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The influence of invasive earthworms on indigenous fauna in ecosystems previously uninhabited by earthworms

Sonja Migge-Kleian · Mary Ann McLean · John C. Maerz · Liam Heneghan

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Abstract Recent studies on earthworm invasion of North American soils report dramatic changes in soil structure, nutrient dynamics and plant communities in ecosystems historically free of earthworms. However, the direct and indirect impacts of earthworm invasions on animals have been largely ignored. This paper summarizes the current knowledge on the impact of earthworm invasion on other soil fauna, vertebrates as well as invertebrates.

Earthworm invasions can have positive effects on the abundance of other soil invertebrates, but such effects are often small, transient, and restricted to habitats with harsh climates or a long history of earthworm co-occurrence with other soil invertebrates. Middens and burrows can increase soil heterogeneity and create microhabitats with a larger pore size, high microbial biomass, and microclimates that are attractive to micro- and mesofauna. Under harsh climatic conditions, the aggregates formed by earthworms may increase the stability of soil microclimates. Positive effects can also be seen when comminution and mucus secretion increase the palatability of unpalatable organic material for microorganisms which are the main food of most micro- and mesofaunal groups. For larger invertebrates or small vertebrates, invasive earthworms may become important prey, with the potential to increase resource availability.

In the longer-term, the activity of invading earthworms can have a strong negative impact on indigenous faunal groups across multiple trophic levels. Evidence from field and laboratory studies indicates that the restructuring of soil layers, particularly the loss of organic horizons, physical disturbance to the soil, alteration of understory vegetation, and direct competition for food resources, lead directly and indirectly to significant declines in the abundance of soil micro- and mesofauna. Though studies of invasive earthworm impacts on the abundance of larger invertebrates or vertebrates are generally lacking, recent evidence suggests that reduced abundance of small soil fauna and alteration of soil microclimates may

S. Migge-Kleian (✉)
Institute of Zoology and Anthropology, University of Göttingen, Berliner Strasse 28, 37073 Göttingen, Germany
e-mail: smigge@gwdg.de

M. A. McLean
Department of Life Sciences, Indiana State University, Terre Haute, IN 47809, USA

J. C. Maerz
Warnell School of Forest Resources, University of Georgia, Athens, GA 30602, USA

L. Heneghan
Environmental Science Program, DePaul University, 2325 North Clifton Avenue, Chicago, IL 60614-3207, USA

be contributing to declines in vertebrate fauna such as terrestrial salamanders. Preliminary evidence also suggests the potential for earthworm invasions to interact with other factors such as soil pollution, to negatively affect vertebrate populations.

Keywords Biological invasion · Collembola · Disturbance · Earthworm invasion · Oribatida · Review · Soil fauna · Salamander

Introduction

The invasion of earthworms into ecosystems previously devoid of earthworms is typical of other biological invasions involving "ecosystem engineers." Ecosystem engineers are organisms which, by their structure or activities, alter physical resource availability for other organisms (Jones et al. 1994, 1997; Crooks 2002). Significant ecosystem effects were observed in North America with an exotic invader, the European wild boar (*Sus scrofa* L.). Rooting in the soil by these animals reduced forest floor depth, altered soil chemistry and increased nutrient leaching (Bratton 1975; Singer et al. 1984). The invasion of North America by exotic earthworms has taken place since the first European settlers landed on the continent (Gates 1982) and has had similar dramatic effects on soil processes (Scheu and Parkinson 1994; Bohlen et al. 2004b); however, this invasion has worked underground and out of the sight of public interest. Even recent reviews on biological invasions of ecosystem engineers failed to recognize the importance of earthworm invasion and completely overlooked the existing literature on this topic. However, earthworms, through their consumption and translocation of organic and mineral materials in soil, strongly alter nutrient availability and the physical structure of the soil (Lee and Foster 1991; Frelich et al. this issue). One major consequence of altering the physical structure of a habitat is the alteration of habitat complexity or heterogeneity. Biotic diversity and abundance tend to be positively correlated with habitat complexity (MacArthur and MacArthur 1961; Hewitt et al. 2005). Impacts of invasion by ecosystem engineers depend on whether they or their activities increase or decrease habitat complexity for other biota (Crooks 2002). In the short term, earthworm activities often increase microhabitat complexity, but decrease it in the longer term. We would then expect that invasive earthworms would initially increase and then later decrease biotic diversity and abundance.

