Front Ecol Environ. Author manuscript; available in PMC 2020 January 06.

Published in final edited form as:
Front Ecol Environ. 2019 November ; 17(9): 502–510. doi:10.1002/fee.2099.

Side-swiped: Ecological cascades emanating from earthworm invasion

Lee E. Frelich[1], **Bernd Blossey**[2], **Erin K. Cameron**[3,4], **Andrea Dávalos**[2,5], **Nico Eisenhauer**[6,7], **Timothy Fahey**[2], **Olga Ferlian**[6,7], **Peter M. Groffman**[8,9], **Evan Larson**[10], **Scott R. Loss**[11], **John C. Maerz**[12], **Victoria Nuzzo**[13], **Kyungsoo Yoo**[14], **Peter B. Reich**[1,15]

[1]University of Minnesota, Department of Forest Resources, 1530 Cleveland Ave. N., St. Paul, MN [2]Department of Natural Resources, Fernow Hall, Cornell University, Ithaca, NY [3]Global Change and Conservation Group, Faculty of Biological and Environmental Sciences, University of Helsinki, Finland [4]Department of Environmental Science, Saint Mary's University, Halifax, Nova Scotia, Canada [5]SUNY Cortland, Department of Biological Sciences, Bowers Hall, Cortland, NY [6]German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Leipzig, Germany [7]Institute of Biology, Leipzig University, Leipzig, Germany [8]Advanced Science Research Center at the Graduate Center, and Brooklyn College Department of Earth and Environmental Sciences, City University of New York, New York, NY [9]Cary Institute of Ecosystem Studies, Millbrook, NY [10]University of Wisconsin-Platteville, Department of Geography, 1 University Plaza, Platteville, WI [11]Oklahoma State University, Department of Natural Resource Ecology and Management, 008C Ag Hall, Stillwater, OK [12]Warnell School of Forestry & Natural Resources, University of Georgia, 180 East Green Street, Athens, GA [13]Natural Area Consultants, 1 West Hill School Road, Richford NY [14]University of Minnesota, Department of Soil, Water, and Climate, St. Paul, MN [15]Hawkesbury Institute for the Environment, University of Western Sydney, Richmond, NSW, Australia

Abstract

Non-native, invasive earthworms are altering soils throughout the world. Ecological cascades emanating from these changes stem from earthworm-caused changes in detritus processing occurring at a mid-point in the trophic pyramid, rather than the more familiar bottom-up or top-down cascades. They include fundamental changes (microcascades) in soil morphology, bulk density, nutrient leaching, and a shift to warmer, drier soil surfaces with loss of organic horizons. In North American temperate and boreal forests, microcascades cause effects of concern to society (macrocascades), including changes in CO_2 sequestration, disturbance regimes, soil quality, water quality, forest productivity, plant communities, and wildlife habitat, and facilitation of other invasive species. Interactions among these changes create cascade complexes that interact with climate change and other environmental changes. The diversity of cascade effects, combined with the vast area invaded by earthworms, lead to regionally important changes in ecological functioning.

Corresponding author: freli001@umn.edu.

Europe PMC Funders Author Manuscripts

Although society usually views earthworms positively in agricultural contexts, as invaders of forests they can have significant deleterious effects. Non-native, invasive earthworms are globally widespread ecosystem engineers that change 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 in this ecological frontier provide a more synthetic understanding of ecological cascades emanating from earthworm invasion and propagating through trophic systems.

These are not familiar bottom-up or top-down cascades, which occur when bottom-level primary producers or top-level predators are added or removed, but instead stem from changes in processing of detritus and soil structure. Invasive earthworms cause cascade effects from sideways entry into the trophic structure, by increasing leaf litter decomposition rate and mixing of soils, with subsequent changes in habitat structure and detritivore, microbial and plant communities that propagate upwards to herbivores and beyond (Figure 1). Detritivores such as dung beetles, also enter the side of 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 USA (Fisichelli *et al*. 2013). The spread of earthworms along waterways and roads by 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 cascades (Panel 1). We divide ecological cascades into two types—*microcascades* and *macrocascades*. Fundamental effects of earthworm invasion on soil properties and functions (microcascades) are separated from the broad-scale effects of concern to society (macrocascades). Furthermore, we introduce the concept of *cascade complexes*, recognizing that earthworms initiate many types of cascades on the same landscape, causing unavoidable interactions among cascades and with environmental factors.

Several overarching questions are woven throughout the paper: What types of cascade effects occur, how do they affect ecosystem functions and human wellbeing, and what is the extent of our knowledge of cascades? We emphasize European earthworm invasions in temperate and boreal forest biomes in North America, where earthworm invasions are best characterized in the peer-reviewed literature.

