Non-native invasive earthworms as agents of change in northern temperate forests

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Exotic earthworms from Europe and Asia are invading many northern forests in North America that currently lack native earthworms, providing an opportunity to assess the role of this important group of invertebrates in forest ecosystems. Research on earthworm invasions has focused on changes in soil structure and carbon (C) and nitrogen (N) cycling that occur following invasion. These changes include the mixing of organic and mineral soil horizons, decreases in soil C storage, and equivocal effects on N cycling. Less well studied are changes in the soil foodwebs that accompany earthworm invasion. Soils of northern temperate forests harbor a tremendous diversity of microorganisms and invertebrates, whose distribution and abundance can be substantially altered by earthworm invasion. Furthermore, invasive earthworms can affect understory plant communities, raising concerns over the loss of rare native herbs in some areas. The ecological consequences of earthworm invasion are mediated through physical, geochemical, and biological effects. These effects vary with different earthworm species, as well as with the characteristics of the site being invaded. Earthworm invasions may have important interactions with other rapid changes predicted for northern forests in the coming decades, including climate and land-use change, increased nutrient deposition, and other biological invasions.

In a nutshell:
- Many northern temperate forests in the US have had no natural earthworm populations since the last glacial period, due to slow northward expansion of native species.
- Exotic earthworm species from Europe and Asia are invading many of these forests, substantially altering forest soils.
- These invasions can alter nutrient storage and availability, and greatly affect populations and communities of other flora and fauna that inhabit forest soils.
- Invasions by earthworms are likely to increase in northern forests with increased human activity and changing climate; the consequences should be considered along with other important changes taking place in these ecosystems.

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(Vitousek 1990). Understandably, much of the focus on exotic species invasions in forests and other ecosystems has been on aboveground invaders, which are the most apparent. However, belowground invasions may be equally widespread and may become better known as more ecologists begin to recognize the importance of links between aboveground and belowground communities (Scheu 2001; Wardle 2002). Invasion of northern forests by exotic earthworms, for example, is receiving increasing attention.

Earthworms are the best known of the large soil fauna, but many northern forests in North America lacked earthworm populations prior to European settlement, probably because of slow northward expansion of native earthworm populations following the last glacial period (James 1995). Foreign earthworm species, mainly of European and Asian origin, are currently invading these forests over a wide geographic area (eg Alban and Berry 1994; Scheu and Parkinson 1994; Bohlen et al. 2004a). The earthworm species involved belong to a group that have been termed the “peregrine” species, representing a small portion of overall earthworm diversity, and are characterized by their ability to colonize new habitats, spread rapidly, and tolerate a wide range of ecosystems and environmental conditions (James and Hendrix 2004). The introduction of these species into new habitats is facilitated by human activity, such as the construction of logging roads, direct releases of unused fishing bait by anglers, and the relocation of fill or horticultural materials (Hendrix and Bohlen 2002).

Earthworm invasions of northern forests can lead to...
rapid and dramatic changes in the soil environment (Langmaid 1964; Alban and Berry 1994) due to the important role of earthworms in modifying soil structure, redistributing organic matter, and altering the habitat of other organisms living in or on the soil (Neilson and Hole 1964). This key role of earthworms in forest humus formation has long been recognized and is captured in the historical mull, moder, and mor terminology used to describe forest soils (Parkinson et al. 2004).

Several excellent recent reviews are available on the ecology of earthworms, their critical role in soil genesis, their effects on nutrient cycling and organic matter breakdown, and their interactions with soil microbial communities (Lavelle et al. 1999; Edwards 2004). The goal of this paper is not to review this extensive literature, but rather to point out that earthworm invasions in northern forests provide an opportunity to examine the generality of current concepts in earthworm ecology and to compare and contrast the importance of different functional groups of organisms in invasion biology. Because earthworms modify the surface soil, which is where the primary interactions between aboveground and belowground communities are mediated, these invasions have important consequences for the soil foodweb, nutrient cycling, and plant communities. The accompanying disturbances may be an important aspect of the current and future environmental change in these forests.

