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Exotic Earthworm Invasions in North America: Ecological and Policy Implications

PAUL F. HENDRIX AND PATRICK J. BOHLEN

Earthworms are the best known and, in many situations, the most important animals that live in soil. Over 3500 earthworm species have been described worldwide, and it is estimated that further surveys will reveal this number to be much larger (Reynolds 1994, Fragoso et al. 1999). Distinct taxonomic groups of earthworms have arisen on every continent except Antarctica, and, through human transport, some groups have been distributed worldwide (Jamieson 1988, Reynolds 1994). The earthworm fauna of North America, including Canada, the continental United States, Mexico, and the islands of the Caribbean, consists of both native (Nearctic and Neotropical) and exotic species imported from many other regions of the world (Fender 1995, Fragoso et al. 1995, James 1995, Reynolds 1995). Any given locality may be inhabited by all native species, all exotic species, a combination of native and exotic species, or by no earthworms at all. Relative abundance and species composition of local fauna depend greatly on soil, climate, vegetation, topography, land use history, and especially on past invasions by exotic species.

Much of our knowledge of the earthworm fauna of North America is based on the work of Gordon E. Gates who, over a 60-year career, collected, described, and cataloged many of the currently recognized taxa, both native and exotic. Beginning in 1949, Gates collaborated with the US Department of Agriculture (USDA), Bureau of Plant Quarantine (now Animal and Plant Health Inspection Service, or APHIS) to intercept oligochaetes found in "plant-associated materials" (mostly soil) being imported into the United States. Over a 32-year period (1950–1982), Gates (1976, 1982) acquired thousands of specimens and was able to determine that earthworms from all over the world were continually being imported. There is no reason to expect that this situation has changed since 1982. Indeed, as with exotic plants, fungi, and insects (Ruesink et al. 1995, Campbell 2001, Mack and Lonsdale 2001), growing global commerce may be increasing the likelihood that exotic earthworms will be introduced, both inadvertently with the importation of soil-containing materials (e.g., agricultural and horticultural products; Gates 1976, 1982, Boag and Yeates 2001, Ehrenfeld and Scott 2001) and intentionally for use in commercial applications (e.g., waste management and land bioremediation; Lee 1995, Edwards 1998). Because previous invasions by exotic earthworms have had significant impacts on soil processes and plant communities in native ecosystems (e.g., Alban and Berry 1994, Groffman and Bohlen 1999, Hale et al. 2000), there may be reason for concern over continued unrestricted importation of earthworms.

EXPANDING GLOBAL COMMERCE MAY BE INCREASING THE LIKELIHOOD OF EXOTIC EARTHWORM INVASIONS, WHICH COULD HAVE NEGATIVE IMPLICATIONS FOR SOIL PROCESSES, OTHER ANIMAL AND PLANT SPECIES, AND IMPORTATION OF CERTAIN PATHOGENS

Regulatory activities have not been effective in reducing earthworm introductions in most areas of the world (Boag and Yeates 2001), probably because legal restrictions traditionally have not targeted earthworms or their propagules. There presently are no specific regulations concerning earth-

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worm imports into the United States. Earthworm importations are regulated by APHIS under the Federal Plant Pest Act because of the potential for introduction of exotic plant pathogens in their guts and in soil that might accompany them (Tracy A. Horner, USDA APHIS, personal communication, 3 January 2002). The recent outbreak of foot-and-mouth disease in Europe has heightened concern about earthworm imports, because some species may be vectors for that viral pathogen and others (Edwards and Bohlen 1996, Jamieson 2000). APHIS is now considering guidelines specifically for the importation of earthworms into the United States. In this article, which is derived from a report prepared recently for APHIS, we review the status of earthworms in North America, address problems associated with exotic earthworm invasions, and discuss criteria for assessing potential risks of earthworm importation.

Native earthworms in North America

Earthworms are classified within the phylum Annelida, class Clitellata, subclass Oligochaeta, order Opisthophora. According to Jamieson (1988), there are 16 families worldwide (table 1). Six of these families (cohort Aquamegadrili plus suborder Alluroidina) comprise aquatic or semiaquatic worms, whereas the other 10 (cohort Terrimegadrili) consist of the terrestrial forms commonly known as earthworms. Two families (Lutodrilidae and Komarekionidae, both monospecific) and genera from three or four others (Sparganophilidae, Lumbricidae, Megascolecidae, and possibly Ocnerodrilidae) are Nearctic (Jamieson 1988, James 1995). No native earthworms have been reported from Canada east of the Pacific Northwest or from Alaska or Hawaii, although exotic species now occur in all of these regions. Native earthworms in the families Ocnerodrilidae, Glossoscolecidae, and Megascolecidae occur in Mexico and the Caribbean islands. Fragoso and colleagues (1995, 1999) discuss native and exotic earthworms in the south Nearctic and north Neotropical regions. In this article, we focus on the Nearctic region north of Mexico.

Table 1. Major families of Oligochaeta (order Opisthophora) and their regions of origin.

Family	Region of origin
Limicolous or aquatic	
Alluroididae	AF, SA
Syngenodrilidae	AF
Sparganophilidae	NA, EU
Biwadrilidae	JA
Almidae	EU, AF, SA, AS
Lutodrilidae	NA
Terrestrial	
Ocnerodrilidae	SA, CA, AF, AS, MA
Eudrilidae	AF
Kynotidae	MA
Komarekionidae	NA
Ailoscolecidae	EU
Microchaetidae	AF
Hormogastridae	ME
Glossoscolecidae	SA, CA
Lumbricidae	NA, EU
Megascolecidae	NA, CA, SA, OC, AS, AF, MA

Note: AF = Africa, AS = Asia, CA = Central America, EU = Europe, JA = Japan, MA = Madagascar, ME = Mediteranean, NA = North America, OC = Oceania, SA = South America
Source: Summarized from Gates (1982) and Jamieson (1988).

