

Invasion patterns of Lumbricidae into the previously earthworm-free areas of northeastern Europe and the western Great Lakes region of North America

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Abstract We examine the patterns of expansion of exotic European earthworms in northeastern Europe and the western Great Lakes region of North America. These areas share many ecological, climatic and historical characteristics and are devoid of indigenous earthworm fauna due to Quaternary glaciations. These regions are being colonized by a similar suite of exotic lumbricid species and it is unlikely that this is the result of chance, but rather indicates that these species have particular characteristics making them successful invaders. The present macro-scale distributions of earthworm species in northern Russia show little connection to the pattern of the last glaciation.

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Rather, the primary factors that determine the current distributions of earthworm species include climatic conditions, the life history traits of different earthworm species, the suitability of habitat and intensity and patterns of human activity. In the western Great Lakes region of North America, there are three primary factors affecting current distributions of exotic earthworm species including the patterns of human activity and land use practices, the composition of particular source populations of earthworms associated with different vectors of transport and the soil and litter properties of habitats across the region. Disturbance of a habitat does not appear to be a prerequisite to the invasion and establishment of exotic earthworms. Analysis of the macro-scale distributions of Lumbricidae species in northeastern Europe may provide important insights into the potential of invasive European earthworm species to spread in North America, and identify potentially invasive species.

Keywords Soil animals · Jump dispersal · Climatic conditions · Frost tolerance · Vegetation type · Disturbance · Fish bait

Introduction

Emerging research on the consequences of exotic earthworm invasion in North America (McLean

and Parkinson 1997; Bohlen et al. 2004a; Hale et al. 2005) has increased interest in understanding the patterns and factors controlling invasion dynamics, particularly in regions that contain no native earthworm species (Bohlen et al. 2004b). In this paper, we examine the patterns of expansion of exotic earthworm populations in northeastern regions of Europe and the cold-temperate western Great Lakes region of North America. These areas share many ecological, climatic and historical features and are devoid of indigenous earthworm fauna due to quaternary glaciations (Gates 1977; Reynolds 1994, 1995). Both areas are currently being colonized by a strikingly similar array of lumbricid species of primarily European origin.

Considering the broad similarity of climatic and edaphic conditions, the processes that determine species distribution and abundance may be analogous on both continents. Analysis of the macro-scale distributions of Lumbricidae species in northeastern Europe may provide important insights into the potential of invasive European earthworm species to spread in North America, as well as identify other potentially invasive species, which have not yet reached North America. Similarly, the regional and stand level patterns and dynamics of earthworm invasions in North America will contribute to an understanding of potential expansion patterns of earthworms in cold-temperate regions of Europe and Asia.

In this paper we first address the macro-scale distribution of peregrine (Lee 1985) earthworm species in northeastern Europe (north of 55° N, east of 30° E). In addition, we briefly describe the preferred habitats of the most active colonizers toward the northeastern border of their natural range in Europe. The data provided here were compiled from a range of soil-zoological surveys performed during the last 30 years. Of course, the intensity of sampling varied, and some less accessible areas are poorly studied. However, we believe that this information may provide basic information on the broad tolerance of earthworm species to climatic and environmental conditions. We then discuss and compare the main factors that govern the distribution of earthworm species in northeastern Europe and in northern hard-

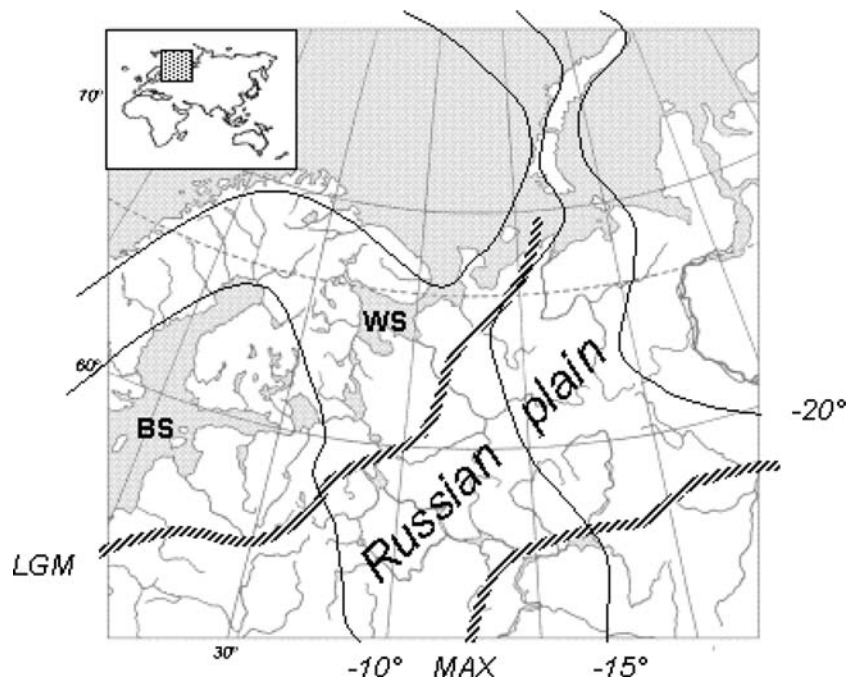
wood forests of the western Great Lakes region of U.S.A.

