

Biological invasions: Linking the aboveground and belowground consequences

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Abstract

The 9th biennial meeting of the Soil Ecology Society held in Palm Springs, CA in May 2003, addressed the theme of “Invasive species and soil ecology”. This meeting prompted interest in pursuing this special issue of Applied Soil Ecology, which includes papers presented at the meeting and other papers contributed after the meeting. This paper highlights some of the major issues addressed at the meeting and in the subsequent papers published in this special issue, and also provides a conceptual framework for examining interactions between aboveground and belowground invasions.

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1. Introduction

Biological invasions have emerged as a major topic in ecology over the past couple of decades, and have even prompted the journal specifically devoted to this topic (Carlton, 1999; Drake and Mooney, 1989; Mack et al., 2000). Most invasion studies have focused on changes in aboveground plant and animal communities, with a focus on losses in biodiversity (Brussaard et al., 1997). However, belowground invasions may be equally widespread. Exploring links between above and belowground communities illuminates the broader ecological implications of species invasions (Wardle, 2002). In the past few years there has been an increased emphasis on the ecosystem consequences of invasion, including the effects of invasion on nutrient cycling processes and nutrient loss (Ehrenfeld et al., 2001; Hooper et al., 2000). These ecosystem consequences obviously

cannot be examined without considering both the aboveground producer community and belowground decomposer community. In this paper I provide a conceptual framework for describing how biological invasions affect ecological systems, considering both the aboveground and belowground components and links between the two, and provide examples from recent literature that illustrate these interactions.

2. Linking biological invasions across the soil divide

Biological invasions influence, or are influenced by, the soil biological community in a variety of ways. Plants or animals that invade the aboveground community can alter the quality or quantity of inputs into the soil and thus alter the resource base for the soil foodweb. Alternatively, the soil community can facilitate invasion by plant species by, for example, creating favorable rhizosphere interactions or lacking root pathogens in the new environment. Yet another example involves the invasion of soil-dwelling organisms, which can in some

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cases completely transform the soil environment, as in the case of invasions of new habitats by ecosystem engineers such as earthworms, or alter plant community structure through invasion by soil-dwelling pests or pathogens.

2.1. Aboveground invaders

The effects of both aboveground and belowground invaders can be divided into their effects on community shifts and disturbance regimes (Fig. 1). In the aboveground realm plant community shifts can alter the quantity or quality of litter inputs or change other soil properties, which can ramify through the system by altering rates of litter decomposition, and accumulation and storage of organic matter as well as nutrient release rates from decomposing litter, possibly facilitating continued invasion (Kourtev et al., 2003; Wardle and Bardgett, 2004). Invasive plants can also alter ecological interactions in the rhizosphere leading to important but poorly understood consequences for microbial dynamics, nutrient uptake and competitive

interactions in the plant community. Secretion of root exudates that have allelochemical effects towards native grasses apparently contributes to the successful invasion of western grasslands in North America by *Centaurea diffusa* (Callaway and Aschehoug, 2000). Another important aspect of rhizosphere interactions involves release from pathogens or other antagonistic soil biota, which can facilitate the establishment and spread of invasive plants. Negative feedback of the soil community on plant growth has been proposed as an important mechanism by which plant species diversity can be maintained in some communities (Bever et al., 1997). Such an effect has been demonstrated in several studies showing that native soils have a negative effect on some native plant species but a positive effect on invasive plant species (Callaway et al., 2004; Reinhart et al., 2003).

Plant invasions and community shifts can also influence soil nutrient or water availability. Invasion by nitrogen-fixing species that increase the distribution of rhizobial or other rhizosphere N-fixing associations can greatly alter N accumulation and transformation

