Paul F. Hendrix
Editor

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Edited by

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Cover Photo: Palu Valley in Sulawesi, Indonesia, showing the contrast between arid and over-grazed land and rich river valley agriculture.
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Table of contents

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INTRODUCTION

Biological invasions belowground—earthworms as invasive species

Paul F. Hendrix

Current views of biological invasions in terrestrial ecosystems have been dominated by what we see above the soil surface–exotic plants, vertebrates and insects (e.g., Pimentel 2002; Sax et al. 2005). Less conspicuous, but equally important with respect to ecosystem processes are invasions by soil organisms, which are occurring literally beneath our feet (Ehrenfeld and Scott 2001). Familiar examples include the South American fire ant (*Solenopis invicta*) which has invaded southern North America and Australia, and the New Zealand flatworm (*Arthurdendyus triangulatus*) which has become wide-spread in the United Kingdom; both have caused considerable ecological and economic damage.

There is mounting evidence that exotic earthworm invasions are increasing worldwide, sometimes with significant effects on soil processes and plant communities. At least 100 earthworm species have achieved distributions beyond their places of origin (Lee 1985; Fragoso et al. 1999). As with other invasive organisms, earthworm introductions appear to be facilitated by global commerce, both inadvertently with the importation of soil-containing materials (e.g., agricultural and horticultural products) and intentionally for use in commercial applications (e.g., waste management and land bioremediation).

Recent reviews have considered earthworm invasions, with a focus on North America where European Lumbricidae have dispersed into previously glaciated regions of Canada and the USA (Hendrix and Bohlen 2002; Bohlen et al. 2004a, b; Parkinson et al. 2004; James and Hendrix 2004). In this special issue of Biological Invasions, we expand on this discussion and explore some of the broader dimensions of earthworm invasions through a series of papers written by an international group of soil ecologists who are studying earthworm invasion biology and ecology worldwide. The papers were conceived at a workshop in Athens, Georgia, USA, in 2003, presented at a special symposium at the 14th International Colloquium on Soil Zoology, in Rouen, France in 2004, and subsequently submitted to rigorous peer-review for the journal. As described in the following synopsis, these ten papers cover several aspects of earthworm invasions, including mechanisms and pathways of invasions and characteristics of invasive species; biogeographic case studies from sub-arctic to tropical regions; effects on other biota and ecosystem processes both in areas devoid of and inhabited by indigenous earthworms; and beneficial aspects of earthworm introductions and means by which invasions might be controlled.

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Characteristics of some earthworm species (e.g., parthenogenesis, environmental plasticity, ability to aestivate) appear to make them particularly successful as invaders (Fragoso et al. 1999; James and Hendrix 2004). Terhivuo and Saura consider in more detail the biology of earthworm invasiveness among the European Lumbricidae, one of the most successful groups of invasive species. Analysis of clone pool structure and dispersal of several parthenogenetic species in Northern Europe shows the importance of different species' adaptations to particular modes of dispersal, such as anthropochory in *Octolasion tyrteum*, and hydrochory in *Eiseniella tetraedra* and *Dendrobaena octaedra*. Rapid adaptation of parthenogenetic clonal populations may be an especially important mechanism for successful invasions. Terhivou and Saura further note that North America ‘‘appears to be a natural laboratory to study the invasion and dispersal of parthenogenetic earthworms.’’ For example, *O. tyrteum* has a somewhat restricted distribution within wetlands and riparian zones in its native Europe, but parthenogenetic descendants have invaded a much wider variety of habitats, including highly disturbed agricultural soils in eastern North America.

Case studies have been useful in the search for spatial and temporal patterns of earthworm invasions, and four are included in this issue. Pop and Pop present a retrospective study of changes in earthworm communities over the past three decades in the Carpathian Mountains of Romania. They show that parthenogenetic *Octolasion lacteum* and the now ubiquitous *Lumbricus terrestris* have replaced endemic or rare species at a number of sites since the original surveys were conducted 20–30 years ago. This rapid transition is attributed to the wide ecological tolerances displayed by the invasive compared to the endemic species. This is one of only a few studies that have documented the change in earthworm community structure during a finite period of time.

Tiunov et al. present one of the first comparative analyses of earthworm invasions in two climatically similar regions (Northeastern Europe and the North American Great Lakes region) that had been earthworm-free since the last Pleistocene glacial retreat. Similar earthworm species (European lumbricids) and similar rates and patterns of spread, particularly as facilitated by human activities, were observed in both cases suggesting some general trends in earthworm invasion ecology. Considerable range expansion of these earthworms is considered likely, especially for the cold-tolerant *D. octaedra*. Interestingly, the other predominant cold-tolerant species in northern Europe and Russia, *Eisenia nordenskioldi*, has not yet been reported in North America but there is no apparent reason why it cannot invade if it is introduced, for example through the mechanism of ‘‘jump dispersal.’’

Frelich et al. review the interesting case study of an earthworm invasion in Minnesota, USA, where exotic lumbricids are associated with significant changes in soil characteristics, understory plant composition, and interactions with deer herbivory. They outline a series of mechanisms that may be contributing to an earthworm-induced ‘‘forest decline syndrome,’’ including mixing of organic and mineral soil horizons, modification of seed and seedling dynamics, changes in mycorrhizal abundance and colonization rates, increases in herbivory, and alteration of nutrient availability and plant productivity. These cascading effects of multi-species earthworm invasions are consistent with an ecosystem scale ‘‘invasional meltdown’’ (Simberloff and Von Hole 1999), and could interact with climate warming to cause major changes in the structure and function of these north-temperate forests.

In a fascinating historical review of earthworm invasions in tropical regions, González et al. note that the history of exotic earthworm introductions ‘‘is much more complex in the tropics than in temperate North America, as it is related to the complex human history of migration and use of the landscape, water barriers and island ecosystems.’’ Using the pan-tropical, peregrine earthworm, *Pontoscolex corethrurus*, as a case study they conclude that land use is a major factor influencing earthworm community structure and the establishment of exotic species in tropical ecosystems. Although *P. corethrurus* has also invaded undisturbed areas (e.g., cloud forests in Puerto Rico and Taiwan) it is most prevalent in disturbed sites such as pastures converted from rain forests, the pastures then becoming likely sources for further invasions into those forests. Particular reproductive features of tropical earthworms (e.g., continuous breeding, high fecundity, short incubation period) may contribute to their invasiveness throughout the tropics.

Impacts of earthworm invasions on soil processes have been well documented (e.g., Scheu and Parkinson 1994, Bohlen et al. 2004a, b) but effects on soil biota whose activities drive many of these processes are not adequately known. Two papers address this problem. McLean et al. review a voluminous literature on earthworm interactions with microbial communities, in comparison with the relatively few studies of microbial responses to recent earthworm invasions. Reduction in fungal abundance and diversity (including disruption of mycorrhizal hyphae) and vertical shifting of microbial biomass from forest floor to mineral soil appear to be consistent microbial responses to earthworm invasion. Furthermore, overall microbial activity may decline initially after invasion but later increase, suggesting an adaptation of the microbial community to invasion-induced changes in soil characteristics. Migge-Kleian et al. explore the little-studied impacts of earthworm invasions on other soil fauna. Evidence suggests that abundance of micro- and macrofauna may actually be enhanced in the short-term following invasion, due to increased habitat heterogeneity (e.g., burrows and middens) and resource availability (earthworms as prey). However, longer-term effects on many faunal groups may be negative due to reduction or loss of litter, mixing of soil horizons, and alteration of microhabitat conditions.

As noted, many of the studies of earthworm invasions have been done in previously glaciated areas devoid of indigenous earthworms. Despite the high level of interest and intensity of this work, these may be more special cases than the invasion of exotic earthworms into temperate, subtropical and tropical regions inhabited by native earthworm fauna. Adding to the discussion by González et al. noted above, Hendrix et al. review the literature on interactions between native and exotic earthworms and explore habitat disturbance, competitive exclusion, co-existence and biotic resistance as factors involved in earthworm invasions. Evidence suggests that co-occurrence of native and exotic species is common and occurs even in relatively undisturbed ecosystems. However, it is not known if co-existence is persistent or a transient state that eventually may lead to competitive exclusion of native species. While numerous extrinsic factors influence the success or failure of earthworm invasions (e.g., propagule pressure, ‘‘open’’ niche space), resistance to invasion may be more related to habitat characteristics than to direct interactions with indigenous earthworms.

The last two papers consider the all-but-neglected problem of dealing with invasive earthworms prior to, during or after their establishment and/or naturalization in new areas. Baker et al. discuss the interesting case of agricultural, pastoral and reclaimed ecosystems where exotic earthworms often are viewed as beneficial to soil properties and plant productivity. In some cases they may have been introduced intentionally, creating experiments for studying basic earthworm invasion biology, as well as potential applications of earthworm inoculation. However, this issue also raises the ‘thorny dilemma’ of achieving the benefits of earthworm introductions for land reclamation at the risk of initiating invasions into nearby pristine ecosystems. Utilization of native earthworms in land restoration and management is an exciting possible alternative, but we lack the necessary knowledge of their ecology and behavior or of management practices that might encourage their recolonization.

Finally, there has been very little discussion of the possibility of preventing or controlling earthworm invasions, despite interest among governmental and private organizations (Hendrix and Bohlen 2002). Callaham et al. provide a thorough analysis of this possibility and propose a decision tree for use by regulatory agencies to screen earthworms or earthworm-containing materials prior to importation. They also consider the interesting idea of ‘‘control by stages of invasion,’’ whereby appropriate control measures are targeted to varying degrees of invasion, for example, eradication at the establishment stage or land management manipulations at expansion or saturation stages. They conclude that prevention of earthworm introductions ultimately will involve a combination of regulatory policy, public education and appropriate land management.

In conclusion, the set of papers in this special issue of Biological Invasions makes clear that general patterns are emerging as to the mechanisms, directions and impacts of earthworm invasions in a variety of habitats and from microsite to regional scales. There are still many unanswered questions and we expect that the ideas set forth in these contributions will lead to specific new areas for research in soil ecology, and broaden the discussion of invasion biology in terrestrial ecosystems generally.

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ORIGINAL PAPER

Dispersal and clonal diversity of North-European parthenogenetic earthworms

Juhani Terhivuo · Anssi Saura

Abstract At least 15 earthworm species are known to reproduce parthenogenetically. Most of these retain meiosis but the chromosome set is duplicated before meiosis; alternatively there is mitosis instead of meiosis. In both cases the offspring are genetic copies of the parent worm. Parthenogens are always polyploid. Parthenogenesis is associated with a dispersal advantage: a single propagule suffices to establish a new population. We have studied the clone pool structure and dispersal of ecologically dissimilar polyploid parthenogenetic lumbricids in northern Europe using enzyme electrophoresis. The anthropochorous *Octolasion cyaneum* has a very low number of clones in populations that are located far away from each other. The opposite is the eurytopic *Dendrobaena octaedra* that has a wide array of clones in each population. The ripicolous *Eiseniella tetraedra* disperses with flowing water and possibly also through zoochory. On subarctic North-European mountains its clone pool decreases with increasing elevation. At the top there are a few but persistent clones. Small brooks carry propagules downstream, so that at the mouths of brooks clone pools are more diverse than higher up; again larger rivers carry clones downstream. Clone dispersal is relatively free in a freely flowing river, while dams stop propagules in harnessed rivers. The mouths of rivers have high *E. tetraedra* clone diversity. Clones disperse from these clone centers to islands formed through land uplift along the northern Baltic Sea. The annual turnover of clones is high on these islands. A survey of epigeic and endogeic parthenogens on the Åland islands which serve as stepping stones between Estonia, Finland and Sweden shows an invasion route of clones across the Baltic Sea. Anthropochory (*Aporrectodea rosea* and *Octolasion cyaneum*) and hydrochory (*E. tetraedra* and *Dendrobaena octaedra*) seem to play important roles in the clone pool formation on the Åland islands. Quite recently an exotic parthenogen *Dichogaster bolaui* has found a curious habitat in human settlements viz., the sewer pipe system. Many clonal earthworms show significant morphological and morphometric diversity in and between sample localities but we have failed to associate this variation with the clonal variability. It seems that local factors modify the morphometrics and morphology ultimately determined by the genotype of parthenogenetic earthworms.

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Introduction

Partenogenesis in earthworms

Parthenogenesis entails a two-fold advantage over sexual reproduction (Williams 1975; Maynard Smith 1978). In sexually reproducing (amphigonic) organisms it normally takes two individuals to produce one offspring per unit time, while each parthenogenetic individual is a reproducing female. Accordingly, two parthenogens produce two offspring at the same time as a male and a female produce just one. Earthworms are largely hermaphroditic, and the advantage of dispensing with sex is not as clear as in otherwise amphigonic animals, which do away with the male sex altogether. In some earthworm species with biparental reproduction there is an exchange of sperm between the partners whereas in some species certain individuals function mostly as males and others again as females (Meyer and Bouwman 1997). Parthenogens can allocate resources efficiently to egg production. Some of them retain, however, unnecessary or potentially costly attributes of sex such as copulation, male genitalia and production of spermatophores, even though there seems to be no sperm production and the male pores may not always open (e.g. Casellato 1987; Terhivuo 1988a). These earthworms share many of these evidently unnecessary features with asexual plants such as dandelions that produce flowers, nectar and empty pollen. Parthenogenetic reproduction in plants goes with the collective name of apomixis. We may here refer to the monograph by Asker and Jerling (1992) that covers the cytological and evolutionary attributes of plant apomixis.

Most parthenogenetic lumbricids retain meiosis. The chromosome number is doubled before meiosis at the last oogonial divisions. This premeiotic doubling is accomplished through a mitosis, in which all resulting chromosomes become included in a single nuclear membrane at telophase. The next step is regular meiosis. In the first meiotic division the chromosomes pair and form bivalents, the number of which is equal to the chromosome number in the somatic cells. The chromosome number is restored and all offspring are genetically copies of their mother (Suomalainen et al. 1987). *Dendrobaena octaedra* produces eggs through mitosis instead of meiosis, i.e. through cloning in the proper sense of the word (Omodeo 1955; Casellato and Rodighiero 1972). Amphigonic *D. octaedra* populations have never been encountered. Most populations are hexaploid (6×) but there are also populations that have high uneven chromosome numbers (Casellato 1987; Suomalainen et al. 1987).

Chromosomal sex determination is the major obstacle for polyploidy in animals. Polyploid animals reproduce in general parthenogenetically (Suomalainen et al. 1987). Hermaphroditic earthworms lack sex chromosomes, and biparentally reproducing earthworms may be either diploid or polyploid while all parthenogenetic earthworms appear to be polyploid or aneuploid (Muldal 1952; Omodeo 1951a–e, 1952, 1953a,b, 1955; Casellato and Rodighiero 1972; Vedovini 1973; Casellato 1987; Terhivuo et al. 1987, 1994; Viktorov 1997. Odd degrees of ploidy (e.g. 3×, 5× etc.) are not compatible with sexual reproduction but do not constitute an obstacle for clonality. Accordingly, clonal earthworms can have either an odd or even degree of ploidy, while sexually reproducing polyploids always have an even multiple of the haploid set.

Parthenogenesis is a condition derived from sexual reproduction. In general sexual forms inhabit the central area of distribution of a species and the parthenogenetic derivatives are found in marginal or disturbed habitats around the sexuals in a pattern called geographic parthenogenesis (Vandel 1928). The asexual polyploids form, likewise, concentric rings around the central diploid populations, so that the lowest degrees are found close to the diploid sexuals and the highest ones farthest away from them, a pattern called geographic polyploidy by Stenberg et al. (2003). Amphigonic polyploid earthworms seem to display a somewhat similar pattern (Omodeo 1951b). Perel and Graphodatsky (1982) have found degrees of polyploidy all the way up to dodecaploidy (12×) in *Eisenia nordenskioldi*. Viktorov (1997) has shown that different polyploid forms have discrete geographic distributions and ecological attributes. Deeply burrowing parthenogenetic *E. nordenskioldi* polyploids inhabit the southern margins and amphigonic epigeic polyploids the northern margins of the total area of distribution across Siberia (also see Tiunov et al. this issue).

Clone diversity, dispersal and occupation of habitats

Dispersal modes and pathways between earthworm populations are not easy to trace, particularly if no obvious human agency is involved. Enzyme electrophoresis is an efficient tool in surveying genetic structure, clonal adaptation and dispersal affinities between populations of polyploid and parthenogenetic earthworms. A clone is identified through an overall enzyme phenotype coded by several independent loci. Clonal offspring are copies of their parent worm. Mutations and eventual effects of transposition will, however, accumulate in the clones. Sexual reproduction in animals is usually tied to diploidy, meiosis, fertilization and Mendelian inheritance. These processes produce new gene combinations in each generation. Some combinations may confer to their bearers a higher fitness, i.e. a potential to produce more surviving offspring than either parent. On the other hand, genetic recombination disrupts adapted gene complexes. Local adaptation can be maintained through inbreeding, low mobility and other attributes of population structure. Alternatively, an animal can dispense with sex altogether and propagate a well-adapted genotype through cloning.

We surveyed parthenogenetic polyploid earthworm species in northern Europe. We have tried to work out how ecologically dissimilar parthenogenetic earthworm species disperse in relation to their genetic variability (i.e. clones) and what kind of clone pool variability they show in northern Europe where they live at the northern limits of their range. The latter area was completely covered with ice during the last glaciation called Weichsel. Earthworms must have colonized it in the course of the past 10,000 years or so.

Terhivuo and Valovirta (1978) and Terhivuo (1988b) have shown that the habitat spectra of earthworm species diminish from the south to the north, i.e. towards the margins of their range in Finland. This also holds true to the parthenogenetic endogeic *Aporrectodea rosea* and the epigeic *D. octaedra* and *Octolasion tyrtaeum* as well as the rather stenotopic epigeic *Eiseniella tetraedra* that we have studied in the Nordic and Baltic countries and in Russia.

In our studies, we have also focused on working out postglacial dispersal routes by means of clone pool affinities between parthenogens along the shores of the northern Baltic Sea and on the Åland Islands lying between Finland and Sweden and Estonia. Their clone pool structure shows that there are dispersal ties between continental populations of the Baltic basin and that the Åland Islands form a stepping stone for the dispersal of many clones across the Baltic sea. We have also posed the questions of how do the clones disperse from high subarctic mountains down to the Baltic sea and how do they disperse to islands that emerge from the northern Baltic Sea at a rate of about 1 cm/year. In this study, *E. tetraedra* has been our target worm.

In general, we have identified variable numbers of clones for the different species by using starch gel enzyme electrophoresis. The technique is simple and repeatable and is to be preferred when one is dealing with polyploids that are difficult to study in other routine molecular methods (see e.g. Saura et al. 1979; Parker and Selander 1980; Stille et al. 1980). Functional alleles at each genetic locus produce a distinct enzyme phenotype and the overall phenotype over all loci is used to identify a clone. Clone pool diversities were estimated using the distribution-free rarefaction method, which avoids sample size differences among populations.

Morphological diversity

We have also studied morphological variability and made morphometric measurements on adults of parthenogenetic lumbricids. By doing this we have aimed at relating observed variability to clone diversity in North Europe. Our surveys often revealed significant differences in somatic and reproductive characters between local populations but with few exceptions we have not recorded any regular pattern of geographical variability (Terhivuo 1988a; Terhivuo and Saura 1993a, b, 1996, 1997). This emphasizes the key role of local environmental factors on the genotype of the worm that ultimately determine the structural characteristics of the species.

Results

About 20 species of earthworms have been recorded in Norway, Sweden, Estonia, Finland and European parts of Russia (Julin 1949; Stöp-Bowitz 1969; Perel 1979; Terhivuo 1988b; Timm 1999). At least nine of these are known to reproduce by facultative or obligate parthenogenesis (Casellato 1987).

We have surveyed a variety of North-European parthenogenetic earthworms that are dissimilar in many ways (Table 1). In Finland *Octolasion cyaneum* is recorded only in southern parts of the country but in North Sweden it is found as far north as the city of Umeå. *Aporrectodea rosea* and *O. tyrtaeum* extend their ranges to central Finland. *D. octaedra* and *E. tetraedra* occur all over the country (Terhivuo 1988b). *Dichogaster bolaui* is an exotic invader found only indoors in Finland (Terhivuo 1991). Some species such as *O. cyaneum*, *A. rosea* and North American populations of *O. tyrtaeum*, appear to be primarily dispersed by human activity but vary in clone diversity in a given locality. On the other hand, northern European *O. tyrtaeum*, *D. octaedra* and *E. tetraedra* have less dependence on anthropochorous dispersal. These species also vary in clone diversity and patterns of clone distribution according to their primary means of dispersal (Table 1). Therefore, we will consider them below one by one.

Octolasion cyaneum and anthropochory

Terhivuo and Saura (1993a, 1996, 2003) studied clonal variation in this endogeic and highly (9× and 10×) polyploid (Muldal 1952; Vedovini 1973) worm with obligate parthenogenesis. The material is geographically extensive. We have worms from the northernmost population ever found (Umeå, Sweden at 63°55′), through central Sweden and southern Finland, England, northern Germany through Switzerland and we have worms from a population in Canberra, Australia.

The number of clones is in general low (mostly one or two), even though some samples are large (ranging from 20 to 42 worms). The sample of

Table 1 Ecological and other characters in peregrine parthenogenetic earthworm species considered in this study

Species	Ecological plasticity			Dispersal and distribution	Clone pool diversity
	1	2	3	4	5
O. cyaneum[a]	end	steno.	anth	Eur, NAm, Me, SAm, Austr,	1/2/1
A. rosea[b]	epi	±eury.	anth	WPa, Ne, SAm, SAfr, Austr,	7.2/7.3/7.0
O. tyrtaeum[a]	end.	±eury.	spont	Eur, NAm, SAm, MiE, NAfr, Austr	3.9/4.2
D. octaedra[a]	epi	eury.	spont	Pa, Me, Ind, Co	7.6/8.3/6.7
E. tetraedra[a]	epi	steno.	spont	WPa, NNe, SAm, SAfr, Aus, Me, Ind	6.4/8.0/5.3
D. bolaui[a]	epi	indoors	anth	Afr, Ind, Austr, Eur	–

[a] Only parthenogenetic strains are known

[b] Besides parthenogenetic strains amphigonic populations are reported from central and southern Europe (Casellato 1987)

Symbols: (1) Vertical distribution in soil; end = endogeic, epi = epigeic. (2) Habitat spectrum; steno = stenotopic, eury = eurytopic, indoors (in N Europe). (3) Main mode of dispersal; anth = anthropochorous, spont = spontaneous (methods not related to human agency). (4) World distribution (introductions included) (Stöp-Bowitz 1969; Sims and Gerard 1985); Eur = Europe, NAm = North America, Me = Mexico, SAm = South America, SAfr = South Africa, NAfr = North Africa, Austr = Australasia (India, Pakistan, Australia, oceanic islands, etc), WPa = Western Palearctic, Ne = Nearctic, SAf = South Africa, Pa = whole Palearctic, Ind = India, Co = Columbia, NNe = Northern Nearctic, Aus = Australia. (5) Clone pool diversity i.e. expected number of clones in a sample of 10 individuals correspondingly from Finland/Sweden/Estonia (Terhivuo and Saura 1996, 1997) nine worms from Switzerland had five clones and the one of 24 worms from Australia had 4 clones. The extent of variation among populations was low so that the northern samples mostly had just one and the same clone. There is no overall pattern that would support a concept of a specific multipurpose genotype. Morphometric variation showed local heterogeneity rather than regional trends; this variation was not associated with the clone(s) at each locality.

Amphigonic forms of *O. cyaneum* are not known but the overall pattern of variation agrees to some extent with the one observed in other clonal organisms, e.g. flightless weevils (Saura et al. 1976; Stenberg et al. 2003). There is high diversity in the area of origin i.e., the Alps and low diversity in the area colonized since the Ice Age. *Octolasion cyaneum* is a commensal of horticulture and it is evidently transported with garden plants, tools or soil. This gives rise to founder effects with the result of low clone diversity. Many of the sites, where we found *O. cyaneum*, were old, some even with continuous cultivation since Roman or Middle ages. Random factors related to the activities of man are the likely explanation for the rather high number of clones in the city of Canberra in Australia, which these worms have reached several times through the agency of man through time.

Today *O. cyaneum* is widening its range in Finland. This takes place mostly through human agency. For instance, at the Lammi Biological Station located about 100 km to the north of the city of Helsinki, these worms increase rapidly in numbers and spread to nearby soils where they were absent some tens of years ago (Karppinen and Nurminen 1964; Terhivuo 1988a). They also spread within the Helsinki and Umeå city areas by means of soil transport (Terhivuo and Saura unpublished).

A. rosea and agriculture

We have sampled populations from the northern margin of distribution of the endogeic *A. rosea* (Terhivuo and Saura 1993b, 1996, 1997). The material comes from Estonia, central Sweden, the Åland islands between Sweden and Finland and southern Finland. *A. rosea* is tied to agriculture but it may be found also in biotopes other than fields and meadows. This indicates that it is less intimately connected with human culture than *O. cyaneum* and can evidently disperse to nearby soils irrespective of human transport. Clone pool diversity was high. A sample of 50 worms could be expected to include about 20 clones in Sweden and Finland, while the Åland populations had about half of that diversity. Åland had few clones that were not found elsewhere. Using the Ochiai and Renkonen number similarity measures we found that the Åland populations shared clones more with Sweden than the Finnish mainland (Fig. 1). This agrees with the cultural and commercial ties that Åland has had with the Swedish mainland. Clone diversity is highest in areas where agriculture is old. We found some evidence for morphological differentiation tied to the genetic constitution of populations. Whether or not that was associated with the level of polyploidy in a given locality is not known (Terhivuo and Saura 1993b).

Octolasion cyaneum and *A. rosea* are often found in the same habitat but the latter has a far wider niche in northern Europe. It almost always has a high clone diversity, which indicates effective clone flow and powers of dispersal. The ties between populations as well as with history of agriculture show that human activity is the main agent of dispersal. The northern limit of distribution is quite sharp in Finland (Terhivuo 1988b). It is difficult to envision any historical or other pattern in agricultural practice that would give rise to such a border. The likely explanation is that the clones share a more or less identical reaction norm that does not allow colonization beyond a certain ecological threshold. One may hypothesize the possibility of multiple evolution of clones in *A. rosea*, combined with clone flow from different sites that would build up a diversity of clones in old agricultural and horticultural sites.

We may mention here that we have found copulating *A. rosea* individuals. We have considered this as a behavioural remnant of an earlier mode of amphigonic reproduction (Terhivuo and Saura 1993b). Evidently pointless sexual reproduction is a common feature in many parthenogenetic animals, such as lizards etc.

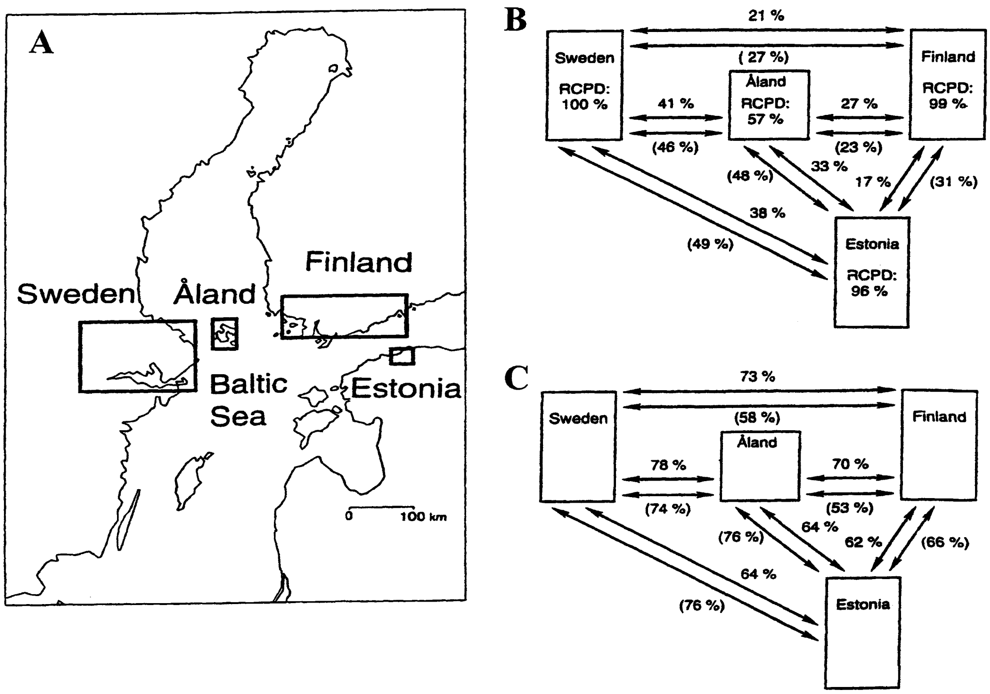

Fig. 1 Study area (**A**), proportions of clones (**B**) and enzyme variants (**C**) shared by the clone pools of the parthenogenetic earthworm *Aporrectodea rosea* on the Åland Islands and the mainlands of Finland, Sweden and Estonia as indicated by the Ochiai and the Renkonen Number (in parentheses) similarity measures (based on Terhivuo and Saura 1997). RCPD = relative clone pool diversity by the rarefaction values for a sample size of 10 worms (the highest regional value denotes 100% and the other values are calculated in relation to it)

O. tyrtaeum, an epigeic of waterlogged and moist soils

These worms seem to be triploid and parthenogenetic (Casellato 1987). In northwestern Europe they inhabit waterlogged soils such as shore meadows and banks of rivers and lakes. *O. tyrtaeum* seems to be capable of dispersing without human agency, i.e. by hydrochory. The populations may reach high densities at shores and shore alder thickets from which they may have dispersed into less moist habitats. Quite recently we have found that some upland *O. tyrtaeum* populations in Finland comprise specimens smaller in size and with more brightly yellow coloured rear end of the body than at wetland populations.

Terhivuo and Saura (1993a, 1997) studied *O. tyrtaeum* clone diversity in an extensive material from Sweden, Finland, Estonia and the Åland islands in between them. Clone diversity was rather low, from about 5–6 clones in a sample of 50 individuals. The amount of clones shared among the three regions was the same. Some clones shared among the regions were remarkably abundant on Åland. There was no clear-cut morphological differentiation among either regions or clones.

The North American continent appears to be a natural laboratory to study the invasion and dispersal of parthenogenetic earthworms. Jaenike and Selander (1979, 1985) and Jaenike et al. (1982) have studied the clonal diversity in *O. tyrtaeum*. While these worms are rather stenotopic inhabitants of wetlands and rivers in northern parts of the Old World, they have successfully invaded all kinds of habitats, including ploughed fields in the eastern United States. In fact, they are the most common earthworms in many localities there. Nevertheless, the clonal diversity is lower than in our material that comes from the northern margin of the species in its European home. Two genotypes, A and B, predominate in an extensive American material that has a total of eight recognized genotypes. Both A and B have a broad niche and their distributions overlap across a range of habitat and soil types. Jaenike and Selander (1985) argue that fluctuating population sizes and stochastic factors explain the coexistence of these two abundant types. Consequently, they have a very broad niche. The low number of clones across the eastern USA seems to indicate the effect of one or more founder events. It also shows that there has evidently been little evolution either through mutation or recombination through some unknown sexual process.

D. octaedra, an eurytopic epigeic with wide clone pools

This hardy worm occupies the widest scope of habitats among north-European lumbricids (Terhivuo and Valovirta 1978). It is by no means dependent on anthropogenic soils but does not avoid them. In Fennoscandia it can be found in the north as far as there is dry land on the coast of Arctic Norway. We have explored its clone composition and morphometrics in a set of papers (Terhivuo et al. 1987; Terhivuo and Saura 1990, 1996, 1997). The worms have been collected from an extensive area extending from Estonia and central Sweden in the south to northernmost Norway.

Clone diversity was always high, from 22 clones up to 26 clones in a sample of 50 worms. It may be pointed out that the sample from Estonia had a slightly lower diversity. In general the number of clones is high and relatively few clones were shared among localities. In Finland, the species seems to be hexaploid (Hongell and Terhivuo 1989). About every third worm sampled had a new overall genotype. All populations sampled had a high diversity, including geologically young islands far from the mainland (Terhivuo and Saura 1990 and unpublished). This shows that *D. octaedra* disperses with mechanisms that are highly efficient and does not rely on the active movements of the worm. The absence of male pores in many specimens and the derived mode of parthenogenesis do not support biparental reproduction as an explanation for high clone diversity.

The *D. octaedra* clone pool on the Åland islands was more similar to Finland than to Sweden. Åland is tied to Finland through thousands of stepping-stone islands, while the sea separating it from Sweden (which is geographically closer) is open and relatively deep. As stated above, cultural contacts to Sweden have been more active than to Finland, a circumstance seen in the clone pool affinities of culture commensals but not with *D. octaedra*.

A transect from northern Norway through southern Finland and another one through the Åland islands in the west to eastern Finland did not show any clear-cut affinities between the *D. octaedra* clone pools. In general, the clone pool in Finland comprised less than ten abundant clones that were recorded along most transects and of a swarm of less abundant clones with restricted distributions. Clone pool diversity increased northwards in open habitats but decreased in forests. The conclusion is that the populations of these worms are always made up of a wide variety of clones. Whether any of them differ in niche parameters remains to be seen. The clone pools along the transects show apparent clinal patterns that may indicate adaptation. The clones in the north deviated more in their enzyme compilations from a norm clone than the ones in the south. There was no evidence for clinal variation in the east-west transect (Fig. 2).

D. octaedra shows extensive morphological variability in North America where the species has come from Europe through human activity Gates (1974). In northern Europe it also has a wide variability in somatic as well as in reproductive characters (Terhivuo 1988a). Though morphological studies on parthenogenetic earthworms often reveal local differences between populations these differences are seldom reported to show any clinal pattern.

D. octaedra adults in southern and central Finland have the same mean number of segments as those in northern Finland and Norway. They show, however, a clinal pattern of increasing body size in different types of biotopes towards the north. Adult *D. octaedra* may lack or possess rudimentary male pore terminalia. The ones that have the pores, have them sometimes (in Sweden and Estonia) on segment XIV but this was never

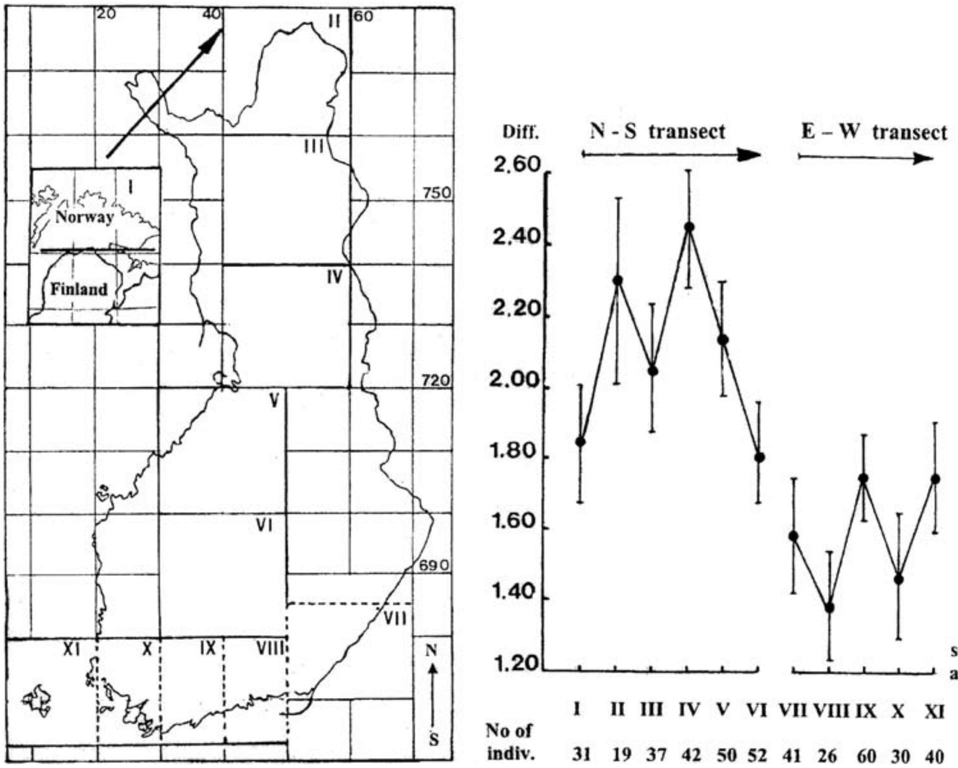

Fig. 2 (**A**) Study area with the north-south transect (subareas I–IV) and the east-west transect (subareas VII–XI). (**B**) Mean enzyme variant differences (mean - SE) among *Dendrobaena octaedra* specimens as measured by the numbers of the enzyme variants deviating from those in the norm clone. Individuals of the norm clone are considered equal to 0. See also the text (based on Terhivuo and Saura 1990)

observed in Finland or Åland. The scope of variation on Åland resembles more that in Finland than in Sweden.

E. tetraedra, a stenotopic epigeic dispersing by hydrochory and zoochory

E. tetraedra is a common inhabitant of shores all the way to Arctic Norway. In the mountains of northern Scandinavia it reaches the middle alpine zone, about 1,000 m above sea level. We may add that glaciers form there at an altitude of 1,300 m. These small worms are short-lived, with a life span of about one and a half years. They are tetraploid (Casellato 1987; Terhivuo et al. 1994).

We (Terhivuo et al. 1994) first compared clone pools in southern Finland with ones in northern Norway. Populations had rather low diversity in general, so that in a sample of 100 worms one can expect to find about 12 clones. The corresponding figure for *D. octaedra* is about 28 clones (Terhivuo and Saura 1990). In the Baltic area, clone diversity is highest on the Swedish mainland, so that a sample of 50 *E. tetraedra* is expected to include about 24 clones, on the Åland islands about 16, and on the Finnish mainland about 12.5 clones. There was considerable variation (presence versus absence and location) in the non-functional male organs among and within populations. Such traits need not be subject to selection (Suomalainen et al. 1987). In the survey by Terhivuo et al. (1994) it turned out that as in *D. octaedra* there are only a few abundant clones and a swarm of less common ones. Moreover, the two most frequent clones A and B were recorded both in the north and in the south. Using these as norm clones, comparisons showed that the clones in North Norway deviated on average less from clone A than from clone B. The opposite was true for clones in South Finland. This may indicate differential adaptation of *E. tetraedra* clone pools in South Finland and North Norway.

