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.

Front Ecol Environ 2019; 17(9): 502–510, doi:10.1002/fee.2099

Although society usually views earthworms positively in agricultural contexts, as invaders of forests they can have substantial deleterious effects. Non-native, invasive earthworms are globally widespread ecosystem engineers that alter physical and biogeochemical soil properties, affecting ecosystem functioning and habitat quality for native species (Hendrix *et al.* 2008). Previous reviews examined basic effects of earthworm invasion and hypothesized that cascade effects (Panel 1) were occurring (eg Frelich *et al.* 2006). However, recent advances provide a more comprehensive understanding of ecological cascades that are triggered by earthworm invasions and propagate through trophic systems.

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

These are not the familiar type of bottom-up or top-down cascades, which occur when bottom-level primary producers or top-level predators are added or removed. Instead, invasive earthworms cause cascade effects from sideways entry into the trophic structure – in effect, ecosystems are "side-swiped" when changes in functions are initiated by the entrance of earthworms into the side of the trophic structure. The earthworms increase leaf litter decomposition rates and soil mixing, thereby altering habitat structure and detritivore, microbial, and plant communities, and these changes affect herbivore communities and beyond (Figure 1). Detritivores such as dung beetles also side-swipe the trophic pyramid, with subsequent effects that cascade both up and down (Pace *et al.* 1999). However, in contrast to other detritivores, cascades caused by invasive earthworms cover entire terrestrial landscapes across vast spatial extents (Hendrix *et al.* 2008). For example, European earthworms inhabit >80% of suitable soils in northern Minnesota, Wisconsin, and Michigan (Fisichelli *et al.* 2013). The spread of earthworms along waterways and roads as a result of human activities (eg fishing bait, nursery stock), with thousands of introduction points across the landscape, allows them to invade most of a region within several decades.

Using earthworm impacts on ecosystems as a case study, we first define the terms *ecological cascade* and *ecological cascade effect*, then propose a novel framework for classifying ecological cascade effects (Panel 1). We divide ecological cascade effects into two types: *microcascade effects* and *macrocascade effects*. Fundamental effects of earthworm invasion on soil properties and functions (microcascade effects) are separated from the broad-scale effects of concern to society (macrocas-

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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.

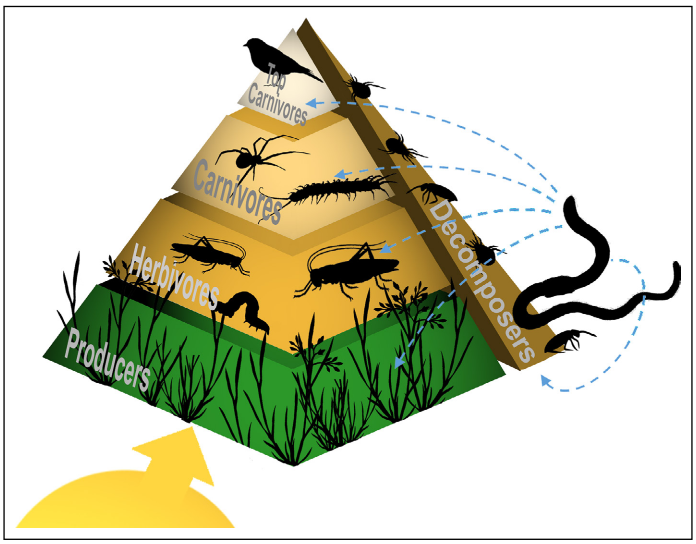

Figure 1. Trophic pyramid showing decomposers interacting with all trophic levels from the side of the trophic structure, as regulators of rate of nutrient return (indicated by brown part of the pyramid). In addition to their role as decomposers (trophic effects), earthworms physically alter the habitat 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.

cade effects). In addition, we introduce the concept of *cascade complexes*, which recognizes that earthworms initiate many types of cascades on the same landscape, causing unavoidable interactions between cascades and with other environmental factors.

