Invasive Soil Organisms and Their Effects on Belowground Processes

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Abstract

Invasive species have a wide range of effects on soils and their inhabitants. By altering soils, through their direct effects on native soil organisms (including plants), and by their interaction with the aboveground environment, invasive soil organisms can have dramatic effects on the environment, the economy and human health. The most widely recognized effects include damage to human health and economies, such as that caused by invasive fire ants and termites. Many other soil invasive species, however, have pervasive but poorly understood effects on terrestrial ecosystems. These species include the following:

1. Invasive plants and their symbionts (e.g., *Falcataria* in Hawaii).
2. Herbivores (e.g., root-feeding weevils).
3. Ecosystem engineers (e.g., earthworms).
4. Keystone species (e.g., terrestrial planaria).

In addition, aboveground invasive species, notably herbivores and pathogens, can have major indirect effects on belowground processes by altering nutrient cycles, plant health, productivity and carbon (C) allocation patterns, demography, and community composition and function.

Given the diversity of invasive soil organisms, there is a need for Forest Service Research and Development (*R&D*) *to develop a prioritized list of invaders and research topics to help guide research and identify research gaps.* Large gaps exist in our knowledge of the identity, distribution, abundance, and effects of most invasive soil organisms. Organisms with uncertain but potentially large ecosystem effects (e.g., invasive planaria) deserve more attention. In addition, we perceive several areas emerging as important research topics for Forest Service R&D. These topics include the widespread increase in propagule pressure of soil invasive species in urban areas and in the wildland-urban interface, the potential for additive and synergistic effects of suites of soil invasive species, the feedbacks between invasive species and soil microbial communities, and the interactions of soil invasive species with global change.

All stages of management of soil invasive species are critical, and Forest Service R&D is poised to play a leadership role. In the prediction and prevention area, we are in need of a more coordinated effort. Forest Service R&D has the expertise to inform the U.S. Department of Agriculture (USDA), Animal and Plant Health Inspection Service (APHIS) and other organizations about gaps in their programs for excluding or limiting dispersal of soil invasive species, but, at present, no comprehensive program exists to generate such information. Some work is being done on biogeographic models of invasive distribution that could inform prediction and prevention efforts. In the detection and eradication, management and mitigation, and restoration and rehabilitation areas, we have scientists directly addressing major soil invasive species issues, including

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effects and control of invasive termites; belowground effects of invasive plant species; interactions of invasive plants with soil microbial and fungal communities; effects and management of invasive earthworms; diversity and effects of urban soil invasive species; diversity, distribution, and effects of root-feeding weevils; and biogeography of invasive soil macroinvertebrates.

The Forest Service has strengths that permit us to directly address these problems, including a network of scientists investigating soil invasive species. Some gaps do exist in our expertise, however; most notably in taxonomy of soil organisms. These gaps should be addressed via either new hires or collaboration with non-Forest Service scientists.

We need to do a better job of communicating the diversity of Forest Service research in this area, both internally and externally. Increased opportunities for communication among Forest Service scientists working in this area would facilitate our efforts, and expansion of the invasive species Web site to include a section on soil invasive species would improve communication of our results. The Forest Service should host regular national meetings on soil invasive species to link Forest Service and other scientists and managers.

The continued erosion of the Forest Service research budget jeopardizes all these efforts. Long-term efforts in managing the effects of invasive species will require significantly expanded investments in Forest Service R&D. Maintenance of the status quo (or, worse, continued budget erosion) will contribute to the Nation's inability to cope with potential ecological disasters, such as the chestnut blight epidemic or, more recently, the emerald ash borer invasion, which have transformed, or are in the process of transforming, entire forest ecosystems.

Introduction

Soils are the foundation of productive ecosystems, providing a matrix within which plant roots provide support and forage for nutrients and water. Their properties derive from complex interactions of physical, chemical, and biological processes that drive the cycling and storage of carbon and nutrients. The biological processes are carried out by a highly diverse and complex array of plants, microorganisms, fungi, invertebrates, and vertebrates. This biodiversity is essential for the production of ecosystem goods and services, such as timber and nontimber forest products; as a source of new pharmaceuticals and other products derived from plants, bacteria, and fungi; for protection of clean air and water; for mitigation of changing atmospheric chemistry via carbon sequestration in soils, in the plants sustained by them, and in forest products; for protection of habitat for game and nongame wildlife alike; and for provision of recreational opportunities for the millions of people who enjoy the Nation's forests every year.

These goods and services are very sensitive to the biotic communities that control them; therefore, invasive species have a large potential effect on them. Plant and animal species can alter nutrient and water cycling, rates of decomposition and storage of soil C, soil structure and fertility, tree growth and mortality, and a host of other properties. For example, the introduction of a single "ecosystem engineer," such as an invasive earthworm species, has the potential to completely alter the chemical and structural properties of soils. In addition to having direct effects on soils, soil organisms can affect other species that live in or use the soil (e.g., via root herbivory or disease). The introduction of predators can alter the invertebrate communities in soils, with potential effects on soil processes and on forest food webs dependent on those soil organisms. The most obvious effects of introduced soil organisms are on human health and economies (e.g., introduced fire ants and Formosan subterranean termites), but the other effects described previously are likely to have more significant environmental and economic consequences that are at present only poorly quantified.