A comparison of clone pool affinities between Estonia, the Åland islands and Sweden and Finland, respectively, showed that similarity was highest between Åland and Sweden, followed by Sweden and Finland, whereas Åland and Finland and Estonia had lower similarities to the above (Terhivuo and Saura 1996, 1997). The results agree roughly with linear distance and suggested that *E. tetraedra* disperses with water.

Northern Scandinavia is subject to the phenomenon of land uplift, a consequence of a rebound of the crust of the earth after having been pressed down by the weight of ice in the not too distant past. In the environs of the town of Umeå in northern Sweden the rate of uplift is about 9 mm a year. This means that new islands rise from the sea at a constant rate, while older islands merge to form larger islands and these join gradually with the mainland. We followed the clone constitution of islands at the Skeppsvik archipelago (Terhivuo and Saura 1999). The river Sävarån feeds clones to the area in the northern part of the Baltic Sea where salinity is low (about 0.3%) and *E. tetraedra* lives all along the shores of the mainland. We first estimated clone diversity along the Sävarån close to the river mouth and then inspected clone diversity on islands of different ages with differing distances from the river mouth. We also followed the turnover of clones within this area for 3 years. A total of 94 *E. tetraedra* clones were found among 449 worms collected during this period. Eighty-one percent of the clones found on the islands was found also along the river but these clones made up a minority (35%) in the river sample. Clone diversities on new islands were low (8–13 clones in a sample of 25 worms) in comparison with the riverside samples (16–21 clones in a sample of 25 worms) and the turnover rate between years was high (about 80%) on the islands. The newest and also the most isolated islands did not have any worms. The structure of the clone pool on the islands differs clearly from that of the mainland and it is subject to a rapid turnover. However, the river feeds new clones to the sea all the time and these fugitive clones colonize the islands. New islands are occasionally submerged through floods and the worms are subject to fish predation. The final stage is a permanent and quite diverse clone assemblage that characterizes the shores of the Baltic Sea.

Northern Sweden has a set of parallel rivers that run from the Scandes mountains to the Baltic sea. Two rivers next to each other constitute an ecological theater, where the process of colonization and adaptation can be observed. We have studied the Ume and Vindel rivers and compared them with the much smaller Sävar river. The Vindel river is one of the few remaining free-flowing large rivers in Europe, while the Ume is harnessed with 20 major dams. The two rivers join before they meet the sea (Terhivuo et al. 2002). The two river mouths (the Ume–Vindel and the Sävar) had highest clone diversities in terms of Swedish clone diversity, i. e. about 18 clones in a sample of 20 worms (Fig. 3). The result seems to be unexpected, as the Sävar is a much smaller river. It is, however, in line with the results of river ecology stating that small rivers behave like large ones. The river mouths did not appreciably have clones in common. This means that they do not represent samples of a large coastal clone pool. In fact, the river mouths experience a rapid turnover of clones between years (Terhivuo et al. 2002).

Populations along the free-flowing Vindel river had higher diversities than corresponding sites along the Ume river. The Vindel river contributed about three times more clones to the common river mouth than the harnessed Ume river. In addition, populations along the Vindel had more clones in common than populations along the Ume river. A stepwise pattern of shared clones is seen along the Vindel. The locality highest upstream shares clones with the next one downstream, which again shares clones with the next one, etc. The localities along the harnessed Ume river do not share any clones with each other. In other words, worms disperse down the Vindel but the dams stop the dispersal along the Ume river. The morphometric characters of *E. tetraedra* adults do not show any association with an area or river. For example mountain brooks could have large worms as well as small ones. There was, however, a between-year difference in samples taken in two consecutive years at the Ume–Vindel mouth. In conclusion, the

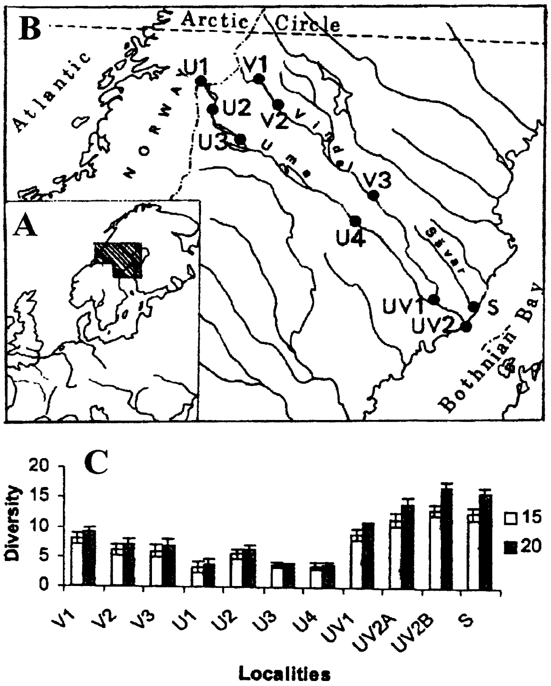

Fig. 3 Study area (**A**) and sample localities (**B**) along the free running Vindel river (V1–V3), the harnessed Ume river (U1–U4), the part of the two rivers joined (UV1–UV2A), and the Sävar river (S). *Eiseniella tetraedra* clone pool diversities (**C**) are indicated according to the rarefaction method. The expected numbers of clones are calculated for sample sizes of 15 and 20 individuals. The bars indicate ±1SD (based on Terhivuo et al. 2002)

results show that worm cocoons float down a free river. Small colored wood cubes do the same; they are also stopped in water reservoirs of a harnessed river (Terhivuo et al. 2002) (Fig. 3).

We have continued the studies of *E. tetraedra* clones along small mountain brooks in the watershed area of the Ume river (Terhivuo and Saura unpublished) on the Scandes. We sampled several brooks as far as up the subarctic mountains where *E. tetraedra* was found and took samples with about even intervals down. Many brooks did not have any worms. On arctic mountains of North Sweden clone pool diversity decreases with increasing elevation. It seems that small brooks carry propagules from wide areas of mountain slopes especially in periods of heavy rainfall and melting snow. Small brooks join and make wider brooks prior to running to large rivers or lakes. At the mouth of the brooks *E. tetraedra* clone pools are considerably more diverse than they are at the top of arctic mountains. Herds of reindeer wander along the mountain slopes, cross brooks, and probably disperse cocoons. Propagules can be spread in pieces of soil attached to the feet of mammals and maybe birds also contribute to their dispersal. Sport fishermen can also spread earthworms along the rivers in Northern Scandinavia but the mountain brooks where we have studied *E. tetraedra* are so small that they are devoid of fish. Our material of *E. tetraedra* clones from northern parts of Russian taiga shows that there are riverside localities with very low clonal variability thus resembling the clone pools at higher elevations of subarctic mountains (Terhivuo and Saura unpublished).

In summary, our surveys point out that *E. tetraedra* is an inhabitant of river and shore soils extending its range up to the Ice Coast in northern Europe. It disperses with flowing water and possibly also through zoochory. On subarctic North-European mountains its clone pools decrease with increasing elevation so that at the top there are a few but persistent clones. Small brooks carry propagules downstream, and at the mouths of brooks clone pools are more diverse than higher up; again larger rivers carry clones downstream. Clone dispersal is relatively free in a freely flowing river, while dams stop propagules in harnessed rivers. The mouths of rivers have high *E. tetraedra* clone diversity. Clones disperse from these clone centers to islands formed through land uplift along the northern Baltic Sea. The annual turnover of clones is high on these islands that occasionally can be submerged. The Åland Islands serve as a stepping stone for the invasion of clones between Estonia, Finland and Sweden across the Baltic Sea.

D. bolaui, a curious parthenogenetic inhabitant of human settlements

D. bolaui (Acanthodrilidae) originates either from India and the nearby areas (Sims and Gerard 1985) or more probably from Africa (Lee 1985; Jamieson et al. 2002). Terhivuo (1991) reported that it has established itself in the sewer systems in Finland. Later similar records have been made in several European cities. It may be considered a minor nuisance as small pink worms appear in swimming pools and toilet bowls. Lee

(1985) proposed *D. bolaui* to be a parthenogen and the preliminary analysis by Terhivuo and Saura (unpublished) showed that in Finland there may be just a single clone of the species.

In Finland the *D. bolaui* individuals recorded in flowerpots of decorative plants imply the arrival of the species with imported plant material. Probably it first arrived in greenhouses and from there was transported with flowerpots to separate localities in Finland. Total lack of *D. bolaui* records prior to 1988 and numerous ones thereafter indicates that it is a rather late arrival among the Finnish earthworm fauna. Its presence in urban sewer pipe systems seems to due to the habit of showering decorative plants in toilets so that individuals or cocoons can easily be carried with water to the sewer pipe system where the species seems to thrive because many of the worms found were adults with well-demarcated secondary reproductive organs (Terhivuo 1991).

Discussion

Dispersal methods

Earthworm movements in soil or on the soil surface are called spontaneous or active dispersal. It is, however, an inefficient method since it does not disperse the worm more than 10–15 m/year (Ghilarov and Perel 1984; Hoogerkamp et al. 1983). If this were the only means of dispersal for lumbricids, northern Scandinavia and Finland should still be devoid of Lumbricidae; since the retreat of the ice sheet after the culmination of the Weichsel glaciation some 15,000 years ago, lumbricids should have spread spontaneously no more than some 200 km northwards from the southernmost edge of the ice sheet.

Stephenson (1930) stressed the importance of anthropochory in earthworm dispersal. Human introductions, either intentional or unconscious, play a key role in earthworm invasions as is well demonstrated by the presence of numerous European Lumbricidae in North America, Asia, New Zealand, Australia, Central and South America and Africa (see e.g. Gates 1982; Lee 1985; Sims and Gerard 1985; also see Baker et al., Frelich et al., and Hendrix et al., this issue).

According to (Schwert and Dance 1979) hydrochory makes an efficient dispersal mechanism especially for earthworms not associated with anthropomorphic soils. Our surveys on *E. tetraedra*, *D. octaedra* and *O. tyrtaeum* also highlight the importance of hydrochory. Moreover, zoochory may be involved as well but we lack actual observations of it.

There are few reports on the role of anemochory in earthworm dispersal in general. However, Stöp-Bowitz (1969) reports an occasion when heavy storm had lifted dead leaves with earthworms and carried them on the ice of a Norwegian lake. Such occasions are hard to detect in other seasons of a year.

The evolution and adaptation of clones

A clone is a reproductively isolated unit. Formation of a new clone through mutation and lack of genetic recombination is a fast process in comparison to the formation of a new species characterized by isolation and cessation of gene flow between populations. Assuming a constant mutation rate *per* locus *per* generation, a hexaploid should have three times as many mutations *per* generation as a diploid with the same haploid number. Thus polyploid clones accumulate mutations and become highly heterozygous for alleles in any locus. Aneuploidy will also change expression of alleles if the chromosome with the allele is lost in a clone. In general, polyploidy complicates the picture since each chromosome in a polyploid may have differentiated widely from its multiple homologs through mutations and transposition. The result is a swarm of new clones that can be derived from one or few frequent and widely distributed parent clones. We do not know, however, whether the clones are monophyletic or how old they are. An old clone or a widely distributed common clone may be monophyletic or through mutations it may result in a huge assemblage of minor derivatives (Terhivuo and Saura 1990; Loxdale and Lushai 2003). In fact, Lushai et al. (2003) have stressed that molecular data from prokaryotes and eukaryotes support the argument that clones possess a highly dynamic and adaptive genome. It should be pointed out that it is likely that more and more clones will be found along with a growing number of polymorphic enzyme systems used to identify clones (Terhivuo and Saura 1990). The detailed phylogeny of clones would be very interesting when done in concert with the geographical data, rivers system data, etc, presented in this paper. Rapidly evolving methods of DNA sequencing could be used together with our enzyme data.

In Central and southern Europe amphigonic strains of *A. rosea* have been recorded but the other lumbricid species studied by us are considered to reproduce by obligate parthenogenesis (Casellato 1987).

Given that a study is done in a sufficiently fine scale, one may expect to find evidence for or against a concept that clones would be ecologically equivalent. Christensen (1980) and Christensen et al. (1978) studied the distribution and long-term changes in parthenogenetic and polyploid populations of the enchytraeid *Lumbricillus lineatus* along short ecological transects on a shore. Seasonal and long-term changes were observed in the genotype distributions. Several genotypes coexisted in a single population. The triploids inhabited the areas highest up on the shore, pentaploids intermediate localities and tetraploids dominated at the lowest sites. Different genotypes divided the transect among themselves and the distributions were similar at two transects. This means that genotypes actively select and use different parts of their niche in a heterogenous environment. Christensen et al. (2002) have shown that the clone pool of the enchytraeid *Buccholzia appendiculata* is stable and can persist for a long time.

In any case, clonal organisms are reproductively isolated from each other and many authors (e.g. Viktorov 1997) point out that clones or degrees of ploidy correspond to good taxonomic entities. In fact, botanists treat clones as good species. Clones should then be expected to share the same niche and be subject to competitive exclusion. Studies on clonal animals have seldom shown such an effect (Suomalainen et al. 1987); clones and degrees of ploidy seem to coexist freely, as shown by the results described above and e.g. by Stenberg et al. (2003).

We have seen that morphological variation exists independently of genetic variation in clonal earthworms. This is an argument against competitive exclusion on the basis of genotype, given that phenotypes are poorly correlated with genotype. The effect of this should be the maintenance of clonal diversity because selection is expected to be somewhat random with genotype in a situation like this. All evidence that we have implies that competitive exclusion does not operate among clonal worms and certainly more work is needed to understand the factors that determine their population structure and geographical range.

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ORIGINAL PAPER

Lumbricid earthworm invasion in the Carpathian Mountains and some other sites in Romania

Victor V. Pop · Adriana Antonia Pop

Abstract Recent field research shows that the ubiquitous *Lumbricus terrestris* and *Octolasion lacteum* (the large parthenogenetic form) have invaded new habitats in Romania, replacing mostly endemic or rare species of the former earthworm communities which were recorded 20–30 years ago. Seven different cases of earthworm invasion are currently described. Invader species have larger ecological tolerances as compared with the endemic species.

Keywords Earthworm invasion · *Lumbricus terrestris* · *Octolasion lacteum* · Romania

Introduction

Biological invasion usually refers to large-scale processes when exotic animal or plant species conquer new, remote and disjunctive biogeographic areas. In this process, as a rule, mostly cosmopolitan earthworm species are involved (Lee 1985). This paper considers an earthworm invasion occurring on a smaller ecological gradient, in the frame of similar biogeographic units.

Site description and background

The Romanian part of the Carpathian Mountains forms a 900 km long, 35–150 km wide mountain chain with a mean altitude of 840 m and a highest peak of 2,544 m. The main vegetation belts of oak, beech, spruce and fir forests, and sub-alpine scrub have developed on cambisols, argiluvisols and spodosols with islands of mollisols. The hilly plain of Transylvania, an area with a diameter of over 100 km inside the Carpathian arch at a general altitude of 450–650 m, is mostly occupied by agricultural land and remnants of oak and beech forests on brown forest soils, spodosols and islands of leached chernozems. In the Carpathians over 40 lumbricid species have been recorded, one third of which are endemic, while in the Transylvanian hilly plain approximately 20 species are known (Pop 1941, 1948, 1964).

In two short reviews (Pop VV 1987, 1997), the structure of the Carpathian earthworm communities in relationship with the vegetation and soils was presented. Six main community patterns were considered as being characteristic for these mountains, four in forest and two in grassland ecosystems. Each community type had a nucleus of characteristic and constant species, and the structural pattern of the community was maintained by substitution of ecologically similar species.

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Recent field research and re-sampling of earthworms in the Carpathians have revealed interesting changes in the earthworm community structure of several mountain habitats. In 2002 and 2003, while looking for particular lumbricid species for a molecular taxonomy research project, we visited some places from the Romanian Carpathians where the first author had worked in 1965–1975. Earthworms were sampled from 5–7 sample units of 50 x 50 cm using formalin extraction (Lee 1985).

Instead of the target species, considered to be very characteristic for the given sites, we found dense populations of *Lumbricus terrestris* L. and to some extent of the large parthenogenetic form of *Octolasion lacteum* (Örley 1881) in places where they were lacking 30 years before. These changes, which seem to be contemporary and quite rapid, should be regarded as a result of an invasion process by some peregrine or ubiquitous Lumbricid species. The invasive species, with wide ecological tolerances, replace partially or totally the local (mostly endemic) species with narrower ecological tolerance.

This paper describes the earthworm invasion observed in seven different types of biotopes, five in the Carpathians and two in the Plain of Transylvania, in Romania. Comparative data in Table 1 shows the structure of the earlier and the present states of the earthworm communities reflected by species structure and relative abundance of the species.

Results and discussion

In two sites from the Vladeasa Mts (1,848 m alt) we carried out medium-term seasonal dynamic studies of the earthworm communities in the period 1974–1976. Characteristic earthworm communities for different vegetation belts were recorded (Pop 1987). In the earthworm communities from this mountain, the endemic epi-endogeic *Dendrobaena clujensis* (Pop 1938), was very characteristic. After 30 years, this species was almost entirely replaced by *L. terrestris*.

In the Valisoara Gorge, from the Trascaul Mts, a limestone area of the Apuseni Mts, we found in 1971 a very vigorous population of *Fitzingeria platyura montana* (Cernosvitov 1932). This species, distributed in South Eastern Europe, is characteristic for the Carpathians. Unfortunately, it seems that it is a vulnerable species, as it has been replaced totally by *L. terrestis*. The disappearance of this species has also been noticed in places other than the Carpathians.

In the Mehedinti and Cerna Mountains, separated by the Cerna valley, the replacement of characteristic species was induced by the same *L. terrestris*, followed by the large, parthenogenetic form of the endogeic *O. lacteum*. Here, in a deciduous mixed forest in 1976–1977, a particular earthworm community with the endemic endogeic *Cernosvitovia opisthocystis* (Rosa 1895) and some other rare species (Table 1) was found; for *Cernosvitovia rebeli* (Rosa 1897) this is the only record from Romania. In 2003 and 2004 some of these species disappeared and their place was occupied by a dense population of the large parthenogenetic form of *O. lacteum*. In a nearby grassland, a dense population of *L. terrestris* occupied the only place in Romania where *Dendrobaena veneta* (Rosa 1886) was found.

In the Transylvanian hilly plain, invasion by *L. terrestris* and *O. lacteum* has so far been observed in two places (Table 1). Near Cluj, in grasslands, the endemic *D. clujensis* was completely replaced by *L. terrestris*. It is important to note that this site represents just the ‘‘*terra typica*’’ from where *D. clujensis* was described; digging, hand-sorting, and formalin extraction in dozens of locations over a large area yielded only the large *L. terrestris*.

The last place where the invasion of *L. terrestris* was found was in arable land near Gherla, in the Northern part of the Transylvanian plain. Here, this species replaced *Octodrilus gradinescui* (Pop 1928), which was highly characteristic for the entire valley of the Somes river. A high density of *O. lacteum* at this site showed that both invader species were involved in the replacement of the former earthworm fauna.

The invasion of new habitats by *L. terrestris* and the partial or total replacement of the original earthworm fauna, especially in forest ecosystems, are remarkable because during 30 years (1965–1995) of field research *L. terrestris* was not found in forests, except in the last few

Table 1 Invasion of *Lumbricus terrestris* and *Octolasion lacteum* and replacement of early earthworm communities in seven sites from Romania

Site	Primary earthworm community (year of recording)	Secondary earthworm community (year of recording)
Vladeasa Mt, Apuseni Mts, the Carpathians, 1,650 m alt., spruce fir forest, crypto-podzolic acid brown soil	(1967) *Dendrobaena alpina* 92 *Dendrobaena byblica* 3 *Dendrobaena clujensis* 5	(2002) *Lumbricus terrestris* 42 *Dendrobaena alpina* 58
Vladeasa Mt, Apuseni Mts, the Carpathians, 1,430 m alt., grassland, acid brown soil	(1967) *Allolobophora rosea* 48 *Dendrobaena clujensis* 50 *Dendrodrilus rubidus* 2	(2002) *Lumbricus terrestris* 63 *Allolobophora rosea* 25 *Dendrobaena clujensis* 12
Valisoara Gorge, Trascau Mts, the Carpathians, 700 m alt., grassland, shallow rendzina, on limestone	(1971) *Fitzingeria platyura* 85 *Dendrodrilus rubidus* 15	(2003) *Lumbricus terrestris* 96 *Dendrodrilus rubidus* 4
Cerna Valley, the South Eastern Carpathians, 400 m alt., grassland, alluvial soil	(1976–1977) *Dendrobaena veneta* 86 *Lumbricus rubellus* 2 *Dendrobaena octaedra* 2 *Dendrodrilus rubidus* 2 *Octolasion lacteum* 8	(2003–2004) *Lumbricus terrestris* 85 *Octolasium lacteum* 10 *Allolobophora caliginosa* 5
Mehedinti Mts, the South–Eastern Carpathians 400 alt., mixed deciduous (oak, beech, hornbeam) forest, eubasic brown earth	(1976–1977) *Cernosvitovia rebeli* 64 *Cernosvitovia opisthocystis* 4 *Fitzingeria platyura* 4 *Lumbricus polyphemus* 4 *Octolasion lacteum* 24	(2003–2004) *Cernosvitovia opisthocystis* 12 *Lumbricus polyphemus* 6 *Octolasion lacteum* 82
Cluj-Napoca, 650 m alt., Grassland, podzolic brown soil	(1971) *Dendrobaena clujensis* 91 *Allolobophora rosea* 9	(2002–2003) *Lumbricus terrestris* 73 *Octolasion lacteum* 27
Gherla, Cluj district, 400 m alt., arable, alluvial soil	(1964) *Allolobophora caliginosa* 15 *Octodrilus gradinescui* 73 *Octolasion lacteum* 12	(2003) *Lumbricus terrestris* 67 *Octolasion lacteum* 33

Relative abundance (%) follows the name (data original in this report)

years. It is important to note that *L. terrestris* has had a peculiar, almost anthropophilic distribution in Romania, as well as in the other Central European countries (also see Tiunov et al. this issue). This species occurs mainly in grasslands of city parks or in smaller arable areas where vegetables may be cultivated. It is customary to say that *L. terrestris* occurs mainly in zoological textbooks, not in forests or other natural habitats (though it is sometimes improperly determined there). Now it seems that this axiom should be corrected. Even more interesting seems to be the expansion and invasion of the large parthenogenetic form of *O. lacteum*. Apart from the sites discussed here, we have observed this process in other places, but unfortunately we overlooked it.

If these clear invasion cases have happened, it is probable that the process is continuing and will occur in other places as well. New field investigations and re-sampling of previously studied sites will provide new evidence on this phenomenon. Therefore, the invasion and the expansion of these ecologically vigorous species inside the European continent should be considered as real and natural processes that change the original local fauna (i.e., a real invasion).

It is quite difficult to determine why this process occurs, and which factors direct it. As a first approximation, it appears that apart from the direct and probably inadvertent transportation of these species by human agricultural activity and the clear cutting of forests, the invasion process is facilitated by environmental disturbances, such as pollution. The use of pesticides, fertilizers and other polluting chemicals could affect (or even kill) the endemic species, which may have narrow ecological tolerances. The more vigorous, ubiquitous, seemingly polymorphic forms, such as *L. terrestris* or the parthenogenetic form of *O. lacteum*, may adapt more easily to disturbed conditions (i.e., anthropochores *sensu* Gates 1970; also see Terhivuo and Saura this issue).

Reduced earthworm species diversity coupled with the disappearance of certain species, could lead to negative consequences in their habitat. The pre-invasion structures of earthworm communities, formed during a long adaptive and co-evolutionary process, have developed as assemblages of epigeic, endogeic and anecic species (Lee 1985). The post-invasion community structures in our studies are usually simplified and often lack surface and deep-soil inhabiting species, the invasive *L. terrestris* taking the place of species from various ecological categories. Any disturbance in the ratio among the previous epigeic, endogeic and anecic earthworm species could affect other components of the ecosystem, especially soil properties. For the time being, we have no clear evidence for the probable changes in vegetation and soil induced by the drastic changes in the structure of the earthworm communities by the new invasive species. Nevertheless, some obvious signs were noticed in our studies, such as the abundance of *L. terrestris* castings on the soil surface. In a few years the whole earthworm burrowing system could be replaced, and a large quantity of earthworm casts will cover the soil. It is likely that this will be soon followed by changes in the vegetation cover (see Frelich et al. this issue).

Conclusion

The process of earthworm invasion should be in no way confounded with the natural or man-induced succession of species in a changing ecosystem. In a succession, the new species come from neighboring ecosystems and the process has the same trend in similar areas. If determined by natural causes, such as climatic changes, the process may occur on a large scale and in different areas with several species from different ecological categories moving at similar rates. The invasive species tend to move individually and replace not just the species from the same ecological category. At least in the first step, the community structure tends to simplify.

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ORIGINAL PAPER

Invasion patterns of Lumbricidae into the previously earthworm-free areas of northeastern Europe and the western Great Lakes region of North America

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Abstract We examine the patterns of expansion of exotic European earthworms in northeastern Europe and the western Great Lakes region of North America. These areas share many ecological, climatic and historical characteristics and are devoid of indigenous earthworm fauna due to Quaternary glaciations. These regions are being colonized by a similar suite of exotic lumbricid species and it is unlikely that this is the result of chance, but rather indicates that these species have particular characteristics making them successful invaders. The present macro-scale distributions of earthworm species in northern Russia show little connection to the pattern of the last glaciation. Rather, the primary factors that determine the current distributions of earthworm species include climatic conditions, the life history traits of different earthworm species, the suitability of habitat and intensity and patterns of human activity. In the western Great Lakes region of North America, there are three primary factors affecting current distributions of exotic earthworm species including the patterns of human activity and land use practices, the composition of particular source populations of earthworms associated with different vectors of transport and the soil and litter properties of habitats across the region. Disturbance of a habitat does not appear to be a prerequisite to the invasion and establishment of exotic earthworms. Analysis of the macro-scale distributions of Lumbricidae species in northeastern Europe may provide important insights into the potential of invasive European earthworm species to spread in North America, and identify potentially invasive species.

Keywords Soil animals · Jump dispersal · Climatic conditions · Frost tolerance · Vegetation type · Disturbance · Fish bait

Introduction

Emerging research on the consequences of exotic earthworm invasion in North America (McLean

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and Parkinson 1997; Bohlen et al. 2004a; Hale et al. 2005) has increased interest in understanding the patterns and factors controlling invasion dynamics, particularly in regions that contain no native earthworm species (Bohlen et al. 2004b). In this paper, we examine the patterns of expansion of exotic earthworm populations in northeastern regions of Europe and the cold-temperate western Great Lakes region of North America. These areas share many ecological, climatic and historical features and are devoid of indigenous earthworm fauna due to quaternary glaciations (Gates 1977; Reynolds 1994, 1995). Both areas are currently being colonized by a strikingly similar array of lumbricid species of primarily European origin.

Considering the broad similarity of climatic and edaphic conditions, the processes that determine species distribution and abundance may be analogous on both continents. Analysis of the macro-scale distributions of Lumbricidae species in northeastern Europe may provide important insights into the potential of invasive European earthworm species to spread in North America, as well as identify other potentially invasive species, which have not yet reached North America. Similarly, the regional and stand level patterns and dynamics of earthworm invasions in North America will contribute to an understanding of potential expansion patterns of earthworms in cold-temperate regions of Europe and Asia.

In this paper we first address the macro-scale distribution of peregrine (Lee 1985) earthworm species in northeastern Europe (north of 55° N, east of 30° E). In addition, we briefly describe the preferred habitats of the most active colonizers toward the northeastern border of their natural range in Europe. The data provided here were compiled from a range of soil-zoological surveys performed during the last 30 years. Of course, the intensity of sampling varied, and some less accessible areas are poorly studied. However, we believe that this information may provide basic information on the broad tolerance of earthworm species to climatic and environmental conditions. We then discuss and compare the main factors that govern the distribution of earthworm species in northeastern Europe and in northern hardwood forests of the western Great Lakes region of U.S.A.

Northeastern Europe: macro-scale distribution of earthworms

The northern part of the Russian plain that lies between Fennoscandia and the Ural mountains is mainly covered by coniferous boreal forests of taiga type, which are gradually replaced by tundra biomes north of 65° latitude. Most of this territory was covered by Pleistocene ice shields (Fig. 1), which presumably eliminated indigenous earthworm fauna. Only a few endemic species (*Eisenia intermedia*, *E. uralensis*, *Perelia tuberosa*, *P. diplotetratheca*) remain in the middle and southern Ural Mountains and adjoining regions, where they often dominate local earthworm communities (Perel 1979; Vsevolodova-Perel 1997). However, the present-day macro-scale distribution of earthworm species shows little connection to the pattern of the last glaciation. The earthworm fauna of the northern Russian plain is composed mainly of peregrine species of European origin (*Aporrectodea caliginosa*, *A. rosea*, *A. longa*, *Allolobophora chlorotica*, *Octolasion tyrtaeum*, *Lumbricus terrestris*, *L. castaneus*, *L. rubellus*, *Dendrobaena octaedra*, *Dendrodrilus rubidus*, *Eisenia fetida* and *Eiseniella tetraedra*). Some other species, e.g., *Aporrectodea icterica* and *Octolasion cyaneum* have been occasionally found in parks and botanical gardens, but never in natural habitats. A few species of Ural and Siberian origin are common east of 50° E, with *E. uralensis* penetrating slightly further westward (Vsevolodova-Perel 1988). An exception is *Eisenia nordenskioldi*, a Siberian species which colonized many localities throughout the eastern Russian plain, from forest-steppe to taiga and tundra biomes.

The eastern Baltic Sea region seems to be a main starting point for many earthworm species colonizing the Russian plain. Some species typical in the temperate zone of Europe, such as *A. chlorotica* and *A. longa*, occur rarely east of 30° E and only in anthropogenic habitats (Vsevolodova-Perel 1988).

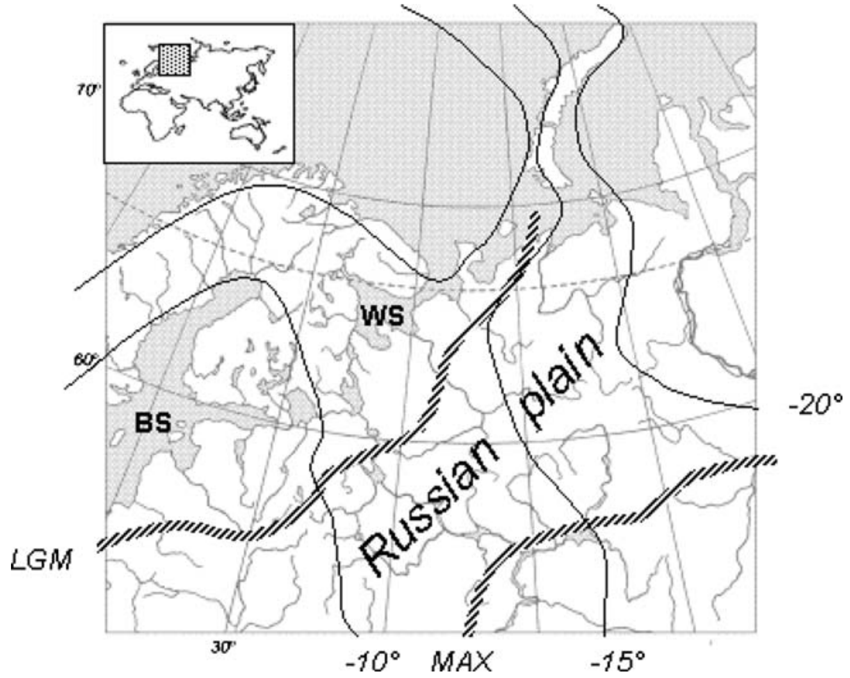

Fig. 1 The furthest glacial maximum (MAX) and last glacial maximum (LGM) of Quaternary glaciation in northeastern Europe and the Russian plain (north of 55°N, east of 30°E). Isotherms indicate the mean air temperature in January. The general areas of the White Sea basin (WS) and the Baltic Sea basin (BS) are indicated

Three endogeic species have successfully colonized the northern part of the Russian plain. *Aporrectodea caliginosa* and *A. rosea* have similar ranges (Fig. 2A) reaching the coast of the White Sea to the north and Ural piedmont to the east. However, toward the eastern extremes of their ranges both species are increasingly restricted to cultivated soil (e.g. vegetable gardens), secondary deciduous forests and river valleys. As a rule, they are absent in pristine coniferous forest stands north of 60° N. *Octolasion tyrtaeum* (*lacteum*) has colonized a considerably larger area and inhabits zonal (boreal) forests of taiga type, though often at a very low density (Fig. 2B). The density is usually much higher (≥30 ind. m^{-2}) in lowlands and hydromorphic habitats such as flooded meadows and lotic bogs (Perel 1979). *Octolasion tyrtaeum* is well adapted to moist habitats and can survive prolonged periods of inundation and oxygen deficiency due to an extensively developed subcutaneous capillary network (Semenova 1968) and high hemoglobin levels (Byzova 1974). In contrast to the *Aporrectodea* species, *O. tyrtaeum* has rarely been documented in anthropogenic habitats.

Lumbricus terrestris is the single anecic species that penetrates slightly farther than 60° N. In the central part of the Russian plain (e.g., around Moscow) this species can be very abundant in unmanaged mixed forests, but in the taiga zone was only found in the vicinity of human settlements (Fig. 2C). The epi-endogeic species *L. rubellus* was found in many places north of 60°, mostly in meadows, secondary forests and in human settlements (Fig. 2C). The smaller epigeic species *L. castaneus* is relatively abundant in the western part of the Russian plain in broad-leaved and mixed forests, but was not recorded north of 60°. *Dendrodrilus rubidus* (Fig. 2D) occupies an area similar to *O. tyrtaeum*, but penetrates further north in the White Sea basin. The strictly anthropochorous "manure worm" *E. fetida* seems to be completely frost-intolerant even as cocoons (Holmstrup et al. 1990), but was regularly found in dung or bark heaps and similar habitats at places north of the Arctic circle in the White Sea basin which have relatively mild winters.

The epigeic species *D. octaedra* and the epi-endogeic species *E. nordenskioldi* (Fig. 3) have much broader distributions than all other species. Both species populate taiga, but also tundra-type biomes, occasionally reaching relatively high densities (≥50 ind. m^{-2}; Perel 1979). *D. octaedra* was reported across northeastern Europe,

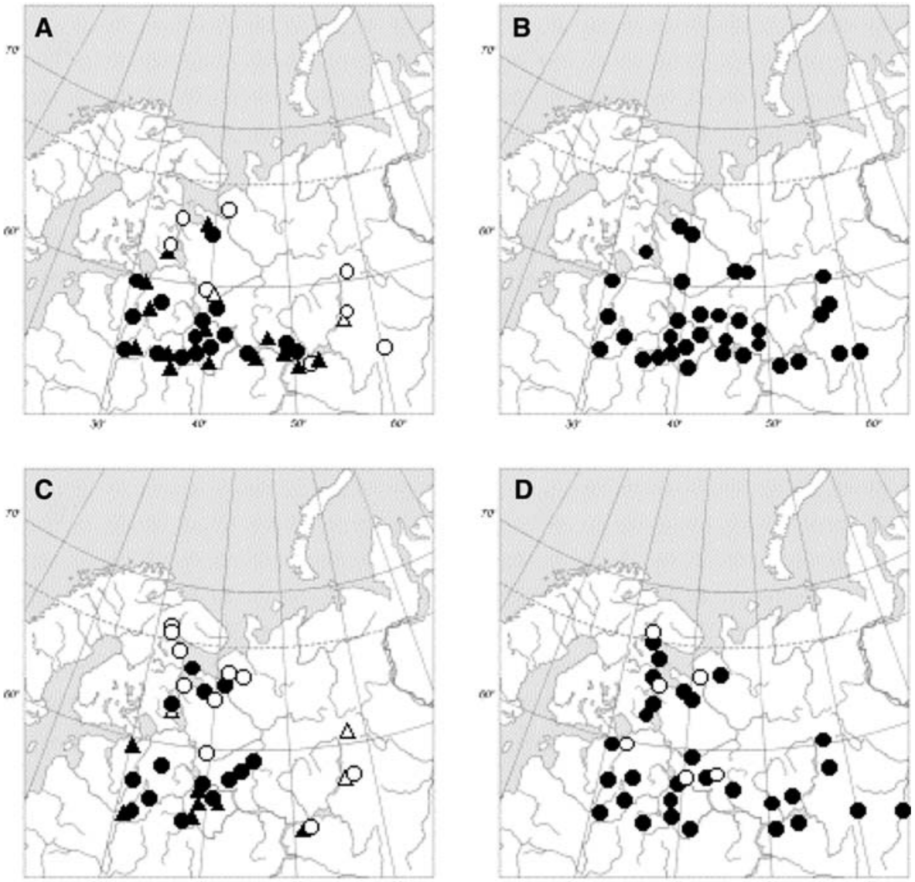

Fig. 2 Macro-scale distribution of earthworm species in northeastern Europe (north of 55°N, east of 30°E). **A**: *Aporrectodea caliginosa* (circles) and *A. rosea* (triangles), **B**: *Octolasion tyrtaeum*, **C**: *Lumbricus rubellus* (circles) and *L. terrestris*(triangles), **D**: *Dendrodrilus rubidus*. Filled symbols indicate natural or moderately transformed habitats; open symbols indicate anthropogenic habitats

including some arctic islands (e.g. Southern Novaya Zemlya; Fig. 3A). Unlike Lumbricidae species of European origin that appear to be invading from the central Russian plain northeastward, *E. nordenskioldi* is apparently colonizing northern Europe westward from Siberia, and was rarely found west of 40° E (Fig. 3B).

Overall, the macro-scale distribution of earthworms in northeastern Europe shows a very characteristic pattern: the number of species is at a maximum in western regions and decreases sharply in a north-eastward direction. In addition, the northern boundary for most species penetrating north of 55° on the Russian plain is between 65 and 68° N in the west and decreases to between 55 and 60° N in the east. Notable exceptions are *D. octaedra* and *E. nordenskioldi*, which occur north of the Arctic Circle even at the northeastern extreme of Europe and in West Siberia.