We also address several overarching questions: What types of cascade effects occur? How do they affect ecosystem functions and human well-being? What is the extent of our knowledge of cascades? We focus on European earthworm invasions in temperate and boreal forest biomes in North America, which is where earthworm invasions are best characterized in the peer-reviewed literature.

Microcascade 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 (Lyttle *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

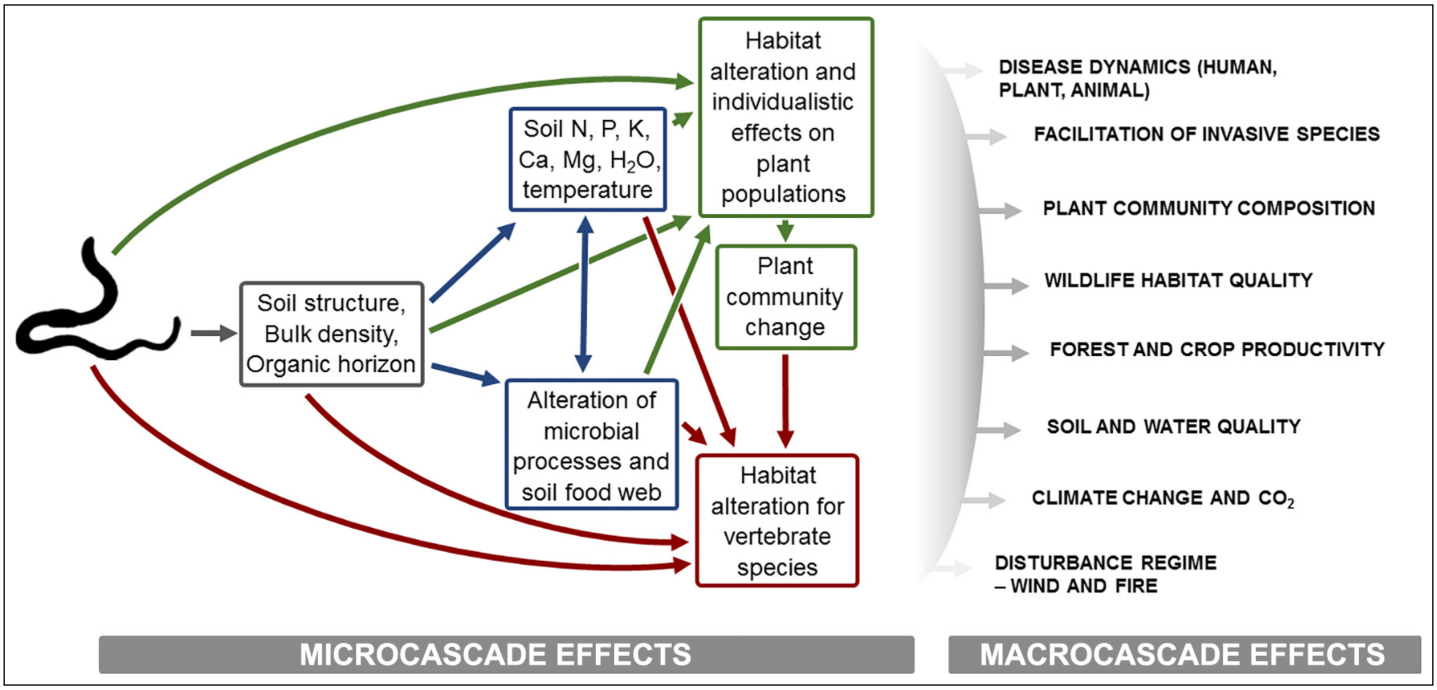

Figure 2. Microcascade effects in the soil leading to alteration of plant and animal habitats and macrocascades of concern to society. Green, red, and blue arrows and boxes represent effects on plants, animals, and soil physical/microbial processes, respectively. Seven of the macrocascades shown correspond to the subsections within the "Macrocascade effects of earthworm invasions of concern to society" section of the main text, while the eighth (disease dynamics) emerges in the synthetic case study.