**Earthworm invasions and nutrient cycling**

Much of the research on earthworm invasions has focused on the consequences for nutrient cycling and soil microbial processes (e.g. Scheu and Parkinson 1994; Bohlen et al. 2004b; Groffman et al. 2004). Earthworms shift the soil system from a slower cycling, fungal-dominated system to a faster cycling, bacterial-dominated system, or at least one that is less fungus dominated (Wardle 2002). This is accomplished through the redistribution and transformation of soil organic matter as earthworms consume organic-rich forest floor material and incorporate it into underlying mineral soil (Figure 1). The degree of mixing of soil layers depends upon the life history traits of particular earthworm species, which are often broadly categorized as belonging to one of three main ecological groups: epigeic, endogeic, and anecic (Edwards and Bohlen 1996). Epigeic species reside mainly in the upper organic layer and may cause limited mixing of mineral and organic soil layers. Endogeic species reside in the mineral or mixed soil layers and often enhance mixing of organic and mineral soil layers. Anecic species (including Lumbricus terrestris, the common nightcrawler) form nearly vertical permanent burrows up to 1–2 m deep. These species incorporate litter into the soil and bring mineral soil from different depths to the surface, resulting in soil mixing that is very different from the mixing caused by epigeic or endogeic species (Figures 1 and 2). Not all species fall neatly into these standard categories, but classification is useful for differentiating major ecological groups and their effects. The physical transformation of the soil is the most obvious sign of earthworm invasion in northern forests. How these physical changes and the associated redistribution of organic matter influence ecosystem level processes such as total C storage, N transformation rates, and loss of nutrients via hydrologic and gaseous pathways, and how these change over time, is not well understood.

A shift towards a faster cycling system implies that earthworm invasion could result in a net loss of C from the soil. Northern forests are important global C sinks, but environmental changes may turn them into C sources (McKane et al. 1997; Hobbie et al. 2002). Earthworm invasion could enhance increased C flux from northern forests due to global warming, especially as the ranges of different ecological groups of earthworms expand into more of these forests. In fact, most studies have docu-
mented an increase in soil C loss following earthworm invasion. Carbon loss of around 600 kg per hectare per year for a period of 14 years was reported for mixed hardwood forests in Minnesota (Alban and Berry 1994), and of 28% of total surface soil C for sugar maple (Acer saccharum) forests in the northeastern US (Bohlen et al. 2004b). Such losses occur because recalcitrant C pools that accumulate at the soil surface in the absence of earthworms are exposed to greater mineralization rates after earthworms invade. The increased mineralization is partly a result of earthworm respiration, but is mostly due to the stimulation of microbial activity in earthworm guts and casts. Mineralization is also increased by the secretion of labile C compounds in mucus and subsequent alteration of soil structure (Edwards and Bohlen 1996). In the long term, however, earthworm activity may contribute to stabilization of soil C in earthworm casts and other stable aggregates formed by earthworm activity (Scheu and Wolters 1991; Tiunov and Scheu 2000).

The effects of earthworm invasion on N cycling and retention are more complex and less conclusive than the effects on C transformations. Nitrogen is both a limiting nutrient and an atmospheric pollutant, so the effects of earthworms on N cycling potentially influence nutrient uptake and the fate of atmospheric N deposited in forest ecosystems. Earthworms have been shown to increase the N mineralization and leaching of N from forest soils in both lab and microcosm studies (Haimi and Huhta 1990; Scheu and Parkinson 1994; Burtelow et al. 1998), indicating that earthworm invasions have the potential to accelerate rates of N transformation. Earthworm activity has been shown to increase denitrification rates in some instances, though not in others, and the question of whether earthworm invasion influences overall gaseous N flux from forest soils remains unanswered (Burtelow et al. 1998; Bohlen et al. 2004b). It is also unclear whether earthworm invasion substantially alters N retention in those systems. They did not lead to large increases in N leaching from surface soil in undisturbed forest plots in New York (Bohlen et al. 2004b).

Analysis of soil C and N content and stable isotope signatures of invaded forest sites in New York suggested that total soil N remained unchanged following invasion, despite the fact that soil C storage decreased substantially (Bohlen et al. 2004b). An increase in total microbial biomass, which may act as a strong immobilization sink for available N in C-rich soils (Groppman et al. 2004), is one possible mechanism for N retention following earthworm invasion. This is an interesting finding because some studies have reported a decrease in microbial biomass in response to earthworm activity (Blair et al. 1997; Hendrix et al. 1998; Wolters and Joergensen 1992). However, most previous studies that reported a decrease in microbial biomass with earthworms involved agricultural or mixed soils, not organic-rich forest soils where earthworms can stimulate microbial biomass by mixing soil layers together (Scheu and Parkinson 1994; Saetre 1998). In the New

Figure 2. Earthworms representative of different ecological groups. (a) Epigeic species, such as Dendrodrilus rubidus, inhabit organic-rich surface layers and feed mainly on surface organic matter. (b) Endogeic species, such as Octolasion tyrtaeum, consume more mineral soil than epigeic species, and mix mineral and organic soil layers together. (c) Anecic species, such as Lumbricus terrestris, live in deep vertical burrows, feed mainly on surface litter, and incorporate litter into the soil as well as transporting mineral soil to the surface from deeper soil layers. (Note that only the anterior end of L. terrestris is shown here; the posterior end remains in its burrow).
Invasive earthworms in temperate forests

PJ Bohlen et al.