North America: European earthworm invasion of northern hardwood forests

Native North American earthworms present in the western Great Lakes region (Michigan, Minnesota and Wisconsin) are thought to have been extirpated by the Wisconsinan glaciers which covered virtually all of the region; recolonization by native North American species from southern refugia has not yet reached most of the area (James 2004). It is assumed that exotic earthworms were originally transported to the region

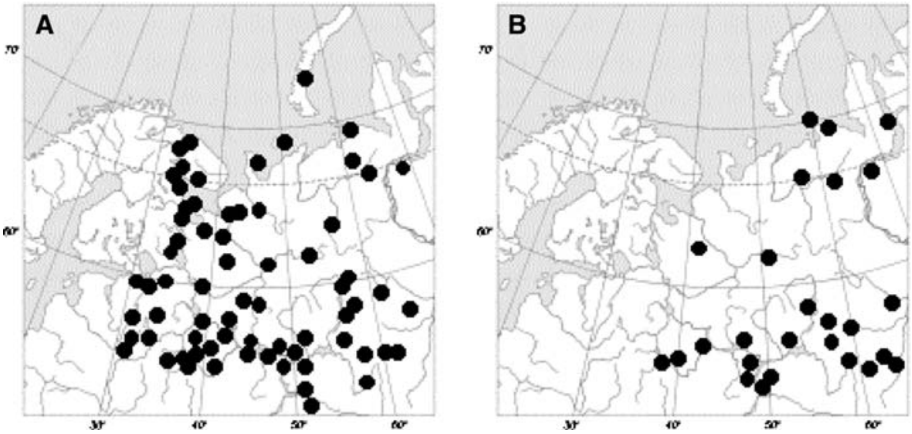

Fig. 3 Macro-scale distribution of earthworm species in natural or moderately transformed habitats in northeastern Europe (north of 55°N, east of 30°E). **A**: *Dendrobaena octaedra*; **B**: *Eisenia nordenskioldi*

during European settlement through the dumping of soil used for ballast in ships and through soils associated with plant material carried by settlers (Reynolds 1977; Gates 1982; Lee 1985; James 2004; Reynolds et al. 2002). Our studies have been restricted to mature sugar maple (*Acer saccharum*) dominated forests of the Chippewa National Forest in north central Minnesota and the Chequamegon National Forest in north-western Wisconsin (Holdsworth et al. 2004; Hale et al. 2005). Secondary tree species include yellow birch (*Betula alleghaniensis*), paper birch (*Betula papyrifera*) and basswood (*Tilia americana*) with ironwood (*Ostrya virginiana*) and American elm (*Ulmus americana*) in the sub-canopy and sapling layers. Soils are generally deep, well-drained and light colored Eutroboralfs (USDA 1997) that, in the absence of earthworms, are characterized by a thick forest floor composed of O_i (L), O_e (F) and O_a (H) layers. These forests exist within a matrix of large and small lakes and a variety of forested and non-forested vegetation communities across a wide range of soil conditions. The climate is humid, continental, cold temperate with a median growing season of 115–134 days and snow cover from late November to early April. Normal mean temperatures in January are −13 to −15°C and 20°C in July.

Most of the peregrine European lumbricids that can survive the winter conditions of this region are present somewhere in the landscape (Reynolds et al. 2002; Hale 2004). Fifteen species of exotic earthworms have been recorded in the three western Great Lakes states (Reynolds 1995; Reynolds et al. 2002). The most common include *D. octaedra*, *A. caliginosa*, *A. tuberculata*, *A. rosea*, *L. rubellus* and *L. terrestris*. *O. tyrtaeum* and *D. rubidus* are also well documented but with less widespread distribution than the other species.

Mechanisms and constraints of earthworm distributions

The primary factors that determine the large-scale distribution of earthworms in northeastern Europe are apparently climatic conditions, suitability of habitat and the patterns of human activity and land use practices. These factors are obviously connected, as more temperate climatic regions often contain habitat types amenable to earthworm colonization. These areas were also colonized the earliest by humans, who subsequently transformed natural habitats and through their activities transported earthworm species to the region. At the smaller scale of the western Great Lakes region of North America, the differences in climatic conditions are presumably of minor importance. The presence, species composition and abundance of earthworms depend on the composition of particular source populations, different vectors of transport, and soil and litter properties of available habitats across the region.

Climatic constraints

Climatic conditions in northeastern Europe become increasingly harsh in a northeasterly direction across the Russian plain. Summer temperatures decrease gradually from south to north with the mean July isotherm of +15°C lying approximately at 65° N. Simultaneously, the mean and minimum winter isotherms lie meridionally, with mean air temperature in January decreasing from −2° to −5°C in the Baltic region to −20°C in the Ural piedmont (Fig. 1). With the exception of *E. nordenskioldi* and *D. octaedra*, earthworm species have very limited ability to withstand soil freezing (Holmstrup and Zachariassen 1996; Petersen and Holmstrup 2000; Berman et al. 2002), and minimal winter soil temperature may be a main determinant of the northern and eastern boundary of their range.

The geographical distributions of earthworm species across northeastern Europe mirror the increasing ability of different earthworm species to withstand severe climatic conditions. A ranking of earthworms species based on laboratory data on their frost tolerance (*A. chlorotica* < *L. castaneus* < *L. terrestris* < *A. rosea* ≤ *A. caliginosa* < *L. rubellus* < *O. tyrtaeum* < *D. rubidus* < *D. octaedra* ≤ *E. nordenskioldi*) closely corresponds to the broad geographical patterns of these species across the region. Species such as *A. chlorotica* are very frost-sensitive even as cocoons (Holmstrup and Zachariassen 1996). Cocoons, but not postembrional stages, of *Aporrectodea* and *Lumbricus* species may withstand cooling to between −5 and −8°C (Holmstrup et al. 1990; Holmstrup and Zachariassen 1996) and the cocoons of *D. rubidus* and *D. octaedra* can survive −35°C (Dymond et al. 1997; Berman et al. 2002).

Most earthworm species (with the possible exception of *D. octaedra* and *D. rubidus*) are not able to complete their life cycle during one growing season at the northern edge of their range, so adults and juveniles must either withstand soil freezing or find appropriate refugia in order to survive until spring. For example, endogeic and anecic species may avoid freezing by hibernating in deep soil layers. However, adult and juvenile *E. nordenskioldi* are able to overwinter in a frozen state at temperatures down to −30°C, whereas cocoons can withstand −35°C (Berman and Leirikh 1985). Berman et al. (2002) also reported that Siberian and some east-European populations of *D. octaedra* are freeze-tolerant at postembrional stages of the life cycle, with about 50% of experimental animals surviving freezing to between −10 and −12°C.

Many of the European earthworm species colonizing the Great Lakes region (e.g., *A. rosea*, *L. rubellus*, *L. terrestris*) are not frost-tolerant. This suggests that they hibernate in deep soil layers, though the question needs further investigation. On the other hand, the cold winter climate of the region may have prevented the expansion of *E. fetida* and Asian species of the genus *Amynthas*. These species prevail in commercial, community and private composting sites across the region (C. Hale personal observations), but have never been documented in natural habitats.

Suitability of habitats

The range of habitats potentially suitable for earthworm colonization decreases sharply across northeastern Europe in a northeastly direction as broad-leaved and mixed forests are replaced by pine, spruce and larch stands of taiga type. Acidic litter of coniferous trees coupled with low evaporation rates during cold summer promote the leaching of base cations and form generally very acidic soils with pH rarely above 5. Acidic soils under coniferous forests are unfavorable for most earthworms, except acid-tolerant species such as *D. octaedra*, *D. rubidus* and *E. nordenskioldi*. The freeze-hardiness and parthenogenic nature of these three species, combined with their ability to tolerate acid soils and exploit poor quality litter, are seemingly the major reasons for their success in colonizing vast areas of northeastern Europe and Siberia, including areas with permafrost soils.

However, even in the taiga zone some deciduous forests are always present as early successional stages following disturbances such as fire or logging. These forests are typically dominated by birch, aspen or alder and, along with meadows in river valleys, penetrate deeply into the taiga zone. They form important corridors for the primary establishment of a range of earthworm populations. For example, zonal *Picea* and *Pinus* forests along the Onega River (ca 63° N, 38° E) are sparsely populated by *D. octaedra* and *D. rubidus*, with total densities of 1–7 ind. m^{-2}. Secondary *Populus* forests of the same area harbor much larger and more diverse populations of earthworms including *D. octaedra*, *L. rubellus* and *O. tyrtaeum* with total densities up to 80 ind. m^{-2}, while on flooded and dry meadows the density of earthworms reaches 42–104 ind. m^{-2} including *D. octaedra*, *D. rubidus*, *L. rubellus*, *O. tyrtaeum*, *A. rosea* and *A. caliginosa* (Perel 1979; Kudryasheva 1997).

In predominately deciduous forests of the western Great Lakes region the expansion of European lumbricids does not appear to be significantly affected by edaphic conditions or inhospitable habitat types even though earthworm populations or species may be limited in some localities by low soil pH (e.g., white cedar bogs) and/or dry, coarse textured soils (e.g., Michigan dune complex; Nordström and Rundgren 1974; Staaf 1987; Pop 1997). However, in areas that have been colonized by exotic earthworms, the population size and species composition of earthworm communities will ultimately be dependent upon soil texture, pH, moisture, and the palatability and quantity of litter (Nordström and Rundgren 1974; Staaf 1987; Judas 1990; Ponge and Delhaye 1995; Lavelle 1997; Pop 1997; Bohlen et al. 2004a). Spruce and pine forests with less palatable litter over sandy, acidic soils will likely have the lowest earthworm biomass and species richness (*D. octaedra* is often the only species present), while sugar maple dominated forests with highly palatable litter and loamy, mesic soils will likely have the highest biomass and species diversity.

Anthropogenic transformation of habitats

Disturbance of natural habitats is thought to facilitate invasions of exotic species, including invasive earthworms (Kalisz and Wood 1995). This is certainly true for northeastern Europe where human activity strongly influenced local vegetation and soils by slash-and-burn and later conventional agriculture, pasturage, intensive logging, and increased frequency of forest fires. Colonization of this region by agrarian human populations started long before 1000 AD, and intensified considerably in the 13th through the 15th centuries (Osipov and Gavrilova 1983). As a consequence of human activity there has been an expansion of meadows and secondary deciduous forests, especially around large settlements, along rivers and other trading routes. Many earthworm species are closely associated with human settlements at the northeastern edge of their range (Fig. 2).

Abandoned human settlements, although already overgrown by taiga vegetation, often form local oases of increased diversity of earthworms, which persist for decades and most likely for centuries (A.V. Tiunov, personal observations). Similar phenomena have been described elsewhere (Enckell and Rundgren 1988; Kalisz and Dotson 1989).

In contrast, natural or anthropogenic transformation of habitats seemingly is not required for successful colonization by exotic earthworm species in the Great Lakes region (see also Frelich et al., this issue). While human activity is certainly an important means of transporting European earthworm species to an area (see below), there is no evidence that disturbance is required to allow establishment of earthworms once they have reached a site. Throughout the western Great Lakes region, managed, unmanaged, and old-growth hardwood forests are being invaded by European earthworm species where source populations are present (Alban and Berry 1994; Hale 2004; Holdsworth et al. 2004; Gundale et al. 2005). The level to which human disturbance of habitats may further facilitate establishment of earthworms is unknown at this time. However, the speed at which pristine habitats can be invaded when earthworms reach a new site suggests that disturbance is of minimal importance to invasion dynamics in the region. Furthermore, the probability of finding exotic earthworm species in any given location is strongly related to the duration, type, and intensity of human use (Holdsworth et al. 2004). In the southern areas of Minnesota and Wisconsin with the longest duration (~150 years) and greatest intensity of human use since European settlement, several European earthworm species (i.e., *L. rubellus* and *Aporrectodea* species) are ubiquitous.

Dispersal by humans

The natural rate of dispersal of an established earthworm population is relatively slow for European lumbricids (5–10 m/year; Marinissen and Van den Bosch 1992; Dymond et al. 1997; Hale et al. 2005). Thus, anthrochorous dispersion has likely played a key role in the spreading of earthworm populations across northeastern Europe, but we are not aware of any study on the history of this process. The continuing use of earthworms as fishing bait ensures a constant introduction of new populations along rivers and lakes. This is particularly true for *L. rubellus*, which forms numerous small isolated populations in White Sea basin, obviously associated with popular fishing spots (A.V. Tiunov, personal observations).

Likewise, in the Great Lakes region, exotic earthworms have been spread as released fishing bait, as indicated by the proximity of many invasion epicenters to lakes shores, boat landings and cabins (Proulx 2003). The expansion of human activities has led to the establishment of thousands of epicenters of earthworm invasion. These epicenters are associated not only with higher earthworm abundance relative to the surrounding landscape, but also with increased species richness because fishing bait often contains other species (i.e., *Aporrectodea* species,*D. octaedra*, *D. rubidus*, *O. tyrtaeum*) in addition to the *L. terrestris* and *L. rubellus* that are marketed (A. Holdsworth and C. Hale, personal observations). Overall, the distribution of most earthworm species is significantly positively related to roads and to fishable streams (Fig. 4, Holdsworth et al. 2004). The spatial distribution of earthworm invasion epicenters is a major factor affecting the distributions of European earthworm species in the early stages of invasion across the landscape.

The composition of exotic earthworm populations in any given location will also be related to the species composition of source populations associated with the dominant vectors of earthworm transport and introduction in the area. Areas with few lakes and little fishing may have earthworm populations dominated by epigeic and endogeic species that are more commonly transported by home and road building activity, logging and off-road vehicles (Dymond et al. 1997; Hale 2004; A. Holdsworth personal observations). Recent increase in the establishment of community yard waste compost sites and personal vermicomposting favors invasion of epigeic and epi-endogeic species such as *L. rubellus* (C. Hale personal observations).

Species traits and ecological relationships

While the distribution of exotic earthworm species overall is strongly affected by human activity patterns and the composition of source populations, life history characteristics of different species also contribute to species-specific distributional patterns (Reynolds 1977; Hale 2004; Holdsworth et al. 2004). In particular, the reproductive strategies employed by different earthworm species may contribute to their geographic distributions. At least four most active invasive species (*E. nordenskioldi*, *D. octaedra*, *D. rubidus*, *O. tyrtaeum*) are either totally or partially parthenogenic (Perel 1979). This trait may facilitate reproduction at very low densities, characteristic of extreme habitats, where a single surviving individual could establish a local population. Parthenogenic reproduction may also contribute to the rapid expansion of a population once a well-adapted morph arrives in a particular location (Jensen and Holmstrup 1997; Holmstrup and Loeschcke 2003). Parthenogenic *D. octaedra* is the most widespread species in both regions, due to high reproductive rate, ability to colonize coniferous forest floors with low pH and poor quality litter, and cold hardiness. Its small body size facilitates accidental spread by vectors such as logging truck tires (Dymond et al. 1997) that are less likely for larger bodied species, such as *L. terrestris*.

While many organisms prey on earthworms (i.e., birds, salamanders, shrews, foxes, badgers and many macro-invertebrates), the impacts of predation on earthworm population dynamics in natural habitats are difficult to estimate and remain generally unknown (Judas 1989). In parts of the United Kingdom there are organisms, such as

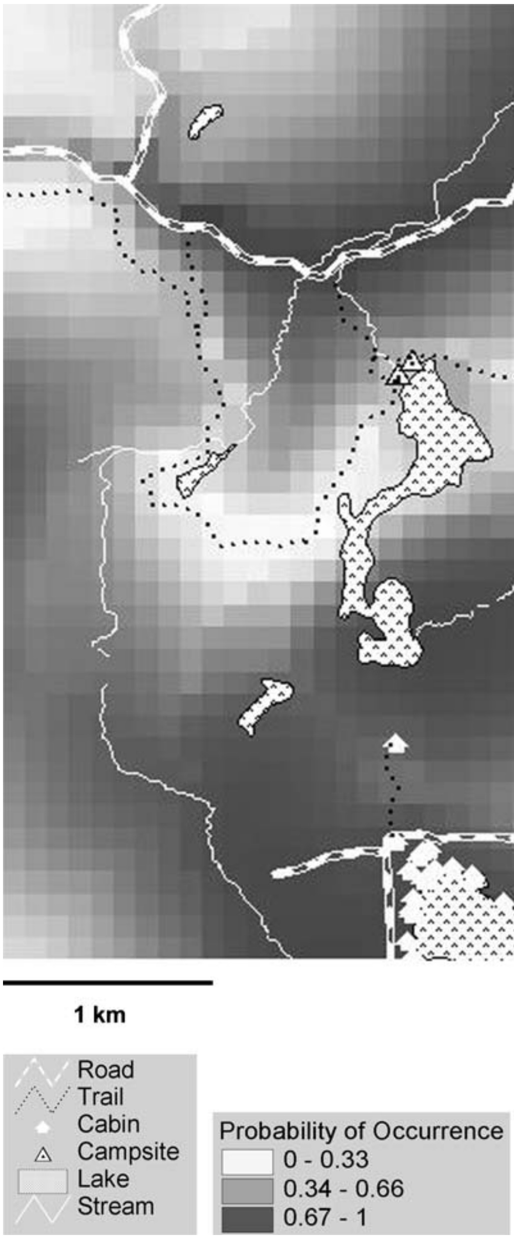

Fig. 4 Estimated probability of occurrence of invasive earthworm species *Lumbricus terrestris* in relation to landscape features in a Wisconsin wilderness area. Estimates are based on regression models using 291 plots from 40 maple-dominated forest stands on well-drained and light coloured Eutroboralfs

the New Zealand flatworm (*Artioposthia triangulata*), that have been credited with significantly limiting earthworm populations (Lillico et al. 1996; Nixon 1996). However, there is no evidence suggesting that such top-down control of earthworm populations is important in northeastern Europe or Great Lakes region (Reynolds et al. 1977; Ducey and Noce 1998).

‘‘Invasional meltdown’’

Soil and litter properties not only shape earthworm populations but are shaped by invading earthworms in ways that may facilitate the invasion by other earthworm species. For instance, endogeic species (i.e., *Aporrectodea* species and *Octolasion tyrtaeum*) are commonly transported via a range of human activities. However, their spread from an introduction site may be limited by the availability of soil organic matter (Hendrix et al. 1999; Shakir and Dindal 1997). In native, earthworm-free hardwood forests that maintain thick organic horizons and have naturally low soil organic matter content, alterations of forest floor material by invading epigeic and epi-endogeic earthworms may facilitate the establishment of endogeic species by mixing O and mineral soil horizons, thereby making this pool of organic material more accessible (Hale et al. 2005). This situation may be regarded as an example of ''invasional meltdown'' (Simberloff and von Holle 1999), in which one species facilitates invasion by another (see also Frelich et al. and Hendrix et al., this issue).

Conclusion

Overall, the pattern of earthworm invasion closely resembles the ''jump dispersal'' model (Shigesada et al. 1995). That is, the probability of colonization of distant localities is directly dependent on the availability of dispersal opportunities, and much less so on the distance from the source and time since initial colonization (MacIsaac et al. 2001). This is especially true for endogeic and anecic earthworm species, which are closely associated with centers of human activity in northeastern Europe and the western Great Lakes region of North America.

The earthworm species colonizing new areas in Russia are largely the same as those invading North America. It is unlikely that this is the result of chance, but rather indicates that this suite of species has particular characteristics that make them successful invaders. The comparison of climatic conditions across the two regions suggests that many European species may considerably extend their range in North America. In particular, Berman et al. (2002) suggested that winter temperature would not constrain the invasion of *D. octaedra* in large areas of North America still devoid of earthworms. *Eisenia nordenskioldi* may deserve special attention. To our knowledge *E. nordenskioldi* is not recorded in North America, though it has a high potential to colonize boreal forests and even tundra biomes in the upper arctic. Its presence on many arctic islands along the Siberian coast (Vsevolodova-Perel 1988) suggests that *E. nordenskioldi* might have been dispersed by humans. Given that it is also common in the Chukotka and Kamchatka Peninsulas of the Russian far east, it could reach North America across both the Atlantic and Pacific Oceans. However, the main area of this species distribution lies far from principal trading routes, making a potential invasion less likely. Models combining habitat suitability parameters, the spatial distribution of source populations, and dispersal vectors could greatly improve our understanding of invasion potential of such exotic earthworm species.

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ORIGINAL PAPER

Earthworm invasion into previously earthworm-free temperate and boreal forests

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Abstract Earthworms are keystone detritivores that can influence primary producers by changing seedbed conditions, soil characteristics, flow of water, nutrients and carbon, and plant–herbivore interactions. The invasion of European earthworms into previously earthworm-free temperate and boreal forests of North America dominated by *Acer*, *Quercus*, *Betula*, *Pinus* and *Populus* has provided ample opportunity to observe how earthworms engineer ecosystems. Impacts vary with soil parent material, land use history, and assemblage of invading earthworm species. Earthworms reduce the thickness of organic layers, increase the bulk density of soils and incorporate litter and humus materials into deeper horizons of the soil profile, thereby affecting the whole soil food web and the above ground plant community. Mixing of organic and mineral materials turns mor into mull humus which significantly changes the distribution and community composition of the soil microflora and seedbed conditions for vascular plants. In some forests earthworm invasion leads to reduced availability and increased leaching of N and P in soil horizons where most fine roots are concentrated. Earthworms can contribute to a forest decline syndrome, and forest herbs in the genera *Aralia*, *Botrychium*, *Osmorhiza*, *Trillium*, *Uvularia*, and *Viola* are reduced in abundance during earthworm invasion. The degree of plant recovery after invasion varies greatly among sites and depends on complex interactions with soil processes and herbivores. These changes are likely to alter competitive relationships among plant species, possibly facilitating invasion of exotic plant species such as *Rhamnus cathartica* into North American forests, leading to as yet unknown changes in successional trajectory.

Keywords *Aporrectodea* · *Dendrobaena* · Exotic earthworm invasion · *Lumbricus rubellus* ·

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Lumbricus terrestris · Keystone species · Minnesota forests · New York forests

Introduction

Invasion by non-native earthworms into previously earthworm-free forest ecosystems has only recently received substantial attention from ecologists. Such ecosystems occur in the temperate and cold-temperate deciduous and mixed deciduous-conifer forests of North America at latitudes of 45–60° N, an area of several million km^2. Earthworms native to North America were unknown in this region prior to the introduction of European earthworm species (*Lumbricidae*) that started in the 1700s and continues today (see Tiunov et al. this issue).

Because earthworms are ecosystem engineers (sensu Jones et al. 1994) that change basic processes such as cycling and movement of water and nutrients, soil structure, and seedbed conditions, their introduction causes profound effects that cascade throughout ecosystems. Earthworms are part of the detritivore community, consuming leaf litter and increasing rates of decomposition. Although it is well known that detritivores and decomposers are necessary for recycling of carbon and nutrients, seldom do scientists have the chance to observe how a major change in the detritivore community affects ecosystems at large spatial scales, as is occurring now with European earthworm invasion in cold-temperate forests. In this paper we review the evidence that earthworms engineer forest ecosystems to the extent that they can be considered a keystone class of organisms that exert control over many aspects of ecosystem structure and function, including the primary producers.

There is a vast scientific literature on earthworm ecology in areas where they are native, and on impacts of exotic earthworms on agricultural systems (Lee 1985; Edwards and Bohlen 1995; Edwards 2004). However, there is little published on the impacts of earthworms on native plants (Scheu 2003). The study of impacts of exotic earthworm species on native soils devoid of earthworms and on the response of native soil food webs and native plant species within these ecosystems is a very recent phenomenon (Parkinson et al. 2004; Bohlen et al. 2004a, b).

The overall objective of this paper is to examine impacts of exotic earthworm introduction on soils and plant communities in a large region that was previously devoid of earthworms. Three major topics are addressed: (1) changes in soil structure and processes caused by exotic earthworms; (2) potential mechanisms by which earthworms influence the soil and plant community and the long-term changes expected; and (3) the current evidence for these mechanisms. Finally, avenues of future research are proposed.

Impacts on soils

Upon invasion, earthworms alter the structure of soil horizons, availability of nutrients, and soil biota. The type and magnitude of these impacts vary with the species of earthworm and characteristics of the soil. Colonization by litter-dwelling, epigeic earthworm species such as *Dendrobaena octaedra* physically disrupts the separation of organic layers by mixing of F (O_e) and H (O_a) materials, but leaves the litter (L or O_i) layer relatively intact and has little impact on the structure of the mineral soil (McLean and Parkinson 1997a, b). Soil dwelling endogeic, epi-endogeic and deep-burrowing anecic earthworm species (e.g. *Aporrectodea* sp., *Lumbricus rubellus*, and *L. terrestris*, respectively) consume the surface organic horizon, mixing surface litter into the upper mineral soil horizons, to an average depth of 25–30 cm (Lee 1985; Edwards and Bohlen 1995). Therefore, the result of multi-species earthworm invasion is conversion from a mor organic horizon structure (consisting of O_i, O_e, O_a subhorizons) over a thin A horizon and well-developed E horizon below, to a mull structure similar to a previously farmed plow layer (only O_i subhorizon present) over a relatively deep (up to 25 cm) organic-rich A horizon (Langmaid 1964; Shaw and Pawluk 1986; Alban and Berry 1994). This post-earthworm structure is similar to soils found under non-acid hardwood forests in northern Europe, where the lumbricid species of earthworms invading North America are native (Kubiena 1948; Bal 1982; Ponge and Delhaye 1995).

Earthworm-free forest soils that have not been previously plowed by humans tend to have very low bulk densities, due to the presence of a thick litter layer and the burrowing action of many species of native invertebrates (McLean and Parkinson 1997a; Bohlen et al. 2004a). The introduction of earthworms increases bulk density by decreasing the thickness of the forest floor, reducing the abundance of native soil dwelling invertebrate species, and cementing soil particles together during burrowing and casting activities (McLean and Parkinson 1998a, b; Scheu and Parkinson 1994a; Alban and Berry 1994; Migge 2001). Although a soil fauna community typical for deciduous mull humus forests in Europe can lead to relatively low bulk densities in the presence of earthworms (Bal 1982; Schaefer 1991), it is unknown whether such adjustments in the soil fauna will lead to recovery of low bulk densities in recently invaded North American forests.

Earthworms strongly affect soil nutrient availability either directly via soil processing or indirectly via changes in the microbial and soil invertebrate community, but exotic earthworm invasions have variable effects on nutrient availability. Laboratory and field microcosm studies have shown increased nutrient availability and plant growth with the presence of earthworms (Scheu 1987; Scheu and Parkinson 1994a, b). Many of the laboratory studies compared earthworm casting material to the surrounding soil, or were done over short time periods (e.g. Lunt and Jacobsen 1944; Syers et al. 1979; Parkin and Berry 1994). It is unclear how applicable these results are to larger spatial and temporal scales. Nutrients mobilized during the rapid incorporation of a multi-year accumulation of surface litter during initial earthworm invasion may ultimately be immobilized or leached out of the ecosystem.

Field studies have shown variable effects of earthworm invasion on soil N dynamics. Invasion of maple forests in New York by *Lumbricus* spp. increased leaching of NO_3 in a historically plowed site, but not at another site that had never been plowed, possibly because of the greater potential for N immobilization in the more C-rich unplowed site. Total soil N was not significantly changed by earthworm invasion (Bohlen et al. 2004c). Nitrogen availability in the A horizon declined after multiple-species earthworm invasion in Minnesota hardwood forests (Hale et al. 2005a).

Phosphorous is more easily leached from ecosystems when European earthworms invade. Suarez et al. (2004) found an increase in P leaching and decrease in P availability on plots in a New York sugar maple forest dominated by *L. rubellus*. Although phosphorous availability in upper soil horizons increased in plots with *L. terrestris*, presumably because *L. terrestris* brought mineral soil from deeper horizons to the surface where it could be weathered, a net leaching loss of P from the ecosystem is still expected. Some soils lack sufficient unweathered P to maintain P availability despite leaching losses, and *L. terrestris* activity may result in lower availability as well as net leaching in some soils. Sugar maple forests in Minnesota invaded by several species including *L. terrestris* and *L. rubellus* had lower P availability than control plots without those earthworm species (Hale et al. 2005a). Loss of P with exotic earthworm invasion has been associated with instances of maple decline in Quebec, Canada (Paré and Bernier 1989). Absorption of P by tree roots through mycorrhizae hyphal networks may also be reduced when earthworms disrupt the hyphal network and reduce infection rates on tree roots (Lawrence et al. 2003).

The magnitude of earthworm invasion impacts on forest soils depends on the species assemblage of earthworms that invade as well as on land-use history. For example, strictly epigeic species, such as *Dendrobaena octaedra*, have minor impacts on soil physical structure, C distribution, bulk density, and nutrient status (McLean and Parkinson 1997a, b). The impacts to these soil characteristics are greatest when earthworm species of all ecological groups invade in concert (Hale et al. 2005a). Cultural history is also important, and impacts of earthworms may be minimal in areas that were previously plowed by humans (Bohlen et al. 2004a), presumably because cultivation mimics changes caused by earthworms, such as disrupting the forest floor and incorporating the organic horizon into the mineral soil, decreasing soil organic matter and increasing bulk density.

The abundance and diversity of earthworms that invade a given ecosystem depends on the available source population, soil texture and moisture, soil pH and litter palatability. Different assemblages of earthworms are favored depending on the vector of transport and introduction (Proulx 2003). For example, fishing bait favors a broad assemblage of epigeic, endogeic and anecic species (Hale personal observations) while transport by logging truck tires may favor only small epigeic species (Dymond et al. 1997). Epigeic or epi-endogeic species that are poorly adapted to tolerate or escape dry conditions may be prevented from colonizing extremely course or dry soil types, or have restricted abundance in drier habitats. Low soil pH may prevent the colonization of all but a few of the small epigeic lumbricid species (Curry 1998). The chemistry of leaf litter is also important; the palatability of plant litter for earthworms increases as the C:N ratio decreases (Hendriksen 1990). Thus, boreal forests composed of pine (*Pinus* sp.) and spruce (*Picea* sp.) on sandy and/or acidic soils are likely to be more resistant to invasion, as they have been in northern Scandinavia despite the presence of lumbricids for thousands of years. The presence of deciduous tree species with low C:N ratio litter, such as aspen (*Populus* sp.) and birch (*Betula* sp.), mixed with pine and spruce is likely to allow earthworms to inhabit a site, especially those species such as *Dendrobaena octaedra* that are tolerant of poor litter quality (Nordström and Rundgren 1974; Dymond et al. 1997).

Impacts on plant communities

The cumulative impact of earthworm invasion on many plant species is likely to be substantial and may result in significant changes in community composition. In uncultivated, mature sugar maple dominated forests of northern Minnesota, earthworm invasion caused significant declines in the diversity and cover of herbaceous plants and abundance of tree seedlings (Fig. 1). Diverse, lush herb communities of spikenard (*Aralia racemosa*), solomon's seal (*Polygonatum pubescens*), bellwort (*Uvularia grandiflora*), nodding trillium (*Trillium cernuum*), large-flowered trillium (*Trillium grandiflorum*), and goblin fern (*Botrychium

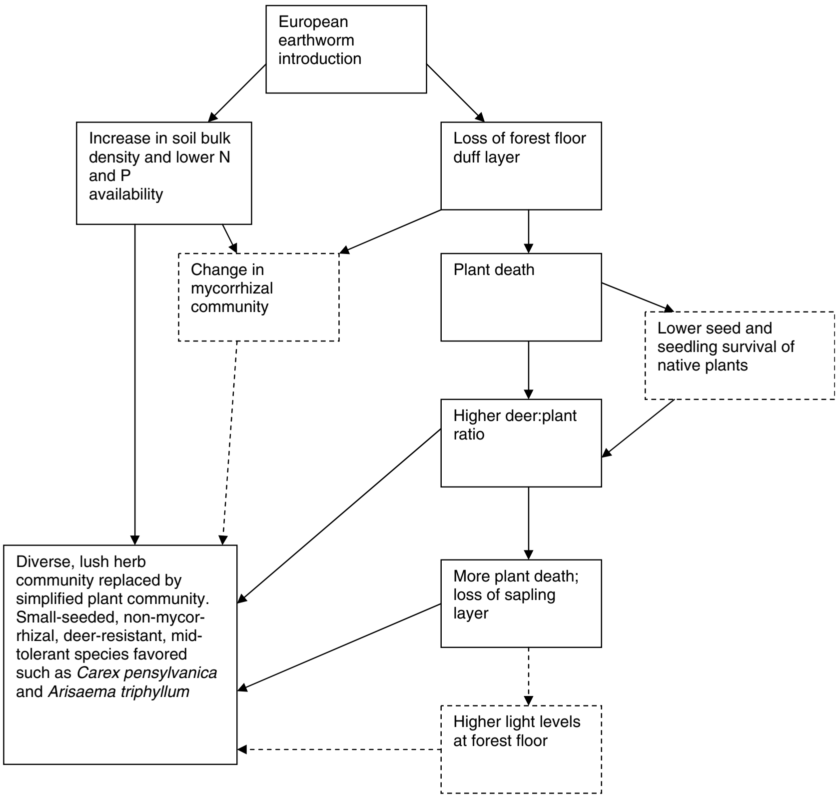

Fig. 1 Conceptual diagram for changes in plant community composition caused by European earthworms in Minnesota, USA, hardwood forests. Dashed boxes and arrows indicate hypothesized processes and connections with little data at this time

mormo) were transformed to simplified communities of only a few species dominated by *Carex pennsylvanica* and *Arisaema triphyllum* (Gundale 2002; Hale 2004) (Fig. 2). There are several possible mechanisms underlying the changes in plant communities during non-native earthworm invasion.

Mechanism 1: removal of the O_e/O_a horizon

The best-known mechanism is the direct removal of the forest floor duff layer (O_e and O_a horizons) by invading earthworms (Nielson and Hole 1963, 1964; Alban and Berry 1994; Bohlen et al. 2004a, c; Hale et al. 2005b). Without earthworms, temperate forests develop an organic forest floor that plays a fundamental role in nutrient cycling and serves as a seedbed and rooting zone for forest plant species. Invading earthworms cause the disappearance of the forest floor and partially or completely uproot herbs and tree seedlings (Hale 2004). This precipitates the first round of plant mortality contributing to a forest decline syndrome (Fig. 1).

Fig. 2 Forest floor and plant community at base of trees before (a) and after (b) European earthworm invasion in a sugar maple-dominated forest on the Chippewa National Forest, Minnesota, USA. Photo credit: Dave Hansen, University of Minnesota Agricultural Experiment Station

Understory plant species that succeed in forests with thick forest floors generally have larger seeds, more complex seed dormancy and germination strategies, and are more shade tolerant than plant species common to thin forest floor environments (Harper et al. 1965; Sydes and Grime 1981; Kostel-Hughes 1995; Baskin and Baskin 1998). Loss of the forest floor also reduces shelter, exposing seeds and seedlings to freezing, desiccation, and predation by insects, small mammals and other organisms (Nielsen and Hole 1964; Nixon 1995; Cothrel et al. 1997). Therefore, dramatic changes in the structure of the forest floor following earthworm invasion are expected to have a negative impact on the survival of understory species adapted to thick forest floors (Grime 1979; Gundale 2002). The thin litter layer remaining after earthworm invasion could favor the emergence of species with narrow, weak stems such as *Carex* species commonly found in earthworm invaded forests (Sydes and Grime 1981). We expect that species preferring a mineral soil seedbed will be favored over those preferring a duff seedbed, and that species dependent on duff, such as saprophytic coral root orchids (*Corallorhiza* ssp.), may be excluded or reduced in abundance following invasion.

In addition to problems with germination and emergence after earthworms change the forest floor, many of the native herbaceous species that decline during earthworm invasion are relatively poor colonizers with short seed dispersal distances (Cain et al. 1998). If nearby source populations do not exist these species are unlikely to recolonize earthworm-infested sites. For canopy tree species such as sugar maple (*Acer saccharum*), seed production does not appear to be affected by earthworms but seedling density clearly declines (Hale 2004).

The rate and magnitude of the removal of the forest floor and the consequences for native forest plant communities depends on the species of earthworms invading (Hale et al. 2005b). The strictly epigeic species, *D. octaedra*, has a limited effect on forest floor thickness and does not lead to increased plant mortality (Gundale 2002).

However, a population of *L. rubellus* can consume 10 cm or more thickness of intact forest floor within one growing season, which is faster than plants rooted in the forest floor can adjust, resulting in increased plant mortality during initial invasion (Hale and Holdsworth, personal observation). In contrast, *L. terrestris* preferentially consumes fresh surface leaf litter rather than intact forest floor leading to a more gradual reduction of the thickness of the forest floor that may allow plants to adjust to changing conditions.

Mechanism 2: direct impact of earthworms on seeds and seedling survival

Regeneration or recovery of the understory plant community following initial earthworm invasion may be greatly affected by seed and seedling dynamics of native plants (Marquis 1975; Mladenoff 1985; Pickett and McDonnell 1989). Passage of seeds through the earthworm gut and deep burial of seeds may decrease the viability of seeds and the soil seed bank in these systems (Leck et al. 1989). For most plant species native to North American forests, little or nothing is known with regard to these impacts on seed germination.

Mechanism 3: change in the mycorrhizal community

The loss of the forest floor duff layer causes changes in the mycorrhizal community, which may indirectly contribute to simplified plant communities (Fig. 1). Changes in soil structure and chemistry and grazing by earthworms lead to changes in the abundance and structure of soil fungal communities (Johnson et al. 1992; McLean and Parkinson 1998b, 2000). The vast majority of native understory plants in northern temperate sugar maple dominated forests are strongly mycorrhizal (Brundrett and Kendrick 1988), and declines in abundance or colonization rates of mycorrhizal fungi or shifts in fungal community composition could lead to changes in the understory plant community. The Goblin fern (*Botrychium mormo*) is strongly mycorrhizal, appears to be dependent on thick organic horizons, and has been completely extirpated in many areas invaded by earthworms (Gundale 2002). The declines in sugar maple (*Acer saccharum*) seedlings during earthworm invasion (Hale 2004) could be partially due to reduced arbuscular mycorrhizal colonization rates (Lawrence et al. 2003). Plants that are non-mycorrhizal and have an extended root growth period may be favored following earthworm invasion. In western Great Lakes hardwood forests, *Carex pensylvanica* increases dramatically following earthworm invasion. It is one of the only non-mycorrhizal native species in these forests and has the ability to produce roots during relatively cold periods of spring and fall (Brundrett and Kendrick 1988). Such soil influences on plant species abundance and diversity have been suggested (Newman and Reddell 1988; Francis and Read 1994; van der Heijden et al. 1998; Brussaard 1999) and are supported by the emerging research on earthworm invasions. Although there are a few mycorrhizal plant species, such as *Arisaema triphyllum* and *Circaea lutetiana* that have a positive relationship with earthworm biomass, a much larger number of plant species is negatively correlated with earthworm biomass (Hale 2004).

