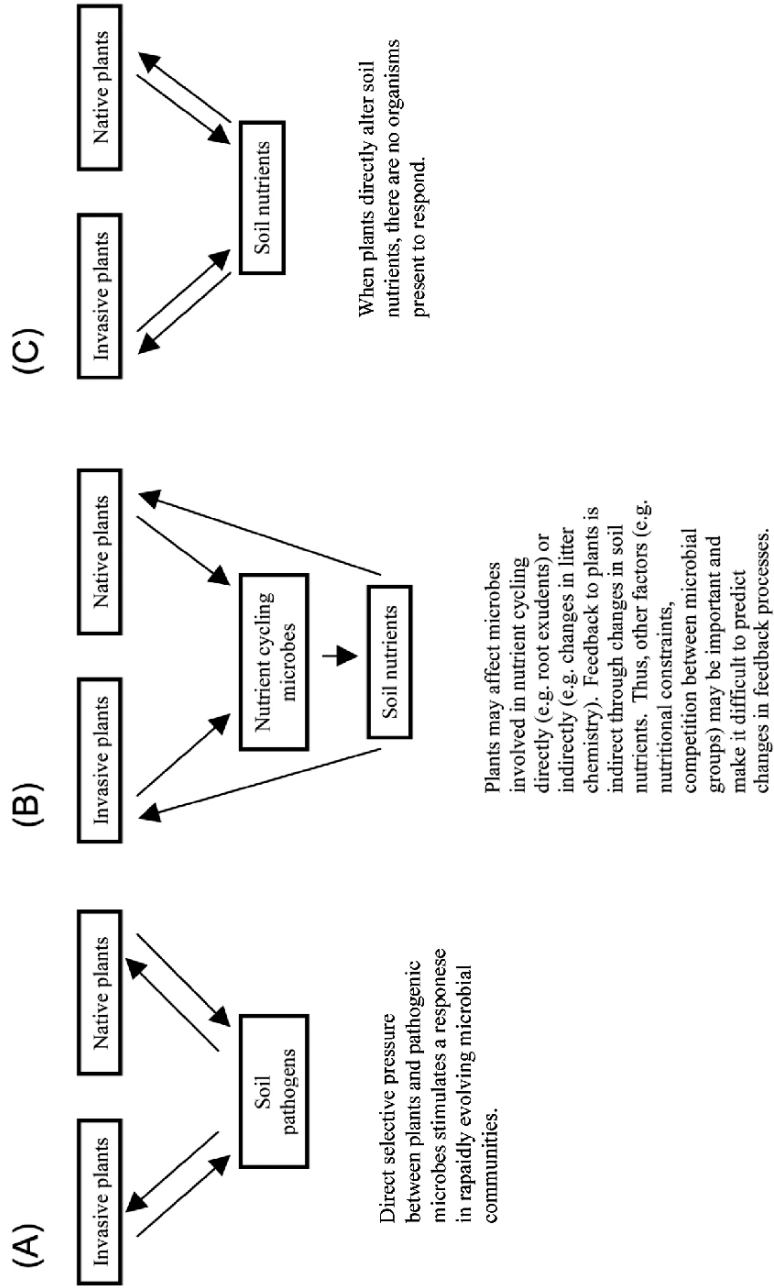


Fig. 2

species are largely free from species-specific soil pathogens but can still interact with less host-specific mutualists such as mycorrhizal fungi and bacteria that drive nutrient cycles.

In this section, first we will describe the evidence that invasive species have escaped pressure from soil pathogens and the potential feedback effects on the fitness of invasive species. Second, we will discuss the implications of this type of feedback for ecosystem stability.

Do invasive species benefit from escaping soil pathogens?

In a review of 473 species that were naturalized in the United States, Mitchell and Power (2003) found that 84% fewer fungi and 24% fewer virus species infected the plant species in their invaded ranges compared to their native ranges. Furthermore, they reported that species that experienced greater release from microbial pathogens were more invasive (Mitchell and Power 2003). However, the relationships were relatively weak, particularly for invaders of natural areas, soil pathogens were not distinguished from other pathogens, and the presence or abundance of pathogens does not necessarily correlate with the strength of their effects.