York study, the increase in microbial biomass was attributed to a more favorable environment that increased the "carrying capacity" of the mixed surface soil relative to undisturbed forest floor. Understanding or predicting the effects of earthworm invasion on N cycling in forest soils depends on the quantity and quality of soil organic matter, because of the tight coupling of soil C and N cycling. Earthworms may increase N flux more in systems fertilized with N, such as agricultural or pasture systems (Knight et al. 1992; Dominguez et al. in press); earthworm invasion might therefore be expected to increase N flux more in forests with high levels of N deposition than in more N-limited systems, though this remains to be investigated.

Earthworm invasion also affects phosphorus (P) cycling in soil, which is strongly influenced by physical and chemical modifications. Trees in areas with an intact forest floor concentrate a large proportion of their fine roots in this layer, where up to 80% of their annual P requirement is met by the tight linking of organic P mineralization and uptake (Wood et al. 1984; Yanai 1992). By eliminating the forest floor and mixing it with the underlying soil, earthworms can greatly alter P cycling by increasing P fixation by soil minerals and by altering the mineralization of organic P. For example, a study of sugar maple stands in Quebec showed that all stands that had forest floors mixed with mineral soil had lower concentrations of available P than did stands with intact forest floors, undisturbed by earthworm activity (Paré and Bernier 1989 a, b). A comparison of plots with and without earthworms in New York suggested that invasive earthworms influenced soil P cycling, but that the effects depended on the species composition of the earthworm community, possibly because various earthworm species differentially affect the degree of mixing of soil layers and the redistribution of organic and mineral components within the soil profile (Suárez et al. 2004). The effect of earthworms on P cycling is largely dependent on regional soil mineralogy, the degree of mixing of soil layers, and the timeframe of the invasion. An initial increase in organic P mineralization in the early stages of invasion may be followed by a decrease in available P as soil minerals fix more P.

Soil microbial community responses

Organic layers in the soil provide microhabitats and resources that support an abundant and diverse soil community. The profound changes in the soil organic layers resulting from earthworm invasion greatly alter microhabitats and resources for microorganisms and invertebrates (Figure 3). However, with the exception of studies in forests in Alberta, Canada, and in a maple forest in New York, data on the effects of earthworm invasions on soil microbial communities in forests are limited.

Studies on the response of soil fungi to the invasion of Dendrobaena octaedra into pine forest soil in Alberta suggest that in the long term, fungal community diversity and richness decreased and dominance among fungi increased, apparently due to the disruption of fungal hyphae, decreased resource availability, and reduced spatial heterogeneity as the organic layers became homogenized (McLean and Parkinson 2000a). Competition among fungi was reduced soon after invasion, possibly through the addition of nutrients or as a result of disturbances due to burrowing and deposition of casts into the organic layers (McLean and Parkinson 1998b).

Given the differences between epigeic, endogeic, and anecic earthworms in terms of feeding behavior and effects on the soil profile, one might expect the response of soil fungi to earthworm invasion to vary in accordance with the ecological group of the invading species. In fact, results from a laboratory mesocosm experiment suggest that some species, including fast-growing species of Trichoderma, are favored by the presence of the epigeic D octaedra, but are inhibited by the presence of anecic and/or endogeic earthworms, indicating that epigeic earthworms favor fungal species that tolerate moderate disturbances. Other fungi, including Mortierella sp (Zygomycetes), uniformly decreased in the presence of epigeic, anecic, or endogeic earthworms, reflecting their inability to tolerate hyphal disruption; this is due to the lack of septa to prevent cell content leakage. With so little data available, conclusions about the effects of earthworms on microfungal communities must remain preliminary.