Microcascade effects of earthworm invasion

Non-native earthworms catalyze a microcascade of 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 play a critical role in protecting the soil from erosion, buffering soil microclimate, and providing habitat for roots and soil organisms. Earthworms eliminate these layers (Figure 3) through elevated decomposition and mixing with underlying mineral soil (Lyttle *et al.* 2015), increasing soil bulk density and aggregation, reducing soil carbon, 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 (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 (deep burrowing) species bring up less-weathered subsoil materials, replenishing total P in topsoils, but coincident changes in macroporosity also promote P leaching losses (Resner *et al.* 2015). Although early stage invasions may increase N and P availability, lower availability occurs after several decades (Hale *et al.* 2005). We note that these studies compare long-invaded sites (several decades) to nearby uninvaded sites and therefore reflect results with earthworm densities that commonly occur in the field, and that are integrated over the time that the sites have been invaded.

Earthworm ecosystem engineering alters the diversity and composition of soil microbial and faunal communities (Burke *et al.* 2011), selecting for fast-growing bacteria (Ferlian *et al.* 2018) and large-bodied fauna (Schlaghamersky *et al.* 2014). The density and diversity of epigeic (surface-litter dwelling) fauna declines 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. More recently, Asian (*Amynthas* spp.) earthworms have begun invading eastern North America, and appear to replace established European species (Dávalos *et al.* 2015b). These invasions are less extensive and the ecosystem impacts are relatively unknown, although Asian earthworms also consume the organic horizon and affect nutrient cycling (Qui and Turner 2017; Laushman *et al.* 2018).

Macrocascade effects of earthworm invasion of concern to society

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

CO_2 sequestration

A global scale macrocascade likely associated with earthworm invasion into northern forests is initiation of a climate change feedback as stored soil C is released into the atmosphere as 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). Thus, the ongoing expansion of earthworms in northern forests is likely releasing significant amounts of soil C to the atmosphere; moreover, continued earthworm expansion is favored by warming soils and northward migrations of preferred food sources, such as *Acer* and *Tilia* species into the boreal forest (Fisichelli *et al.* 2013). In the short to mid-term this cascade contributes to anthropogenic factors (eg fossil fuel burning) that are driving increases in 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 and mineralization of soil C (Zhang *et al.* 2013). In particular, earthworm feeding and burrowing activity can result in the formation of microaggregates and carbon sorption on mineral surfaces in which 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 carbon in forest soils depends on a complex suite of biotic and environmental factors including soil mineralogy, texture, earthworm assemblage, and vegetation community composition.

Disturbance regimes

Invasive earthworms act directly and indirectly as disturbance agents. Direct disturbances 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 by consuming the organic horizon in which they are rooted (Hale *et al.* 2006). Impacts on decomposition and plant communities can indirectly alter disturbance regimes, including changing frequency, intensity, or timing of disturbances. Decreased tree growth and litter inputs and increased litter decomposition reduce 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 forests to maple (mesophication) in the north central U.S. (Frelich *et al.* 2017). In boreal forests, simulation modelling indicates the amount of C lost from the forest floor is greater with earthworms and fire present together than with either disturbance alone (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 the effects of wind disturbances, as dieback favors smaller trees with thinner crowns that are likely more resistant to wind. Overall, little research has examined 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

The effects of earthworms on surface water quality result primarily from their bioturbation activity and consequent changes in soil porosity. In compacted agricultural soils, anecic earthworms create macropores and facilitate water infiltration, which promotes transport of contaminants (eg pesticides) to subsoil drains (Villholth *et al.* 2000). In contrast, in northern forests, non-native earthworms 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 subject to rain-splash and runoff, which is a substantial component of soil erosion (Darwin, 1881).

Lower N retention in forest soils after earthworm invasion results from destruction of the forest floor, although the ability of mineral soil to retain N varies, likely depending on earthworm community composition (Crumsey *et al.* 2015; Groffman *et al.* 2015). For example, in a mesocosm experiment, *Aporrectodea caliginosa* caused more leaching of nitrate and ammonium from riparian areas into streams than *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 invasions with well-established *Lumbricus terrestris* (Loss *et al.* 2013) result in deterioration of soil quality, with visible effects on forest productivity and plant communities described below.

Forest productivity

The sensitivity of forest canopy trees to changes caused by earthworm invasions is a relatively little-studied topic, yet evidence suggests that profound effects occur. Loss of the O 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 are vital for trees to acquire water and nutrients are disrupted upon 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 for a major role of drying soils as a driver 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 facilitate non-native plant invasions of garlic mustard (*Alliaria petiolata*), Japanese barberry (*Berberis thunbergii*), Japanese stiltgrass (*Microstegium vimineum*), and common buckthorn (*Rhamnus cathartica*) in eastern North American forests (Nuzzo *et al.* 2009; Craven *et al.* 2017), multitiple non-native grasses in California (Clause *et al.* 2015), and fire tree (*Myrica fava*) in Hawaii (Aplet 1990). Enhanced seedbed conditions by removal of leaf litter was a significant factor facilitating germination of common buckthorn (Figure 3, Roth *et al.* 2015). Earthworm abundances are also higher in the presence of invasive non-native plants compared to adjacent uninvaded areas (Dávalos *et al.* 2015a).

