A History of Earthworms in North America from the Pleistocene till Now

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Introduction

The discovery of North America by European explorers and the subsequent Columbian exchange and colonization of the New World fundamentally changed the ecology of North America through the introduction of a myriad of new species to the continent. One of these species was the humble earthworm, which had not been present in the northern reaches of North America since the Pleistocene; however, its reintroduction was profound and continues to affect the ecology, environment, and climate to this day.

Background

Before the Columbian Exchange, the northern forests of North America had long been devoid of earthworms, a consequence of the last Ice Age, which wiped out many species. While southern regions of the continent harbored healthy populations of earthworms, the glacial history of the north meant that these areas lacked earthworms, significantly affecting the soil composition and forest floor dynamics. Earthworms play a crucial role in breaking down organic matter, aerating the soil, and enhancing nutrient cycling; therefore, their absence or presence can dramatically alter an ecosystem. North America had been devoid of these invertebrates since the Pleistocene, the great Ice Age, which started about 2.8 million years ago (mya) and ended only about 0.012 mya and allowed for the introduction of humans in the hemisphere via the Bering Sea land bridge (Lecturer).

During the Ice Age, glaciation events profoundly impacted the distribution and survival of earthworm populations across the continent. As the glaciers advanced, they reached latitudes as far south as 37° N, effectively decimating earthworm communities in their path (Editors of Encyclopedia Britannica). This period was characterized by significantly lower temperatures that affected not just the directly glaciated regions but the broader continent as well. The colder climate led to the expansion of permafrost areas. The effects of these conditions are visible in the form of periglacial weathering patterns within the rock strata (Marshall et al.). Such geological evidence provides insights into the climatic conditions during the Ice Age and their impact on the terrestrial landscape and its inhabitants.

During the Ice Age, earthworms were all but wiped out of the continent's northern reaches, where the glacial advance extended to the 37° N latitude mark. This period of low temperatures affected the rest of the continent in myriad ways and included a larger spread of permafrost, evidenced by periglacial weathering in the rock strata (Marshall et al.). This weathering allows us to see which portions of the continent would have been habitable for the North American earthworm; the habitable zone existed below the frost line, where the ground remained unfrozen. At its maximum spread, the frost line extended as far south as Atlanta and Dallas (Marshall et al.). Figure 1 represents these phenomena visually, illustrating the southward advance of the frost line and the glaciated areas. This map provides a crucial reference for understanding the geographical extent of habitable zones during the Ice Age and the significant challenges faced by earthworms and other organisms in finding suitable habitats amid the advancing ice sheets and expanding permafrost.

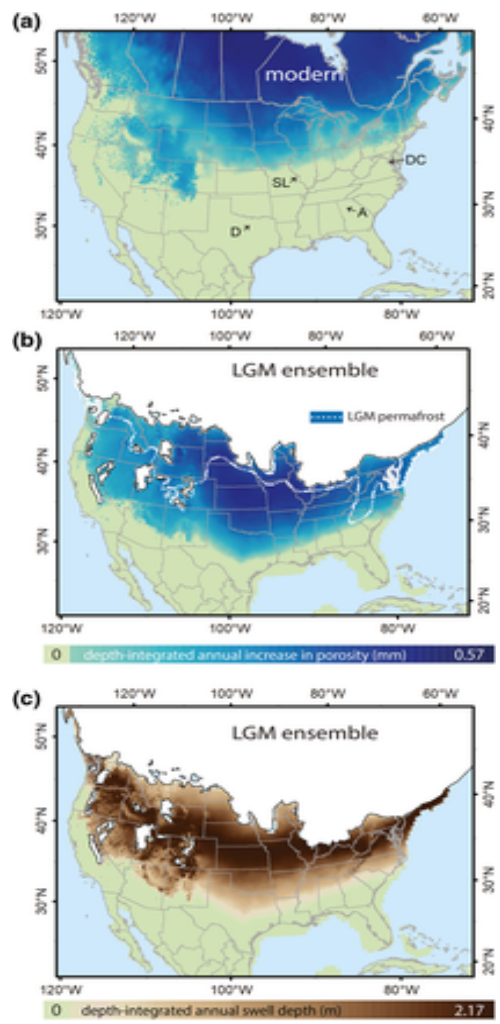

Figure 1: Extent and magnitude of modern versus Last Glacial Maximum (LGM) frost weathering lifted from Marshall et al, 2021