It is probable that earthworm invasions not only affect saprophytic but also mycorrhizal fungi, but this has not been well studied. Results from a laboratory study on the impacts of earthworms on mycorrhizal fungi are congruent with observations on saprophytic microfungi. The presence of earthworms of different ecological groups decreased colonization rates and abundance of arbuscular mycorrhizae of sugar maple, most likely due to physical disruption of fungal mycelia (Lawrence et al. 2003). Changes in the abundance and functioning of arbuscular mycorrhizal fungi probably contributed to alterations in forest herb communities.

Soil invertebrate community responses

Earthworm invasions can rapidly alter soil structure, humus forms, and plant communities, and some of these changes can occur in as short a period as 2 to 5 years (Langmaid 1964). However, the influence of these ecosystem engineers on other soil biota, eg microarthropods (mites, collembolans), enchytraeids (potworms), or nematodes is poorly understood, especially with respect to changes that occur following earthworm invasions in forest ecosystems. Soil-inhabiting vertebrates and their responses to invading earthworms as new food resources have only recently been examined in more detail (Maerz et al. in press), although the importance of earthworms as a food source for a wide variety of vertebrates is well

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The diversity of soil mixing effects of different ecological groups of earthworms in boxes containing reconstructed soil layers from an aspen forest in southwest Alberta, Canada. (a) Boxes with no earthworms; (b) boxes containing individuals of the epigeic earthworm species, D. octaedra, which have mixed the organic layer into the mineral soil; and (c) boxes containing individuals of the endogeic species, O. tyttaeum, which have thoroughly mixed the mineral and organic layers together. For more details see Scheu & Parkinson (1994).

established (Edwards and Bohlen 1996).

The rapidly spreading earthworm D. octaedra mainly inhabits the forest floor, which is also the major habitat for soil-inhabiting microarthropods. Studies in a pine forest in Alberta confirmed the expected, positive influence of earthworm activity on soil invertebrates (Wickenbrook and Heisler 1997; Loranger et al. 1998), but only either in the short term or in unfavorable habitats. A high biomass of D. octaedra resulted in increased oribatid mite diversity; in a laboratory experiment, intermediate levels of earthworm activity tended to increase microarthropod abundance after 3 months, probably due to an increase in microhabitats and microbial food resources (McLean and Parkinson 1998a). Similarly, the dry and unfavourable pine litter (L-layer) was modified by earthworm activity in a way that resulted in increased oribatid mite species richness and diversity (McLean and Parkinson 1998a). However, high earthworm biomass and activity in the longer term and in the lower organic layers, the main habitats of microarthropods in climates with hot and dry summers and cold winters, resulted in strong decreases in diversity and abundance. These declines can be attributed to the restructuring of the organic layer into earthworm casts and associated mechanical disturbance, as well as the competition for microbial food resources.

More dramatic decreases in microarthropod diversity and abundance were observed in aspen forest soil in Alberta when L. terrestris, an anecic species, and O. tyttaeum and Aporrectodea calignosa, both endogeic species, invaded soils previously devoid of earthworms. These large earthworm species mix organic material and mineral soil in much greater quantities than D. octaedra, and therefore compete vigorously with microarthropods for microbial and organic food. They alter habitat and food resources more strongly and create mechanical disturbances which, as demonstrated in a 1-year laboratory experiment, may result in lower microarthropod abundances than are found in agricultural soils under conventional tillage (Migge 2001). The same processes occur in the field; these will be slower in dry continental climates such as in the forests of southern Alberta, but are likely to be much faster in the milder climates of the eastern forests. To date, there are no comparable data available from other regions, and data on enchytreaids, nematodes, and macroarthropods are lacking.

Soil inhabiting vertebrates

Recent studies on the foraging behavior of salamanders (Plethodon sp) suggest that introduced earthworms may play an important role in salamander diets, especially in lowland forests and during rainy seasons (Maerz et al. in press). Earthworms apparently increase the fecundity of adult salamanders by providing a high protein food source, but decrease the survival rates of young salamanders, presumably by reducing populations of smaller...
invertebrate food sources, or by altering the habitat in other ways. Further investigations are needed to understand how this influences salamander population dynamics and what impacts the invading earthworms will have on other predators, such as birds or small mammals. The changes observed in decomposer and plant communities, as well as vertebrate foraging strategies, imply that belowground invasions can also dramatically alter the aboveground food web.

**Plant community responses to earthworm invasions**

The abundance and diversity of native plant species and tree seedlings can decline steeply following earthworm invasion (Figure 1). Some hardwood forest stands in northern Minnesota that had lush and diverse understory plant communities only 40 years ago now have only one species of native herb and virtually no tree seedlings remaining after earthworm invasion, although other factors may also have contributed to these changes (Hale 2004). Concerns have therefore been raised about the potential for widespread loss of native forest plant species and the stability of their communities in hardwood forest ecosystems following earthworm invasion.