Pleistocene glaciations are thought to have eliminated the earthworm fauna from most of Canada and the northern portion of the continental United States (Gates 1970). The southern limits of defaunation at the peak of the Wisconsinan glaciation may have extended to the edge of permafrost, a significant distance beyond the ice terminus (Gates 1970, Pielou 1991). Glacial refugia apparently remained along the Pacific Coast, where a number of native genera in the families Megascolecidae and Sparganophilidae now occur (Fender and McKey-Fender 1990, Fender 1995), and in the eastern United States, where all of the other Nearctic groups occur (figure 1; Gates 1982, James 1995). Colonization of previously glaciated areas was apparently slow, and few native earthworms inhabited northern regions of North America at the time of European settlement (Gates 1967).

Approximately 70 species of native earthworms have been described from the eastern United States and another 28 species from the Pacific region (table 2). An isolated group of megascolecids has recently been described in southern California, possibly as a relict of previously more widespread groups (Wood et al. 1997). With further surveys, more species will very likely be described in all of these regions (James 1995). North America thus has a rich and diverse indigenous earthworm fauna, which probably reaches its highest species diversity and exerts its greatest influence on soil processes in forest and grassland ecosystems (Fender 1995, Fragoso et al. 1995, James 1995, Kalisz and Wood 1995, Hendrix 1996). Remnants of native ecosystems in unglaciated areas have shown the most pristine communities of native earthworms, but the relative importance of these species in disturbed and intensively managed ecosystems has received little study. Habitat alteration and introduction of exotic earthworms may have reduced the abundance and ecological importance of native species.

Exotic earthworms in North America

In addition to the 100 or more native earthworm species in North America north of Mexico, at least 45 exotic species have been introduced (Gates 1976, 1982, Reynolds 1995). Exotics include European Lumbricidae (25 species); African (2 species), Asian (14 species of the "pheretimoid" group), and South American (2 species) Megascolecidae; African Eudrilidae (1 species); and South American Glossoscolecidae (at least 1 species) and Ocnerodrilidae (2 species). It is possible that other species, including some from other families, have been introduced but not yet reported in the literature.

As with insect introductions into North America (Simberloff 1989), the preponderance of European species of earthworms is probably due to habitat similarities in these generally temperate regions and to historically high levels of commerce between them. European Lumbricidae are the most common exotic earthworms north of the glacial margins, and several species have become notorious for their effects on forest floors in northern forests formerly devoid of earthworms (Alban and Berry 1994, Scheu and Parkinson 1994, McLean and Parkinson 1997, Hale et al. 2000). The Asian megascolecid (*Amynthas* sp.) also is invading forests in the northeastern United States (Steinberg et al. 1997, Burtelow et al. 1998, Groffman and Bohlen 1999). Most of the nonlumbricid exotic species in North America occur in the southeastern and Pacific regions of the United States. In general, exotic earthworm distributions are patchy across the continent and appear to overlap with distributions of native species. There is debate as to whether exotic earthworms displace native earthworms in undisturbed habitats (Kalisz and Wood 1995).