The extent of the permafrost and the reach of the glacial ice have significant implications for understanding which areas of the continent could have supported earthworm populations. Regions below the shifting frost line provided a refuge for earthworms, along with small pockets not covered by glaciers in which native earthworms survived but from which they rarely spread (Alberta Worm Invasion Project). Following these events and the end of the great Ice Age, the native earthworm populations moved back at a slow rate of up to 16m each year in forest conditions (Gorder). This population change would have had minimal effects if there had not been a source of invasive earthworms introduced further north.

The European powers that discovered and colonized the continent brought along invasive species. This fundamentally changed the landscape as the European earthworms expanded from their colonial origins in the 1600s (Smithsonian Environmental Research Center). These introductions took place in the early European settlements, mainly on the eastern seaboard, where they were in root balls and ballasts of ships and likely imported for agricultural purposes and spread rapidly by humans for the same reason (Brown). In modern times, they have spread through human interaction on car tires and boots and as bait for fishing (Alberta Worm Invasion Project). As they spread, they drastically changed the soil conditions that had been devoid of worms for over ten millennia. The subterranean invaders would have had a profound effect on the ecosystem. Unfortunately, given the state of science at the time, this went largely unnoticed, along with the myriad of other things introduced in the Columbian Exchange. Given that no useful data on this issue was even considered until well after the scientific revolution, especially in the Americas, we can look at the current frontline of this invasion further north, with its lowest extent in northern New England and the Midwest and into lower Canada.

Importance

These invasive invertebrates are wreaking havoc on the northern forests as they are spread by human interaction, and their habitable range is expanding due to climate change. The European earthworms fundamentally break up the soils in the upper layers; this can lead to "conspicuously different nutrient dynamics than uninvaded forests." (Dobson et al.) This benefits deep-rooting plants at the expense of the native medium and shallow-rooting species (Dobson et al.). It is precisely this movement of nutrients from the middle of the soil column that benefits species that root deeper and disadvantages those in the middle. As fewer nutrients exist in this range, for native plants in their ideal rooting depth: "early successional and non-native species that can establish successfully" with these new dynamics introduced by invasive earthworms (Dobson et al.). Figure 2 represents how the mineral cycle changes with the introduction of non-native earthworms.

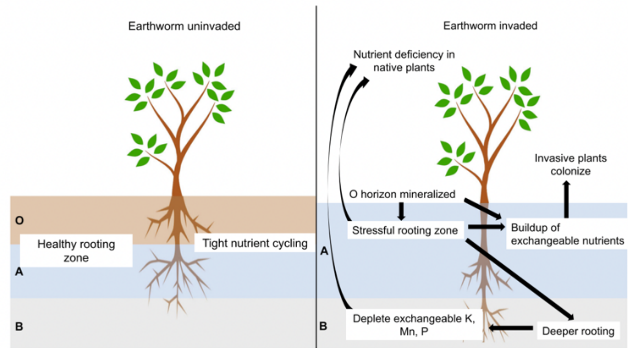

Figure 2: Proposed mechanism for earthworm disruption of nutrient cycling in forests left from Dobson et al, 2017

The organic horizon (O horizon) is a layer of built-up organic material at the surface of the soil, consisting of leaves and other organic material that would usually be left to its own devices to lock nutrient cycling into this productive soil band; these thick organic soil layers develop over many centuries, playing an essential role in the forest ecosystem (Frelich et al.). Without earthworms, there is a duff layer that holds nutrients and minerals deeper in the soil; it is precisely this layer that is broken up by these invasive species (Brown).