Another major consequence of earthworm activity in the soil is the frequent disturbance of the soil habitat. Soils containing dense earthworm populations are characterized by large pores and aggregate structures offering many microhabitats for other soil fauna. Conversely, bioturbation, the mixing of substrates due to earthworm burrowing and casting activity, may impose high levels of disturbance especially for soil fauna of smaller body sizes. The degree of disturbance varies with the community structure of the earthworm population. In communities dominated by epigeic earthworm species, activities are restricted to the upper layers of the soil profile, where they may strongly influence the processing of organic material and create aggregates of smaller size (Lee and Foster 1991; McLean and Parkinson 1997). In contrast, soils inhabited by mainly endogeic earthworm species often exhibit a more or less intact litter layer while the mineral soil has been heavily disturbed, a network of burrows persists and organically enriched mineral aggregates are formed (Edwards and Shipitalo 1998). In the presence of anecic earthworm species, the level of disturbance for other soil fauna increases since organic material at the surface is reduced and incorporated into the soil matrix. Biotic diversity can be positively associated with intermediate levels of disturbance (Connell 1978; Foissner et al. 2005); thus we would expect a higher diversity and abundance of soil fauna in invaded sites with moderate densities of earthworms, whereas high earthworm densities would likely decrease soil fauna diversity and abundance.

Many soil organisms live in the rich organic layers of soils because those layers provide moisture and more climatically stable living spaces and food, either from decomposing plant organic matter or other fauna. Disturbance to organic layers by earthworms may pose a challenge to other soil fauna, and adaptation over long periods of time has generated species-rich communities in habitats where earthworms are present (Schaefer 1999). However, the invasion of earthworms into ecosystems previously devoid of earthworms and the rapid transformation of soils that follows may pose significant challenges to organisms not adapted to earthworm activities (Bohlen et al. 2004a; Hale 2004; Hale et al. 2005; McLean et al., this issue). Consequently, the influences on soil fauna can be great. In North America, for example, vast areas of the northern parts of the continent remained free of earthworms after the last glaciation and have only in the last century been invaded by European and Asian earthworm species. In addition, many areas of North America that had native earthworm fauna have experienced a turnover to exotic species. The extensive invasion of North America provides excellent research grounds to investigate the impacts of earthworm invasions on historically earthworm-free ecosystems (Parkinson et al. 2004) and ecosystems with a history of similar taxa having been present (Hendrix et al., this issue). In the following sections, we review the current literature on the short- and long-term impact of earthworms on other fauna and we evaluate the empirical evidence for potential impacts. Available information on the impacts of earthworm invasion comes largely from increasing numbers of studies of earthworm invasions of north temperate forests that were historically earthworm-free.

Impact on microarthropods

The influence of earthworms on soil mesofauna (mainly microarthropods and enchytraeids) differs strongly between systems where co-existence of these two groups has a long history and those systems previously devoid of earthworms. Additionally it is important to separate between long-term and short-term effects of earthworm activity on these small invertebrates. Few studies are available that investigate the effects of earthworms on microarthropods and, of those, mainly Collembola and oribatid mites have been studied.

