Community Assembly of Earthworms in Previously Glaciated Regions of North America: Current Knowledge, Gaps in Research, and Future Directions

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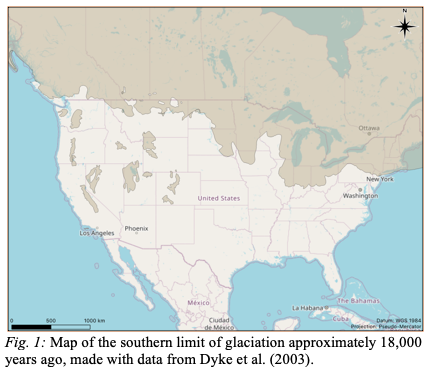
*Introduction:*

Currently, we are in the midst of a large-scale biological invasion that often goes unnoticed. Earthworms have been introduced into North America from Europe, Asia, and other parts of the world and are continuing to spread. While earthworms have many positive effects on certain ecosystems, they can also be harmful, especially when they are invasive (Ferlian et al., 2018).

Understanding earthworm community assembly patterns is consequential to invaded terrestrial ecosystems because they are ecosystem engineers, meaning they contribute greatly to the overall ecosystem structure and functioning (Kooch & Jalilvand, 2008). Community assembly refers to the structure of a group of species that live and interact in the same place (Weiher et al., 2011). Negative effects of earthworms vary based on taxonomy (Greiner et al., 2012; Qiu & Turner, 2017) and functional group (Cope & Burns, 2019; Ferlian et al., 2018; Huang et al., 2020), making it vital to understand how assemblages of earthworms form in invaded habitats.

*Historical Background:*

*i. Glaciation and the post-quaternary hypothesis:* Some North American forests likely evolved without the presence of the major terrestrial ecosystem engineer, the earthworm (Phylum *Annelida*, Order *Oligochaeta*) (Gates, 1966; Reynolds, 1995). During the last glacial period of the Pleistocene which ended approximately 11,000 years ago (Reynolds, 1995), glaciers covered Canada and the northern United States (Fig. 1), which likely made it impossible for earthworms to live in these regions (Fender, 1995; Reynolds, 1995). This is known as the post-quaternary hypothesis (Gates, 1966; Reynolds, 1995). There is also evidence that native earthworms from more southern habitats have been slow to migrate north into this region and recolonize it post-glaciation.



*ii. Introduction of Earthworms to North America:* Since the time of European colonization of North America, non-native earthworms have been introduced to these previously earthworm-free ecosystems, likely transported in the ballasts of ships, in the soil of plants being sold commercially, and as fishing bait (Fender, 1995). European earthworms (Family *Lumbricidae*) were introduced to North America at the time of European colonization, about 500 years ago (Fender, 1995). More recently, the Family *Megascolesidae* of earthworms from Asia have been introduced as well, and are known for their erratic behavior and snake-like movements, which have earned them the common names “jumping worms,” “snake worms,” and “crazy worms.” Increased commerce and a cosmopolitan world have likely led to their introduction in North America from Asia in the past hundred years (Moore et al., 2018).

Both families of earthworms have been shown to pose threats to northeastern temperate forests, but further research is needed to have a full understanding of their impacts and also to inform efforts to suppress their invasion. There is less research on the impacts of jumping worms, but existing studies indicate that due to different behavior and life-history traits, impacts may be worse than those of the lumbricids (Price-Christenson et al., 2020; Suárez et al., 2006).

*Overview of Community Assembly:*

Community assemblages, or the array of species found in a specific place that interact with each other (Weiher et al., 2011), have been studied extensively to understand what factors are responsible for their dynamics and composition. Diamond (1975) proposed that species assemblages of ecologically similar organisms are determined by interspecific (between species) competition. Conner & Simberloff (1979) established the need for a method to analyze community assemblage data using null models before concluding that assemblage rules are occurring. Their paper calls into question Diamond’s (1975) assumption that island species distributions are indeed due to assembly rules such as competition without a sufficient null model. Nonetheless, Diamond’s concept of such assembly rules has persisted and other studies now show evidence for these trends, including in earthworm communities (Ikeda et al., 2018; Sheehan et al., 2007).

*Research on Earthworm Community Assembly:*

Earthworm community assemblages have been studied in many areas of the world, but are lacking in previously glaciated regions of North America. Existing literature on earthworm assemblages in other areas, however, can help us better understand the patterns that may be found in previously-glaciated habitats.