More recently, experiments using soils from native and invaded ranges have suggested that some invasive species have escaped from soil pathogens. If invasive species suffer from the effects of soil pathogens in their native soils, then sterilization of native soils should result in an increase in the growth of the invasive. In contrast, in invaded soils, the invasive should be relatively free from pathogens but may benefit from less host-specific mutualistic microbes. If so, sterilization of invaded soils should result in a neutral to negative effect on the invasive species. These interactions have been explored for *Prunus serotina* (black cherry), *Centaurea maculosa* (spotted knapweed) and two *Acer* (maple) species.

Reinhart *et al.* (2003) compared the effects of soil microbes on the growth of *Prunus serotina* in both its native and invaded ranges. In its native, North American range, the soil microbial community occurring near *P. serotina* strongly inhibited the establishment of neighboring conspecifics and reduced seedling performance in the greenhouse. In contrast, in its non-native European range, *P. serotina* readily establishes in close proximity to conspecifics, and soil microbial communities enhance the growth of seedlings. Previous research in the native range of *P. serotina* demonstrated that soil-borne *Pythium* species (Oomycota) inhibit the survival, growth, and abundance of *P. serotina* (Packer and Clay 2000, 2002). Although the genus *Pythium* is found around the world, genotypes are often host-specific (Deacon and Donaldson 1993; Mills and Bever 1998). Thus, in the native range, *P. serotina* experiences negative plant-soil feedback interactions, likely due to the negative effects of *Pythium*. In contrast, in the invaded region, *P. serotina* experiences positive feedbacks due to escape from its main natural enemy (Reinhart *et al.* 2003).

Centaurea maculosa is one of western North America's worst invasive weeds. In several experiments, Callaway *et al.* (2004) have compared the effects of soil microbes from the native range in Europe to the effects of soil microbes collected from invasive populations in the northwestern United States. European soil biota had much stronger inhibitory effects on *C. maculosa* than North American soil biota. Sterilization of European soils caused, on average, a 166% increase in the total biomass of *C. maculosa*, suggesting a release from pathogenic microbes. In contrast, sterilizing invaded North American soils led at most to a slight increase in total biomass of 24%. For most North American soils, sterilization led to a decrease in growth of 20-30%, suggesting that *C. maculosa* had benefited from mutualistic soil microbes. These results support Mitchell and Power's (2003) conclusion that invasive species should suffer much higher fungal and viral infection in their home ranges compared to invaded ranges. They also suggest that in some cases, mutualisms may be more beneficial in non-native ranges because the negative effect of natural enemies do not attenuate the positive effect of mutualists.

Mutualists have also been found to play an important role in the plant-soil feedback interactions of two *Acer* species (Reinhart and Callaway, 2004). In the field, distances between *Acer* conspecifics were 56-77% less in their invaded ranges than in their native ranges. In a greenhouse experiment, the effect of soil microbial communities also differed between native and invaded ranges. Relative to sterilized controls, soil associated with both conspecifics and heterospecifics from the native range decreased the total biomass of *Acer* seedlings by 35% suggesting inhibition by pathogenic microbes. In the invaded range, soil associated with conspecifics decreased the biomass of *Acer* seedlings by an even greater magnitude, 112%. However, soil associated with heterospecifics in the non-native ranges increased biomass of *Acer* seedlings by 13%. Thus, while *Acers* accumulate pathogens in their invaded range, the surrounding soil is relatively free from inhibitory microbes, potentially enhancing invasion by these trees.

Thus, there is evidence that, not only do invasive species escape the negative effects of soil pathogens in their invaded ranges, but that potentially due to the effects of mutualists, feedback effects in invaded ranges are often positive. Next, we will explore the potential for these feedback effects to affect community stability.

Will escape from negative feedbacks from soil pathogens persist?