Observations in soils with a long history of earthworm activity show that soil processed by earthworms or mixed with their excreta can be attractive in the short-term for collembolans (Salmon and Ponge 1999; Salmon 2001; Wickenbrock and Heisler 1997). The positive short-term response may be due to increased habitat complexity, i.e., the addition of mucus which supports bacterial and fungal growth, and the increased pore size of soil which enables more species to also inhabit deeper layers of the soil profile (Marinissen and Bok 1988). Midden formation by some earthworm species such as *Lumbricus terrestris* L. creates microhabitats on the soil surface which can attract not only saprophagous mesofauna (Hamilton and Sillman 1989) but also their predators (Maraun et al. 1999). However, findings are not always consistent in these studies even when conducted in similar habitat types such as deciduous forests in central Europe: while Bayoumi (1978) reported higher densities of oribatid mites in earthworm burrows compared to the surrounding soil, Maraun et al. (1999) showed that Oribatida were more abundant in non-midden soil compared to the middens of *L. terrestris*. These differences could be due to investigations on different microhabitats (burrows in the soil constructed by several earthworm species compared to middens on the surface by *L. terrestris*). Microarthropod densities in earthworm middens may also vary seasonally, being high in late summer when old middens are enriched in organic matter but undisturbed by recent earthworm activity, and low in fall when middens are disturbed (Hamilton and Sillman 1989). Positive responses in microarthropod density are often small in magnitude (<100% increase). For example, Loranger et al. (1998) reported an increase in Collembolan density from 8,900 to 13,300 ind m^{-2} between low and high-density earthworm plots, and Maraun et al. (1999) reported an increase in density from 32,200 to 52,400 ind m^{-2} between midden and non-midden soils. In habitats used in the latter study, natural long-term variation in Collembola abundance ranged between 18,600 and 46,800 ind m^{-2} (Wolters 1998), so the positive effect of earthworm middens was relatively small and remained within the natural range of Collembola density.

Investigations at the frontier of earthworm invasions into historically earthworm-free soils show that the invasion of epigeic species such as *Dendrobaena octaedra* (Savigny) in pine forests can have complex effects on microarthropod density and diversity (Parkinson and McLean 1998; McLean and Parkinson 2000a). In the pine forests of western Alberta (West Canada) where harsh climatic conditions of the continental climate limit microbial, micro- and mesofaunal activity in the upper litter layers, earthworm activity was positively correlated with species richness and diversity of oribatid mites (McLean and Parkinson 2000a). This could be explained by the occasional casting activity by *D. octaedra* in this horizon during conditions of higher moisture which could increase microhabitat heterogeneity in this layer (Anderson 1978). Again, the positive effects of earthworm invasion appeared small and relatively ephemeral. When earthworms were added to intact soil cores containing indigenous soil fauna, densities of Collembola and tarsonemid mites in treatments with earthworms were significantly higher than in treatments where no earthworms had been added; however, the abundance of the dominant oribatid mite species, *Oppiella nova* (Oudemans) declined (McLean and Parkinson 1998a). The relatively harsh habitats for these studies may partly explain the positive effects of earthworms on microarthropods. In addition, the short-term positive response of some microarthropods may have been the indirect result of the negative effect of earthworms on the dominant mite species, or reflect species-specific responses to invasion.

Despite the potential for relatively small, short-term positive responses to earthworm invasion, several recent studies indicate that over the long-term, earthworm invasions have significant, negative impacts on soil microarthropods. Reduced habitat complexity due to litter consumption, competition for organic resources, and mechanical disturbance due to earthworms processing and burrowing through the mineral soil and organic horizons are implicated in long-term negative effects of earthworms on microarthropods, especially the hemi- and epedaphic types (Maraun and Scheu 2000; Maraun et al. 2003). Competition for food between large earthworms and small saprophagous microarthropods has been postulated to be important (Brown 1995), but good experimental evidence for this is still lacking. In laboratory experiments with earthworms and microarthropods of Spanish meadow soil, microarthropod density was generally lower within cages where earthworms were present than outside of the cages, indicating that the small animals either had been destroyed by the earthworms or had moved into the undisturbed soil outside of the cages (Gutiérrez López et al. 2003). Other manipulative studies, such as the increase of earthworm populations beyond natural levels due to the addition of glucose-fertilizer (Maraun et al. 2001) or the mechanical perturbation of the forest floor by sieving (Maraun et al. 2003), show that the majority of microarthropods are very sensitive to increased levels of disturbance. Oribatid mite and Collembolan density and diversity were lowest in highly disturbed field plots.

