Side-swiped: ecological cascades emanating from earthworm invasions

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Non-native, invasive earthworms are altering soils throughout the world. Ecological cascades emanating from these invasions stem from rapid consumption of leaf litter by earthworms. This occurs at a midpoint in the trophic pyramid, unlike the more familiar bottom-up or top-down cascades. These cascades cause fundamental changes (“microcascade effects”) in soil morphology, bulk density, and nutrient leaching, and a shift to warmer, drier soil surfaces with a loss of leaf litter. In North American temperate and boreal forests, microcascade effects can affect carbon sequestration, disturbance regimes, soil and water quality, forest productivity, plant communities, and wildlife habitat, and can facilitate other invasive species. These broader-scale changes (“macrocascade effects”) are of greater concern to society. Interactions among these fundamental changes and broader-scale effects create “cascade complexes” that interact with climate change and other environmental processes. The diversity of cascade effects, combined with the vast area invaded by earthworms, leads to regionally important changes in ecological functioning.

In a nutshell:
• Non-native earthworms accelerate leaf litter decomposition and soil mixing in the upper layers, leading to rapid loss of the litter layer and higher bulk density
• These changes in soil structure result in warmer, drier soils, and changes in nutrient availability
• Resulting cascade effects of concern to society include changes in carbon sequestration, disturbance regimes, soil and water quality, forest productivity, plant communities and wildlife habitat, and facilitation of other invasive species
• Cascade effects occur across large landscapes, and interact with each other and with other factors (eg climate change, deer herbivory), to cause important changes in ecological functioning

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Panel 1. Definitions of terms relating to ecological cascades

**Ecological cascade**: an inevitable chain of events resulting from an initial change in an ecosystem. There are many possible causes of initial changes including disturbances, changes in the environment, species extinctions, and (as in this paper) addition of invasive species.

**Ecological cascade effect**: traditionally defined as secondary effects (including extinctions) that occur after one species goes extinct (most common usage) or a novel species joins a community. A trophic cascade effect is caused by removal of a predator (top-down effects) or primary producer (bottom-up effects) (eg removal of a top predator results in an increase in the population of a herbivore that, in turn, decreases populations of primary producers). Here, however, we define “ecological cascade effect” broadly to include the trophic and non-trophic effects of introducing an ecosystem engineer (earthworm) that alters food webs and physiochemical soil environments in ways that ripple through the ecosystem. For example, removal and/or mixing of the soil organic horizon affects the distribution and activity of soil organisms, which in turn affects processing and ultimately storage and loss of carbon (C) and nitrogen (N). We term these sideways ecological cascade effects.

**Microcascade effect**: fundamental effects of an ecological cascade on populations, species, communities, and ecosystem processes—in this case, the effects of earthworm invasion on the environment in which they live, including processing of materials, nutrient cycles, physical changes and resulting impacts on other taxonomic groups.

**Macrocascade effect**: cumulative effects of microcascades that change ecosystem functions at a broader level, affecting services that society receives from ecosystems and the associated goals, including maintenance of biodiversity, water quality, and ecosystem health and productivity.

**Cascade complex**: linked macrocascade effects that interact with other environmental changes (eg high deer density, climate change) to influence ecological dynamics at landscape or regional scales, spanning (among many possibilities) forest–agricultural field and rural–urban boundaries.

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Figure 1. Trophic pyramid showing decomposers interacting with all trophic levels from the side of the trophic structure, as regulators of rate of nutrient return (indicated by brown part of the pyramid). In addition to their role as decomposers (trophic effects), earthworms physically alter the habitat of soil organisms, primary producers, and consumers (non-trophic effects, indicated by the dashed blue arrows). Yellow arrow indicates input of solar energy to primary producers.

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Cascading effects of earthworm invasion

Non-native earthworms catalyze many changes in soil physical, chemical, and biological properties (Figure 2). In earthworm-free conditions, northern forests develop thick organic soil layers over many centuries that protect the soil from erosion, buffer soil microclimate, and provide habitat for roots and soil organisms. Earthworms eliminate these layers (Figure 3) by increasing decomposition rates and mixing them with underlying mineral soil (Lytte et al. 2015); this enhances soil bulk density and aggregation, and reduces soil carbon (C), carbon-to-nitrogen (C:N) ratios (Fahey et al. 2013), and cation exchange capacity (CEC; Resner et al. 2015), leading to altered soil water dynamics and variable effects on pH (Eisenhauer et al. 2007). The net effect of these changes is to reduce forest soil fertility. Tree-ring analyses and observations of invading earthworm fronts on permanent plots indicate that changes in soil morphology occur within 10 years, and persist for at least 40–60 years (Larson et al. 2010; Resner et al. 2015).