In this vision paper, we describe what we see as the most pressing issues surrounding the question of invasive species in soils, highlighting both what we already know and what we consider to be important knowledge gaps. We address specific taxonomic/functional groups, emerging broad issues, and issues related to the specific steps involved in responding to invasive species. We also highlight important strengths and weaknesses of Forest Service R&D in our capacity to address soil invasive species issues.

Effects of Taxonomic and Functional Groups on Belowground Processes

Taxonomic and functional groups differ in their mode of effect, so we present here a brief summary of the direct effects of the major groups of invasive soil organisms and the Forest Service R&D efforts related to each group.

Plants

Invasive plant effects on ecosystems can be substantial. They have been summarized in extensive reviews of this topic elsewhere (e.g., Ehrenfeld 2003, Reichard and Hamilton 1997, Stohlgren et al. 2004) and are being addressed in another vision paper, so we mention them only briefly in the context of belowground effects. Plant belowground effects are expected to be greatest when a new functional group enters a region; for example phreatophytic *Tamarix* in riparian zones leading to degradation of riparian zones, nitrogen fixing *Myrica faya* and *Falcataria* in Hawaii leading to loss of native biological diversity (Vitousek and Walker 1989), and alien plants with traits leading to enhanced fire regimes with devastating effects on native organisms and dramatic alterations of ecosystem processes (Brooks et al. 2004). Forest Service R&D has extensive efforts addressing invasive plant species effects on belowground processes (see “The Role of Forest Service in Nonnative Invasive Plant Research,” chapter 3, Sieg et al. 2010 in this document).

Aboveground Diseases and Herbivores: Indirect Effects

The pathogen and insect vision papers will be addressing these topics in detail, so we address these only lightly here. Indirect effects of aboveground herbivores occur via alteration of aboveground conditions or processes in ways that have belowground effects. These effects include those of aboveground herbivores on rates of plant growth, mortality, and litterfall. These changes can significantly alter nutrient cycles and disturbance regimes (e.g., windthrow, fire), with consequences within the affected site and with downstream effects on hydrology and stream chemistry (Ellison et al. 2005). Forest Service R&D has extensive research in these areas (see “Forest Service R&D—Invasive Insects: Visions for the Future” and “Invasive forest pathogens: Summary of issues, critical needs, and future goals for USDA Forest Service Research and Development,” chapter 2, Klopfenstein et al. 2010 in this document).

Similarly, changes in belowground communities have the potential to affect aboveground herbivores and diseases by a variety of pathways (Scheu 2001).

Belowground Diseases and Herbivores

In addition to the indirect effects of aboveground diseases and herbivores, there are direct belowground effects of root diseases and herbivores. The disease effects are exemplified by *Phytophthora lateralis* root rot on Port Orford cedar. Forest Service pathologists have been involved in investigating this disease for decades (e.g., Greenup 1998, Zobel et al. 1982). An emerging area of interest is the potential for soil microbial communities to structure the interactions between native and invasive plant species (Klironomos 2002). This topic will be addressed in more detail below (see Key Issues).

Root-feeding herbivores can also have large effects on plants and ecosystems, although our understanding of the importance of this phenomenon is hindered by the paucity of studies of root herbivory compared with aboveground herbivory (Blossey and Hunt-Joshi 2003, Hunter 2001, Masters 2004). Root feeders come from a variety of taxonomic groups but are especially well represented in the Coleoptera, Lepidoptera, and Nematoda. Effects of these herbivores can be seen in altered root demography (Stevens et al. 2002, Wells et al. 2002), plant growth and seed production, root:shoot ratios, nutrient status (Masters 2004), multitrophic interactions, (Masters 2004, Van der Putten et al. 2001), and plant community structure (Gange and Brown 2002). One indication of the importance of root-feeding herbivores is found in the literature on classical biological control. Approximately 65 percent (20 of 31) of intentionally released Coleoptera in the Chrysomelidae (8 of 12), Curculionidae (9 of 14), Cerambycidae (1 of 3), and Buprestidae (2 of 2) have contributed to control of invasive plant species (Blossey and Hunt-Joshi 2003).

Therefore, the widespread abundance of a variety of invasive root herbivores is likely to have far-reaching ecological effects in natural forests. Although only a small proportion of these species are introduced, they are often widely distributed and abundant and can locally outnumber native root herbivores (Pinski et al. 2005a, 2005b). The Forest Service Northern Research Station (NRS) (Mattson, Friend, Lilleskov) and collaborators (K. Raffa, D. Coyle) are leading this research effort in the northern region. Biogeographic patterns of their distribution have also been investigated, pointing to northern peaks in abundance of introduced root-feeding weevils (Lilleskov et al. 2008).