Earthworms also may influence other soil faunal invasions. For example, invasive earthworm effects on surface organic horizons result in lower micro- and macro-arthropod abundance (Burke *et al.* 2011), but it is unknown whether earthworm activities favor introduced and

Europe PMC Funders Author Manuscripts

historically co-existing European or Asian invertebrates. Earthworm invasions also alter plant nutritional quality and defense chemistry, resulting in changes in non-native slug herbivory in experimental communities and the field (Dávalos *et al.* 2014).

Plant community changes

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). 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 observed (Fisichelli *et al.* 2013) with extensive sedge lawns on some sites. A recent meta-analysis concluded that plant diversity in North American forests significantly declined 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). Earthworm abundance and plant community composition are both influenced by legacy effects of human land use, forest age, herbivory, and climate (Simmons *et al.* 2015) and synergistic interactions among stressors (eg non-native plants, earthworms, deer) are common.

Wildlife habitat changes

Earthworm-caused changes to the soil and plant communities have cascading effects to 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 (Maerz *et al.* 2005); however for other taxa (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 may negatively impact moisture or temperature-sensitive taxa (Reich *et al.* 2018). The above-described vegetation changes associated with earthworm invasions negatively affect some ground-nesting songbirds by reducing habitat availability and causing a reduction in concealment that elevates nest predation rates (Loss and Blair 2014).

Europe PMC Funders Author Manuscripts

Synthesis of case studies: an example of a cascade complex

Currently, the most extensive example of linked cascade effects 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*) that cause human allergies (Heimpel *et al.* 2010); (2) without insulation from the organic horizon, the soil becomes warmer and drier at midsummer, exacerbating drought effects and impacts of a warming climate (Reich *et al.* 2018); (3) there is enhanced leaching of nutrients and consequently reduced availability of N, P and cations, with impacts on soil and water quality; (4) forest floor fuel contiguity is reduced, reducing effectiveness of prescribed burns needed to maintain the oak component of maple-dominated forests, consequently reducing diversity in food sources (ie acorns) for wildlife (Frelich *et al.* 2017); (5) habitat for ticks that carry Lyme Disease (*Borrelia burgdorferi*) is changed in complex ways, with potential for positive and negative impacts on human health (Burtis *et al.* 2014); and (6) heavy metals accumulated in forest floor leaf litter from burning fossil fuels are bioaccumulated in earthworms, raising concerns about newly developed food webs based on the presence of 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 activity in rural areas leads to enhancement of Giant ragweed (*Ambrosia trifida*) establishment (Regnier *et al.* 2008), a major human allergen producer.

This synthesis of multiple case studies reveals a cascade complex in which several of the macrocascades initiated by earthworm invasion co-occur in one region, creating long cascade sequences with several links and branches. The cascade effects cross (i) spatial scales from stand to landscape, (ii) land cover types including woodland, cropland and urban, and (iii) ecosystem types from terrestrial to aquatic. The cascade complex includes interactions with other environmental factors such as high deer populations and climate change (Fisichelli *et al.* 2013) and an invasion sequence from earthworms to invasive plants and insects (Heimpel *et al.* 2010), with complex influences on human health, the economy and 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. Potential impacts of these cascades have been explored to varying degrees, although many of their connections remain to be investigated. For example, in contrast to many studies of earthworm impacts on leaf litter and plant communities, aquatic consequences of nutrients and sediment 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 considered here have up to four links; strong effects are limited to the first two–three links, with dampened effects at three-four links. For example, factors other than earthworms also contribute to abundances of Asian lady beetles and ragweed, and many factors besides these contribute to human allergies. Important factors outside of these 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 cascade effect sequences in the cascade complex (Figure 4) have negative effects on forest productivity and diversity, and that earthworms are likely to exacerbate increasing drought effects caused by a warming climate, which likely have dramatic impacts on whether climate warming is positive or negative for forests (Reich *et al.* 2018). These effects can occur throughout temperate and boreal forest biomes, and although most studies cover North America, similar earthworm invasion effects occur 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—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 seem likely to continue in a new, more persistent state (eg novel soil morphology and plant communities). The future stability of earthworm-invaded ecosystems is unknown and this review suggests 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 more droughty, 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 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 impacts on human wellbeing.