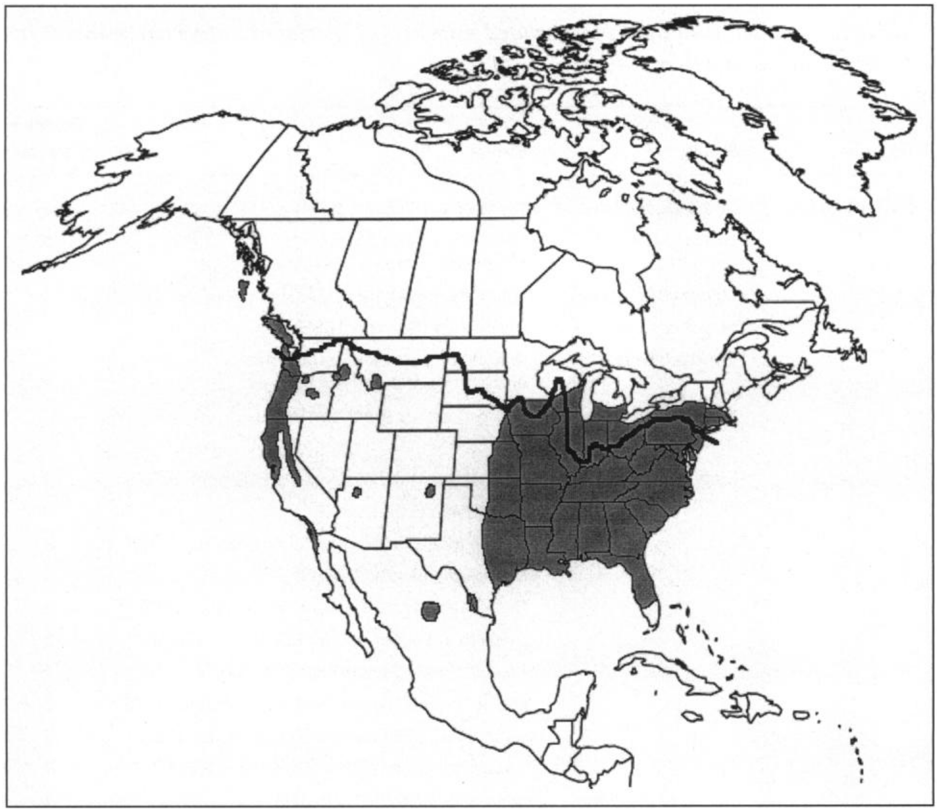

Figure 1. Approximate distributions of Nearctic earthworms in eastern and Pacific regions of North America in relation to Wisconsinan glacial margins (heavy line). Shaded areas represent combined ranges of approximately 100 species, some tentative and some with very limited distribution. See Fender (1995), Fragoso and colleagues (1995), James (1995), and Reynolds (1995) for detailed distribution maps.

Ecological considerations

Earthworms occur in a wide range of habitats where soil water and temperature are favorable for at least part of the year; across this range, they display a variety of adaptations to environmental conditions. Even in unsuitable regions, earthworms may inhabit local microsites where conditions are favorable (e.g., urban gardens, desert oases), especially if well-adapted species have been introduced. Within habitats, earthworms often show clumped spatial distributions that correspond to such factors as vegetation, soil texture, or soil organic matter content. Feeding behavior, in particular, dictates horizontal and vertical distributions of earthworm species within a soil volume and determines their effects on soil processes.

Ecological "strategies" of earthworms. Several earthworm species (typically a half-dozen or less) may coexist at a given location by partitioning available resources in the soil. Different feeding strategies result from a variety of behavioral, morphological, or physiological adaptations (Lee 1985, Barois et al. 1999): Epigeic, epi-endogeic and epi-anecic species inhabit and feed on litter and organically enriched surface layers of soil; poly-, meso-, and oligohumic and endo-anecic endogeic species inhabit mineral soil within the rhizosphere and beyond; and anecic species feed on surface litter but reside in burrows in the mineral soil (table 3). Furthermore, these feeding activities influence how different earthworm species affect soil processes. For example, epigeic species facilitate the breakdown and mineralization of surface litter, while anecic species incorporate surface litter deeper into the soil profile and enhance aeration and water infiltration through their deep vertical burrows (Lee 1985, Edwards and Bohlen 1996). Understanding the ecological role of invasive species is key to predicting their potential effects on soil processes and on other organisms.

Beneficial effects of earthworms. Concern over potentially harmful effects of exotic earthworms runs counter to the general view of earthworms being beneficial to soils. Darwin (1881) was the first to show that earthworms significantly influence soil processes important to the functioning of terrestrial ecosystems. Subsequent research, mainly in agricultural and pastoral systems, has shown that earthworms often have favorable effects on soils, particularly in systems under conservation management (e.g., no tillage). Earth-

Table 2. Families, genera, and estimated numbers of species of native earthworms in North America, north of Mexico.

Region	Family	Genus	Number of species
Eastern region	Komarekionidae	*Komarekiona* (Gates 1974)	1
	Lumbricidae	*Bimastos* (Moore 1893)	10
		Eisenoides (Gates 1969)	2
	Lutodrilidae	*Lutodrilus* (McMahan 1976)	1
	Megascolecidae	*Diplocardia* (Garmon 1888)	42
	Ocnerodrilidae	Unidentified species in California and North Carolina	?
	Sparganophilidae	*Sparganophilus* (Benham 1892)	11
Pacific region	Megascolecidae	*Arctiostrotus* (McKey-Fender and Fender 1982)	2
		Argilophilus (Eisen 1893)	9
		Chetcodrilus (Fender and McKey-Fender 1990)	3
		Diplocardia (Garmon 1888)	4
		Drilochaera (Fender and McKey-Fender 1990)	1
		Driloleirus (Fender and McKey-Fender 1990)	6
		Kincaidodrilus (McKey-Fender 1982)	1
		Macnabodrilus (Fender and McKey-Fender 1990)	2
		Nephrallaxis (Fender and McKey-Fender 1990)	2
		Toutellus (Fender and McKey-Fender 1990)	4
	Sparganophilidae	*Sparganophilus* (Benham 1892)	1

Source: Summarized from Gates (1982), Fender (1995), Fragoso et al. (1995), and James (1995). See Reynolds and Cook (1993) for taxonomic source information.

worm activity has been reported to speed rates of plant litter decomposition, increase nutrient transformation and plant nutrient uptake, improve soil aggregation and porosity, and enhance water infiltration and solute transport (Satchell 1983, Lee 1985, Hendrix 1995, Edwards and Bohlen 1996, Edwards 1998, Lavelle et al. 1999). Where earthworms are abundant, direct fluxes of nutrients through their biomass can be considerable; for example, up to 150 kilograms of nitrogen per hectare per year have been reported to turn over in earthworm tissues (Lee 1985). Studies in managed grassland have shown that earthworm activity results in an increase in forage quantity and quality in reclaimed polders in the Netherlands (Hoogerkamp et al. 1983) and in subtropical pastures in Australia (Blakemore 1997). Beneficial effects of earthworms on plant growth may come about through increased nutrient and water availability, stimulation of microorganisms that enhance plant growth, or possibly through direct production of substances that promote plant growth (Edwards and Bohlen 1996, Lavelle et al. 1999).