In the short term, losses of inorganic nutrients from surface horizons (layers) (Resner et al. 2015) may be offset by increased nutrient availability in underlying soil layers (Eisenhauer et al. 2007). Moreover, earthworms facilitate the flow of litter N into stable soil organic matter (Fahey et al. 2013), and may either stimulate or inhibit hydrologic and gaseous losses of N (Groffman et al. 2015). Anecic (ie deep burrowing) species transfer less-weathered subsoil materials to
upper horizons, replenishing total phosphorus (P) in topsoils, but concurrent increases in macroporosity (resulting from burrows) also promote P leaching losses (Resner et al. 2015). Although early stage invasions may increase N and P availability, lower N and P availability occurs after several decades (Hale et al. 2005). These studies compare long-invaded sites (several decades) to nearby non-invaded sites, which means they offer a realistic picture of earthworm densities that commonly occur in the field, and their results show cumulative earthworm effects over the time that the sites have been invaded.

Earthworm ecosystem engineering also alters the diversity and composition of soil microbial and faunal communities (Burke et al. 2011), promoting the proliferation of fast-growing bacteria (Ferlian et al. 2018) and large-bodied fauna (Schlaghamersky et al. 2014). At the same time, the density and diversity of epigeic (i.e., surface-litter dwelling) fauna decline due to removal of their habitat (Frelich et al. 2006).

Earthworm invasions show successional dynamics, and larger magnitude microcascade effects occur as more earthworm species/functional groups become established (Hale et al. 2006; Ferlian et al. 2018). Most areas with invasive earthworms in North America are occupied by European species, but Asian (particularly Amythnas spp) earthworms have recently been introduced into eastern North America, where they appear to be replacing established European populations (Dávalos et al. 2015b). Although these invasions are less extensive and their ecosystem impacts relatively unknown, it has been shown that Asian earthworms consume the organic horizon and affect nutrient cycling (Qui and Turner 2017; Laushman et al. 2018).

Macrocascade effects of earthworm invasions of concern to society

The fundamental impacts of earthworms on litter and soils combine to form myriad macrocascade effects. These fall into categories related to major environmental issues. We highlight seven categories with sufficient coverage in the peer-reviewed literature to be addressed (Figure 2).

Carbon dioxide sequestration

A global-scale macrocascade effect likely associated with earthworm invasion into northern forests is a climate-change feedback, as stored soil C is released into the atmosphere in the form of carbon dioxide (CO$_2$). Northern forests that lacked earthworms in the Holocene contain large amounts of C in surface organic horizons. Feeding by epigeic and anecic earthworms can eliminate these layers over decadal time scales (Hale et al. 2005), directly releasing CO$_2$ into the atmosphere (Fahey et al. 2013). As such, the ongoing expansion of earthworms in northern forests could be releasing large amounts of soil C to the atmosphere; moreover, continued earthworm expansion is promoted by warming soils and northward migrations of preferred food sources, such as Acer spp and Tilia spp into the North American boreal forest (Fisichelli et al. 2013). In the short to mid-term, this
cascade effect adds to anthropogenic factors (eg burning of fossil fuels) that are driving increases in atmospheric greenhouse-gas concentrations (Lubbers et al. 2013).

In the long term, the ultimate effects of earthworm invasion on forest C storage are uncertain, and depend on the balance between earthworm processes promoting stabilization (retention) and mineralization (decomposition) of soil C (Zhang et al. 2013). In particular, earthworm feeding and burrowing activity can form microaggregates and cause C sorption (in which C molecules leave solution and accumulate on mineral surfaces where soil C is stabilized; Lyttle et al. 2015), but they can also disrupt existing aggregates and stimulate C mineralization (Fahey et al. 2013). Whether the net effect is to increase or decrease long-term stabilization of detrital C in forest soils depends on a complex suite of biotic and environmental factors, including soil mineralogy, soil texture, earthworm species assemblage, and vegetation community composition.