Mechanism 4: increased deer:plant ratio

Aboveground grazers can have large effects on plant composition and diversity, particularly large ungulates like the North American white-tailed deer (*Odocoileus virginianus*) (Pastor et al.1998; Horsley et al. 2003). Deer herbivory and earthworm invasion could have a synergistic effect on plant communities. The initial plant mortality resulting from the removal of the forest floor by earthworms increases the deer:plant ratio, so that deer consume a much larger proportion of plants than they would in the absence of earthworms. Shifts in the deer:plant ratio can lead to extirpation of plants, and to alternate states with lush and sparse plant communities, especially if the deer:plant ratio shifts such that annual consumption by deer is greater than annual growth among plants (Augustine et al. 1998; Côté et al. 2004;). High deer:plant ratios favor plant species that produce high levels of secondary compounds. The relative abundance of two such species, *Arisaema* *triphyllum* and *Allium tricoccum*, was unaffected by earthworms (Hale 2004), perhaps because herbivores avoid grazing them.

Mechanism 5: changes in productivity and nutrients

Changes in soil chemical composition and nutrient dynamics have been documented following earthworm invasion in previously earthworm-free soils (Scheu and Parkinson 1994a; Tomlin et al. 1995; Blair et al. 1997; Burtelow et al. 1998; Bohlen et al. 2004a, c) and will likely influence future plant communities. Increases in nitrogen and phosphorous loss due to leaching (Suárez et al. 2004) and decreased nitrogen and phosphorous availability (Bohlen et al. 2004b, Hale et al. 2005a) could reduce forest productivity and benefit some species over others.

Summary and future research

Earthworms are a keystone group of detritivores that affect composition of primary producers and ecosystem productivity by changing seedbed conditions, soil characteristics, flow of water, nutrients and carbon in ecosystems, and relationships between plants and herbivores. There is evidence that they strongly influence the composition of the herbaceous plant community. Changes in the tree seedling community attributed to exotic earthworms suggest that the composition of the tree layer will ultimately be altered as well.

The impact of earthworm invasion on ecosystem productivity in previously earthworm-free forests has not been studied at this point. However, reduced availability of key nutrients such as N and P, increased soil bulk density, and reduced diversity of the plant community could lead to reduced productivity through a cascade of ecosystem impacts. Long-term studies that follow individual tree growth and ecosystem-level measures of productivity such as litterfall and woody biomass production before and after earthworms invade will be necessary to ascertain impacts.

Because adult trees are not killed when earthworms invade, changes in successional trajectory and productivity may take decades or longer to detect. Therefore a way of dating earthworm invasion would be of value, so that impacts could be examined in stands invaded some time ago. Changes in soil chemistry caused by earthworms may create some sort of tree-ring signature, and if so this would be an ideal way to date time of invasion. Because earthworm invasion has been progressing through northern forests for a century, such a dating technique would allow the construction of a chronosequence of stands with varying time since invasion by earthworms. This in turn would greatly facilitate the investigation of slowly-developing, cascading ecosystem impacts of European earthworm invasion.

The impacts of earthworms on native forest soils are similar in some ways to plowing by humans. The mixing of forest floor material into the mineral soil to produce a 20–30 cm thick A horizon enriched with organic matter is similar in plowed soils and unplowed soils with earthworms. The findings of Bohlen et al. (2004a, c) are consistent with this hypothesis in that distribution of organic matter and nutrients within the soil were similar between areas with and without earthworms on a study site that was farmed and reforested, while invasion of earthworms into another location with primary soils (i.e. never plowed soils) caused large changes, making the soil similar to that found on the previously farmed site (Bohlen et al. 2004a, c). Based on historical information from New England, recovery of soils from farming takes centuries (Motzkin et al. 1996), and similar time frames for recovery would probably be required if exotic earthworms were somehow removed from these systems.

Earthworm invasion in some forests starts a forest decline syndrome that results in replacement of a lush diverse understory herb and tree seedling community with a sparse community of relatively low diversity (Figs. 1, 2). The degree to which the forest understory community declines depends on differential effects of various assemblages of invading earthworm species. These differential effects of earthworm species have two implications for impacts of invasive earthworms on native plant communities. First, the dominant earthworm species in a given area can influence the magnitude and rapidity of the invasion impacts. *Lumbricus rubellus* is a rapid, large impact ecosystem engineer, *L. terrestris* is a slow but large impact engineer, and *Dendrobaena* is a slow, small impact engineer of the forest floor environment. There is some empirical evidence for the ranking of impacts. Large areas have *Dendrobaena* as a dominant earthworm species and apparently retain high diversity and abundance of plants. On one Minnesota site dominated by *L. terrestris* several species of herbs persisted that disappeared from another site with *L. rubellus* (Hale 2004). Second, in areas with multiple species of earthworms invading, the order of invasion is important. If *L. terrestris* invades before *L. rubellus*, and the forest floor gradually disappears, then *L. rubellus* may have little additional effect if it invades later, and plants would have had time to adjust to the changing environment. The reverse order of invasion may be devastating to the plant community (Gundale 2002, Hale 2004). Experimental, controlled introductions of single earthworm species on field plots will be necessary to verify these field observations.

The forest decline syndrome may extend to more than just simplification of the understory herb community. Invasive plant species, successional trajectory of the tree canopy, and productivity may also be influenced by earthworm invasion. Whereas native plant species are negatively impacted by processes shown in Fig. 1, the spread of exotic plant species, such as European buckthorn (*Rhamnus* sp.) and garlic mustard (*Alliaria officinalis*), that are better adapted to the presence of earthworms than native plant species, may be enhanced by earthworm invasion. For instance, biomass and abundance of invasive earthworms increased in plots dominated by European buckthorn (Heneghan and Steffen, unpublished). European buckthorn produces leaf litter with a relatively low C:N ratio which decomposes rapidly (Heneghan et al. 2002). Elevation of earthworm populations in soils dominated by buckthorn is therefore expected and this increase in population has some important functional implications. In an urban woodland where buckthorn was the dominant understory species and where earthworm activity was high, leaf litter of buckthorn was fully lost from litterbags within 2 months. Decomposition rates were lower in parts of the woodland where buckthorn was not present and earthworms were less abundant. Soils in plots containing buckthorn had higher %N and %C, elevated pH and gravimetric water content, and modified microbial communities (Heneghan et al. 2002). This combination of altered ecosystem properties resulted in a soil that may be less suitable for natives than for the propagules of invaders. In this case the reciprocal relationship between the invasive shrub and earthworms resulted in a situation where each species positively reinforced the population of the other species (Heneghan 2003).

Following earthworm invasions, the increase in soil bulk density and loss of the duff, which absorbs water during rainfall events and slowly releases it into the soil, could lead to a more xeric ecosystem. In many temperate forest ecosystems this could lead to changing dominance from mesic to dry-mesic species. Often this means transition from sugar maple and American basswood (*Tilia Americana*), which prefer mesic conditions, to oaks and red maple (*A. rubrum*) (Curtis 1959), species which cast less shade than the mesic forest species (Canham et al. 1994). Gradual depletion of the tree sapling layer caused by reduced seedling recruitment after earthworm invasion (and reinforced by deer herbivory) could lead to more light at the forest floor. If future studies do find this effect, then a group of tree species mid-tolerant of shade may be favored, including northern red oak (*Quercus rubra*), white oak (*Q. alba*), American basswood, green ash (*Fraxinus pennsylvanica*) and red maple. Duff thickness and deer browsing, however, may also have other effects that could negate changes in water status and light. For example, thick duff favors red oak germination and survival, whereas thin duff favors white oak (Rogers 1990; Sander 1990), so that white oak may be favored in forests with earthworms. Deer also favor red oak, ash and red maple relative to sugar maple for winter browsing, and may therefore help sugar maple maintain dominance (Beals et al. 1960).

Changes in forest composition after earthworm invasion will be complex, and will interact with other agents of global change, such as warming climate. Long-term studies that follow soil water, nutrients, light levels, and plant community composition inside and outside of large deer exclosures, replicated in areas with and without exotic earthworms, will be necessary to examine how the cascade of impacts starting from earthworm invasion will influence the successional trajectory of the forest. At this point it appears likely that warming climate will allow higher deer populations in northern forests as well as faster northward expansion of invading earthworm populations. Thus we can hypothesize that warmer temperatures, deer and earthworms will work synergistically to change temperate forest ecosystems much faster than any one of these factors would by itself.

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ORIGINAL PAPER

Earthworm invasions in the tropics

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Abstract The effects and implications of invasive species in belowground terrestrial ecosystems are not well known in comparison with aboveground terrestrial and marine environments. The study of earthworm invasions in the tropics is limited by a lack of taxonomic knowledge and the potential for loss of species in native habitats due to anthropogenic land use change. Alteration of land use plays a major role in determining the abundance and community structure of earthworms and the establishment of exotic earthworms in areas previously inhabited by worms. Once an exotic species has become established into a new place, site and species characteristics seem to be key factors determining their spread. We reviewed the literature on the distribution and effects of exotic earthworms to understand the interactions of earthworm invasion and land use history in the tropics. Patterns in the abundance, effects and mechanisms of earthworm invasions on ecosystem processes in the tropics are elucidated using *Pontoscolex corethrurus* as a case study.

Keywords Tropics · Earthworms · Exotic · Native · Caribbean · Invasion

Introduction

Invasive species have become a major research issue in ecology, particularly due to the deleterious or unknown effects that non-indigenous species can have on ecosystem health and functioning. Ecologists continue to pursue fundamental questions related to biological invasions (i.e., why some communities are more invaded than others, or why some invading species are widespread and abundant; Colautti et al. 2004) yet have not unraveled the effects and implications of invasive species in belowground terrestrial ecosystems.

Invasive species include those organisms whose distribution and abundance are changing within historical times to include geographic regions in which they have not been present, and whose

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migration is not always directly related to range shifts associated with changing climate or habitat. Invasion follows a predictable set of stages including arrival, establishment, and spread (Hager and Treple 2003). Ecological consequences and management options differ at all stages, and individual species will exhibit variation in success at each stage. Invasive species successful at establishment and spread typically lack natural checks on population growth and can have important ecological consequences in a system.

Earthworms are the best known and often the most important animals influencing the functioning of soil ecosystems (Hendrix and Bohlen 2002). Earthworms significantly influence soil structure, nutrient cycling and crop productivity. In terms of biomass, they often dominate the fauna of soil food webs (Lavelle et al. 1999; Lee 1985) and their casting and burrowing activities increase soil porosity, stimulate microbial activities, and accelerate litter decay and the release of nutrients into the soil (Lee 1985; Lavelle et al. 1999; González and Seastedt 2001; González 2002; Liu and Zou 2002). The mechanisms by which land use history and exotic species invasions affect the relative abundance and species composition of local earthworm fauna are different than those caused by soil, climate, vegetation, and topography (Hendrix and Bohlen 2002).

Invasions of exotic earthworms in areas inhabited by indigenous earthworms can lead to the exclusion of either species group or to their co-occurrence. The potential mechanisms explaining the relative abundance of native and exotic species and the success or failure of the establishment of an exotic earthworm after an invasion include the intensity of propagule pressure, and the degree of habitat matching and biotic resistance (for details see Hendrix et al. this issue). Earthworms have also invaded areas previously devoid of earthworms (e.g., north of the Pleistocene glacial margin) (Hendrix 1995). In those areas, exotic European lumbricids have been shown to alter forest floor, change nutrient cycling rates and the distribution and function of microbes and roots, and negatively impact the native vegetation (e.g., Alban and Barry 1994; Gundale 2002; Bohlen et al. 2004; also see Frelich et al. McLean et al. and Tiunov et al. this issue).

Land use history plays a major role in determining the abundance and community structure of earthworms and the establishment of exotic earthworms in areas previously inhabited by native worms. For example, in the tropics, conversion of forest to pastures has been associated with significant decreases in soil macro-invertebrate diversity (Lavelle and Pashanasi 1989) and with the dominance of a few exotic earthworm species that can persist along gradients of plant succession after disturbance (Zou and González 1997; Sánchez-de León et al. 2003). Land use alteration in the tropics has historically been dominated by a shift from forest to agriculture, but there are also land use trends towards increasing urbanization and reforestation. The role of exotic earthworms includes influence on current pasture ecosystems, their potential invasion into surrounding forests and consequent ecosystem effects, their influence on regenerating secondary forests in abandoned pasture, and their overall effects on tropical biodiversity. Many of these potential effects are unstudied and remain unknown.

We have reviewed the literature on the distribution and effects of exotic earthworms to understand the interacting effects of earthworm invasion and land use history in the tropics. In the following sections, we evaluate the history of earthworm invasions in the tropics and the status of native and exotic earthworm species in this region. We elucidate patterns in earthworm abundance, effects of earthworm invasions on ecosystem processes and mechanisms of those effects in the tropics, using *Pontoscolex corethrurus* as a case study in many examples. Finally, some implications for management and future research directions are explored.

History of earthworm invasions in the tropics

James (1998) argued that earthworms are biogeographically model organisms, with poor dispersal and with distributions largely explained by past land connections and salt water barriers between land. Indeed, the absence of native earthworms from mid-oceanic volcanic islands, such as the Hawaiian and Canary Islands (Nakamura 1990; Loope et al. 1988; Talavera 1990), suggest great difficulty of earthworms crossing salt water (Stephenson 1930). Also, earthworms have failed to colonize the Lesser Antilles by over-water dispersal from nearby land masses inhabited by indigenous earthworms; there is no evidence of spread from South America into the Lesser Antilles or from the Greater Antilles to the east and south (James 1998).

When considering the history of invasions of exotic earthworms in the tropics we need to consider their transport by humans. The invasions of exotic earthworms in the tropics can be explained to a great extent by the historical dispersal of humans and commerce (e.g., trade routes). For example, *Gordiodrilus peguanus* and *Eudrilus eugenia* (African species) are present mainly in former European colonies such as the Greater Antilles (Gates 1972) that were inhabited by African slave populations. These species are not present in countries such as Perú and México where African slaves were practically non-existent (Fragoso et al. 1999). Similarly, the dispersal to the Caribbean Islands of three native genera of South America (*Pontoscolex*, *Onychochaeta* and *Eukerria*) can be explained by human migration prior to European colonization (Righi 1984; Lavelle and Lapied 2003). Humans arrived in the Greater Antilles from South America some 2200 years ago by island hopping (Domínguez-Cristóbal 2000). At least three successive groups or cultures of indigenous people from South America had arrived in Puerto Rico before 1493 (Gómez-Acevedo and Ballesteros-Gaibrois 1980). Some of those indigenous groups mastered agriculture (Gómez-Acevedo and Ballesteros-Gaibrois 1980) and their activities modified the flora and fauna by introducing new species to Puerto Rico (Francis and Liogier 1991). Also in Puerto Rico, exotic earthworms such as *Dichogaster* sp., *P. corethrurus* and *Amynthas rodericensis* have been reported in caves (Peck 1974) which were commonly used by indigenous people and African emancipated slaves (Ayes-Suárez and Otero-López 1986). Rightly so, Fragoso et al. (1999) stated that the absence from a given tropical country of native earthworms with wide range distributions can be explained by human activities rather than ecological factors. Merging rigorous scientific methodologies between ecology and human history could provide insights (James 1998) in the study of tropical earthworm invasions.

In recent times, commercial transport of earthworms or earthworm-containing media has advanced the proliferation and establishment of non-indigenous earthworms into new areas (see Baker et al., and Callaham et al. this issue). The major sources of non-indigenous earthworm introductions are the fishing-bait, horticulture and waste management industries. Advances in communication technology (e.g., internet access) have facilitated the promotion of lucrative businesses that sell and export exotic earthworms internationally. Most of the exotic earthworms used for waste management require high organic inputs and moisture conditions that can be met easily in forested landscapes in the tropics; shipment through the mail for waste management industries seem to be a key source of transport of non-indigenous earthworms into new areas. Recreational fishing has been related to the spread of exotic earthworms in the temperate forests of Minnesota, USA, where comprehensive educational efforts to stop the invasion have been well received (Callaham et al. this issue). The prevention of introductions of exotic earthworms in the many countries of the tropics should be based in education but also on the development of effective policy and management plans.

Native and exotic earthworm species in the tropics

During the early 1980's, researchers generally believed that earthworms had a low abundance and thus had little influence on soil processes in tropical forests as compared to tropical savannas and pastures where earthworms were more abundant. However, several studies completed in tropical forests have pointed out that earthworms are relevant to the soil macro-fauna in tropical ecosystems (Fragoso and Lavelle 1992). Taxonomists have described over 3600 earthworm species in the world with an average annual addition of 68 species. As more field surveys are conducted, especially in tropical regions where the great majority of species is unknown, the global earthworm richness could be at least twice the present count (Fragoso et al. 1999; Reynolds 1994). Fragoso et al. (1999) suggested that nearly 500 new native species could be expected to be discovered in Central America and the Caribbean islands once the surveys are completed. However, it has also been found that several peregrine earthworm species have invaded these tropical areas due to human activities (Fragoso et al. 1999), and the distribution of these exotic earthworms overlaps the range of native earthworms. In fact, results from Lavelle and Lapied (2003) indicate that many native earthworm species are in danger of extinction or have already disappeared in Amazonia due to the colonization by exotic species.

Fragoso et al. (1999) listed 51 exotic earthworms commonly distributed across the tropics. About 28 of them are present in the Caribbean Islands (Table 1). Over 50% of these exotic earthworms were originally from Europe and Asia (29 and 23%, respectively), 18% were from South America and 16% were from West Africa. They mainly belong to the Families Megascolecidae (35%) and Lumbricidae (33%) (calculated from data by Fragoso et al. 1999) and are widely distributed in different land-use systems, including natural ecosystems, croplands, pastures, tree plantations, fallows and are also present in organic wastes. There are about 400 native species of earthworms described in the tropics, with 67 % restricted to a single locality (Fragoso et al. 1999); approximately one third of those single localities are due to endemic species in the Caribbean Islands (Rodríguez et al. 2006). Native species in the Caribbean Islands mostly belong to the families Octochaetidae (65%) and Glossoscolecidae (17%) (Rodríguez et al. 2006). Jamaica and Hispaniola have the greatest percentage of native earthworm species (Rodríguez et al. in press), despite the scarcity of intensive surveys in both islands (Fragoso et al. 1999) and the extensive land use changes in Hispaniola. Therefore, the native earthworm fauna of the Caribbean Islands, like those of Amazonia, could be in danger of not being described or of extinction.

Table 1 The exotic earthworms of the Caribbean Islands (from Rodríguez et al. 2006)

Family	Species
Acanthodrilidae	*Pontodrilus litoralis* (Grube 1855) (=*P. bermudensis*)
Almidae	*Drilocrius hummalineki* (Michaelsen 1933)
Eudrilidae	*Eudrilus eugenieae* (Kinberg 1867)
Glossoscolecidae	*Pontoscolex corethrurus* (Müller 1856)
	Onychochaeta windlei (Beddard 1890)
	O. elegans (Cognetti 1905)
	Periscolex brachycystis (Cognetti 1905)
Lumbricidae	*Eisenia andrei* (Bouché 1972)
Megascolecidae	*Amynthas corticis* (Kinberg 1867)
	A. rodericensis (Grube 1879)
	A. gracilis (Kinberg 1867)
	Polypheretima elongata (Perrier 1872)
	Pheretima violacea (Beddard 1895)
	Perionyx excavatus (Perrier 1872)
	Pithemera bicincta (Perrier 1875)
	Metaphire houlleti (Perrier 1872)
Moniligastridae	*Drawida barwelli* (Beddard 1886)
Ocnerodrilidae	*Nematogenia panamensis* (Eisen 1900)
	Ocnerodrilus occidentalis (Eisen 1878)
	Eukerria kükenthali (Michaelsen 1908)
	E. saltensis (Beddard 1895)
	Gordiodrilus paski (Stepheson 1928)
Octochaetidae	*Dichogaster bolaui* (Michaelsen 1891)
	D. affinis (Michaelsen 1890)
	D. modiglianii (Rosa 1896)
	D. annae (Horst 1893)
	D. saliens (Beddard 1893)
	D. gracilis (Michaelsen 1892)

Mechanisms of earthworm invasions in the tropics – *Pontoscolex corethrurus* as a case study

Pontoscolex corethrurus, which was originally derived from South America, is now a dominantly invasive species around the world. Because of its superior capacities of adaptation, *P. corethrurus* has established populations throughout the moist tropical regions of over 56 tropical countries across the world (Fragoso et al. 1999). In Puerto Rico, *P. corethrurus* invaded primary cloud forests at the top of the Luquillo Mountains (Hendrix et al. 1999). An invasion of *P. corethrurus* has also been noticed in the Najenshan Nature's Reserve in southern Taiwan, a primary tropical rain forest (Zou et al. unpublished data). However, the invasion of tropical exotic earthworms occurs most frequently in disturbed habitats.

Establishment of exotic earthworms in a new area can occur (1) when they can compete successfully with native species in the new site, or (2) after they colonize disturbed habitats where human activities have reduced or eliminated native earthworms (Fig. 1). Kalisz (1993) suggested that whether native earthworms will coexist with or be replaced by exotic earthworms depends on the disturbance history of the areas and the state of naturalness of the landscape. As shown in Fig. 1, in native ecosystems native earthworms may completely impede the invasion of exotic earthworms because of their better adaptability to the original environments. But, disturbance (due to human activities or natural events) could result in extirpation or reduction of native species populations due to sharp changes in soil physical structure, nutrient cycling (litter input), and microclimate (e.g., logging and deforestation), conditions that may reduce native earthworm populations prior to the invasion of exotic earthworms. Opportunity for invasion in disturbed ecosystems occurs when native earthworms leave vacant niche spaces that are available for the introduction and colonization of exotic species (Kalisz and Wood 1995). It is then when the competitive relationship between native and exotic earthworms will become important for the coexistence of native and exotic earthworms or the presence of either population in a disturbed area (also see Hendrix et al. this issue).

Disturbance due to anthropogenic practices seems to be the major cause of spread of exotic earthworms in the tropics. Exotic earthworms can establish their populations in sites modified after deforestation (e.g. forest–pasture conversion), in tree plantations and in cultivated areas, as well as in areas inhabited by humans (González et al. 1996; Zou and González 2001; Lapied and Lavelle 2003; Fig. 2).

Some studies have argued that the increase in densities of *P. corethrurus* might directly cause the disappearance of native species populations (Fragoso et al. 1995; Lapied and Lavelle 2003). However, disturbed sites with a combination of both native and exotic species have been found (González et al. 1996; Kalisz 1993; Lapied and Lavelle 2003). This suggests that some native species might compete with exotic species and then exclude or co-exist with the exotics (Fig. 1). Certainly, more studies related to the relationships and consequences of native vs. exotic earthworm species are needed.

The reasons for failure or success of establishment of exotic earthworms include invasion history (e.g., frequency and duration of the introductions), site characteristics (e.g., climatic and edaphic conditions), and the characteristics of the species involved (see details in Hendrix et al.

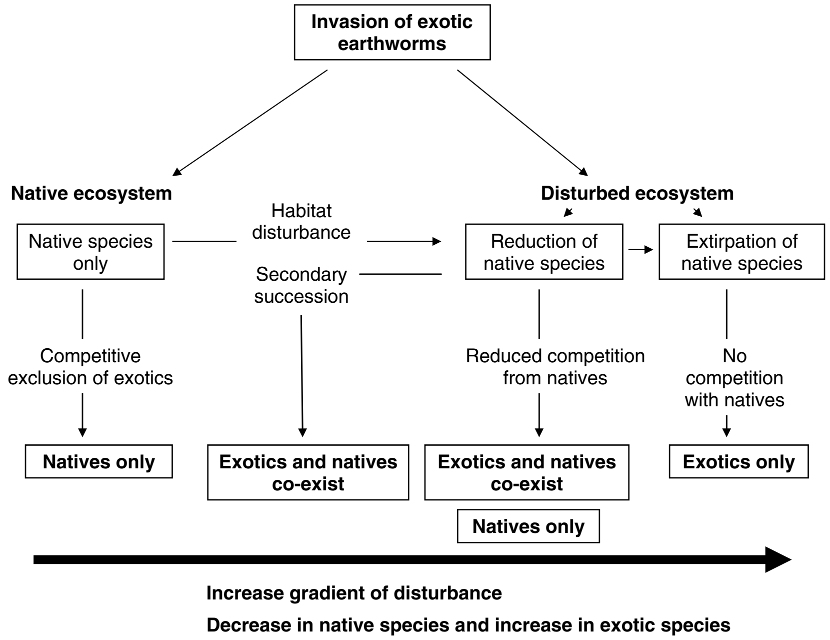

Fig. 1 Model illustrating the paths by which invasion of exotic earthworms affects native earthworm species in undisturbed and disturbed ecosystems

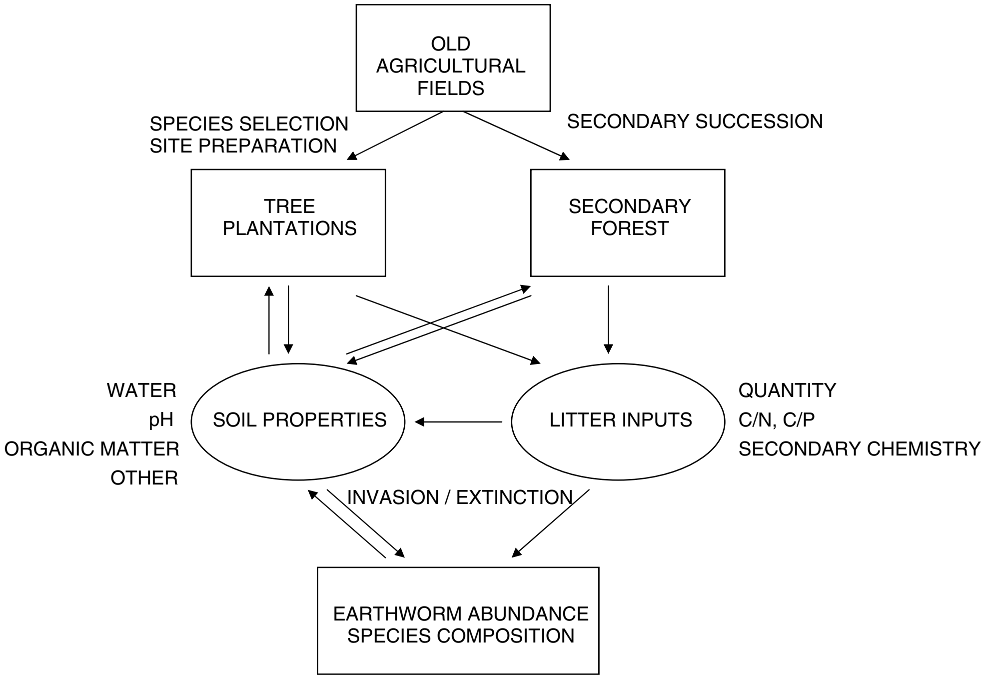

Fig. 2 Conceptual model illustrating the mechanisms by which tree plantations and secondary forests affect earthworm abundance and species composition in abandoned croplands (from González et al. 1996)

this issue). Once an exotic species has been established in a new place, the site and species characteristics seem to be key factors determining their spread. In contrast to exotic species, native earthworms are not as tolerant of a shift to dryer grassland microclimate conditions, and are mostly restricted to natural ecosystems (González et al. 1996; Zou and González 1997; Fragoso et al. 1999; Lapied and Lavelle 2003; Sánchez-De León and Zou 2003; Decaëns et al. 2004). For example, *P. corethrurus* can reach an abundance of 1000 individuals per square meter (25 cm deep) in disturbed agricultural pastures (Zou and González 1997). It has also been shown to inhabit soils that are highly compacted, have low pH, high temperature and low moisture regimes, and poor organic inputs (e.g., Henrot and Brussaard 1997; Römbke et al. 1999; García and Fragoso 2002; Decaëns et al. 2004; among many others).

The reproductive biology of exotic species is an important characteristic to consider in the context of invasion. Tropical peregrine earthworms (e.g., *P. corethrurus*, *Perionex excavatus*, *Dichogaster modigliani* and *Polypheretima elongata*) are often considered to be continuous breeders with high fecundity (Bhattacharjee and Chaudhuri 2002). Thus, on the basis of response to selection pressure, high fecundity, short incubation period with high hatching success are probably adaptative strategies of *r*-selected organisms that enable them to survive drastic environmental changes, especially heat, drought and predation in the soil (Pianka 1970; Bhattacharjee and Chaudhuri 2002). Thus far, endogeic earthworms have been more frequent invaders of disturbed tropical pastures than epigeic species. Interestingly, exotic endogeic species (e.g., *P. corethrurus*, *P. elongata* and *Drawida nepalis*) have been shown to increase their rate of cocoon production and incubation period with increased temperature (Fig. 3) while epigeics decreased their reproductive capabilities (Bhattacharjee and Chaudhuri 2002). One more reason for the absence of epigeic invasive earthworms in the tropics is due to the presence of abundant vertebrate predators such as frogs and lizards. Thus, the interactions between the characteristics of the exotic earthworm species, particularly their functionality and activities, could determine their potential for establishment.

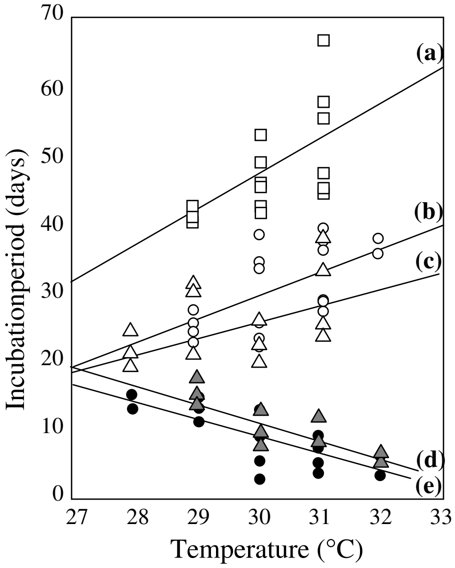

Fig. 3 Relationship between temperature and incubation period in different earthworm species (**a**) *Polypheretima elongata*, (**b**) *Drawida nepalensis*, (**c**)*Pontoscolex corethrurus*, (**d**) *Dichogaster modiglianii*, and (**e**) *Peryonyx excavatus*. Endogeic species are represented with open symbols and epigeic species are represented with filled symbols (modified from Bhattacharjee and Chaudhuri 2002)

Another characteristic that makes *P. corethrurus* a successful invader is the ability of juveniles to enter diapause and to regenerate after amputation, independent of soil moisture conditions (Fragoso and Lozano 1992). Parthenogenesis is common for most tropical exotics (Fragoso et al. 1999). All of the above characteristics could be adaptive strategies of tropical exotic earthworms to cope with climatically harsh environments, making them without doubt strong invaders.

Ecological consequences of earthworm invasion in the tropics

Ecosystem properties

Ecosystem properties may change after an invasion by exotic earthworms. In undisturbed ecosystems, native earthworms could either outcompete an invasive earthworm or the invasion itself could lead to a disturbed ecosystem. Exotic earthworms in disturbed ecosystems could cause the reduction or extirpation of native species and such invasion could result in changes in soil properties and biogeochemical processes (Fig. 1). There is little information on changes in ecosystem species composition and structure following tropical earthworm invasion. Vitousek et al. (1987) showed that invasion of the dinitrogen-fixing tree, *Myrica faya*, affected plant species composition, net ecosystem productivity and nitrogen cycling in Hawai'i. But these changes also coincided with the presence of the exotic earthworm *P. corethrurus* (Aplet 1990; Zou 1993). Therefore, it is unclear whether these changes resulted from the invasion of trees, earthworms, or both. Knowledge of ecological consequences for soil biological diversity following tropical earthworm invasion is also scarce because of the absence of data on soil biota before invasion occurred (also see McLean et al. and Migge-Kleian et al. this issue). Nevertheless, there is scattered information available for the effects of tropical earthworm invasion on soil physical properties and biogeochemical processes.

Soil physical properties

Earthworms have typically been thought to improve soil physical properties through their borrowing and casting activities. In contrast, Chauvel et al. (1999) and Barros et al. (2001) reported that the invasion of *P. corethrurus* after forest clearing and introduction of exotic grasses resulted in a large increase in earthworm population density (400 ind. m^{-2}). This consequently produced an impermeable crust (up to 20 cm thick) of compact castings which decreased soil macro-porosity and increased soil erosion in Amazonian pastures. However, this finding was not consistent with a study conducted in Puerto Rico, where *P. corethrurus* did not cause significant changes in soil bulk density in a pasture and mature tabonuco forest (Liu and Zou 2002), even though earthworm population density reached 840 ind. m^{-2} in the pasture site (Zou and González 1997). In contrast to the findings of Barros et al. (2001), Larsen et al. (unpublished data) found that soil erosion and surface water runoff were significantly reduced with the presence of *P. corethrurus* in a tabonuco forest in Puerto Rico. We need more studies to understand the effects of invasive tropical earthworms on soil physical properties. Interaction effects between the earthworms and specific soil characteristics may dominate hydrologic responses.

Biogeochemical processes

Changes in soil physical properties such as aeration can alter soil oxidation/reduction and leaching processes. Changes in the activities of the soil community may also regulate biogeochemical reactions in the soil. A reduction in soil aeration can increase the production of methane and nitrous oxide, enhancing the greenhouse effect. The consequences of tropical earthworm invasion on soil oxidation and reduction status and its subsequent effect on greenhouse gas production remain poorly known. An increase in the density of tropical invasive earthworms can accelerate the mineralization of nitrogen and the decomposition of plant litter. Pashanasi et al. (1992) found exotic species (*P. corethrurus*) enhanced N mineralization with a trend of increasing microbial biomass in a pot experiment containing three tropical fruit seedlings. Similarly, González and Zou (1999) found that *P. corethrurus* increased soil N availability in a pot experiment containing the tropical pioneer tree species *Cecropia*. Liu and Zou (2002) suggested that *P. corethrurus* increased litter decomposition rates by elevating rates of litter consumption or microbial activity in a tropical pasture and a wet forest in Puerto Rico. These findings that tropical invasive earthworms accelerate biogeochemical fluxes are in accordance with those found in temperate systems.

Concluding remarks

Great advances in our knowledge of the ecology and taxonomy of earthworms in the tropics, especially in tropical moist and wet forests, have occurred during the past quarter of a century. Still, the study of earthworm invasions in the tropics is limited by a lack of taxonomic knowledge and is challenged by the potential for loss of species in native habitats due to anthropogenic land use change. The history of the introductions of non-indigenous earthworms is much more complex in the tropics than in temperate North America as it is related to the complex human history of migration and use of the landscape, water barriers and island ecosystems. An interdisciplinary approach (i.e., history and ecology) can help elucidate the spread of non-indigenous species in the tropics and help develop policy on invasive earthworms as related to land management (also see Baker et al. and Callaham et al. this issue).

There are a few examples of exotic earthworms known to invade relatively undisturbed forest remnants in the tropics. However, disturbance due to anthropogenic practices seems to be a major prerequisite for earthworm invasion in the region. The peregrine earthworm *P. corethrurus* seems to be the dominant species in pastures established after deforestation. Depending on the type and frequency of a disturbance, however, we can find sites exclusively dominated by exotics or native species, or by a combination of both. Thus, studying the differences in adaptative strategies between invasive and native earthworms can help explain the success in survival and establishment of non-indigenous earthworm species in disturbed sites. In the tropics, the ecosystem consequences of (1) a mixed native and exotic earthworm community, (2) an exclusively exotic earthworm community, and (3) the dominance of single exotic species in sites previously inhabited by native earthworms have yet to be determined. The general contention that earthworms increase soil fertility and plant productivity could be applied to examples from both native and exotics species. Also, there are conflicting results on the effects of *P. corethrurus* on soil physical properties in active and abandoned pastures in different parts of the tropics. Therefore, studies that deal with the effects of the different mixtures or scenarios of native vs. exotic earthworm species on soil physical and biogeochemical properties and overall ecosystem species composition are needed. An important level of complexity to consider is the functionality (epigeic vs. anecic vs. endogeic) of the native and/or exotic species involved as their functionality could be as important as the combination of the species assemblage. Since the effects of the introductions and establishment of non-indigenous earthworms are not fully understood, a prudent management strategy should focus on the prevention and study of these invasions. Earthworm invasions can have profound implications in the conservation of biodiversity, natural habitats and overall ecosystem health in the tropics.

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ORIGINAL PAPER

Earthworm invasions of ecosystems devoid of earthworms: effects on soil microbes

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Abstract Recent studies document North American earthworm invasions and their profound effects on the structure of the soil profile, which is the habitat for soil microorganisms (mainly fungi and bacteria). Dramatic alterations made to these layers during earthworm invasion significantly change microbial community structure and therefore microbial activities such as C transformations. Understanding the impacts of earthworm invasion on the microbes themselves will give insight into earthworm effects on microbial activities. Bacterial and actinomycete communities in earthworm guts and casts have not been studied in environments recently invaded by earthworms. Earthworm invasion tended to decrease fungal species density and fungal species diversity and richness. The presence of earthworms decreased zygomycete species abundance probably due to disruption of fungal hyphae. Physical disruption of hyphae may also explain decreased mycorrhizal colonization rates, decreased mycorrhizal abundance and altered mycorrhizal morphology in the presence of earthworms. Mixing of organic layers into mineral soil during earthworm invasion tended to decrease microbial biomass in forest floor materials while increasing it in mineral soil. In newly invaded forest soils, microbial respiration and the metabolic quotient tended to decline. In forests where either the microbial community has had time to adapt to earthworm activities, or where the destruction of the forest floor is complete, as in invasions by the Asian *Amynthas hawayanus*, the presence of earthworms tends to increase the metabolic quotient indicating a shift to a smaller, more active microbial community.

Keywords Bacteria · Disturbance · Earthworm invasion · Enzyme activity · Fungal community · Microbial biomass · Mycorrhizae

Introduction

Soil microbes

It is estimated that half of Earth's biomass is microbial (Whitman et al. 1998). Soils contain an incredible genetic and functional diversity of microbes (primarily bacteria and fungi) (Swift et al.