Europe PMC Funders Author Manuscripts

Acknowledgements

We gratefully acknowledge support from the following sources: University of Minnesota Center for Forest Ecology and Geraldine and Darby Nelson (LEF), the Strategic Environmental Research and Development Program (SERDP) of the U.S. Department of Defense (BB, AD, JM, VN), Oklahoma Agricultural Experiment Station (SRL), European Research Council (ERC) under the European Union's Horizon 2020 research and innovation program (grant no 677232) and German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, funded by the German Research Foundation (FZT 118) (NE), Wisconsin Alliance for Minority Participation (ERL), CFANS faculty development support and Institute for Advanced Study residential fellowship (KYoo), Natural Sciences and Engineering Research Council of Canada (NSERC) and Academy of Finland (285882) (EKC).

References

Aplet GH. Alteration of earthworm community biomass by the alien *Myrica faya* in Hawai'i. Oecologia. 1990; 82:414–416. [PubMed: 28312719]

Bal T, Storer AH, Jurgensen MF. Evidence of damage from exotic invasive earthworm activity was highly correlated to sugar maple dieback in the Upper Great Lakes region. Biol Invasions. 2018; 20:151–164.

Burke JL, Maerz JC, Milankovich JR, et al. Invasion by exotic earthworms alters biodiversity and communities of litter- and soil-dwelling oribatid mites. Diversity. 2011; 3:155–175.

Burtis JC, Fahey TJ, Yavitt JB. Impact of invasive earthworms on *Ixodes scapularis* and other litter dwelling arthropods in hardwood forests, central New York State, USA. Appl Soil Ecoly. 2014; 84:148–157.

Cáceres-Charneco RI, Ransom TS. The influence of habitat provisioning: use of earthworm burrows by the terrestrial salamander, Plethodon cinereus. Pop Ecol. 2010; 52:517–526.

Cameron EK, Shaw CH, Bayne EM, et al. Modelling interacting effects of invasive earthworms and wildfire on forest floor carbon storage in the boreal forest. Soil Biol Biochem. 2015; 88:189–196.

Cameron EK, Bayne EM. Invasion by a non-native ecosystem engineer alters distribution of a native predator. Diversity and Distrib. 2012; 18:1190–1198.

Clause J, Forey E, Lortie CJ, et al. Non-native earthworms promote plant invasion by ingesting seeds and modifying soil properties. Acta Oecolgia. 2015; 64:10–20.

Costello DM, Lamberti G. Non-native earthworms in riparian soils increase nitrogen flux into adjacent aquatic ecosystems. Oecologia. 2008; 158:499–510. [PubMed: 18825416]

Craven D, Thakur M, Cameron E, et al. The unseen invaders: introduced earthworms as drivers of change in plant communities in North American forests (a meta-analysis). Global Chang Biol. 2017; 23:1065–1074.

Crumsey JM, Capowiez Y, Goodsitt MM, et al. Exotic earthworm community composition interacts with soil texture to affect redistribution and retention of litter-derived C and N in northern temperate forest soils. Biogeochemistry. 2015; 126:379–395.

Darwin, CR. The formation of vegetable mould, through the action of worms, with observations on their habits. London: John Murray; 1881.

Dávalos A, Nuzzo V, Blossey B. Demographic responses of rare forest plants to multiple stressors: the role of deer, invasive species and nutrients. J Ecol. 2014; 102:1222–1233.

Dávalos A, Nuzzo V, Blossey B. Single and interactive effects of deer and earthworms on non-native plants. Forest Ecol Manag. 2015a; 351:28–35.

Dávalos A, Simpson E, Nuzzo V, Blossey B. Non-consumptive effects of native deer on introduced earthworm abundance. Ecosystems. 2015b; 18:1029–1042.

Dobson A, Blossey B. Earthworm invasion, white-tailed deer and seedling establishment in deciduous forests of north-eastern North America. J Ecol. 2015; 103:153–164.

Eisenhauer N, Partsch S, Parkinson D, Scheu S. Invasion of a deciduous forest by earthworms: changes in soil chemistry, microflora, microarthropods and vegetation. Soil Biol Biochem. 2007; 39:1099–1110.

Fahey TJ, Yavitt JB, Sherman RE, et al. Earthworm effects on the incorporation of litter C and N into soil organic matter in a sugar maple forest. Ecol Appl. 2013; 23:1185–1201. [PubMed: 23967585]

Ferlian O, Eisenhauer N, Aguirrebengoa M, et al. Invasive earthworms erode soil biodiversity: A meta-analysis. J Animal Ecol. 2017; 87:162–172.

Fisichelli NA, Frelich LE, Reich PB, Eisenhauer N. Linking direct and indirect pathways mediating earthworms, deer, and understory composition in Great Lakes forests. Biol Invasions. 2013; 15:1057–1066.