**Disturbance regimes**

Invasive earthworms act directly and indirectly as disturbance agents. Direct disturbance effects include dieback of canopy sugar maple (*Acer saccharum*) trees (Bal et al. 2018) and increasing mortality in the standing crop of herbaceous plants and tree seedlings, which occur when earthworms consume the organic horizon in which these plants are rooted (Hale et al. 2006). Impacts on decomposition and plant communities can indirectly alter fire and wind regimes, including changing the frequency, intensity, or timing of disturbances. Reduced tree growth and litter inputs and increased litter decomposition decrease fuel loads available for fires, making prescribed fires used in forest management more difficult to carry out. Therefore, despite causing dieback of maple trees, invasive earthworms are one of several factors driving conversion of fire-dependent oak (*Quercus* spp) forests to maple (ie mesophication) in the North Central US (Freligh et al. 2017). In boreal forests, simulation modeling indicates that the amount of C lost from the forest floor is higher when earthworms and fire co-occur than with either disturbance in isolation (Cameron et al. 2015). Earthworm invasions can also interact with changes in fire frequency to affect C storage, such as increases in fire frequency have a stronger effect on long-term C storage in the forest floor when earthworms are present (Cameron et al. 2015). Furthermore, earthworms may alter wind disturbance effects, as dieback favors smaller trees with thinner crowns that are likely to be more resistant to strong winds. Overall, there has been little research on interactions between invasive earthworms and disturbance regimes, and it remains unclear how frequently and strongly earthworm invasions will cause cascading effects on disturbance regimes.

**Soil and water quality**

Earthworms affect surface water quality primarily through bioturbation and by changing soil porosity. In compacted agricultural soils, anecic earthworms create macropores that facilitate water infiltration, which promotes transport of contaminants (eg pesticides) to subsoil drains (Villholth et al. 2000). In contrast, non-native earthworms in northern forests eliminate the surface organic horizon, and in many cases increase bulk density of the surface mineral horizon (Hale et al. 2005), potentially promoting overland flow and soil erosion (Figure 3). Moreover, surface earthworm casts are easily dislodged when subject to rain-splash and runoff, leading to soil erosion (Darwin 1881).

Lower N retention in forest soils following earthworm invasion results from destruction of the forest floor, although the ability of mineral soil to retain N varies, and likely depends on earthworm community composition (Crume et al. 2015; Groffman et al. 2015). For example, in a mesocosm experiment, the presence of *Aporrectodea caliginosa* resulted in more leaching of nitrate and ammonium from riparian areas into streams than did the presence of *Lumbricus* spp (Costello and Lamberti 2008), indicating that species-specific effects on nitrification occur through ammonium excretion and soil burrowing. Lower availability of N and P, lower CEC, and loss of the moderating influence of the organic horizon on erosion and water balance in late-stage *Lumbricus terrestris* invasions (Loss et al. 2013) resulted in deterioration of soil quality, with visible effects on forest productivity and plant communities, which are described in more detail below.

**Forest productivity**

The sensitivity of forest canopy trees to changes caused by earthworm invasions has not been studied in great depth, but there is some evidence that profound effects occur. Loss of the organic horizon common in northern forests increases susceptibility to drought, much like removing mulch from a garden bed. Fine root networks and associated arbuscular mycorrhizal communities that allow trees to acquire water and nutrients are disrupted following earthworm invasion (Paudel et al. 2016). In response to these changes, mesic tree species such as sugar maple exhibit increased drought sensitivity, crown dieback, and reduced (by 30–40%) basal area increment (Larson et al. 2010; Bal et al. 2018). These results are troubling given the recent evidence that drying soils are major drivers of negative effects of climate change on mid-latitude forests, where invasive earthworms are most problematic (Reich et al. 2018).

**Facilitation of other non-native species**

Earthworm invasions may facilitate non-native plant invasions of garlic mustard (*Alliaria petiolata*), Japanese barberry (*Berberis thunbergii*), Japanese stillgrass (*Microstegium vimineum*), and perhaps common buckthorn (*Rhamnus cathartica*) in eastern North American forests (Nuzzo et al. 2009; Roth et al. 2015; Craven et al. 2017), multiple non-native grasses in California (Clause et al. 2015), and fire tree (*Myrica faya*) in Hawaii (Aplet 1990). Enhanced seedbed conditions through removal of leaf litter was a key factor facilitating germination of common buckthorn (Figure 3;
Earthworm abundances may also be higher in the presence of invasive non-native plants than in adjacent non-invaded areas (Dávalos et al. 2015a). There is evidence of a positive feedback cycle in which earthworms facilitate plant invasion and later benefit from the presence of the non-native plants (Madritch and Lindroth 2009; Roth et al. 2015).

Earthworms also may influence other soil faunal invasions. For example, invasive earthworm effects on surface organic horizons result in lower micro- and macroarthropod abundance (Burke et al. 2011), but it is not known whether earthworm activities favor introduced and historically co-existing European or Asian invertebrates. Moreover, non-native earthworms may alter the nutritional quality and defensive chemistry of selected understory plant species, as indicated by changes in herbivory by non-native slugs observed during a field experiment (Dávalos et al. 2014).

