

Pandora's Box Contained Bait: The Global Problem of Introduced Earthworms*

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Key Words

biological invasions, exotic species, oligochaete biogeography, soil fauna

Abstract

Introduced exotic earthworms now occur in every biogeographic region in all but the driest or coldest habitat types on Earth. The global distribution of a few species (e.g., *Pontoscolex corethrurus*) was noted by early naturalists, but now approximately 120 such peregrine species are recognized to be widespread from regional to global scales, mainly via human activities. Species adapted to human transport and to colonization of disturbed habitats are most widespread and are the principal invasive species. We identify a number of endogenous and exogenous factors that may contribute to the successful establishment and spread of peregrine species. Quantification of these factors may help to determine why certain species become invasive while others do not. Recent advances in theory and modeling of biological invasions and in molecular techniques should prove fruitful in improving our understanding of invasive earthworms, as well as in predicting their impacts on ecosystems.

Invasive: refers to a nonnative or exotic species that causes disturbance to the ecosystem that it invades

Exotic: not naturally occurring in the location in which it is found (also referred to as alien)

Introduced: brought to a location by intentional and/or accidental human action

Peregrine: widely ranging, often owing to human action

INTRODUCTION

Apart from the familiar cases of Argentine fire ants (*Soleopsis invicta*) in Oceania and North America, the Formosan termite (*Coptotermes formosanus*) in South Africa and the southeastern United States, and the New Zealand flatworm (*Arthurdendyus triangulatus*) in the British Isles, subterranean biological invasions have gone largely unnoticed until recently (Ehrenfeld & Scott 2001). Exotic earthworms in particular escaped the attention of all but a few biologists interested in the distribution and ecology of soil invertebrates. The earliest surveys of terrestrial oligochaetes revealed that several earthworm species had achieved distributions well beyond their expected realms and were possibly displacing indigenous fauna (Beddard 1912, Eisen 1900). Throughout the ensuing century there has been a steady accumulation of evidence of earthworm introductions worldwide (e.g., Gates 1972, Ljungstrom 1972, Stebbings 1962). Gates (1982), Jamieson (1981), Sims (1980), and later Omodeo (2000) presented modern syntheses of earthworm biogeography. Despite continuing phylogenetic uncertainties (Jamieson et al. 2002), these works represent our understanding of the distributions of the major earthworm taxa, both indigenous and exotic, throughout the world. However, it was probably the observations of dramatic changes in forest soil profiles caused by exotic European lumbricid earthworms (e.g., Alban & Berry 1994, Nielsen & Hole 1964, Scheu & Parkinson 1994) that stimulated recent efforts to understand earthworm invasions better. The past decade has seen a surge in research on earthworm invasion ecology and several recent reviews have detailed effects of introduced earthworms on soils, biota, and ecosystem processes in temperate and tropical regions (Bohlen et al. 2004a, Groffman & Bohlen 1999, Hendrix 2006, Hendrix & Bohlen 2002, Lavelle et al. 1999, Parkinson et al. 2004). It is clear that introduced earthworms can significantly alter soil structural properties, organic matter and nutrient dynamics, and plant and animal communities above and belowground (see **Table 1** for a summary of documented impacts of five widespread introduced earthworm taxa). In spite of increasing knowledge of these impacts, there is still considerable uncertainty about the earthworms themselves, their distributions, and mechanisms by which they come to be introduced and invasive in new areas. Our aim in this review is to address these uncertainties by attempting to answer the following questions:

- How widespread are exotic earthworms and what factors affect their distribution?
- Can we recognize characteristics of earthworms that contribute to their invasiveness?
- How can we predict which species will be invasive, which geographic areas are vulnerable, and what the consequences of earthworm invasions will be?

BIOGEOGRAPHY AND GLOBAL EXTENT OF EARTHWORM INVASIONS

Historical Perspective

Exotic earthworms now occur on every continent (except Antarctica), on oceanic islands, in every biogeographic region, and in nearly every type of ecosystem (including desert oases) on the planet. Early records identified a dozen or more species that were termed peregrine by Michaelsen (1900), i.e., “those species which possess some powers of migration over the sea, denied to the majority of worms, and probably due to the direct interference of man” (Beddard 1912). These included the apparently ubiquitous *Pontoscolex corethrurus* and *Eudrilus eugeniae* in the tropics (each, interestingly, being the only peregrine representative from the families Glossoscolecidae and Eudrilidae, respectively); several species from the genera *Amyntas*, *Microscolex*, *Dichogaster*, and *Perionyx* (all Megascolecidae); and at least 10 species of Lumbricidae, which include “by far the greatest number of peregrine forms” (Beddard 1912). Beddard also drew several conclusions from his early survey

Table 1 Distributions and known impacts for select well-known invasive earthworm taxa

Taxa	Biogeographic realm(s) (see Figure 1)		Impacts and selected references
	Indigenous	Introduced	
Lumbricidae			
<i>Aporrectodea</i> spp.	Western Palearctic	ALL ^{a,b}	Native earthworms (Winsome et al. 2006)
			Plant growth (Doube et al. 1997, Welke & Parkinson 2003)
			Nutrient cycling (Bohlen et al. 2004)
<i>Dendrobaena octaedra</i>	Western Palearctic	ALL except Ethiopian ^{a,b}	Microarthropods (McLean & Parkinson 2000)
			Forest floor (Parkinson et al. 2004)
			Soil structure and function (Hale et al. 2005)
<i>Lumbricus rubellus</i> and <i>L. terrestris</i>	Western Palearctic	ALL ^{a,b}	Microarthropods (Eisenhauer et al. 2007)
			Plant community composition (Frelich et al. 2006, Holdsworth et al. 2007)
			Nutrient cycling (Bohlen et al. 2004)
			Soil structure and function (Hale et al. 2005)
Megascolecidae			
<i>Amyntas</i> spp.	Eastern Palearctic	ALL ^{a,b}	Macroarthropods (B.A. Snyder, unpublished data)
			Plant growth (Brown et al. 2006)
			Nutrient cycling (Burtelow et al. 1998, Lavelle et al. 1999, Steinberg et al. 1997)
			Soil structure (B.A. Snyder, unpublished data)
Glossoscolecidae			
<i>Pontoscolex corethrurus</i>	Neotropical	ALL ^a	Plant community (Gonzalez et al. 2006)
			Litter decomposition (Liu and Zou 2002)
			Nutrient cycling (Lavelle et al. 1999)
			Soil structure (Lavelle et al. 1999)

^aGates 1972.