The experiments described above indicate that invasive species are likely to experience positive feedback in their invaded habitat because they escape specialist soil pathogens at home but can utilize generalist mutualists where they invade. What remains to be determined is how this feedback affects community dynamics. Plants participating in strong positive feedbacks with soil biota are more likely to become community dominants than those that do not. The most complete study of these interactions was done by Klironomos (2002), who explored feedback

interactions among plant species and soil microbial communities in grasslands in eastern North America. In experiments using only the mycorrhizal fraction of the microbial community, he found that the origin of the filtrate (from soils in which the same species or a different species had previously been grown) did not alter the response (either positive or neutral) to mycorrhizal fungi. In contrast, in experiments using only the pathogenic/saprobic fractions, the rare native species experienced negative feedbacks when the fractions were from soils that had previously grown the same species. However, the origin of the pathogenic/saprobic fraction had no effect on the growth of invasive species. Overall, relatively rare native species consistently exhibited negative feedback interactions with the soil microbial community (a relative decrease in growth on 'home' soil in which conspecifics had previously been grown), whereas invasive species consistently exhibited positive feedback interactions with the soil community. Similarly Agrawal *et al.* (2005) found that introduced plants were subject to half the negative soil feedback as congeneric species. How long, in terms of evolutionary time scales, such positive interactions will be maintained remains an unknown.

The basic nature of microbes suggests that they will be able to respond relatively quickly to pressures exerted by invasion by exotic plants. As discussed above, soil-borne pathogens can be relatively host specific (Neergaard 1977; Kirkpatrick and Bazzaz 1979; Agarwal and Sinclair 1997; Mills and Bever 1998). However, many soil-borne pathogens are generalists (Dix and Webster 1995). For example, Blaney and Kotanen (2001) found that seed germination of 15 congeneric pairs of invasive and native plant species from western Ontario displayed a similar positive response to the application of fungicide, suggesting non-species specificity of fungal seed pathogens in their system. Furthermore, microbes have a short generation time and thus can respond to evolutionary pressures within a short timeframe. Thus, pathogenic microbes may be able to rapidly switch to a new invasive host. *Sclerotinia sclerotiorum*, a fungus native to intermountain prairies invaded by *C. maculosa*, has been found to damage *C. maculosa* when applied to the rhizospheres at high concentrations (Jacobs *et al.* 1996, Ridenour and Callaway 2003). As described above, Reinhart and Callaway (2004) found that while the soil community associated with other tree species had a positive effect on the growth of invasive *Acers*, soils associated with conspecifics had a negative effect. This suggests that the pathogenic soil microbial community may have been able to adapt to this new host, and accumulation of soil pathogens eventually suppresses the offspring of *Acer* recruits.

In summary, some invasive species appear to have escaped pressure from soil pathogens and thus benefit from positive feedback interactions with the soil biota where they invade. Although not yet explicitly addressed in the literature, microbial communities may change over time and thus break down positive plant-soil microbial feedbacks. If this occurs, the abundance of the invasive species should decrease, and the community should move to a point where negative feedback interactions restrict the invasive's dominance. This was originally suggested by

Klironomos (2002) who observed that plant-specific pathogen loads are maximized under high population densities, particularly monocultures such as those created by some invasive species, and will eventually result in negative feedback on abundant plants. Next we consider how feedbacks driven by microbes in nutrient cycles might respond differently over evolutionary time than feedbacks driven by soil pathogens.

INVASIVE PLANTS AND SOIL NUTRIENT CYCLING

In general, plant-soil feedbacks are thought to be determined by the direct effects of pathogens and mutualists (Bever 1994; Mills and Bever 1998; Packer and Clay 2000; Bever 2002; Klironomos 2002), but other components of the soil ecosystem may participate in feedbacks. In particular, individual plant characteristics, such as phenology, nutrient uptake, litter-fall, tissue chemical composition, and association with symbiotic microbes, can have significant effects on soil nutrient cycles (Hobbie 1992; Angers and Caron 1998; Berendse 1998; Binkley and Giardina 1998; Northrup *et al.* 1998; Schlesinger and Pilmanis 1998; Van Breemen 1993; Wardle *et al.* 1998; Chen and Stark 2000; Eaton and Farrell 2004) which may, in turn, alter the growth and survival of the species that drive these effects. Because they are novel, may have different biochemical constituents (Bais *et al.* 2003, Vivanco *et al.* 2004), and are often dominant components of plant communities, invasive plants can have unusually strong effects on soil nutrient cycles (Vitousek 1986; Vitousek *et al.* 1987; Vitousek 1990; D'Antonio and Vitousek 1992; Ehrenfeld *et al.* 2001; Ehrenfeld and Scott 2001; Ehrenfeld 2003).