Northeastern Europe: macro-scale distribution of earthworms

The northern part of the Russian plain that lies between Fennoscandia and the Ural mountains is mainly covered by coniferous boreal forests of taiga type, which are gradually replaced by tundra biomes north of 65° latitude. Most of this territory was covered by Pleistocene ice shields (Fig. 1), which presumably eliminated indigenous earthworm fauna. Only a few endemic species (*Eisenia intermedia*, *E. uralensis*, *Perelia tuberosa*, *P. diplotratheca*) remain in the middle and southern Ural Mountains and adjoining regions, where they often dominate local earthworm communities (Perel 1979; Vsevolodova-Perel 1997). However, the present-day macro-scale distribution of earthworm species shows little connection to the pattern of the last glaciation. The earthworm fauna of the northern Russian plain is composed mainly of peregrine species of European origin (*Aporrectodea caliginosa*, *A. rosea*, *A. longa*, *Alolobophora chlorotica*, *Octolasion tyrtaeum*, *Lumbricus terrestris*, *L. castaneus*, *L. rubellus*, *Dendrobaena octaedra*, *Dendrodrilus rubidus*, *Eisenia fetida* and *Eiseniella tetraedra*). Some other species, e.g., *Aporrectodea icterica* and *Octolasion cyaneum* have been occasionally found in parks and botanical gardens, but never in natural habitats. A few species of Ural and Siberian origin are common east of 50° E, with *E. uralensis* penetrating slightly further westward (Vsevolodova-Perel 1988). An exception is *Eisenia nordenskioldi*, a Siberian species which colonized many localities throughout the eastern Russian plain, from forest-steppe to taiga and tundra biomes.

The eastern Baltic Sea region seems to be a main starting point for many earthworm species colonizing the Russian plain. Some species typical in the temperate zone of Europe, such as *A. chlorotica* and *A. longa*, occur rarely east of 30° E and only in anthropogenic habitats (Vsevolodova-Perel 1988).

Fig. 1 The furthest glacial maximum (MAX) and last glacial maximum (LGM) of Quaternary glaciation in northeastern Europe and the Russian plain (north of 55°N, east of 30°E). Isotherms indicate the mean air temperature in January. The general areas of the White Sea basin (WS) and the Baltic Sea basin (BS) are indicated



Three endogeic species have successfully colonized the northern part of the Russian plain. *Aporrectodea caliginosa* and *A. rosea* have similar ranges (Fig. 2A) reaching the coast of the White Sea to the north and Ural piedmont to the east. However, toward the eastern extremes of their ranges both species are increasingly restricted to cultivated soil (e.g. vegetable gardens), secondary deciduous forests and river valleys. As a rule, they are absent in pristine coniferous forest stands north of 60° N. *Octolasion tyrtaeum (lacteum)* has colonized a considerably larger area and inhabits zonal (boreal) forests of taiga type, though often at a very low density (Fig. 2B). The density is usually much higher (≥ 30 ind. m^{-2}) in lowlands and hydromorphic habitats such as flooded meadows and lotic bogs (Perel 1979). *Octolasion tyrtaeum* is well adapted to moist habitats and can survive prolonged periods of inundation and oxygen deficiency due to an extensively developed subcutaneous capillary network (Semenova 1968) and high hemoglobin levels (Byzova 1974). In contrast to the *Aporrectodea* species, *O. tyrtaeum* has rarely been documented in anthropogenic habitats.