Predators/Keystone Species

Introduced predators have been described as keystone species when their actions have significant top-down effects on food web structure, community composition, and ecosystem processes, although some question the usefulness of this concept (e.g., Kotliar 2000). Groups of ecologically important introduced predators affecting soil communities include ground beetles, centipedes, and planaria. Invasive terrestrial planaria could have major effects on ecosystem processes, because many of these species of flatworms are predators of earthworms, attacking and killing individuals more than 10 times their size (Ducey et al. 1999). One species, *Bipalium adventitium*, has been found in at least eight States (Ogren and Kawakatsu 1998) and preys on a diversity of earthworm species (Ducey et al. 1999, Fiore et al. 2004, Zaborski 2002). They are currently concentrated in human-altered habitats such as lawns and gardens, and it is not known whether this constrained habitat range is due to environmental limitations or slow dispersal into native habitats (Ducey and Noce 1998). Another invasive planarian has been shown to significantly reduce the abundance of earthworms, with apparent cascading effects on other earthworm predators (Boag and Yeates 2001). Thus, it may function in North America as a broad host range biological control agent with negative effects on native as well as introduced earthworm species. The ecological consequences will depend on the rate of spread and efficacy of these predators but could have significant effects on earthworm-mediated processes in both agroecosystems and forests. Other introduced predators of concern are Carabidae (ground beetles), which can become numerically dominant in certain habitats. Their effects on communities and ecosystems are unclear, beyond possible reductions in native ground beetle abundance (Spence and Spence 1988). Introduced centipedes could also have significant effects via predation and competition with native predators, but relatively little work has been done on their diversity, distribution, and effects (Hickerson et al. 2005). Forest Service R&D active research on keystone species in soils is limited to a recent analysis of biogeography of introduced ground beetles (Lilleskov et al. 2008).

Ecosystem Engineers

Many invertebrates have been characterized as ecosystem engineers (Jones et al. 1994) because of their ability to alter ecosystem properties and processes disproportionately to their biomass or food consumption. Some of the best examples of invasive ecosystem engineers include earthworms, ants, and termites.

Earthworms

By consuming soil organic matter and mixing soils, earthworms have a dramatic effect on soils and the ecosystems they support. Two distinct science problems associated with invasive earthworms in North America are (1) invasions north of the Wisconsinan glacial boundary where no native earthworm species reside and (2) invasions south of this boundary where invasive species may interact with native earthworms. In some regions of North America, invasive earthworm species often have greater species richness and abundance than natives. In fact, in much of the previously glaciated regions of North America, the earthworm fauna is composed exclusively of invasive species (Lilleskov et al. 2008, Reynolds and Wetzel 2004).

Forest Service scientists in the International Institute of Tropical Forestry (IITF) (González) and Southern Research Station (SRS) (Callaham) have been working on problems associated with invasive earthworms for about 10 years each in the Caribbean tropics and the Southern United States, respectively (Callaham and Blair 1999, Callaham et al. 2003, Callaham et al. 2006a, Callaham et al. 2006b, González 2002, González 2006, González and Seastedt 2001, González and Zou 1999, González et al. 1996, González et al. 1999, González et al. 2003, González et al. 2006a, González et al. 2006b, González et al. 2007a, González et al. 2008, González et al. 2007b, Huang et al. 2006, Yiqing and González 2008, Zou and González 1997). They have been involved with an international group of researchers who are concerned with earthworm invasions, and both contributed to a special issue of the journal *Biological Invasions,* which focused on the topic (Callaham et al. 2006a, González et al. 2006, Hendrix et al. 2006). In addition, IITF (González) hosted the second Latin American Symposium of Earthworm Ecology and Taxonomy. The peer-reviewed proceedings of the meeting were published as a special issue in the *Caribbean Journal of Science* (González 2006).

In regions where only nonnative earthworms are present, we are seeing a fundamental shift in soil properties from unmixed soils with distinct organic horizons (mor) to well-mixed soils without organic horizons (mull). These changes have profound effects on soil properties and processes that ramify throughout ecosystems, including emerging problems such as siltation of water sources resulting from increased soil erosion and threats to endangered herbaceous plants (e.g., Bohlen et al. 2004a, Bohlen et al. 2004b, Gundale 2002, Hale et al. 2005, Hale et al. 2006, Steinberg et al. 1997). Reductions in arbuscular mycorrhizal fungal abundance and colonization in the presence of invasive earthworms have already been demonstrated (Lawrence et al. 2003) and are implicated as one of the factors in sugar maple decline and loss of understory species (Bohlen et al. 2004b, Frelich et al. 2006, Holdsworth et al. 2007). NRS scientists are studying ecosystem effects of earthworm invasions in urban ecosystems (Pouyat) and north of the glacial boundary (Lilleskov, Kolka, Swanston) to determine how forest management must be adapted to this state-shift in soil properties.

Termites

Termites have major economic and ecological effects via their consumption of wood and other organic matter, via bioturbation, and via emissions of the greenhouse gas methane. Given the large economic effects, most efforts on invasive termites have focused on their effects on manmade structures; however, the effects of invasive termites on forest ecosystems are less studied and in need of more attention. Termites have been considered ecosystem engineers (Dangerfield et al. 1998) because they have the potential to significantly alter rates of bioturbation of soils, carbon cycling, trace gas emissions (Sugimoto et al. 1998, Wheeler et al. 1996), and other ecosystem properties. The most widespread and economically costly invasive termite in the United States is the Formosan subterranean termite (*Coptotermes formosanus*). This species can form supercolonies and hollow out live trees for its nests. The potential economic and ecological effects of these changes in forest ecosystems are extensive and are being investigated by Forest Service scientists in the SRS (T. Wagner).