In the previous section we showed that many invasive species exhibit positive feedbacks after escaping soil pathogens, and then speculated that these feedbacks may eventually become neutral or negative as generalist pathogens switch to the host or specialists adapt. In contrast to this scenario in which invasive dominance may fade, positive feedbacks between invasive plants and soil nutrient cycles may lead to much longer time periods of invasive dominance. Nutritional constraints may lead to significant shifts in microbial communities, resulting in long-term changes in nutrient pools and cycling rates. These changes may also occur due to the introduction of novel plant-microbe interactions, such as symbiotic nitrogen-fixation. Similarly, the direct effects of invasive plants on soil nutrients may be particularly long-lived because there is no mediation by another organism with the potential to evolve.

In this section, we briefly review the mechanisms by which invasive species may alter soil nutrient cycles and illustrate the potential for long-lived positive feedback interactions by describing the interactions of *Bromus tectorum* (cheatgrass, downy brome) and *Myrica faya* (fire tree) with soil nutrient cycles in invaded communities in the western United States and Hawaii.

The effects of invasive species on nutrient cycles

There are many mechanisms by which invasive species may alter soil nutrient cycles (see review by Ehrenfeld 2003). Through changes in litter production and quality, invasive plants may increase (Ehrenfeld *et al.* 2001; Mack *et al.* 2001) or decrease (Saggar *et al.* 1999; Ehrenfeld *et al.* 2001; Evans *et al.* 2001) microbially-mediated decomposition and/or mineralization rates. For example, litter of *Microstegium vimineum*, an exotic C4 grass that has invaded Eastern deciduous forests, has a higher C:N ratio, decomposes slower, and immobilizes more N than litter from uninvaded forests (Ehrenfeld *et al.* 2001).

Invasive species may also alter the input of nitrogen by nitrogen-fixing bacteria. Nearly 10% of the invasive species listed by the U.S. Department of Agriculture are in the Fabaceae family (Ehrenfeld 2003), and changes in ecosystem nitrogen availability due to association of invasive plants with symbiotic nitrogen-fixing bacteria have been documented in several ecosystems (Versfeld and van Wilgren 1986; Vitousek *et al.* 1987; Stock *et al.* 1995; Yelenik *et al.* 2004). Furthermore, changes in litter quality from non-nitrogen fixing invaders may alter the abundance and activity of non-symbiotic nitrogen-fixing bacteria, as found in Hawaiian forests invaded by African grasses (Ley and D'Antonio 1998).

Invasive species may affect soil nutrient cycles through the production of secondary chemicals. Roots of *Centaurea maculosa* exude the polyphenol, (\pm)-catechin. (+)-Catechin displays strong antimicrobial properties for at least some groups of bacteria (Bais *et al.* 2002, 2003) and appears to affect at least some aspects of the soil nitrogen cycle (A. Thorpe, unpublished data). Furthermore, by chelating metal-phosphorus complexes, catechin may increase phosphorus availability in phosphorus-limited soils (Thorpe *et al.* in press; Stevenson and Cole 1999). An allelochemical produced by *Centaurea diffusa*, 8-hydroxyquinoline, may also alter nutrient cycling through antimicrobial (Vivanco *et al.* 2004) and chelation (The Merck Index 1996) properties. The dry mass of leaves of *Melaleuca* spp. (paperbark), which has invaded large areas of the coastal southeast United States, particularly the Everglades, is up to 7% monoterpenes (Boon and Johnstone 1997). These compounds inhibit microbial colonization and decomposition of leaf litter in both the native and invaded ranges of *Melaleuca* spp. (Boone and Johnstone 1997). It has also been suggested that allelopathic chemicals released by some invasive species may alter nitrogen-fixation in neighboring plants (Wardle *et al.* 1994, 1995). Many other invasive species produce chemicals with antimicrobial activity (Rice 1964; Ehrenfeld 2003), however, the role of these chemicals in the plants' invasive success is generally unknown.

In sum, there is good evidence that by introducing a novel characteristic (e.g. a higher C:N ratio, association with nitrogen-fixing bacteria, or exudation of an anti-microbial chemical), invasive species can alter soil nutrient cycles in invaded communities. Although explicit studies of the ramifications of such alteration of nutrient cycles are rare, these effects may ultimately feedback to

the plants that cause them and affect the organization of plant communities. Two different species, *Bromus tectorum* and *Myrica faya* provide excellent examples of (1) how invasive plants may affect the soil, and (2) how soil changes affect the survival of invasive and native species. These studies also illustrate how positive feedbacks between invasive plants and soil nutrient cycles may persist in an ecosystem.