Earthworms and their activities have been put to a number of uses, including processing of organic wastes through vermicomposting, which has become a sizable industry in North America (Edwards 1998, Lavelle et al. 1999); restoration of degraded soils, using earthworms as agents of bioremediation (Satchell 1983, Lee 1995, Edwards and Bohlen 1996); and culturing or harvesting of earthworms for fishing bait, which has reached a large economic scale in the United States and Canada (Edwards and Bohlen 1996). These enterprises are responsible for much of the commercial distribution of earthworms and mostly involve a few exotic, anthropochorus species (i.e., those adapted to and often introduced into human-managed ecosystems) in the families Lumbricidae, Glossoscolecidae, and Eudrilidae. Many of these species are now established in North America, either

Table 3. Ecological categories, habitat, feeding, and morphological characteristics of earthworms.

Category	Subcategory	Habitat	Food	Size and pigmentation
Epigeic	Epigeic	Litter	Leaf litter, microbes	< 10 cm, highly pigmented
	Epi-anecic/ Epi-endogeic	Surface soil	Leaf litter, microbes	10–15 cm, partially pigmented
Anecic	Anecic	Burrows	Litter and soil	> 15 cm, anterodorsal pigmentation
Endogeic	Polyhumic	Surface soil or rhizosphere	Soil with high organic content	< 15 cm, filiform, unpigmented
	Mesohumic	Upper 0–20 cm of soil	Soil from 0–10 cm strata	10–20 cm, unpigmented
	Endo-anecic	0–50 cm of soil, some make burrows	Soil from 0–10 cm strata	> 20 cm, unpigmented
	Oligohumic	15–80 cm of soil	Soil from 20–40 cm strata	> 20 cm, unpigmented

Source: Modified from Barois et al. (1999).

in contained vermiculture or as naturalized populations in the wild. These commercial interests also appear to be the major source of demand for importation of exotic earthworm species (Tracy A. Horner, USDA APHIS, personal communication, 3 January 2002).

Detrimental effects of earthworms. Despite the many documented and putative beneficial effects of earthworms on soil structure, nutrient dynamics, and plant growth, some aspects of earthworm activities are considered undesirable (Edwards and Bohlen 1996, Lavelle et al. 1998, Parmelee et al. 1998). Detrimental activities include removing and burying of surface residues, which would otherwise protect soil surfaces from erosion; producing fresh casts that increase erosion and surface sealing; increasing compaction of surface soils; depositing castings on the surface of lawns and golf greens, where they are a nuisance; dispersing weed seeds in gardens and agricultural fields; transmitting plant or animal pathogens; riddling irrigation ditches, making them less able to carry water; increasing losses of soil nitrogen through leaching and denitrification; and increasing loss of soil carbon through enhanced microbial respiration.

It is the net result of positive and negative effects of earthworms that determines whether they have detrimental impacts on ecosystems (Lavelle et al. 1998). Obviously, an effect such as mixing of organic and mineral soil horizons may be considered beneficial in one setting (e.g., urban gardens) and detrimental in another (e.g., native forests). The undesirable impacts of exotic species are central to assessing the risks associated with their introduction and spread.

Impacts of exotic earthworms

The major concerns about exotic earthworms have been the potential for certain species to invade new habitats and, once established, the effects they may have on other organisms and soil processes within those habitats (Alban and Berry 1994, Dalby et al. 1998, Hale et al. 2000).

Exotic earthworm invasions. As observed for many other exotic species (e.g., Simberloff 1989, Williamson 1996, Mack and Lonsdale 2001), the principal mechanism for the introduction of exotic earthworms into new areas has been through human migration and commerce over the past several centuries (Gates 1967, Lee 1985). Historically, introductions were probably unintentional—for example, earthworms may have been in soil dumped from ship's ballast or in imported plant roots—but more recently, earthworms have also been imported and distributed intentionally. Once imported, there is a potential for exotic earthworms to become established and invade wherever they are released or allowed to escape into the environment. Whether or not they become pests depends on circumstances, such as the type of ecosystem they invade and their effects on soil processes or other species.

In North America, the most dramatic effects of exotic earthworm invasions on soil processes have been in areas previously devoid of earthworms (e.g., north of Pleistocene glacial margins). Gates (1967) reviewed two early accounts of exotic earthworm effects on soil properties. In one case, introduced *Lumbricus terrestris* reportedly obliterated soil horizonation to a depth of approximately 1 meter over a six-county area (> 3000 km^2) in South Dakota; in another, the upper soil horizons in a cut-over forest site in New Brunswick, Canada, were mixed by introduced *Aporrectodea tuberculata* and *L. terrestris* during a 4-year period. More recently, significant effects of exotic earthworms on soil profiles, on nutrient and organic matter dynamics, on other soil organisms, or on plant communities have been reported in chaparral in southern California (Graham and Wood 1991); tallgrass prairie in Kansas (James 1991, Callaham et al. 2001); temperate forests in Minnesota (Alban and Berry 1994, Hale et al. 2000), New York (Steinberg et al. 1997, Burtelow et al. 1998, Groffman and Bohlen 1999), New Jersey (Kourtev et al. 1999), and Alberta, Canada (Scheu and Parkinson 1994, McLean and Parkinson 1997). Significant effects of exotic earthworms in terrestrial ecosystems have also been reported in other parts of the world (Stockdill 1982, Hoogerkamp et al. 1983, Lee 1985, Zou 1993, Edwards and Bohlen 1996, Edwards 1998, Lavelle et al. 1999).