Long-term field studies of earthworm invasion are rare since most European habitats that are suitable for earthworms in terms of climate and soil conditions are already inhabited by them (see Pop and Pop, and Tiunov et al., this issue). However, even in Europe there are landscapes in which earthworm colonization and the succession of animals could be observed. For example, following accumulation of organic material and colonization of microarthropods in reclaimed opencast coal mining areas in Germany, densities of microarthropods increased over time until earthworms colonized those soils (Wanner and Dunger 2002). As earthworm populations increased, a correlated decline in microarthropod populations was observed until a lower but more constant population density was reached (Dunger 1991). In the eastern Rocky Mountains of Alberta, Canada, where *Dendrobaena octaedra* has been invading forest soils historically free of earthworms, long-term negative effects of earthworm invasion on microarthropod diversity and abundance are apparent once earthworm biomass and activity are high in the lower organic layers (F and H layer). In this environment, microarthropods prefer habitats in lower organic layers of the well-stratified soil (Mitchell 1978; McLean and Parkinson 2000a), and these layers become homogenized into earthworm casts by invading epigeic earthworm species. As in other studies, competition for food resources may also contribute to the long-term negative effects of earthworm invasion on microarthropods in this environment (e.g., McLean and Parkinson 1998b, 2000b).

One reason that earthworm invasions may have greater negative long-term impacts is the increase in earthworm abundance and species richness over time. In Western Canada, epigeic species often move into habitats faster and are recorded in higher numbers than endogeic or anecic species (Scheu and McLean 1993). At the time of Scheu and McLean's study in 1993, the anecic species *L. terrestris* was found frequently only in gardens within the city or village limits. During the last decade this earthworm species, which is sold as fishing bait, has been invading natural ecosystems such as aspen forests and riparian habitats (D. Parkinson, S. Migge-Kleian, S. Scheu personal observation). Studies investigating the influence of *L. terrestris* alone and in combination with endogeic earthworms (*Octolasion tyrtaeum* Örley and *Aporrectodea caliginosa turgida* Savigny) have documented dramatic changes in the soil and organic layer profile (Migge 2001). These larger earthworm species mix organic material and mineral soil in much greater quantities than *D. octaedra*, and therefore, more strongly compete with microarthropods for microbial and organic food, and alter the habitat through strong mechanical disturbances. In the laboratory, the addition of *L. terrestris* and endogeic earthworms to aspen forest soil incubated for 12 months at constant temperature and moisture resulted in dramatic decreases of microarthropod diversity and abundance. Oribatid mite abundance, for example, declined from 127,000 to 4,000 ind m^{-2}, an effect that was similar for all microarthropod groups examined (Migge 2001). Results from this laboratory experiment indicate that the endogeic earthworm species' impact is mostly due to mechanical disturbance (i.e., burrowing pressure and soil movement) rather than to direct alteration of the habitat (i.e., litter disappearance and aggregate formation, Migge 2001).

Field studies of earthworm impacts in historically earthworm-free aspen forests showed similar declines in Collembola and gamasid mite populations (Migge 2001). In the field, however, seasonally drier conditions slow down earthworm impacts on soil profiles considerably. Many earthworm species become inactive (quiescence or even diapause) when soil moisture content drops below critical levels (Edwards and Bohlen 1996). In milder climates of the north-eastern United States, earthworms can have a dramatic impact upon the structure of soils, resulting particularly in the virtual elimination of the litter layer (Bohlen et al. 2004b). The process of shifting woodlands from those that have an accumulation of slowly decomposing litter to ones where the litter layer disappears during the course of the year is exacerbated by a combination of earthworm invasion and the proliferation of invasive shrubs, many of which have a low C:N ratio (Heneghan et al. 2002). For instance, woodlands that are invaded by *Rhamnus cathartica* (European buckthorn) and earthworms have little leaf litter during the growing season. This results in the virtual collapse of both oribatid mite and collembolan communities (L. Heneghan unpublished data). Heneghan and Bernau (unpublished) sampled these communities in invaded areas and compared them to the litter in non-invaded areas in June and December of 2002, and April 2003. There was a consistently lower abundance of collembolans and mites in *R. cathartica* plots. For instance, in June 2002 there was an average of 3,255 ind m^{-2} in uninvaded areas, and 235 ind m^{-2} in invaded plots. To a large extent this was a function of the amount of dead organic matter (DOM) in the plots. However, even when abundances were expressed per unit mass of DOM there were differences between plots in the April 2003 samples, indicating direct earthworm effects.