Lumbricus terrestris is the single anecic species that penetrates slightly farther than 60° N. In the

central part of the Russian plain (e.g., around Moscow) this species can be very abundant in unmanaged mixed forests, but in the taiga zone was only found in the vicinity of human settlements (Fig. 2C). The epi-endogeic species *L. rubellus* was found in many places north of 60°, mostly in meadows, secondary forests and in human settlements (Fig. 2C). The smaller epigeic species *L. castaneus* is relatively abundant in the western part of the Russian plain in broad-leaved and mixed forests, but was not recorded north of 60°. *Dendrodrilus rubidus* (Fig. 2D) occupies an area similar to *O. tyrtaeum*, but penetrates further north in the White Sea basin. The strictly anthropochorous “manure worm” *E. fetida* seems to be completely frost-intolerant even as cocoons (Holmstrup et al. 1990), but was regularly found in dung or bark heaps and similar habitats at places north of the Arctic circle in the White Sea basin which have relatively mild winters.

The epigeic species *D. octaedra* and the epi-endogeic species *E. nordenskioldi* (Fig. 3) have much broader distributions than all other species. Both species populate taiga, but also tundra-type biomes, occasionally reaching relatively high densities (≥ 50 ind. m^{-2} ; Perel 1979). *D. octaedra* was reported across northeastern Europe,

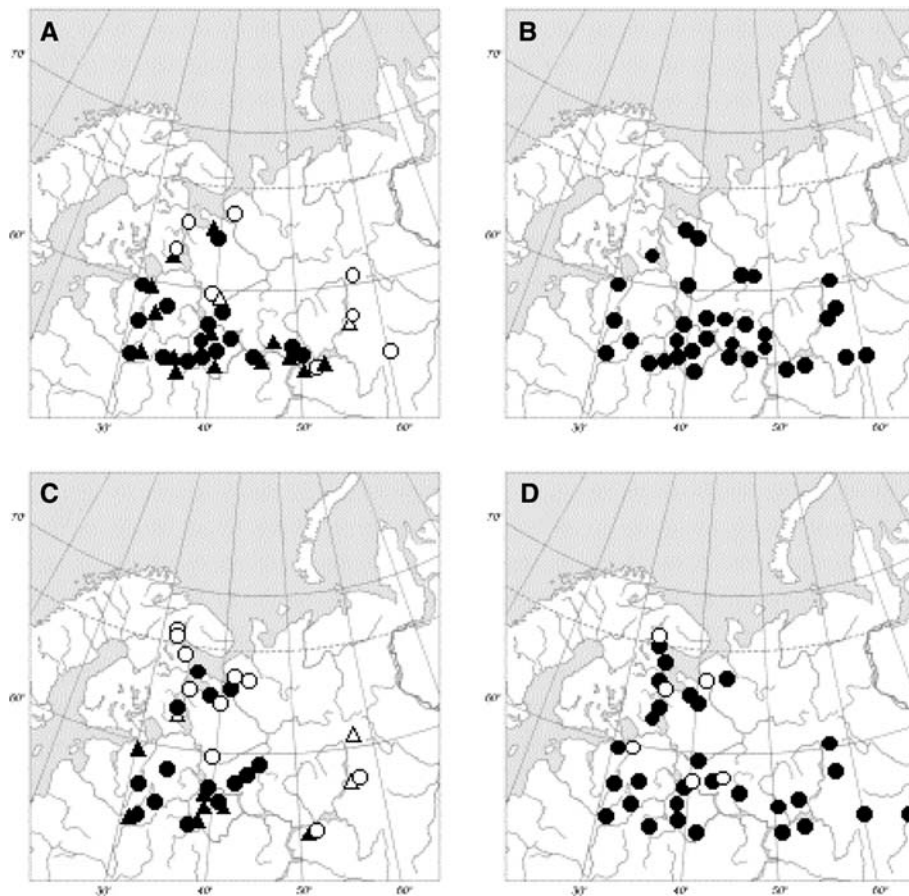


Fig. 2 Macro-scale distribution of earthworm species in northeastern Europe (north of 55°N, east of 30°E). **A:** *Aporrectodea caliginosa* (circles) and *A. rosea* (triangles), **B:** *Octolasion tyrtaeum*, **C:** *Lumbricus rubellus* (circles)

and *L. terrestris* (triangles), **D:** *Dendrodriilus rubidus*. Filled symbols indicate natural or moderately transformed habitats; open symbols indicate anthropogenic habitats

including some arctic islands (e.g. Southern Novaya Zemlya; Fig. 3A). Unlike Lumbricidae species of European origin that appear to be invading from the central Russian plain north-eastward, *E. nordenskioldi* is apparently colonizing northern Europe westward from Siberia, and was rarely found west of 40° E (Fig. 3B).

Overall, the macro-scale distribution of earthworms in northeastern Europe shows a very characteristic pattern: the number of species is at a maximum in western regions and decreases sharply in a north-eastward direction. In addition, the northern boundary for most species penetrating north of 55° on the Russian plain is between 65 and 68° N in the west and decreases to between 55 and 60° N in the east. Notable exceptions are *D. octaedra* and *E. nordenskioldi*,

which occur north of the Arctic Circle even at the northeastern extreme of Europe and in West Siberia.