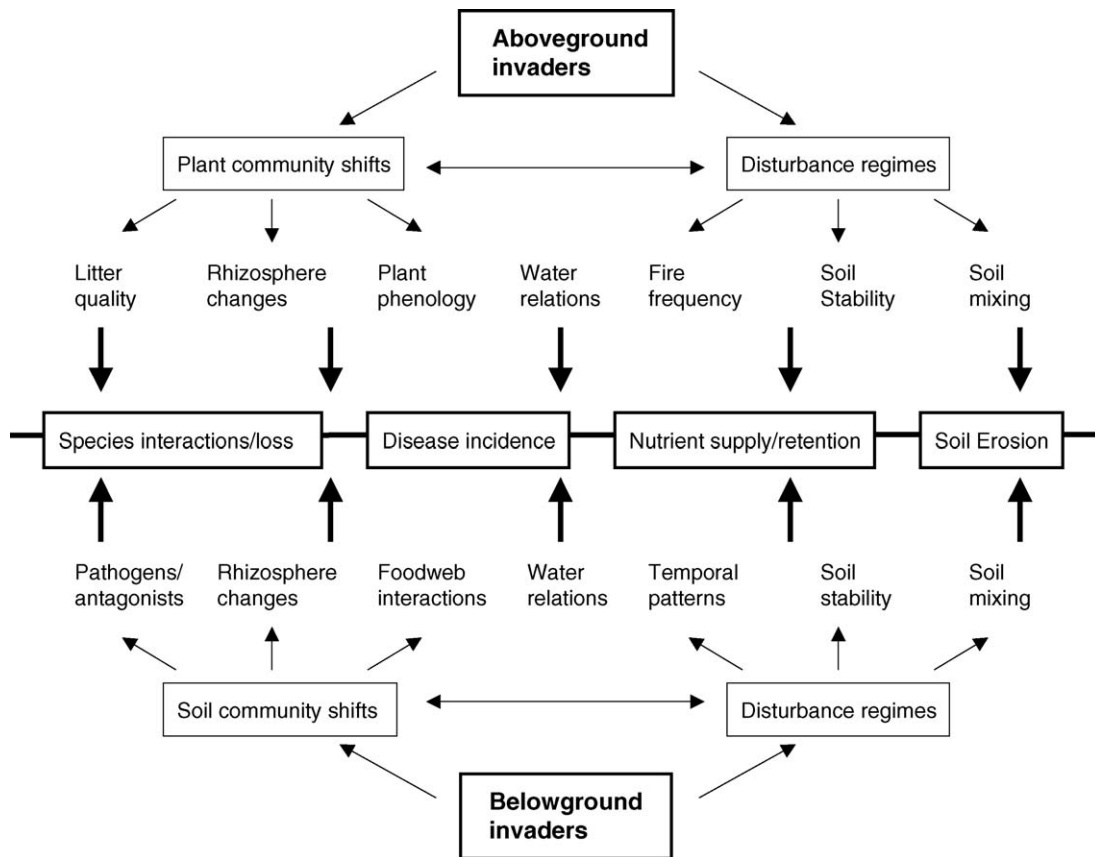


Fig. 1. Diagram illustrating the various mechanisms by which aboveground and belowground invaders influence ecosystem structure and function. Please see text for discussion.

rates in ecosystems (Corbin and D'Antonio, 2004; Rice et al., 2004). It has been suggested that the combined influence of increased N and changes in light regimes associated with invasive tree species in grasslands can facilitate further invasion and encroachment of grasslands by trees (Siemann and Rogers, 2003). Conversely, invasive plants may inhibit N-fixation and possibly lead to long-term declines in N inputs to soil (Wardle et al., 1994). The complex interactive effects of invasion on soil N-cycling are illustrated by grass invasion into submontane woodlands in Hawaii in which the grass increased net mineralization in the wet season due to changes in soil organic matter, but decreased net mineralization in the dry season due to decreases in soil moisture (Mack and D'Antonio, 2003). Plant phenology or growth form is another important mechanism by which plants can alter ecosystem function by changing the timing of nutrient uptake, but also by influencing timing and availability of fuel loads in fire-prone ecosystems, thus altering fire regimes in some invaded ecosystems (Levine et al., 2003). Changes in plant water use patterns by invasive species, which can be influenced both by the timing and amount of water uptake, can significantly alter soil moisture depletion and availability, which can impact the soil community and nutrient turnover (Enloe et al., 2004).

Change in soil disturbance is another major aspect of invasion ecology that can have a major impact on community structure and ecosystem function. This is especially true of introduced large herbivores, such as cattle, deer or goats, which can have a negative impact on soil macrofauna and other litter inhabiting soil invertebrates, and which can also destabilize soils and increase erosion (Wardle and Bardgett, 2004; Wardle et al., 2001; Yates et al., 2000). Rabbit warrens in Australia degrade the soil surface and reduce native mosses and lichens leading to an increase in cover of exotic plants and increased fuel loads that can enhance the spread of fire (Eldridge and Simpson, 2002). The ecological effects of soil disturbance by large introduced mammals might be viewed as positive in some instances; for example, soil disturbance by feral hogs increases species richness and diversity of microhabitats in floodplain marshes in central Florida (Arrington et al., 1999).

2.2. *Belowground invaders*

Invasion by belowground organisms have received less attention than invasion by aboveground organisms, in part due to the cryptic nature of the soil environment and the less apparent consequences of such invasions. It is likely that many exotic species occur among the soil

fauna of any particular region, but that these species are not readily recognized, due to the relatively small number of researchers working on the taxonomy and distribution of these groups. Because there has been less notice of belowground invaders literature on the consequences of belowground invasions is lacking.