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 (ie 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 *Amynthas* 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 (Frelich *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 that 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 (Crumsey *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 stiltgrass (*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;

D Wallace

A Roth

G Schlaghamersky

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.

Roth *et al.* 2015). 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 (Fisichelli *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).

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 impacts 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

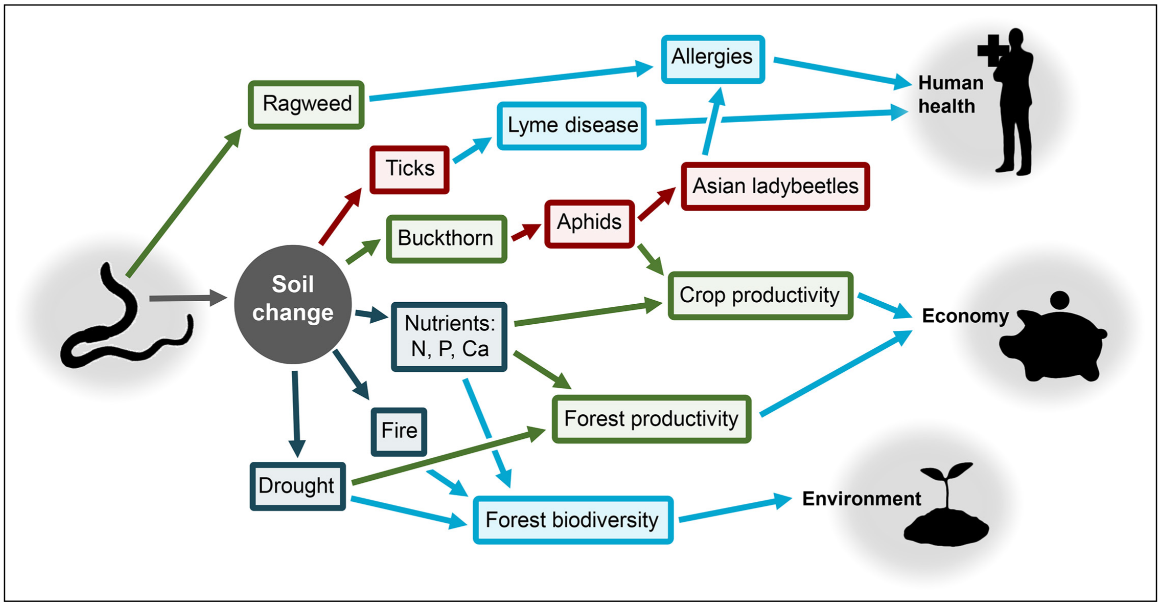

Figure 4. Cascade complex initiated by earthworm invasion in the northern hardwood forest region, Minnesota to New England. Microcascade changes caused directly by earthworms and soil changes (black silhouette and circle, left side), lead to interlinked macrocascade effects shown by the rectangles, which ultimately affect societal well-being, represented by the silhouettes on the right. Arrow and box colors show effects involving plants (green), animals (red), alterations of the environment (dark blue), and issues of concern to society (light blue). Terrestrial–aquatic linkages are not included.

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 – ie 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 (eg N and P leaching, excess CO_2 emissions), while others will probably continue in a new, more persistent state (eg 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.

Acknowledgements

We gratefully acknowledge support from the following sources: University of Minnesota Center for Forest Ecology and G Nelson and D Nelson (LEF); the Strategic Environmental Research and Development Program of the US Department of Defense (BB, AD, JCM, VN); Oklahoma Agricultural Experiment Station (SRL); European Research

Council under the European Union's Horizon 2020 research and innovation program (grant no 677232) and German Centre for Integrative Biodiversity Research Halle-Jena-Leipzig, funded by the German Research Foundation (FZT 118) (NE); Wisconsin Alliance for Minority Participation (EL); CFANS faculty development support and Institute for Advanced Study residential fellowship (KY); and Natural Sciences and Engineering Research Council of Canada, and Academy of Finland (285882) (EKC).

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