North America: European earthworm invasion of northern hardwood forests

Native North American earthworms present in the western Great Lakes region (Michigan, Minnesota and Wisconsin) are thought to have been extirpated by the Wisconsinan glaciers which covered virtually all of the region; recolonization by native North American species from southern refugia has not yet reached most of the area (James 2004). It is assumed that exotic earthworms were originally transported to the region

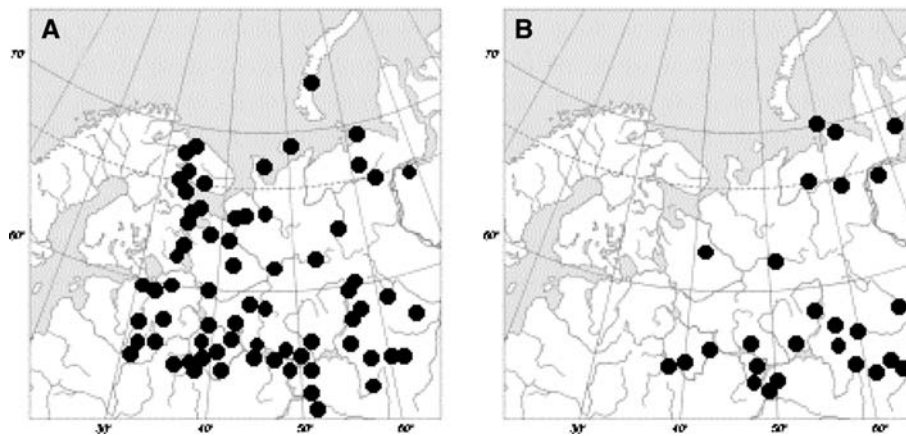


Fig. 3 Macro-scale distribution of earthworm species in natural or moderately transformed habitats in northeastern Europe (north of 55°N, east of 30°E). **A:** *Dendrobaena octaedra*; **B:** *Eisenia nordenskioldi*

during European settlement through the dumping of soil used for ballast in ships and through soils associated with plant material carried by settlers (Reynolds 1977; Gates 1982; Lee 1985; James 2004; Reynolds et al. 2002). Our studies have been restricted to mature sugar maple (*Acer saccharum*) dominated forests of the Chippewa National Forest in north central Minnesota and the Chequamegon National Forest in north-western Wisconsin (Holdsworth et al. 2004; Hale et al. 2005). Secondary tree species include yellow birch (*Betula alleghaniensis*), paper birch (*Betula papyrifera*) and basswood (*Tilia americana*) with ironwood (*Ostrya virginiana*) and American elm (*Ulmus americana*) in the sub-canopy and sapling layers. Soils are generally deep, well-drained and light colored Eutroboralfs (USDA 1997) that, in the absence of earthworms, are characterized by a thick forest floor composed of O_i (L), O_e (F) and O_a (H) layers. These forests exist within a matrix of large and small lakes and a variety of forested and non-forested vegetation communities across a wide range of soil conditions. The climate is humid, continental, cold temperate with a median growing season of 115–134 days and snow cover from late November to early April. Normal mean temperatures in January are –13 to –15°C and 20°C in July.

Most of the peregrine European lumbricids that can survive the winter conditions of this region are present somewhere in the landscape (Reynolds et al. 2002; Hale 2004). Fifteen species

of exotic earthworms have been recorded in the three western Great Lakes states (Reynolds 1995; Reynolds et al. 2002). The most common include *D. octaedra*, *A. caliginosa*, *A. tuberculata*, *A. rosea*, *L. rubellus* and *L. terrestris*. *O. tyrtaeum* and *D. rubidus* are also well documented but with less widespread distribution than the other species.

Mechanisms and constraints of earthworm distributions

The primary factors that determine the large-scale distribution of earthworms in northeastern Europe are apparently climatic conditions, suitability of habitat and the patterns of human activity and land use practices. These factors are obviously connected, as more temperate climatic regions often contain habitat types amenable to earthworm colonization. These areas were also colonized the earliest by humans, who subsequently transformed natural habitats and through their activities transported earthworm species to the region. At the smaller scale of the western Great Lakes region of North America, the differences in climatic conditions are presumably of minor importance. The presence, species composition and abundance of earthworms depend on the composition of particular source populations, different vectors of transport, and soil and litter properties of available habitats across the region.

