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ORIGINAL PAPER

Invasion of exotic earthworms into ecosystems inhabited by native earthworms

P. F. Hendrix · G. H. Baker · M. A. Callaham Jr · G. A. Damoff · C. Fragoso · G. González · S. W. James · S. L. Lachnicht · T. Winsome · X. Zou

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

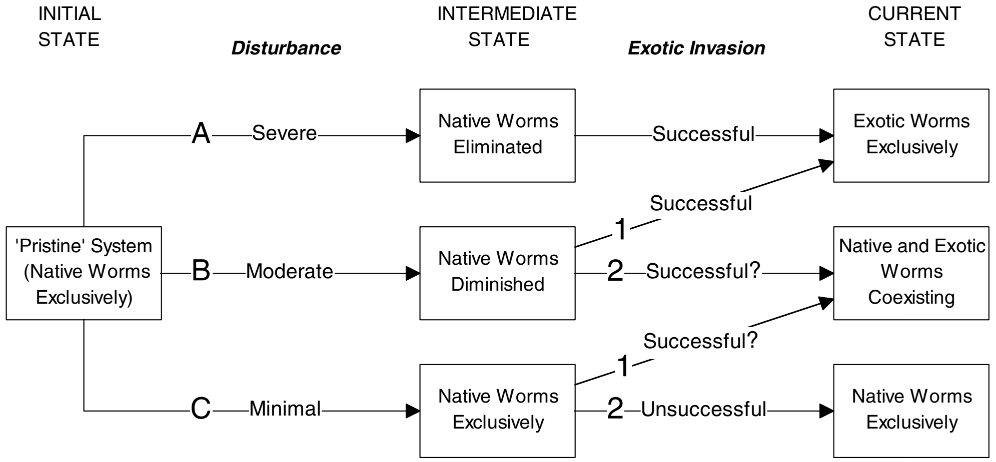

Fig. 1 Hypothesized sequences of invasion depending on degree of habitat disturbance and invasion success by exotic earthworms invading ecosystems inhabited by native earthworms. See text for description of pathways

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 forest cloud forest	Minimal	++	+		
		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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