Frelich LE, Hale CM, Scheu S, et al. Earthworm invasion into previously earthworm-free temperate and boreal forests. Biol invasions. 2006; 8:1235–1245.

Frelich LE, Reich PB, Peterson DW. The changing role of fire in mediating the relationships among oaks, grasslands, mesic temperate forests, and boreal forests in the Lake States. J Sust Forestry. 2017; 36:421–432.

Griffith B, Türke M, Weisser WW, Eisenhauer N. Herbivore behavior in the anecic earthworm species *Lumbricus terrestris* L.? Eur J Soil Biol. 2013; 55:62–65.

Groffman PM, Fahey TJ, Fisk MC, et al. Earthworms increase soil microbial biomass carrying capacity and nitrogen retention in northern hardwood forests. Soil Biol Biochem. 2015; 87:51–58.

Gundale MJ. Infleunce of exotic earthworms on the soil organic horizon and the rare fern Botrychium mormo. Cons Biol. 2002; 16:1555–1561.

Hale CM, Frelich LE, Reich PB. Changes in cold-temperate forest understory plant communities in response to invasion by European earthworms. Ecology. 2006; 87:1637–1649. [PubMed: 16922315]

Hale CM, Frelich LE, Reich PB. Effects of European earthworm invasion on soil characteristics in northern hardwood forests of Minnesota, U.S.A. Ecosystems. 2005; 8:911–927.

Heimpel GE, Frelich LE, Landis DA, et al. European buckthorn and Asian soybean aphid as part of an extensive invasional meltdown in North America. Biol Invasions. 2010; 12:2913–2931.

Hendrix PF, Callaham MA Jr, Drake JM, et al. Pandora's box contained bait: the global problem of introduced earthworms. Ann Rev Ecol, Evol Syst. 2008; 39:593–613.

Holdsworth AR, Frelich LE, Reich PB. Effects of earthworm invasion on plant species richness in northern hardwood forests. Cons Biol. 2007; 21:997–1008.

Larson E, Frelich LE, Reich PB, et al. Tree rings detect earthworm invasions and their effects in northern hardwood forests. Biol Invasions. 2010; 12:1053–1066.

Laushman KM, Hotchkiss SC, Herrick BM. Tracking an invasion: Community changes in hardwood forests following the arrival of *Amynthas agrestis* and *Amynthas tokioensis* in Wisconsin. Biol Invasions. 2018; 20:1671–1685.

Loss SR, Blair RB. Earthworm invasions and the decline of clubmosses (*Lycopodium* spp.) that enhance nest survival rates of a ground-nesting songbird. For Ecol Manag. 2014; 324:64–71.

Loss SR, Hueffmeier R, Hale CM, et al. Earthworm invasions in northern hardwoods forests; a rapid assessment method. Nat Areas J. 2013; 33:500–509.

Lubbers IM, Van Groenigen KJ, Fonte SJ, et al. Greenhouse gas emissions from soils increased by earthworms. Nature Climate Change. 2013; 3:187–194.

Lyttle A, Yoo K, Hale CM, et al. Impact of exotic earthworms on organic carbon sorption on mineral surfaces and soil carbon inventories in a northern hardwood forest. Ecosystems. 2015; 18:16–29.

Maerz JC, Nuzzo VA, Blossey B. Declines in woodland salamander abundance associated with non-native earthworm and plant invasions. Cons Biol. 2009; 23:975–981.

Maerz JC, Karuzas JM, Madison DM, Blossey B. Introduced invertebrates are important prey for a generalist predator. Divers Distrib. 2005; 11:83–90.

McCormick MK, Parker KL, Szlavecz K, Whigham DF. Native and exotic earthworms affect orchid seed loss. AoB plants. 2013; 5doi: 10.1093/aobpla/plt1018

Nuzzo VA, Maerz JC, Blossey B. Earthworm invasion as the driving force behind plant invasion and community change in northeastern North American forests. Cons Biol. 2009; 23:966–974.

Pace ML, Cole JJ, Carpenter SR, Kitchell JF. Trophic cascades revealed in diverse ecosystems. TREE. 1999; 14:483–488. [PubMed: 10542455]

Paudel S, Longcore T, MacDonald B, et al. Belowground interactions with aboveground consequences: Invasive earthworms and arbuscular mycorrhizal fungi. Ecology. 2016; 97:605–614. [PubMed: 27197388]

Europe PMC Funders Author Manuscripts

Qui J, Turner MG. Effects of non-native Asian earthworm invasion on temperate forest and prairie soils in the Midwestern US. Biol Invasions. 2017; 19:73–88.