Climatic constraints

Climatic conditions in northeastern Europe become increasingly harsh in a northeasterly direction across the Russian plain. Summer temperatures decrease gradually from south to north with the mean July isotherm of +15°C lying approximately at 65° N. Simultaneously, the mean and minimum winter isotherms lie meridionally, with mean air temperature in January decreasing from -2° to -5°C in the Baltic region to -20°C in the Ural piedmont (Fig. 1). With the exception of *E. nordenskioldi* and *D. octaedra*, earthworm species have very limited ability to withstand soil freezing (Holmstrup and Zachariassen 1996; Petersen and Holmstrup 2000; Berman et al. 2002), and minimal winter soil temperature may be a main determinant of the northern and eastern boundary of their range.

The geographical distributions of earthworm species across northeastern Europe mirror the increasing ability of different earthworm species to withstand severe climatic conditions. A ranking of earthworms species based on laboratory data on their frost tolerance (*A. chlorotica* < *L. castaneus* < *L. terrestris* < *A. rosea* ≤ *A. caliginosa* < *L. rubellus* < *O. tyrtaeum* < *D. rubidus* < *D. octaedra* ≤ *E. nordenskioldi*) closely corresponds to the broad geographical patterns of these species across the region. Species such as *A. chlorotica* are very frost-sensitive even as cocoons (Holmstrup and Zachariassen 1996). Cocoons, but not postembryonic stages, of *Aporrectodea* and *Lumbricus* species may withstand cooling to between -5 and -8°C (Holmstrup et al. 1990; Holmstrup and Zachariassen 1996) and the cocoons of *D. rubidus* and *D. octaedra* can survive -35°C (Dymond et al. 1997; Berman et al. 2002).

Most earthworm species (with the possible exception of *D. octaedra* and *D. rubidus*) are not able to complete their life cycle during one growing season at the northern edge of their range, so adults and juveniles must either withstand soil freezing or find appropriate refugia in order to survive until spring. For example, endogeic and anecic species may avoid freezing by hibernating in deep soil layers. However, adult and juvenile *E. nordenskioldi* are able to overwinter in a frozen state at temperatures down to

-30°C, whereas cocoons can withstand -35°C (Berman and Leirikh 1985). Berman et al. (2002) also reported that Siberian and some east-European populations of *D. octaedra* are freeze-tolerant at postembryonic stages of the life cycle, with about 50% of experimental animals surviving freezing to between -10 and -12°C.

Many of the European earthworm species colonizing the Great Lakes region (e.g., *A. rosea*, *L. rubellus*, *L. terrestris*) are not frost-tolerant. This suggests that they hibernate in deep soil layers, though the question needs further investigation. On the other hand, the cold winter climate of the region may have prevented the expansion of *E. fetida* and Asian species of the genus *Amyntas*. These species prevail in commercial, community and private composting sites across the region (C. Hale personal observations), but have never been documented in natural habitats.

Suitability of habitats

The range of habitats potentially suitable for earthworm colonization decreases sharply across northeastern Europe in a northeasterly direction as broad-leaved and mixed forests are replaced by pine, spruce and larch stands of taiga type. Acidic litter of coniferous trees coupled with low evaporation rates during cold summer promote the leaching of base cations and form generally very acidic soils with pH rarely above 5. Acidic soils under coniferous forests are unfavorable for most earthworms, except acid-tolerant species such as *D. octaedra*, *D. rubidus* and *E. nordenskioldi*. The freeze-hardiness and parthenogenic nature of these three species, combined with their ability to tolerate acid soils and exploit poor quality litter, are seemingly the major reasons for their success in colonizing vast areas of northeastern Europe and Siberia, including areas with permafrost soils.

However, even in the taiga zone some deciduous forests are always present as early successional stages following disturbances such as fire or logging. These forests are typically dominated by birch, aspen or alder and, along with meadows in river valleys, penetrate deeply into the taiga zone. They form important corridors for the primary

establishment of a range of earthworm populations. For example, zonal *Picea* and *Pinus* forests along the Onega River (ca 63° N, 38° E) are sparsely populated by *D. octaedra* and *D. rubidus*, with total densities of 1–7 ind. m⁻². Secondary *Populus* forests of the same area harbor much larger and more diverse populations of earthworms including *D. octaedra*, *L. rubellus* and *O. tyrtaeum* with total densities up to 80 ind. m⁻², while on flooded and dry meadows the density of earthworms reaches 42–104 ind. m⁻² including *D. octaedra*, *D. rubidus*, *L. rubellus*, *O. tyrtaeum*, *A. rosea* and *A. caliginosa* (Perel 1979; Kudryasheva 1997).

