Molecular Ecology (2008) **17**, 1165–1169

NEWS AND VIEWS

PERSPECTIVE

Evidence for human-mediated dispersal of exotic earthworms: support for exploring strategies to limit further spread

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Abstract

As potent ecosystem engineers, non-native earthworms are altering the fundamental structure and function of previously earthworm-free cold-temperate hardwood forests in North America. Discarded earthworms used for fishing bait has been presumed to be an important vector for the continued spread of non-native earthworms because epicentres of invasion often include boat landings, lakeshores and roads. However, controversy has remained about the overall importance of human-mediated spread vs. natural expansion of established earthworm populations. In this issue of *Molecular Ecology*, Cameron *et al.* explore the continued role of humans in dispersing non-native earthworms.

Received 20 November 2007; revision accepted 10 December 2007

European earthworms have been invading hardwood forests in the northern USA and Canada since Europeans settled there. These forests developed over thousands of years in the absence of earthworms (James 1995) and historically had thick layers of leaf litter that serve as rooting medium for herbaceous and woody species. Following invasion of a northern forest by non-native earthworms, a cascade of ecological effects can occur (Frelich *et al*. 2006). The most obvious change initially is the loss of the previously thick forest floor. This loss is associated with large declines in native plants and tree regeneration, surface soil in these forests is compacted, soil erosion increases, and nutrient leaching occurs (Bohlen *et al*. 2004; Holdsworth *et al*. 2007a). These structural and functional changes in a forest can also result in the collapse of a previously diverse arthopod community, declines in forest salamanders, ground-nesting forest birds and shifts in small mammal populations. Therefore, concern is growing about the potential widespread loss of native forest species as well as the overall sustainability of northern hardwood forests.

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Research in the past decade has begun to illuminate landscape patterns of invasion and impacts of earthworms, the dynamics of forest change in response to earthworms, and the differential consequences of earthworm invasion in different ecosystems (Bohlen *et al*. 2004). This research also indicates that invasions of northern hardwood forests are occurring throughout the range of this ecosystem in North America (Holdsworth *et al*. 2007b). The magnitude and regional scale of these invasions suggest that a substantial portion of these forests will be impacted by earthworms to some degree within the next few decades. Nevertheless, findings also suggest that local control of invasions into areas that are currently earthworm-free or minimally impacted may be possible. Cameron *et al*. (2008) further illuminate the patterns and mechanisms of earthworm invasion which will be critical to the development of policies and management strategies to address this threat.

In North America, earthworm diversity and abundance is strongly associated with the duration and intensity of human activity (Fig. 1, Reynolds 1977; Holdsworth *et al*. 2007b). Urban areas are largely colonized by a wide variety of earthworms. However, in rural landscapes earthworm populations are concentrated around features such as boat landings, fishing resorts, roads, campsites, and trails. In areas with numerous lakes, dumping of earthworms used for fishing bait appears to be a very important vector since many leading edges of earthworm invasion radiate from boat landings, cabins, and fishing resorts. However, in areas with few lakes, earthworm populations are more strongly associated with roads, suggesting that the movement of compost or soil from earthworm-infested areas via all-terrain vehicles and logging equipment may transport earthworm eggs or cocoons on vehicle tires and underbodies. While these relationships with human landscape features strongly suggest that human-mediated dispersal is important to the continued spread of these species, the relative importance of natural expansion by established populations has been difficult to assess.

With few exceptions, the vast majority of earthworms sold for bait or composting are non-native; *Dendrobaena octaedra* is a common contaminant in compost and bait (Fig. 2). It is also the most widely distributed earthworm species found across the landscape, and therefore, understanding the patterns and mechanisms of dispersal of this species provides a context in which to evaluate the relative distributional dynamics of other non-native earthworm species (Cameron *et al*. 2008; Holdsworth *et al*. 2007b).

Cameron *et al*. (2008) use mitochondrial DNA sequencing to examine the relationship between genetic distances and geographical distances and the relative genetic diversity in populations of *D. octaedra*. Their objective was to investigate the relative importance of human-mediated dispersal of earthworms compared to diffusive spread from established populations in explaining the spread of non-native earth-

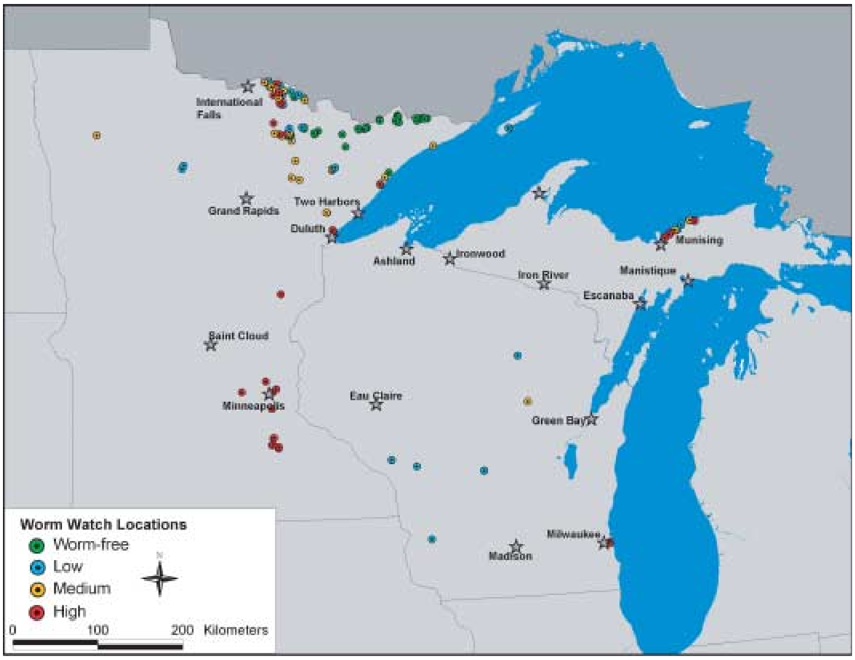

Fig. 1 The distributions and relative abundance of non-native earthworms in sites across the western Great Lakes region illustrate the relationship between urban centres and high abundance and diversity of earthworms, while the most remote areas are earthworm-free. Data provided by Great Lakes Worm Watch, <http://www.greatlakeswormwatch.org/> 0.