In most of these ecosystems, exotic earthworms apparently were introduced inadvertently at some time in the past and effects observed over a period of years to decades. In Minnesota, several species of European lumbricids formed successive "wave fronts" across the forest floor, led by *Dendrobaena octaedra,* followed by *Lumbricus rubellus, Aporrectodea* spp., and lastly by *L. terrestris.* These species apparently dispersed into the forests from nearby lakeshores where, over several decades, they were released as fishing bait (Hale et al. 2000). Similar effects on soil processes have been reported for a mixed assemblage of European lumbricids in association with exotic plant species introduced into parklands in New Jersey (Kourtev et al. 1999). Both of these situations, in which one exotic species facilitates invasion by another, are examples of "invasional meltdown," described by Simberloff and von Holle (1999).

Competitive exclusion or ecosystem disturbance. Since the time of early observations, there has been debate over mechanisms by which exotic earthworms become dominant in certain ecosystems (Eisen 1900, Stebbings 1962). In many of the cases cited above, exotic species invaded ecosystems previously devoid of earthworms. In areas inhabited by native earthworms, exotic invasions often are preceded by disturbance of soils or vegetation (e.g., Kalisz and Dotson 1989, Fragoso et al. 1995, 1999, Callaham and Blair 1999). Although competitive exclusion of native earthworms by exotic ones has been postulated, little direct evidence of this can be found. Kalisz and Wood (1995) suggested four stages in the establishment of exotic earthworm populations in soils inhabited by native species: (1) habitat disturbance, (2) extirpation or reduction of native populations, (3) introduction of exotic species, and (4) colonization of vacant niche space by exotic species. Even in the absence of obvious habitat disturbance, some minimum habitat patch size may be required to maintain native earthworm assemblages; increased edges and potential vectors for invasion by exotic species into small ecosystem remnants may lead to displacement of native populations (Kalisz and Wood 1995). Thus, as with other exotic species (Williamson 1996), the principal mechanism for displacement of native earthworm populations is assumed to be habitat alteration rather than direct competition, although the relative contributions of these two factors remain to be clarified.

Interestingly, the most dramatic effects of exotic earthworms on soil processes have not been reported from areas inhabited by native earthworms, particularly where soils and vegetation are undisturbed. In some cases where invasions have occurred, native species have remained dominant over exotic species (Fragoso et al. 1995, 1999, Callaham and Blair 1999, Bhadauria et al. 2000). In deciduous forests in Kentucky, only native earthworms occur in undisturbed or slightly disturbed sites, whereas exotic species occur only in severely disturbed sites (Kalisz and Dotson 1989). Microcosm studies indicate that the European lumbricid *Aporrectodea longa* cannot successfully invade forest soils inhabited by native megascolecid earthworms in South Australia (Dalby et al. 1998). Studies of an invasion of European lumbricids into a tallgrass prairie in Kansas suggest competitive displacement of native *Diplocardia* spp. by exotic *Aporrectodea* spp. in disturbed areas but continued dominance of the native species under natural conditions. It has been suggested that native earthworms are better adapted than invading European lumbricids to local soil and climatic conditions and hence maintain longer periods of activity and effects on nutrient dynamics in prairie soils (James 1991, Callaham and Blair 1999, Callaham et al. 2001). These observations suggest that certain endemic earthworm fauna or characteristics of their native habitats or both may be resistant to invasion by some exotic earthworm species and, consequently, may reduce the impact of exotic species on soil processes. The possibility of biotic resistance (Simberloff 1989, Williamson 1996) in the context of earthworm invasions deserves further research.

Exotic earthworms as disease vectors. There have been reports of earthworms transmitting pathogens, either as passive carriers or as intermediate hosts (Lee 1985, Edwards and Bohlen 1996, Jamieson 2000), which raises the concern that exotic earthworm introduction could be a mechanism for the introduction of pathogens into new areas. The potentially most serious case, given the recent outbreak of foot-and-mouth disease in Europe, is a report of *L. terrestris* carrying a virulent strain of that disease virus (reviewed by Edwards and Bohlen 1996). This observation was made in a lab culture study, where the virus remained virulent for 3 to 7 days after ingestion by the earthworm, suggesting that *L. terrestris* could serve as a reservoir and dispersing agent for the disease under field conditions. Moreover, some cases of human infections of lungs, kidneys, and mesenteries by nematodes apparently derived from earthworms (species not given) have been reported. Other animal parasites and pathogens reportedly carried by earthworms include protozoan and nematode parasites of wild and domestic birds and nematode and helminth parasites of pigs, small mammals, and birds (Lee 1985, Edwards and Bohlen 1996).

Earthworms also have been reported to carry and spread plant pathogens, including spores of *Fusarium, Pythium,* and potato wart disease, and cysts of plant parasitic nematodes (e.g., potato root eelworm). The most studied earthworm species have been European lumbricids *(L. terrestris, A. longa),* but one megascolecid *(Megascolex insignis)* also reportedly increased the spread of a fungal pathogen (Lee 1985, Edwards and Bohlen 1996). Conversely, there are reports that lumbricid earthworms reduce the density of pathogenic nematodes and the severity of symptoms of *Rhizoctonia* infections of wheat seedlings, as well as aid in the dispersal through soil of disease biocontrol agents or genetically modified bacteria used in bioremediation (Edwards and Bohlen 1996, Daane and Haggblom 1999); Daane and Haggblom (1999) also showed that bacteria might be transported inside earthworm cocoons. Although there are no reported links between exotic earthworms and the introduction of significant pathogens, the potential for pathogens to be carried by earthworms warrants development of policies to minimize such introduction.