^bDoes not include biogeographic realm of origin, as there is debate on the size of the region of origin for most earthworm taxa. *P. corethrurus* is a notable exception (Lavelle & Lapid 2003).

of peregrine earthworms: (a) The capacity of “extending their range beyond the limits assigned by nature is not confined to any one family.” He further suggested that the disproportionate numbers of peregrine Lumbricidae, relative to other families, is a consequence of the “newness” of the family coupled with the “vigour seen in new races.” (b) “Some species are more capable of extending themselves than others.” In the tropics, for example, *E. eugeniae* and *P. corethrurus* are already circummundane, whereas *Dichogaster bolau*, *Nematogonia panamaensis*, and *Pheretima taprobanae* occur in increasingly more restricted areas outside their indigenous home. (c) There appear to be no “peculiarities of structure” common to all peregrine forms that might account for their success, other than the fact that all are small to moderate in size. Whereas intolerance to low temperature appears to limit success of tropical peregrines in temperate climates, the opposite does not seem to be true, as a number of lumbricid species have become established in the tropics (e.g., Gates 1972).

Although temperate earthworms introduced into the tropics appear best adapted to montane temperate areas, this latter conclusion by Beddard is of great modern interest as we attempt to

Megadrile: large terrestrial and semiaquatic segmented worms, commonly referred to as earthworms, cf. microdrile

Microdrile: small, mostly aquatic oligochaete worms, but also including the terrestrial Enchytraeidae

understand mechanisms of invasiveness and develop models to predict where and how extensively earthworm invasions might occur.

Systematics and Evolutionary History

Earthworms are classified within the phylum Annelida, class Clitellata, subclass Oligochaeta (increasingly, Crassicitellata). Seventeen families are usually recognized worldwide, making up the semiaquatic and terrestrial forms commonly known as earthworms (Jamieson et al. 2002). Approximately 3700 species of these megadrile oligochaetes have been described, and it is estimated that total global species richness may exceed 7000 (Fragoso et al. 1999, Lavelle & Lapid 2003, Reynolds 1994). Current distributions of the major families are shown in **Figure 1**.

The broad outlines of earthworm distributions were set by geological and biological evolution: diversification, dispersion, and extinction on slowly shifting land masses (James 2004). On smaller spatiotemporal scales, changing climate and ecological processes affect earthworm distributions. We present a brief overview of these subjects to clarify two points. First is how it is possible to know that a particular species is exotic to a location. Second, it is important to know why some locations were or are naturally devoid of earthworms, because such locations may respond very differently to earthworm invasions than places where an indigenous earthworm community exists (or once existed).

Earthworms have left no known pre-Neogene fossils of any kind, save possibly ichnofossils of form consistent with modern earthworm-created structures (S. Hasiotis & S. James, personal

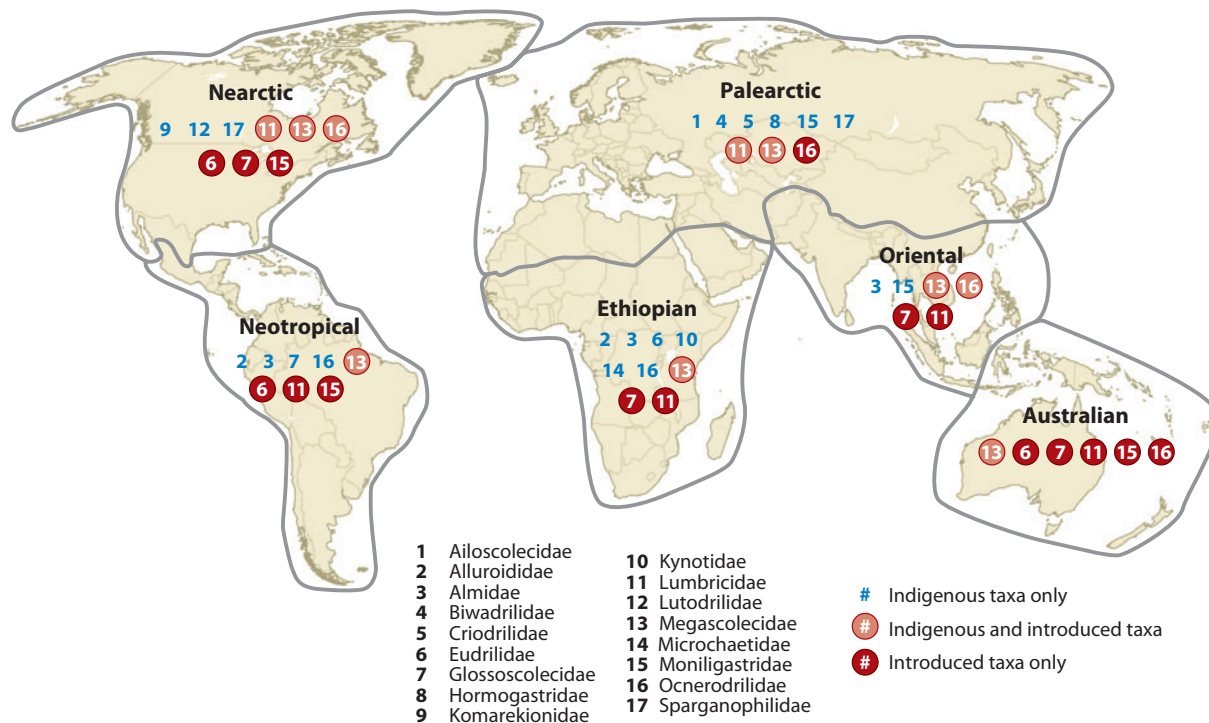


Figure 1

Global distribution of indigenous and introduced species within earthworm families in each biogeographic realm (modified from Reynolds 1994, with data from Gates 1982, Jamieson 1981, Omodeo 2000, Sims 1980).

observation). Thus the origins of earthworms are uncertain in time and space, but their position on the phylogenetic tree of Annelida: Clitellata is probably as a sister group to the Enchytraeidae (Erséus 2005). In this view, the basal clitellates were aquatic, and ancestors of earthworms and Enchytraeidae were most likely aquatic clitellates because the sister clade is the largely aquatic Lumbriculidae leeches.

