



Soil fauna responses to natural disturbances, invasive species, and global climate change: Current state of the science and a call to action



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ABSTRACT

Environmental disturbances seem to be increasing in frequency and impact, yet we have little understanding of the belowground impacts of these events. Soil fauna, while widely acknowledged to be important drivers of biogeochemical function, soil structure and sustainability, and trophic interactions, are understudied compared to other belowground organisms such as archaea, bacteria, and fungi. In this review we summarize the current state of knowledge of soil fauna as it relates to and is influenced by various disturbances. We focus our review on three main natural and anthropogenic disturbance types: 1) natural disturbances, including damage from wind and flooding; 2) invasive species, including above and belowground flora and fauna; and 3) climate change impacts on the atmosphere and temperature. We do not address the impacts of wildfires, forestry, agricultural practices, mining, or human-caused pollution, as these topics have all been covered in other works. We highlight knowledge gaps and suggest future avenues of research, with hope that the importance of soil fauna and their influences on ecosystems will be given greater emphasis in future research.

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1. Introduction

Natural disturbances such as wind, flood, drought, and fire have shaped ecosystems and organisms within the global biosphere for millennia, and their influence on the structure and function of ecosystems has long been recognized by ecologists. Indeed, some of the earliest ecological research addressed plant community succession in disturbed habitats (e.g., work in the late 1800s by Eugen Warming) (Coleman, 1986). More recently, ecologists have come to appreciate that anthropogenic disturbances also can shape ecosystem properties, and similar to natural disturbances, span a vast range of intensity, and spatial and temporal scales (Fig. 1). The Earth is currently experiencing an unprecedented period of

anthropogenic disturbances, and climate models predict increased intensity and frequency of future natural disturbances (Dale et al., 2001; IPCC, 2014). Although the discipline of “Disturbance Ecology” is fairly well developed for plant community ecology, including treatment in several book-length syntheses, little effort has been made to synthesize soil responses to disturbances. Further, despite the documented importance of soil organisms on ecosystem functioning (Coleman et al., 2004; Fierer et al., 2007; Wall, 2012; Wardle et al., 2004; Zak et al., 2003), even less attention has been given to soil ecological responses. Here we present a focused review of soil fauna responses to major classes of natural and anthropogenic disturbances across global ecosystems. Due to the prevalence of microbially-focused scholarship in recent years (Fig. 2), we intentionally emphasize *fauna* and exclude discussion of soil microbial responses to disturbances. At the heart of this work is our position that an appreciation and deeper understanding of the relationships between disturbance processes, soil fauna, and ecological function are of critical importance to the future

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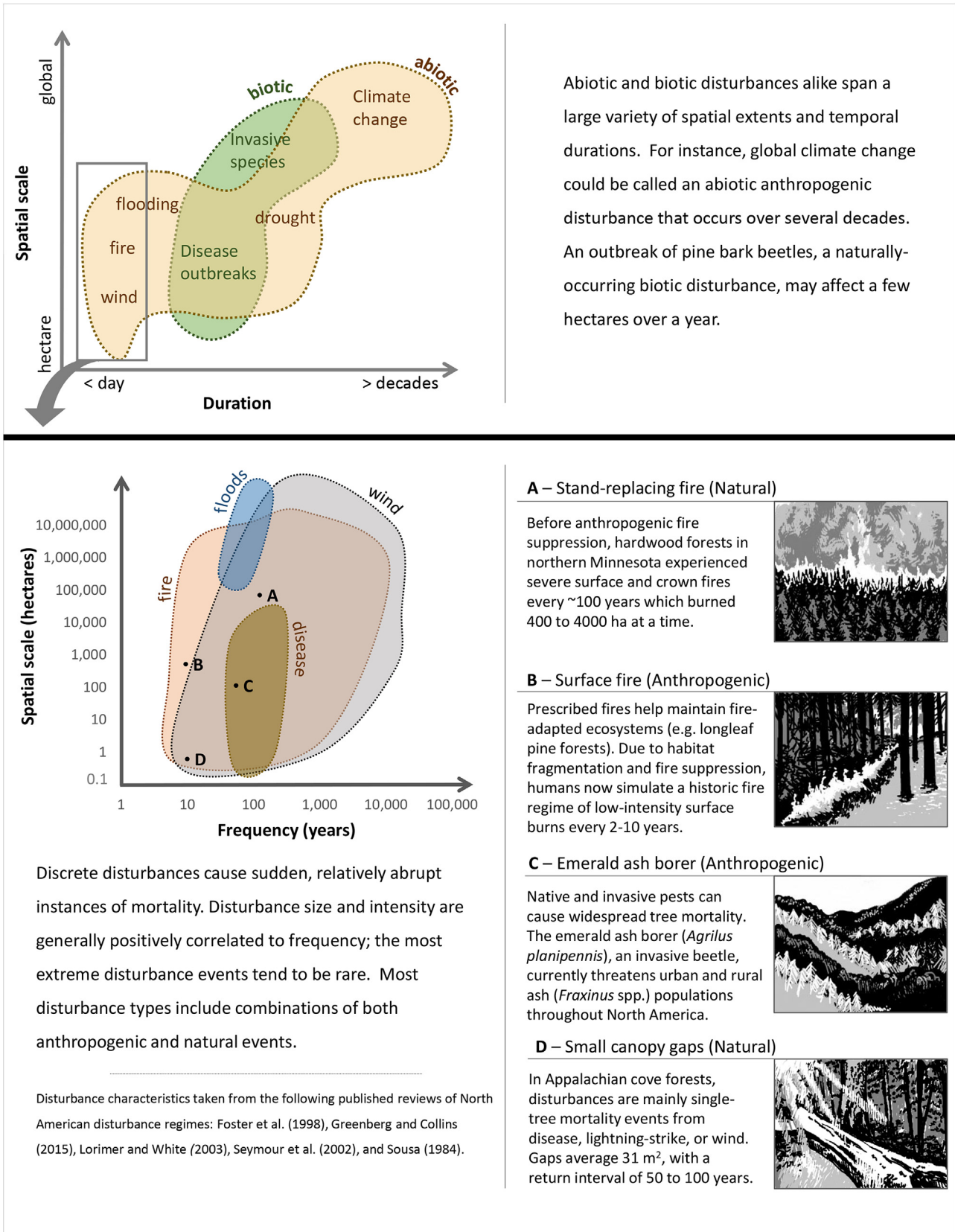


Fig. 1. Disturbance types, scales, and their interactions as they pertain to and impact soil fauna. Disturbance characteristics taken from the following published reviews of North American disturbance regimes: Foster et al. (1998), Greenberg and Collins (2015), Lorimer and White (2003), Seymour et al. (2002), and Sousa (1984).