Ants

Large numbers of invasive ant species exist, especially in the Southern United States (Lilleskov et al. 2008). Invasive ants affect the economy and human health (e.g., fire ants), ecological processes such as pollinator interactions, seed dispersal, and native biodiversity (Christian 2001, Holway et al. 2002). Invasive ants such as *Linepithema humila* and *Solenopsis* sp. have reduced parasite loads in their introduced ranges and are likely candidates for introduction of biocontrol agents (Chen 2004, Feener 2000), because their lower genetic diversity may make them particularly sensitive to this form of management. The potential exists for invasive wood ants to have significant effects in northern forests, such as populations intentionally established in eastern Canada in misguided biocontrol efforts (Jurgensen et al. 2005). In addition, invasive European fire ants are spreading in the Northeastern United States (Groden et al. 2005) and could have significant effects on human and ecosystem health as they aggressively attack organisms near their nests. Beyond a biogeographic review of invasive ants (Lilleskov et al. 2008), we are not aware of any Forest Service R&D active projects on invasive ants.

Other Invertebrates

Millipedes, isopods, and gastropods can all be numerically important invasive species in some ecosystems. Their effects on ecosystem processes have only been superficially examined. Detritivory, fungivory, herbivory, and predation by invasive gastropods could have significant effects (e.g., Tupen and Roth 2001). Invasive isopods may have significant effects via direct feeding on fungal sporocarps. Like earthworms, the isopod fauna north of the glacial maximum is dominated by introduced Eurasian species (Jass and Klausmeier 2000), but little investigation into their effects and potential for spread into undisturbed ecosystems has been carried out. The native vs. introduced status of many taxa, especially meso- to microinvertebrates (e.g., mites and collembola), which are numerically dominant in northern forest soils, cannot be assessed because of incomplete knowledge of taxonomy and biogeography.

Vertebrates

Invasive vertebrates with indirect effects are covered in another vision paper. The invasive with the greatest direct effects on forest soils is the feral pig (*Sus scrofa*). This species is of great concern in both the continental United States and Hawaii (Singer 1981) via its role in uprooting plants, bioturbation, and facilitation of invasive plant species.

Plant Symbionts: *Mycorrhizal fungi*

Recognition of the need to consider the possible negative effects of introduction of nonnative mycorrhizal fungi is growing (Schwartz et al. 2006). Fungi from different parts of the world have been introduced with plants or in soil (e.g., in Puerto Rico, Florida, and California, along with nonnative *Pinus*, *Eucalyptus*, *Allocasuarina*, or *Casuarina*). *Eucalyptus* is widespread in California and has slowly escaped from its original plantings to occupy nearby habitat, leading to the replacement of native ectomycorrhizal fungi with the introduced species associates (Castellano 2008). One area in need of investigation is the potential for invasive species to cause the extirpation of rare or threatened ectomycorrhizal fungi (e.g., in coastal California). Another area of concern is the redistribution of native ectomycorrhizal fungi via inoculation or plantings and the potential for these fungi to alter local genetic diversity. In addition, a real potential exists that importation of mycorrhizal inoculum could result in the introduction of diseases that could attack native fungi or plants, with serious but as yet unexplored consequences (Schwartz et al. 2006). Pacific Northwest Research Station (PNWRS) scientists (Castellano, Smith) are investigating some aspects of this problem. As the climate changes, we will see invasions of ectomycorrhizal species from the south, as evidenced from biogeographic studies (Mueller et al. 2007, Ortiz-Santana 2006). Biogeographic studies of ectomycorrhizal fungi and other root-associated fungi are of critical importance for invasive species predictions and are being conducted by Forest Service scientists in the NRS and PNWRS (Lodge 2001, Mueller et al. 2007, Ortiz-Santana 2006). Large-scale integrated approaches to characterizing these communities are essential to our ability to be able to define baseline biogeographic patterns and the effect of invasive species and other agents of environmental change (Lilleskov and Parrent 2007).

Role of Forest Service R&D at Different Stages of Invasion

Different strategies are appropriate at the various stages of invasion. In the following paragraphs we identify the key actions that are being taken or should be taken by Forest Service R&D at different stages of invasion.

Prediction and Prevention

Forest Service R&D can contribute to prediction and prevention of soil invasive species via a variety of actions, including characterizing invasion pathways and modeling efforts.