Regnier E, Harrison SK, Liu J, et al. Impact of an exotic earthworm on seed dispersal of an indigenous US weed. J Appl Ecol. 2008; 45:1621–1629.

Reich PB, Sendall KM, Stefanski A, Rich RL, Hobbie SE, Montgomery RA. Effects of climate warming on photosynthesis in boreal tree species depend on soil moisture. Nature. 2018; 562:263–267. [PubMed: 30283137]

Resner K, Yoo K, Hale C, et al. Invasive earthworms deplete key soil inorganic nutrients (Ca, Mg, K and P) in a northern hardwood forest. Ecosystems. 2015; 18:89–102.

Richardson JB, Görres JH, Jackson BP, Friedland AJ. Trace metals and metalloids in forest soils and exotic earthworms in northern New England, USA. Soil Biol Biochem. 2015; 85:190–198. [PubMed: 25883392]

Rooney TP. High white-tailed deer densities benefit graminoids and contribute to biotic homogenization of forest ground-layer vegetation. Plant Ecol. 2009; 202:103–111.

Roth AM, Whitfeld TJS, Lodge AG, et al. Invasive earthworms interact with abiotic conditions to influence the invasion of common buckthorn (*Rhamnus cathartica*). Oecologia. 2015; 178:219–230. [PubMed: 25481818]

Schlaghamersky J, Eisenhauer N, Frelich LE. Earthworm invasion alters enchytraeid community composition and individual biomass in northern hardwood forests of North America. Appl Soil Ecol. 2014; 83:159–169.

Simmons W, Dávalos A, Blossey B. Forest successional history and earthworm legacy affect earthworm survival and performance. Pedobiologia. 2015; 58:153–164.

Villholth KG, Jarvis NJ, Jacobsen OH, de Jonge H. Field investigations and modeling of particle-facilitated pesticide transport in macroporous soil. J Env Quality. 2000; 29:1298–1309.

Wackett AA, Yoo K, Olofsson J, Klaminder J. Human-mediated introduction of geoengineering earthworms in the Fennoscandian arctic. Biol Invasions. 2017; 20:1377–1386.

Zhang W, Hendrix PF, Dame LE, et al. Earthworms facilitate carbon sequestration through unequal amplification of carbon stabilization compared with mineralization. Nature Comm. 2013; 4doi: 10.1038/ncomms3576

Europe PMC Funders Author Manuscripts

In a nutshell

- Non-native earthworms speed up decomposition of leaf litter and soil mixing in the upper horizons, leading to loss of the litter layer and higher bulk density.
- These changes in soil structure lead to warmer, drier soils, and changes in nutrient availability.
- Resulting cascade effects of concern to society include changes in CO_2 sequestration, disturbance regimes, soil quality, 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 other factors (eg climate change and deer herbivory), to cause important changes in ecological functioning.

Panel 1

Definitions of terms relating to ecological cascades

Ecological cascade. 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* refers to effects caused by removal of a predator (top-down) or primary producer (bottom-up), eg, removal of a top predator results in an increase in population of an herbivore that in turn decreases populations of primary producers. Here, however, we define ecological cascade broadly to include the trophic and non-trophic effects of introducing an ecosystem engineer (earthworms) that alters food webs and physiochemical soil environments in ways that percolate 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 cascades; in effect ecosystems are ‘side-swiped’ when changes in functions are initiated by entrance of earthworms into the side of the trophic structure.

Microcascade. Fundamental effects of addition or removal of organisms on the environment in which they live, including processing of materials, nutrient cycles, and physical changes.

Macrocascade. 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, health and productivity of ecosystems.

Cascade complex. Linked macrocascades that interact with other environmental changes (eg high deer populations and climate change) to influence ecological dynamics at landscape or regional scales, spanning (among many possibilities) forest-agricultural field and rural-urban boundaries.