*Potential Drivers:* As in the assemblages of other taxonomic groups, there are multiple potential drivers of earthworm community composition, and it is likely that multiple will be significant to different extents. These “assembly rules” will vary depending on context. Environmental or habitat traits are one major category, and earthworm functional traits and interactions are another major category of drivers of community composition (Curry, 2004).

*i. Environmental and Habitat Traits:* One category of potential drivers of earthworm assemblages are environmental and habitat traits, such as climate, elevation, pH, and vegetation cover (Curry, 2004).

Many studies have addressed the effects of vegetation cover on earthworms. Ammer et al. (2006) studied the drivers of earthworm community composition in Scotts pine forests at 19 sites in Bavaria. All forest stands were dominated by Scots pine (*Pinus sylvestris*), with some all conifers and others mixed with hardwood tree species such as European beech and pedunculate oak (Ammer et al., 2006). They found a non-significant trend of increasing earthworm abundance in sites with broadleaf trees and a significant increase in earthworm diversity at these sites as well (Ammer et al., 2006). Aubert et al. (2003) studied the effect of tree canopy on earthworm and other macro-invertebrate compositions in beech forests of Normandy, France. They compared pure beech to mixed beech-hornbeam forests and found that *Lumbricidae* earthworms were significantly more abundant in pure beech stands (Aubert et al., 2003). After analyzing their other variables with respect to site and season, Aubert et al. (2003) concluded that patchiness and resource diversity (i.e., different litter types from different tree species) do *not* lead to more diverse and heterogeneous communities in this case.

Besides vegetation type, habitats have been analyzed for community assembly by other variables, such as altitude, moisture, and other abiotic conditions. Salomé et al. (2011) examined the effects of altitude, forest successional stage, and soil characteristics on earthworm community composition in alluvial (subject to flooding and sediment deposits) forests. They found 27 species of earthworms at their sites in Switzerland across all elevations except the alpine level (Salomé et al., 2011). They found that soil texture, which was siltier in this habitat, significantly affected epigeic earthworm abundance. They concluded that soil parameters in alluvial habitats matter most in determining earthworm species richness and abundance, followed by altitude.

Soil characteristics are unsurprisingly also important in determining earthworm assemblages. De Wandeler et al. (2016) conducted a field study on earthworms across European forests to examine what factors determine their incidence and abundance. They found that soil characteristics and vegetation composition were the most important and that climate factors were surprisingly less consequential (De Wandeler et al., 2016). When soil C:N was above 22, the probability of finding earthworms decreased significantly. Earthworms were also less abundant in acidic soils and only in areas with a soil pH above 4.0 was there more earthworm biomass.

Land-use type has also been found to affect earthworm abundance and diversity. Decaëns et al. (2008) studied earthworm community assembly rules in North-West France. They found that land-use type significantly affected which lumbricid earthworms were found at the sites, with grasslands the most and croplands the least rich in species (Decaëns et al., 2008). Whalen (2004) also sampled earthworm communities from patches in different land-use types in Quebec, Canada. They found that earthworm communities varied across cornfield, hayfield, and forest sites, with the highest abundance found at the forest sites. Earthworm composition across and within habitats was highly variable and patchy (Whalen, 2004). Nuutinen et al. (1998) conducted a field study of earthworm spatial variation and abundance in a grass and clover field in Finland. They found a total of five earthworm species and correlated their data with soil properties (Nuutinen et al., 1998). Nuutinen et al. (1998) found that earthworm abundance was positively correlated with soil infiltration, clover productivity, and soluble soil phosphorus. In this case, correlation should not be mistaken for causation, because it is quite possible that the increased earthworm abundances caused increases in these variables, not the other way around. This nuance will be important to consider in future research on the drivers of earthworm community assemblages.

Land-use type also includes habitats that are heavily affected by human disturbance, such as urban and suburban areas. Tiho & Josens (2007) studied the drivers of earthworm assemblages of urban environments in the city of Brussels, Belgium. They found that two of their five sites had less species co-occurrence than expected in the null model and that this is a result of competition between ecologically similar earthworm species (Tiho & Josens, 2007). Smetak et al. (2007) also studied earthworm diversity within urban systems.

Differential results across these studies highlight that community assembly is context-dependent and assumptions about earthworm communities cannot be made on habitats for which no data exists. Therefore, these are all potential patterns that may exist in previously-glaciated regions of North America, but field studies from the northern U.S. and Canada will still be indispensable in furthering scientific knowledge of earthworm communities and invasion in this region.