Impact on Enchytraeidae and microfauna

Enchytraeids are abundant in rich organic layers of well-stratified mor and moder soils, and play an important role in soil organic matter fragmentation and humification (Koutika et al. 2001) especially in the absence of earthworm activity. Data on the impact of earthworm invasion on indigenous Enchytraeidae, such as in northern North America, are not yet available. However, in European systems where enchytraeids and earthworms are both native, negative effects of earthworms on enchytraeid abundance appear comparable to the effects of invasive earthworms on microarthropods in other systems. Compared to the organic layers of moder soils, where enchytraeid density can be 108,000 ind m^{-2}, enchytraeid density in mull soils characteristic of the conditions created by earthworm invasion may only be 22,300 ind m^{-2} (Schaefer and Schauermann 1990). In laboratory studies, Enchytraeidae abundance was reduced when they were incubated with epigeic (*Lumbricus rubellus* Hoffmeister, [Haimi and Boucelham 1991]; *D. octaedra* [Huhta and Viberg 1999]), endogeic (*Aporrectodea caliginosa* [Räty and Huhta 2003]) or anecic earthworm species (*L. terrestris* [Lagerlöf and Lofs-Holmin 1987]). As with soil microarthropods, competition with earthworms for organic resources and physical disturbance to organic horizons may contribute to the negative effects of earthworms on enchytraeids. In addition, Dash et al. (1980) suggest selective predation by earthworms on enchytraeids. Reports of positive influences of earthworms on Enchytraeidae are rare and mainly involve special microhabitats such as middens of anecic *Lumbricus* species. In forests of long co-existence history such as oak-hornbeam forests in Hungary (Dózsa-Farkas 1978) or highly disturbed habitats like agricultural soil (Schrader and Seibel 2001), the formation of middens is beneficial to enchytraeid populations compared to the surrounding soils, probably due to the increased quantity of organic material.

The influence of earthworms on microfauna groups (Protozoa, Nematoda) has been reviewed by Brown (1995), and recent studies have added to the understanding of these macrofauna-microfauna interactions (Huhta and Viberg 1999; Tiunov et al. 2001; Ilieva-Makulec and Makulec 2002; Aira et al. 2003; Räty and Huhta 2003). In general, two effects can be distinguished. Earthworms produce casts, burrows and/or middens which are enriched in readily available nutrients, thus changing bacterial and fungal composition and promoting microfloral growth (e.g. Tiunov and Scheu 2000a, b). This forms attractive microhabitats for protozoa and nematodes compared to surrounding soil (Shaw and Pawluk 1986, Tiunov et al. 2001, Aira et al. 2003). On the other hand, earthworms process organic and/or mineral material and thereby ingest Protozoa (Bonkowski and Schaefer 1997) and Nematoda (Dash et al. 1980) and most likely also digest them, thus using them as a food source (Piearce and Phillips 1980), and reducing their numbers. In laboratory mesocosms of coniferous or mixed forest floor with added *D. octaedra* or *L. rubellus* and *A. caliginosa*, nematode abundance decreased remarkably and nematode community structure changed significantly (Huhta and Viberg 1999, Räty and Huhta 2003). Apparently the first contact with earthworm activity is crucial to nematode communities: Bacterial feeding nematodes declined strongly during the first weeks of incubation when *L. rubellus* was added to meadow soil (Ilieva-Makulec and Makulec 2002) or European earthworm species were introduced to New Zealand pastures (Yeates 1981).

Investigations on protozoans and nematodes in areas previously devoid of earthworms are still lacking. Therefore, we can only speculate as to the impact invading earthworms will have on the microfauna. In addition to structural changes in the habitat, earthworm invasion will change the food source (e.g., organic matter and microorganisms) for these organisms quite strongly (McLean and Parkinson 1998b, 2000b, Scheu and Parkinson 1994, Groffman et al. 2004; also see Frelich et al. and McLean et al., this issue). Changes in the fungal and bacterial community will inevitably induce changes in the microfaunal community. A shift towards dominance of bacterivorous nematodes and a reduction of fungivorous nematodes, for example, could be the consequence. Plant parasitic nematodes might be affected only indirectly by invasion of epigeic earthworm species through dramatic and rapid changes in the forest floor and understory plant communities of hardwood forests (Frelich et al. this issue). There is still much need for investigations on the microfauna in these systems since, for example, protozoan activity is tightly linked to plant growth (Bonkowski 2004), and might help restore equilibrium in the heavily earthworm-impacted plant communities of the north-central USA described by Hale (2004) and Hale et al. (2005).