Characterizing Invasion Pathways

Understanding pathways of introduction, pools of potential invaders, and the risk of invasion for specific regions is critical to prevention and prediction of invasive species. For invasive species with large effects on belowground processes, the primary historic pathway of introduction was likely the transport of soils for ballast, planting medium, or other purposes. Prevention measures should continue to be coordinated with other agencies, such as APHIS, to intercept new species at ports of entry. Although many invasive soil organisms are not currently targeted by APHIS, current APHIS regulations severely limit the transport of soils, which presumably has greatly reduced the influx of invasive soil organisms. This presumption, however, should be tested; to test this presumption, we need better characterization of the diversity and distribution of invasive soil organisms already present and determination of the rate of new introductions. Very little of this type of work has been done for soil organisms (see, for example Larson and Langor 1982), although existing quarantine records could be analyzed for trends in interception of soil organisms.

Within the United States, restrictions on soil movement are in place only for specific quarantine areas (e.g., for fire ants), which do not cover many invasive soil organisms. Suggestions for control will depend on the taxonomic group. For example, in the case of earthworms, stricter guidelines for the bait and horticultural industries would be needed to contain invasions (Callaham et al. 2006a). For the fish-bait industry, these regulations would ideally eliminate the commercial availability of the more aggressive and generalist species (in terms of habitat requirements). For the horticultural industry, we suggest minimum guidelines that would ensure materials shipped from areas with invasive earthworms into areas not yet affected by those species be certified “worm-free” (this is not unprecedented for soil invertebrates, *c.f.* the imported fire ant). In the case of other groups (e.g., gastropods), although existing regulations limit their distribution, these species are readily available for sale on the Internet, and the regulations do not appear to be rigorously enforced (Tupen and Roth 2001).

Other invasive species with direct and indirect effects on soils, including plants, pathogens, and insects (herbivores, predators, and saprotrophs), are being vectored at high rates in other ways (intentional and unintentional plant transport, wood products, etc.) that are discussed more fully in their taxonomic treatments contained in this volume. These groups deserve the greatest attention in prediction and prevention efforts because of their high likelihood of both transport and negative effects on natural and managed ecosystems.

Modeling

A variety of modeling approaches are necessary to optimize our response to invasive species. Bioeconomic models define the best targets for response to invasive species (Leung et al. 2002). Ecological niche models define potential distribution of invasive species (Peterson and Vieglais 2001) and could be used to define the likely ranges and effect of potential soil invaders. Related risk models are currently in development for prediction of likely invasions of exotic earthworms and their effects on soil properties and processes. Such models need to be developed on a species-specific basis for different species of actual or potential soil invasive species. *Forest Service R&D should coordinate with other Government agencies to develop predictive models as one means of prioritizing risks for soil invasive species for prevention efforts.*

Detection and Eradication

Detection and eradication, both key components of efforts to respond to invasive species, each provide specific challenges to Forest Service R&D.

Detection

Reliable and effective detection of invasive soil organisms will require extensive monitoring and survey of sensitive habitats combined with the ability to recognize invasive species when they are encountered. Taxonomic resources (scientists and state-of-the-art identification facilities) must be available to rapidly determine the identity of novel organisms. In addition to facilitating the critical abilities of traditional taxonomists, we must avail ourselves of molecular identification tools when appropriate. A network of monitoring sites combined with a centralized facility to process the sampled material from a given taxonomic group would be one workable solution to the problem of invasive species detection. Whatever the approach, these efforts require first and foremost a more thorough understanding of the diversity and distribution of soil invasive species in North America and the ability to respond rapidly.

Eradication

Eradication efforts for soil organisms are challenging because of the difficulty of determining presence of cryptic species and because of the severe disruption of soils that might be involved. Appropriate methods and intensity of effort will depend on the taxonomic group. Taxa must be ranked in terms of probability of invasion and the costs of invasion vs. eradication. Although the economic costs of some invasions are obvious (e.g., Formosan subterranean termite), the costs of other taxa are beginning to be appreciated but have not been fully quantified (e.g., invasive earthworms).

Approaches that attempt eradication or control at the stage of initial establishment can be potentially cost effective. *Knowing which introduced and naturalizing species to target for eradication is the greatest challenge in management of invasive species, because we have only limited ability to predict which subset of introduced species will result in ecosystem-modifying invasions. The modeling approaches discussed under prevention should be developed as a prioritization tool for determining appropriate responses.*

Direct Treatment Approaches. Chemical treatment is feasible when the distribution of populations of invasive soil organisms is well known and limited spatially (e.g., Arango and Green 2007). Research is critical in the areas of what compounds are effective, how and when they should be applied in a forestry or urban setting, what size of invasion can be treated effectively, which invasive species can be treated in this way, and what potential nontarget effects might result from such treatment.

Management and Mitigation

Efforts to manage and mitigate soil invasives must include a variety of approaches, including efforts to slow the spread of key invasives; characterization of environmental constraints and habitat, landscape, and risk modeling to better understand the areas most likely to be strongly affected by specific invasives; land management approaches to minimizing the impacts of invasives; and biological control of invasives when appropriate.

Slowing the Spread

A variety of approaches are available to either slow the spread or reduce the effects of invasive species. These approaches include comprehensive programs, such as Slow the Spread for gypsy moths, which combine education, biological control, trapping, and other approaches to reduce the rate of gypsy moth spread.