In predominately deciduous forests of the western Great Lakes region the expansion of European lumbricids does not appear to be significantly affected by edaphic conditions or inhospitable habitat types even though earthworm populations or species may be limited in some localities by low soil pH (e.g., white cedar bogs) and/or dry, coarse textured soils (e.g., Michigan dune complex; Nordström and Rundgren 1974; Staaf 1987; Pop 1997). However, in areas that have been colonized by exotic earthworms, the population size and species composition of earthworm communities will ultimately be dependent upon soil texture, pH, moisture, and the palatability and quantity of litter (Nordström and Rundgren 1974; Staaf 1987; Judas 1990; Ponge and Delhaye 1995; Lavelle 1997; Pop 1997; Bohlen et al. 2004a). Spruce and pine forests with less palatable litter over sandy, acidic soils will likely have the lowest earthworm biomass and species richness (*D. octaedra* is often the only species present), while sugar maple dominated forests with highly palatable litter and loamy, mesic soils will likely have the highest biomass and species diversity.

Anthropogenic transformation of habitats

Disturbance of natural habitats is thought to facilitate invasions of exotic species, including invasive earthworms (Kalisz and Wood 1995). This is certainly true for northeastern Europe where human activity strongly influenced local vegetation and soils by slash-and-burn and later conventional agriculture, pasturage, intensive

logging, and increased frequency of forest fires. Colonization of this region by agrarian human populations started long before 1000 AD, and intensified considerably in the 13th through the 15th centuries (Osipov and Gavrilova 1983). As a consequence of human activity there has been an expansion of meadows and secondary deciduous forests, especially around large settlements, along rivers and other trading routes. Many earthworm species are closely associated with human settlements at the northeastern edge of their range (Fig. 2).

Abandoned human settlements, although already overgrown by taiga vegetation, often form local oases of increased diversity of earthworms, which persist for decades and most likely for centuries (A.V. Tiunov, personal observations). Similar phenomena have been described elsewhere (Enckell and Rundgren 1988; Kalisz and Dotson 1989).

In contrast, natural or anthropogenic transformation of habitats seemingly is not required for successful colonization by exotic earthworm species in the Great Lakes region (see also Frelich et al., this issue). While human activity is certainly an important means of transporting European earthworm species to an area (see below), there is no evidence that disturbance is required to allow establishment of earthworms once they have reached a site. Throughout the western Great Lakes region, managed, unmanaged, and old-growth hardwood forests are being invaded by European earthworm species where source populations are present (Alban and Berry 1994; Hale 2004; Holdsworth et al. 2004; Gundale et al. 2005). The level to which human disturbance of habitats may further facilitate establishment of earthworms is unknown at this time. However, the speed at which pristine habitats can be invaded when earthworms reach a new site suggests that disturbance is of minimal importance to invasion dynamics in the region. Furthermore, the probability of finding exotic earthworm species in any given location is strongly related to the duration, type, and intensity of human use (Holdsworth et al. 2004). In the southern areas of Minnesota and Wisconsin with the longest duration (~150 years) and greatest intensity of human use since European settlement, several European

earthworm species (i.e., *L. rubellus* and *Aporrectodea* species) are ubiquitous.

Dispersal by humans

The natural rate of dispersal of an established earthworm population is relatively slow for European lumbricids (5–10 m/year; Marinissen and Van den Bosch 1992; Dymond et al. 1997; Hale et al. 2005). Thus, anthrochorous dispersion has likely played a key role in the spreading of earthworm populations across northeastern Europe, but we are not aware of any study on the history of this process. The continuing use of earthworms as fishing bait ensures a constant introduction of new populations along rivers and lakes. This is particularly true for *L. rubellus*, which forms numerous small isolated populations in White Sea basin, obviously associated with popular fishing spots (A.V. Tiunov, personal observations).

Likewise, in the Great Lakes region, exotic earthworms have been spread as released fishing bait, as indicated by the proximity of many invasion epicenters to lakes shores, boat landings and cabins (Proulx 2003). The expansion of human activities has led to the establishment of thousands of epicenters of earthworm invasion. These epicenters are associated not only with higher earthworm abundance relative to the surrounding landscape, but also with increased species richness because fishing bait often contains other species (i.e., *Aporrectodea* species, *D. octaedra*, *D. rubidus*, *O. tyrtaeum*) in addition to the *L. terrestris* and *L. rubellus* that are marketed (A. Holdsworth and C. Hale, personal observations). Overall, the distribution of most earthworm species is significantly positively related to roads and to fishable streams (Fig. 4, Holdsworth et al. 2004). The spatial distribution of earthworm invasion epicenters is a major factor affecting the distributions of European earthworm species in the early stages of invasion across the landscape.