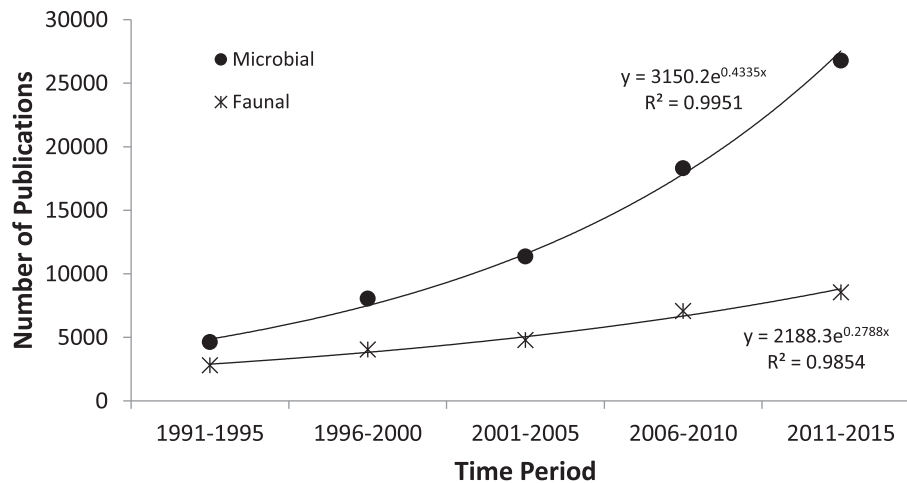


Fig. 2. Number of titles returned in Web of Science searches on the terms “soil + microb^{***}” and the sum of terms “soil + several faunal terms including earthworm, millipede, Collembola, mite, Acari, Oribatid^{*}, centipede, ant, Formicidae, Enchytraeidae, macroinvertebrate, macroarthropod, and nematode.” Searches were performed 12/28–31/2015. Only journal articles and reviews are reported. Number of titles in each category was summed for five year intervals from 1991 to 2015. Exponential curves were fitted to both categories.

sustainability of global food and fiber production systems.

Our review examines how a suite of natural and anthropogenic disturbance types affect soil fauna. We limit our treatment of anthropogenic disturbances to invasive species and climate change, although we fully acknowledge the impacts direct human-mediated disturbances such as certain agriculture and forestry practices, pollution, mining, and climate change-induced alterations to biogeochemical cycles can have on soil biota. Many of these topics have already been reviewed, and while there is considerable difference in the level of impact to soil fauna based on the specific ecosystem/environment, several patterns are evident. For instance, in the short term, most soil invertebrates in forests are rather resilient in their responses to forest management practices or harvesting activities (Marshall, 2000; Setälä et al., 2000). Plant species composition is usually impacted by human activity, and can greatly impact soil fauna in some cases (Frouz et al., 2013; Heděnc et al., 2014), though these impacts are highly variable (Korboulewsky et al., 2016). Pollutants either negatively impact soil fauna or have neutral effects, and changes to aboveground plant community composition can greatly impact soil fauna (Cortet et al., 1999; Coyle et al., 2011; Halling-Sørensen et al., 1998; Kapusta et al., 2011; Kapusta and Sobczyk, 2015). Soil invertebrates are more negatively impacted by mining activities immediately following the disturbance, and as time passes these impacts lessen and the community may return to pre-disturbance conditions (Frouz et al., 2001, 2006, 2008; Roubíčková and Frouz, 2014). Agricultural practices such as fertilization, tillage, and grazing usually have species-specific impacts – which, depending on intensity of agricultural practices, may be positive, negative, or neutral – on belowground fauna (e.g., Ayuke et al., 2011; Cavigelli et al., 2012; Lordache, 2012; Schon et al., 2010; Topoliantz et al., 2000; Witmer et al., 2003; Zida et al., 2011).

For each disturbance type, we will review the available literature for epigeic and endogeic fauna, as these are often treated separately in the literature. Epigeic organisms are those that live on the surface and upper layers of soil (i.e., litter layer and O horizon), and generally consist of both micro- and macroinvertebrates. These organisms are generally responsible for helping convert organic matter that falls to the ground into soil. These organisms are also likely to be immediately and abruptly impacted by acute natural disturbances (e.g., tornados) and may experience large fluctuations in temperature and moisture compared to their deeper-dwelling counterparts.

By contrast, endogeic fauna are those that dwell mostly, or exclusively, in the mineral portion of the soil, rarely venturing to the surface. Of course, some fauna engage in behavior that involves occupying both surface and mineral soil horizons (e.g., anecic earthworms and ants). Organisms in these groups are responsible for the majority of “soil engineering” by invertebrates (e.g., creating tunnels and holes). These organisms may drag organic matter deeper into the soil, and in contrast to their epigeic counterparts, move vertically through soil horizons. They also have a greater ability to escape or avoid soil surface perturbations than do epigeic organisms.

We will adhere to the general categories of epi- and endogeic with occasional reference to other categories (for examples of the fauna reviewed, see Table 1) for this review. Much more work has been done evaluating epigeic fauna, likely because sampling is easier to accomplish (i.e., one does not have to dig a hole to study these organisms).