Formosan subterranean termites are prime candidates for such an effort, especially given their potential effect on forest ecosystems. Forest Service R&D has efforts aimed at controlling the damage caused by invasive termites. The Forest Service, Forest Products Laboratory (FPL), in collaboration with the Southern Regional Research Center, is working on new wood preservatives (Clausen et al. 2007, Lebow et al. 2006) and termite bait toxicants (Rojas et al. 2004) to prevent damage by native and Formosan subterranean termites. In certain instances, native subterranean termites (e.g., *Reticulitermes flavipes*) can be transported out of their endemic area, thus becoming invasive in a new ecological environment (Arango and Green 2007) (FPL, S. Lebow and F. Green; SRS, Wagner).

Forest Service work being done on termite control will be most effective as part of a coordinated effort to slow the spread of invasive termites (e.g., the USDA Agricultural Research Service (ARS) Operation Full Stop [Lax and Osbrink 2003]). In any effort of this sort, one of the critical questions to ask is, what are the costs and benefits of slowing the spread vs. not acting? Analyses of these sorts require collaboration among biologists, ecologists, and economists.

Characterization of Environmental Constraints and Habitat, Landscape, and Risk Modeling

To manage for invasive species, it is critical that we develop an understanding of basic life history and habitat tolerances of key species already introduced. This effort involves a comprehensive laboratory- and field-based approach to determine physical and chemical constraints on species distribution. Combined with landscape and risk modeling, this information is a key tool in developing appropriate management strategies for the key invasive species.

Land Management Approaches

Evidence indicates that certain types of land management can limit the encroachment of nonnative soil organisms. Maintenance of ecosystem-appropriate disturbance regimes appears to have promise as a means of limiting the spread of introduced soil organisms (Callaham et al. 2003, Callaham et al. 2006b). Research into the mechanisms behind this observation will lead to better understanding of invasion dynamics and, ultimately, to the development of management prescriptions that take invasive species into account.

Biological Control

Biological control is a key tool for control of invasive species and should be used when appropriate. Despite its potential, our ability to use biological control has limitations. One of the greatest limitations is potential serious nontarget effects of control organisms (Simberloff and Stiling 1996). The risks of these nontarget effects have to be carefully weighed vs. the potential benefits of control. In addition, for certain invasive species, competing economic interests could limit the applicability of biological control. For example, biological control of the earthworm *Lumbricus terrestris* (the nightcrawler), even if ecologically viable, is unlikely to be a socially and economically acceptable option because of the importance of this species to the bait industry. We are aware of no Forest Service biocontrol programs addressing invasive soil organisms, although ARS collaborators are investigating the potential for biocontrol of the Formosan subterranean termite.

Restoration and Rehabilitation

Many soil invasive species are so completely naturalized that our only option is to adapt to their presence. Potential for restoration and rehabilitation depends on the invasive species and system invaded. For example, work on earthworm effects should help to inform management for native plant species of concern in the presence of certain species of nonnative earthworms (e.g., Gundale 2002). In some cases, significant alterations in forest management strategies may be necessary to adapt to the changes caused by earthworm invasion. Forest Service R&D can contribute significantly to such efforts, some of which are already under way in the NRS (Lilleskov, Swanston, Kolka). Certain invasive plants are also known to produce allelopathic chemicals, which can reside in soils long after the aboveground portions of the plant have been treated or removed (Kulmatiski and Beard 2006). The soil-mediated legacy effects of invasive plants are in much need of further research.

Application and Communication

From the current effort it is clear that the Forest Service has a diversity of research programs on a broad range of invasive soil organisms and other species that affect belowground processes. The dispersed structure of our organization constrains communication among the scientists working on these diverse programs and does not emphasize to our customers the diversity and magnitude of our efforts. We suggest that, to improve internal information sharing and to emphasize our strengths in this area to our customers, the Forest Service produce a central Web-based clearinghouse of Forest Service research on soil invasive species on the Forest Service invasive species Web site. We also recommend regular national meetings on invasive soil organisms hosted by the Forest Service. To reduce costs and carbon footprints, some of these meetings should be videoconferences. Establishment of a Forest Service listserv on invasive species would also facilitate communication among Forest Service scientists.

Key Issues

In addition to listing the activities and general recommendations in the previous text, we have identified several key issues in need of coordinated effort in the future.

Identification, Distribution, and Effects of Key Invaders

One of the greatest challenges in characterizing invasive species and their distribution is our lack of thorough taxonomic and biogeographic treatments for many of these groups. Until we have this information it will be impossible to make informed decisions about how to prevent and manage invasions. *Therefore, maintaining and expanding sources of taxonomic and biogeographic knowledge, either within the Forest Service or among our collaborators, should be a key priority of Forest Service R&D.*

Prioritized List of Soil Invasive Species

Given the large number of soil invasive species, it becomes imperative that we prioritize our efforts to address the most pressing issues first. This approach requires a synthesis of expert knowledge on the topic. This document serves as a starting point for such a synthesis and prioritization, but we must be aware that, as our understanding of the actual or potential effects of certain groups increases, our priorities will be likely to shift and that more formalized efforts are necessary to ensure adequate prioritization. *To aid in prioritization efforts, we should initiate a formalized Forest Service R&D prioritization effort* (*e.g., via a national task force of Forest Service R&D and current and potential academic collaborators on soil invasive species*).