Apart from some uncertainties about the phylogenetic positions of the Syngenodrilidae, Al-luroididae, and Moniligastridae, the distributions of the family-level taxa are mainly consistent with post-Pangaeian land area relationships (James 2004, Jamieson 1981, Sims 1980) insofar as the phylogeny is known. This is important in the discussion of invasive earthworms because to know if something is outside its natural range, one must have some basis for determining what the natural range is. Until considerable knowledge of earthworm distributions accumulated, specialists were not surprised to find what we now know to be Asian and European species in various other locations, and to name them for those locations as if the species were indigenous to the places. Some examples are *Amyntas hawayanus* (junior synonym of *A. gracilis*, material for which was also first found well outside of Asia), and *Allolobopohora iowana* (syn. *Aporrectodea caliginosa*). *Amyntas loveridgei* is not yet known from inside the natural genus range, only from the Western Hemisphere, but no one would consider it native to any of the places it has been found.

In the pre-plate tectonics era, biologists often invoked long-distance dispersal and land bridges to explain observed distributions (Stephenson 1930). However, some earthworm specialists suggested that human activity was responsible for certain common introduced species' presence, noted the associated disappearance of indigenous species, and correctly identified the continents of origin of the exotics (Eisen 1900, Ljungstrom 1972). Eventually, plate tectonics models of Earth's crust removed the hypothetical imperative for land bridges and other esoteric dispersal scenarios. Thus, support dwindled for considering multicontinental distributions of some exotic species as natural (e.g., Omodeo 1963), and it became more straightforward to speak of native and exotic species of earthworms.

To know if a species is not native to a site, we first refer to the primary concentration of the relevant supraspecific taxon, such as *Amyntas* in mainland Asia, *Pontoscolex* in the Guyanan Shield, or the Lumbricidae in Europe. Then we note that of the particular taxon, a subset is widely distributed outside its presumed natural range, and the species in question belongs to that subset. The evidence is circumstantial but is credible in light of the facts that there were no remarkable land bridges and long-distance prehistoric dispersal is not a necessary condition to achieve present-day natural and artificial distributions. Indeed, it is highly improbable that in the absence of human transport, a single species would exist in numerous widely scattered locations across the globe, such as the artificially pan-tropical *P. corethrurus*.

Pleistocene glaciations are thought to have eliminated the earthworm fauna from most of the northern temperate regions of Earth (Gates 1982, Tiunov et al. 2006). Natural refaunation by dispersal from glacial refugia in North America, Europe, and Asia has been slow [~ 10 m year⁻¹ (Terhivuo & Saura 2006)], leaving large areas of northern temperate forest, boreal forest, and tundra devoid of native earthworms. In these areas, invasions take place in soils unoccupied by earthworms (e.g., Alban & Berry 1994, Frelich et al. 2006, Tiunov et al. 2006). This is an important distinction from regions inhabited by native earthworms because, compared with the latter sites, naturally earthworm-free ecosystems have different soil process characteristics, different organic matter breakdown regimes, and will show greater change when invaded by an ecosystem engineer class that previously was absent (Bohlen et al. 2004). Where invasions take place into occupied soils (or heavily disturbed soils where natives have been negatively impacted), soil structure may not be so drastically altered, although it is still possible to have major structural changes (Hendrix et al. 2006). Other soil biota and vegetation are likely to be adapted to the influence of earthworms and

Native: a taxon that occurs naturally in the location where it is found

may be less affected by a change in earthworm community composition than biota unaccustomed to earthworm presence.

Distributional Patterns of Introduced Earthworms

Among the approximately 3700 described species, about 3% (~120) have been identified as peregrine (Fragoso et al. 1999, Lee 1985), but the current state of knowledge allows few generalizations about distributional patterns of introduced earthworms. At global scales, Beddard's (1912) observations still hold: Temperate regions tend to be invaded by temperate species, and tropical regions by tropical species (with some temperate species also invading montane temperate elevations in the tropics). Given that there are many more tropical than temperate earthworm species (Fragoso et al. 1999, Lavelle & Lapied 2003), it is interesting that the proportion of peregrines is much higher among temperate species (tropical: 51 of an estimated several thousand species; temperate: 45 of an estimated 500–600). This suggests that there are many more tropical peregrines that have not yet been discovered; that many more tropical species have yet to become peregrine, but could under appropriate conditions; that temperate species are inherently more prone to invasiveness, possibly through more euryoecious adaptations; or that current distributions of introduced earthworms are mostly a function of global commerce that has favored transport of temperate more than tropical species over the past centuries. The last two hypotheses seem the most likely, but the emergence of new tropical invasive species is an intriguing possibility, that is, that regional peregrines have the potential to become global peregrines, including several species of the pheretimid genus *Amyntas* in Thailand (e.g., *A. alexandri*) and subtropical China.

At regional to local scales, it has long been held that exotic earthworms tend to colonize and become established in disturbed habitats (Eisen 1900, Lee 1985, Sims 1980, Smith 1928, Stebbings 1962). Whether or not they become invasive appears to depend on local climatic, edaphic, and land-use factors. For example, several studies found that introduced earthworms failed to disperse into surrounding undisturbed areas even decades after introduction (Abbott 1985, Kalisz & Dotson 1989, Lavelle & Pashanasi 1989). However, other studies have shown that introductions of exotic species may create hotspots that then become hubs for further invasion into surrounding areas (e.g., Holdsworth et al. 2007). It is commonly believed that exotic earthworms displace native species through competitive interactions, or that they occupy niches vacated by extirpated native species. Kalisz & Wood (1995) summarized the prevailing idea that physical disturbance or habitat fragmentation is 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. Undisturbed soils occupied by native earthworms may exclude exotic species (e.g., Wood et al. 1997), but coexistence of native and exotic species, however transient it may be, has been reported in a number of locations (e.g., Callaham et al. 2003, Grosso et al. 2006, Hendrix et al. 2006). The extent to which native species persist in the presence of exotics may be attributable to the degree of habitat disturbance (**Figure 2**).

Regions of Origin and Introduction of Exotic Earthworms

As noted above, some representatives from most earthworm families have become established as exotic species in other biogeographic realms (**Figure 1**). The ~120 known peregrines include ~50 Megascolecidae, ~30 Lumbricidae, and ~40 species from 10 other families, at least one of which can be traced to an origin in each realm (Gates 1982, Jamieson 1981, Lee 1985, Omodeo 2000, Reynolds 1994, Sims 1980).

