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Historical patterns of exotic earthworm distributions inform contemporary associations with soil physical and chemical factors across a northern temperate forest

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ABSTRACT

Understanding environmental factors related to exotic earthworm distributions across invasion stages (i.e., introduction, colonization, regional spread) is critical for assessing long-term impacts on previously earthworm-free forests. Studies following earthworm community establishment in North America, however, remain limited. We address this by characterizing historical and current exotic earthworm distributions in a regionally representative aspen-dominated forest, where their presence was first documented in the early 1900s. We map historic earthworm distribution records in a 360-km^2 area surrounding our current study site, and re-analyze data collected nearly 60 years ago to inform contemporary associations between species densities and environmental factors. Field surveys were conducted over two years (2008–2010) using 10 permanent plots, with concurrent measurements of environmental 'effect factors' determined by large-scale ecosystem processes (leaf litter inputs, soil physical properties, soil C and N content), and environmental 'response factors' likely impacted by earthworm activity over short time scales (annual litter mass loss and soil isotopic values). Present-day communities included five exotic species with varying densities: *Lumbricus rubellus* ≥ *Lumbricus terrestris* >> *Dendrobaena octaedra* ≥ *Aporrectodea* spp. (*Aporrectodea trapezoides* + *Aporrectodea caliginosa*). These species were also present in the landscape in the early to mid-1900s though shifts in species composition, particularly the movement of *L. terrestris* into upland forest soils, were evident. Over two years, earthworm community composition did not show strong temporal or spatial trends characteristic of incipient invasions. However, species-specific associations with environmental factors were observed: *L. terrestris* and *L. rubellus* densities were positively associated with soil C and N content, *Acer rubrum* (red maple) inputs, and soil moisture; and were negatively associated with *Pinus strobus* (white pine) inputs. *D. octaedra*, and *Aporrectodea* spp. densities were positively associated with % sand; and negatively associated with plot-to-road distance. Soil moisture and texture were significant drivers of earthworm species abundance in historical surveys, though associations with soil C were only evident for *Aporrectodea* spp. Contemporary associations between earthworm species and soil C and N content suggest greater nutrient limitation in upland forest soils, while the importance of plot-to-road distance suggests the persistence of dispersal limitation and repeated introductions as a mechanism maintaining population densities. Species-specific associations with environmental response variables were also observed, where: surface soil δ^{13}C depletion was associated with *Aporrectodea* spp. and *D. octaedra* biomass; δ^{15}N enrichment was associated with total earthworm biomass, but negatively associated with *L. rubellus* biomass; and increased leaf litter mass loss was associated with *L. terrestris* and juvenile biomass. As soil C and N pools were not higher in plots with higher earthworm biomass, these results suggest earthworm activity may influence soil nutrient cycling by decreasing turnover times of nutrient pools over the long-term. Our results characterize exotic

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earthworm distributions at scales relevant to forest ecosystem processes, and allow for future extrapolation of laboratory and controlled field studies assessing impacts on soil nutrient cycling across northern temperate forests.

1. Introduction

Quaternary glaciations resulted in the removal of earthworms from northern temperate and boreal regions in North America and northeastern Europe, and northward migrations of endemic earthworm species following glacial retreat have been limited (James, 1995). The reintroduction of earthworm species into northern temperate and boreal regions has instead been facilitated by European human migration and disturbance; beginning in Europe in the 13th–15th centuries, and in North America in the 17th–19th centuries (Tiunov et al., 2006). Interestingly, European migrations into these regions have resulted in a common suite of what are now considered "peregrine" earthworm species of the Lumbrucidae family, including *Aporrectodea caliginosa*, *Dendrobaena octaedra*, *Lumbricus rubellus*, and *Lumbricus terrestris* (James and Hendrix, 2004; Holdsworth et al., 2007). The relatively recent establishment of exotic earthworm populations (i.e., within the last 150 years) in previously earthworm-free North American landscapes has been facilitated by similar climate regimes of northeastern European where these species have been naturalized (Reynolds, 1995; Tiunov et al., 2006). Although climatic drivers determine macro-scale distributions of earthworm species (Lavelle, 1983; Edwards and Bohlen, 1996; Tiunov et al., 2006), regulation of earthworm community composition and density at smaller regional and landscape scales is largely determined by mechanisms of reintroduction and environmental factors.