Effects of Invasive Species on Interactions Between Plants and Soil Microbial Communities

At present the feedbacks between invasive and native plant species, soil organisms, and soil microbial communities are poorly understood, yet the potential for large-scale shifts in biodiversity and ecosystem processes driven by symbiotic (whether beneficial or detrimental) organisms is large. To the examples of invasive N-fixing plant species and ectomycorrhizal fungi described previously can be added a host of other interactions. These interactions include the escape of invasive organisms from biological control agents such as root pathogens, resulting in increased competitive advantage for the invasive species (e.g., Callaway et al. 2001, Callaway et al. 2004, Klironomos 2002, Mitchell and Power 2003, Wolfe and Klironomos 2005); the introduction of sublethal root pathogens that will affect plant productivity yet remain undetected; alterations of soil microbial communities by invasive plants (e.g., Kourtev et al. 2002, 2003); and changes in soil microbial communities mediated by the interactions of disturbance and invasive plant species and resulting effects of these changes on native plant regeneration (e.g., Hebel et al. 2009). We face enormous challenges in detection of these interactions, requiring utilization of rapidly developing molecular approaches for characterization of microbial (including both bacterial and fungal) communities. *At present, although local Forest Service R&D efforts on these problems exist* (*e.g., PNWRS, J.E. Smith*), *no unified effort is in place for determining a Forest Service strategy to respond to this suite of interrelated problems. Coordination of research efforts among spatially diffuse groups* (*e.g., via creation of a Forest Service listserv on invasive species*) *would increase the probability of research coordination among regions.*

Invasive-Dominated Communities in Urban and Agricultural Ecosystems

Areas with higher human population density are exposed to higher loading of introduced soil organisms (Lilleskov et al. 2008). As a result, urban areas have fundamentally different soil arthropod communities with a much higher proportion of introduced species when compared with those in areas of lower human population density (e.g., Bolger et al. 2000, Connor et al. 2002, McIntyre 2000, Pouyat et al. 1994, Spence and Spence 1988). This pattern is likely a function of rates of propagule input, greater disturbance, and other mechanisms such as higher success rates of human-associated faunas because of the match of source and destination habitats. *With the expansion of the wildland-urban interface, the area with dramatically altered communities of soil organisms is also likely to expand. The Forest Service should be prepared to predict the effects of these changes and develop proactive approaches to this problem.* The

NRS (Pouyat) has a program specifically addressing the effects of invasive soil organisms in the urban matrix and exploring soil community and process changes in forests along urban-rural gradients in New York City and Baltimore (Pouyat and Carriero 2003, Steinberg et al. 1997, Szlavecz et al. 2006). A related problem is the interface between wildland and agricultural systems, which could be a major steppingstone for exotic species introductions into wildlands.

One uncertainty is whether urban/human dominated forest soil communities are constrained to their urban matrix or if they will spread into nonurban environments in the future. Patterns of apparent synanthropy (close association with humans) can be driven by slow rates of dispersal or by absolute environmental constraints that limit dispersal into natural ecosystems; i.e., some species may be obligate synanthropes constrained to human-altered environments, whereas others may be facultative synanthropes capable of spreading into ecosystems not dominated by humans (Bolger et al. 2000, Kavanaugh and Erwin 1985, Niemelä and Spence 1991, Niemelä et al. 2002, Spence and Spence 1988). The importance of spread out of these systems will depend on the biotic and abiotic resistance of wildlands to the invaders from urban and agroecosystems (e.g., Hendrix et al. 2006). *To predict future patterns of invasion and community change, it is essential that we determine which key invaders are capable of crossing from human-dominated ecosystems into wildland ecosystems.*

Additive and Synergistic Effects of New Suites of Soil Invasive Species

The concept of an invasional meltdown (i.e., synergistic interactions between invasive species facilitating more invasions and leading to rapid ecosystem change [Simberloff and Von Holle 1999]) has received considerable attention (Simberloff 2006). The potential for invasional meltdown in response to soil invasive species has not been fully explored but has been demonstrated to some degree in interactions between introduced earthworms and introduced plants (Heneghan et al. 2007, Kourtev et al. 1999) and between invasive plants and their mycorrhizal partners (Richardson et al. 2000). Wholesale soil community changes in urban ecosystems and the likely expansion of these invasive-dominated communities highlight the necessity of determining whether such synergistic interactions among invasive species occur among the species in these communities. The Forest Service has researchers with expertise and active research programs on urban invasive soil organisms and their effects on soil processes (NRS, R. Pouyat), and the expertise of other scientists with relevant interests and skills could be brought to bear on this problem as well. *Better communication, coordination, and collaboration between Forest Service scientists working on invasive plants and those with expertise in soil ecology will help to determine the importance of interactions among invasive species in forest ecosystems.*