*ii. Earthworm Traits:* Other potential drivers of earthworm assembly fall under the category of earthworm traits, such as functional group, behavior, and interspecific competition.

Ikeda et al. (2018) examined the mechanisms of earthworm community assembly using biogeographical analysis. They collected molecular taxonomic data from three genes of 553 earthworms from a mountainous primary forest in Japan. These data allowed them to analyze two possible factors in community assembly: dispersal ability, which is a biogeographic driver, and habitat adaptation, which is an evolutionary driver of community assembly. The two families of earthworms that they examined, the *Lumbricidae* and the *Megascolecidae*, have different cecum types. Their results indicate that while the two taxa live together, cecum type may influence community assembly as a key evolutionary trait that determines habitat suitability (Ikeda et al., 2018).

Jégou et al. (2001) conducted a mesocosm study on earthworm interspecific interactions and how this affects burrowing systems of different species. After eight months with *Lumbricus rubellus*, *Aporrectodea giardi,* and *A. caliginosa* in either single or paired species treatments, Jégou et al. (2001) X-rayed the mesocosms and made models of their burrow systems. They found that *L. terrestris* made more shallow but longer burrows in the presence of *A. caliginosa* (Jégou et al., 2001). *A. caliginosa* made deeper burrows when in the presence of *A. giardi*, but the total length of the burrow was about the same (Jégou et al., 2001). This study shows that interspecific relationships influence earthworm burrowing behavior, which means that resource partitioning is likely occurring. Evidence for niche partitioning means that functional ecology of earthworms should be important in determining community assembly.

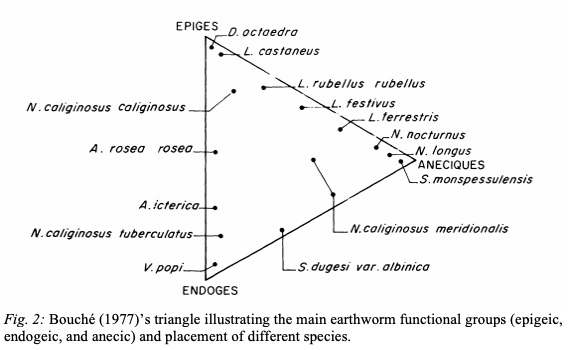
Functional groups are another possible driver of earthworm assembly. Functional groups divide organisms based on their role in the ecosystem, as opposed to their taxonomic identity (Weiher et al., 2011). Marcel Bouché was a French ecologist who studied earthworms and was the first to categorize them into functional groups based on their feeding and burrowing habits (Bouché, 1977).

The three main groups Bouché identified, which have generally been accepted by other scientists since, include anecic, epigeic, and endogeic earthworms. Sometimes other special functional groups are used to describe the behavior of wetlands and bark-dwelling earthworms more accurately (Reynolds, 1977), but these are the foremost accepted functional groups of earthworms. Anecic earthworms make long burrows and live deep in the soil. They go to the top of the burrow to forage and bring food such as leaf detritus and other organic matter down into the burrow. Endogeic earthworms live in the upper layer of the soil, which is rich in organic matter. Epigeic earthworms live near the top of the soil and often eat the leaf litter. (Bouché, 1977). Intermediary categories, such as epi-endogeic or epi-anecic, describe earthworm with behaviors that are between two or sometimes all three categories (Fig. 2).

Bouché (1977) organized these functional groups into a triangle that reflects the variable nature of earthworm functional groups (Fig. 2). Besides basic burrowing patterns, other common characteristics can be attributed to the different functional groups. Anecic species are often larger in body size (adults can be 200 to 1100 mm) and dull pigmentation. They often forage on leaves at night (Bouché, 1977). The endogeic earthworms inhabit a more shallow layer of the soil than the anecic earthworms and are diverse in size. They often have little pigmentation and eat dead roots in the soil (Bouché, 1977). Bouché (1977) also notes their robustness to environmental stress through their ability to hibernate in cold conditions and estivate in dry conditions. The epigeic earthworms are more pigmented and smaller in size (about 10 to 30 mm). Living so close to the surface, they are subject to higher levels of predation than other functional groups and often have certain corresponding adaptations (small tail, mobile, high reproductive rate) (Bouché, 1977). All of these variations in earthworm traits could affect competition assemblage dynamics.

