



Forest successional history and earthworm legacy affect earthworm survival and performance



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ABSTRACT

Introduced European and Asian earthworms, considered ecosystem engineers due to their ability to rapidly deplete leaf litter layers and alter forest floor communities and processes, continue to spread in North America. Environmental factors facilitating or limiting earthworm distributions are poorly understood. We experimentally assessed how successional age of forests in the Finger Lakes Region of New York, USA, and soil microbial communities (i.e. biotic resistance) influence earthworm communities and survival and growth of two common earthworms, *Lumbricus rubellus* and *Dendrobaena octaedra*. We used historic aerial photos and ArcGIS to establish a forest regeneration chronosequence where we surveyed earthworm communities. In addition, we collected forest soils from adjacent earthworm-invaded and earthworm-free zones, and followed survival and growth of individuals in sterilized or untreated soils over a seven week period. Our results show that both forest successional age and earthworm legacy effects influence earthworm performance. Younger forests had higher earthworm populations compared to older forests despite similar overstory tree composition, highlighting the importance of local conditions and land-use histories. Individual earthworms grew faster in soils with earthworm legacies compared to individuals in previously earthworm free soils. Contrary to our expectations, soil sterilization reduced earthworm performance, potentially through elimination of food items. Earthworms modify soil conditions, creating positive soil feedback loops favoring their own growth. Patchy earthworm distributions may be a function of earthworm preference for favorable conditions created by conspecifics, and there appears little biotic resistance to limit their spread.

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Introduction

Introduced European and Asian earthworms have been identified as major transformative species and ecosystem engineers in previously earthworm-free North American forests (Bohlen et al., 2004a,b; Hale, 2008; Hale et al., 2006; Hendrix and Bohlen, 2002; Holdsworth et al., 2007; James, 1995; Nuzzo et al., 2009; Ransom, 2011). Before earthworm invasions, soils are characterized by a thick, stratified humus layer and fungal-dominated decomposition. Earthworm-invaded forests usually lack stratified soil profiles (and often have bare mineral soil) with bacterial dominated decomposition (Bohlen et al., 2004a,b; Dempsey et al., 2013; Groffman et al., 2004). Earthworm invasions affect decomposition (Suarez et al., 2006b), fine root dynamics and mycorrhizal associations (Fisk

et al., 2004; Gilbert et al., 2014; Lawrence et al., 2003), seedling survival and growth (Dávalos et al., 2013, 2014; Dobson and Blossey, 2015), seed bank dynamics (Nuzzo et al., 2015), foliar chemistry, and predator, parasite and pathogen communities (Cameron and Bayne, 2012; Frelich et al., 2006). Earthworm invasions generally promote grasses, sedges, non-mycorrhizal and non-native plants at the expense of native, herbaceous understory plants (Fischelli et al., 2013; Hale et al., 2006; Heneghan et al., 2006; Kourtev et al., 1999; Madritch and Lindroth, 2009; Nuzzo et al., 2009), although recent studies have shown negative earthworm impacts on sedges (Dávalos et al., 2013; Dobson and Blossey, 2015). Earthworm activity has negative ripple effects extending to other taxa on the forest floor such as invertebrates, salamanders, ground-nesting birds (Loss et al., 2012; Maerz et al., 2009; Ransom, 2011; Snyder et al., 2009) and below-ground food webs (Szlavec et al., 2011).

The true diversity of introduced earthworm taxa, their distribution, origins, taxonomy and systematics remain poorly documented and contested (Blakemore, 2008; Hendrix, 1995; Reynolds and Wetzal, 2011). Well over a dozen introduced species are common in

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the northeastern United States with variable numbers of species in the most common genera of *Amyntas*, *Aporrectodea*, *Dendrobaena*, *Lumbricus* and *Octolasion* (Bohlen et al., 2004a; Dávalos et al., 2015). Different earthworm life histories and feeding strategies (epigeic, endogeic, and anecic) are expected to have different impacts on forest fauna and flora, soil biota and nutrient dynamics, but these effects have not been well investigated until recently (Dempsey et al., 2013; Eisenhauer et al., 2012; Greiner et al., 2012; Nechitaylo et al., 2010; Sackett et al., 2013; Straube et al., 2009).

Despite the ubiquitous nature of earthworms close to human habitations, earthworms show patchy distributions in eastern forests (Bohlen et al., 2004a; Dávalos et al., 2015; Dobson and Blossey, 2015; Sackett et al., 2012; Szlavecz and Csuzdi, 2007), and distinct invasion fronts (Hale et al., 2005, 2008). The presence, dispersal and distribution of non-native earthworms appears inextricably linked to human activities. Roads and boat launches serve as invasion hubs and provide important source populations even in remote areas (Cameron et al., 2008; Frelich and Reich, 2009; Gundale et al., 2005; Hale, 2008; Holdsworth et al., 2007; Sackett et al., 2012). The positive attitudes toward earthworms and their assumed beneficial effects in gardens, fields and forests are deeply ingrained in human populations in North America (Seidl and Klepeis, 2011) and many species are accidentally and purposefully distributed through the sale of ornamental plants and fishing bait (Keller et al., 2007).