Plant community changes

Earthworm invasion profoundly changes the composition of deciduous forest understories by altering seedbed conditions, nutrient dynamics, and root mycorrhization rates (Hale et al. 2006; Paudel et al. 2016). Earthworms affect plant species directly as seed predators (McCormick et al. 2013) or as seedling herbivores (Griffith et al. 2013). Their spread has been linked to declines in a rare fern and sugar maple seedlings (Gundale 2002; Hale et al. 2006). In one study, seedling survival of 12 of 15 native forest understory species was negatively affected by non-native earthworm abundance (Dobson and Blossey 2015). Selective facilitation or suppression of individual species (native or introduced) can lead to wholesale changes in herbaceous plant communities and reduced diversity in response to earthworms (Holdsworth et al. 2007). Increasing abundance of native sedges, especially Pennsylvania sedge (Carex pensylvanica), has been reported (Fischelli et al. 2013), with extensive sedge lawns observed at some sites. A recent meta-analysis concluded that plant diversity in North American forests declined significantly with increasing functional earthworm diversity; native graminoid and non-native species cover increased while native cover declined (Craven et al. 2017).

Figure 3. Impacts of European earthworm invasions on North American forests. (a) Base of a sugar maple (Acer saccharum) tree in a temperate forest in southern Minnesota, showing loss of the organic horizon and subsequent soil erosion; (b) base of a balsam fir (Abies balsamea) tree in a boreal forest in northern Minnesota, showing recession of the forest floor and exposure of roots leading to drought stress; (c) invasion front of common buckthorn (Rhamnus cathartica) in an earthworm-infested oak and maple forest in southern Minnesota; (d) Lumbricus rubellus, a European earthworm species responsible for consumption of the organic horizon in forests.
Evidence for causal effects of introduced earthworms on plant diversity needs to be examined using a multiple stressor framework (Fisichelli et al. 2013; Dávalos et al. 2014). Both earthworm abundance and plant community composition are influenced by human land use, forest age, herbivory, and climate legacy effects (Simmons et al. 2015), and synergistic interactions among stressors (eg non-native plants, earthworms, deer herbivory) are common.

Changes in wildlife habitats

Earthworm-caused changes to soil and plant communities have cascading effects on vertebrates. These impacts may be complex, involving direct and indirect effects on habitat structure and food availability. Earthworms are a potentially bountiful food resource for some wildlife taxa (Maerz et al. 2005), whereas for others (eg woodland salamanders), invasions might have a net negative indirect effect on food resources by reducing abundance of invertebrates that are important prey (Maerz et al. 2009). For birds, invasive earthworms can provide a novel food source, and invasions altered distribution of a generalist avian predator at local and landscape scales (Cameron and Bayne 2012). Invasive earthworms also indirectly affect wildlife by altering habitat structure. Their extensive networks of burrows may benefit some wildlife (Cáceres-Charneco and Ransom 2010), but by eliminating leaf litter layers, earthworms may exacerbate soil warming or drying that could negatively affect moisture- or temperature-sensitive taxa (Reich et al. 2018). The vegetation changes associated with earthworm invasions described above have also been shown to reduce habitat availability for some ground-nesting songbirds and to reduce visual nest concealment, which increases nest predation rates (Loss and Blair 2014).

Synthesis of case studies

Currently, the most extensive example of a cascade complex can be assembled from studies of earthworm impacts in the cold-temperate biome of eastern North America, from Minnesota to New England. At least six cascade sequences emanate from changes to soils when European earthworms invade (Figure 4): (1) common buckthorn invasion is facilitated; buckthorn is the overwintering host for soybean aphids (Aphis glycines) that reduce agricultural yields and are the food source for Asian ladybeetles (Harmonia axyridis), which cause human allergies (Heimpel et al. 2010); (2) without insulation from the organic horizon, the soil becomes warmer and drier in midsummer, exacerbating drought effects and impacts of a warming climate (Reich et al. 2018); (3) nutrient leaching increases; as a result, availability of N, P, and cations declines, with impacts on soil and water quality; (4) forest floor fuel contiguity is reduced, decreasing the effectiveness of prescribed burns needed to maintain the oak (Quercus spp) component of maple-dominated forests, thereby reducing diversity in food sources (ie acorns) for wildlife (Frelich et al. 2017); (5) habitat for ticks that carry the spirochete (Borrelia burgdorferi) responsible for Lyme disease is changed in complex ways, with potential for positive and negative impacts on human health (Burtis et al. 2014); and (6) heavy metals in forest floor leaf litter from the burning of fossil fuels bioaccumulate in earthworms, raising concerns about toxicity for wildlife species that consume earthworms (Richardson et al. 2015). The combined effects of (1), (2), and (3) lead to reduced productivity of sugar maple, the most dominant tree species in the region, and – together with deer herbivory – simplification of the herb community, favoring native graminoids and non-native plant species. The combined effects of (2) and (3) could lead to declines in water quality due to erosion and leaching of nutrients from terrestrial to aquatic ecosystems. Finally, earthworm (L terrestris) activity in rural areas promotes establishment of giant ragweed (Ambrosia trifida), a major human allergen producer, by collecting and providing safe sites for giant ragweed seeds (Regnier et al. 2008).