Assessing risks of exotic earthworm invasions

Assessing the risk of earthworm invasions is challenging because there is no evidence of clear economic impacts and because the linkages between ecological processes below ground and above ground are poorly understood. Much of the research on invasions by terrestrial invertebrates has focused on insects, particularly those that have become economically important pests. Because of their relatively high mobility and fecundity, a number of insect invaders have shown rapid spread and have become the subject of intensive research and control efforts (Simberloff 1989). Invasion biology of soil invertebrates has not been as well studied (Ehrenfeld and Scott 2001), with the exception of some ant, termite, and nematode species of economic importance. Invasions by more cryptic and less mobile soil fauna appear to be qualitatively and quantitatively different from those of other invertebrates and may even be more similar to plant invasions than to those of other animals (Di Castri 1991). Invasions by terrestrial planarians (Boag and Yeates 2001) may be the best model for understanding and controlling earthworm invasions because of similarities between these groups with respect to ecology, life history, and modes of transport.

Identifying problematic earthworm species before importation. It is difficult to predict which species in any taxonomic group of animals or plants will be successful invaders, or even to list characteristics common to those that have been successful (Simberloff 1989, Williamson 1996, Mack et al. 2000). In the case of earthworms, most of the morphological and behavioral traits listed in table 3 can be found in at least some invasive species. Nor does success of one species necessarily indicate success of related species. For example, *Pontoscolex corethrurus* and *Aporrectodea trapezoides* are highly successful invaders in tropical and temperate climates, respectively, whereas their congeners, *Pontoscolex spiralis* and *Aporrectodea icterica*, appear to be much less so, possibly because they have not been as widely introduced or they are not as well adapted to a wide range of environmental conditions.

Numerous indicators of successful invaders have been postulated (e.g., high intrinsic rate of increase, certain reproductive and genetic characteristics, high abundance and wide range in native habitat, taxonomic isolation or occupancy of vacant niche in new habitat), but many of these are difficult to determine or do not hold in practice. Nonetheless, some generalizations about invasive species, concerning propagule pressure, habitat matching, and previous success at invasion, may be useful in developing criteria for earthworm importation (Simberloff 1989, Ruesink et al. 1995, Williamson 1996, Mack et al. 2000).

Propagule pressure is a function of inoculum characteristics of an introduced species—the probability of establishment of a species in a new area increases with increasing size of the introduced population, with increasing frequency of introduction, or both. In addition to initial population size, a high reproductive output after introduction may increase the likelihood of dispersal into a new environment. Other ecological characteristics of earthworms may affect their establishment, including resting stages (e.g., estivation and diapause) and production of resistant cocoons, both of which allow populations to survive adverse conditions. Also, a number of earthworm species display parthenogenesis (obligate or facultative), a trait that may enhance the establishment of new populations (Lee 1985, Fragoso et al. 1999). Thus, high density or frequent introductions of parthenogenetic species with high fecundity may indicate a high probability of successful invasion if the target habitat is suitable.

Habitat matching refers to conditions in the habitat of origin relative to those of proposed or suspected areas of introduction. As a general rule, species that exhibit a wide range of environmental plasticity in their native habitats are likely to be more successful as invaders than species with more restrictive environmental requirements (Williamson 1996). Earthworm species from northern latitudes (e.g., European lumbricids and some Asian megascolecids) are poor colonizers in tropical or subtropical climates (except in localized temperate situations), and vice versa. For example, despite continued and widespread introduction throughout the United States, *Eisenia fetida*, the lumbricid "manure worm" commonly used in vermicomposting, is not often found in natural habitats in the southern United States. Likewise, *Pontoscolex corethrurus* (Glossoscolecidae) and *Eudrilus eugeniae* (Eudrilidae), both now distributed throughout the tropics, apparently have not become established in natural habitats in the continental United States where they have been introduced, with the exception of *P. corethrurus* in south Florida (Gates 1970, 1982, Fragoso et al. 1999).

Assessment of matching with specific subhabitats may be possible, based on information about behavioral or morphological characteristics of introduced species (table 3). Although these characteristics may not be good predictors of invasion success, they could be helpful in estimating the kinds of effects an exotic earthworm may have if it is released into new environments. For example, in Alberta, Canada, the exotic epigeic, *Dendrobaena octaedra*, mixed the surface litter and upper mineral layers of soil in a lodgepole pine forest (McLean and Parkinson 1997), whereas a combination of epigeic *(D. octaedra)*, endogeic *(Aporrectodea* spp.), and anecic *(L. terrestris)* species transformed the forest floor to a depth of up to 50 centimeters in hardwood forests in Minnesota (Alban and Berry 1994, Hale et al. 2000).

Previous success at invasion may be one of the clearest indicators of a species' potential to invade new habitats, at least for the well-known anthropochorus earthworms. There are documented reports of earthworm invasions throughout the world, and a number of species are known to have achieved wide distributions beyond their places of origin in tropical and temperate regions, presumably because of their ability to invade and become established in a wide variety of habitats. Lee (1985) suggests that there are about 100 such "peregrine" species, representing all families and presumably transported by humans "across otherwise impassable barriers." Some of the widely distributed, potentially invasive earthworm species and some of their ecological characteristics are listed in table 4.