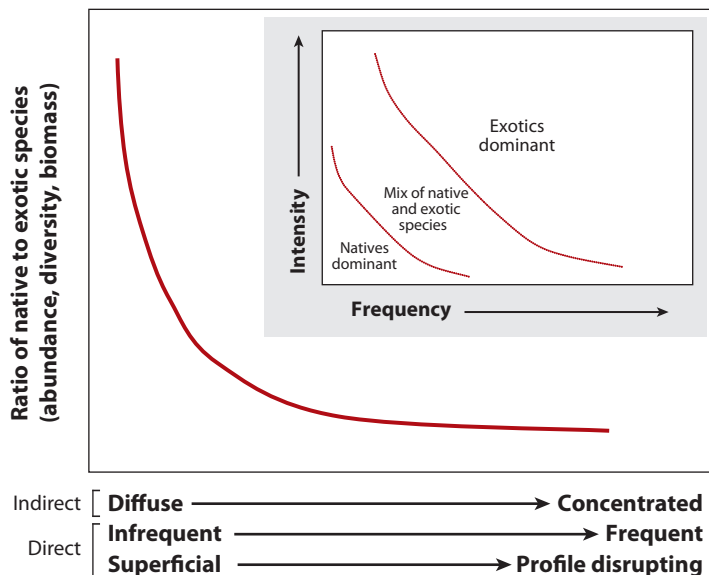


Figure 2

Hypothesized relationships between types of disturbance and expected proportions of native and exotic species. Direct disturbances are categorized by frequency of occurrence and by intensity or degree of physical perturbation of the soil profile. Frequency and intensity are related, but we envision a scenario where extreme disruption of the soil profile need not be frequent to effect change in earthworm communities (*inset*). Indirect disturbances include road density, human population density, degree of fragmentation, and diversity of land-use types, among others.

The most widespread exotic earthworms come from the Palearctic European Lumbricidae, including 20–30 species from the genera *Lumbricus*, *Aporrectodea*, *Allolobophora*, *Octolasion*, *Dendrobaena*, *Eisenia*, and *Eiseniella* that can now be found in temperate habitats throughout the world (Lee 1985, Reynolds 1995, Sims 1980). The highest diversity of the approximately 385 species of Lumbricidae occurs in the unglaciated regions of southern Europe, only approximately 5% of those species having spread into northern areas either by natural dispersion or through human transport (Sims & Gerard 1999, Tiunov et al. 2006). The families Criodrilidae, Hormogastridae, and Ailoscolecidae also occur in Europe but are not known to have become established widely outside of the western Palearctic region. Interestingly, the now Holarctic genus *Sparganophilus* (Sparganophilidae) may have been introduced into Great Britain and France from southeastern North America, where it presumably originated. Introduced earthworms in Europe include *Amyntbas* spp., *Dichogaster* spp., *Pontodrilus* spp., *Microscolex* spp. (Megascolecidae), *Ocnerodrilus occidentalis* (Ocnerodrilidae), and *E. eugeniae* (Eudrilidae), among others (Omodeo 2000, Sims & Gerard 1999).

The Palearctic and Oriental biogeographic regions of East Asia contain a large diversity of earthworms in the Megascolecidae, Lumbricidae, Biwadrilidae, Almididae, and Ocnerodrilidae. These regions are also the origins of several important groups of invasive earthworms, including the pheretimoid group of Megascolecidae and *Lampito mauritii*. Among the pheretimoids, *Amyntbas* and *Metaphire* are the dominant genera in southern China (Chen 1956, Zeng et al. 1982), represented by 86 and 34 endemic species, respectively, mostly distributed in southern China except for eight species also found in northern China. Of the 244 reported species in China, approximately 32 are introduced, belonging to 7 families and 18 genera (Huang et al. 2006, Xu

1996). Collectively, 68% of nonnative earthworms in China belong to the Lumbricidae and are distributed mainly in northern China; 57% of known species in northern China belong to the Lumbricidae and their proportion of the total earthworm fauna decreases from north to south across the country (Huang et al. 2006).

The Indian subcontinent has a large and diverse native fauna and is home to the pantropical *Perionyx excavatus*, which is widespread in India owing to its importance in vermicomposting. Additional *Perionyx* species may be locally invasive, and there is enough morphological diversity within compost operations to suggest that more than one species may be involved. Other exotic species are *Bimastos parvus* and European Lumbricidae (in higher elevations of the Western Ghats and in the Himalayas), *P. corethrus*, various pheretimoids (*Amyntas*, *Metaphire*), a few Ocnodrilidae and *Dichogaster* species, and some regional peregrines such as *Lampito mauritii* (Stephenson 1923; S.W. James, personal observation).

European Lumbricidae, Asian pheretimoids, and South American Glossoscolecidae (*P. corethrus*) are the main invasive earthworms in Australia, New Zealand, Papua New Guinea, and the South Pacific islands. In Australia, there are at least 66 introduced earthworm species and ~350 described native species (Jamieson 1981). Two lumbricids, *Aporrectodea trapezoides* and *A. caliginosa*, are especially common in agricultural lands and pastures of Australia (Baker 2004, Mele & Carter 1999). Similarly, a nationwide survey in New Zealand found that 64% of 216 farms assessed were inhabited by at least 3–4 European lumbricid species, *A. caliginosa* being the most widely distributed (Springett 1992). Lumbricid earthworms were introduced with early European settlements in Australia and New Zealand for agricultural purposes. Peregrine earthworms in the southwestern Pacific islands belong to the families Lumbricidae, Moniligastridae, Glossoscolecidae, and Megascolecidae, the latter including *Dichogaster* spp, which collectively constitutes 14 of 26 recorded species in this area. *Pontoscolex corethrus* is particularly widespread in the islands of Fiji, Samoa, Tonga, and Niue (Easton 1984).