Functional group has been shown to impact earthworm community assembly, interspecific interactions, effects on the ecosystem, and dispersal patterns. While anecic earthworms are very poor dispersers due to the tendency to establish a burrow in the autumn and remain there (Mazaud & Bouché, 1980), the epigeic and endogeic earthworms likely are able to disperse at greater rates. Overall, however, earthworms are all poor dispersers and their invasion and colonization must for the most part be mediated by another organism, most commonly humans (Lavelle, 1988).

Regardless of their poor dispersal abilities, functional groups of earthworms (and thus their behavior), have been cited as an explanation for the differential impacts of invasive earthworms on ecosystems (Hale et al., 2005; Lavelle, 1988).

 Sheehan et al. (2007) conducted a mesocosm experiment on different functional groups of earthworms and how different availability of resources affected the community dynamics. They created mesocosms with different proportions of anecic, epigeic, and endogeic earthworms. This included monocultures, even mixtures, and different levels of domination of each functional group. Sheehan et al. (2007) also factored in initial biomass and food availability as variables. They found that all mesocosms moved towards domination by anecic species (Sheehan et al., 2007). Interestingly, epigeic survival increased with a higher proportion of anecic earthworms in the same mesocosm. Endogeics survived better with a low food supply and low initial biomass (Sheehan et al., 2007). Anecics exhibited stronger intraspecific competition, doing significantly worse when there were lots of other anecics. Epigeics were negatively affected by higher biomass of the other groups of earthworms, indicating more interspecific competition than intraspecific competition (Sheehan et al., 2007). This study is useful in understanding how the functional groups of earthworms may interact with each other in their natural environment, which should be reflected in the community assembly of earthworms.

A recent study from Bottinelli et al. (2020) rejects the idea that earthworm ecological categories in fact do *not* serve as functional groups. They argue that the original system, invented by Bouché with data that was primarily on European lumbricid earthworms, does not account for all of the nuances of earthworm functional diversity. They recommend that further research is done to expand the number of categories or at least re-evaluate characterization by taxonomic traits (Bottinelli et al., 2020). Nevertheless, these categories are still useful for understanding the general functional traits of earthworms and until researchers create a better system of classification, they should still be used.

Competition and niche partitioning is another likely mechanism by which earthworm communities may assemble. Fox’s rule hypothesizes that communities of similar organisms or organisms that live together will assemble with a diversity of species from different and complementary ecological niches before there are multiple species of the same niche (Fox, 1987). While Fox based this rule on rodent assemblages, the same ecological principles can be applied to earthworm assemblages. In a soil ecosystem with limited space and resources, we would expect to see earthworms of different functional groups before we see many species of a single functional group. The mechanism for this could include local extirpation via competition, unsuccessful colonization via competition, or even evolutionary processes leading to speciation into different functional niches over longer periods of time (Sheehan et al., 2007).

The functional groups of earthworms may very well be useful in understanding the competition and niche partitioning of different earthworm species within a community. Thus, these earthworm-trait-based drivers of community assemblage are all interconnected.

*Threats of Earthworms in Previously Earthworm-Free Habitats:*

Understanding earthworm community assemblage is important given the impact earthworms have on terrestrial ecosystems, including negative impacts on ecosystems that evolved without earthworms.

Earthworms are key ecosystem engineers, changing soil components such as the leaf litter layer, soil horizons, and nutrient cycling (Greiner et al., 2012; Gundale, 2002; Lawrence et al., 2003; Resner et al., 2015; Qiu & Turner, 2017). These changes in the soil ecosystem have recorded downstream effects on plants (Alexander, 2018; Cassin & Kotanen, 2016; Eisenhauer et al., 2007; Eisenhauer & Scheu, 2008; Gundale, 2002; Hale et al., 2008; Lawrence et al., 2003) which in turn effects the overall structure and functioning of ecosystems.

*Differential Effects of Earthworms:* Given the negative effects of invasive earthworms on ecosystems, it is important to understand where earthworms have invaded and to what extent. Furthermore, community assembly is a vital part of understanding the effects invasive earthworms will have on habitats because earthworms are not all the same. Studies have shown that the type and degree of effects vary depending on taxonomic group (Greiner et al., 2012; Qiu & Turner, 2017) and functional group (Cope & Burns, 2019; Ferlian et al., 2018; Huang et al., 2020). Therefore, being able to predict earthworm community composition as invasion continues will be key to predicting the responses of these ecosystems to the specific earthworm assemblages that are established.