Europe PMC Funders Author Manuscripts

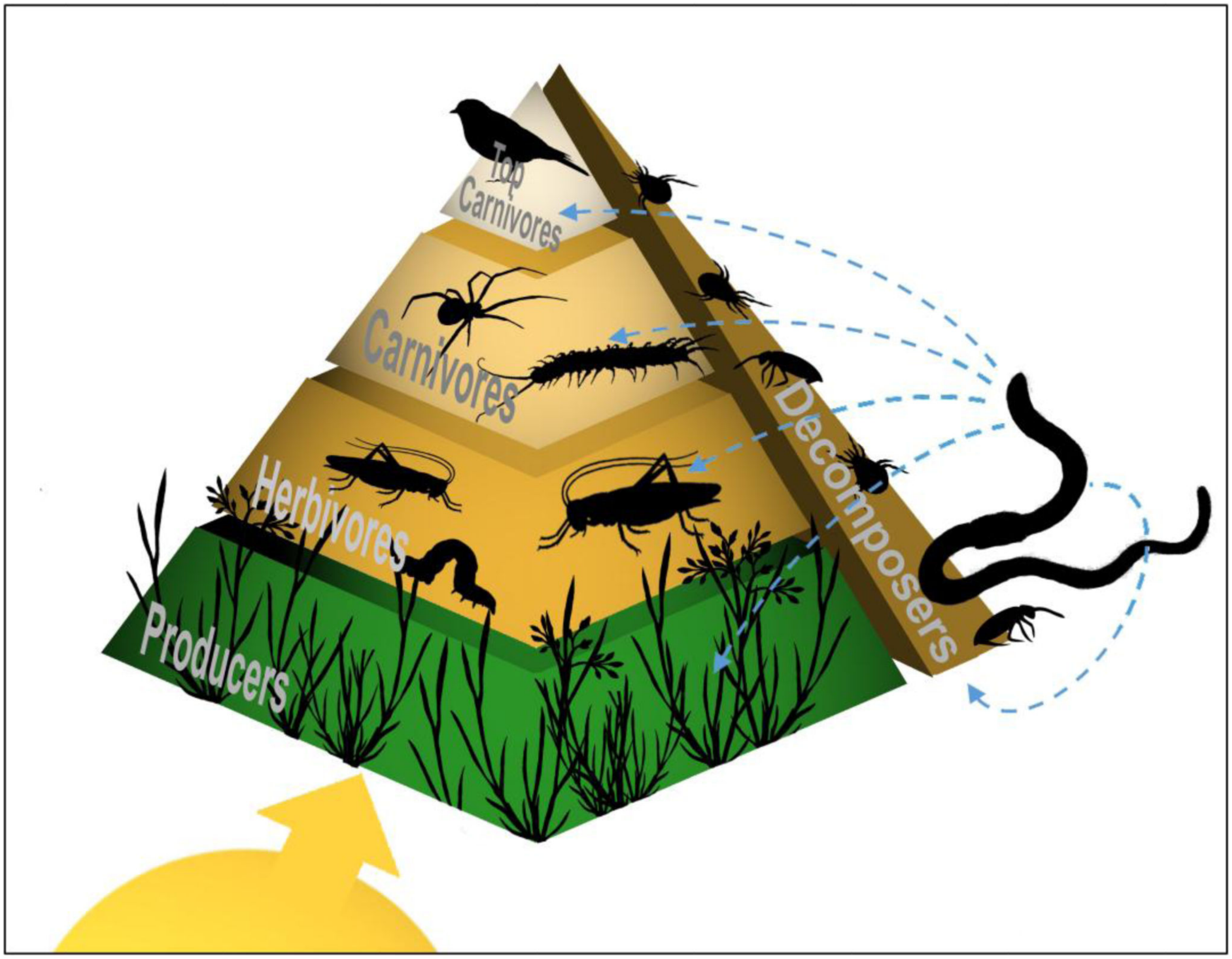

Figure 1.

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 for 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.

