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Earthworm invasions in the tropics

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

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

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Introduction

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

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

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

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

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

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

History of earthworm invasions in the tropics

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

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

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

Native and exotic earthworm species in the tropics

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

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

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

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

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

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

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

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

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

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

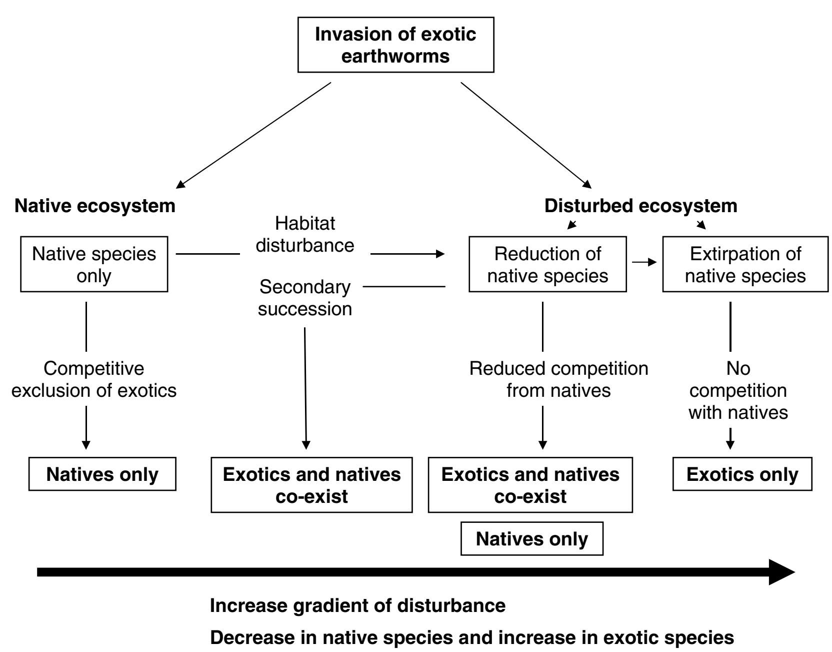

Fig. 1 Model illustrating the paths by which invasion of exotic earthworms affects native earthworm species in undisturbed and disturbed ecosystems

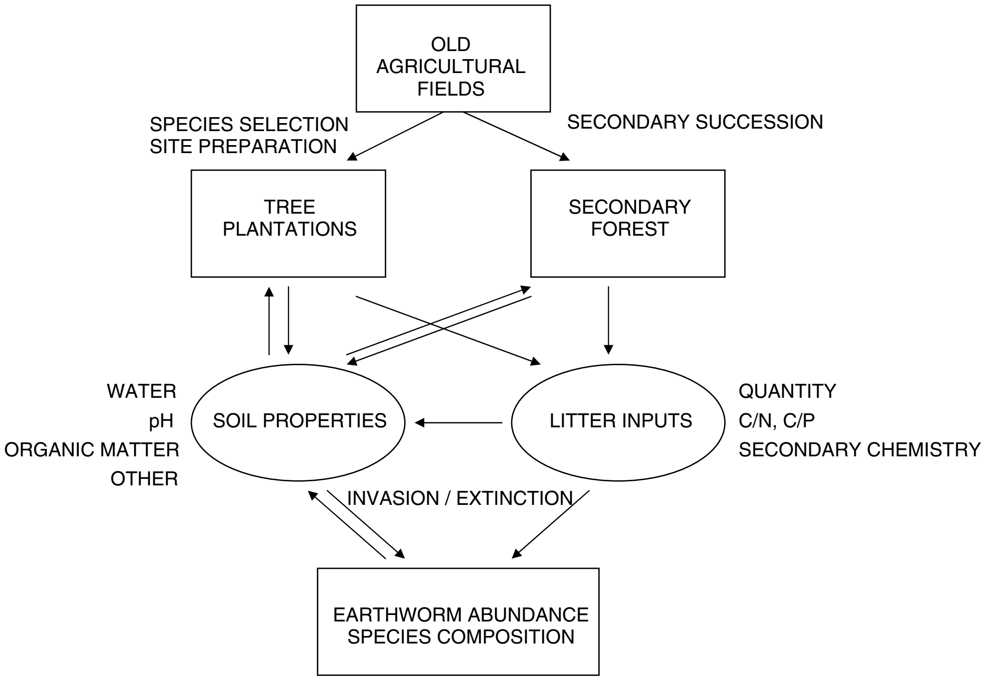

Fig. 2 Conceptual model illustrating the mechanisms by which tree plantations and secondary forests affect earthworm abundance and species composition in abandoned croplands (from González et al. 1996)

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

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

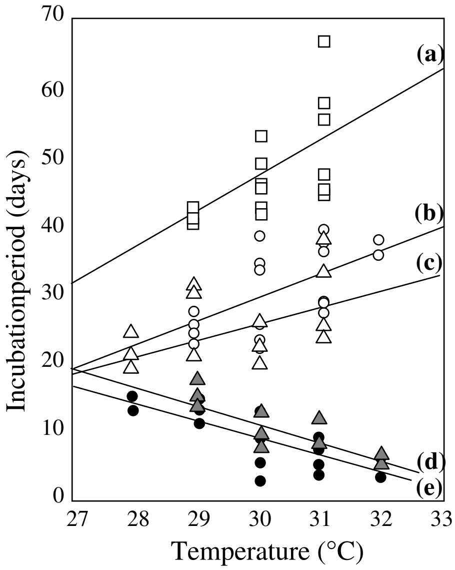

Fig. 3 Relationship between temperature and incubation period in different earthworm species (**a**) *Polypheretima elongata*, (**b**) *Drawida nepalensis*, (**c**)*Pontoscolex corethrurus*, (**d**) *Dichogaster modiglianii*, and (**e**) *Peryonyx excavatus*. Endogeic species are represented with open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

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

Ecological consequences of earthworm invasion in the tropics

Ecosystem properties

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

Soil physical properties

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

Biogeochemical processes

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

Concluding remarks

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

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

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