worms across the landscape. If diffusive spread of earthworm populations was the primary source of expansion, genetic distance would be expected to be correlated with geographical distance. But this was not the case. Instead, genetic distance and geographical distance were unrelated, suggesting that human-mediated jump dispersal was much more important in explaining the landscape patterns of earthworm spread. Further, genetic diversity was higher at boat landings than roads, likely the result of multiple introductions at boat landings where anglers dump unused fishing bait. These results support evidence from other studies that human activity is the primary source of continued earthworm introductions and spread across the landscape and provides valuable insight into the patterns of non-native earthworm invasion.

Interest is growing to devise strategies for limiting the spread of earthworms into earthworm-free or minimally impacted areas (Callaham *et al*. 2006). Since there are no known ways to extirpate or control earthworms once they have colonized an area, some people suggest that there is nothing to be done since earthworms will simply spread on their own once a population has established. However, earthworm spread is estimated to be slow, between 5 m and 10 m a year, or about 0.5–1 km every 100 years (Hale *et al*. 2006). Cameron *et al*. (2008) provide evidence through their mitochondrial DNA analysis that diffusive spread of established earthworm populations is less important than human-mediated jump dispersal to the continued spread of non-native earthworms.

Evidence of increased genetic diversity at boat landings suggests that multiple introduction events have occurred there and are more likely to occur there in the future (Cameron *et al*. 2008). This fact has big ecological and policy implications, given that the magnitude and types of impacts by non-native earthworms on forested ecosystems are related to the biomass and species of earthworms present (Hale *et al*. 2006; Holdsworth *et al*. 2007a). In Minnesota and Wisconsin, it is estimated

Fig. 2 This very small species, *Dendrobaena octaedra*, lives strictly in the litter layer and feeds primarily on fungi and bacteria found there. It is the most common and widely distributed non-native earthworm in North America and is a very common contaminant in earthworms sold for compost and fishing bait worms. (Photo credit: Erik Hahn).

that approximately 80% of the landscape is invaded by earthworms to some degree. However, only about 50% of invaded sites contain more than four earthworm species, and sites with only one or two species present appear to have relatively minor ecological impacts. In contrast, in the boreal forest of Alberta where Cameron *et al*. (2008) conducted their study, they estimate that only 9% of forest habitat is likely invaded due to the more recent history of human development. Moreover, threats posed by earthworm species just beginning to expand across North America, such as the Asian genera *Amynthas*, are not yet fully appreciated (Kourtev *et al*. 1999; Hale 2007). Areas likely to have multiple, ongoing introductions would be places where decisive action now could mitigate against the introduction of non-native earthworms species still uncommon in most of North America yet are known to cause severe impacts outside of their native ranges. Therefore, even in areas that have been invaded to some degree by earthworms, efforts to prevent future introductions of new species or additional genetic variability of species already present could help to limit the level of impacts.

Cameron *et al*. (2008) demonstrate how the use of relatively simple and inexpensive molecular techniques developed in recent years can provide tools to address otherwise difficult questions. Molecular biology can now play a powerful role in the battle against non-native species by illuminating many of the patterns of introduction and spread that are otherwise difficult or impossible to ascertain. This study is the first to directly determine that human-mediated dispersal is much more important to the continued expansion of non-native earthworm species than is natural spread from diffusion of existing populations. Further, the fact that multiple introductions appear to be clustered at sites like boat landings provides clear support for the idea that changes in human behaviour can have pivotal affects on the future trajectory of these invasions. The prevention of future introduction is key to the protection of northern forests and the resources they provide, and this study will no doubt lead to more effective targeting of limited resources in education and research as well as inform potential regulatory or policy decisions.

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doi: 10.1111/j.1365-294X.2007.03678.x

PERSPECTIVE

Can we stop transgenes from taking a walk on the wild side?

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Abstract

Whether the potential costs associated with broad-scale use of genetically modified organisms (GMOs) outweigh possible benefits is highly contentious, including within the scientific community. Even among those generally in favour of commercialization of GM crops, there is nonetheless broad recognition that transgene escape into the wild should be minimized. But is it possible to achieve containment of engineered genetic elements in the context of large scale agricultural production? In a previous study, Warwick *et al.* (2003) documented transgene escape via gene flow from herbicide resistant (HR) canola (*Brassica napus*) into neighbouring weedy *B. rapa* populations (Fig. 1) in two agricultural fields in Quebec, Canada. In a follow-up study in this issue of Molecular Ecology, Warwick *et al.* (2008) show that the transgene has persisted and spread within the weedy population in the absence of selection for herbicide resistance. Certainly a trait like herbicide resistance is expected to spread when selected through the use of the herbicide, despite potentially negative epistatic effects on fitness. However, Warwick *et al.*'s findings suggest that direct selection favouring the transgene is not required for its persistence. So is there any hope of preventing transgene escape into the wild?

Keywords: *Brassica napus*, *Bo rapa*, gene flow, hybridization, transgene

Received 9 November 2007; revision accepted 13 November 2007

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