The breakdown of the O horizon promotes the growth of non-native species and does not allow the conditions for native trees to grow in the early stages of life. Additionally, many native plants have evolved shallow roots that rely on the unique microhabitat disrupted by non-native earthworms (Dobson et al.). As this leaf litter vanishes from the forest floor, the nutrients held in by this layer are made readily available to plants in a way that was absent before the change in dynamics produced by earthworms.

Earthworms build extensive burrows that fundamentally change the relationship between fungi and plants; this also alkalizes the soil, affecting its pH. The lack of leaf litter allows for water normally stored in this range to decrease, in turn "increasing susceptibility to drought" in forests, as it locks in moisture into the lower soil layers, resulting in diebacks in some areas. (Frelich et al., 2019; Halle-Jena-Leizig, 2016). There is an effect on diversity, as they affect not only the soil dynamics but, in some cases, directly ingest seeds of defenseless native plants and, in some circumstances, increase runoff (Craven et al.). This change introduces better conditions for non-native plants, including garlic mustard (*Alliaria petiolata*), Japanese barberry (*Berberis thunbergii*), Japanese stiltgrass (*Microstegium vimineum*), common buckthorn (*Rhamnus cathartica*) as well as non-native grasses (Frelich et al., 2019).

Given that non-native species evolved to live with earthworms and their increased nutrient release, earthworms are more abundant in the presence of non-native species (Frelich et al., 2019). This simultaneously destroys the conditions for native species to survive.

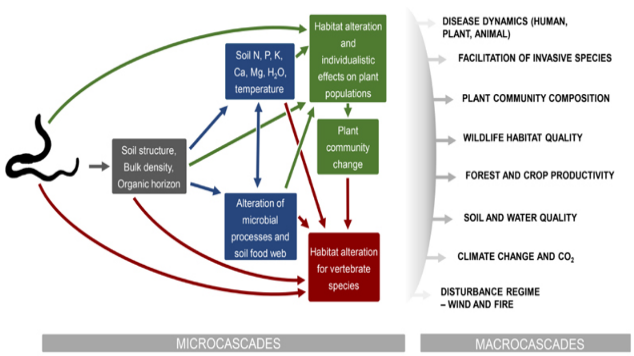

Figure 3: Microcascade effects in the soil leading to alteration of plant and animal habitats and macrocascades of concern to society left from Frelich et al., 2019. The green, red, and blue represents the effects on plants, animals, and soil physical/microbial processes, respectively.

There is also the issue of the release of carbon into the atmosphere, given the effects on northern boreal forests. This has caused a cascade changing the ecosystem at a broader level as carbon in the surface horizons, accumulated over centuries, is now breaking up due to earthworm invasions (Frelich et al., 2019). Figure 3 represents the earthworm cascades and their various effects. As earthworms facilitate the mixing of soil layers, releasing this stored carbon, it is estimated that earthworms are responsible for an “increase in CO2 loss from soil by an average of 33% globally” (Cameron et al.). This, in turn, along with climate change, exacerbates and allows for the northward migration of not only earthworms but also the invasive species that follow them. The leaf litter and organic materials that stored carbon at the top levels of the soil were traditionally burned off by forest fires as part of the carbon cycle. Earthworms reduce the fuel available for forest fires so much that, in some areas, it makes “prescribed fires used in forest management more difficult to carry out.” (Frelich et al., 2019; Lejoly et al., 2019). However, forest fires are increasing due to climate change and other factors, only further exacerbating the release of carbon and loss of forest ecosystems, helping the spread of earthworms in North America.

Conclusion

There is no way of knowing what the state of forests looked like before the re-establishment of earthworms (Brown). However, their reintroduction has fundamentally changed North America’s ecosystem and landscape, making our forest ecosystems more susceptible to drought, resulting in diebacks in some areas, and forever altering the understory and soil nutrient cycles; they have paved the way for many invasive species. This fundamental shift from pre-earthworm to post-earthworm North America can be mitigated but not easily reversed. It has fundamentally changed the entire ecosystem of a continent in a way that rarely gets noticed, and it is hard to fully quantify or understand all the cascading effects of this introduction. One thing is clear: a pre-earthworm North America, in many ways, is completely unrecognizable.

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