Earthworm invasions in sugar maple-dominated forests in northern Minnesota were first noted 15 to 20 years ago (Mortensen and Mortensen 1998). Many stands contained discrete, visible leading edges of invasion where forest floor thickness decreased from 10 cm to zero in distances as short as 75 meters. Associated with the loss of the forest floor across the leading edges were rapid increases in earthworm biomass, the successive appearance of up to eight earthworm species, and substantial changes in soil physical and chemical properties (Hale et al. in press). When not associated with some underlying gradient in initial soil conditions, this leading edge of earthworm invasion provides an opportunity to assess the relationships of earthworm biomass and species assemblages to changes in the understory plant community, while controlling for site-specific factors that often thwart field-based comparative studies.

In study plots in northern Minnesota, the abundance and diversity of the herbaceous plant species and tree seedlings across leading edges of earthworm invasion decreased with increasing total earthworm biomass, but the magnitude of change depended on the species assemblage of the earthworm community (Hale 2004). Herbaceous plant communities were more strongly affected when the epi-endogeic species *Lumbricus rubellus* was present. A diverse community of herbaceous plants, including species that are often used as indicators of rich sugar maple-dominated hardwood forests in the Great Lakes region (such as *Caulophyllum thalictroides*, *Uvularia grandiflora*, *Trillium* spp, *Osmorhiza claytonii*, *Asarum canadensis*, and *Polygonatum pubescens*; Kotar 2002), could be found in areas where *L. rubellus* was not present. This diverse community of herbs was present even in some areas that supported a high biomass of earthworm species other than *L. rubellus*. However, where the *L. rubellus* biomass reached its maximum, the herbaceous plant community was dominated by *Carex pensylvanica* and *Arisaema triphyllum*, with rare occurrences of other native plant species. The disappearance of established populations of the rare goblin fern (*Botrychium mormo*) were also associated with the invasion of this earthworm (Gundale 2002).

Earthworm invasion of hardwood forests can have both direct and indirect effects on the understory plant community. Direct mortality of herbaceous plants and small tree seedlings rooted in the forest floor occurs when earthworms eat the forest floor out from under them (James and Cunningham 1989; Hale 2004). Earthworms may reduce plant regeneration by ingesting and burying seeds and by reducing the shelter offered by the forest floor layer, thus exposing seeds and seedlings to desiccation and predation by insects, small mammals, and other organisms (Leck 1989; Kostel-Hughes 1995). After initial earthworm invasion, smaller understory plant populations become more vulnerable to the impacts of deer grazing, which can lead to local extirpation (Augustine et al. 1998). Changes in soil nutrient dynamics, including increases in N and P loss due to leaching and decreased availability, may also affect the growth and composition of herbaceous plant communities following earthworm invasion (Bohlen et al. 2004b; Hale 2004).

Individual responses of plant species to earthworm invasion will be important in determining the trajectory of compositional changes in hardwood forests following earthworm invasion (Schau 2003; Hale 2004). In a greenhouse experiment, the addition of earthworms increased plant mortality and altered root-to-shoot ratios, but the magnitude and direction of those changes depended on both the plant species and the particular species of introduced earthworm. In field studies, *Arisaema triphyllum* (Jack in the pulpit) and *Allium tricoccum* (wild leeks) were both positively associated with increasing earthworm biomass (Hale 2004). Changes in the soil fungal community following earthworm invasion (Johnson et al. 1992; McLean and Parkinson 2000a; Lawrence et al. 2003), may have consequences for native understory plants, the vast majority of which are strongly mycorrhizal in northern forests (Brundrett and Kendrick 1988; Baskin and Baskin 1998). The dominance of earthworm-invaded sites by non-mycorrhizal herbs such as *C. pensylvanica* in Minnesota and *Allia petiolata* (garlic mustard) throughout the eastern US suggests that earthworms may enhance the competitive success of non-mycorrhizal herb species at the expense of mycorrhizal ones (Francis and Read 1994; Brussaard 1999; Hale 2004).