A sparse but growing literature deals with introduced earthworms in the Neotropics. For example, it is estimated that 17% of the known species in Brazil are invasive (Brown et al. 2006), but in the heavily populated state of São Paulo nearly 40% of all species collected were introduced (Brown & James 2006). These introduced species included the ubiquitous *P. corethrus* and *E. eugeniae*, but also many other species representing the families Megascolecidae (11 species), Lumbricidae (2 species), Acanthodrilidae (6 species), Ocnodrilidae (5 species), and Glossoscolecidae (1 species other than *P. corethrus*). Other parts of South America where information is available include Argentina [25 species, 6 megascolecids, and 19 lumbricids (Mischis & Herrera 2006)], Uruguay [11 Megascolecidae and Lumbricidae that dominate Uruguayan soils, particularly in more disturbed sites (Grosso et al. 2006)], and Andean Colombia [5 introduced species of 18 collected from forested and pasture soils (Feijoo-Martinez et al. 2006)]. Regional sampling in Mexico showed relatively few introduced species, but that these (particularly *P. corethrus*, *P. elongata*, and *Ocnodrilus occidentalis*) were widespread (Fragoso et al. 1995). In Puerto Rico, *P. corethrus* and *Amyntas* spp. make up the majority of invasive species, and these are known to dominate soils where primary forest has been cleared (Gonzalez et al. 2006). Likewise, on the islands of the Caribbean basin, there are relatively few invasive earthworms species, but these are ubiquitous. *Pontoscolex corethrus* occurs across the basin, and various *Amyntas* spp. are also common (Fragoso et al. 1995).

African records of introduced earthworms, as is the case for many sparsely studied regions, are mainly found scattered in the taxonomic literature where the specimens were found in collections examined by specialists (Pickford 1937). Ljungstrom (1972) commented on the large extent of invasions in urbanized and cultivated parts of South Africa. Recently, some ecological and agricultural studies have provided indications of the extent of invasions in Africa. S.W. James

(unpublished data) has found several *Amyntas* species and *Octolasion tyrtaeum* in KwaZulu Natal, South Africa. *Pontoscolex corethrurus* is known from Kenya and probably inhabits almost all other nondesert regions. North Africa is home to many European species in the wetter areas (Omodeo 2000), and the Canary Islands are entirely populated with exotic species (Talavera 2007).

In addition to the approximately 102 described native earthworm species in North America north of Mexico (Fender 1995, James 1995; the former suggesting another 80+ undescribed species), at least 45 exotic species have been introduced. As of the early 1990s, known exotics included European Lumbricidae (25 species), African Acanthodrilidae (two species), Asian Megascolecidae (14 species of the pheretimoid group), South American Acanthodrilidae (two species), African Eudrilidae (*E. eugenia*), South American Glossoscolecidae (*P. corethrurus*), Asian Moniligastridae (1 species), and Ocnerodrilidae (2 species) (Gates 1982, Reynolds 1995). It is likely that other species have been introduced but have not yet been reported in the literature. Interestingly, only one Nearctic earthworm, *Bimastos parvus*, is known to have become established as an exotic species outside of North America [e.g., in Europe, Nepal, East Asia, and Brazil (Brown et al. 2006, Gates 1982)].

From our current knowledge of the distributions of introduced earthworms, an important question arises: What accounts for the biogeographic asymmetry in exotic species distributions; that is, why are some areas more highly invaded than others? This could be partly due to lack of information from areas that have not been adequately surveyed (e.g., Africa), such that earthworm introductions may be even more extensive than we currently know. But in regions of known introductions, factors contributing to high species richness of exotic earthworms probably include the history of introductions in the wake of human colonization and commerce and environmental tolerances of introduced earthworms relative to conditions in their new habitats (Gonzalez et al. 2006, James & Hendrix 2004). Our ability to predict future invasions will require a much better understanding of the biological and ecological mechanisms involved.

MECHANISMS OF EARTHWORM INVASIVENESS

What biological traits predispose species to be invasive is a fundamental question of invasion biology (Simberloff 1989). A number of indicators of invasiveness have been postulated, including high fecundity, single-parent reproduction, high genetic variability, phenotypic plasticity, high abundance and wide range in native habitat, taxonomic isolation, and occupancy of vacant niche in new habitat. Beddard (1912) lamented that there appear to be no “peculiarities of structure” common to all peregrine earthworms. Nearly a century later, Lodge (1993) remarked with respect to invasive species in general “[that] because all patterns are characterized by large variance and exceptions, we cannot with any confidence predict the outcome of any particular introduction.” However, recent advances in data mining and statistical learning have reversed this conclusion. Taxonomically grouped reliable predictors of invasiveness have now been identified for birds (Jeschke & Strayer 2006, Sol et al. 2005), fishes (Jeschke & Strayer 2006, Kolar & Lodge 2002, Marchetti et al. 2004), mammals (Jeschke & Strayer 2006), mollusks (Keller et al. 2007), pine trees (Rejmánek & Richardson 1996), and woody plants (Reichard & Hamilton 1997).

Such findings have not been reported for invasive earthworms. Rather, where studies have been performed, counterexamples have been identified. Thus, a number of morphological and behavioral traits found in invasive species are also common to noninvasives (Hendrix & Bohlen 2002). Further, it appears that invasion success of one species is a poor indicator of invasion success of closely related species. As examples, there are hundreds of *Amyntas* species, but only approximately 10 are widely invasive. Until recently, *Pitbamera* was only known from approximately eight invasive species (mostly in Pacific islands and Southeast Asia), but recent surveys in the Philippines

Anthropochorous:
primarily associating
with human habitation

have discovered at least 50 noninvasive species (Hong et al. 2008). Thus, taxonomic sampling bias must be considered because several years ago we might have believed that all *Pitheclimber* are invasive.

Other generalizations, however, might be useful in identifying potentially invasive earthworms. For example, species that exhibit a wide range of environmental plasticity in their native habitats are likely to become more widespread than species with more restrictive environmental requirements (Fragoso et al. 1999, Williamson 1996). Although not satisfying from a mechanistic standpoint, prior invasion success may be one of the clearest indicators of a species' potential to invade new habitats, at least for the well-known, anthropochorous earthworms (**Table 1**). A systematic comparative study of the characteristics of invasive versus noninvasive earthworms would be timely.

Invasiveness Characteristics and Vectors of Earthworm Transport

It has been suggested that biological invasions by cryptozoans are more similar to plant than to animal invasions (di Castri 1991). This may be particularly true for earthworms because of certain reproductive (e.g., cocoon production), behavioral (e.g., diapause), and economic (e.g., use in vermiculture) features of these organisms. A number of factors, both inherent to earthworms (endogenous) and to agents of their environment (exogenous), may contribute to the invasiveness of at least some species (Fragoso et al. 1999, James & Hendrix 2004).