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1979; Lavelle and Spain 2001; Buckley and Schmidt 2002). Microbes are enzymatically very versatile and are able to degrade a vast range of organic substrates including recalcitrant biopolymers such as lignin and cellulose (Atlas and Bartha 1998). Both bacterial and fungal nutrition are heterotrophic and absorptive in nature but differences in bacterial and fungal growth patterns account for their differing impacts in the soil habitat. Bacteria are unicellular, or, in the case of actinomycetes, finely filamentous, but both tend to be clustered in discrete microhabitats only a few micrometers in volume (Swift et al. 1979; Coleman and Crossley 1996). Bacterial cells are confined to the surface of soil particles and bacterial activity is related to the surface area of these particles (Gunnarsson et al. 1988). Their small size allows efficient dispersal through water films and permits colonization of all available crevices and pores where they rapidly exploit available resources (Swift et al. 1979). Actinomycetes can comprise 10 to 33% of the soil bacteria and are relatively drought tolerant (Swift et al.1979; Atlas and Bartha 1998; Brady and Weil 2002). In contrast, fungi are multicellular and their filaments (hyphae) penetrate many microhabitats where they secrete enzymes, degrade complex substrates and absorb the degradation products (Swift et al. 1979; Coleman and Crossley 1996; Carlile et al. 2001). These absorbed nutrients can be translocated along the hyphae to supply nutrients to parts of the hyphal network which are nutrient limited (Swift et al. 1979). Although many species of soil fungi occur as free-living microbes, some occur as symbionts with plant roots, in which the fungus becomes integrated into the physical structure of the roots (Atlas and Bartha 1998). These mycorrhizae occur in most families of plants. Mycorrhizae extend from the root into the soil and increase plant uptake of nutrients, especially phosphorus and nitrogen and in return the fungal partner is supplied with carbon substrates (Carlile et al. 2001).

Earthworm impacts on forest soil

In the absence of earthworms, forest soils typically contain organic layers of varying thickness, consisting of relatively unaltered leaf litter (Oi or L), fragmented, darkened litter (Oe or F) and amorphous, humified, unidentifiable litter (Oa or H). These organic layers are the site of the majority of microbial biomass and activity and contain a wide range of microhabitats and substrates for microbial exploitation (Atlas and Bartha 1998; Lavelle and Spain 2001). The invasion of earthworms results in reduction of the thickness, heterogeneity and organic matter content of these organic layers, an increase in the thickness of the upper mineral horizon, and increased or decreased organic matter content of the upper mineral horizon (Alban and Berry 1994; McLean and Parkinson 1997a; b; Burtelow et al. 1998; Hale 2004; Bohlen et al. 2004b). Earthworms also have profound effects on nutrient availability, through the addition of nutrients from urine, mucus and dead tissue as well as through chemical and physical alterations during gut passage (e.g. Scheu 1991; Brown et al. 2000). In general, earthworms increase N availability and may increase or decrease C accessibility depending on the type of earthworm, age of fecal material and soil layer (e.g. Brown et al. 2000; Lavelle and Spain 2001; also see Frelich et al., and Baker et al., this issue).

Potential impacts of earthworms on soil microbes

The complex ways in which earthworm activities alter soil habitats for microbes may result in overall positive or negative effects on microbial activities and communities. Increased C and N availability in mucus and urine might be expected to increase microbial growth and activity, particularly in mineral soils where microbes are thought to be inactive most of the time. In contrast, gut passage may have positive or negative effects on microbes depending on the type of microbe and degree of disturbance. Degree of disturbance during gut passage relates to the length of time spent in the gut; typically, from 3–8 h for epigeics and 12–20 h for anecics (e.g. Parle 1963b; Edwards and Fletcher 1988).

Gut passage through epigeic earthworms results in litter fragmentation and some mixing with mineral material (Ponge 1991). Particle surface area is an important parameter for bacteria and there has been speculation that comminution, or the reduction to small fragments, would have potentially positive effects on bacterial activity (e.g. Gunnarsson et al. 1988). One might expect then that epigeic gut passage would result in increased bacterial activity and growth due to the increased particle surface area and the accompanying substrate accessibility. One might also expect that litter comminution during epigeic gut passage might either increase or decrease fungal growth and activity depending on the degree of hyphal disruption. The importance of the integrity of the hyphal links between parts of a fungal mycelium has led to much speculation about the potential effects of earthworm disturbance on fungi (e.g. Pattinson et al. 1997; McLean and Parkinson 2000; Lawrence et al. 2003).

In addition to causing physical disturbance, earthworms also chemically alter microbial substrates, thus altering nutrient availability (see Frelich et al.; Baker et al., in this volume for a discussion of earthworm effects on nitrogen; this review will be limited to earthworm effects on C transformations). Passage through guts of anecic or endogeic earthworms results in much more complete mixing of organic and mineral materials than through epigeic guts. The formation of stable organo-mineral complexes during anecic or endogeic gut passage may reduce C availability to microbes in casts depending on the time scale (e.g. Lavelle and Spain 2001). In the short term, (few days) microbial activity is often stimulated in casts, but over weeks, stabilization begins and over months to years, there is generally a protection of C in casts and a decrease in C mineralization (Brown et al. 2000). One might expect that anecic or endogeic gut passage would result in an initial stimulation and later a reduction in microbial activity due to the addition of soluble C in intestinal mucus followed by a long-term reduction in available C substrates. And anecic and endogeic gut passage is expected to have more negative impacts on fungal growth and activity due to more intense hyphal disruption, relative to that caused by epigeic gut passage.

A further potential impact of earthworms on microbes is that of transport of microbial propagules. Earthworm activities have been shown to increase microbial distributions in soils (Hutchinson and Kamel 1956; Doube et al. 1995; Harinkumar and Bagyaraj 1994; Daane et al. 1997) which may translate into overall effects on microbial growth and community structure.

In the following sections, we consider effects of earthworms on several aspects of soil microbial community structure and activity. In each case we first discuss the situation in which microbes and earthworms occur together in the same habitat, and then the situation where earthworms have recently invaded habitats devoid of earthworms.

Earthworm impacts on microbial species and communities

Bacteria—co-occurring with earthworms

Whether the microbes observed in earthworm guts are permanent residents of the gut or are transient reflections of the microbial community on ingested materials is not yet clear. It seems likely that at least some bacteria may be permanent components of earthworm guts. That bacterial numbers varied in a uniform way from crop to hind gut in *Lumbricus terrestris* irrespective of litter substrate (Wolter and Scheu 1999) is consistent with this idea. Comparison of bacteria isolated from the guts of starved earthworms and earthworms fed farmyard manure led Toyota and Kimura (2000) to conclude that the *Aeromonas* species found in the guts of starved *Eisenia foetida* was indigenous to the earthworm. They also concluded that *Bacillus* species, which were abundant in earthworm guts reflected the bacterial community on the farmyard manure fed to the earthworms (Toyota and Kimura 2000).

Bacterial diversity in earthworm guts can be quite high; several hundred bacterial strains have been isolated from earthworm guts (Khambata and Bhat 1957; Márialigeti 1979). Gut bacteria are also functionally diverse, digesting a wide range of compounds including amino acids, sugars, cellulose, chitin, lignin, starch, polylactic acids (Khambata and Bhat 1957; Parle 1963a; b; Márialigeti 1979; Makulec 2002).

Bacterial abundances tend to be higher in earthworm guts, relative to the soil (Parle 1963b; Shaw and Pawluk 1986; Karsten and Drake 1997), but see Makulec (2002). During passage through the gut bacterial numbers may increase or decrease depending on earthworm species, bacterial species and part of the gut (Parle 1963b; Kristufek et al. 1992; Pedersen and Hendriksen 1993; Karsten and Drake 1997). Increased bacterial abundance during gut passage was observed in the anecic *L. terrestris* as well as the epigeic *L. rubellus*, but not in the endogeic *Aporrectodea caliginosa* (Parle 1963b; Kristufek et al. 1994; Karsten and Drake 1997). These differences may be due to differences in earthworm digestion. For example, the release of labile substrates during comminution by epigeic and anecic earthworms may stimulate bacterial multiplication while ingestion of recalcitrant humified organic matter by endogeics may suppress bacterial multiplication in earthworm guts (Parle 1963b; Kristufek et al. 1992). Bacterial abundances increased logarithmically during *L. terrestris* gut passage suggesting bacterial growth and not selection of food materials rich in bacteria (Parle 1963b). Also differential susceptibility to digestive enzymes in *L. rubellus* and *L. festivus* foregut may explain the observed reduced bacterial abundance in the foregut, but increased abundance in the hind gut suggests growth (Pedersen and Hendriksen 1993). Differential susceptibility to digestive enzymes may in part relate to the ability of the bacterial species to insulate itself in bacterial microaggregates in the gut. In *L. rubellus* guts, Kristufek et al. (1994) observed metabolically active bacteria enveloped by layers of clay particles in an exopolysaccharide matrix. As biofilms protect bacteria from antibiotics and environmental stresses (Davey and O'Toole 2000), these microaggregates may protect the bacteria from digestive enzymes and abrasion.

Not only are bacteria found in earthworm guts, but bacteria added to earthworm substrates can survive passage through earthworm guts. Even gram-negative non-spore forming bacteria can survive gut passage through lumbricid earthworms (Pedersen and Hendriksen 1993; Thorpe et al. 1993; Doube et al. 1995; Daane et al. 1997). Bacterial communities in fresh earthworm casts reflect the particular bacterial community of the ingested substrate and the differential survival of bacterial cells and spores during gut passage. For example, lower abundance of *E. coli* and *Pseudomonas* spp. in casts than dung suggested that these species did not survive gut passage as well as *Enterobacter* spp. and *Aeromonas* spp. whose abundance was similar in dung and casts.

Earthworms may also alter the distribution of bacteria in the soil due to their burrowing activities. In laboratory microcosms, the influence of earthworm activities on plasmid transfer between spatially separated donor and recipient bacteria was studied (Daane et al. 1997). Limited vertical movement of donor and recipient bacteria occurred in the absence of earthworms while earthworm activities significantly increased vertical bacterial distributions (Daane et al. 1997).

Bacteria—recent earthworm invasion

To our knowledge the bacterial communities in earthworm guts and casts in ''pristine'' environments have not yet been investigated. If at least some members of the earthworm gut bacterial community are permanent gut residents, then earthworms arriving in North America from Europe and Asia, for example, may still possess characteristic bacterial species. This needs to be determined. Since at least some members of the earthworm gut bacterial community appear to reflect the bacterial community on the substrates ingested, one might expect to find similar patterns in environments previously devoid of earthworms as those found in habitats with long-term earthworm occurrence.

Actinomycetes—co-occurring with earthworms

Actinomycetes associated with earthworms have not been well studied. Not only is it unclear whether any of the actinomycetes isolated from earthworm guts are permanent residents or merely reflections of the actinomycete community on ingested substrates, studies are also lacking on interactions between earthworms and actinomycetes.

One estimate of temperate forest soil actinomycete diversity indicates that 90–130 species may be isolated from different soil layers (Lavelle and Spain 2001). Sixty species of actinomycetes were isolated from the guts of Indian earthworms (Khambata and Bhat 1957). Kristufek et al. (1990) isolated 14 species of *Streptomyces* from meadow soil and 12 species from the guts of *L. rubellus* and *Octolasion montanum*. In both soil and earthworm guts, 5–36% of the bacteria isolated were actinomycetes, but this varied with earthworm species (Khambata and Bhat 1957; Kristufek et al. 1993; Atlas and Bartha 1998). Kristufek et al. (1993) attributed the low proportion in *L. rubellus* guts to the low proportion of actinomycetes on the organic matter consumed by *L. rubellus*. This suggests that the actinomycete community in earthworm guts reflects the actinomycete community on the ingested substrate rather than being permanent gut residents. Consistent with this idea are the observations that (i) different streptomycete species were dominant in *L. rubellus* and *O. montanum* guts, and (ii) the streptomycete communities in these earthworm guts were very similar to those in the soil in spring but very different from those in the soil in summer (Kristufek et al. 1990).

Actinomycete survival and abundance during earthworm gut passage depends on the earthworm species. Actinomycete abundance increased during *L. terrestris* gut passage but did not increase during *A. caliginosa* gut passage (Parle 1963b; Kristufek et al. 1992). These observations may indicate effects of differences in earthworm digestion and/or differential susceptibility to digestive enzymes in a manner similar to other bacteria (see above). Possibly longer gut transit time for *L. terrestris* would allow time for actinomycete multiplication while the short gut transit time for *A. caliginosa* would not.

Data on abundances of actinomycetes isolated from earthworm guts and casts are few and contradictory, and do not appear to relate to either the ecological strategy of the earthworm species or soil pH (Parle 1963b; Kristufek et al. 1993; Makulec 2002). These differences may reflect the different isolation media used in each study and point up the necessity for further investigation of this important microbial group. One microcosm study suggests that earthworm activities may also increase actinomycete abundance in the whole soil (as characterized by the phospholipid fatty acid (PLFA) 10Me18:0, which is an indicator of actinomycetes) (Saetre 1998).

Actinomycetes—recent earthworm invasion

To our knowledge there are no data on the effects of earthworm invasions on actinomycete communities in pristine soils. Since this group of microbes produce many antibiotics which may have significant negative impacts on the growth and activity of other soil microbes, this is a subject that needs to be explored.

Microfungi—co-occurring with earthworms

It seems likely that gut fungi are transient reflections of the substrate microbial community. This is supported by the observation that the fungal community in fresh *L. terrestris* casts appears to reflect the fungal community on the litter substrates consumed (Tiunov and Scheu 2000b). Fungal hyphal length was maximal in *L. terrestris* crop/gizzard but tended to decline during gut passage, and was generally greater than hyphal length in the soil; this indicated selective grazing on microbe-rich substrates (Wolter and Scheu 1999).

Data on fungal diversity in earthworm guts are very limited. Six fungal species were isolated on nitrogen-free media and 36 taxa were isolated on cellulose medium from the guts of Indian earthworms; 17 species were isolated from guts of *L. terrestris* and 16 from *Drawida calebi* (Hutchinson and Kamel 1956; Khambata and Bhat 1957; Dash et al. 1979). Presumably these are underestimates and more fungal species would have been isolated from these guts had the authors examined more samples or used more types of isolation media.

Transmission electron microscopy of *L. rubellus* earthworm gut contents revealed few fungal hyphae (Kristufek et al. 1994), although fungal colony-forming units (CFUs) increased during gut passage to a maximum in the hind gut (Kristufek et al. 1992). Dash et al. (1979) observed that size of hyphal fragments decreased during gut passage suggesting that increased CFUs is a result of comminution of hyphae into smaller, but still viable fragments during gut transit. Conversely, fungal CFUs decreased from the foregut to the hindgut in *A. caliginosa* suggesting that endogeic gut passage results in more damage to fungal hyphae and fewer viable CFUs relative to epigeic gut passage (Kristufek et al. 1992). Further evidence that fungal survival during gut passage depends on the earthworm and the fungal species is given by Moody et al. (1996) and Shankar et al. (2002). Fungal spore viability differed between two anecic species, *L. terrestris* and *A. longa*. In general, gut passage through either earthworm species significantly reduced spore viability of all four fungal species tested except that *Chaetomium globosum* was slightly reduced by *L. terrestris* and significantly enhanced by *A. longa* (Moody et al. 1996). Germination of *Mucor hiemalis* spores was reduced by exposure to *L. terrestris* intestinal fluids and tended to be higher following mechanical abrasion (Moody et al. 1996).

Fungal diversity in earthworm casts is not well studied, ranging from 6 genera (not identified to species) to 61 species in the few observations that have been made (Parle 1963a; Tiwari and Mishra 1993; Tiunov and Scheu 2000b; Orazova et al. 2003). Even the highest estimates may underestimate actual species richness; plating more particles would probably yield more species. With these limitations in mind it appears that cast fungal community structure depends on the differential survival of fungal propagules, the substrates ingested by the earthworms and cast age. There are not enough data to conclude whether the species of earthworm is an important factor although it would be surprising if it were not, given differences seen in bacterial and actinomycete communities.

Fungal community structure in earthworm casts has recently been investigated in detail. Tiunov and Scheu (2000b) observed a tendency for two species of Mucorales and two species of *Alternaria* to be less abundant and for *Trichoderma* species to be more abundant in fresh casts than in the original litter, possibly due to differential survival of fungal propagules during gut passage. An investigation of the importance of improved microhabitat conditions in *L. terrestris* middens revealed that microhabitat conditions were less important than gut passage in structuring the cast fungal community (Orazova et al. 2003). Cast fungal communities are also affected by substrate consumed by earthworms. Fungal communities on fresh *L. terrestris* casts were more similar to communities on litter than to communities on soil (Tiunov and Scheu 2000b). Cast fungal communities of worms consuming beech (*Fagus*) differed from those consuming linden (*Tilia*) litter and these differences were maintained for at least 100 days during aging (Tiunov and Scheu 2000b). Cast age also affects cast fungal community structure. Fungal communities of aged casts were easily differentiated from those of fresh casts (Tiunov and Scheu 2000b). Aged casts containing either beech or lime litter retained their differences from each other and from aged casts without litter for 100 days (Tiunov and Scheu 2000b). As casts aged, the number of uncolonized particles decreased while the number of fungal taxa isolated, fungal and yeast CFUs, and abundance of two species of Mucorales increased (Parle 1963b; Tiunov and Scheu 2000b). Fungal CFUs in recently deposited casts were higher than in soil, possibly due to increased C availability in casts which contained 1.5 times more organic C and total N than the soil (Parle 1963a; Tiwari and Mishra 1993; Makulec 2002).

Microfungi—recent earthworm invasion

Prior to earthworm invasion, the organic layers in soil provide many microhabitats and resources to support an abundant and diverse soil biota. The profound changes in soil organic layers resulting from earthworm invasion significantly alter microhabitats and resources for these microorganisms. However, data are very limited and refer only to effects of invasive earthworms on the fungal community in soil, not in earthworm guts or casts. Studies on gut and cast fungi of invasive earthworms are needed.

Effects of the invasion of *D. octaedra* into pine forest soil in Alberta were studied in laboratory mesocosms and in field plots, which are thought to represent the early and later stages in the invasion, respectively. Early in the invasion the number of fungal isolates per particle (a measure of competition between fungi) first increased, then decreased as worm activities intensified (McLean and Parkinson 1998). The increase in number of isolates per particle suggests that competition between fungi was reduced, possibly through the addition of nutrients or increasing spatial heterogeneity as the worms deposited casts in the organic layers. This was followed by a decrease in number of isolates per particle suggesting that further worm activities decreased resource availability or reduced spatial heterogeneity, as the organic layers became homogenized. Later in the invasion, fungal community diversity and richness decreased and dominance by one fungal species increased, apparently due to the disruption of fungal hyphae (McLean and Parkinson 2000). Evidence for this included (i) positive correlation of the occurrence of fast growing species such as *Trichoderma polysporum* with high worm biomass, (ii) negative correlation of the occurrence of slow growing species such as *Oidiodendron echinulatum* with high worm biomass, and (iii) decreased occurrence of Zygomycetes such as *Mortierella ramanniana* and species of *Mucor* in plots containing high worm numbers. Zygomycetes have few septa and are more susceptible to cell content leakage following hyphal damage than are fungi with more septa.

Given the differences between epigeic, endogeic and anecic earthworms in terms of their preferred food and effects on the soil profile, one might expect significant differences between the invasion of epigeic earthworms and either anecic or endogeic earthworms. In a laboratory mesocosm experiment, the anecic earthworm *L. terrestris* and/or the endogeic earthworm *O. tyrtaeum* were introduced into previously worm-free aspen forest soil. The presence of either or both earthworms did not affect fungal community diversity. The frequency of occurrence of *Trichoderma* species tended to decrease in the earthworm treatments. The frequency of occurrence of *Oidiodendron* species and *Pseudogymnoascus roseus* increased in the presence of *L. terrestris*, while that of *Mortierella* species decreased (Migge 2001).

With so few data, general conclusions about the effects of earthworm invasions on microfungal communities cannot be drawn, but some suggestions are possible. Frequency of occurrence of *Mortierella* species, which are Zygomycetes, was lower in the presence of epigeic, anecic or endogeic earthworms, reflecting their inability to tolerate hyphal disruption due to their lack of septa to prevent cell content leakage. That the occurrence of fast-growing species of *Trichoderma* was favoured by the presence of the epigeic *D. octaedra* but inhibited by the presence of anecic and/or epigeic earthworms may indicate that these microfungal species can only tolerate moderate amounts of disturbance induced by invasive earthworms.

Mycorrhizae—co-occurring with earthworms

Mycorrhizal spores may be better protected than microfungal spores from digestive enzymes and abrasion during earthworm gut passage. The few studies indicate that arbuscular mycorrhizal (AM) propagules and spores can survive gut passage and remain infective, and that casts may contain higher numbers and similar diversity of AM spores and propagules than surrounding bulk soil (Reddell and Spain 1991; Gange 1993).

Data on the interactions between earthworms and mycorrhizal colonization are few and somewhat contradictory. The presence of earthworms may increase (Patron et al. 1999; Brown et al. 2000), decrease (Pattinson et al. 1997; Brown et al. 2000) or not affect (Wurst et al. 2004) AM colonization. Positive effects of earthworms on mycorrhizal colonization may occur in poor soils where earthworm activities increase nutrient availability. For example, the addition of the tropical earthworm, *Pontoscolex corethrurus*, to unfertilized poor soil (low C, N, P) resulted in more root fragments infected by AM fungi (Patron et al. 1999; Brown et al. 2000). However, when NK fertilizers were added, earthworms decreased AM colonization (Brown et al. 2000). The observed decrease in AM colonization may reflect increased grazing on roots and AM fungal hyphae by the earthworms or the negative impacts of increased physical disturbance by earthworm activities.

Mycorrhizae—recent earthworm invasion

There are even fewer studies of the effects of invasive earthworms on mycorrhizae. Results from a study of the impacts of earthworm activities on mycorrhizal colonization of sugar maple are congruent with observations on microfungi. The presence of *L. rubellus*, *O. tyrtaeum* and *L. terrestris* all decreased colonization rates and total abundance of AM, likely due to physical disruption of fungal mycelium (Lawrence et al. 2003). Arbuscular mycorrhizal morphology was also altered in the presence of these earthworms, suggesting carbon stress due to loss of external hyphae (Lawrence et al. 2003).

In a greenhouse experiment investigating the effects of AM fungi and the endogeic earthworm *A. caliginosa* on plant growth and ^{32}P transfer between plants, there were very few significant effects (Tuffen et al. 2002). The authors speculated that the benefits of increased P availability due to earthworm activities was offset by the negative impacts of hyphal disruption on AM mycelium (Tuffen et al. 2002). To separate the effects of earthworm impacts on P availability from impacts via physical disruption of mycelium, the authors also included a mechanical disruption treatment. Mechanical disruption tended to produce shoot/root ratios more typical of non-mycorrhizal plants but few significant effects (Tuffen et al. 2002). Although these results suggest few significant effects of earthworms on AM and ^{32}P transfer between plants, it is likely that the experimental design hindered the observation of significant effects. Of necessity, earthworm activities and mechanical disruption occurred to only a quarter of the root/AM system; thus, although earthworms may have affected AM hyphal connections and activities, it was not possible to observe this.

Negative impacts on mycorrhizal colonization of seedlings have also been observed in earthworm-worked soils. Mycorrhizal colonization was reduced in soil from pure fir and mixed birch-fir stands that had been previously worked by earthworms, compared to controls not worked by earthworms (Welke and Parkinson 2003). Since earthworms were not present in the worm-worked soils during the experiment, it is possible that differential spore survival during gut passage or preferential grazing on species observed only on Douglas fir reduced the inoculum in the worm-worked Douglas fir soils. Another study showed that there is at least one mycorrhizal species that occurs only on these Douglas fir roots, which tends to support this idea (Jones et al. 1997).

These few studies, in combination with evidence that invasive earthworms can significantly decrease undisturbed forest floor thickness and alter nutrient cycling and fine root biomass, point up the need for further studies of the implications of earthworm invasion on mycorrhizal communities and functions.

Earthworm impacts on microbial biomass

Microbial biomass—co-occurring with earthworms

As earthworm effects on microbial biomass have been recently reviewed by several authors (see Edwards and Bohlen 1996; Brown et al. 2000; Lavelle and Spain 2001), we will summarize the conclusions briefly. From the few data available, it appears that fungal biomass (hyphal length) is much greater in the earthworm crop/gizzard than in the soil, indicating selective grazing on microbe-rich substrates by *L. terrestris*; the subsequent decline during gut passage may indicate digestion by the worms (Wolter and Scheu 1999). Microbial biomass tends to be higher in fresh casts, relative to uningested soil, and begins to decline within a few hours (Parle 1963a; Edwards and Bohlen 1996; Tiunov and Scheu 2000a). The relative increase in microbial biomass in casts depends on the available-C content of the uningested soil, with a higher relative increase in soils with low C content (Scheu 1987; Edwards and Bohlen 1996; Subler and Kirsch 1998; Haynes et al. 1999).

In an experiment to separate the effects of substrate and gut processes on microbial biomass and respiration, Tiunov and Scheu (2000a) used microcosms containing lime (*Tilia*) or beech (*Fagus*) soil in combination with lime or beech litter. In fresh cast material, type and quantity of ingested litter appeared to be more important than available C content. Microbial respiration, glucose-active biomass (GAMB) and biovolume were significantly higher in casts from treatments containing lime litter (Tiunov and Scheu 2000a). Fungal, bacterial and total microbial biovolume correlated significantly with litter content indicating the importance of the litter microbes (Tiunov and Scheu 2000a). The importance of the litter substrate and therefore litter microbes is also evident in an investigation of cast-lined *L. terrestris* burrow walls (Tiunov and Scheu 1999). GAMB was significantly higher in burrow walls than in bulk soils in both *Tilia* and *Quercus* forest but not in *Fagus* forest (Tiunov and Scheu 1999). In *Fagus* forest soil, *L. terrestris* burrow walls were not lined with casts, unlike those in *Tilia* forest soil; the authors suggested this was due to the inadequacy of *Fagus* litter as a food source, so overall soil GAMB did not increase (Tiunov et al. 2001).

The presence of earthworms may increase (Zhang et al. 2000; Scheu et al. 2002), decrease (Saetre 1998; Scheu et al. 2002; Caravaca and Roldán 2003) or not change (Zhang et al. 2000) microbial biomass in the bulk soil. The results depend on the earthworm species, the component of microbial biomass being assessed, the available C in the uningested soil and earthworm abundance. Endogeic species tend to decrease (Saetre 1998; Scheu et al. 2002) and anecic and epigeic species tend to increase (Zhang et al. 2000; Makulec 2002; Scheu et al. 2002) microbial biomass. A classic example of this is an experiment by Scheu et al. (2002) in which GAMB declined in the presence of endogeic earthworms but returned to control levels if both endogeic and epigeic earthworms were present; the authors suggested that epigeic incorporation of organic materials increased resource availability (Scheu et al. 2002).

The activities of earthworms tend to increase microbial biomass in low-C soils presumably by increasing C availability, while in high-C soils, earthworm activities tend to decrease microbial biomass, perhaps due to OM consumption. In low-C soil, intense short-term (24 h) activity by anecic earthworms increased total microbial biomass (chloroform fumigation), but decreased GAMB (Zhang et al. 2000). The results of Caravaca and Roldán (2003) appear to contradict the general trend of increased microbial biomass in low-C soils and decreased microbial biomass in high-C soils. The addition of *E. foetida* to sandy soil significantly decreased microbial biomass while increasing water-soluble C and water-soluble carbohydrates (Caravaca and Roldán 2003). However, although the original sandy soil was low in C, the soils were amended with composted residues which significantly increased the C content (Caravaca and Roldán 2003). In effect, this was a high C situation, and as expected, microbial biomass decreased in the presence of earthworms. Earthworm activities also generally decrease the fungal:bacterial ratio in soil (Saetre 1998; Makulec 2002), presumably due to damage of fungal hyphae.

Microbial biomass—recent earthworm invasion

Studies of invasive earthworm impacts on microbial biomass are contradictory. Most occurred in different forest types invaded by different earthworm species, making it difficult to draw overall conclusions about the relative importance of earthworm species, available-C and soil type to microbial biomass.

To our knowledge there are no studies on microbial biomass in guts or casts of invasive earthworms. However, a study of *L. terrestris* burrow walls revealed significantly lower microbial biomass-C in burrow walls than in control maple-oak forest soil (Görres et al. 1997). This is an unexpected result, given that maple-oak leaf litter was presumably an adequate food resource for *L. terrestris* (see Tiunov et al. 2001). However, this may reflect the soil type or more complex interactions with other soil biota. The soil was very sandy and to ensure physical stability of the soil cores during the experiment, the A horizon was mixed with the C horizon resulting in a low initial microbial biomass-C content (Görres et al. 1997). The authors suggested that burrow walls attracted nematodes which grazed and reduced microbial biomass (Görres et al. 1997).

Studies of the invasion by several different earthworm species into maple forests in New York offer a chance to assess the importance of earthworm species on microbial biomass in the soil as a whole. In some maple stands invasion by a mixed community of lumbricids has been observed, in contrast to other stands where the Asian species *Amynthas hawayanus* has invaded. The mixed community of lumbricids significantly reduced the forest floor in the previously uncultivated site, mixing the forest floor into the upper mineral horizon (Bohlen et al. 2004b) resulting in significantly lower forest floor microbial biomass C and N, increased readily mineralizable C and significantly higher microbial biomass C and N in the A horizon (Groffman et al. 2004). Although plots investigated by Burtelow et al. (1998) contained *Aporrectodea* species and no *Amynthas*, the forest floor had been completely transformed into a granular surface layer typical of *Amynthas* activities. The transformation of the forest floor into casts resulted in a significant decrease in forest floor OM but no increase in A horizon OM, indicating OM consumption by the earthworms (Burtelow et al. 1998). But the end result was increased microbial biomass C and N in the forest floor, increased readily mineralizable C and increased microbial biomass N in mineral soil of worm-worked patches (Burtelow et al. 1998). From these limited data, it appears that both types of earthworms release C, supporting a larger microbial biomass in the A horizon. Differences in the restructuring of the forest floor by these two earthworm types resulted in either increased or decreased forest floor microbial biomass.

A comparison of New York maple forests with differing land use histories illustrates the importance of previous cultivation on the effects of earthworm invasion. Previously cultivated (until 1920) versus logged (late 19th century) but never cultivated maple forests in NY contained a mixed community of lumbricids dominated by *L. terrestris* and *L. rubellus L. terrestris* or by *L. terrestris* (Bohlen et al. 2004a). In both forests, earthworm activities decreased forest floor depth and microbial biomass C and N, and increased A horizon microbial biomass C and N. But the magnitude of the effect related to the original forest floor available for incorporation into the mineral horizon (Groffman et al. 2004); in the previously cultivated site, there was little forest floor to be mixed into the mineral horizon and the increases in microbial biomass in the mineral horizon were less dramatic (Groffman et al. 2004).

Several studies were conducted in forests in Alberta, Canada, following the invasion of epigeic earthworms into *Populus* and *Pinus* forests. Comparisons of these studies may indicate the importance of earthworm species and forest type to microbial biomass. In *Populus* microcosms, the activities of *D. octaedra* mixed organic layers into the upper mineral horizon, significantly decreasing GAMB in L/F layer and increasing GAMB in the H layer and A horizon (Scheu and Parkinson 1994a). Similar results were obtained in field microcosms although the effects were less pronounced (Scheu and Parkinson 1994b). These effects were attributed to the mixing of the organic layers into the mineral upper horizon since *D. octaedra* decreased GAMB in all layers and horizons when incubated separately (Scheu and Parkinson 1994a). *Octolasion lacteum* mixed organic and mineral materials in *Populus* microcosms more thoroughly than *D. octaedra*; effects on the GAMB were similar except that H layer GAMB was significantly decreased (Scheu and Parkinson 1994a) possibly reflecting more intense feeding activities in the H layer by this endogeic species, which is known to preferentially consume humified OM typical of H layers. In contrast, in *Pinus* mesocosms, *D. octaedra* significantly decreased GAMB in the F/H layer and mineral horizon (McLean and Parkinson 1997a) as was observed when the *Pinus* F/H layer was incubated separately (Scheu and Parkinson 1994a). Incorporation of OM from the upper layers deeper into the soil by *D. octaedra* cannot be the sole explanation here, since there was no corresponding increase in GAMB in the lower soil layers. The authors attributed this to consumption of organic matter by the worms (McLean and Parkinson 1997a).

In *Pseudotsuga*, *Betula* or mixed *Pseudotsuga* + *Betula* forest microcosms, the activities (but not the presence) of *A. caliginosa* did not affect forest floor GAMB (Welke and Parkinson 2003). However, in the mineral soil, the effect of *A. caliginosa* depended on the forest type (Welke and Parkinson 2003). GAMB was significantly lower in worm-worked *Betula* and mixed *Pseudotsuga* + *Betula* soils and significantly higher in pure *Pseudotsuga* soil (Welke and Parkinson 2003). Lower GAMB in the *Betula* and mixed *Pseudotsuga* + *Betula* soils may reflect consumption of OM and microbial biomass. Increased

GAMB in *Pseudotsuga* mineral soil may reflect mixing of OM into the mineral horizon similar to that seen in aspen soil (Scheu and Parkinson 1994b). In general, the fungal:bacterial ratio was reduced by the activities of *D. octaedra* and *O. lacteum* (Scheu and Parkinson 1994a), presumably due to damage to fungal hyphae.

Earthworm impacts on microbial activity

Respiration and metabolic efficiency—co-occurring with earthworms

Earthworm activities tend to increase microbial respiration in casts, burrow walls or in bulk soil (Shaw and Pawluk 1986; Scheu 1987; Haimi and Huhta 1990; Görres et al. 1997; Saetre 1998; Haynes et al. 1999; Zhang et al. 2000; Tiunov et al. 2001) due to the addition of readily accessible C substrates. However, the effects may depend on earthworm species, soil type, available C in uningested materials, and cast age. Also see reviews by Edwards and Bohlen (1996), Brown et al. (2000), Lavelle and Spain (2001).

Soil type affected the impact of *L. terrestris* on microbial respiration (Shaw and Pawluk 1986), which increased in clay loam and silty clay loam soil, but decreased in sandy loam soil. The decrease was accompanied by increased C associated with clay particles, indicating net storage of OM (Shaw and Pawluk 1986).

Several studies have shown that microbial respiration in casts depends on available C content (Scheu 1987; Haynes et al. 1999; Tiunov and Scheu 2000a) and cast age (Scheu 1987; Tiunov and Scheu 2000a). Scheu (1987) showed that although microbial respiration in *A. caliginosa* casts was higher than that of bulk soil, the cast microbial community was C-limited and respiration declined over time. In another study, Tiunov and Scheu (2000a) showed that in fresh *L. terrestris* casts, C content and litter type significantly correlated with cast respiration which declined over time. In *L. terrestris* burrow walls microbial respiration was significantly higher than in control soil (Tiunov and Scheu 1999); a small but significant proportion of the variation in respiration was explained by soil type (*Fagus*, *Quercus* and *Tilia* forest) and season (Tiunov and Scheu 1999).

Metabolic quotient ($q\mathrm{CO}_2$) is the ratio of the amount of CO_2 respired per unit microbial biomass and is an index of the relative activity of the microbial biomass. Earthworm activities tend to increase the metabolic quotient (Wolters and Joergensen 1992; Görres et al. 1997; Haynes et al. 1999; Tiunov and Scheu 1999; Zhang et al. 2000), suggesting a switch to a smaller, but more active microbial community. This may relate to the decrease in the fungal:bacterial ratio commonly seen in earthworm-worked soils and thought to result from disruption of fungal hyphal links. Bacteria are less efficient at assimilating C and therefore have a higher $q\mathrm{CO}_2$ than fungi (Adu and Oades 1978; Sakamoto and Oba 1994).

Litter quality affects $q\mathrm{CO}_2$ in *L. terrestris* burrow walls (Tiunov and Scheu 1999). The increase in $q\mathrm{CO}_2$ was relatively small in *Tilia* soil and larger in *Fagus* and *Quercus* soil (Tiunov and Scheu 1999). Other soil characteristics also affect the impact of earthworms on the $q\mathrm{CO}_2$ (Wolters and Joergensen 1992). The stimulation of $q\mathrm{CO}_2$ by *A. caliginosa* declined with increasing acidity, organic C, total N, exchangeable Ca and cation exchange capacity (Wolters and Joergensen 1992), suggesting that stimulation of microbes by earthworms is smaller in nutrient-rich soils.

Earthworm effects on microbial biomass and $q\mathrm{CO}_2$ in pasture soil are similar to results in forest soils given above, indicating a switch to a smaller but more active microbial community (Haynes et al. 1999). In arable soil, with much lower organic and microbial C, microbial biomass and $q\mathrm{CO}_2$ increased significantly (Haynes et al. 1999). Addition of either *A. caliginosa* or *E. foetida* to arable soils amended with organic residues significantly decreased microbial biomass and increased $q\mathrm{CO}_2$ in casts, also indicating a more active microbial community (Haynes et al. 1999; Caravaca and Roldán 2003).

Respiration and metabolic efficiency—recent earthworm invasion

In general, earthworm activities increase soil respiration and thus earthworm invasions are expected to increase respiration in invaded sites due to the increase in readily accessible C substrates through the addition of mucus. The underlying assumption is that microbes are C limited, but in newly invaded, C-rich organic layers this may not be true. That microbial respiration declined or was unaffected by invasive earthworms in several North American forests may reflect this. In aspen field microcosms microbial respiration in L/F material decreased and that in H material increased in the presence of *D. octaedra* (Scheu and Parkinson 1994b). In pine mesocosms representing the initial invasion by *D. octaedra*, earthworm density did not significantly affect microbial respiration although in field plots representing later stages of invasion, microbial respiration declined with increasing earthworm biomass particularly in the F/H layer (McLean and Parkinson 1997a, b). These data are consistent with microcosm studies indicating that aspen L, F and pine F/H layer microbial respiration was N-limited and therefore would not be enhanced by earthworm activities, whereas aspen H, A and pine L and B layer microbial respiration was C-limited and therefore more likely to be enhanced by earthworm activities (Scheu and Parkinson 1995).

Data from other forests suggest that this may be a general pattern in newly invaded forest soils. In fir, birch or mixed fir/birch forest floor worked by *A. trapezoides* microbial respiration was not significantly different from control forest floor (Welke and Parkinson 2003). However, respiration was significantly higher in worm-worked birch or fir/birch mineral soil and significantly lower in worm-worked fir mineral soil compared to the respective controls (Welke and Parkinson 2003). In New York maple forests with mixed communities of lumbricids the presence of earthworms did not significantly affect total soil respiration (Fisk et al. 2004). However, the forest floor and mineral soil were not separated in this study obscuring respiration differences between layers in the presence of earthworms.

In contrast, in maple forest plots worked by the invasive earthworm *Amynthas hawayanus*, microbial respiration from the organic horizon was significantly higher than in uninvaded plots (Burtelow et al. 1998). This earthworm species completely consumed the forest floor reducing it to granular cast material. This complete consumption of OM may have reduced microbial activity to the point where accessible C additions enhanced microbial respiration.