In addition to effects on understory herbs, earthworm invasion may influence overstory trees by influencing root distribution and function (Fisk et al. 2004). Invading earthworms can lower the soil surface by removing the forest floor, thus leaving tree roots exposed and changing
their distribution in the soil (Figure 1b). Forest sites in New York overrun by earthworms had fewer fine roots than sites without earthworms, while the higher N concentration in roots in invaded sites indicated that earthworms altered allocation and possibly also functioning of fine roots and the efficiency of N uptake. The long-term consequences of such changes for tree nutrition, seedling establishment, and seed survival are unknown.

## Conclusions

Earthworm invasion of northern forests is influenced by many factors and has multiple ecological effects mediated through the physical, geochemical, and biological changes that occur following invasion (Figure 4). The ecological consequences of these invasions depend upon which species or species complexes invade and the characteristics of the site being invaded. Enough evidence exists to generalize about some of these consequences, such as carbon loss and gross changes in microbial communities. Yet, despite the vast literature on earthworm ecology, too little evidence is available to make general predictions about their effects on nutrient availability or loss, soil erosion, and native microbial, plant, or invertebrate communities. Examining the response of the soil ecosystem to earthworm invasion may help clarify current concepts in earthworm ecology. It may even lead to new concepts that will supplant long-held views about the role of earthworms in forest ecosystems.

Most research on earthworm invasions has focused on the consequences of invasion at particular forest sites, with much less emphasis on the mechanisms of invasion and the broader landscape- and regional-scale factors that contribute to, or limit, invasion. These factors include agents of dispersal, the quantity and quality of resources at invaded sites, the nature of the overstory vegetation, and soil characteristics (Figure 4). Human activity has been implicated as an important cause of earthworm dispersal, including anglers dumping unused fishing bait, logging trucks carrying mud that contains earthworms or cocoons into newly logged areas, and the spreading of horticultural materials such as mulch or compost in gardens or along trails. Factors that affect either the quantity or quality of soil organic matter are important because organic matter is the primary resource base for invading earthworms. Low quantities of organic matter may represent an inadequate food source for earthworms with rapid growth rates. The quality of soil organic matter or plant litter, including such properties as the C:N ratio, or tannin (polyphenol) content, is known to influence earthworm feeding, growth, and fecundity. Forests with large amounts of soil organic matter but poor food quality may prevent establishment or limit growth and expansion of earthworm populations (Edwards and Bohlen 1996). Finally, soil factors, such as texture, acidity, richness of base cations, and moisture, influence the establishment and size of earthworm populations. These various factors may affect different species in dissimilar ways, so that conditions that prevent colonization by one species may not prevent the establishment of another.

The potential widespread loss of native understory plant species that could result from expanding earthworm invasion of northern hardwood forests raises the question of whether strategies could be developed to prevent further invasions or provide for restoration following invasion (Proulx 2003). Although local control of invasions may be possible in some situations, the magnitude and regional scale of invasion by non-native earthworms suggest that in the next few decades many northern temperate forests that currently lack earthworms will be invaded to some degree, rendering regional control strategies impractical. Reducing agents of dispersal by, for example, educating fishermen about the effects of earthworm introductions, limiting the spread of horticultural materials containing earthworms, or limiting new road con-
Invasive earthworms in temperate forests

PJ Bohlen et al.

stru ction into forest tracts, may help slow dispersal of exotic earthworm species. The decline in some under-
story plant species following invasion is due to the co-
ocurrence of other factors, such as high deer densities (Augustine et al. 1998). In this situation, control of earth-
worms, even if it were possible, may not be sufficient to enhance recolonization of understory herbs without efforts to control deer densities.

Northern temperate forests are facing rapid environ-
mental transformations that include climate change, species invasion, changes in land-use patterns, and con-
tinued atmospheric deposition. Earthworm invasion is an additional factor that may interact with, and contribute to, these changes. Positive or negative interactions may occur, such as an acceleration of C loss (climate warming and earthworm invasion), increased gaseous or hydro-
logic flux of N (atmospheric deposition and earthworm invasion), or nutrient stress (drought or pollution and earthworm invasion). The increasing length of growing seasons and enhanced productivity currently occurring at northern latitudes (Papadopol 2000; Zhou et al. 2001) are likely to contribute to a more rapid northward expansion of earthworm populations and introductions of exotic species formerly limited by colder temperatures. Earthworm invasions are likely to interact with other biolo-

gical invasions occurring concurrently or predicted to occur in forest ecosystems (Hansen et al. 2001). These invasions will have important consequences, not only for biodiversity and conservation, but also for nutrient cycling and ecosystem processes in northern forest ecosys-
tems.

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