The effects of *Bromus tectorum* on soil nutrient cycles

Bromus tectorum is an annual (occasionally biennial) Eurasian grass that has invaded over 40.5 million ha in the Intermountain West of North America (Ypsilantis 2003). The effects of *B. tectorum* on nutrient cycles differ in fire-prone and non-fire-prone systems.

Bromus tectorum tends to germinate and complete its life cycle earlier than most native species in the systems it invades, and its dead, dry stems create an unusually large fuel load in the summer (Harris 1967; Mack 1981; Upadhyaya *et al.* 1986; Ypsilantis 2003). In fire-prone sagebrush-grassland ecosystems, fire recurrence intervals decrease from 20-100 years to 3-5 years (Mack 1981; Upadhyaya *et al.* 1986; Ypsilantis 2003). Since *B. tectorum* germinates earlier and grows faster than most native species (Harris 1967; Mack 1981; Upadhyaya *et al.* 1986; Ypsilantis 2003), this invader appears to take better advantage of the post-fire flush of nitrogen than native species (Lowe *et al.* 2003). Early nitrogen uptake by *B. tectorum* reduces total soil nitrogen and creates higher soil carbon to nitrogen ratios than native vegetation (Blank *et al.* 1994; Halvorson *et al.* 1997). *Bromus tectorum* may also limit nitrogen availability by shading biological soil crusts that fix nitrogen (Ypsilantis 2003).

In ecosystems that lack fire, there are very different interactions between *B. tectorum* and the soil ecosystem. Grassland communities in Utah invaded by *B. tectorum* have higher levels of exchangeable potassium and ratios of potassium or phosphorus to calcium carbonate and magnesium or iron oxides than uninvaded soils (Belnap and Phillips 2001; Belnap *et al.* 2003). It is unknown whether these nutrient differences are due to *B. tectorum* invasion or if *B. tectorum* preferentially invades sites with these characteristics, however it is clear that *B. tectorum* can dramatically alter phosphorus cycling in invaded soils. Although there is no net change in total soil phosphorus pools, *B. tectorum* appears to access forms of P that are recalcitrant and unavailable to natives, which increases levels of labile phosphorus (R.L. Sanford, *personal communication*).

By altering the biotic and abiotic components of nutrient cycles, *B. tectorum* alters nutrient availability in ways that ultimately feedback to increase its own survival relative to native species (Belnap and Phillips 2001; Evans *et al.* 2001). By altering fundamental ecosystem characteristics, these effects may significantly alter plant community structure and dynamics.

The effects of *Myrica faya* on soil nutrient cycles

Invasion of Hawaiian ecosystems by the nitrogen fixing tree *Myrica faya* (Gerrish and Mueller-Dombois 1980; Vitousek 1986; Vitousek and Walker 1989; Aplet 1990; Hughes *et al.* 1991) provides an example of how ecosystem scale changes may result in “invasional meltdown” (Box 2; Simberloff and van Holle 1999). The volcanic soils of Hawaii are usually nitrogen-limited (Vitousek 1986; Vitousek and Walker 1989). There are no native nitrogen-fixing plants that colonize early successional habitats in these systems (Vitousek 1986; Vitousek and Walker 1989), and invasion by *M. faya* introduces a novel ecosystem process that results in substantial increases in soil nitrogen (Vitousek 1986; Vitousek and Walker 1989). Most successful invasions in Hawaii have occurred on soils that are relatively fertile (Gerrish and Mueller-Dombois 1980) and the nitrogen fertilization that results from invasion by *M. faya* may facilitate invasion by other species with higher nitrogen requirements. For example, another invasive tree, *Psidium cattleianum* (strawberry guava) grew much larger when grown in soil from under *M. faya* than from soil collected under the native *Metrosideros polymorpha* (‘Ohi‘a lehua; Hughes *et al.* 1991). *Myrica faya* also enhances populations of exotic earthworms, which increase nitrogen burial and further alter nutrient cycling (Aplet 1990). Thus, invasion by *M. faya* results in positive feedbacks that not only enhance the invasion of this species, but promote invasion by other invasive species and lead to fundamental ecosystem changes.