2. Impacts of natural disturbances

2.1. Wind

Wind disturbances, such as hurricanes, tornadoes, and derechos (i.e., straight-line winds), affect a wide range of forest ecosystem types including coastal, inland, and mountainous zones. The size of the ecological impact can range from a few square meters (e.g., small tree-fall gaps or root tip-up mounds) to hundreds of square kilometers (e.g., hurricanes) (Fischer et al., 2013). Hurricanes and other natural disasters are predicted to increase in frequency and intensity under most climate change scenarios (IPCC, 2014). The sporadic nature and variable spatial impacts of wind disturbances makes carefully planned ecological studies difficult, but recent efforts to artificially recreate hurricane impacts in a controlled setting have been successful (<http://luq.lternet.edu/>). Wind disturbances result in two important structural changes to the physical environment: the removal of canopy material (e.g., branches, leaves) and the deposition of that material on the forest floor or the total removal and export of that material from the local system (Lugo, 2000; Shiels and González, 2014). Thus, these disturbances can lead to sudden inputs of organic matter and increased light penetration to the forest floor, and in some cases, high numbers of uprooted trees (Lugo, 2008; Peterson et al., 1990). Such sudden inputs from treefalls, broken branches, litter, and roots can boost

Table 1
Fauna groups (and their characteristics) covered in this review.

| Group | Habitat | Phylum | Class | Order | Family |
|---------------------|--|------------|-------------|-----------------------------|---|
| Earthworms | Some Epigeic Most Endogeic/Anecic Some at all levels | Annelida | Oligochaeta | Haplotaxida | Lumbricidae Megascolecidae |
| Springtails | Majority Epigeic Few Endogeic/Anecic | Arthropoda | Entognatha | Collembola | Isotomidae |
| Snails | All Epigeic | Mollusca | Gastropoda | Stylommatophora | Clausiliidae Pleurodontidae |
| Mites | Majority Epigeic Few Endogeic/Anecic | Arthropoda | Arachnida | Acari | |
| Millipedes | All Epigeic | Arthropoda | Diplopoda | Polydesmida Spirobolida | Xystodesmidae Polydesmidae Megascolecidae Spirobolidae |
| Proturans | Endogeic/Anecic | Arthropoda | Entognatha | Acerentomata Eosentomata | Protentomidae Acerentomidae Eosentomidae |
| Leaf beetles | Epigeic and Endogeic | Arthropoda | Insecta | Coleoptera | Chrysomelidae |
| Ground beetles | All Epigeic | Arthropoda | Insecta | Coleoptera | Carabidae |
| Saproxyllic beetles | All Epigeic | Arthropoda | Insecta | Coleoptera | Various Families |
| Termites | All levels | Arthropoda | Insecta | Isoptera | Rhinotermitidae Termitidae |
| Enchytraeids | All Epigeic | Annelida | Clitellata | Haplotaxida | Enchytraeidae |
| Wireworms | All Endogeic/Anecic | Arthropoda | Insecta | Coleoptera | Elaterridae |
| Ants | All levels | Arthropoda | Insecta | Hymenoptera | Formicidae |
| Rove beetles | All Epigeic | Arthropoda | Insecta | Coleoptera | Staphylinidae |
| Centipedes | All Epigeic | Arthropoda | Chilopoda | All | All |
| Spiders | All Epigeic | Arthropoda | Arachnida | Araneae | Salticidae Gnaphosidae Thomisidae Lycosidae Agelenidae Dictynidae Linyphiidae |
| Rotifers | All Epigeic | Rotifera | All | All | All |

decomposition rates for years after a disturbance event and release nutrients to the soil, while uprooted trees can contribute to heterogeneity in soil microsite characteristics through the creation of root pits and mounds (Lugo, 2008; Peterson et al., 1990). Consequently, changes to decomposer community composition and structure can result in changes to litter quality and quantity, which in turn can influence multi-trophic food webs, species-specific interactions, and ecosystem stability (González et al., 2014; Turner et al., 1998). In general, most research involving wind disturbance has thus far focused on aboveground impacts, but there is a growing literature examining the effects of wind disturbances on soil biota.

2.1.1. Effects on epigeic organisms

Many epigeic invertebrates depend on moist litter material for food and resources. Wind disturbances can increase the amount of debris on the ground (Everham and Brokaw, 1996), but at the same time, the open canopy and increased air circulation associated with such disturbances can dry the litter layer and soil surface (Richardson et al., 2010). The combination of increased litter, but decreased moisture, often results in decreased abundance and diversity of epigeic fauna such as snails (Bloch and Willig, 2006; Prates et al., 2011), millipedes (Greenberg and Forrest, 2003; Urbanovicová et al., 2014), and ground beetles (Bouget and Duelli, 2004; Gandhi et al., 2008; Greenberg and Forrest, 2003; Richardson et al., 2010; Sklodowski and Garbalińska, 2011; Urbanovicová et al., 2014) in wind disturbed forests. This general decrease in detritivores (e.g., Schowalter, 1994) may lead to effects at higher trophic levels evidenced by reductions in surface predators, such as spiders, centipedes, and predatory ground beetles (Bouget and Duelli, 2004; Greenberg and Forrest, 2003; Richardson

et al., 2010). Litter accumulation is heavily influenced by canopy openness and wind speed, and tends to correlate with earthworm abundance and community composition. For example, presence of the epigeic earthworms *Lumbricus rubellus*, *Eisenia fetida*, *Dendrobaena octaedra*, and *Dendrodrius rubidus* were positively correlated with litter amount in windthrown areas in France (Campana et al., 2002).