The composition of exotic earthworm populations in any given location will also be related to the species composition of source populations associated with the dominant vectors of earthworm transport and introduction in the area. Areas with few lakes and little fishing may have

earthworm populations dominated by epigeic and endogeic species that are more commonly transported by home and road building activity, logging and off-road vehicles (Dymond et al. 1997; Hale 2004; A. Holdsworth personal observations). Recent increase in the establishment of community yard waste compost sites and personal vermicomposting favors invasion of epigeic and epi-endogeic species such as *L. rubellus* (C. Hale personal observations).

Species traits and ecological relationships

While the distribution of exotic earthworm species overall is strongly affected by human activity patterns and the composition of source populations, life history characteristics of different species also contribute to species-specific distributional patterns (Reynolds 1977; Hale 2004; Holdsworth et al. 2004). In particular, the reproductive strategies employed by different earthworm species may contribute to their geographic distributions. At least four most active invasive species (*E. nordenskioldi*, *D. octaedra*, *D. rubidus*, *O. tyrtaeum*) are either totally or partially parthenogenic (Perel 1979). This trait may facilitate reproduction at very low densities, characteristic of extreme habitats, where a single surviving individual could establish a local population. Parthenogenic reproduction may also contribute to the rapid expansion of a population once a well-adapted morph arrives in a particular location (Jensen and Holmstrup 1997; Holmstrup and Loeschcke 2003). Parthenogenic *D. octaedra* is the most widespread species in both regions, due to high reproductive rate, ability to colonize coniferous forest floors with low pH and poor quality litter, and cold hardiness. Its small body size facilitates accidental spread by vectors such as logging truck tires (Dymond et al. 1997) that are less likely for larger bodied species, such as *L. terrestris*.

While many organisms prey on earthworms (i.e., birds, salamanders, shrews, foxes, badgers and many macro-invertebrates), the impacts of predation on earthworm population dynamics in natural habitats are difficult to estimate and remain generally unknown (Judas 1989). In parts of the United Kingdom there are organisms, such as