One of the most apparent and dramatic examples of belowground invaders is the invasion of northern forest by non-native earthworm species, a subject that has received much attention in recent years (Bohlen et al., 2004a,b). In the case of earthworms, much of their effect occurs because of their role as ecosystem engineers capable of substantially changing the physical and chemical characteristics of the soil environment, with consequences for the entire soil foodweb, nutrient distribution, and even vertebrate and understory plant communities. Introduced ants are another important ecosystem engineer that can have significant impact on soil turnover and microtopography. The imported red fire ant (*Solenopsis invicta*) can have a large impact on landscape development in seasonally flooded ecosystems in their native Argentina and it remains to be seen whether this large scale effect will manifest itself in the invaded areas of North America (Cox et al., 1992).

Beyond their engineering effects on soil, invasive ants can also affect animal and plant communities crossing the soil divide to act as both aboveground and belowground invaders. Invasive imported fire ants can disrupt native ant communities, although some native ants persist in invaded areas (Morris and Steigman, 1993; Rao and Vinson, 2004; Sanders et al., 2003). These ants can also influence seed dispersal distances because of their smaller size relative to some native ant species that they displace (Ness et al., 2004). Selective seed predation by red imported fire ants contributed to success of ragweed plants growing in an old-field community (Seaman and Marino, 2003). As with the example of earthworm invasions, the example of fire ant invasions illustrates how one group of invading organisms, in this case a single species of ant, can have multiple ecological consequences mediated through their effects both on soil disturbance and on species interactions in aboveground and belowground communities. Other such effects are probably quite common and provide fertile ground for examining the effects of species on ecosystem structure and function.

2.3. *The special case of pathogens and pests*

Invasive pathogens are a special case of invasion that can alter communities and disturbance regimes through

the effects on specific hosts. The classic example is the case of chestnut blight in eastern North America in which a dominant canopy species was virtually eliminated from a diverse temperate forest. Although the path of invasion of pathogens and pests are quite different from that of other invasive species their ultimate effects on ecological interactions occur by similar mechanisms of altering communities and disturbance regimes both above and belowground.

Some of the most dramatic effects of invasive pathogens have occurred in forest ecosystems. Pathogens that influence dominant canopy species include aboveground pathogens, such as the ascomycete, *Cryphonectria parasitica*, attacking American chestnut, *Castanea dentata*, in the eastern US, and invasive root pathogens, such as *Phytophthora lateralis* attacking Port Orford cedar (*Chamaecyparis lawsoniana*) in the northwestern US (Jules et al., 2002), or *Phytophthora cinnamomi* causing dieback in eucalypt forests in western Australia. In the case of *Phytophthora cinnamomi* the dieback of susceptible eucalyptus trees leads to shifts in plant and animal communities both above and belowground (Newell, 1998; Postle et al., 1986; Weste et al., 2002). In one affected *Eucalyptus marginata* forest there was a large decline in litter inputs, reduction in soil invertebrate populations, and an increase in litter decomposition, probably due to changes in litter microclimate (Postle et al., 1986). In the case chestnut blight, the American chestnut was replaced by other canopy species and the effects are more difficult to discern because of the many changes that have occurred in these forests over the past century since the chestnut declined. The major mechanism by which pathogen or pest invasions influence ecological systems is through changes in the plant community by replacement or decline of a dominant species, which ramify thought the belowground system by altering the quantity and quality of litter inputs with consequences for the decomposer community, decomposition rates, and nutrient cycling.

2.4. Closing the loop

Understanding ecosystem functioning in terrestrial ecosystems requires a consideration of both the aboveground community, which supplies carbon through primary production, and the belowground community, which supplies nutrients through recycling and decomposition of decaying organic matter (Wardle, 2002). In addition to these primary functions of production and decomposition are the complex species interactions, physical transformations through activities

of ecological engineers, and pathogenic and mutualistic associations, all of which can be affected by ecological invasions. The papers in this special issue illustrate various aspects of these interactions, such as how invading plants affect or are affected by the soil community, how soil differences influence competitive interactions between invasive and native earthworms, and how soil pathogens affect invasive plants in their native habitat. As is so often the case in ecology, consideration of biological invasions shows that you cannot change one thing without changing another. A more complete understanding of the ecological consequences of invasion depends upon understanding the ways in which invasions influence shifts in species interactions, community structure, and ecosystem processes both above and belowground.

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