In soils invaded by earthworms, one might expect to see increased $q\mathrm{CO}_2$ indicating a switch to a smaller but more active microbial community similar to that seen in situations where the microbial community has evolved in the presence of earthworms. However, it may be that in recently invaded soils, there has not been enough time for the microbial communities to adapt to earthworm activities and therefore the switch to a more active microbial community is not observed. In maple-oak forest soil in Rhode Island, USA, there was evidence of a switch to a smaller, more active microbial community in *L. terrestris* burrow walls (Görres et al. 1997). In these burrow walls, microbial biomass C was significantly lower and $q\mathrm{CO}_2$ was significantly higher than in control soil (Görres et al. 1997). The earthworm fauna of Rhode Island is completely exotic and these species have been present for at least 30 years (Reynolds 1973, 2002). We suggest that the addition of *L. terrestris* to a Rhode Island soil resulted in a switch to a smaller, more active microbial community because the microbial communities have had a chance to adapt to the presence of earthworms. A similar result was seen in aspen field microcosms in Alberta, Canada; low microbial biomass and high $q\mathrm{CO}_2$ in L/F material in the presence of *D. octaedra* suggest a switch to a smaller, more active microbial community in this layer (Scheu and Parkinson 1994b). Earthworms were first observed in this study site in 1984, 8 years before this experiment was conducted. We suggest that 8 years is long enough for the microbial community to adapt to the presence of earthworms.

In contrast, in more recently invaded forests, there is evidence that the microbial community has not yet adapted to the presence of earthworms. In mesocosms, representing the initial stages of the invasion of *D. octaedra* into *Pinus* forest, earthworm density did not significantly affect $q\mathrm{CO}_2$, while in field plots representing later stages in the initial invasion by *D. octaedra*, $q\mathrm{CO}_2$ declined with increasing earthworm biomass (McLean and Parkinson 1997a, b). The activities of *A. trapezoides* did not affect $q\mathrm{CO}_2$ in forest floor materials (Welke and Parkinson 2003). However, $q\mathrm{CO}_2$ was generally lower in worm-worked *Pseudotsuga*, *Betula* or *Pseudotsuga + Betula* mineral soil compared to the respective controls (Welke and Parkinson 2003). The decreases in $q\mathrm{CO}_2$ observed in both studies suggest that the microbial community has not been able to switch to a smaller, but more active microbial community and/or that the fungal community remains dominant but is becoming less active in the presence of earthworms.

C substrate use—co-occurring with earthworms

To our knowledge, there is only one investigation of the impact of earthworms on microbial C substrate use in sites with earthworms. In general, the presence of endogeic and/or epigeic earthworms decreased actual catabolic activity, attributed to decreased resource availability due to consumption by the earthworms (Scheu et al. 2002). The presence of endogeic and/or epigeic earthworms increased potential catabolic activity indicating a shift by the microbial community to more rapidly respond to resource pulses (Scheu et al. 2002). This is congruent with the observation that the presence of earthworms tends to produce a shift to a more active microbial community (see Wolters and Joergensen 1992; Görres et al. 1997; Haynes et al. 1999; Tiunov and Scheu 1999; Zhang et al. 2000). The earthworm species and number of species in an ecological group also affected actual and potential microbial catabolic potentials. Although two earthworm species may be epigeic, differences in gut transit, preference for organic or mineral material may significantly affect microbial C substrate use, emphasizing the importance of earthworm species diversity (Scheu et al. 2002).

C substrate use—recent earthworm invasion

Data on $q\mathrm{CO}_2$ from recently invaded soils suggest that microbial communities in these soils have not yet developed into the smaller, more active communities typical in the presence of earthworms. If these communities are not yet adapted to the presence of earthworms, one might also reasonably expect that the presence of earthworms would not increase the diversity of C substrates used by these microbes. Contrary to this expectation, results from recently invaded forests in British Columbia, Canada, indicate that the activities (though not the presence) of *A. trapezoides* increased total potential bacterial activity, substrate richness and diversity (as assessed using BIOLOG plates) compared to control soils (Welke and Parkinson 2003). Similar results were obtained using BIOLOG plates in a field study where endogeic and anecic lumbricids had recently invaded aspen forests in Alberta (Migge 2001). These observations suggest that the microbial community is able to respond rapidly to resource pulses, including those caused by earthworm activities, due to high enzymatic versatility and not necessarily to changes in community structure (Lavelle and Spain 2001; Buckley and Schmidt 2002).

Enzyme activities—co-occurring with earthworms

Activities of a broad range of enzymes have been reported from earthworm guts, including cellulase, chitinase, phosphatase, protease, xylanase, mannanase, urease, dehydrogenase, and various glucosidases (Khambata and Bhat 1957; Parle 1963b; Márialigeti 1979; Zhang et al; 1993, 2000; Mba 1997; Lattaud et al. 1998; Haynes et al. 1999; Makulec 2002; Prat et al. 2002; Caravaca and Roldán 2003).

There has been much discussion about whether these enzymes are of microbial or earthworm origin. Enzyme analysis of earthworm gut contents and gut wall tissue culture enabled Zhang et al. (1993) to differentiate enzymes produced by gut microbes from those produced by the tropical endogeic earthworm *P. corethrurus*. Gut (gut wall + contents) activities included *N*–acetylglucosaminidase, maltase, laminaribiase, cellulase, as well as a range of polysaccharides (including amylase, xylanase, glucomannanase, carboxymethylcellulase, and galactomannanase etc.) (Zhang et al. 1993). Tissue culture of the washed gut wall revealed a similar range of enzyme activities with the exception of cellulase and mannanase (Zhang et al. 1993). Of three tropical endogeic earthworms, gut wall tissue cultures showed that *Polypheretima elongata* was able to synthesize all its required enzymes while *Millsonia anomala* relied on microbes for cellulose and mannan digestion (Lattaud et al. 1998).

Different earthworm species have different ranges of enzymatic capabilities depending on their normal substrates: epigeic earthworms tend to possess higher cellulase activities than anecic or endogeic earthworms, reflecting relatively undecomposed organic matter as their primary food resource (e.g. Urbasek 1990; Zhang et al. 2000; Prat et al. 2002). High chitinase activity is thought to indicate the importance of fungi as a food resource (Zhang et al. 1993). Gut enzyme capabilities also differ between species within an ecological group, for example between three tropical endogeic earthworms (Lattaud et al. 1998). High amylase and maltase specific activities in *P. elongata* guts suggest that this species feeds mainly on roots, while glucosidic activities in *M. anomala* indicate that this species can degrade fungal cell walls and roots (Lattaud et al. 1998).

Gut enzyme activities differ both between species and in location of major activity within the gut (Zhang et al. 1993; Lattaud et al. 1998; Prat et al. 2002). In *P. corethrurus* and *M. kerguelensis* the majority of the activity was observed in the foregut and midgut, while in *D. rubidus tenuis*, the highest enzyme activities occurred in the anterior tract (Zhang et al. 1993; Prat et al. 2002).

Enzyme activities—recent earthworm invasion

To our knowledge, there are no studies on gut enzymes in earthworms invading areas historically devoid of earthworms. Earthworms invading new areas are expected to carry with them those microbes that are a permanent component of their guts. These, presumably, would be the producers of essential enzymes for degradation of their normal substrates. Transient gut microbes (and their enzymatic capabilities) are expected to vary between habitats and with differences in ingested substrates.

Conclusions

It is not yet clear whether or which earthworm gut microbes are permanent gut residents or merely transients reflecting the microbial community on consumed substrates. To resolve this, comparisons of the gut microbes of the same species ingesting the same or different litters are needed. Further, comparisons across habitats where earthworms and microbes have co-occurred for years with those where earthworms have recently invaded would clarify to what extent invading earthworms carry their original gut microbes with them (also see Hendrix et al., this issue).

Earthworm interactions with bacteria and microfungi have been studied more thoroughly than those with other microbes. However, although it is commonly assumed that the negative impacts of earthworm invasions on fungi are due to hyphal disruption, this has yet to be tested convincingly. Studies are particularly needed for Zygomycetes which appear to experience more severe negative impacts from hyphal disruption.

Despite the importance of actinomycete antibiotic production which may have negative impacts on other soil microbes, and the importance of mycorrhizae for plant growth, remarkably little is known about the interactions of either of these groups with earthworms. Both groups need more thorough study in habitats where they co-occur with earthworms and in recently invaded ones. Additionally, mycorrhizal studies should include a range of mycorrhizal types (AM, ectomycorrhizae, ericaceous, orchidaceous) to allow predictions of the probable impact of earthworm invasions on different plant species.

Earthworms tend to increase microbial biomass and respiration in low-C soils and decrease them in high-C soils. This becomes particularly important when considering the effects of earthworm invasions in forest soils, which typically have high organic matter contents in the forest floor. Studies of the effects of earthworm invasion in low-C soils would provide an interesting test of the importance of soil C status.

From the studies available, it appears that the microbial community adapts to the presence of earthworms by switching to a smaller, but more active microbial community. Long-term studies of the invasion of earthworms could assess whether or how quickly the various components of the microbial community adapt to the presence of earthworms.

There is evidence that earthworm gut enzymes reflect their primary food substrates. Further studies are needed to determine whether these are (i) of earthworm or microbial origin, (ii) independent of food substrates and (iii) carried with the earthworms as they invade a new environment.

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ORIGINAL PAPER

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

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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

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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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ORIGINAL PAPER

Invasion of exotic earthworms into ecosystems inhabited by native earthworms

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Abstract The most conspicuous biological invasions in terrestrial ecosystems have been by exotic plants, insects and vertebrates. Invasions by exotic earthworms, although not as well studied, may be increasing with global commerce in agriculture, waste management and bioremediation. A number of cases has documented where invasive earthworms have caused significant changes in soil profiles, nutrient and organic matter dynamics, other soil organisms or plant communities. Most of these cases are in areas that have been disturbed (e.g., agricultural systems) or were previously devoid of earthworms (e.g., north of Pleistocene glacial margins). It is not clear that such effects are common in ecosystems inhabited by native earthworms, especially where soils are undisturbed. We explore the idea that indigenous earthworm fauna and/or characteristics of their

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native habitats may resist invasion by exotic earthworms and thereby reduce the impact of exotic species on soil processes. We review data and case studies from temperate and tropical regions to test this idea. Specifically, we address the following questions: Is disturbance a prerequisite to invasion by exotic earthworms? What are the mechanisms by which exotic earthworms may succeed or fail to invade habitats occupied by native earthworms? Potential mechanisms could include (1) intensity of propagule pressure (how frequently and at what densities have exotic species been introduced and has there been adequate time for proliferation?); (2) degree of habitat matching (once introduced, are exotic species faced with unsuitable habitat conditions, unavailable resources, or unsuited feeding strategies?); and (3) degree of biotic resistance (after introduction into an otherwise suitable habitat, are exotic species exposed to biological barriers such as predation or parasitism, ''unfamiliar'' microflora, or competition by resident native species?). Once established, do exotic species co-exist with native species, or are the natives eventually excluded? Do exotic species impact soil processes differently in the presence or absence of native species? We conclude that (1) exotic earthworms do invade ecosystems inhabited by indigenous earthworms, even in the absence of obvious disturbance; (2) competitive exclusion of native earthworms by exotic earthworms is not easily demonstrated and, in fact, co-existence of native and exotic species appears to be common, even if transient; and (3) resistance to exotic earthworm invasions, if it occurs, may be more a function of physical and chemical characteristics of a habitat than of biological interactions between native and exotic earthworms.

Keywords Native earthworms · Exotic earthworms · Biological invasions · Disturbance · Competition

Introduction

Research over the past century has shown that where earthworms are abundant, they significantly influence soil processes and are integral to the functioning of terrestrial ecosystems. Documented effects of earthworms include accelerated plant litter decomposition, nutrient transformations and plant nutrient uptake; increased soil aggregation and porosity; and enhanced water infiltration and solute transport (see Satchell 1983; Lee 1985; Hendrix 1995; Edwards and Bohlen 1996; Lavelle et al. 1999; Edwards 2004). While these effects are usually considered desirable in agricultural soils, recent interest has focused on detrimental impacts of invasive, exotic earthworms on soil processes in wildland ecosystems (Hendrix and Bohlen 2002; Bohlen et al. 2004a,b; James and Hendrix 2004). Exotic earthworms are capable of significantly affecting soil profiles, nutrient and organic matter dynamics, other soil organisms, and plant communities. Impacts have been reported in tropical forests (Zou and González 1997; Zou and Bashkin 1998; González and Zou 1999; Fragoso et al. 1999; Liu and Zou 2002; Decaëns et al. 2004); chaparral shrublands (Graham and Wood 1991; Graham et al. 1995); grasslands (Stockdill 1982; James 1991; Callaham et al. 2001); and particularly in temperate forests (Langmaid 1964; Alban and Berry 1994; Scheu and Parkinson 1994; Steinberg et al. 1997; Burtelow et al. 1998; McLean and Parkinson 2000; González et al. 2003; Bohlen et al. 2004b; Hale et al. 2005; also see Frelich et al. this issue).

Most of the work on earthworm invasions has focused on a relatively few species (e.g., European lumbricids, *Amynthas* spp., *Pontoscolex corethrurus*) that have achieved wide distributions and are now abundant in many ecosystems. Moreover, the most dramatic effects of exotic species on soil organic matter dynamics have been observed in areas previously uninhabited by earthworms (e.g., north of Pleistocene glacial margins; see Frelich et al., McLean et al., Migge-Kleian et al. and Tiunov et al., this issue) or where native populations have been reduced by disturbance (e.g., pastures in Australia and Puerto Rico; see Baker et al. and González et al. in this issue). Effects of exotic earthworms have not been as frequently reported from invasions of ecosystems inhabited by native earthworm assemblages where soils and vegetation are undisturbed (e.g., Abbott 1985; Kalisz and Dotson 1989; Lavelle and Pashanasi

1989; Callaham and Blair 1999; Fragoso et al. 1995, 1999). These observations suggest that some characteristics of indigenous earthworm fauna and/or their native habitats may be resistant to invasion by exotic earthworm species and thus may reduce the impact of exotic species on soil processes. In this paper, we explore the interactions between native and exotic earthworms and factors that may facilitate or inhibit invasions by exotic species into areas inhabited by native earthworm species.

Interactions between native and exotic earthworms

Habitat disturbance or competitive exclusion

Exotic earthworms have been spread throughout the world, aided by human colonization and commerce for at least the past few centuries; several peregrine species are now prevalent in many soils impacted by human activity (Ljungstrom 1972; Lee 1985; Kalisz 1993; Fragoso 1995, 1999; Reynolds 1995; Bhadauria et al. 2000). Where these introductions have occurred in areas inhabited by indigenous earthworms, exotic earthworms may not persist, they may occur exclusively, or they may co-occur with the native earthworm species. Reasons for success or failure of establishment, or for varying densities of exotic species at any particular site may not be known with certainty, but probably include site characteristics (e.g., soil and climatic conditions), invasion history (e.g., frequency and duration of introductions), and characteristics of the exotic and native species involved. Site disturbance, including natural phenomena (e.g., tree fall, floods) that can create conditions favorable for establishment or proliferation of exotic species, may be a particularly important factor.

Since the time of early observations, mechanisms by which exotic earthworms come to dominate in certain ecosystems have been debated (Eisen 1900; Beddard 1912; Smith 1928; Lee 1961; Stebbings 1962). Do exotic species displace native species through direct or indirect competition, or do exotic species occupy vacant niches following disturbance and the demise of native species? Kalisz and Wood (1995) summarized the prevailing idea that physical disturbance or habitat fragmentation are prerequisite to establishment of and domination by exotic earthworms in soils occupied by native species. The proposed sequence is (a) habitat disturbance, (b) decline or extirpation of native species, (c) introduction of exotic species, and (d) colonization of empty habitat by exotic species. By considering the currently observed state of any particular earthworm assemblage, we can trace several possible series of events that may have led to that state from a presumed indigenous community in a pristine ecosystem (Fig. 1).

Pathway A represents the extreme case described by Kalisz and Wood (1995), through which disturbance leads to exclusively exotic assemblages, as often observed with ‘‘anthropochorous’’ earthworms in agricultural soils (e.g., Parmelee et al. 1990; Baker et al. 2002). We can speculate that the same outcome may occur under less severe disturbance but perhaps with more aggressive exotic invaders, as in pathway B-1. Pathways B-2 and C-1 lead to the often observed co-occurrence of native and exotic species (Stebbings 1962; Abbott 1985; James 1991; Fragoso et al. 1999) through varying levels of habitat disturbance and invasion intensity. The B-2 case again assumes at least moderate levels of disturbance, which reduce native population density and alter habitat conditions prior to invasion. The C-1 pathway suggests that competitive displacement of native species by exotic species may occur even in relatively undisturbed ecosystems; this possibility, whereby forest fragmentation for example, may foster exotic invasions without direct habitat disturbance, was termed ‘‘invisible disturbance’’ by Kalisz and Wood (1995). The idea is controversial and is supported by little empirical data. Furthermore, whether co-occurrence is a stable condition or whether native or exotic species maintain dominance in any particular situation are interesting long-term questions, as noted by the question marks for ‘‘successful’’ invasion on these pathways in Fig. 1. Finally, pathway C-2 represents the idea that native earthworm assemblages or properties of their minimally disturbed habitats are resistant to invasion by exotic species. There

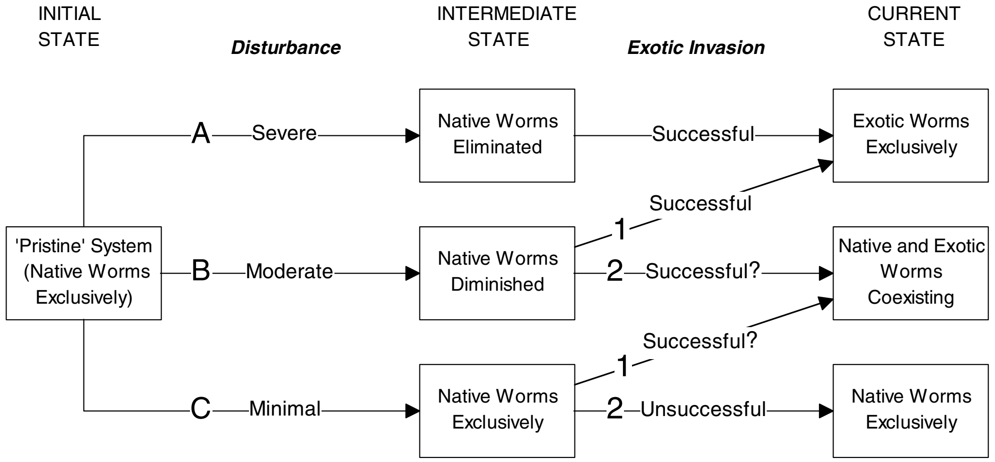

Fig. 1 Hypothesized sequences of invasion depending on degree of habitat disturbance and invasion success by exotic earthworms invading ecosystems inhabited by native earthworms. See text for description of pathways

also is very little information with which to test this idea, as discussed below.

Case studies

As noted earlier, much of the research on earthworm invasions has been conducted in ecosystems previously devoid of earthworms. However, a few studies have examined interactions between native and exotic earthworms (Table 1).

Abbott (1985) in Western Australia and Kalisz and Dotson (1989) in Kentucky, USA, found that exotic earthworms occurred only in severely disturbed forest sites, whereas native earthworms occurred in undisturbed to slightly disturbed sites, sometimes in association with exotics. They noted that the exotics had failed to disperse into undisturbed areas even decades after introduction. Dalby et al. (1998) concluded from microcosm studies that the European lumbricid, *Aporrectodea longa*, would not successfully invade forest soils inhabited by native megascolecid earthworms in South Australia because of its strong preference for nearby pasture soils. In the central Himalayas of India, Bhadauria et al. (2000) reported declines in endemic earthworm abundances with disturbance pressure in natural and regenerating forests; exotic species did occur in the undisturbed climax forest but certain exotic species were restricted to the regenerating forest.

Studies of an invasion of European lumbricids into a native prairie in Kansas, USA, suggested competitive displacement of native *Diplocardia* spp. by exotic *Aporrectodea* spp. in disturbed areas, but continued dominance by the native species under natural conditions (James 1982; Callaham and Blair 1999); regular prescribed fires appeared to favor the diplocardians. Studies in California, USA, grasslands (Winsome 2003; Winsome et al. 2006) showed that exotic species predominated only in areas within fertilizer-amended pastures and on sedimentary soils within unamended pastures. Native species were present in abundance equal to or greater than exotic species in all other habitat types, including oak woodland reserves within the amended pastures and on serpentine soils. These results suggested that displacement of native by exotic species in these grasslands occurred only where resource quality and/or disturbance were at a maximum (i.e., presence of high-quality forage grasses in the heavily grazed, amended pastures). Damoff (2005) found co-occurrence of the exotic *Amynthas diffringens* with several native earthworm species in a secondary bottomland hardwood forest in eastern Texas, USA. *Diplocardia komareki* was the largest and deepest-burrowing of the native species and may have interacted least with *A. diffringens*; all other species appeared to occupy the same vertical position (large niche overlap) in the soil profile with *A. diffringens*.

In Puerto Rico, the exotic earthworm, *Pontoscolex corethrurus*, was found to dominate both disturbed and little-disturbed sites, whereas native

Table 1 Relative occurrence of native and exotic earthworm in ecosystems subjected to varying types and degrees of disturbance. Minus, single plus and double plus signs indicate absence, presence and dominance, respectively, of native or exotic earthworm species

Earthworms						
Location	Ecosystem type	Disturbance	Native	Exotic	Earthworm species (native/exotic)	References
Western Australia	Eucalyptus forest	Minimal	+	–	“Indiginous” species/ *Aporrectodea trapezoides*, *A. caliginosa*, *Eisenia fetida*, *Octolasion cyaneum*, *Microscolex dubius*	Abbott (1985)
		Forest clearing/replacement	+	+		
South Eastern Australia	Pasture	Converted	+	++	*Spenceriella* spp./ *A. caliginosa*, *A. trapezoids*, *A. tuburculata*, *A. rosea*, *O. cyaneum*, *L. rubellus*, *M. dubius*, *M. phoshoreus*, *Microscolex spp*.	Mele and Carter (1999a, b)
	Crops	Converted	+	+		
	Acidified crops	Converted	++	+		
South Australia	Eucalyptus forest	Minimal	++	+	*Gemascolex lateralis*/*A. caliginosa*, *A. trapezoides*	Dalby et al. (1998)
India	Broad-leaf temperate forest	Undisturbed	++	+	*Drawida* sp. *Eutyphoeus nanianu*, *Eu. festivus*, *Eu. waltonii*/*Amynthas corticis*, *Bimastos parvus*, *O. tyrtaeum*, *Octochaetona beatrix*	Bhadauria et al. (2000)
	Subclimax mixed forest	Minimal	+	+		
	Pasture/pine plantation	Deforested/converted	+	++		
Ivory Coast	Savanna/gallery forest	Minimal	+	–	13 spp., esp.*Chuniodrilus* spp., *Millsonia anomala*, *Dichogaster agilis*, *Dichogaster. spp*./None	Lavelle (1978), Fragoso et al. (1999)
	Pasture	Converted	+	–		
	Agroecosystems	Converted	+	–		
Colombia	Savanna	Minimal	+	–	Indigenous acanthodrilids, glossoscolecids, ocnerodrilids	Jiménez et al. (1998, 2001)
		Grazed pasture	+	–		
South Eastern Mexico	Tropical rainforest	Minimal	++	+	69 native spp, esp. *Dichogaster bolaui*, *D. saliens*, *Balanteodrulus pearsei*, *Lavellodrilus parvus*, *Diplotrema murchiei*/26 exotic spp., esp. *Pontoscolex corethrurus*, *Polypheretima elongata*	Fragoso et al. (1995, 1999)
	Tropical deciduous	Minimal	++	+		
	forest cloud forest	Minimal	++	+		

Table 1 continued

Earthworms						
Location	Ecosystem type	Disturbance	Native	Exotic	Earthworm species (native/exotic)	References
	Crops	Deforested/converted	+	++		
	Tropical pasture	Deforested/converted	+	++		
	Tree plantation	Deforested/converted (exotic abundance increases with level of disturbance)	+	++		
Costa Rica	Tropical pasture (non-grazed)	Deforested/converted	+	++	*Glossodrilus nemoralis*/ *P. corethrurus*, *Metaphire californica*	Fragoso et al. (1999)
Peru	Tropical rainforest	Minimal	++	+	“Native forest spp.”/ *P. corethrurus*	Lavelle and Pashanasi (1989), Fragoso et al. (1999)
	Agroecosystems	Deforested/converted	+	++		
Puerto Rico	Tropical rainforest	Minimal	++	+	*Estherella sp.*, *E. gatesi*, *E. montana*, *Trigaster longissimus*/*P. corethrurus*, *Amynthas rodericensis*	Zou and Gonzalez (1997), González and Zou (1999), Hendrix et al. (1999a), Liu and Zou (2002), Lachnicht et al. (2002)
	Tropical cloud forest	Minimal	++	+		
	Tropical pasture	Deforested/converted	+	+		
	Pine and mahogany plantations	Deforested/converted	–	+	None/*P. corethrurus*, *A. rodericensi*	González et al. (1996)
	Secondary forests	Deforested/converted	+	+	*Pontoscolex spiralis*, *E.gatesi*, *E.montana*/*P. corethrurus*, *A. rodericensis*	
Kentucky, USA	Deciduous forest	Minimal	+	–	*Bimastos spp.*, *Diplocardia* spp. *Eisenoides carolinensis*, *Komarekionia etoni*/*A. Allolobophora chlorotica*, *Ap*.	Kalisz and Dobson (1989), Dobson and Kalisz (1989), Kalisz (1993), Kalisz and Wood (1995)
		Logged	+	+		
		Severely disturbed	–	+		
Georgia, USA	Mixed forest	Moderate	+	++	*Bimastos sp.*, *Diplocardia sp.*/*A. caliginosa*, *Lumbricus rubellus*, *L. terrestris*, *M. dubius*	Parmelee et al. (1990), Hendrix et al. (1992), Callaham and Hendrix (1997)
		Deforested/cultivated	+	++		
Florida, USA	Longleaf pine/wiregrass savanna	Minimal	+	–	*Diplocardia* spp.	Hendrix et al. (1999b)
Kansas, USA	Tallgrass prairie	Minimal	+	–	*Bimastos welchi*, *Diplocardia* spp./*A. caliginosa*, *O. cyaneum*,	James (1991), Callaham and Blair (1999), Callaham et al. unpublished
		Fire suppression	+	+		
		Conversion to pasture	+	++		
	Gallery forest	Encroachment into prairie	+	++		

Table 1 continued

Earthworms

Location	Ecosystem type	Disturbance	Native	Exotic	Earthworm species (native/exotic)	References
Missouri, USA	Riparian alluvium	Minimal	+	+	*Bimastos zeteki, Diplocardia* spp./*A. trapezoides, O. lacteum*	Stebbings (1962)
	Mixed forest	Moderate	++	+		
Texas, USA	Bottomland hardwood forest	Moderate	+	+	*Diplocardia spp./ Amynthas diffringens*	Damoff (2005)
California, USA	Chaparral	Minimal	+	–	*Diplocardia sp./ A. caliginosa*	Graham and Wood (1991), Wood et al. (1997), Peterson et al. (2001)
		Exotic vegetation	+	+		
		Severe soil disturbance	–	+		
	Oak savanna	Minimal	+	–	*Argilophilus marmoratu/ A. trapezoides*	Winsome et al. (2003)
	Pasture	Converted/fertilized	+	++		
Oregon, USA	Temperate coniferous forest	Minimal	+	–	Indigenous Megascolecids/*A. caliginosa*	Hendrix and Cromack unpublished
		Logging/campsites	+	+		

earthworms were present in undisturbed sites. Exotic earthworms occurred in mahogany and pine plantations as well as in naturally regenerated secondary forests; native species were only present in the secondary forests (González et al. 1996). *Pontoscolex corethrurus* also was present in the relatively undisturbed tabonuco forest (with selective logging) and cloud forest at the top of undisturbed Luquillo Mountains (Zou and González 1997; Liu and Zou 2002; Hendrix et al. 1999b; also see González et al. in this issue).

A survey of 84 cropping and pasture systems in southeastern Australia showed that exotic species were dominant, but a single native species co-occurred with exotics in both systems (Mele and Carter 1999a). The native species occurred with higher abundances in the less disturbed pasture systems, but was also the dominant species in acidified cropping systems (Mele and Carter 1999a, b). An examination of earthworm populations under different tillage or stubble management showed that less disturbance (no-tillage verses plowing) favors greater earthworm populations, and can preserve native species in both temperate (Parmelee et al. 1990; Mele and Carter 1999b) and tropical (Fragoso et al. 1999) ecosystems (also see Baker et al. and González et al. in this issue). In eastern Colombia, exotic earthworms were apparently excluded from native savannas converted into man-made pasture systems because native conditions were relatively maintained (Jiménez et al. 1998).

Finally, recent studies using stable isotopic techniques in a variety of ecosystems suggest the potential for direct competition between native and exotic species for food resources, based on overlap in ^{13}C and ^{15}N signatures (Hendrix et al. 1998, 1999a, b; Callaham et al. 2001; Lachnicht et al. 2002; Winsome 2003). These relatively short-term studies do not show actual displacement of native species; longer-term observations or studies of well-characterized chronosequences might be more conclusive.

Overall, these case studies suggest that exotic earthworms are able to invade and become established in a variety of ecosystems currently or previously inhabited by native earthworms. They also appear to co-occur with native earthworms in at least some, usually disturbed, conditions. As discussed below, it is not clear if co-occurrence is persistent or only a transient situation.

Invasion resistance by native earthworms and their habitats

A number of general mechanisms have been proposed that explain why exotic species may succeed or fail to invade new habitats (Simberloff 1989; Williamson 1996; Mack et al. 2000). Specific to earthworms, Hendrix and Bohlen (2002) discuss several mechanisms that may be particularly important determinants of success or failure along the C-2 pathway in Fig. 1.

Propagule pressure

In any area vulnerable to invasion, it is possible that exotic species simply have not yet been introduced or had adequate time to spread from local points of introduction. Dispersal of earthworms is relatively slow (10–15 m y^{-1}; Hoogerkamp et al. 1983; Ghilarov and Perel 1984; also see Terhivuo and Saura, this issue), and years to decades may be required for proliferation of an exotic population after it has been introduced. Observations by Alban and Berry (1994) and Hale et al. (2005) suggest extended periods of time between introduction of European lumbricid species and their invasion of earthworm-free forests in Minnesota (also see Frelich et al. and Tiunov et al., this issue). Repeated introductions of an exotic species (i.e., high propagule pressure) may increase the likelihood of its establishment. However, other factors also influence invasion potential, including species characteristics such as fecundity and parthenogenesis; habitat characteristics such as dominant vegetation, soil and climatic conditions; and indigenous biota, such as predators, parasites and competitors (possibly including native earthworms). These factors may impart invasion resistance to a given habitat.

Habitat matching

Once introduced, exotic earthworms may fail to become established if they are not pre-adapted to a local habitat. A number of abiotic factors are known to influence earthworm distribution and abundance, and hence the success of introduced species. Temperature and water regimes appear to be controlling factors for many invasive taxa on a global scale, for example limiting European lumbricids to temperate regions or *Pontoscolex corethrurus* to the tropics (Gates 1970; Fragoso et al. 1999). At local scales, soil properties such as texture, pH, Ca/Mg ratios, and soil organic matter content are important determinant of invasion success (Lee 1985; Edwards and Bohlen 1996).

Introduced earthworms also may not become established if resources in a new site are limiting to growth and reproduction. It has been suggested that habitat disturbance, such as fertilizer amendments or vegetation conversion, increase resource availability to anthropochorous earthworms thus enhancing their ability to invade disturbed sites (Fragoso et al. 1999; Winsome et al. 2006). Even in the absence of disturbance, it would be expected that an invader's feeding strategy would have to match the resource base in a new habitat for it to become established (e.g., epigeic species would be unsuccessful in areas devoid of surface litter).

In microcosm experiments, exotic earthworms have shown both reduced and increased survival, growth and reproduction in soils from invaded habitats, apparently depending on species and site characteristics. For example, *A. trapezoides*, *A. caliginosa* and *Octolasion cyaneum* did better in South Australian scrub vegetation soils containing indigenous earthworm casting than in nearby pasture soils in which they had become established (Lawson 1993). Conversely, *A. trapezoides* lost weight and *A. longa* failed to reproduce in Eucalyptus forest soils in Western and South Australia, respectively (Abbott 1985; Dalby et al. 1998). Abbott (1985) concluded that *A. trapezoides* was not well adapted to low organic matter content of these forest soils. In California grasslands, Winsome et al. (2006) found that invasive *A. trapezoides* was better adapted (in terms of growth) to heavily amended pasture soils than to relatively less enriched native grassland soils.

Exotic species' adaptations to temperature and precipitation regimes are reasonably predictive of invasion success on a broad scale (Lee 1985), but predictions at a finer scale appear difficult because of the high degree of local variability within many ecosystems. Furthermore, while establishment of an exotic earthworm species in a new habitat may suggest that it has overcome the hurdles of propagule pressure and habitat matching, it does not necessarily guarantee successful invasion of intact native earthworm communities.

Biotic resistance

Once introduced into a habitat to which they are otherwise adapted, exotic species may fail to become established for biological reasons, such as predation (e.g., by birds, lizards or moles), parasitism (e.g., ecto- or intra-coelomic nematodes), or effective competition by resident native species, including indigenous earthworms. Indirect evidence of biotic resistance comes from studies in undisturbed ecosystems where well-adapted exotic earthworms are known to have been introduced or have become established nearby, but have failed to invade a particular habitat occupied by native earthworms (e.g., several of the minimally disturbed sites in Table 1). However, of those cases where natives occur exclusively, many appear to be explainable on the basis of habitat factors (e.g., low pH and coarse textured soils in Florida or Ivory Coast; serpentine soils in California oak savanna), which may be unfavorable to the exotic earthworms. Exceptions are forests studied by Abbott (1985), Lavelle and Pashanasi (1989) and Kalisz (1993), where there is no apparent reason why exotic species have not dispersed from old logging, homestead or cultivated sites into native earthworm communities within the forest.

Microcosm studies give some support to the biotic resistance hypothesis, and specifically to direct competitive interactions between native and exotic earthworms. Winsome et al. (2006) found that native *Argilophilus marmoratus* negatively affected *Aporrectodea trapezoides* growth and development in native California grassland soils, but not in enriched pasture soils nearby; *A. trapezoides* was the stronger competitor when resources were not limiting, but *A. marmoratus* was better adapted to the low-productivity grasslands and exacerbated the effects of resource limitation on *A. trapezoids* in the native habitat.

A further aspect of biotic resistance may relate to interactions between introduced earthworms and soil microflora. Daane and Häggblom (1999) found that earthworm cocoons in sterile medium did not develop as successfully as those in non-sterile medium, suggesting a functional linkage between earthworms and the ambient soil microflora. Furthermore, Gilot-Villenave (1994) has proposed that earthworms introduced into a new habitat may be impaired if they encounter an unfamiliar microflora, whereas cocoons of the same species may survive if they carry an indigenous microbial inoculum. If true, this phenomenon raises interesting questions for earthworm invasion ecology: Do sites inhabited by native earthworms maintain microbial populations unfavorable to exotic earthworms? Do wormless sites have a different microflora that offers less resistance (implying that earthworms can build resistance by modifying microfloras)? Do disturbed areas have depauperate (or even exotic) microfloras that do not offer this resistance to invasion by pre-hatched earthworms? Are there practical implications for intentional introduction of earthworms (e.g., for land reclamation efforts)? Some studies do suggest an internal or external ''rumen'' in earthworm feeding whereby soil or gut microbes facilitate catabolism and assimilation of organic substrates by earthworms (Lavelle et al. 1995; Brown and Doube 2004). An analysis of the microbial flora of earthworm gut material demonstrated that 12 phospholipid fatty acid markers occurred only in gut compartments and not in the bulk soil (Sampedro et al. 2003). Bacteria phylotypes isolated from intestinal tissue of *Lumbricus rubellus* were not detected in cast material or bulk soil, but it was suggested that the association was opportunistic rather than obligate (Singleton et al. 2003). There are few data with which to test the idea of obligate or antagonistic microbial associations with earthworms, or their implications for invasion ecology, but these are important questions for further research.

Differences between native and exotic earthworm assemblages

Based on general knowledge of earthworm ecology, some potential differences between native and exotic earthworm populations might affect the likelihood and outcome of exotic invasions into native earthworm communities. First, native earthworm densities and fecundities may be lower than those of invasive species, even in undisturbed soils (Lee 1985; Fragoso 1999; Winsome 2003). This situation could give r-selected, rapidly growing exotic species populations a competitive advantage over native fauna for common resources. Second, at least some native earthworm assemblages appear to be dominated by endogeic species (Kalisz 1993; Fragoso et al. 1999), possibly providing open niches in the O-horizon which could be readily exploited by epigeic exotic species, for example *Amynthas agrestis* in deciduous forests occupied by native earthworms in north Georgia, USA (Callaham et al. 2003). Third, native earthworms may be better adapted to local conditions and thus have a competitive advantage over exotic species during periods when climatic conditions force exotics into dormancy, as observed in prairie soils in Kansas, USA (James 1991; Callaham et al. 2001). These situations are somewhat speculative, but may be involved in some cases of exotic invasions into native earthworm communities.

Co-existence of native and exotic earthworms

Table 1 summarizes information from studies that have assessed the status of native and exotic earthworm species in ecosystems under various degrees of disturbance. Native earthworms appear to occur exclusively or to predominate over exotic earthworms mostly in relatively undisturbed sites. Nonetheless, co-occurrence of native and exotic species, especially in disturbed or managed sites, appears to be common across a range of ecosystem types. Intensity of and time since disturbance appear to be important correlates of relative abundances of native and exotic species (Fragoso et al. 1999). Biotic resistance, if it exists in earthworm communities, may be more a matter of degree than an absolute outcome of native and exotic species interactions. From a practical standpoint, perhaps the more important questions are: under what circumstances do native and exotic species co-exist in a given volume of soil, and are these situations persistent in the long term? Again, there are only limited data with which to address these questions.