Working criteria for assessing potentially invasive earthworms. Any one of these attributes—propagule pressure, habitat matching, or previous success at invasion—probably is not sufficient to evaluate the invasion potential of an earthworm species. Furthermore, these attributes are related primarily to mechanisms and ecological consequences of invasions and not to the possibility that earthworms may be vectors of pathogens. Both aspects of risk are combined in box 1 as working criteria for assessing invasion and disease–vector potential of exotic earthworms. These criteria represent a subset of protocols summarized by Ruesink and colleagues (1995).

This set of information for any earthworm species should help decisionmakers identify which species may present high invasive potential if introduced into new areas, but it is unlikely that all of the necessary information will be available for all introduced species. In the case of intentional introductions, prospective importers might be made to bear the responsibility of providing as much information as possible (Ruesink et al. 1995), which then could be confirmed and augmented by import authorities. For inadvertent introductions, authorities or others concerned with earthworm invasions would need to acquire the information, a considerable amount

Table 4. Characteristics of some "peregrine" earthworm species now widely distributed beyond their regions of origin. Most are anthropochorus, with high climatic and edaphic plasticity.

Species	Ecological category	Partheno-genetic	Origin
Tropical or subtropical			
Amynthas gracilis (Kinberg 1867)	Uncertain	+	Asia
Amynthas corticis (Kinberg 1867)	Uncertain	+	Asia
Dichogaster affinis (Michaelsen 1890)	Endogeic polyhumic	+	West Africa
Dichogaster bolaui (Michaelsen 1890)	Epigeic	+	West Africa
Dichogaster saliens (Beddard 1893)	Endogeic polyhumic	+	West Africa
Drawida barwelli (Beddard 1886)	Endogeic polyhumic	+	India
Eudrilus eugeniae (Kinberg 1867)	Epi-endogeic, polyhumic	?	West Africa
Microscolex dubius (Fletcher 1887)	Endogeic	+	South America
Microscolex phosphoreus (Dugès 1837)	Uncertain	+	South America
Ocnerodrilus occidentalis Eisen 1878	Endogeic polyhumic	+	Central America
Polypheretima elongata (Perrier 1872)	Endogeic mesohumic	+	Asia
Pontoscolex corethrurus (Müller 1856)	Endogeic mesohumic	+	South America
Temperate			
Amynthas agrestis (Goto and Hatai 1899)	Epi-endogeic	+	Asia
Amynthas hawayana (Rosa 1891)	Epigeic	–	Asia
Amynthas hilgendorfi (Michaelsen 1892)	Epigeic	+	Asia
Allolobophora chlorotica (Savigny 1826)	Endogeic	–	Europe
Aporrectodea caliginosa (Savigny 1826)	Endogeic	–	Europe
Aporrectodea trapezoides (Dugès 1828)	Endogeic	+	Europe
Aporrectodea tuberculata (Eisen 1874)	Endogeic	–	Europe
Bimastos parvus (Eisen 1874)	Epigeic	+	North America
Dendrobaena octaedra (Savigny 1826)	Epigeic	+	Europe
Eisenia fetida (Savigny 1826)	Epi-endogeic, polyhumic	–	Europe
Lumbricus rubellus (Hoffmeister 1843)	Epi-endogeic	–	Europe
Lumbricus terrestris (Linnaeus 1758)	Anecic	–	Europe
Octolasion tyrtaeum (Savigny 1826)	Endogeic	–	Europe

Source: Summarized from Gates (1967), Lee (1985), Reynolds (1995), and Fragoso et al. (1999). See Reynolds and Cook (1993) for taxonomic source information.

of which is in the literature but scattered in text and reference books, scientific journals, popular or gray literature, and Internet Web sites. Creation of a data bank with information on reproductive potential, habitat conditions, previous invasion success, disease vectors, and so on would be useful. Table 4 contains a limited set of such information for some of the known invasive species. Such a data bank should also reference oligochaete specialists worldwide.

Policy options

Exotic earthworms have been introduced into most regions of the world principally through human commerce over the past few centuries. Many species were probably introduced and established before there was any consideration of potential impacts, possibly without even knowledge that importation was taking place. As a result, historically, importations of earthworms were not regulated; only recently, as the impacts of importations have become apparent, have regulations been implemented.

Risk assessment protocols have been developed for other invasive organisms (e.g., Ruesink et al. 1995, Reichard and Hamilton 1997). In terms of risks associated with earthworm invasions, three categories warrant attention: (1) the potential impacts on soil processes and environmental quality (e.g., an increase in the turnover of carbon in soil), (2) the potential impacts on beneficial or desirable microbial, animal, and plant species (e.g., native earthworm populations and rare or threatened plants), and (3) the potential for earthworms to be vectors for the import or dispersal of pathogens (e.g., animal or plant diseases). Overall risk may be defined as the product of the probability of establishment and magnitude of potential effects (Ruesink et al. 1995), both of which might be estimated from the criteria in box 1 and an analysis of a species' likely impacts within these categories of risk. Regulatory response to importation requests or to inadvertent

Box 1. Working criteria for assessing potentially invasive earthworm species.

Propagule pressure
- Frequency and inoculum size of introductions
- Fecundity
- Parthenogenesis

Habitat matching
- Characteristics of native habitat
- Proposed or suspected "target" habitat
- Likelihood of introduction into matched habitat
- Ecological characteristics (table 3)

Invasion history
- Location of species origin
- Current distribution
- Previous invasions
- Types of habitats invaded
- Rate of dispersal in invaded habitats

Disease vector potential
- Known or suspected pathogens carried
- Incidence of potential earthworm-borne diseases in region of export

importation would then depend on the level of risk perceived. There are several possible degrees of regulation.