Earthworms have dispersed from points of introduction and source populations to colonize large portions of historically earthworm-free North America. In the Great Lakes region, earthworm 'invasion fronts,' or the leading edge of discernible earthworm impacts, expand at an average rate of 7.5 m/year (Hale et al., 2005) and have progressed substantially over a decade (Eisenhauer et al., 2011). However, recent studies highlight the dynamic nature of earthworm invasion fronts and demonstrate that steady range expansion of earthworms is not always the case. Long-term monitoring of an earthworm invasion front in a central New York forest found no evidence of range expansion (Stoscheck et al., 2012). In Virginia, the distribution of a common invasive earthworm species was far less extensive than anticipated given documented dispersal rates in other areas, time since introduction, and seemingly favorable environmental conditions in surrounding soils (Ransom and Billak, 2015). While many earthworm fronts progress into earthworm-free soils, others stall or expand slowly and unevenly for reasons that are not readily apparent and do not appear to be strictly a function of time.

While human aided dispersal and local climate, leaf litter types, particularly C:N and Ca concentration, and previous land-use history (Hendrix, 1995; Hendrix et al., 2006; Ma et al., 2013) have important consequences for earthworm establishment and survival, the current presence/absence patterns or differences in earthworm abundance and community composition remain poorly understood. It is possible that predation and parasitism may affect earthworm populations and distribution patterns since earthworms are well integrated into local food webs (Maerz et al., 2005), but the demographic consequences of these interactions are unknown. The apparently distinct successional pattern of earthworm colonization beginning with epigeic species and followed by endogeic and ultimately by anecic species (Hale et al., 2006; Suarez et al., 2006b) remains poorly understood. The invasion pattern may reflect different dispersal rates, resource partitioning and competition, or varying tolerances to biotic and abiotic factors. Facilitation through positive habitat alteration, whereby epigeic species disturb and alter forest floors in a manner that allows for successful colonization by endogeic and anecic species, was proposed as a mechanism (Hale et al., 2005; Suarez et al., 2006a), but Cameron and Bayne (2011) found no evidence for facilitative interactions.

Evidence from Europe and North America suggests that not just previous land-use history and dispersal limitation but other forms of biotic resistance may affect earthworm invasion success. For example, isolated forests that have never been clear cut in the heavily fragmented landscapes of Maryland show no evidence of earthworm invasion (Szlavecz and Csuzdi, 2007), and earthworm populations decline with forest successional age in North America (Crow et al., 2009) and Europe (Hedde et al., 2007; Trap et al., 2011). We also have evidence for failure of apparently well-adapted earthworms to spread or increase in abundance in minimally disturbed locations away from human altered habitats, including some with presence of native earthworms in eastern North America (Kalisz, 1993; Stoscheck et al., 2012). Soil biotic resistance as a structuring factor of earthworm distribution was rejected (but not experimentally tested) by Hendrix et al. (2006), who instead favored habitat-specific physical and chemical characteristics as explanatory factors. But forest successional age substantially influences soil microbial communities (Jangid et al., 2011), which in turn may have important effects on earthworm invasion and performance as they constitute both potential food items as well as potential antagonists, although the latter has not been investigated.

At present we do not know whether earthworm invasions into less obviously disturbed forests are a function of time, distance to source populations or a function of forest successional age and land-use histories, which in turn could influence the composition and strength of biotic resistance exerted by resident soil biota. Earthworms are considerably more mobile than previously expected, and are able to select preferred habitats dependent upon habitat and food quality (Mathieu et al., 2010). Interestingly, in choice experiments species such as *Aporrectodea icterica* and *L. terrestris* preferentially select areas with current or previous presence of earthworms (Mathieu et al., 2010; McTavish et al., 2013) suggesting a beneficial conditioning of soils by earthworms (Daane and Häggblom, 1999), particularly by conspecifics (Zhang et al., 2010). Species such as *Eisenia fetida* transfer beneficial bacteria through cocoons to their offspring (Daane and Häggblom, 1999; Davidson et al., 2010) and many earthworm species have species-specific symbionts in their nephridia (Zirbes et al., 2012). Whether species-specific and gut-specific symbionts contribute to food processing and assimilation remains under investigation (Drake and Horn, 2007; Singleton et al., 2003; Zirbes et al., 2012).

In the secondary forests of the Finger Lakes Region in central New York State, and in the surrounding region, we frequently encounter earthworm free zones and areas without discernible earthworm impacts (Burtelow et al., 1998; Dávalos et al., 2015; Dobson and Blossey, 2015; Stoscheck et al., 2012; Suarez et al., 2006a) surrounded by a matrix of earthworm occupancy. These invasion fronts appear to remain stable over extended time periods (>10 years, Blossey, pers. obs.) without apparent encroachment (Stoscheck et al., 2012). We used this existing patchy distribution to assess importance of multiple factors in determining colonization dynamics and earthworm performance using a combination of field assessments and soil feedback experiments. We were guided in our investigations by the following hypotheses:

1. Earthworm abundance declines with forest successional age
2. Earthworm abundance decreases with distance from forest edge
3. Earthworms perform better in soils previously occupied by other earthworms
4. Biotic communities in earthworm-free zones reduce earthworm survival and growth
5. The early colonizing species *Dendrobaena octaedra* is less dependent on soil conditioning by other earthworms than the later colonizing *Lumbricus rubellus*

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