In addition to greater inputs of leaf litter, wind disturbances also result in large inputs of woody material to the forest floor in the form of treefalls, snaps, and broken branches, and these can boost numbers of saproxyllic insects. It is notable however that the increase in specialist wood-feeding fauna can be substantially delayed, but once established can persist for many years (Skłodowski and Garbalińska, 2011). Increased woody debris in gaps creates “dead wood islands” (Bouget and Duelli, 2004) in otherwise debris-poor forests. Saproxyllic insects respond to the increase in fine (and especially) coarse woody debris, exposed roots of downed trees, and whether the material is within the forest or in a gap (Grove, 2002). Gaps can also serve as hotspots of saproxyllic beetle diversity, sometimes providing habitat for rare species (Bouget and Duelli, 2004). This benefit to diversity is more likely in debris-poor conifer forests. In ecosystems where the ecological contrast between interior forest and gaps is not as strong, gaps may only be slightly more diverse (Bouget, 2005a, 2005b; Bouget and Noblecourt, 2005). The consistent positive response of this group to woody debris has prompted management recommendations to preserve at least 50% of windthrown areas in their natural state (Wermelinger et al., 2002). Although saproxyllic insects are recognized as an integral part of the forest landscape and in the breakdown of dead woody tissue (Grove, 2002), their impact on biogeochemistry has only recently been explored (Cobb et al., 2010;

Ulyshen, 2015).

Abundance and diversity of small-bodied litter organisms (e.g., Collembola, Acari) tend to increase as a result of wind disturbance (Cuchta et al., 2012a, 2012b; Richardson et al., 2010) but community structure was altered through differing responses of individual taxa. These responses may be driven by debris additions (Cuchta et al., 2012a) or canopy openness (Richardson et al., 2010), although high variation in intraplot abundance was evident (e.g., Cuchta et al., 2012a, 2012b), and in some cases no differences were observed between windthrown and reference stands (Urbanovicová et al., 2014).

2.1.2. Effects on endogeic and anecic organisms

Taxa that are highly mobile or can utilize soil environments at multiple depths (e.g., ants and earthworms) have the potential to escape the desiccating effects of a wind-generated canopy opening, and may be considered more tolerant of wind disturbances. For instance, Hurricane Floyd significantly changed, but did not eliminate, ant communities on several Bahamian islands (Morrison, 2002a), while abundance of several ant species increased near edges of disturbed forest and in windthrown areas in Germany (Theobald-Ley and Horstmann, 1990). Multiple forest disturbances – all that resulted in a decrease of leaf area and branches – had varying impacts on ant species in Korea, where some species increased, some decreased, and some were unaffected by these disturbances (Kwon et al., 2014). In addition to large-scale canopy openings from hurricanes, soil pits and mounds from windthrown trees are another consequence of wind disturbance that can have profound impacts on soil biota. In beech forests of northern Iran, endogeic and anecic earthworms, in particular, were rarely found in soil mounds, but were common in soil pits (Kooch et al., 2014, 2015). This contrasts with work in beech and poplar forests in Belgium, where windthrow pits had very low earthworm abundance (Nachtergale et al., 2002). Although leaf and limb litter are often considered in instances of wind disturbance, tree falls due to wind often result in an influx of root litter and those potential effects on organisms are poorly understood.

2.2. Flooding and water stress

The primary impact of flooding is restricted to the soil environment, yet this disturbance can impact multiple ecosystem components, including biota, hydrological and biogeochemical cycles, and the physical structure of the environment. Overland water flow can alter the abundance, diversity, and composition of soil fauna by redistributing organic materials, sediments, contaminants, and even the fauna themselves (Argerich et al., 2008; Tronstad et al., 2005; Wheatcroft et al., 1997). While some areas experience seasonal or periodic flooding, others suffer rare but substantial flooding events that can have effects on soil properties and organisms that can persist for decades or even centuries. Moisture is a key driver of terrestrial organism activity, and terrestrial invertebrates cope with periods of hypoxia or anoxia caused by fluctuating soil moisture levels by altering their behavior, cellular and physiological functioning, and level of activity (Harrison et al., 2006; Hoback and Stanley, 2001; Marx et al., 2009, 2012). As such, it is not surprising that nearly all soil-dwelling species exhibit distinct responses when subjected to regular flooding. Further, once an environment has flooded, it can take several years for the invertebrate community to return to its pre-disturbance state (Gerisch et al., 2012a, 2012b; Tuf, 2003; Tuf et al., 2008). Of the major disturbances discussed in this review, flooding is arguably the most easily simulated under controlled conditions, and thus, much of the information we have on this topic comes from laboratory or mesocosm studies.

2.2.1. Effects on epigeic organisms

Flooding has distinct, yet relatively short-lived, impacts on many epigeic taxa. Ground beetle abundance usually decreases (Gerisch et al., 2012b; Tuf et al., 2008), but species diversity tends to increase following flooding (Gerisch et al., 2012a; Lessel et al., 2011; Schowalter, 2012). In addition, functional diversity can decrease (Gerisch et al., 2012a), although this is highly dependent on the initial community assemblage (Gerisch, 2014). Thus, community changes after flooding may not be attributable to greater resource availability, but instead may be due to significant environmental selection for certain functional types. Traits such as large body size or dormancy in egg stage may allow some beetle species to survive inundation; alternatively, highly mobile species rapidly immigrate or recolonize sites after flooding (Lambeets et al., 2008; Rothenbücher and Schaefer, 2006).

Collembola are the most well-studied epigeic group with regard to flooding impacts. Many collembolan species have evolved strategies to survive periods of inundation, such as a buoyant integument that allows for flotation (Witteveen and Joosse, 1988), responsiveness to rapid temperature changes following inundations (Tamm, 1984, 1986), and numerous additional physiological, physical, and behavioral adaptations (Marx et al., 2012). The most flood-resistant collembolans use egg diapause and passive drifting strategies to cope with flooding (Marx et al., 2009). Even with these adaptations to inundation, most collembolan species decrease in abundance and show physiological impairment after flooding. Flooding tends to increase site heterogeneity, allowing for the colonization of more water-tolerant species (Marx, 2008; Marx et al., 2009) – this can lead to increased species and functional diversity that differs depending on the current inundation level (Russell et al., 2004). Flood frequency can directly impact the species assemblage of collembolans, as frequently flooded sites showed lower species richness, but greater abundance of individual species compared to less frequently flooded sites (Russell, 2008). Heterogeneous populations and metapopulation dynamics likely contribute to the varied response of collembolan communities to flooding (Russell et al., 2004).