Impact on macro- and megafauna

Earthworm invasions have been the focus of soil biologists only for the last 15 years, so it is not surprising that very little data are available on the influence of these invasions on macrofauna of the above-ground food web. There have been few studies to evaluate earthworm impacts on invertebrate macrofauna, either saprophages (e.g., isopods, diplopods) or predators (e.g., spiders, beetles, centipedes). Earthworm-free forests of North America included native and introduced isopods and diplopods prior to widespread invasion by earthworms, so presumably the strong effect of earthworms on eliminating forest organic horizons will have a negative effect on these fauna. Earthworm invasion impacts on predatory macroinvertebrates may be more complicated. Since earthworms are prey for some large invertebrate predators, such as carabid beetles (Lukasiewicz 1996) and centipedes (Poser 1988), one might predict the effects of earthworm invasion on predator populations to be positive. In agricultural systems in the United Kingdom for example, the predatory carabid *Pterostichus melanarius* (Illigers) preys on earthworms when densities of other prey are low (Symondson et al. 2000). The presence of earthworms appears to prevent *P. melanarius* population crashes during periods of low abundance in their primary prey. Despite their potential value as prey, invasive earthworms may have indirect, negative effects on predatory macroinvertebrates. Many forest floor macroinvertebrates rely on thick organic layers as habitat to protect against dehydration, extreme temperatures, and predators, thus they could be negatively affected by the loss of organic layers during earthworm invasion. Predators that rely on other soil fauna as prey, particularly species or individuals that cannot prey on earthworms, may also be indirectly negatively impacted by declines in soil arthropods that result from earthworm invasion.

A similar argument could be made for the potential impacts of earthworm invasion on predatory vertebrates that now exploit introduced earthworms. Ovenbirds (*Seiurus* spp.) feed on insects, spiders and other invertebrates found on or near the forest floor. One might expect that ground foraging birds would profit from the introduction of earthworms as a food supply. However, the Minnesota Breeding Bird Survey reported a nearly 50% decline in ovenbird nesting success in the Chippewa National Forest associated with decreases in forest floor thickness believed to be the result of earthworm invasion (Mattsson 2001). A survey of small mammals across a leading edge of earthworm invasion was conducted in a sugar maple forest on the Chippewa National Forest (Buech et al. unpublished data). Red-backed vole and shrew abundance declined from the non-invaded forest areas to the earthworm-invaded areas only ~150 m away where the forest floor had been nearly eliminated. Woodland salamander abundance and diversity have declined in relation to earthworm invasion in Sylvania Wilderness Area in the Ottawa National Forest of Michigan (Bergeson, personal communication), and declining salamander abundance has been linked to earthworm associated declines in forest litter across 10 sites in New York and Pennsylvania (Maerz et al. unpublished data).

Currently, the strongest evidence of the potentially complex effect of earthworms on some vertebrate populations comes from studies in historically earthworm-free forests of New York and Pennsylvania. Maerz et al. (2005) found that adult red-backed salamanders (*Plethodon cinereus Green*) consume large numbers of introduced earthworms in such forests, leading to increases in adult salamander food availability compared to forest habitats that remain free of earthworms. However, exploitation of earthworms was strictly limited by climate to cool spring and autumn evenings when there was rain. Consequently, earthworms are a potentially profitable but unpredictable resource for *P. cinereus* compared to the more abundant macro- and meso-invertebrates that characterize their diets in forests free of earthworms (Maerz et al. 2005; Burton 1976). The consequences of this new resource dynamic for salamander populations has not been fully investigated, but, as one might predict, the positive effects of earthworms on adult salamander resources are associated with increased female fecundity (Maerz 2000) and reduced territorial behaviour (Maerz and Madison 2000). However, there is no evidence that access to earthworms has a positive effect on *P. cinereus* abundance (Maerz and Madison 2000). Rather, recent evidence suggests that earthworm invasions may lead to salamander population declines (Maerz et al. unpublished data). Salamander abundance is known to decline with disturbance that leads to the loss of the forest floor organic layer (Petranka et al. 1993; Pough et al. 1987). *P. cinereus* respire through moist skin, thus the strongly dependent on moist organic layers to protect against dehydration and high temperatures (Feder 1983). Further, juvenile salamanders too small to prey on earthworms depend on abundant soil mesofauna such as Collembola and mites as prey. The effects of earthworm invasions on soil microclimate and the availability of small invertebrates are likely to reduce forest habitat quality for salamander populations and other vertebrate with similar needs.