Interactions of Invasive Species and Global Environmental Change

Managing in the face of global change is one of the key challenges facing the Forest Service. As climate and atmospheric chemistry change, ecosystems will change in their susceptibility and response to invasions (Dale et al. 2000). Species with direct and indirect effects on soils are likely constrained by the bioclimatic match between source and receptor regions (Lilleskov et al. 2008), so a thorough understanding of how ranges are likely to change as a function of climate change is essential. Other factors, such as nitrogen deposition, provide further stresses on native ecosystems that have a potential for accelerating invasions or increasing their effects (e.g., Fenn et al. 2003). Increasing carbon dioxide will drive alterations in plant tissue chemistry or competitive interactions in ways that could favor or inhibit invasive species. Our understanding of such interactions is poor, but Forest Service research on the interaction of climate and pine beetle outbreaks in the Rocky Mountains (Rocky Mountain Research Station, Logan) indicates the strong nonlinear changes in pest effects that can occur in response to small changes in climate (Logan and Powell 2001). Similar changes could be expected in some invasive soil organisms. For example, invasive native (*Reticulitermes flavipes*) and nonnative (e.g., *Coptotermes formosanus*) termite species are spreading northward but, at present, are apparently limited bioclimatically to the Southern United States and in the North to urban areas (e.g., Arango and Green 2007). Populations resident in urban areas could rapidly expand and coalesce as climate changes. *Understanding the constraints on their distribution and potential for control is critical to our ability to manage and adapt to these invasions.*

Forests are an important sink for carbon, potentially providing an important negative feedback to global climate change. This carbon is stored in both soils and biomass. Changes in soil processes can change the pools of soil carbon. One area in need of investigation is the effect of invasive soil organisms in general, and earthworms in particular, on the storage of carbon in soils. It has been established that short-term losses of soil carbon occur during earthworm invasion. These losses can be significant, on the order of 0.6 Mg C ha^{-1} yr^{-1} (Alban and Berry 1994). How long these losses persist and how these losses are modulated by soil texture is only poorly understood, yet such knowledge is essential to our ability to manage forests for carbon storage. It is possible that, although short-term effects include carbon losses, long-term effects include increased physical and chemical protection of soil organic matter, leading to net accumulations of soil carbon. A Forest Service researcher (NRS, Pouyat) and collaborators have compared the effects of invasive earthworms on soil carbon dynamics in forest stands along an urban-rural gradient in the New York City metropolitan area (Groffman et al. 1995, Pouyat et al. 2002), and an existing Forest Service project addresses this question in nonurban forests (NRS-Lilleskov, Swanston, Kolka). *Understanding the effects of invasive species on climate is critical to our ability to manage forests to mitigate climate change.*

Overarching and Concluding Remarks

The Forest Service has the unique opportunity to provide information that will improve our ability to predict, prevent, detect, eradicate, and manage invasive organisms that affect the belowground component of ecosystems, but only if we make it a priority to develop an integrated program that takes full advantage of the unique strengths that we offer.

These strengths include (1) a national network of capable and motivated scientists dedicated to protecting the sustainability, biodiversity, health, and ecosystem goods and services of our forests; (2) a network of long-term ecological research projects, sites, and associated databases, especially Forest Inventory Analysis and our invaluable network of Long Term Ecological Research Network studies and experimental forests and ranges; (3) a long-term perspective; and (4) the flexibility to respond to problems as they arise. *Our customers—the public, land managers, other scientists, policymakers, other Government organizations such as APHIS—do not have the expertise or focus on forests that would permit them to make informed decisions necessary to protect forests from soil invasive species. It is, therefore, our responsibility to ensure that information needed is developed and disseminated to these customers.* APHIS needs our help in identifying organisms of greatest concern to forests and their mode of entry, land managers need to recognize the signs of invasive species and know how to respond, other scientists need unfettered access to the information we collect, and the public and policymakers need to be educated about the issues we face and the collective and individual actions required.

To provide this information, we must maintain a vital and comprehensive research program that includes both internal Forest Service research and collaboration with academic institutions and scientific societies. Given the range of taxonomic groups and ecological roles encompassed by soil invasive species, **it is also essential that Forest Service R&D maintain diverse expertise in soil science, pathology, entomology, mycology, taxonomy (especially of invertebrates and fungi), biological and other methods of control, ecology, ecosystem science, biogeochemistry, and hydrology.** The trend toward declining research budgets must be reversed if we are to maintain the expertise needed to address these problems. To address these problems, we need to communicate the economic, social, and environmental benefits of expanding our research program.

We can scale the organization to focus on the highest priority issues/needs if we remain flexible; keep lines of communication open among different research groups; minimize top-down control of the research process, allowing individual scientists to recognize and respond to emerging issues; provide resources for research collaborations among units and regions, and between units and universities; and provide central databases of scientists, expertise, publications, and long-term datasets. It is essential that within Forest Service R&D we share data and protocols to maximize comparability of collected data, and when appropriate seek additional resources to fund collaborative efforts that synthesize existing data or permit national-scale efforts. In order to provide greater integration, it is also critical that we increase incentives, such as targeted funding, for collaboration among regions. Providing opportunities for unstructured communication among researchers (*e.g., national meeting of researchers focusing on belowground invasive species, perhaps in partnership with the Soil Ecology Society*) *will also facilitate such efforts.*

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