Flooding can also induce changes in mite (Griegel, 2008; Marx et al., 2009) and ground beetle populations (Lessel et al., 2011). Generally, more hydrophilic or hydrotolerant species occur in flooded areas, especially for taxa that are relatively mobile. At extreme ends of a hydrologic gradient, harsh conditions cause significant community changes in floodplain snails and selection for traits such as calcified shells and uniparental reproduction (Ilg et al., 2009, 2012).

2.2.2. Effects on endogeic and anecic organisms

Although surface fauna are more susceptible to being washed away by running water, belowground macrofauna are more vulnerable to inundation and hypoxic conditions due to their inability to avoid or quickly escape flood water. Thus, belowground macrofauna – especially earthworms (Ivask et al., 2007; Plum and Filser, 2005; Zorn et al., 2005), termites (Osbrink et al., 2008; Schowalter, 2012), ants (Beuzelin et al., 2009; Mertl et al., 2009; Schowalter, 2012), and proturans (Sterzynska et al., 2012) – tend to decrease in abundance after floods. Changes in earthworm abundance may be highly dependent on particular conditions, especially soil type and flooding duration (Plum and Filser, 2005).

Increases in flooding frequency and duration generally lead to decreases in soil macrofauna abundance and biomass (Ausden et al., 2001; Frouz et al., 2004; Plum, 2005). Flooding effects on diversity, however, appear to be highly variable, and dependent upon the general flooding regime, regardless of the intensity of an individual flood (Horrocks et al., 2012; Soares et al., 2013; but see Ballinger et al., 2007; Mertl et al., 2009). However, short flooding

periods followed by long recovery periods can benefit certain earthworm species (e.g., *L. rubellus* and *Allolobophora chlorotica*), which showed increased abundance and biomass in intermittently-flooded areas (Schütz et al., 2008), and led to compositional shifts favoring epigeic earthworms (Bullinger-Weber et al., 2012). Flooding can also change ant community composition, mainly by reducing specialist predators and facilitating the integration of terrestrial and floodplain species (Mertl et al., 2009; Schowalter, 2012). Termites generally show reduced activity and abundance as a result of flooding (Osbrink et al., 2008; Ulyshen, 2014).

The deleterious effect of flooding on economically important edaphic pests may – in certain situations – have positive impacts. For instance, corn rootworms (*Diabrotica* spp.), and the citrus root weevil (*Diaprepes abbreviatus*) all show increased mortality during periods of inundation, especially at high temperatures (Hoback et al., 2002; Shapiro et al., 1997), and larval abundance is negatively correlated with soil moisture content (Li et al., 2004, 2007; Toepfer et al., 2007). While the wireworm *Melanotus communis* also shows increased mortality with increasing temperature during flooding (Hall and Cherry, 1993), the use of flooding as a management tool produced inconsistent results (Traugott et al., 2015; and references therein). Flooding regimes can be effective for managing some rhizophagous pest populations (Genung, 1970; Van Herk and Vernon, 2006). If flooding decreases abundance of the pest's natural enemies, however it can actually boost pest populations and contribute to economic losses (Beuzelin et al., 2009; Genung, 1970).

2.3. Drought

Drought has both direct and indirect impacts on the soil environment. Water content in upper soil layers is usually reduced relatively quickly, but deeper soil layers may not be immediately impacted (Nepstad et al., 2002). Lower soil water content increases soil hardness (Anh et al., 2014), increases soil shrinkage (Lauritzen and Stewart, 1941), and reduces water films (Coleman et al., 2004), making movements by many soil fauna more difficult. Drought can result in reduced cover of aboveground flora (Franklin et al., 2016; Garssen et al., 2014), which can lead to increased temperatures and altered microclimate on the soil surface.

2.3.1. Effects on epigeic organisms

The impacts of drought are variable and inconsistent within and among epigeic taxonomic groups. Potential reasons for this inconsistency may be a function of the phenotypic plasticity of each group as a whole or due to a lack of taxonomic resolution in reporting of results. Because ants are relatively easily identified and one of the most studied arthropod taxa in the world, much species-specific information exists regarding the impacts of drought (and other natural and anthropogenic disturbances) on this group. As an example, drought resulted in a decrease of Argentine ant (*Linepithema humile*) abundance and a reduction in the amount of ant-occupied area (Menke and Holway, 2006). Conversely, drought caused an increase in nest abundance and population density of the fungus-gardening ant *Trachymyrmex septentrionalis* McCook (Seal and Tschinkel, 2010). For other groups such as mites or collembolans, it is frequently neither possible nor practical to identify all individuals to the species level (e.g., Holmstrup et al., 2013; Whitford and Sobhy, 1999; Xu et al., 2012), and even when species-level identifications are reported, individual species are often lumped into larger taxonomic groups for analyses (e.g., Turnbull and Lindo, 2015). Patterns at the species level provide insight to the effects of drought. For instance, populations of the collembolan *Protaphorura quadriocellata* were twice as high under control compared to drought conditions (Pflug and Wolters, 2001), and in a separate study the mite *Opiella ornata* was significantly

less abundant under drought compared to control conditions (Tsiafouli et al., 2005). These contrasting results serve to illustrate one serious dilemma facing researchers of soil ecology, which is that soil faunal communities are incredibly diverse, are complex in their responsiveness to perturbation, and changing the level of taxonomic resolution at which data are analyzed can significantly change the interpretation of results.

Enchytraeidae and other oligochaete worms show a consistent negative response to drought, likely due to the fact that most species do not have physical adaptations to limit water loss through the skin (Preston, 2008). For instance, survival and reproduction of *Enchytraeus albidus* and *E. crypticus* was reduced by >23% under drought conditions, especially chronic drought exposure (Maraldo et al., 2009). Drought reduced enchytraeid populations and biomass in certain, but not all, soil types (Plum and Filser, 2005) indicating that soil texture and/or microclimate (and in this case, water holding capacity) has important implications for enchytraeid population dynamics under drought conditions. A severe drought reduced populations of the epigeic earthworm *D. octaedra* so much that adults were not captured at all during the four driest months of one summer whereas they were routinely collected during wetter summers of the six year study period (Eggleton et al., 2009).