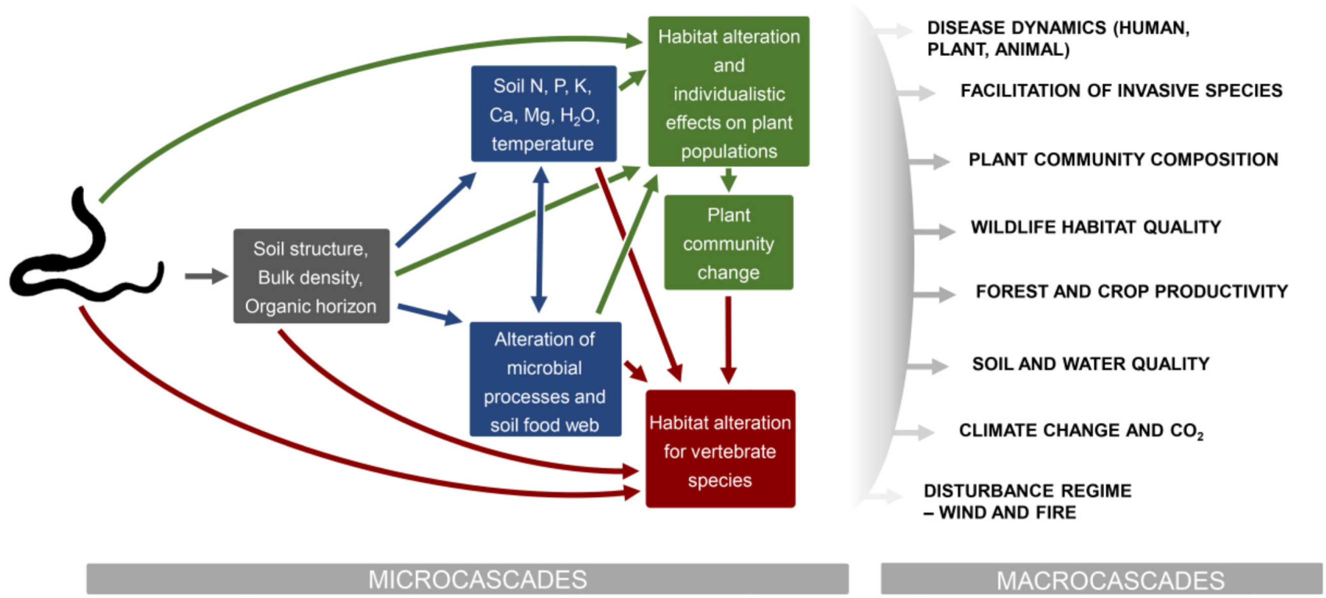

Figure 2.

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 of **Macrocascade effects of earthworm invasion of concern to society,** while the eighth (disease dynamics) emerges in the synthetic case study.

Figure 3.

European earthworm impacts in North American forests. (a) Base of a sugar maple tree in a temperate forest, southern Minnesota, showing loss of the organic horizon and subsequent soil erosion; (b) Base of a balsam fir (*Abies balsamea*) tree in boreal forest, northern Minnesota, showing recession of the forest floor and exposure of roots leading to drought stress; (c) Invasion front of common buckthorn in an earthworm-infested oak and maple forest, southern Minnesota; (d) *Lumbricus rubellus* is a European earthworm species responsible for consumption of the organic horizon in forests. Photo credits: (b) Doug Wallace; (c) Alex Roth; (d) George Schlaghamersky.

Europe PMC Funders Author Manuscripts

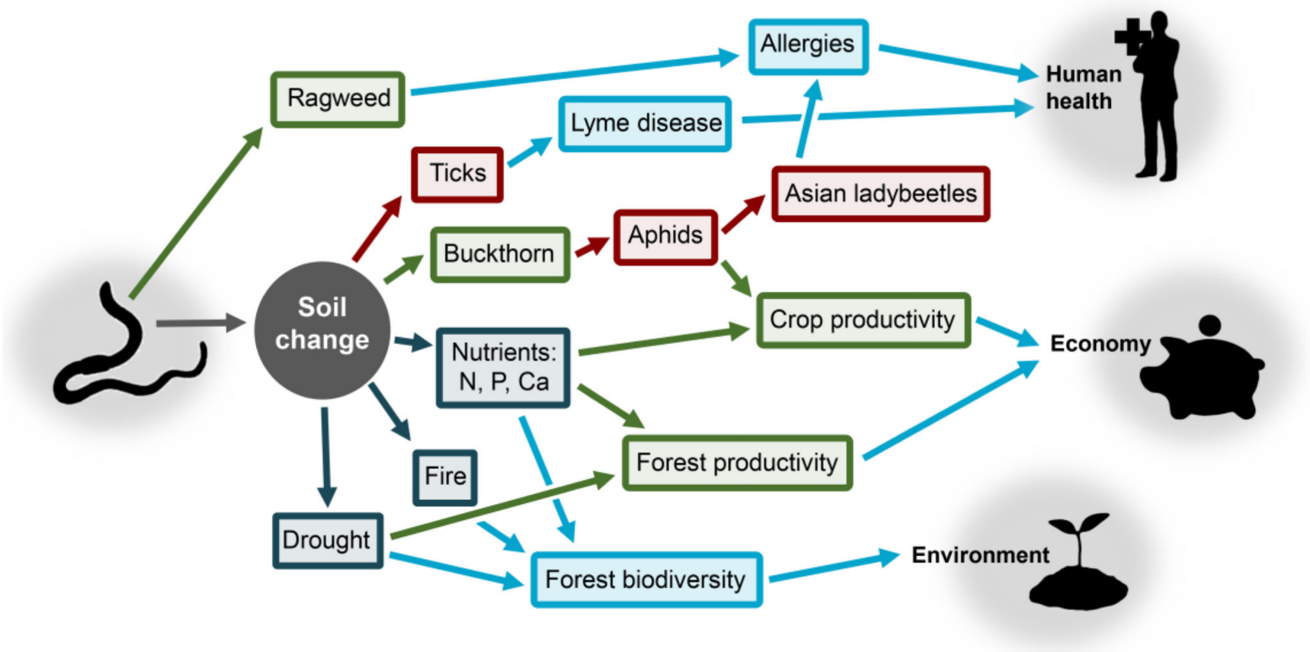

Figure 4.

Cascade complex initiated by earthworm invasion in the northern hardwood forest region, Minnesota to New England, USA. 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.