In North America, the earliest mechanisms of reintroduction were both passive, such as when earthworms were introduced through the removal of soils used as ballast for ships, and active, following the purposeful reintroduction of earthworm species for agriculture (Gates, 1942; Schwert, 1980; Edwards and Bohlen, 1996; Eijsackers, 2011). The latter mechanism is still operative, but is accompanied by a suite of other mechanisms that include the inclusion and release of peregrine earthworm species as fishing bait, and passive dispersal facilitation through road construction, vertebrate transport, and imports of soil-containing materials (Gates, 1982; Ehrenfeld and Scott, 2001; Cameron et al., 2007; Hendrix et al., 2008; Cameron and Bayne, 2009). Although the presence of exotic earthworm species in northern temperate and boreal forests were first documented in the early 1900s, historical patterns of earthworm species abundance and distributions are largely unknown for most areas where incipient invasions are occurring.

Characterization of earthworm community association with environmental factors in European forests accompany a larger understanding of top-down controls such as predation and disease (though this is still limited) (Curry, 1994), the importance of earthworm activity in the remediation of acidified forest soils (Deleporte and Tillier, 1999; Potthoff et al., 2008; Hirth et al., 2009), and the importance of human disturbance and land management in regulating earthworm community establishment (Muys and Granval, 1997; Tiunov et al., 2006; Eisenhauer et al., 2009). In northern temperate and boreal forests of North America, these associations have largely been used to understand the likelihood of invasion success given active mechanisms of introduction. For example, previous work has determined that the primary factors determining invasion success in northern temperate forests include propagule pressure (Hale et al., 2005), seasonal abundance dynamics (Callaham and Hendrix, 1997), and environmental factors including soil pH, temperature, soil moisture, and litter palatability (Decaëns and Rossi, 2001; Whalen, 2004; Reich et al., 2005; Sackett et al., 2012; Fisichelli et al., 2013). Further, in areas where human-mediated dispersal of earthworm species occurs, distance from roads and cabins within forested areas have also been reported as major predictors of earthworm species abundances (Hale et al., 2005; Holdsworth et al., 2007). What remains is a limited understanding of how these associations might change as earthworm communities become established across landscapes. Better understanding of environmental controls on exotic earthworm distributions following regional establishment is essential to extrapolating from laboratory and small plot studies to ecosystem scales at which nutrient dynamics are studied (Whalen and Costa, 2003).

Similarly, earthworm impacts on temperate forest ecosystems have primarily been characterized during incipient invasions in North America, and impacts on some ecosystem processes and properties are better understood than others. Areas of dense earthworm invasion have shifted understory plant diversity and diminished forest floor horizons (Bohlen et al., 2004b; Hale et al., 2006). These invasions have also been linked to decreased soil C stocks (Burtelow et al., 1998; Lachnicht and Hendrix, 2001; Bohlen et al., 2004b; Marhan and Scheu, 2006; Eisenhauer et al., 2007; Sackett et al., 2012), soil C redistribution (Burtelow et al., 1998; Lachnicht and Hendrix, 2001; Bohlen et al., 2004a; Wironen and Moore, 2006; Straube et al., 2009), and increased soil CO_2 exports (Marhan and Scheu, 2006). However, limited information is available on how different earthworm species affect leaf litter disappearance in temperate forest ecosystems (cf. Suárez et al., 2006b; Holdsworth et al., 2008, 2012) and particulate organic matter chemistry in surface soils (Marhan et al., 2007; Crow et al., 2009; Crumsey et al., 2013; Fahey et al., 2013). Therefore, it is necessary to characterize impacts on leaf litter mass loss and soil chemistry following earthworm community establishment to enhance understanding of the ecological consequences of exotic earthworm distributions.

In this study, we analyze two historical data sets to map approximate geographic locations of earthworm species collections in a regionally representative hardwood forest, and characterize relationships between the relative abundances of earthworm species and soil physical and chemical properties qualitatively evaluated approximately 30 years after major logging and fire disturbances. We then report the results of field surveys conducted over two years, nearly 60 years following previous studies, examine contemporary patterns of exotic earthworm species densities, and characterize environmental correlates of species distributions; we consider site distance from potential introduction sites (lake shore and roads) and environmental factors. We divided environmental factors into 'effect factors' determined by large-scale ecosystem processes (leaf litter inputs, soil physical properties, soil C and N content), and 'response factors' likely impacted by earthworm activity over short time scales (litter decomposition, soil isotopic values). We address the following questions: (1) How have the relative abundances of earthworm species and interactions with environmental variables changed as communities become established across the landscape? (2) Considering earthworm species biomass as a proxy for earthworm activity, to what extent do earthworm species distributions affect ecosystem processes