2.3.2. Effects on endogeic and anecic organisms

Unlike floods, which can occur over the course of hours and quickly inundate areas, the impacts of droughts manifest much more slowly on the soil environment. As such, organisms below the surface may have the capacity and opportunity to move in order to avoid the impacts of drying soil. For instance, Fraser et al. (2012) found that when soils were irrigated, earthworm abundance was nearly equal in upper (0–5 cm), middle (5–10 cm) and lower (10–25 cm) soil depths. However, under dry conditions nearly all earthworms were found in the lower soil depth, suggesting a downward movement in response to drying soil. While there was a general trend of decreasing earthworm abundance with increasing drought in the UK, this earthworm community (dominated by five species) recovered within months after the end of the drought, likely because of their ability to move downward to more moist soil, and their ability to wait out unsuitable conditions in the cocoon stage (i.e., aestivate) (Fraser et al., 2012). Endogeic earthworm responses to drying are species specific, however, as Callahan et al. (2001) observed that native North American *Diplocardia* spp. remained active throughout the hot and dry late summer months in a tallgrass prairie site, whereas an introduced European species (*Octolasion tyrtaeum*) burrowed to the deepest depth possible in field mesocosms and ceased activity during the dry months.

2.4. Fire

Fire is one of the most widespread disturbances across the globe and has profound effects in structuring and regulating entire ecosystems both spatially and temporally. Some ecosystems (e.g., grasslands, savannas, and temperate coniferous forests) are adapted to the periodic occurrence of low-intensity surface fires that mainly impact topsoil and the plant understory (e.g., Hartnett and Fay, 1998; O'Brien et al., 2008), whereas others are regulated by less frequent, but more intense crown fires that rarely touch the ground and instead sweep through only the forest canopy (e.g., Agee, 1993). Of course, other ecosystems are fire-sensitive, and the occurrence of fire (either rare, natural ignition, or intentional anthropogenic prescribed fire) is catastrophic and results in a state change from one ecosystem to another (e.g., burning of tropical rain forest and conversion to agricultural land-use [Cochrane, 2003]). For soil fauna, the responses to natural or anthropogenic fire disturbances are generally linked to the fire dependence/sensitivity of

the ecosystem in question, the frequency and intensity of fires, and the life-history traits of the soil organisms themselves. Surface fires, whether prescribed or naturally occurring, have a number of direct and indirect effects on the soil that affect soil faunal communities. Taxa that are unable to retreat to deeper, cooler soil suffer direct mortality from the extreme heat. Surface fires remove some portion of the upper organic horizon, sometimes removing it altogether. This reduces both habitat availability (i.e., litter and topsoil) and food resources (especially fungal hyphae and fungivorous prey species). Among the most important life-history traits are epigeic/endogeic habitat use and dispersal capacity (Siepel, 1994). In any case, whether prescribed or natural, low intensity or catastrophic, fire dependent or fire sensitive ecosystems, all fires result in physical, chemical and biological changes to soils that have the potential to influence soil fauna (Callaham et al., 2012). And, while there is a paucity of data pertaining to the impact of wildfires on soil fauna (but see Zaitsev et al., 2016), some patterns are evident.

2.4.1. Effects on epigeic organisms

Epigeic organisms, compared with endogeic organisms, are more often affected by surface fires (Coleman and Rieske, 2006). This is likely due to the inability of some epigeic macro- and mesofauna to quickly penetrate deeply enough into the soil to escape the extreme heat during fires, and also due to the loss of substrate/habitat to combustion. Frequency and intensity of the fire regime determines how much of the litter layer is left behind and/or how much litter persists. These factors are critical for the effect of an individual fire event on the litter invertebrates. Detritivores in particular may increase if combustion of the surface fuels is only superficial and leaves detritus on the soil surface, but these organisms decrease in abundance if the fire is more severe and combusts the majority of the litter layer. Millipedes, for instance, show strong decreases in abundance after fire (Neumann and Tolhurst, 1991; Radea et al., 2010), although the effects vary by season. Frequent fires do not appear to impact the presence of termites (Avitabile et al., 2015; Hanula et al., 2012), although as noted in a review by Davies et al. (2010), more intense fires may negatively impact termite populations. Ikeda et al. (2015) suggested prescribed fire might be a potential management approach to controlling populations of invasive epigeic earthworms (*Amyntas agrestis*) in the Southern Appalachian mountains and found that although experimental fires did not significantly reduce numbers of adult earthworms, the fires had strong effects on the viability of cocoons, and these hatched at a much lower rate than cocoons from unburned plots.

Smaller-bodied fauna, such as mites, nematodes, and collembolans, may have an elevated level of resiliency to fire, so long as they are able to move further down in the soil when the fire occurs (Barratt et al., 2006; Gongalsky et al., 2012; Malmström et al., 2009; Wikars and Schimmel, 2001). Composition changes in collembolan communities may last for up to a decade (Malmström, 2010, 2012) or recover within a year (Neumann and Tolhurst, 1991). There is still some disagreement as to whether epigeic or endogeic Collembola recover more quickly after fire; Huebner et al. (2012) found that smaller-bodied endogeic species replaced the larger-bodied epigeic species, but Malmström (2012) found selection for well-dispersing surface-dwelling collembola. These differences in response may be related to life history traits like tolerance to disturbance (e.g., burying into the ground favors small-bodied endogeic) or recolonizing strategies (rapidly dispersing and sexually reproducing). Fire effects on mite populations are often minimal or transient (Barratt et al., 2006; Grabczyńska et al., 2009; Jung et al., 2010; Malmström et al., 2009). Decreases in abundance or diversity may not last more than a few months, although the community composition may remain altered. This quick recovery is attributed to the relatively

thick cuticle and ability of mites to move within the soil (Wikars and Schimmel, 2001). Nematode abundance and biomass were generally unaffected by wildfires, though abundance of plant- and hyphal-feeding nematode groups was reduced, while abundance of bacteria-feeding nematodes increased following forest fires (Butenko et al., 2017).