Endogenous factors include characteristics such as wide environmental tolerance (e.g., edaphic plasticity), which, for example, allows anthropochores to establish in disturbed habitats; ability to survive travel in dormancy or as cocoons; dispersal ability (e.g., mass migrations on rainy nights); and reproductive strategies of high fecundity, continuous breeding (especially in tropical species), short incubation time, high hatching success, and, important for colonizing species, parthenogenesis, through which a single organism can establish a population (Fragoso et al. 1999, Terhivuo & Saura 2006). Cocoon production may be particularly important. For example, in Southeast Asia it is common at the end of the rainy season to see mass migrations and mass death of earthworms (Gates 1972), possibly following mass reproduction and production of cocoons that will endure the dry season. This adaptation may also allow such species to survive winter in northern climates where they have been introduced, if timing of tropical dry seasons is similar to that of northern winters [e.g., *Amyntas* spp. in the northern United States (Burtelow et al. 1998, Steinberg et al. 1997)]. Feeding behavior or ecological strategy may also be important for habitat matching at fine spatial scales, such that epigeic earthworms are less likely than endogeic ones to colonize open or grassland habitats without substantial surface litter layers (Hendrix & Bohlen 2002). Sims (1980) noted that the most successful invasive lumbricid species are generalist, edaphophagous feeders that inhabit temporary burrows and are able to withstand soil disturbances.

Several exogenous factors are important in facilitating movements of earthworms across areas they are not likely to traverse on their own. As noted previously, over geologic time, drifting land masses distributed ancestral stock from which contemporary earthworm taxa have evolved. On shorter timescales, natural vectors of transport may include phoresy [e.g., transport of cocoons on birds' feet (see Sims 1980)]; gravity, whereby earthworms and their cocoons roll downslope or wash downstream in watersheds; winds, such as in convective storms that transport earthworm-containing soil and forest floor material; and ocean currents that, for example, raft euryhaline *Pontodrilus litoralis* or their cocoons in tropical seas, where these earthworms tend to live on protected shorelines (Sims 1980, Terhivuo & Saura 2006). Anthropogenic vectors now dominate movements of earthworms and their propagules on a global scale. Historically, early agriculture, commerce, and exploration by Chinese, Polynesian, and European mariners probably first introduced many of the common peregrine earthworms that Eisen (1900), Beddard (1912), and their predecessors reported (James & Hendrix 2004). Over the following century, expanding

international trade has undoubtedly accelerated transport of the same peregrines as well as many other earthworm species. In fact, Gates (1982) monitored oligochaetes intercepted with imported plants and soils quarantined by the U.S. Department of Agriculture over a 32-year period (1950–1982) and found that earthworms from all over the world were continually being imported into the United States. At regional to local scales, modern commerce in horticulture, forestry, and vermiculture introduces earthworms widely in urban and managed ecosystems, whereas back-country fishing and off-road recreation (pack animals and motorized vehicles) may be significant vectors of transport into remote areas (e.g., Callaham et al. 2006, Holdsworth et al. 2007).

Recognition of these endogenous and exogenous factors involved in earthworm introductions raises some interesting questions. Are all exotic/peregrine species invasive and do they display degrees of invasiveness? After all, to become invasive, that is, a self-sustaining, spreading, dominant species, a species must transit several phases of invasion: entrainment in a pathway for redistribution, transport, establishment, and spread (Kolar & Lodge 2001, box 1). Or is invasiveness more a matter of opportunism or stochasticity? Does one invasive species facilitate establishment of others as in the relay effect described by Frelich et al. (2006), and could earthworm invasions manifest as an invasional meltdown (Simberloff & von Holle 1999)?

Ultimately, it would be useful to identify characteristics that might aid in predicting invasiveness of introduced earthworms. Measurable features or predictors might include feeding behavior or life history strategy (i.e., epigeic, endogeic, anecic), environmental tolerances (e.g., soil pH, temperature, water, and organic matter), reproductive characteristics (uni- versus biparental, cocoon production rate and incubation time, parental investment in cocoons/embryos), morphological features (e.g., length, width, mass; pigmentation; gut length; typhlosole development), locomotion (activity, dispersability), travelability (ability to survive transport, response to vibration, mode and length of dormancy), and tolerance to disturbance (maybe even commensalism with humans, e.g., anthropochory). Habitat legacy effects might also be important predictors. For example, of grassland, forest, or riparian species, what fraction is known or is likely to be invasive? Interestingly, *Octolasion tyrtaeum*, a wetland species in its Palearctic home range, is now widespread in a variety of habitats, including agricultural soil, in eastern North America (Terhivuo & Saura 2006), suggesting the possibility of rapid phenotypic or genetic adaptations in at least some species.

MODELING EARTHWORM INVASIONS

Models and Prediction of Earthworm Invasion

Formal approaches to modeling invasions have rarely been applied to earthworms (e.g., Holdsworth et al. 2007), although models could be used to better understand many aspects of earthworm invasions. A first step is modeling suitable habitat, a necessary condition for invasion. Recent decades have seen rapid advances in computational methods for habitat modeling, including the Genetic Algorithm for Rule Set Production [GARP (e.g., Drake & Bossenbroek 2004)], maximum entropy methods (Phillips et al. 2006), and a wide range of statistical and machine learning methods (e.g., Leathwick et al. 2006). With care, each of these can be used to identify habitable environments from information on native range, museum records, and/or initial records from within the invaded range (but see Meynard & Quinn 2007, Stockman et al. 2006). A second condition for invasion success is introduction in numbers adequate to ensure persistence. For species associated with human activity, (i.e., virtually all invasive earthworms) the dominant mode of long-distance dispersal is attendance on mechanisms of human transportation, for example, association with horticulture. Such human activities may be modeled using spatial interaction or gravity models in which zones of attractiveness to traveling people are represented

as discrete sites (e.g., Leung et al. 2006). The final condition for invasion to occur is local spread and dominance. Reaction-diffusion and integrodifference equations are models that integrate population growth and spread for species that reproduce continuously or in discrete time steps, respectively (Neubert & Parker 2004, Shigesada & Kawasaki 1997). Both families of models have been widely used to understand and predict the spread of invasive species from many taxonomic groups (e.g., Buckley et al. 2005, Krkosek et al. 2007). These models have rarely been applied to earthworms or other soil invertebrates, probably because key data have not been collected. We submit that if future studies make an effort to integrate theory and data, our understanding of earthworm invasions will better inform invasion theory overall and our general understanding of population growth and spread will aid the control and management of spreading earthworm species.