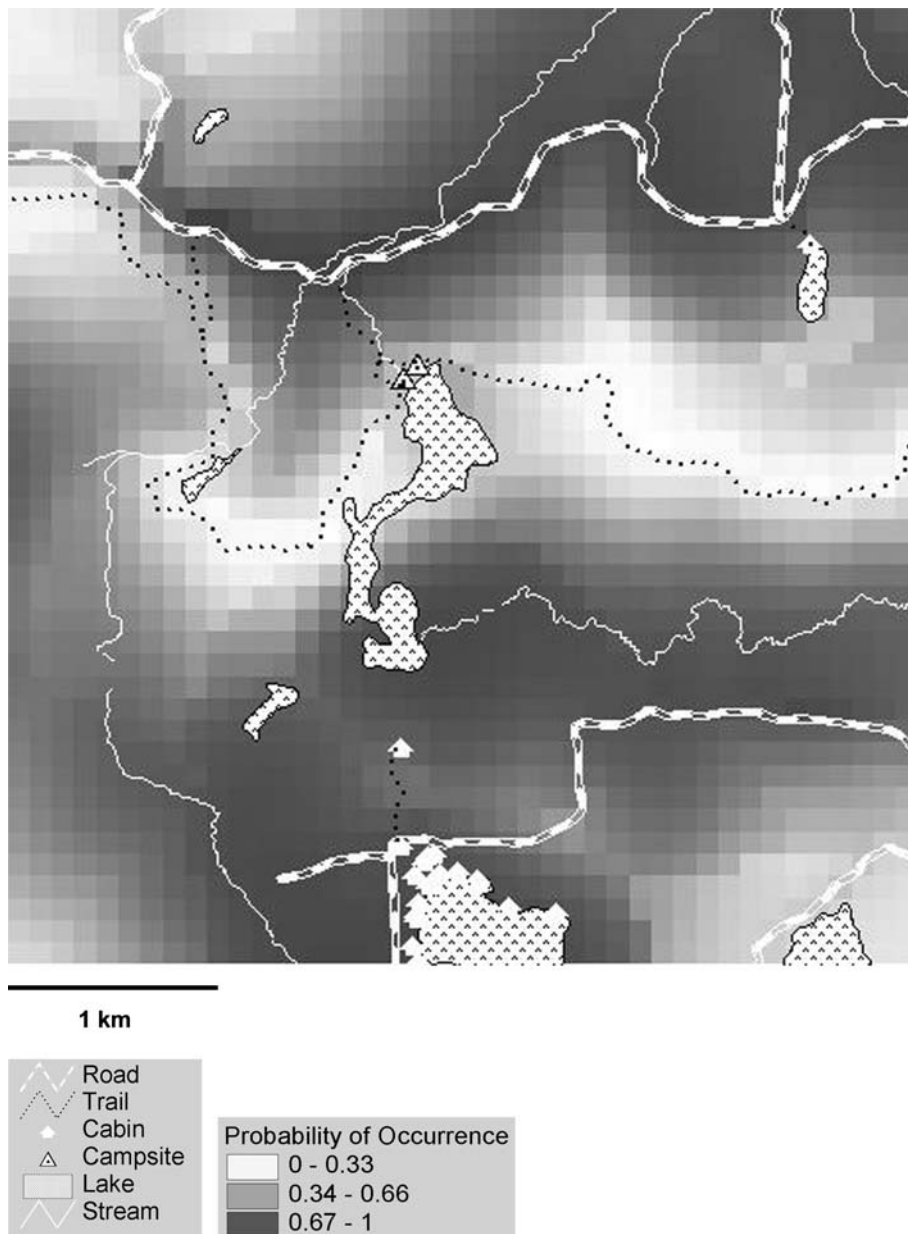


Fig. 4 Estimated probability of occurrence of invasive earthworm species *Lumbricus terrestris* in relation to landscape features in a Wisconsin wilderness area. Esti-

mates are based on regression models using 291 plots from 40 maple-dominated forest stands on well-drained and light coloured Eutroboralfs

the New Zealand flatworm (*Artioposthia triangulata*), that have been credited with significantly limiting earthworm populations (Lillico et al. 1996; Nixon 1996). However, there is no evidence suggesting that such top-down control of earthworm populations is important in northeastern Europe or Great Lakes region (Reynolds et al. 1977; Ducey and Noce 1998).

mates are based on regression models using 291 plots from 40 maple-dominated forest stands on well-drained and light coloured Eutroboralfs

“Invasional meltdown”

Soil and litter properties not only shape earthworm populations but are shaped by invading earthworms in ways that may facilitate the invasion by other earthworm species. For instance, endogeic species (i.e., *Aporrectodea* species and *Octolasion tyrtaeum*) are commonly transported

via a range of human activities. However, their spread from an introduction site may be limited by the availability of soil organic matter (Hendrix et al. 1999; Shakir and Dindal 1997). In native, earthworm-free hardwood forests that maintain thick organic horizons and have naturally low soil organic matter content, alterations of forest floor material by invading epigeic and epi-endogeic earthworms may facilitate the establishment of endogeic species by mixing O and mineral soil horizons, thereby making this pool of organic material more accessible (Hale et al. 2005). This situation may be regarded as an example of “invasional meltdown” (Simberloff and von Holle 1999), in which one species facilitates invasion by another (see also Frelich et al. and Hendrix et al., this issue).

Conclusion

Overall, the pattern of earthworm invasion closely resembles the “jump dispersal” model (Shigesada et al. 1995). That is, the probability of colonization of distant localities is directly dependent on the availability of dispersal opportunities, and much less so on the distance from the source and time since initial colonization (MacIsaac et al. 2001). This is especially true for endogeic and anecic earthworm species, which are closely associated with centers of human activity in northeastern Europe and the western Great Lakes region of North America.

The earthworm species colonizing new areas in Russia are largely the same as those invading North America. It is unlikely that this is the result of chance, but rather indicates that this suite of species has particular characteristics that make them successful invaders. The comparison of climatic conditions across the two regions suggests that many European species may considerably extend their range in North America. In particular, Berman et al. (2002) suggested that winter temperature would not constrain the invasion of *D. octaedra* in large areas of North America still devoid of earthworms. *Eisenia nordenskioldi* may deserve special attention. To our knowledge *E. nordenskioldi* is not recorded in North America,

though it has a high potential to colonize boreal forests and even tundra biomes in the upper arctic. Its presence on many arctic islands along the Siberian coast (Vsevolodova-Perel 1988) suggests that *E. nordenskioldi* might have been dispersed by humans. Given that it is also common in the Chukotka and Kamchatka Peninsulas of the Russian far east, it could reach North America across both the Atlantic and Pacific Oceans. However, the main area of this species distribution lies far from principal trading routes, making a potential invasion less likely. Models combining habitat suitability parameters, the spatial distribution of source populations, and dispersal vectors could greatly improve our understanding of invasion potential of such exotic earthworm species.

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