Ground beetles' thick cuticles may help them survive during fires (Wikars and Schimmel, 2001), although their responses to fire are quite variable (Cook and Holt, 2006; Iglay et al., 2012; Roughley et al., 2010; Willand et al., 2011). Increases in abundance and diversity are often driven by species-specific patterns (Cobb et al., 2007; Wikars and Schimmel, 2001). A few taxa have been observed to possibly be pyrophilic and prefer recently burned habitats (Buddle et al., 2006; Gandhi et al., 2008). Even for those instances where ground beetle populations decrease after fire, the effects are often temporary or less severe than for more soft-bodied taxa (Radea et al., 2010; Saint-Germain et al., 2005; Sasal et al., 2010; Schowalter, 2012).

Fungivores consistently decline in abundance after fire, sometimes quite drastically (Buddle et al., 2006; Wikars and Schimmel, 2001). This response is attributed to the limited fungal resources in post-fire soil and changes to soil pH (Buddle et al., 2006; Malmström et al., 2009).

The effect of fire on soil predators generally reflects the effects of their prey species (Schowalter, 2012). This often results in a decrease in abundance, although the magnitude of that decrease is variable (Gongalsky et al., 2012; Hanula and Wade, 2003; Malmström et al., 2009; Pryke and Samways, 2012). Centipedes, for instance, show relatively weak decreases in abundance (Radea et al., 2010; Sileshi and Mafongoya, 2006). Spider abundance and diversity show both strong and weak decreases, due to species-specific responses (Sileshi and Mafongoya, 2006; Underwood and Quinn, 2010). Unlike ground beetles, however, there is no evidence for the existence of pyrophilic spider species (Malmström et al., 2009). While some spider groups (e.g., Linyphiidae, Lycosidae) may be more common in post-fire environments, spider populations overall may take decades to recover to pre-disturbance levels (Buddle et al., 2000).

2.4.2. Effects on endogeic and anecic organisms

Species that utilize more (and deeper) portions of the soil profile (e.g., ants) tend to be more resistant or resilient to fire (Andersen et al., 2014; Parr and Andersen, 2008; Silveira et al., 2013). Most ant populations are often either unaffected (Barrow et al., 2007; Parr and Andersen, 2008; Silveira et al., 2013), or experience weak decreases in abundance that recover to pre-disturbance levels within a year (Neumann and Tolhurst, 1991; Pryke and Samways, 2012; Underwood and Quinn, 2010); however, in some cases ant communities may be altered up to a decade post-fire (Silveira et al., 2013). Similarly, earthworms can exhibit temporary decreases in abundance following fires (Callaham et al., 2003a,b; Malmström et al., 2009; Neumann and Tolhurst, 1991; Sileshi and Mafongoya, 2006), and earthworm responses to fire highlight the importance of the overall fire regime. In a fire-regulated prairie, repeated fires were shown to maintain native endogeic earthworm assemblages, whereas invasive earthworm species dominated the community when fire was excluded from the system (Callaham and Blair, 1999; Callaham et al., 2003a), and these authors suggested the effects of fire to the earthworm community were likely mediated by plant community responses to fire, highlighting the complexity of plant/soil/fauna/disturbance interactions. The seasonality of fires may also influence earthworm communities; earthworms were relatively unaffected by an autumn burn, but populations were drastically reduced for three years after a spring burn (Neumann and Tolhurst, 1991).

Severity and seasonality seem to be the most important fire regime characteristics that determine the long term consequences of a given fire (Andersen et al., 2014; Malmström, 2010). Changes to invertebrate assemblages can alter ecosystem processes, especially decomposition rates (Brennan et al., 2009). It should be noted, however, that as for all disturbances, changes in soil communities during recovery from fire may not be due to the direct impacts of the actual disturbance, but instead due to changes in the plant community during succession, and/or the quality and quantity of organic matter inputs to the system (Callaham et al., 2003a; Radea et al., 2010).

3. Impacts of invasive species

3.1. Invasive plants

North America now harbors over 1650 non-native plant species in all types of environments (<http://www.invasive.org/species/weeds.cfm>; accessed 16 January 2017). While many species are found outside their native ranges, only a small percentage of non-native species become invasive, dominating or significantly altering ecosystem function in their new ranges and causing substantial ecological or economic impacts (Duncan et al., 2004; Ehrenfeld, 2003; Vila et al., 2011). The principle mechanism through which invasive plants alter the soil environment is by shifting the floristic composition and functional groups present, which in turn affects net primary productivity (NPP), nutrient cycling, and ecosystem capacity to acquire carbon (C) due to differences in morphology, phenology, and growth rate (Ehrenfeld, 2003; Reinhart and Callaway, 2006; Vila et al., 2011). These changes in ecosystem C acquisition may also alter litter decomposition rates, accumulation, and nutrient release from the pool of stored organic matter, while simultaneously affecting rhizosphere interactions that can impact the soil microbial community, nutrient cycling, and plant community interactions (Bohlen, 2006). Invasive plants commonly establish in disturbed areas (Sher and Hyatt, 1999), though evidence suggests that plant invasions are becoming more common in pristine environments (Pauchard et al., 2009). Unfortunately, soil faunal responses are not often included in most examinations of plant invasion ecology.

3.1.1. Effects on epigeic organisms

Plant invasions tend to produce mixed effects on the communities of many litter-dwelling taxa, including changes in abundance, community diversity, and species composition (Bultman and DeWitt, 2008; Christopher and Cameron, 2012; Gu et al., 2008; Kappes et al., 2007; Lindsay and French, 2006; Robertson et al., 2011; Schirmel et al., 2011). As such, impacts on specific taxa are likely tied to interactions with particular plant species. For instance, areas invaded with garlic mustard, *Alliaria petiolata*, had nearly three times more collembolans than uninvaded areas (Alerding and Hunter, 2013), but ant community abundance was unaffected (Ivanov and Keiper, 2011). The invasive tree-of-heaven, *Ailanthus altissima*, can substantially alter ecosystem structure and function (Constán-Nava et al., 2015), yet this species has inconsistent effects on the soil arthropod community (Gutiérrez-López et al., 2014; Motard et al., 2015). Unfortunately, the taxonomic resolution in these and other studies was also inconsistent, ranging from Order or Family for some groups (Gutiérrez-López et al., 2014), to species level for others (Motard et al., 2015), and functional group for others (Xu et al., 2011). In some cases, impacts of invasive plants depended on the inclusion or exclusion of certain taxa during analyses (Standish, 2004).