Models of Earthworm Effects on Ecosystem Processes

Recently, simulation models have been applied in soil ecology for evaluation and prediction of potential impacts of soil organisms on ecosystem functions, such as soil organic matter decomposition and carbon cycling (Chertov & Komarov 1997, Fu et al. 2000, Hairiah et al. 2006, Lavelle et al. 2004). The potential impacts of earthworms on ecosystem function can also be evaluated by their regulation of soil nutrient dynamics, especially in the case of earthworm invasions (Bohlen et al. 2004). Barot et al. (2007) ran a model of limiting nutrient cycles following three pathways: without earthworms, with earthworm trophic (direct) effects, and with earthworm nontrophic (indirect) effects. Their simulation results indicated that the presence of earthworms could increase primary production through trophic and nontrophic effects because of the conservation of nutrients in ecosystems. For earthworm invasions, simulation models might also apply to the estimation of invasion history and to the prediction of the magnitude of their impacts on soil nutrient cycles. Simulation models can give a rough calculation of time that has elapsed since the introduction of earthworms and an assessment of potential influences on soil nutrients based on the knowledge of impacts of invasive earthworms on decomposition and mineralization processes (C.-Y. Huang, unpublished data). However, more work is needed for the development of a theoretical model that is also supported by field experiments or observations of earthworm invasions.

Earthworms as Model Systems in Invasion Biology

Earthworms are underexploited as a model for invasion biology. Many recent studies have adopted a comparative approach, taking advantage of uncontrolled invasions of plants, birds, fishes, mammals, and invertebrates to answer a range of ecological questions. Thus, researchers have identified traits correlated with invasion success (Hamilton et al. 2005, Kolar & Lodge 2001, Marchetti et al. 2004), tested hypotheses about the integration of introduced species into resident communities (Menke & Holway 2006), and characterized transient biological phenomena such as population growth at small population sizes (Davis et al. 2004) and species spread (Johnson et al. 2006). Invasion biology would benefit by comparable studies on earthworms.

A first question is whether earthworms exhibit the same patterns as other invasive species. Do earthworm invaders act like other invasive species, or are there unexplored mechanisms at work in earthworm invasions? Are there different classes of earthworm invaders, or are all invasive earthworms alike? Do the same traits that predispose other species groups to establish new populations or dominate resident communities also facilitate earthworm invasions? At what spatial scales are native and introduced species richness positively versus negatively correlated (Stohlgren et al. 2003)?

Several characteristics lend earthworms to experimental research. At least some species are easily cultured. Collection and relocation by researchers is rarely regulated. Natural source populations are abundant in many places in the world. Individuals are large enough to be located in experimental media, but small enough to be studied at the mesocosm scale. As a model for population ecology they are nearly ideal: Short generation times, small individual home ranges, and representatives of both selfing and nonselfing forms are available. Growth and fitness are easily observed. We think the following questions could be answered using experimental earthworm systems as models:

1. What are the relative roles of propagule pressure (Williamson 1996) and habitat suitability (Menke & Holway 2006) in population establishment? What role do biotic interactions play in establishment (Mitchell et al. 2006)? What role does disturbance play in establishment (Buckley et al. 2007)? How does the timing of introduction affect establishment (Drake et al. 2006)?
2. Do particular biological traits predispose species to traverse successfully the different transitions of a biological invasion, that is, transport, establishment, population growth, community dominance (Kolar & Lodge 2001)?
3. Are sequences of species introductions facilitative, resulting in invasional meltdown, or are they saturating or idiosyncratic (Frelich et al. 2006, Ricciardi 2001, Simberloff & von Holle 1999)?
4. What role do coevolved versus novel natural enemies play in population establishment, growth, and dominance (Colautti et al. 2004, Torchin et al. 2003)?
5. Under what conditions do invasive species displace resident species? How do invasive species displace residents, that is, evolution of increased competitive ability (EICA) (Blossey & Notzold 1995, Joshi & Vrieling 2005), novel weapons hypothesis (Callaway & Ridenour 2004)? When do invasive species increase versus reduce species richness (Gurevitch & Padilla 2004, Sax & Gaines 2003; cf. Clavero & García-Berthou 2005, Ricciardi 2004)?
6. How do species spread in naturally heterogeneous environments (Hastings et al. 2005, Melbourne et al. 2007)? When do long-distance and diffusive spread occur (Muirhead et al. 2006, Shigesada et al. 1995)? What biological characteristics cause species to spread rapidly (Kinlan & Hastings 2005)?
7. Do genetic characteristics (e.g., outcrossing, heterosis) predispose species to invasiveness (Drake 2006, Lee 2002)? How much adaptation occurs between introduction and growth of invasive populations [e.g., via clone pool variability in parthenogenetic earthworms (Terhivuo & Saura 2006)]? Does genetic adaptation explain observed lags between introduction and detection (Shigesada & Kawasaki 1997)?

FUTURE PERSPECTIVES

Implications of Climate Change for Earthworm Distributions

Possible interactions between global change and earthworm invasions are of considerable interest (Bohlen et al. 2004, Frelich et al. 2006). First, the distributions of invasive earthworms worldwide could be altered with changes in land use and climate. Land transformation provides more opportunities for invasion, and, conversely, invasions enhance and drive land transformation (Hobbs 2000). For example, deforestation and other human disturbances could create more habitats suitable for occupation by introduced species. Climate change has the potential to modify impacts of invasive species by affecting their sources, pathways, and destinations (Sutherst 2000). Furthermore, with a warming climate, the demarcation lines of earthworm distributions might