One mechanism for co-existence of exotic and native species may be spatial partitioning of resources. In tropical forests of Chajul, Mexico, Fragoso (personal observation) found that exotic *P. corethrurus* was well established in a low-species-diversity earthworm community (6 species) in a poor forest soil (ferralitic) near a small village, and accounted for more than 84% of total earthworm abundance and biomass. Old alluvial soils, in which a tropical forest was well established, harbored a richer community (11 species) but with *P. corethrurus* still the most important species (41 and 35% of total abundance and biomass). Nonetheless, there was evidence of changes in the community in response to the presence of the invader. For example, *Balanteodrilus pearsei* (a very common species in southeast tropical Mexico) was relatively thin and small, compared to individuals in other populations located 70 km north, where *P. corethrurus* was absent. The vertical distribution of *P. corethrurus* was more superficial in the alluvial soils than in the ferralitic ones, suggesting that other mesohumic endogeic species inhabiting alluvial soils (e.g., *Ramiellona strigosa* and *Lavellodrilus ilkus*) impeded *P. corethrurus* utilization of deeper strata. Thus, we can hypothesize that native endogeic species prevented the invasion of deeper soil by the exotic *P. corethrurus* which instead concentrated in the upper layers where it negatively affected the native polyhumic *B. pearsei*. Lachnicht et al. (2002) also observed spatial partitioning of the soil volume in microcosms derived from tabonuco forests in Puerto Rico. *Pontoscolex corethrurus* was active in the upper mineral soil and forest floor layers, whereas the native *Esthrella* sp. (possibly an anecic species) occupied the deeper mineral soil after a 30-day incubation.

Co-existence may also be facilitated by temporal separation of activity between native and exotic earthworms. For example, James (1991) and Callaham et al. (2001) suggested that native *Diplocardia* in tallgrass prairie soils were adapted to higher temperatures than were the invading European lumbricids, and thus maintained activity during warmer periods when lumbricids became dormant. Regardless of the mode of action, these studies suggest the potential for co-existence of native and exotic earthworms and for resource partitioning in the same soil volume. However, it is unknown whether such co-existence is a transient or long-term phenomenon.

Finally, an intriguing aspect of co-existence is the possibility that native species actually facilitate the establishment of exotic species. Lawson's (1993) microcosm studies (reviewed above) suggested that several invasive European lumbricid species were better adapted to or perhaps able to more effectively exploit resources in soils containing castings from native earthworms than in the pasture soils they had successfully invaded. If this phenomenon is generally observed, it may change our view of exotic earthworm invasions in areas inhabited by indigenous earthworms.

Implications of native–exotic earthworm interactions for soil processes

A key functional question regarding exotic invasions into native earthworm communities is whether or not the impacts of exotic species on soil processes are altered in the presence of native species in their native habitats. Once again, there are very few data with which to address this question. The extreme-case affirmative answer would of course be where exotic species fail to establish after being introduced into a habitat. However, the more interesting situations would be where native and exotic species co-exist. If impacts are observed on soil processes, they might be expected to be related to relative population densities of natives and exotics at times of peak activity (Winsome et al. 2006).

As noted above, James (1991) suggested that native earthworms were better adapted to local soil and climatic conditions, and hence maintained longer periods of activity and effects on nutrient dynamics in tallgrass prairie soils than did invading European lumbricids. This is not necessarily always the case, however, for example where exotic species invade an area to which they are climatically well matched (e.g., Asian subtropical *A. agrestis* in Georgia, USA; Callaham et al. 2003). Finally, the microcosms experiment by Lachnicht et al. (2002) showed significant reductions in C and N mineralization rates induced by *P. corethrurus* when it was incubated in soils with native *Estherella* sp. compared to when it was incubated alone. Whether or not these effects would occur under field conditions is not known, but this is clearly a topic in need of further research.

Conclusions

Although the database is limited, a few conclusions can be drawn from this review. First, exotic earthworms do invade ecosystems inhabited by indigenous earthworms, even in the absence of obvious disturbance (Table 1). Kalisz and Wood (1995) referred to this phenomenon as ''invisible'' disturbance, such as forest fragmentation in which native species may experience local extinction in small remnants. In some cases, native species appear to remain dominant, usually in undisturbed soils; in other cases (both disturbed and minimally disturbed soils), the exotics predominate (Fragoso et al. 1995, 1999). A number of factors are probably involved in these outcomes, including physical and ecological characteristics of the habitat, biological characteristics of native and exotic earthworm species, influences of other indigenous biota, and time and frequency of invasions. In many cases, there must certainly be an element of chance that introduction of exotic species even occurred. Thus, the challenge for developing predictive models of exotic earthworm invasions is significant.

Second, direct competitive exclusion of native earthworms by exotic earthworms seems plausible in theory, but is not easily demonstrated in practice. In fact, field studies suggest that co-existence of native and exotic species is common (Table 1), even if transient. Competitive interactions may occur, as suggested by several microcosm studies, but it also appears that at least some exotic earthworms may utilize resources not fully exploited by native species, especially in disturbed soils. Because many of the invasive species show considerable flexibility in their use of resources and/or microhabitats (Fragoso et al.

1999), they may be well adapted to establish populations within areas occupied by native earthworm communities. The example from Chajul, Mexico cited above illustrates a certain amount of flexibility by an exotic species. An extreme case of this flexibility is the observation by S. James (unpublished data) of *P. corethrurus* occupying arboreal habitats in a montane cloud forest on Nevis Island in the Lesser Antilles; the site had no native earthworms and *P. corethrurus* was found in the soil and in the trees. The possible combination of exotic species flexibility and ‘‘open’’ niche space left by native species raises interesting evolutionary questions.

Third, resistance to exotic earthworm invasions, if it occurs, may be more a function of physical and chemical characteristics of a habitat than of biological interactions with native earthworms.

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ORIGINAL PAPER

Introduced earthworms in agricultural and reclaimed land: their ecology and influences on soil properties, plant production and other soil biota

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Abstract Accidental and deliberate introductions of earthworms into agricultural and reclaimed land are natural experiments that provide opportunities to understand the attributes of successful invaders and their impacts on local biota and ecosystem processes. We consider various case studies (e.g., earthworm invasions in agricultural soils in Australia and Brazil) and deliberate introductions of earthworms into reclaimed mine sites, landfills and cutaway peat in the U.K. and Ireland. Invasions of exotic earthworms, such as European Lumbricidae in Australia, have been geographically extensive, but remain very patchy at regional and field scales. Their impacts on soil properties, plant production and other biota are therefore also likely to be patchy. Various methods have been developed to deliberately inoculate exotic earthworms into disturbed lands, with varying degrees of success. The factors controlling success are, in general, poorly understood. A broad range of impacts of invasive earthworms on soil properties (e.g., soil structure, nutrient availability, burial of surface materials, incidence of root diseases) and plant yield and quality have been reported. Less is known of the impacts of invasive earthworms on other soil fauna, but they are likely to occur due to alterations in food availability and habitat structure. Influences on other biota are likely to extend to aboveground communities as well as those belowground. Introductions of earthworms to disturbed lands can yield substantial benefits in agricultural productivity and amelioration of soil degradation. However, the potential impact of the promotion or control of such introductions on non-target biota and ecosystem processes in pristine ecosystems nearby should be considered.

Keywords Disturbed land · Earthworms · Exotic · Plant production · Soil biota · Soil properties

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Abbreviations

EIU	(Earthworm Inoculation Unit) method a technique incorporating adults and their cocoons in a protective soil microenvironment
NT	No-till agricultural practice

Introduction

Invasions of exotic earthworms have significantly damaged pristine, native ecosystems (see other papers in this issue). However, earthworms have also been both accidentally and deliberately introduced to a wide variety of agricultural habitats, with major benefits accruing to land owners (Lee 1985; Edwards and Bohlen 1996). Deliberate introductions have sometimes been part of more extensive restoration programs following habitat degradation (e.g., mining, peat harvesting) or reclamation of land from the sea (e.g., polders) (Hoogerkamp et al. 1983; Curry and Boyle 1987, 1995; Scullion et al. 1988, Scullion and Malik 2000; Butt 1999; Butt et al. 2004). Introductions have been on both a large scale (many hectares) and much smaller scale (enclosures of a few square metres or less) (Stockdill 1982; Baker 2004). Motivation for such earthworm introductions has been driven by needs to improve soil properties (e.g., nutrient turnover, soil structure and water flow, pH, functional biodiversity, food sources for vertebrate predators) and to increase plant production. Frequently, exotic earthworms comprise the majority of the earthworm fauna in agricultural land (e.g., accidental introductions in New Zealand and Australia) and these earthworms provide various beneficial ecosystem services. However, the impacts of introduced earthworms have not always been positive and rates of improvement in site characteristics have frequently been slower than desired following deliberate introductions. Careful site selection and preparation is often paramount for success. "Non-target" effects of exotic earthworms have rarely been considered prior to deliberate introduction, in comparison with some other exotic introductions (e.g., release of biocontrol agents to control agricultural pests).

This paper provides an overview, illustrated with case studies, of accidental and deliberate earthworm introductions to disturbed land, taken from different parts of the world with varying climatic regimes, and reviews the impact that has occurred on soil properties, plant production and the abundance and diversity of other soil biota (both invertebrates and microbes, but native earthworms especially). We also briefly explore the potential of invasive earthworms to influence the abundance of above ground taxa (pests and beneficial species). In addition, studies of the patterns of establishment of introduced earthworm populations and the development of rearing methods for large scale inoculations into farms and reclaimed land have provided insight into the capacity of these invertebrates to disperse, as well as revealing some of the environmental factors that influence their abundance. We will discuss these issues as well as spatial and temporal patterns in establishment that have been observed or predicted in disturbed habitats.

Distributions of exotic earthworms: "Accidental" establishment at different scales, using Australia as an example

Perhaps the best known group of invasive earthworms in agricultural soils are the peregrine members of the European Lumbricidae (Lee 1985), which have colonised all continents of the world, with the exception of Antarctica (see Frelich et al., and Tiunov et al. in this issue). These include several species of *Aporrectodea*, *Allolobophora*, *Lumbricus* and *Octolasion*. Other families, with origins elsewhere in the world, have also contributed frequent invaders, such as *Microscolex*, *Dichogaster* and *Amynthas* (Megascolecidae) and *Pontoscolex* (Glossoscolecidae). For example, all of these genera have invaded Australian agricultural and urban habitats (Mele et al. 1996; Baker et al. 1997a). A similarity in exotic fauna, originating from Europe, could be expected between southern Australia, Canada, USA, southern South America, South Africa and parts of Asia, based on similarities in climate and similar opportunities to colonise through accidental transport (Baker et al. 1994).

Whilst some earthworm species have colonised very broadly on a geographic scale within Australia, others remain very restricted in their distribution (Baker and Barrett 1994; Baker et al. 1997a) (Fig. 1). Factors controlling these distributions are poorly understood. It is quite probable that the potential extent of at least some invasions has yet to be realised, held back thus far through lack of opportunity to colonise (Baker 1998a, 2004). However, ecological boundaries to distribution are occasionally apparent. For example, Baker (1998a) surveyed pastures extensively throughout south-eastern Australia and showed that *Aporrectodea caliginosa* was common at sites receiving >600 mm annual rainfall, but rare where rainfall was less. The closely related *A. trapezoides* was found more commonly at sites with < 600 mm annual rainfall. This apparent difference in tolerance of aridity between the two species accords well with their observed European distributions (e.g., in France where *A. trapezoides* has the more southern distribution of the two) (Bouché 1972). It is perhaps remarkable that the distributions of some exotic lumbricid species are as extensive as they are in Australia, given that the most likely date of introduction was approximately 200 years ago (when European humans first settled Australia and probably brought exotic earthworms with them accidentally in potted plants, ship's ballast, etc). There has been very little deliberate attempt to enhance their distributions since then (Noble et al. 1970; Blackwell and Blackwell 1989; Baker 1998a, 2004).

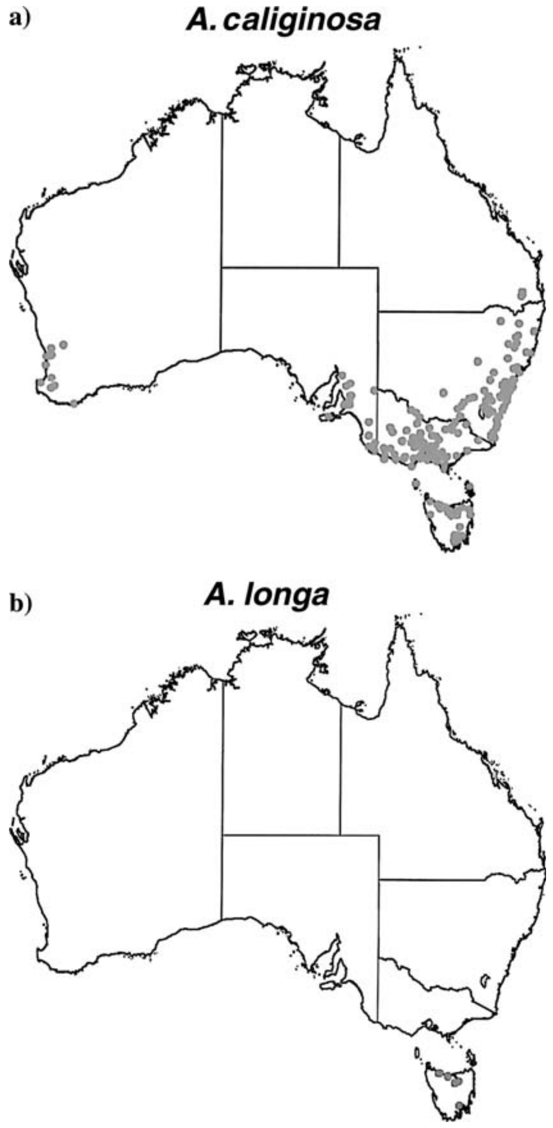


Fig. 1 Distributions of *Aporrectodea caliginosa* and *A. longa* (Lumbricidae) within sites surveyed throughout Australia. Redrawn from Baker et al. (1997a)

At a more regional level, the abundance of exotic earthworms can vary markedly between sites (Baker 2004) (Fig. 2). On some farms, exotic earthworms predominate over native species, and vice versa. Again, lack of opportunity to colonise (and multiply) may explain some of the observed patterns in abundance of the exotic species. Abundance has also been correlated with local rainfall and various soil properties such as carbon content, particle size and pH (Baker et al. 1992b; Baker 1998a). Within individual farms, some fields can contain invasive species, whilst adjacent fields, with apparently similar management and soil type, do not (G. Baker, unpublished data). Within individual fields, invasive earthworms have colonised some soil types more than others (Baker et al. 1993b), and at a finer scale, some exotic earthworms (e.g., *A. trapezoides* and *Microscolex dubius*) aggregate differently under various dung types produced by grazing vertebrates (Scown and Baker, submitted).

The most common invasive earthworms in agricultural soils in south-eastern Australia are *A. trapezoides*, *A. caliginosa* and *A. rosea*, all of

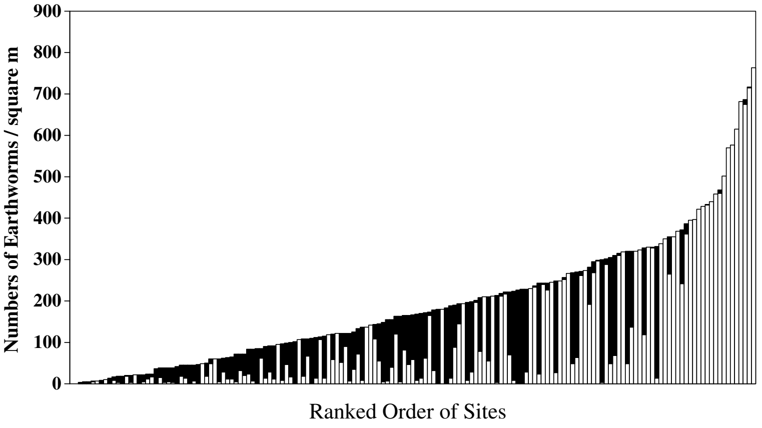


Fig. 2 The abundance of native and exotic earthworms in 163 pastures that were surveyed in late winter-early spring in western Victoria, Australia (see Baker 1998a for more details of survey location). Sites are arranged along the X axis in ascending order of overall population density. Dark bars indicate native species; light bars indicate exotic species. Redrawn from Baker (2004)

which are endogeic species (Baker et al. 1992b; Baker 1998a, 2004). The epigeic species, *M. dubius*, is widespread, but rarely occurs in large numbers. Another epigeic species, *Lumbricus rubellus*, can be locally abundant, but is generally restricted to damp situations. The only anecic invasive species is *A. longa*, but it is mostly restricted to Tasmania. All of these species are only active from early winter to early spring, when soils are cool and moist. Very little is known about the temporal and spatial aspects of the burrowing and feeding of native Australian earthworms, but some marked differences compared with exotic species have been reported. For example, Baker (1996) reported *Gemascolex lateralis* (Megascolecidae) active in leaf litter in the middle of a hot dry summer.

The distribution and abundance of invasive earthworms are thus highly patchy and variable, both at large geographic and local spatial scales, as is the case with earthworms and other soil fauna in general. Earthworm abundance can vary markedly between years as well (Baker 1999). Given this, the influences that invasive earthworms will have on soil properties and other biota will likewise be highly variable. The seasonal activity patterns and particular styles of burrowing and feeding of the invasive species will further determine the nature of these influences (Baker et al. 1992a, 1993a, b; Baker 2004).

Managing deliberate introductions

One of the best known deliberate introductions of earthworms is the case from New Zealand, where lumbricids (most notably *A. caliginosa*) were redistributed to pastures lacking them (Stockdill and Cossens 1966; Stockdill 1982). These managed pastures were sown with exotic plant species. Native earthworms fared poorly under such pastures, leaving a void amongst the soil macrofauna, an accumulation of turf thatch and restricted nutrient cycling. Water infiltration was also impeded. Exotic earthworms were harvested from pastures where they were abundant, using sod-cutting machinery, and then inoculated at regular intervals across pastures devoid of earthworms. Wide-spread establishment within the targeted pastures was achieved within 7 years at economically acceptable costs and with substantial benefits (e.g., increases of 25% in pasture carrying capacity in the long term). Similar strategies have been used in northern Tasmania (Farquhar 1992), with large economic benefits for land-owners and in shorter time frames.

The sod transplantation method might be expected to work better for endogeic compared with anecic earthworms, given the former species' shallower burrowing behaviour, and thus greater potential to be collected in sods. However, information on this topic is scarce. In Tasmanian pastures, where both *A. caliginosa* (endogeic) and *A. longa* (anecic) have been introduced together in sods, the relative success achieved for the two species is not known. Topsoil-dwelling species have established better than deep-burrowing species in reclaimed cutaway peat soils in Ireland following sod transplantation, but this difference is probably better explained in terms of post-introduction survival than by the size of the inoculum (J. Curry, unpublished data). Curry and Schmidt (submitted) noted that the anecic *L. terrestris* was only very sporadic in occurrence in 20–30 year old reclaimed peat, possibly because of insufficient depth of aerobic soil.

The scarcity of anecic earthworms in agricultural soils in southern, mainland Australia has prompted consideration of how the functional diversity of earthworm communities might be improved there (Baker 1998a, 2004). Springett (1985), Temple-Smith et al. (1993) and Baker (1998b) have shown in both field and laboratory experiments in New Zealand and Australia that the addition of *A. longa* to soils already containing *A. caliginosa* and *L. rubellus* can increase pasture production (see other benefits mentioned below). Clearly, there is an additive effect of functional diversity on plant production. Baker (1998a) made a crude prediction of where *A. longa* might establish in Australia if given the chance, based on annual rainfall matching with its known distribution in Europe. Baker and Whitby (2003) have since suggested that the length of time the soil remains sufficiently moist during the year (and hence adequate for cocoon development) may be a better predictor for the successful establishment of *A. longa*. Other edaphic factors, such as soil pH, also need to be considered (Baker and Whitby 2003). Baker et al. (1999a) inoculated *A. longa* in cages into several different soil types in south-eastern Australia and recorded establishment, in the short-term (5 months). *A. longa* survived in all cases. Unencumbered releases have also been made in pastures (Baker 2004). *A. longa* has established and spread at least 7 m from inoculation points within 3 years (with one exceptional individual found at 20 m).

The rate of spread observed for *A. longa* in Australia is similar to those recorded for invasions of lumbricid earthworms in newly formed polders in The Netherlands (Hoogerkamp et al. 1983; Marinissen 1991; Marinissen and van den Bosch 1992; Stein et al. 1992), within land reclaimed following landfill with municipal solid wastes (Butt et al. 2004) (Fig. 3) and on restored surface mine sites in the U.K. (Scullion et al. 1988). Given their different burrowing behaviours and fecundities (hence rates of population growth) (Lee 1985), epigeic, endogeic and anecic earthworms might be expected to disperse and establish away from inoculation sites at different rates, anecic species performing slowest in this regard. Indeed, J. Scullion (unpublished data) showed that the anecic species, *L. terrestris* and *A. longa*, colonised restored mine site soils in the U.K. at slower rates than other more horizontally burrowing species over a 6 year period. Curry and

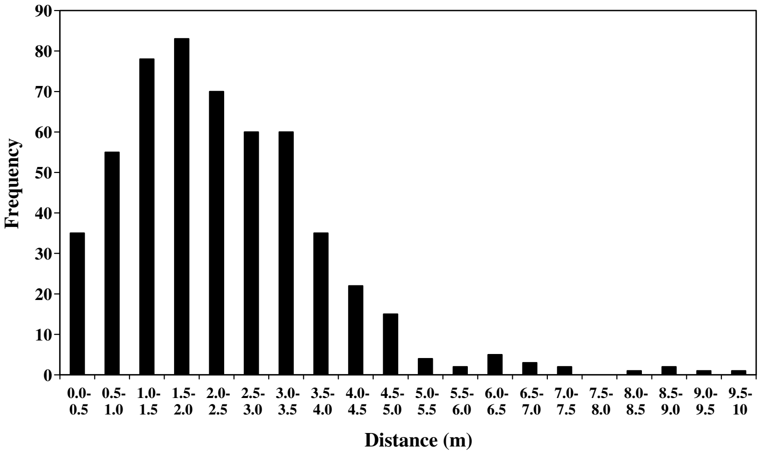


Fig. 3 Distance of casts of *Aporrectodea longa* from point of inoculation, 5 years after introduction to a reclaimed landfill site in the U.K. Data represent total counts of surface casts within 0.5 m radial lengths from the nearest points of *A. longa* inoculation. Redrawn from data in Butt (1999)

Boyle (1987) reported that *A. longa* (and the endogeic *A. rosea*) dispersed more slowly within 1 year from transplanted sods in reclaimed cut-away peat sites than several endogeic and epigeic species (e.g., *A. chlorotica*, *A. caliginosa*, *Dendrodrilus rubidus*, *L. festivus* and *L. rubellus*). Hoogerkamp et al. (1983) found that *A. caliginosa* dispersed at twice the rate of *L. terrestris* in a reclaimed polder in The Netherlands. On the other hand, Butt et al. (2004) recorded *A. longa* at greater distances from inoculation points than *A. chlorotica*, 11 years after introduction to landfill sites. The dispersal of earthworms from release sites can of course easily be confounded by ''natural'' dispersal from other nearby sites and the finding of individuals at particular distances away from inoculation points also does not necessarily infer successful establishment (i.e., a breeding population). Such data thus need cautious interpretation. Earthworm spread can be enhanced accidentally by agricultural machinery (e.g., cocoons can be picked up in mud clinging to tractor tyres and thus transferred within and between fields, Marinissen, 1991), thus blurring observations of innate capacity for dispersal.

One of the most ambitious introductions of earthworms occurred in Russia, where various lumbricids, most notably *A. rosea* and *A. trapezoides*, were transported 700 km (taking 12 days) from the Zaravshanski Mountains to oases in the Kyzylkum Desert (Ghilarov and Mamajev 1967). Agricultural soils at the inoculation sites were devoid of earthworms and dung from grazing vertebrates was accumulating, until successful establishment occurred and local lucerne production was doubled.

Different methods of inoculation can influence establishment success. At mine sites undergoing rehabilitation in the U.K., several introduction techniques have been used on an experimental basis (Scullion et al. 1988; Scullion and Malik 2000). In one trial, mixed populations of earthworms, collected during cultivation of local undisturbed land, were introduced directly at 2 m intervals into mole plough slits at a newly restored site. In another trial at the same site, strips of topsoil containing viable earthworm populations were placed at 50 or 100 m intervals during replacement of the final soil layer at the restored site. Soil in intervening areas was largely devoid of earthworms. In the direct inoculation trial, observations of casting activity suggested that colonisation was almost exclusively along the mole plough slits during the first 12 months. Colonisation of the soil between slits occurred in the second year of the trial. Then, within 4 years, the population on areas to which earthworms were introduced was similar to that of adjacent and similarly managed undisturbed pasture. At the same time, populations in the inoculation strips had lower numbers of *A. longa* and *L. terrestris* compared with the direct introduction plots, but similar numbers of other numerically dominant species (*L. rubellus*, *A. chlorotica* and *A. caliginosa*). This finding may partially reflect the fairly low residual population of the former species in strip soil.

In another study in the U.K., Butt et al. (1997) reported that the use of a technique incorporating adults and their cocoons in a protective soil microenvironment (The Earthworm Inoculation Unit (EIU) method, Butt 1992) was superior to broadcasting of adults of *A. longa* onto compacted soil at a landfill site (Calvert). A viable population of *A. longa* was recorded over the following decade after using the EIU technique (Butt et al. 2004). This technique was also shown to be of value for endogeic species such as *A. chlorotica* and for mixed species inocula. No earthworms were present at the Calvert landfill site when the capping process was completed in 1991. Butt et al. (1999) recorded the spread of *A. longa* and *A. chlorotica* following their introduction in 1992 and also noted that the abundance of the latter increased in the presence of the former. Natural colonisation of the site by earthworms was recorded after a period of 7 years, when *Eiseniella tetraedra* and *L. rubellus* were located. After a further 4 years, *L. castaneus* and *A. rosea* were also found. At this point (2002), the *A. longa* and *A. chlorotica* still accounted for over 65% of earthworms found on site (Butt et al. 2004). By 2003, dispersal of inoculated species and colonisation of other species meant that distribution patterns no longer equated to inoculation treatments. However, the presence of viable trees (*Alnus glutinosa*), planted at the time of inoculation, led to significantly greater earthworm densities compared to areas where *Acer pseudoplatanus* had been planted and subsequently died (Butt et al. 2004). But the surviving trees (*A. glutinosa*), with associated nitrogen-fixing root nodules, were stunted and only attained a height of 3 m (max) after 11 years, with die back each year. This was attributed to limiting soil factors which were not assisted by the presence of inoculated earthworms.

Other local management practices can influence the establishment of exotic species. For example, in the southern Brazilian state of Paraná, exotic *Amynthas corticis* and *A. gracilis* have extensively colonised croplands in regions with cool, sub-tropical climates (Voss 1986; Tanck et al. 2000; Brown et al. 2003). In these areas, no-tillage (NT) practices have spread widely in the past ten years and now cover 5.5 million ha (25% of the state's land surface). Under NT, organic matter content in the topsoil has increased (Sá et al. 2001). Consequently soil macrofauna, such as earthworms, have increased in abundance (Brown et al. 2001, 2003). The adoption of NT is believed to have encouraged the invasion of *A. corticis* and *A. gracilis*, and build-up of their populations has been rapid. Voss (1986) observed an increase in the abundance of *Amynthas* spp. from 0 to 108 individuals m^{-2} within 4 years of adoption of NT, and Peixoto and Marochi (1996) reported similar increases (0 to >200 individuals m^{-2} in 6.5 years). In addition, several farmers have developed a method of field inoculation which consists of spreading batches of composted manures containing high populations of *Amynthas* spp. at selected sites within their fields (e.g., close to bunds used for erosion control) and at prescribed distances apart to promote earthworm colonisation.

Invasive species often exhibit a ''boom-and-bust'' cycle as they establish (Simberloff and Gibbons 2004). Over-exploitation of resources, disease or arrival of competitors have been suggested as mechanisms for the observed collapses in abundance. However, causes frequently remain poorly understood. Examples for soil fauna are rare in this context (e.g., see Baker 1985 for a millipede example). Although invasive earthworms should offer good opportunities to follow temporal and spatial patterns in abundance following establishment, and the environmental factors which drive such patterns, little data are available. Stockdill (1982) reported that pasture production in New Zealand peaked a few years after the introduction of *A. caliginosa*, and then stabilised at a lower level in subsequent years. This pattern in production may, but need not necessarily, have reflected a ''boom-and-bust'' in earthworm abundance (no data are available). The peak in production may simply have reflected a flush of nutrient release from the decomposing thatch that had accumulated prior to earthworm introduction.

Influences on soil properties and plant production

Earthworms can influence soil properties and plant productivity in several ways (Lee 1985; Lavelle 1988; Curry 1994) and there are many examples in the literature of the contributions exotic earthworms make in this regard in agricultural soils and reclaimed land throughout the world. In southern Australia, for example, several studies have shown the influences of exotic earthworm species in agricultural soils on soil structure (Barley 1959b; Doube et al. 1994b, c; Friend and Chan 1995; Hindell et al. 1994a, b, c, 1997; Hirth et al. 1994, 1996; Chan et al. 1997; Curry and Baker 1998), nutrient availability (Barley and Jennings 1959; Baker et al. 2003a), burial of surface organic matter and lime (Barley 1959a; Baker et al. 1993c, 1998, 1999c; Chan et al. 2004), distribution of beneficial microorganisms (Stephens and Davoren 1994; Stephens et al. 1993b, 1994a, b; Doube et al. 1994a, d), reduction of incidence of root diseases (Stephens et al. 1993a, 1995; Stephens and Davoren 1997), and plant yield and quality (Abbott and Parker 1981; Temple-Smith et al. 1993; Garnsey 1994; Stephens et al. 1994a; Baker et al. 1997b, 1999b, 2003b). Several studies have demonstrated that such influences vary markedly between earthworm species, soil types and plant species (Doube et al. 1997; Baker et al. 1999b, 2003a, Baker submitted; Chan et al. 2004).

In reclaimed polders in The Netherlands, conditions for pasture root growth were improved by earthworm colonisation through increased water infiltration and aeration and decreased compaction of the upper soil layers (Hoogerkamp et al. 1983). Earthworms redistributed surface organic matter throughout the soil, and grass production and pasture quality increased. Stockdill (1982) reported similar benefits from introducing earthworms to pastures in New Zealand. Earthworms however also rendered the soil more liable to damage from treading by domestic animals and invasion of moles as they searched for earthworm prey in the Dutch polders.

Curry and Boyle (1987) studied the impact of earthworms on soil properties and herbage production in a field microplot experiment in central Ireland, where the study site had been reclaimed following industrial peat extraction, and seeded with perennial ryegrass and white clover. The presence of earthworms had little apparent effect on herbage production in the first year, but total herbage yield was 25% greater in the second year and 49% greater in the third year in microplots receiving annual topdressing of cattle slurry, compared with similarly-treated microplots without earthworms. No effect of earthworms on herbage yield was detected in microplots receiving inorganic fertilizer only. However, the control microplots did not remain entirely free of earthworms, and considerable heterogeneity in soil conditions masked any impact that earthworms might have had on soil properties in the field. Glasshouse studies were therefore conducted to assess the role of earthworms under more controlled conditions (Boyle et al. 1997) (Fig. 4). Cumulative herbage yields over a period of 20 months were 89% higher in buckets with earthworms fertilised with cattle manure, and 19% higher in buckets receiving only inorganic fertilizer, compared with comparable treatments without earthworms. Grass growth response to earthworms was most pronounced under conditions of declining fertility (+114% to +222%) when manure and fertilizer applications were discontinued, suggesting that growth response to earthworms was mainly due to enhanced organic matter mineralisation. Soil subsidence rates, hydraulic conductivity, moisture characteristics, bulk density, porosity, fibrosity and soil morphology and micromorphology were all found to be significantly influenced by the presence of earthworms, suggesting that earthworm activity can markedly affect the process of soil maturation and profile development in reclaimed peat soils.

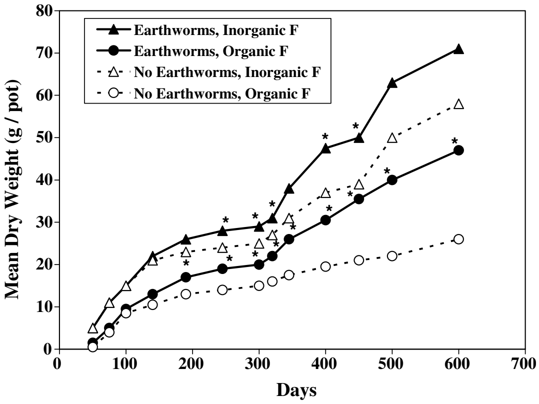
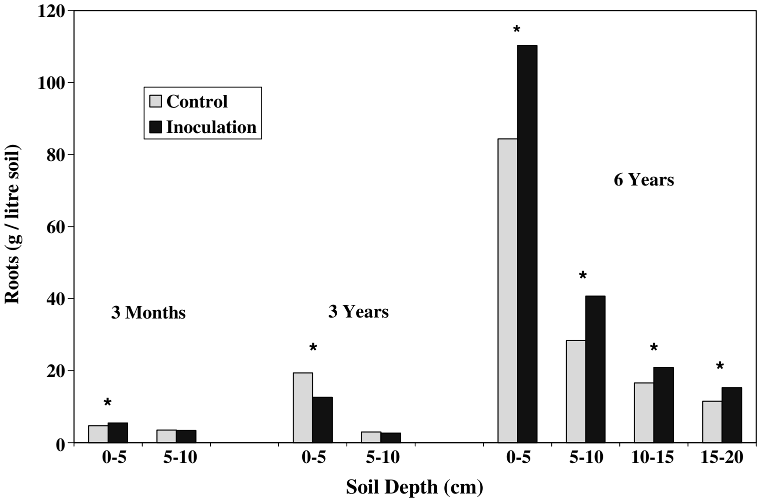


Fig. 4 Cumulative perennial ryegrass (*Lolium perenne*) yields with and without earthworms (mix of *Aporrectodea*, *Allolobophora* and *Lumbricus* spp.) under inorganic or organic fertiliser regimes in glasshouse studies using a mixture of peat and relict degraded mineral soil from reclaimed cutaway peatland. Asterisks indicate significant earthworm effects, within fertiliser treatments. Redrawn from data in Boyle et al. (1997)

In restored mine site soils, Marashi and Scullion (2004) found that inoculation of earthworms increased soil porosity throughout the top 20 cm of soil. However, this increase in porosity was associated with greater soil water-logging, despite the site having been drained and subsoiled. Earthworm activity enhanced water infiltration and artificial drainage was not effective in removing excess water from the soil profile. As a result, the surface of inoculated soils was more prone to treading damage.

Stability of soil aggregates was little influenced by earthworm inoculation in restored mine site soils within 3 years, but by 6 years, aggregation had improved throughout the top 20 cm of soil, especially near the surface (Scullion 1994; Marashi and Scullion 2003). Organic matter content was significantly higher on control compared with inoculation plots to 5 cm depth, but the situation was reversed below this depth. Other work on these soils (Scullion and Malik 2000) showed that increased carbohydrate levels provided the most marked effect of earthworms on organic matter content. Root contents within the soil on inoculated plots were significantly higher than for controls, at all sampling depths (Fig. 5).

Fig. 5 Root biomass at varying depths, 3 months, 3 years and 6 years after earthworm inoculation to soil at a reclaimed mine site in the U.K. Asterisks indicate significant differences. Redrawn from data in Marashi and Scullion (2003)



Earthworms have an important role in mixing organic matter with mineral soils at reclaimed sites. Ultrasonic dispersion showed that organic carbon was better mixed with clays where earthworms were present (Scullion and Malik 2000). Physical protection of organic matter through close association with mineral components results in a lower decomposition rate.

J. Scullion (unpublished data) has also investigated the influences of earthworm inoculation at mine site rehabilitation sites on % root infection by arbuscular mycorrhizal fungi (same sites as referred to in Fig. 5). Overall, there was no difference in % infection, although total root length infected would have been markedly higher on inoculated sites, given the greater (25–43%) development of roots there.

In Paraná, Brazil, the invasion front of *Amynthas* into NT cropland significantly altered soil structure and water holding capacity (Peixoto and Marochi 1996). Most of the top 10 cm of the soil consisted of earthworm castings, and these had a major effect on increasing water infiltration and the availability of several plant nutrients. In the invaded area, grain yields of wheat and soybean increased by 47 and 51%, respectively, while the dry mass of black oat increased 22%. Similarly, Kobiyama et al. (1994) found enhanced growth of tree seedlings (*Mimosa scabrella*) when *Amynthas* were inoculated in field mesocosms. Earthworms influenced saturated hydraulic conductivity and total soil porosity down to 30 cm depth, especially increasing the number of pores with diameter >0.06 mm. Consequently, soil water holding capacity and plant growth increased (Kobiyama 1994). However, Santos (1995) found few significant differences in soil properties (nutrients, bulk density, water infiltration) and no differences in yields of wheat or black beans (*Phaseolus vulgaris*) when *Amynthas* were inoculated into field mesocosms. Furthermore, Kusdra (1998) observed negative effects of inoculations of *Amynthas* spp. on black bean shoot and root biomass and nodulation by symbiotic *Rhizobia* spp. in greenhouse trials. Santos (1995) and Kusdra (1998) conducted their work in disturbed soils, compared with the undisturbed soils used by the other authors. This difference, as well as the variation in plant type across the studies, may help explain the different results. Brown et al. (1999) have also illustrated how earthworms can have varied (positive and negative) impacts on tropical grain crop yields, but reasons for the variability they observed in plant response are unclear.

Very few studies have compared the impacts of invasive earthworm species with those of native species on soil structure, fertility and plant production in agricultural settings. In Australia, some work (Baker et al. 1996, 2003b; Blakemore 1997; Baker 1998a) has shown that native Megacolecidae, e.g., species of *Spenceriella* and *Gemascolex*, are inferior to exotic lumbricids, such as *A. caliginosa*, *A. trapezoides* and *A. longa*, in improving soil structure and water infiltration, burying surface dung, and improving plant production. In contrast, James (1991) argued that introductions of exotic lumbricids to tallgrass prairie in the USA had negative influences on soil properties through a reduction in the abundance of more useful native species.

Interactions with other fauna

Evidence for interactions (positive or negative) between invasive and native earthworms in agricultural soils is limited, although it seems likely to occur, if only at a small scale (Baker 2004). Probably, the scarcity of native earthworms following agricultural disturbance has stifled scientific inquisitiveness on this topic (see González et al., and Hendrix et al., this issue).

In southern Australia, regional surveys have provided no persuasive evidence of interactions between exotic and native earthworm species. For example, a survey of 104 pastures in southern New South Wales (Baker 2004) provided no correlation between the abundance of native and exotic earthworms. But in a similar survey of 163 pastures in western Victoria, native earthworms were generally absent where exotic abundance exceeded about 400 earthworms m^{-2} (Fig. 2). This is suggestive at first glance of possible competitive exclusion. However, the majority of sites with high numbers of exotic earthworms occurred in dairy or sheep pastures in the higher rainfall portion of the region that was surveyed. The scarcity of the native species may well reflect different responses to management practices compared with the exotic species.