Box 2

In 1999, Simberloff and van Holle introduced the concept of “invasional meltdown”. During this process, invasion by one exotic species promotes invasion by other exotic species. These species interact synergistically, causing ecosystem scale changes (such as more frequent fire cycles or more rapid nitrogen cycling through increased nitrogen fixation) that ultimately result in the collapse of native ecosystems.

Will positive feedbacks between invasive plants and soil nutrient cycles persist?

As described above, since invasive plants often differ from native species in characteristics such as phenology, nutrient uptake, litter-fall, tissue chemical composition, and association with symbiotic microbes, they can have significant effects on soil nutrient cycles. Similar effects are often seen during succession (Berendse 1998; Schimel and Bennett 2004). We speculate that, in contrast to our predictions for evolutionary change for interactions between invasive plants

and soil pathogens, positive feedbacks between invasive plants and soil nutrient cycles are more likely to result in long term shifts in community composition that resemble succession. These changes may provide examples of invasional melt-down (Simberloff and Von Holle 1999).

We know of no examples where, during succession, characteristics of the soil ecosystem revert back to those resembling the initial characteristics after disturbance. What little is known about the biotic components of the soil ecosystem during succession indicates that change in the microbial community is towards populations that are better adapted to the new nutrient conditions of the later successional stages (Schimel *et al.* 1998; Schimel and Bennett 2004). These successional shifts appear to be ecological in nature, not evolutionary, and driven by shifts in the species composition of communities over time. In contrast, in the case of alterations to abiotic components of the soil ecosystem, there is no direct selective pressure to stimulate adaptation. Ultimately, these types of changes require that the soil and plant communities may have to respond adaptively to new nutrient conditions.

When invader-soil ecosystem feedbacks occur through effects on nutrient cycles, we suggest that long term effects will be similar to those that occur during succession, the development of a new community composed of species that are better adapted to the specific nutrient conditions of the soil (e.g. Berendse 1998). This has been observed in systems invaded by both native (Maron and Jefferies 1999) and invasive (Hughes *et al.* 1991) nitrogen-fixing species. In California, Maron and Connors (1996) found that nitrogen-rich patches that were left by death of *Lupinus arboreus* (bush lupine) were invaded by exotic annual grasses. Similarly, as described in the preceding section, soils that have been enriched by the exotic nitrogen-fixer *M. faya* are more prone to invasion by other exotic plants, including *Psidium cattleianum* (strawberry guava; Hughes *et al.* 1991). In addition, although only a few native species have been found to “monopolize” sites by creating positive feedbacks (van der Putten 1997), invasive species may be particularly capable of this, especially if they introduce a novel ecosystem process to which native species are not adapted. For example, although *B. tectorum* first became established in fire-prone communities in the Great Basin over 100 years ago (Mack 1981), no other species, either native or invasive, have since been able to establish in substantial numbers. These examples show how ecosystem changes involving exotic species can result in unpredictable successional trajectories.

CONCLUSION

Exotic plant invasions can often involve positive feedbacks between the invader and the native soil community. Positive feedbacks have the potential to lead to long-lasting dominance in communities. However, these feedbacks can be caused by a number of different reasons, and different drivers of positive feedbacks may result in different predictions of how long invaders may dominate a community.

Typically, positive feedbacks are thought to be caused by the absence of soil pathogens but the presence of soil mutualists in invaded soils. Such pathogen-driven positive feedbacks may result in long term invasive dominance, but evolutionary changes in native pathogens might ultimately lead to suppression of the invader and a return to native coexistence. Positive feedbacks can also be caused by the effects of invasive plants on the soil biota that drive nutrient cycles or on the abiotic components of the nutrient cycles themselves. We hypothesize that positive feedbacks caused by the effects of the invader on the soil biota involved in nutrient cycles are likely to lead to community shifts resembling succession and perhaps invasional meltdown. Dominance by invaders that drive positive feedbacks through abiotic components of nutrient cycles may persist for much longer than dominance occurring through positive feedbacks involving the microbial community due to the lack of mediation by an organism with the potential to adapt. However, understanding potential evolutionary changes among invaders and soil ecosystems will help us to accurately predict the long-term effects of biological invasions.

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