Earthworm invasions of North American forests may also interact with other factors to affect vertebrate populations. Burning of fossil fuels has caused widespread deposition of high concentrations of heavy metals and other pollutants across north-eastern North America. Once incorporated into the soil, these metals have the potential to enter the food chain. Whether earthworms are relatively more effective than other soil fauna at moving metals into food webs has not been addressed empirically, but several adaptations of earthworms make them particularly effective at absorbing and accumulating heavy metals from soils into their tissues (Reinecke et al. 2000). In addition, earthworm guts often contain large amounts of soil that are ingested secondarily by predators consuming earthworms. Several studies have documented high concentrations of heavy metals in earthworm tissues at polluted sites (Ireland 1979), and that earthworms are an effective conduit of those metals into the tissue of vertebrate predators, including amphibians (Ireland 1977) and small mammals (Reinecke et al. 2000).

Conclusions

Studies of microarthropods in western Canada and the mid-western USA, and vertebrates in the north-eastern USA demonstrate the large potential impact of earthworm invasions on a range of small and large fauna across multiple trophic levels. Over the long-term, soils that are suitable for earthworms will, if the nutrient status permits, be transformed into mull humus that may be species rich but support lower abundances of many fauna that typically inhabit moder or mor humus soils (Schaefer and Schauermann 1990; Schaefer 1999). Species that are adapted to disturbance and change in habitat structure and food resources, or those that are able to adapt quickly, may be more likely to persist or colonize earthworm-invaded ecosystems. Species that are disturbance-sensitive or that compete with earthworms are likely to show marked declines as a consequence of earthworm invasion. The effects of earthworm invasions may also depend on other factors, such as tree or understory composition. Effects may be larger in forests composed of trees with ‘‘high quality’’ litter, such as maple and aspen that dominate much of the north temperate forests of North America, compared to forests dominated by trees with more recalcitrant litter such as oak or beech species. In the latter forests, the accelerated decomposition of less palatable litter by earthworms may have a positive effect on some native fauna (Tiunov et al. 2001). The invasion of endogeic and/or anecic earthworm species into coniferous forests, a process that has already been observed in the eastern Canadian Rocky Mountains, will be especially interesting (Dymond et al. 1997, D. Parkinson, personal communication; see also McLean et al., this issue). Mixing of nutrient rich mineral soil with acidic coniferous forest floor material could change the whole understory and soil community.

In many forests, earthworm invasions continue as new species spread from human habitations into natural areas. In addition, new species, such as members of the Asian genus *Amynthas*, are rapidly spreading into new areas. Ultimately, the cumulative impact on an ecosystem and its animal community may depend on the succession and total diversity of invading earthworm species. Impacts will be different if endogeic rather than epigeic earthworm species are the first to invade an ecosystem previously devoid of earthworms. Many questions arise, e.g., what will happen if an anecic earthworm species invades simultaneously? How could this affect the previous invader? Studies show that growth rates of earthworms can be negatively affected if other earthworm species are present (Lowe and Butt 1999).

Invading earthworms will dramatically alter not only soil structure, nutrient cycles and the community of microorganisms and plants (Hale 2004; Frelich et al. and McLean et al., this issue) but also animal communities, including small invertebrates, mammals, birds and other vertebrates. All levels of the food web, below- as well as above-ground, may be affected. The expanding frontiers of earthworm invasion provide an opportunity to investigate soil food web interactions but also may reveal hitherto unrecognized links between above- and below-ground communities in forests.

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