This synthesis of multiple case studies reveals a cascade complex in which macrocascade effects from the six sequences above co-occur in one region, so that their effects are intertwined. The cascade effects cross (1) spatial scales, from stand to landscape; (2) land-cover types, including woodland, cropland, and urban; and (3) ecosystem types, from terrestrial to aquatic. The cascade complex includes interactions with other environmental factors, such as high deer density and climate change (Fisichelli et al. 2013), and an invasion sequence from earthworms to invasive plants and insects (Heimpel et al. 2010), with complex implications for human health, the economy, and the environment (Figure 4).

Conclusions

“Sideways” entrance into ecosystem trophic structure – in essence, stepping on the gas pedal for processing detritus – can initiate strong cascade effects when earthworms invade forests. These ecological cascades have been explored to varying degrees, although many of their connections remain unexamined. For example, in contrast to the many studies of how earthworms affect leaf litter and plant communities, the aquatic consequences of nutrients and sediment being exported from terrestrial ecosystems when earthworms invade have received little attention. These impacts will be a growing problem as earthworm invasions spread from introduction points along waterways, where earthworms are used as fishing bait and, over time, occupy ever-larger proportions of watersheds.

The cascades addressed here have up to four links; strong effects are limited to the first two or three links, while later links in a given cascade sequence are weaker. For example, factors other than earthworms also contribute to abundances of
Asian ladybeetles and giant ragweed, and many factors besides these contribute to human allergies. Important factors outside of these ecological cascades influence the issues of concern to society – including fossil-fuel burning, habitat conversion, and land management practices. Nevertheless, due to their diverse alterations of the environment, non-native earthworms have profound impacts on soil quality and conservation of native species at regional scales. Of particular concern is that four of the six ecological cascades within the broader cascade complex described earlier (Figure 4) negatively affect forest productivity and diversity, and that earthworms are likely to exacerbate increasing drought effects caused by a warming climate; those effects will likely have dramatic impacts on whether climate warming increases or decreases forest productivity (Reich et al. 2018). These effects of earthworm invasion can occur throughout temperate and boreal forest biomes, and although most studies cover North America, similar earthworm invasion effects have taken place near the northern edge of the boreal forest in Europe (Wackett et al. 2017).

Although it is generally true that any major environmental change bad for one suite of species is good for another – i.e. that there are “winners” among native species – the overall impact of earthworms on forest diversity is negative because they contribute to biotic homogenization. The “winner” plant species that tolerate other homogenization factors – deer browsing, changing climate, and human disturbance – are generally those that also respond positively to earthworm invasion (Rooney 2009; Craven et al. 2017).

Some effects reviewed here are transitional during earthworm invasion (e.g. N and P leaching, excess CO₂ emissions), while others will probably continue in a new, more persistent state (e.g. novel soil morphology and plant communities), so that the future stability of earthworm-invaded ecosystems is unknown. We suggest three logically sequenced questions to guide future research. First, to what extent can earthworm-invaded ecosystems recover? Over centuries to millennia, native soil fauna and plant species may undergo selection to better compete with earthworms or tolerate new environmental conditions, eventually restoring ecological processes similar to the pre-earthworm ecosystem. Second, are ecosystems with long-term presence of earthworms subject to more frequent drought, less biodiverse, and more susceptible to invasive species than earthworm-free ecosystems, implying that recovery from invasion may be limited? Third, how will earthworm invasion interact with habitat loss, deer herbivory, and climate change to threaten the survival of native species? Linkages between cascades emanating from earthworm invasion and other environmental factors could lead to synergistic effects and more rapid ecosystem change than from any single cascade. An interdisciplinary perspective is needed to understand and manage the growing complexity of environmental changes and their effects on human well-being.

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