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INTRODUCTION

Biological invasions belowground—earthworms as invasive species

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

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

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

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

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

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

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

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

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

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

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

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

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

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