One major difference among invasive earthworms in North America is their taxonomy. Two major families, the *Lumbricidae* from Europe and the *Megascolecidae* from Asia, are now found in many previously earthworm-free habitats and have significantly different life history traits. A substantial number of studies have found that non-native lumbricid earthworms negatively alter ecosystem dynamics and services in hardwood forests of North America (Bohlen et al., 2004; Hale et al., 2005; Lawrence et al., 2003).

Lawrence et al. (2003) studied the impacts of non-native earthworms on *Acer saccharum* (sugar maple) mycorrhizal communities in Cayuta, New York. They sampled tree roots throughout the growing season from paired sample plots that were alike in topography, soil type, and other attributes, save for the presence or absence of earthworms. The percentage of mycorrhizal-colonized root length was measured by dividing the number of hyphae, vesicles, and hyphal coils at intersections of roots by the total number of intersections (Lawrence et al., 2003). Plots colonized by earthworms had significantly less mycorrhizal colonization of the sugar maple roots than plots not colonized by earthworms. Root depth was a significant factor in their models, with the surface layer of soil more colonized by fungus than the subsurface layer. While there was 56% fungal colonization of roots at the forest floor in no-earthworm plots, this level of the soil ecosystem did not exist at all in earthworm plots, a result of them eating leaf litter (Lawrence et al., 2003). This study showed that non-native lumbricid earthworms decrease mycorrhizal colonization of tree roots and also deplete the forest floor layer where mycorrhizal colonization is the highest.

The negative effects of earthworms extend beyond just the soil ecosystem. These effects cause upstream impacts within the trophic levels. Loss et al. (2012) found that decreases in ground-nesting songbird populations may be related to the presence of invasive earthworms in these habitats. Sites in the Chequamegon-Nicolet (Wisconsin) and Chippewa National (Minnesota) Forests with *Lumbricus spp.* Present had significantly lower populations of *Seiurus aurocapilla* (Ovenbirds) (Loss et al., 2012). While it is not clear what effects of earthworms may indirectly lead to declines in Ovenbird populations, possible factors include changes in the macroinvertebrate community, plant community, and other drivers. More research is needed to fully understand these relationships between earthworms and other animals at higher trophic levels.

Some studies on the impacts of megascolecid earthworms compared to their earlier invading counterparts, the lumbricid earthworms, indicate that their significantly different behavior may change how they interact with invaded ecosystems (Greiner et al., 2012; Qiu & Turner; 2017). Jumping worms are usually epigeic or epi-endogeic and able to reproduce parthenogenetically, which leads to high abundances in invaded sites and subsequent domination of the soil community (Price-Christenson et al., 2020). They eat away the litter layer at much higher rates than the lumbricid earthworms and create a much thicker layer of castings (earthworm feces), creating a larger soil aggregate size (Greiner et al., 2012) and affecting water percolation, as well as soil chemistry (Saurez et al., 2006).

Greiner et al. (2012) measured the differences between an invasive Asian and an invasive European earthworm on a temperate deciduous forest. Leaf litter decomposition and soil mineralization were measured. They found that *L. rubellus* increased leaf litter decomposition rates more than *Amynthas hilgendorfi*, the Asian invasive. Soil mineralization was more heavily impacted by *A. hilgendorfi,* however, as was the soil aggregation, caused by their castings. Soil organic matter (SOM) significantly increased with earthworms (regardless of species) in laboratory experiments, but not in the field. Increased SOM likely came from leaf litter that was digested by earthworms and deposited in the soil. There was no interaction between the two species.

One of the few studies to examine Asian earthworms and nutrient cycling, Qiu & Turner (2017) conducted a mesocosm experiment and field study on the impacts on forest and prairie litter and soil nutrients by two invasive Asian “crazy” worms, *Amynthas agrestis* and *Amynthas* *tokioensis*, in southern Wisconsin. Both species significantly reduced the amount of leaf litter by 84-95% while increasing C, N, and available P over the four month study period (Qiu & Turner, 2017). While more nutrients seem positive for plant communities, these nutrients are being mineralized, which makes the soils more susceptible to nutrient loss, and could have cascading effects on nutrient uptake of plants. Price-Christenson et al. (2020) studied the effects of earthworms in the Megascolecid genus *Amynthas* on soil chemistry and soil microbial communities of Wisconsin forests. They found that *Amynthas spp.* have a unique assemblage of gut bacteria and that their presence as invasives in forests sampled in Wisconsin changes the soil microbiome (Price-Christenson et al., 2020).