No action. As noted previously, current regulations applicable to earthworm importation into the United States are based on the Federal Plant Pest Act, under which APHIS controls imports containing soil that might carry pathogens. In the absence of pathogens, it appears that any earthworm species may be imported, that is, there is no specific consideration of earthworms as invasive organisms. This is essentially an "innocent until proven guilty" approach, which has been criticized as ineffective against introductions of potentially invasive species whose risks have not yet been assessed (Ruesink et al. 1995, Mack et al. 2000). With no change in this policy, it seems likely that invasions by new as well as already established species will occur, considering Gates's (1970, 1982) observation that exotic earthworms are being introduced continually into the United States from many areas of the world. New introductions could also increase the risk of introduction of pathogens carried by earthworms imported from affected regions.

Selective importation of earthworms. A policy allowing importation only of approved earthworm species would require the development of an approval process, possibly similar to that recommended for control of terrestrial flatworm invasions in Europe, Australia, and New Zealand (Alford et al. 1998). In Canada, earthworms can be imported only from the Netherlands (only *L. terrestris)* and the United States (only species that are known to already occur in Canada) (see *www.cfia-acia.agr.ca/english/plaveg/protect/dir/d-00-04e.shtml*). Such a "clean list" or "guilty until proven innocent" approach (Reichard and Hamilton 1997, Mack et al. 2000) could be applied on a case-by-case basis, with certification by authorities to ensure that only desired species are imported. It would be helpful under this scenario to have listings of both acceptable and unacceptable species of earthworms. This policy would most likely reduce ecological risks of invasion by species known to be successful invaders, but without research on other species, it could not guarantee that those approved for importation do not themselves become invaders. Also, this policy may not reduce the risks of pathogen introduction, which could occur through approved earthworms.

Severe restrictions on imported earthworms. A policy allowing importation only of approved earthworms and appropriately treated earthworm materials would require an approval system, as well as measures such as quarantine of all materials before entry, importation in pathogen-free packaging (as is required in Canada), and perhaps pest monitoring and control during production in the exporting country. Further measures might include admission only of surface-sterilized cocoons and of adults with no soil in their digestive tracts. This policy would be similar to those already in use for restricted importation and release of biocontrol agents and genetically modified organisms (Ruesink et al. 1995). Such a policy would probably significantly reduce the risks of accidental disease importation via earthworms (although microorganisms may be transported inside cocoons; Daane and Haggblom 1999) and the risks of exotic earthworm invasions.

Complete ban on imported earthworms. This policy would be expected to greatly reduce the risks of introduction of earthworm-borne diseases and of new invasions by exotic species. Earthworm users would have to rely on species populations already present in North America. Because so many exotic species are already established, this action may not be an excessive burden on those desiring earthworms for vermicomposting, fish bait, and so on; it might even stimulate development of native earthworm-based culturing and distribution enterprises and greater exploration of possible uses of native earthworm species. However, a complete importation ban might also impede scientific research on earthworms or oligochaetes in general and discourage development of innovative technologies utilizing earthworms (e.g., waste processing). Therefore, this policy option might include special exceptions for importing earthworms for research or technology development. Undoubtedly, a complete ban would be difficult to enforce, particularly with regard to inadvertent introductions of earthworms or cocoons in horticultural or agricultural materials.

Conclusions

A range of policy options for controlling earthworm importation is desirable. A combination of aspects of selective importation and severe restriction might provide a reasonable level of risk reduction, while allowing continued commerce in and development of earthworm-related enterprises. Of course, a complete ban may be necessary on an ad hoc basis to prohibit importation of earthworms from countries afflicted with pathogens known or suspected to be carried by earthworms (e.g., foot-and-mouth disease).

Enough information probably is available for screening those exotic species with the highest invasion potential. However, as with many other groups of invasive organisms (Simberloff 1989, Mack et al. 2000), more basic knowledge is needed of the natural history and ecology of invasive earthworms in their native habitats and in ecosystems where they have invaded and had significant impacts. What factors control their populations under native conditions? Which characteristics of the organisms and of the habitats have contributed to successful invasions and to invasion failures? How important is biotic resistance, which may occur in ecosystems inhabited by native earthworms? Are native species competitive with aggressive exotic species under native conditions? Is habitat disturbance a prerequisite to invasion? Case studies and experimental manipulations are needed to answer these and other pertinent questions. Additionally, there is still a need for basic survey and taxonomic work to assess the diversity and distribution of native earthworm species, some populations of which may be vulnerable to exotic invasions (James 1995).

Prevention of local invasions and restoration of invaded sites have received little attention. As noted above, activities of earthworms are often considered beneficial in agricultural soils, and there probably would be little incentive to eradicate exotic species or replace them with native species in those situations. The focus should be on preventing new invasions from such areas into surrounding ecosystems where exotic species are expected to have adverse impacts. Extirpation of exotic earthworms from soil is not likely to be feasible on a large scale, but possible barriers to further expansion, such as buffer zones of unsuitable habitat which might impede migration, should be studied.

In addition to controls on importation at national borders, regulations at state and provincial or regional levels may be needed to prevent transport of exotic earthworms into remote or sensitive areas. Efforts by conservation and outreach groups (e.g., Minnesota Worm Watch; see *www.nrri.umn.edu/worms*) are helpful in raising public awareness of problems associated with earthworm invasions in such areas.

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