advance poleward and to higher elevations, where few or no earthworms occur owing to continental and alpine glaciations. Some European lumbricid species (e.g., *Dendrobaena octaedra* and *Eisenia nordenskioldi*) already occur near the Arctic Circle in Russia (Tiunov et al. 2006) and could be expected to advance more rapidly northward into thawing permafrost. Even at lower latitudes altered temperature and precipitation patterns could have more localized effects such as restriction of temperate-adapted lumbricids in tropical areas or expansion of the ranges of regional peregrines such as pheretimoid species in East Asia. Warming at high elevations might be a particular problem for biodiversity conservation; high endemism in mountainous areas could be threatened by invading earthworms (e.g., Pop & Pop 2006). Second, the impacts of earthworms on global change are likely to be complex. In the short term, especially in areas previously devoid of earthworms, invasive earthworms may increase the decomposition of soil organic matter and release more CO₂ into the atmosphere (Potthoff et al. 2001, Speratti & Whalen 2008), and in some cases also more N₂O (Rizhiya et al. 2007). In the longer term, earthworm activities may increase sequestration of organic carbon in soil via protection from decomposition within water-stable aggregates resulting from earthworm castings (Bossuyt et al. 2005, Martin 1991). Finally, it is interesting to speculate on possible changes in the pool of candidate invasive earthworm species that could result from changing climate, altered land use patterns, and expanding global commerce. In addition to the possible expansion of regional peregrines noted above, rapid adaptations (phenotypic and genetic) among known invasive species should be considered as possible mechanisms that could accelerate their spread into new habitats (Terhivuo & Saura 2006). Conversely, introduced species with narrower temperature or moisture tolerances may become more restricted in distribution under warmer or dryer conditions induced by climate change.

Molecular Approaches to Invasion Analysis

Molecular data applications to invasive earthworms have yet to take root. It is now possible to use genetic markers to identify earthworm prey from the guts of predators (Admassu et al. 2006, Harper et al. 2006a, Juen & Traugott 2006), and therefore to look at dietary shifts in predators after the arrival of invasive prey. However, Harper et al. (2006a) mention that intraspecific earthworm haplotype diversity was an impediment to prey identification.

Perhaps more important at this early stage is to improve identification of the earthworms because there are many problems with the taxonomy of invasive species. Some invasive species are known or suspected to be two or more genetically isolated lineages with little morphological distinction, and there are cases of molecularly definable subspecific taxa within what we identify as a single species. *Eisenia fetida* and *E. andrei* are nearly identical except for pigmentation pattern but are isolated (Domínguez et al. 2005), and the former appears to contain a truly cryptic subspecies or species (Perez-Losada et al. 2005). *Lumbricus terrestris* cytochrome oxidase I (COI) barcode region sequences (Hebert et al. 2003) show the presence of two distinct groupings (T. Decaens, B. Richard, and R. Rougerie, unpublished data). *Allolobophora chlorotica* has two color forms (pink and green), each composed of two reproductively isolated, sympatric lineages with >10% COI barcode divergence (King et al. 2006).

Some invasive species contain many parthenogenetic lineages, and some have been named as separate species (Gates 1972). In two cases so far lacking molecular data, the body size, tail setal dimensions, and setal shape vary independently and widely in *P. corethrurus*, and body size and pigmentation vary widely in *Octolasion tyrtaeum*. In the latter, this variation seems to be related to habitat. The common invasive *Aporrectodea caliginosa* is diploid (Omodeo 1955), and the similar, but only quantitatively distinguishable, *A. trapezoides* is a parthenogenetic triploid (Mezhzherin et al. 2007, Garbar et al. 2007) or tetraploid (Omodeo 1955). Often, certain sexual characteristics

used in taxonomy are deleted or strongly modified in parthenogenetic lineages and are different in what appear to be lineages of the same species. Where different clonal populations vary in their properties as invasive agents, molecular data such as microsatellite DNA (Harper et al. 2006b, Velavan et al. 2007) or the ITS region may be the best way to reliably distinguish among them.

To date, little has been done with earthworms in DNA barcoding, but this is changing rapidly. The COI barcode region apparently works well to recover morphologically distinguished presumptive species as monophyletic groups (H. Chang, S. James, Y. Hong, H.-P. Shen, and J.-H. Chen, unpublished data), although the interspecific divergences were higher than the norm among metazoans and have shown cryptic species in *Lumbricus terrestris* and *E. fetida*. The preparation of DNA extracts, COI PCR, and sequencing are completely routine for earthworms, so there are no barriers to further progress in this area. For large numbers of specimens, costs are nearly competitive with specialist time.

Policy and Economic Implications of Earthworm Introductions

The continuing introduction and spread of invasive earthworms seem inevitable, as public policy has hardly dealt with the issue, despite the significant impacts on natural resources (Callaham et al. 2006, Hendrix 2006, Hendrix & Bohlen 2002). However, a public education campaign has proven somewhat effective in reducing introductions to not-yet-invaded areas [Great Lakes Worm Watch Program (see <http://www.nrri.umn.edu/worms/>; also Callaham et al. 2006)]. Therefore, broad-scale public education about earthworms and the invasive earthworm issue may have a considerable impact on new earthworm introductions. In addition to policy and educational solutions, land management can influence the spread of invasive earthworms into soils with a native earthworm fauna present. Strategies to optimize the biotic resistance capacity (sensu Hendrix & Bohlen 2002, Hendrix et al. 2006) of native earthworms and their habitats should be identified and developed. These may range in scope from intensive practices designed to mimic historical disturbance regimes such as annual fire (e.g., Callaham et al. 2003) to simply allowing native vegetation to recover following disturbance (e.g., Sanchez-de Leon et al. 2003).

CONCLUSIONS

Earthworms function as consumers, decomposers, modulators, and food resources for other animals (Edwards 2004, Lee 1985, Zhang et al. 2007). These functions operate at a range of spatial scales from microhabitat to ecosystem and even to regional or global scales (Lavelle et al. 2004). Introduction and invasion of exotic earthworm species into new habitats may extend these functions or alter existing processes. There is urgent need for more detailed field surveys worldwide to reveal the full extent of earthworm introductions and ultimately their impacts; collaborative, international studies across continents and biogeographic regions will be needed to achieve this. In addition to surveys, future research should focus on comparisons of characteristics of invasive and noninvasive species to elucidate mechanisms that might contribute to the invasiveness of introduced earthworms. Modeling and molecular techniques will provide insights into many aspects of earthworm invasion biology, from impacts on predator communities to the genetic underpinnings of the traits that determine invasiveness. Because of these future research directions, there is tremendous potential for earthworm invasions to function as a model system for invasion biology.

DISCLOSURE STATEMENT

The authors are not aware of any biases that might be perceived as affecting the objectivity of this review.

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