Where native earthworms have been accidentally caged in the field in southern Australia with exotic lumbricids, some reduction in the abundance and/ or biomass of the native species has been observed (Baker et al. 1999a, 2002b). Similarly, the introduction of some exotic lumbricids (e.g., *A. longa*) has reduced the abundance and biomass of other established exotic species (e.g., *A. caliginosa*, *M. dubius*) (Baker 1997; Dalby et al. 1998; Baker et al. 2002a). Possible competitive interactions, such as removal of food and habitat and consumption of cocoons, have been suggested as mechanisms for the effect of *A. longa* on *M. dubius* (Dalby et al. 1998). Similar mechanisms could well operate between invasive and native earthworm species.

In Paraná, Brazil, Brown et al. (in press) found native earthworms at only three of 18 sites with row-crops. Exotic species (mainly *Amynthas* and *Dichogaster* spp.) were found only in secondary vegetation (forests and disturbed grasslands) and agricultural areas (approximately 50 sites sampled in the state). Under well-conserved native vegetation, exotics were absent and native species were common. Some native species (particularly Glossoscolecidae) were also found in disturbed areas such as pine forests, grazed grasslands, introduced pastures and home gardens (low-input). Native earthworms appear not to be well suited to survive under conventional agricultural practices, while exotic or peregrine earthworms may be better suited to the conditions created by cropping. Alternatively, the latter species may be just opportunistic invaders that are occupying empty niches left by native species that disappeared after transformation of the native or former vegetation (e.g., tropical forests) for agricultural uses. Tanck et al. (2000) also found abundant populations of exotic *A. corticis* and *A. gracilis* in long-term NT crops and an adjacent secondary forest, but no exotic earthworms in native grassland.

An exception to these rules in Brazil is *Pontoscolex corethrurus*, a species that has been present in southern Brazil for more than a century (Muller 1857). The origin of *P. corethrurus* is thought to lie further north in the Guyanan Shield area of Brazil (Righi 1984). *P. corethrurus* must be therefore considered an invader in most of Brazil, although it has not been treated as an exotic earthworm in that country and little has been done to reduce its spread to new areas (a phenomenon that has occurred regularly with deforestation and other land transformations). Such invasions of *P. corethrurus* have been associated with negative effects on soil structure (Barros et al. 2004; Chauvel et al. 1999) and perhaps native earthworm communities (Lavelle and Lapied 2003).

Dung from grazing vertebrates represents a resource for which various invertebrates can compete (e.g., dung beetles and fly larvae) (Waterhouse 1974). Earthworms can consume and bury large amounts of dung (Holter 1979; Martin and Charles 1979), thus potentially competing with other dung-dependent fauna. However, we are unaware of any studies that have experimentally explored this possibility in the context of invasive earthworms in agricultural systems. Similarly, negative interactions between invasive earthworms and microarthropods have been demonstrated in forests (e.g., McLean and Parkinson 1998, 2000; see McLean et al. and Migge-Kleian in this issue), and the excreta, burrows, and organic middens that anecic earthworms create at the surface openings of their burrows are known to influence the distribution and abundance of microarthropods and other earthworms (Maraun et al. 1999; Salmon and Ponge 1999; Salmon 2001, 2004; Tiunov 2003); but no similar influences on local fauna have, to our knowledge, been attributed to earthworm invasion of agricultural fields.

The importance of ecological linkages between above and below ground communities is gaining increased recognition (Wardle 2002). A few studies (Scheu et al. 1999; Wurst and Jones 2003; Newington et al. 2004) have recently implicated earthworms as influencing the abundance of above-ground herbivores and their natural enemies, as well as Collembola. The study of earthworms generally, and invasive species in particular, in the dynamics of agricultural pests (e.g., influences on weed seed distribution in the soil [Thompson et al. 1993], or insect pests) seems a particularly fruitful research topic to pursue.

Conclusions

Biological invasions usually invoke serious concerns with respect to negative impacts on the conservation of native biological communities. However, biological invasions also provide opportunities to understand the attributes of successful colonists and their impacts on ecosystem processes (Brown and Sax 2004). Earthworm invasions, especially within disturbed habitats, have thus far provided very fruitful opportunities to demonstrate the influences of these fauna on soil processes and plant production, but their impacts on other fauna have been poorly explored.

Many of the impacts of invasive earthworms on soil processes and plant production, when viewed in an agricultural or land reclamation context, can be viewed positively. But a thorny dilemma is struck when considering the ethics of deliberately redistributing exotic earthworms to achieve additional benefits further afield from where they initially colonise (see also Callaham et al., this issue). A value judgement must be made between the conservation of native fauna and ecosystem function in pristine lands adjacent to the disturbed lands (and thus at risk of invasion) and (re)establishment of ecosystem services that are sorely needed to offset soil degradation that previous management practices have created (Baker 2004). For example, Sharpley et al. (1979) have demonstrated the importance of exotic earthworms in influencing the quality (nutrient content) and quantity of water in runoff from New Zealand pastures. This runoff has the potential to pollute water catchments and represents loss of nutrient resources for farmers. Should these exotic species be further spread to pastures lacking them, and also lacking native earthworms due to habitat destruction, to capture similar benefits? In part, we are particularly hamstrung through our lack of knowledge of the ecology and behaviour of native earthworms in many parts of the world, especially their potential role in ecosystem processes and the management practices that need to be implemented to encourage such species back into disturbed lands.

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ORIGINAL PAPER

Policy and management responses to earthworm invasions in North America

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Abstract The introduction, establishment and spread of non-native earthworm species in North America have been ongoing for centuries. These introductions have occurred across the continent and in some ecosystems have resulted in considerable modifications to ecosystem processes and functions associated with above- and belowground foodwebs. However, many areas of North America have either never been colonized by introduced earthworms, or have soils that are still inhabited exclusively by native earthworm fauna. Although several modes of transport and subsequent proliferation of non-native earthworms have been identified, little effort has been made to interrupt the flow of new species into new areas. Examples of major avenues for introduction of earthworms are the fish-bait, horticulture, and vermicomposting industries. In this paper we examine land management practices that influence the establishment of introduced species in several ecosystem types, and identify situations where land management may be useful in limiting the spread of introduced earthworm species. Finally, we discuss methods to regulate the importation of earthworms and earthworm-containing media so that introduction of new exotic species can be minimized or avoided. Although our focus in this paper is necessarily North American, many of the management and policy options presented here could be applicable to the problem of earthworm invasions in other parts of the world.

Keywords Biological invasion · Quarantine · Biogeography · Earthworms · Lumbricidae · Megascolecidae · Glossoscolecidae · Introduced species · Exotics

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Patterns of earthworm invasion in North America

The present-day biogeographical distributions of earthworms in North America are the product of two dramatic events in relatively recent geologic time. The first of these events was the Wisconsinan Glaciation ending about 12,000 years BP, and the second was the rapid colonization of the continent by humans of European origin beginning about 400 years BP.

The principal effect of the Wisconsinan glaciation was to influence the distribution of the native North American earthworm fauna, with total extirpation of earthworms from soils directly affected by ice sheets and permafrost. Since the recession of the glacial ice sheets, climatic factors have been the primary drivers in the distribution of native earthworm fauna, with major refugia for native earthworms developing in wet and humid regions of the continent such as the Pacific northwest, the southeastern US, and parts of southern California and Mexico (Gates 1966; James 1990, 1995; Fender and McKey-Fender 1990; Fragoso et al. 1995). Recolonization of formerly glaciated soils by native species has been slow, and the southern boundary of the glacial ice sheets still provides an approximation of the northern extent of native earthworm distributions (Fig. 1).

More recent, but no less profound than the effects of glaciation, have been the effects of human colonization on the biogeographical distributions of earthworms in North America. The human mediated changes in earthworm biogeography are the focus of this paper. There have been three general manifestations of these effects. First, and perhaps the most important factor affecting current distributions of exotic earthworm species, is the historic transport of exotic earthworms via human activities associated with European settlement and the continued spread of introduced species by the use of earthworms as a commodity, as in the fish-bait and vermicomposting industries (Edwards and Bohlen 1996; Edwards and Arancon 2004). Second, international commerce involving horticultural materials has been identified as a source of propagules for new earthworm species (Gates 1982; Hendrix and Bohlen 2002). Finally, soil disturbances associated with agricultural development, logging or other perturbations appear to be associated with

Fig. 1 The southern extent of the Wisconsinan Glaciation (bold line), and approximate present day distributions of native earthworm species in North America (hatched area). Redrawn from Hendrix and Bohlen 2002

successful establishment of introduced earthworms in some areas (e.g. Kalisz and Dotson 1989; González et al. 1996; Zou and González 2001; Callaham et al. 2003) due to changes in soil physical and chemical properties, net primary productivity, and plant litter chemistry (Fig. 2). Taken together, these three factors provide criteria by which we can make informed predictions about the likelihood that a site will become inhabited by non-native species (i.e., distance from roads, agricultural fields, waters frequented by fishermen, or human habitations are good predictive variables). One important geographical distinction in the patterns of earthworm invasion and establishment involves the presence or absence of a native earthworm community (see Fig. 1). Whereas establishment of exotic earthworm species often appears to be less successful in soils where native earthworm populations and/or native vegetation is intact (Kalisz and Dotson 1989; Callaham et al. 2003; Zou and González 1997; Sanchez et al. 2003; Hendrix et al., this issue), it is clear that soils without a native earthworm fauna are susceptible to invasion and

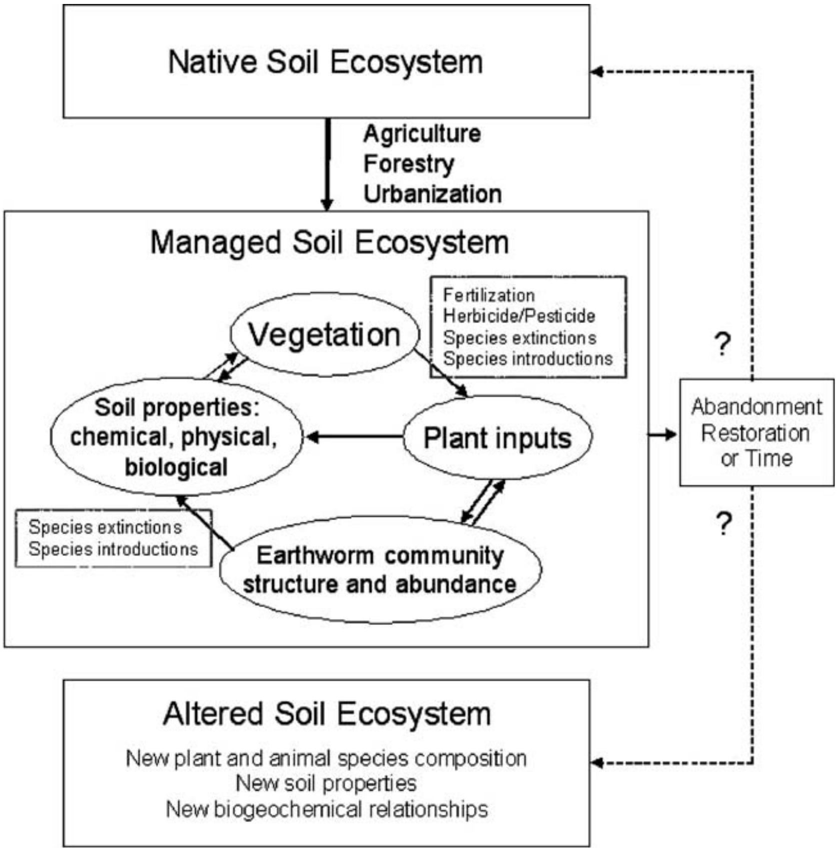


Fig. 2 Conceptual model depicting hypothesized linkages between land use, vegetation change, earthworm community change, and changes to soil properties (based on González et al. 1996). These interactions are seen to have two eventual outcomes in the event of land abandonment and restoration through natural succession or other means. The first is a return to the native state with a full complement of native species of plants and animals (in this case soil invertebrates, including earthworms), and the second is transition to an altered state consisting of a mixture of native species and exotic species with uncertain biogeochemical properties. Evidence suggests that introduced earthworms contribute to the movement of soil ecosystems toward altered states that are not likely to revert to the native condition. Indeed, introduced earthworms can be the primary drivers of such changes even in the absence of large disturbances, as has been observed in soils previously devoid of native earthworms (see text for examples)

introduced earthworms are able to establish even in pristine, undisturbed areas (Dymond et al. 1997; Bohlen et al. 2004; Hale et al. 2005; Frelich et al., this issue).

Ecological effects of introduced earthworms

The question of whether policy and procedures are needed to manage the introduction of new species of earthworms may be best answered by an analysis of the ecological and economic risks associated with such introductions. Earthworms are widely considered to be ‘‘good’’ for soil by the general public, and are usually suggested to be beneficial for soil fertility and other soil characteristics. Indeed, earthworms have frequently been purposely introduced to soils with the objective of soil improvement in agricultural settings (Baker 2004), and in soil reclamation projects (e.g., Butt et al. 1999; Curry and Boyle 1995; Baker et al., this issue). Nevertheless, in spite of the beneficial effects usually associated with earthworms, it has also long been proposed that earthworms are undesirable in certain situations. For example, Walton (1928) tested several chemical treatments for control of unwanted earthworms on golf courses where the castings of earthworms interfered with smooth play on the putting greens. Later, Stebbings (1962) suggested that interactions between native and introduced species could be leading to the competitive exclusion of native earthworm assemblages. However, only recently have there been thorough assessments of the effects that introduced earthworms can have on ecological properties and processes in natural systems (Fig. 2). The most dramatic of these effects was observed in areas that had previously been devoid of any earthworm fauna (i.e. areas north of Pleistocene glacial margins; Frelich et al., and Tiunov et al., this issue).

In the aspen and pine forests of Alberta, Canada, where the European earthworm *Dendrobaena octaedra* was accidentally introduced, the influence of this earthworm on the forest floor was dramatic in terms of microbial characteristics, changes in the community of other invertebrates, changes in nutrient cycling, and even effects on soil horizonation (Scheu and Parkinson 1994; McLean and Parkinson 2000a, b). Further, introduced European earthworms play an important role in litter decomposition in aspen forests in the Rocky Mountains of Colorado, USA (González et al. 2003). Similarly, in undisturbed sugar maple forest soils of New York, recent work has shown that introduced European earthworms of several species had effects on forest floor structure, distribution of microbial biomass, soil C storage, phosphorus cycling and fine root distributions (Bohlen et al. 2004; Groffman et al. 2004; Suárez et al. 2004; Fisk et al. 2004).

In the north temperate forests of Minnesota, invasions of European earthworms resulted in dramatic changes to soil structure; these changes were associated with declines in soil nutrient availability, as well as declines in diversity and abundance of tree seedlings and herbaceous plants (Hale et al. 2005). Also in Minnesota, one study linked the local extirpation of populations of a rare fern, *Bostrychium mormo*, with the presence of the introduced earthworms *Lumbricus rubellus* and *Dendrobaena octaedra* (Gundale 2002). In this study, the dramatic changes in forest floor structure associated with the mixing activity of the epigeic and epi-endogeic earthworms was implicated in the destruction of appropriate habitat for the fern.

The effects of earthworm introductions into ecosystems where a native earthworm assemblage is already present are less well known, but some work detailing differences between the ecological roles of native and introduced earthworms has been reported. In tropical forests of Puerto Rico, the introduced species *Pontoscolex corethrurus* increased rates of litter decomposition and CO_2 efflux from the forest floor relative to rates observed in the presence of native species alone (Liu and Zou 2002). Also in Puerto Rican soils, native and introduced earthworm species had differential effects on soil processes such as nitrogen mineralization and microbial respiration (González et al. 1999; Lachnicht et al. 2002). In the North American tallgrass prairies of Kansas, non-native earthworms were dormant during the summer growing season, whereas native species remained active, suggesting that the influences on soil processes of the different species are different depending on season, and may have important implications for nutrient cycling in the system (Callaham et al. 2001). Other examples of ecological impacts of introduced earthworms on native assemblages are discussed by Hendrix et al., this issue.

Control of earthworm invasions

Policy context

Increasingly, environmental policy has been developed in a context of formal risk analysis. Development of ‘‘rational policy’’ is possible when a problem is well defined, complete information regarding risk is available, a range of policy alternatives has been assessed, and the goals of the policy are agreed upon (Fiorino 1995). That is, in such circumstances, a theoretical benign autocrat could weigh the pros and cons of a given situation and create uncontroversial and effective policy. Situations where the ‘‘rational policy’’ model is applicable are rare.

In the case of developing strategies to mitigate problems associated with invasive earthworms, none of the aforementioned conditions for a simple rational policy approach are adequately met. First, the problem is multifaceted and eludes simple definition—that is, the problem can be stated as one concerning biodiversity decline, harm to critical ecological services, loss of aesthetic value (e.g., loss of native species), and impairment of recreational opportunity (e.g., earthworms damaging putting greens, or limiting the use of non-native earthworms for fishing bait). Secondly, although research on this topic has become more intensive in recent years, the conclusions are not definitive and the risks associated with earthworm invasion are not thoroughly understood or quantified for all species and all potentially impacted ecosystems. Thirdly, policy alternatives have yet to be fully developed and their efficacy is untested. Development of policy alternatives awaits the outcome of a number of different research programs which should evaluate the effectiveness of eradication, control, and management of invasions. Finally, the goals of policy formulation for invasive earthworms are not broadly agreed upon. Although there is a virtual consensus among ecologists on the risks associated with unchecked proliferation of invaders, public awareness of these problems is more limited (Colton and Alpert 1998) and this severely limits the political will to act. This problem is exacerbated when considering earthworms as potential pests since the general perception is that earthworms are ‘good’. Furthermore, policies limiting the sale or distribution of non-native earthworms (or earthworm-containing materials) have the potential to result in negative economic impacts for people involved in these trades, and as such, should be expected to meet with strong opposition. Crafting and implementing effective policy in this circumstance depends upon promoting a more balanced and scientifically informed view of the effects of non-native earthworms on ecosystems.

Cost-benefit analysis has been promoted as a useful economic tool to serve as the analytical basis for policy (Patton and Sawicki 1993). Conceptually, assessing both the negative and positive impacts associated with decisions is straightforward. However, cost-benefit evaluation is analytically complex. Commonly, the approach is based upon incremental costs, that is, the cost associated with moving to a new (usually more stringent) level of control. In the case of policy regarding earthworm invasions, there are currently no specific controls, so an assessment of marginal cost of going from no regulation to regulation is difficult to assess. Moreover, as is the case in most policy development associated with ecological risks, a subset of the objectives has a moral basis. That is, although there are clear economic benefits associated with conserving species threatened by invasive earthworms, not all of the motivation for limiting invasive earthworm damage is based upon utility. Conservation is also based upon a sense of responsible stewardship. Addressing policy alternatives to halt biodiversity decline may therefore not be a tractable problem for economic cost-benefit analysis to arbitrate (Roughgarden 1995). Nevertheless, a quantitative and explicitly monetary assessment of policy decisions regarding earthworm invasion may still prove to be useful. Additionally, when performing such an assessment, it is critical to consider that benefits of conservation accrue over the long term, whereas costs associated with regulation and management are both immediate and ongoing. Depending upon the discount rate used in evaluating cost and benefit accruals stemming from conservation policy, investing in conservation can seem unattractive to decision-makers (Krautkraemer 1995). Therefore, creative incentive schemes may be needed to make the benefits arising from seemingly esoteric policy (such as regulation and management for invasive earthworms) appear more attractive. Incentives are also crucial to make the benefits credible to those organizations and individuals who bear the costs of implementing the policy.

Control by stages of invasion

In developing effective approaches to minimizing the risks associated with invasions it is useful to recognize a variety of stages associated with the phenomenon of invasion. These include introduction, establishment, expansion, and saturation by an invader (Shigesada and Kawasaki 1997). Each of these stages will require a different policy approach to be most effective.

Arguably, the lowest cost associated with containing a major invasion is prevention, that is, regulation of materials deemed to harbor a potential invader. However, since not all introduced species will mount a large-scale invasion (Williamson 1996) it would clearly be onerous and prohibitively expensive to quarantine or restrict all such importations. Therefore, a mechanism for assessing risk associated with particular introductions has considerable value. Most of these predictive tools are qualitative and based upon expert assessment (Reichard and Hamilton 1997), though some are quantitative (Kolar and Lodge 2002). Below we recommend an assessment approach suitable for peregrine earthworms.

Approaches that attempt eradication or control at the stage of establishment can be potentially cost-effective. For instance, if one considers the probable costs associated with containing the gypsy moth in Medford, Massachusetts in the 1860s, relative to the current and ongoing costs of controlling this insect invader, the cost-benefits of early intervention seem obvious. Once again, however, knowing which introduced and naturalizing species to target for eradication is made problematic by our limited ability to predict which subset of introduced species will launch major ecosystem-modifying invasions (Williamson 1996). In the case of earthworms a systematic evaluation of which earthworm species may have the greatest impact, and which ecosystems are likely to be most impacted, will allow informed development of effective eradication and control strategies.

Finally, when an invader is expanding rapidly or has reached a saturation point in the invaded systems, eradication is usually not the most feasible alternative. In this case, control of the species through land management practices or other large-scale remediation of the damage caused by the species is most likely to be effective.

Below, we evaluate regulation and control strategies for earthworm invaders. This includes discussion on regulating the importation or movement of soils containing earthworm propagules and discussion on the role of the management of site disturbances in influencing the impact and spread of introduced earthworms.

Regulation of earthworm-containing materials

Regulation of other soil dwelling organisms

Regulation of soil-borne organisms has been standard practice in the USA and Canada for many years, in an attempt to limit introductions or to control spread of agricultural or other plant pests. Examples within the USA include the root knot nematode (*Meloidogyne* spp.), soybean cyst nematode (*Heterodera glycines*), and the imported fire ants (*Solenopsis invicta* and *Solenopsis richteri*). There is a full list of regulated organisms for Canada as well (see http://www.inspection.gc.ca/english/plaveg/protect/dir/d-00-04e.shtml). All of these organisms are subject to some form of quarantine when propagules of the organism are detected in materials flowing into an uninfected region. For example, in the case of fire ants in the southern USA, soil may be transported from areas that have been infested into areas not infested only when the destination is a laboratory that has been issued a special permit to receive such soils. In all other cases, soil or equipment originating from infested areas must be certified to be free of fire ants, farming implements or earthmoving equipment must be cleaned of all soil capable of transporting fire ant propagules (USDA 2004), and horticultural materials must be certified to be ant-free before shipment to non-infested regions can be made. Measures of this type could easily be adapted for use in the regulation or limitation of transport of earthworm propagules from place to place within North America.

Regulation of earthworms through policy

Given the long time-frame and wide geographical extent of earthworm introductions across North America and the globe, it may be tempting to subscribe to the opinion that it is too late for any regulatory action to have meaningful results. However, the most recent work to address this issue quantitatively (Gates 1982) indicates that the rate at which new species are introduced has increased with the increase in international trade in materials that may contain earthworms or earthworm cocoons. These observations were based on collections made at USDA agricultural inspection stations where materials from around the world were examined for presence or absence of earthworms. Furthermore, there still exist large areas of the North American continent that have yet to be invaded by exotic earthworms, and the potential ecological effects of invasion of these areas are not well known (Hendrix and Bohlen 2002).

For nations where no importation guidelines exist, regulatory actions for dealing with the potential introduction of new species of earthworms range from ‘‘do nothing at all’’ to ‘‘do everything possible’’. In practice, a resolution to ‘‘do something effective and efficient’’ is likely the most desirable outcome. Decisions about whether and how to regulate the introduction of earthworms must be based upon the best information available about the ecological characteristics of the earthworm species in question and the susceptibility of invasion for the ecosystem where the exotic earthworm will be introduced (Hendrix and Bohlen 2002). For example, there may be certain behavioral, physiological, or reproductive characteristics that cause certain earthworm species to be of particular concern in terms of ecological risk associated with introduction. Likewise, the locality into which species are introduced may have much to do with the success or failure of new species introductions. One example of the influence of habitat matching is the case of the African earthworm species *Eudrilus eugeniae* which is adapted to tropical lowlands. Although this species has been successfully cultured for sale in the fish-bait industry across the USA and Canada, there have been no published records of this earthworm existing anywhere in temperate North America outside the controlled environments found in gardens and culture beds (Gates 1970; Reynolds 1994a, b). However, this species has been reported from natural systems in the American tropics (Puerto Rico) where it may present serious ecological risks to native earthworm communities or ecosystem properties (Borges and Moreno 1994; G. González, personal observation). Thus, it is clear that regulation of material containing earthworms could be unnecessary and counterproductive in certain cases, but it is equally clear that each case should be examined carefully before the introduction of a new species is allowed; i.e., the possibility of widespread colonization should not be left to chance.

Here, we propose one potential decision-making tool with regard to handling of earthworm-containing media at inspection stations where the destination may be sensitive to the importation of new earthworm taxa (Fig. 3). Formalized decision-making processes such as the one proposed could be a helpful alternative to the *ad hoc* requests for guidance regarding earthworm importations sometimes sought by regulating agencies. This decision-making process allows for the quarantine of materials containing propagules of earthworms that have not been identified or widely introduced previously. These quarantines would provide time to determine the ecological risk posed by the introduction of a given earthworm species into particular systems. Suggested types of information needed to determine ecological risk associated with a quarantined earthworm species are listed in Table 1.

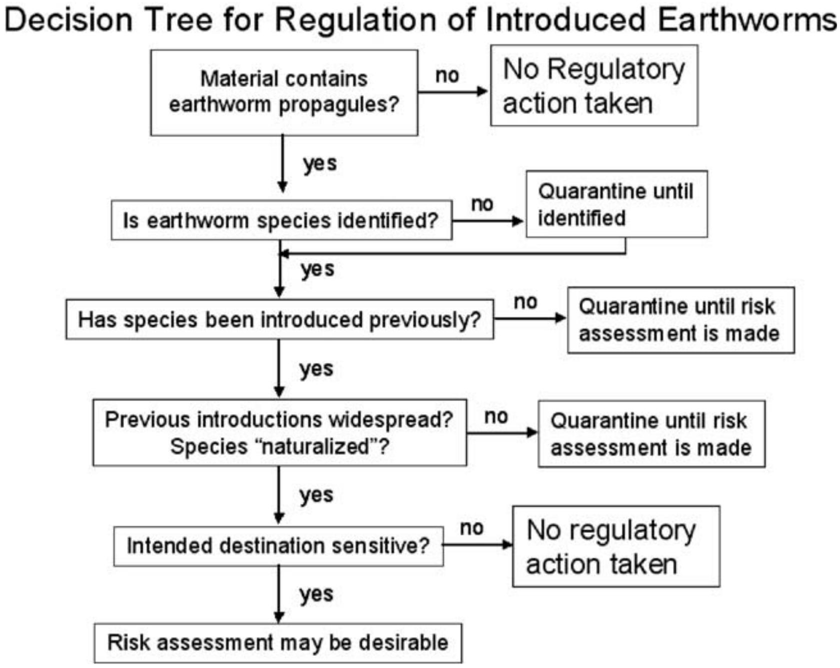


Fig. 3 A prototype decision tree for regulation of earthworms or earthworm-containing media. The initial box represents a source of earthworms or earthworm cocoons, with the ideal scenario being that potential sources (horticultural materials or other soil cargos) could be certified as ''worm-free'', resulting in no regulatory action

Whereas areas supporting both native vegetation and native earthworm communities may possess a certain level of resistance to exotic earthworm invasions (Hendrix et al., this issue), areas without a native earthworm fauna may be particularly susceptible to invasions whether the native vegetation is intact or not (Hale et al. 2005; Frelich et al., this issue). In these areas, the impact of human activity is related to the probability that such activities may transport invasive earthworm species. Given these general observations, when decisions are made about importation of earthworm-containing materials special attention should be directed toward areas where no earthworms (native or exotic) are currently present, where human activities with a high

Table 1 Suggested biological and ecological data to collect for complete risk assessment of new earthworm species potentially entering a new geographic area

Characteristic	Reason for test	Preferable result
Mode of reproduction	Determine if parthenogenic or amphimictic	Amphimictic
Number of embryos per cocoon	Numerous embryos per cocoon increases propagule pressure	One or few embryos per cocoon
Ecological ''strategy''	Determines type of food resource and soil stratum likely to be exploited by species	Depends on locality where introduced. If food resource or habitat of species is scarce, invasion less likely a problem
Temperature/moisture/pH tolerances	Determines habitats and ecosystems where invasion could occur.	Narrow tolerances limit areas where invasion could occur. Mismatch of temperature and moisture requirements to these conditions is desirable

probability of transporting earthworms occur, or where human disturbances have been limited (and native earthworms are present).

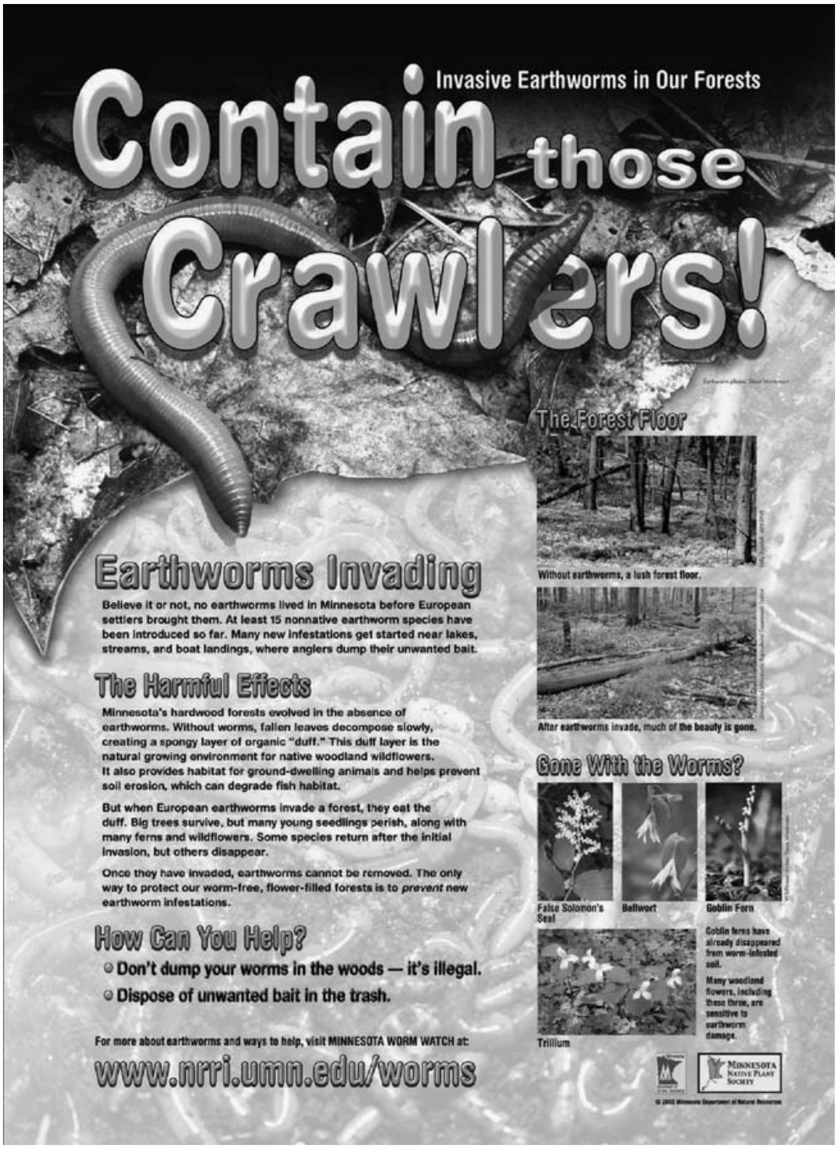
Influence of management practices on introduced earthworms

Once introduced, the success or failure of exotic earthworms to establish large populations appears to be influenced at least in part by the past management of the site. In areas where native earthworm populations are present this effect is generally related to the degree of disturbance the site has experienced: the less disturbed the site, the lower the likelihood of exotic earthworm establishment. This type of disturbance relationship has been documented in forested systems of temperate and tropical North America. Kalisz and Dotson (1989) and Dotson and Kalisz (1989) found differences in the frequency of exotic earthworms in soils of Kentucky to be dependent upon the continuity of forest vegetation and proximity to roads or other severe anthropogenic disturbance. In these studies the principal finding was that the fragmented forestlands of the Bluegrass physiographic region were largely dominated by exotic earthworm species, whereas the extensive non-fragmented forests of the Cumberland Plateau were dominated by native species except where severe disturbances had occurred. In tropical systems of Puerto Rico, Zou and González (1997) and González et al. (1999) found that conversion of native forest to pasture systems resulted in dramatic differences in the earthworm assemblages with nearly total dominance of the pasture systems by the pan-tropical exotic species *Pontoscolex corethrurus*. Although *P. corethrurus* was also present in forested systems, the earthworm species native to Puerto Rico were still dominant in the forest earthworm assemblages. However, the regeneration of secondary forest through natural succession in abandoned pastures was shown to promote the recovery of native earthworms, and the reduction of *P. corethrurus* density (Sanchez et al. 2003).

In another system where introduced earthworms coexist with native earthworms, the tallgrass prairie ecosystems of North America, disturbance is an important determinant of the earthworm community composition. The tallgrass prairie system is one that has been subject to chronic disturbance since its beginnings, and indeed the system appears to rely on disturbances such as grazing, fire, and drought to maintain its characteristic vegetation (Knapp and Seastedt 1986). In this case, disturbances vital to the maintenance of tallgrass vegetation were also associated with maintenance of native earthworm communities (James 1988). Further work in this system showed that relatively short-term departures from the natural disturbance regime (i.e., the absence of regular fire) resulted in a shift in dominance of the earthworm community to introduced species (Callaham and Blair 1999; Callaham et al. 2003).

Land management may be influential even in systems where no native earthworm species are present. Heneghan (2003) documented a synergistic relationship between an invasive shrub, and non-native earthworms in oak woodlands of the upper Midwest of the USA. Invasion of buckthorn shrub into oak woodlands in the Chicago area had strong effects on several ecosystem properties, including negative effects on understory vegetation (Heneghan et al. 2002). If the shrub was removed from an area soon after invasion, then these negative effects on native vegetation were short-lived. However, the presence of buckthorn was also associated with high biomass of invasive European earthworms and the additional effects of these earthworms on soil processes and soil structure caused negative effects on the understory plant community to persist for longer periods of time (Heneghan 2003). Thus, early control measures to limit the encroachment of the invasive shrub in these systems may also indirectly limit the size of non-native earthworm populations, and benefit restoration efforts in impacted areas.

Where non-native earthworms are not well established or are found in discrete populations, the use of chemical treatments to eradicate undesirable worms may be a successful strategy. This approach has long been used in the management of golf courses (e.g., Walton 1928; Schread 1952), and has also been successfully used in experimental manipulations of earthworm



Invasive Earthworms in Our Forests

Contain those Crawlers!

Earthworms Invading

Believe it or not, no earthworms lived in Minnesota before European settlers brought them. At least 15 nonnative earthworm species have been introduced so far. Many new infestations get started near lakes, streams, and boat landings, where anglers dump their unwanted bait.

The Harmful Effects

Minnesota's hardwood forests evolved in the absence of earthworms. Without worms, fallen leaves decompose slowly, creating a spongy layer of organic "duff." This duff layer is the natural growing environment for native woodland wildflowers. It also provides habitat for ground-dwelling animals and helps prevent soil erosion, which can degrade fish habitat.

But when European earthworms invade a forest, they eat the duff. Big trees survive, but many young seedlings perish, along with many ferns and wildflowers. Some species return after the initial invasion, but others disappear.

Once they have invaded, earthworms cannot be removed. The only way to protect our worm-free, flower-filled forests is to *prevent* new earthworm infestations.

How Can You Help?

- Don't dump your worms in the woods — it's illegal.
- Dispose of unwanted bait in the trash.

For more about earthworms and ways to help, visit MINNESOTA WORM WATCH at:

www.nrri.umn.edu/worms

The Forest Floor

Without earthworms, a lush forest floor.

After earthworms invade, much of the beauty is gone.

Gone With the Worms?

False Solomon's Seal

Bellwort

Goblin Fern

Goblin ferns have already disappeared from worm-infested soil.

Many woodland flowers, including these three, are sensitive to earthworm damage.

Trillium

Minnesota Native Plant Society

© 2003 Minnesota Department of Natural Resources

Fig. 4 Reproduction of a poster placed in bait shops and other public locations in Minnesota directed at educating consumers about the problem of earthworm introductions. Reproduced courtesy of Minnesota Department of Natural Resources

communities (e.g., Parmelee et al. 1990). Although these treatments are known to be highly effective for earthworm control, it is clear that non-target effects of chemicals on the system should be carefully examined before large-scale use of such chemicals is recommended.

Given the diffuse nature of the spread of earthworms via a range of seemingly benign human activities (such as recreational fishing or planting of ornamental vegetation), public educational efforts will be a critical component of any comprehensive effort to control the spread of exotic earthworms. One example of this type of effort is the Minnesota Worm Watch Program initiated by scientists at the University of Minnesota. In a cooperative effort between the Minnesota Department of Natural Resources, Minnesota Worm Watch, and the Minnesota Native Plant Society, the program focuses on halting the spread of non-native earthworms into remote areas of Minnesota by educating the public about the ecological consequences of introducing earthworms. A variety of educational materials regarding earthworms is available on the internet (http://www.nrri.umn.edu/worms/default.htm). A poster and exotic earthworm fact sheet were distributed to more than 1500 bait shops, as well as hundreds of nature centers, park visitor centers, and other venues across the state (Fig. 4). Public response to these efforts has been generally favorable, and the basic message to avoid dumping unused bait in remote areas has been well received.

Conclusions

Although earthworm introductions have a long history in North America, there are still many areas on the continent where no exotic species occur. Efforts to prevent the introduction of exotic earthworms into these areas are most likely to be successful through some combination of regulatory policy, public education, and implementation of appropriate land management practices. We have suggested a decision-making strategy for regulation of earthworm-containing materials flowing into North America as well as movement of such materials from place to place within North America, but the data needed to efficiently implement this strategy are scarce. More research into the characteristics of earthworm species likely to become successful invaders of North American ecosystems is needed. Likewise, more research on land management effects on earthworm communities should result in better strategies for containment of non-native species and conservation of native species.

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