Of the two main families of non-native earthworms found in North America, the *Megascolecidae* seem to be more robust invasives, especially in forest ecosystems, where the eat down the litter layer, create and thick cast layer of large soil aggregates, and outcompete other invertebrates, including the *Lumbricidae* earthworms (Price - Christenson et al., 2020). More research is needed, however, to confirm the differences between these two families.

*Future Directions*

There are very few studies on earthworm community composition and assembly, and especially very few from North America in previously glaciated regions. This gap in the literature is an issue as we see the increase of invasive lumbricid and megascolecid earthworms into previously earthworm-free habitats. Many studies have found that invasive earthworms have major negative impacts in habitats that evolved without them, such as the temperate forests of the northern U.S. and Canada (Bohlen et al., 2004; Frelich et al., 2006; Hale et al., 2004). A more robust understanding of earthworm community ecology and assemblage in previously glaciated habitats will help us better predict which taxonomic and functional groups of earthworms will be found and what their effects will be. This will also allow scientists to recommend better adaptive management strategies based on the functional traits of different invading earthworms.

Meta-analyses that can comprehensively evaluate the existing literature to understand the community dynamics of earthworms will be useful. This would include evaluating if assembly rules exist, if nestedness occurs, and what the drivers of these community dynamics are. As seen earlier in the section on potential drivers of community assembly, these variables could include temperature, elevation, precipitation, soil moisture, soil pH, and functional group. More specific to earthworm community assemblages in previously glaciated areas, latitude and time may be significant given that these should correlate with patterns of invasion.

Besides meta-analyses, more studies sampling earthworms in the field are needed, especially in areas recently disturbed by humans or where human-mediated invasions are predicted to occur. More community assemblage data from sites invaded by megascolecids is especially needed given its current scarcity in the literature.

One unique method for evaluating earthworm community assemblages at large scales that may become more feasible as genetic analysis becomes quicker and cheaper is analyzing DNA found in the soil (Pansu et al., 2015). Pansu et al. (2015) created a protocol to assess the effect of land-use on earthworm diversity in a mountain landscape in the Northern French Alps. Their environmental DNA barcoding methods include extracting extracellular DNA from soil cores, performing DNA polymerase chain reaction amplifications of the mitochondrial 16S gene, and sequencing the DNA. To test the efficacy of these methods compared to classic earthworm sampling methods, they sampled earthworms from the same plots where soil samples were taken (Pansu et al., 2015). They found 13 species using the classical sampling method and 16 molecular operational taxonomic units (MOTUs; a proxy for species with the proper context) using environmental DNA barcoding (Pansu et al., 2015). While DNA barcoding yields messy results that can be difficult to categorize into species, these methods may be useful for evaluating earthworm community assemblages on a larger scale than is possible with traditional field sampling methods.

When studying the patterns of community assembly, there are multiple measures that can be assessed. Assemblages of species are considered nested when smaller assemblages are a subset of larger ones (Almeida-Neto et al., 2008). Fox (1987) proposed that one mechanism of community assembly and nestedness is differing functional groups of taxonomically similar species. He proposed that in a community of species that exploit similar resources, there will be one species of each functional group before there are two or more species of a single functional group (Fox, 1987). This hypothesis draws on the concept of ecological niches and resource partitioning theory (Schoener, 1974). Succession of biologically similar organisms is closely related to nestedness.

*Conclusion:*

While earthworm community assemblage dynamics have been well-studied in certain regions of the world, such as Europe (Ammer et al., 2006; Aubert et al., 2003; Decaëns et al., 2008), large gaps remain in the research in North America in previously glaciated habitats. These habitats, located primarily in the northern U.S. and Canada, generally evolved without earthworms (Gates, 1966; Reynolds, 1995). This makes them highly susceptible to the negative effects of invasive earthworms because of how drastically these ecosystem engineers (Ferlian et al., 2018) alter both abiotic and biotic factors. These factors include soil properties, microbial, invertebrates, and plant communities (Bohlen et al., 2004), and even vertebrate communities (Loss et al., 2012). Many studies have found that these negative effects on previously-glaciated forests vary across earthworm taxonomic and functional groups. Studies on community assembly dynamics of invasive earthworms in previously-glaciated regions of North America, in conjunction with data on the differential impacts between different types of earthworms, will be key to creating adaptive management strategies for conservation of these ecosystems.

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