Perhaps no study illustrates the difficulties encountered when trying to make generalizations regarding impacts of various factors

on soil macrofauna communities better than Brown et al. (2004). Their study examined soil macrofauna in pastoral systems throughout a 30-year period over a large geographical region of Mexico, during a time when these pastures were converted from native to invasive grasses. Earthworms, ants, and termites dominated soil fauna abundance and biomass; however, impacts of invasive grasses depended on site, year, time sampled during a year, and faunal group. Communities were different under native and invasive grasses, but it is unknown if these changes resulted in net benefit or detriment to ecosystem function. Results from these studies serve once again to demonstrate the complexity of plant-soil-fauna interactions and argue for increased attention from future researchers employing complex experimental designs focusing on the net effects of disturbances on ecosystem function.

3.1.2. Effects on endogeic and anecic organisms

While few studies examine the impacts of invasive plants on soil endogeic and anecic fauna, there is mounting evidence that invasive flora can affect the earthworm community, and vice versa. The invasive shrub, European buckthorn (*Rhamnus cathartica*), is associated with the presence of earthworms in soils of the Great Lakes region in North America (Heneghan et al., 2006), and the removal of this shrub has been shown to result in decreased abundance of the non-native earthworms (Madritch and Lindroth, 2009). However, other studies dispute the clarity of this relationship as Wyckoff et al. (2014) failed to find a strong relationship between earthworm and *R. cathartica* abundances. However, in a greenhouse study, Roth et al. (2015) found evidence that earthworm interactive effects on light and leaf litter were clearly related to buckthorn germination and growth. In other invasion systems, the presence of the invasive shrub *Chromolaena odorata* caused increases in earthworm density (Mboukou-Kimbatsa et al., 2007) and species richness (Kone et al., 2012) in areas with early compared to older plant invasion. Greater earthworm abundance and biomass was present in longleaf pine (*Pinus palustris*) stands infested by cogongrass (*Imperata cylindrica*) compared to non-infested areas (Martin, 2012). In yet another shrub invasion system in the southeastern USA, Lobe et al. (2014) found the invasive plant, Chinese privet (*Ligustrum sinense*) was associated with higher abundances of European earthworm species (primarily *Aporrectodea caliginosa*), but when the shrub was removed, populations of the introduced earthworms declines and populations of a native species (*Diplocardia michaelsonii*) rebounded.

3.2. Invasive macrofauna

Invasive species of two major soil-inhabiting faunal groups – ants and earthworms – have been intensely researched, and their environmental impacts can be immense. Ants and earthworms can change soil physical properties, decomposition rates, and nutrient dynamics (Bohlen et al., 2004; Dunham and Mikheyev, 2010; Greiner et al., 2012; Holdsworth et al., 2012; Hopfensperger et al., 2011; Stanley and Ward, 2012; Szlavecz et al., 2011). Invasive ants such as the red imported fire ant, *Solenopsis invicta*, or tawny crazy ant, *Nylanderia fulva*, can cause millions of dollars in damage and have broad negative impacts on livestock and crops (Lard et al., 2002), wildlife (Allen et al., 1994), biodiversity (LeBrun et al., 2013), infrastructure (Lard et al., 2006), and human health (Kemp et al., 2000). Invasive earthworms have been implicated in significantly altering forest system structure and functioning in some of the most pristine areas of North America (Addison, 2009; Bohlen et al., 2004; Cameron and Bayne, 2009; Frelich et al., 2006; Hendrix et al., 2008), although this largely occurs in areas that were not previously occupied by earthworms (Hendrix et al., 2006; Migge-Kleian et al., 2006). Because of high public visibility and

relatively easy identification of these invertebrates relative to other groups, there has been a great deal of research pertaining to their impacts on other organisms.

3.2.1. Effects on epigeic organisms

Invasive ants generally decrease the abundance of soil macrofauna directly via predation or indirectly by competing for resources. For example, native ant populations commonly decline in richness and abundance when invasive ants are present (Carpintero et al., 2005; Hoffmann et al., 1999; Holway et al., 2002; Wagner and Van Driesche, 2010; Walker, 2006). In some cases, however, native ant populations may return to pre-invasion levels provided sufficient time passes - in one case where *S. invicta* invaded, the time required for recovery of native species populations was 12 years (Morrison, 2002b). Invasive ants can reduce predatory arthropod abundance by displacement (Causton et al., 2006; Human and Gordon, 1997; Lubin, 1984; O'Dowd et al., 2003), and negatively impact grazing and detrital communities through predation (Dunham and Mikheyev, 2010; Human and Gordon, 1997). While there will always be exceptions (e.g., Stanley and Ward, 2012), invasive ants tend to give us the most consistent ecological response in that they negatively impact populations of other soil macrofauna. For example, Stanley and Ward (2012) examined the impacts of an invasive ant, *L. humile*, on soil macrofauna by assessing biodiversity and ecosystem function in areas that have and have not been invaded. Collembolan abundance was greater, while isopod, amphipod, and ant abundance was reduced in areas invaded by *L. humile*. Unfortunately, none of these groups were identified to species, resulting in analysis and interpretation of *L. humile* impacts at the taxonomic level of Order. Overall, ant abundance decreased, but this trend was driven by species-specific interactions: *Mayriella abstinens* was 743% more abundant in invaded compared to non-invaded areas, while *Prolasius advenus*, *Tetramorium grassii*, and *Nylanderia* spp. were not found in areas invaded by *L. humile*. Similar patterns were evident for several beetle groups, few of which were identified below the genus level. A closer inspection of beetle abundance shows that as taxonomic resolution decreases, species-specific responses become less influential to the overall data interpretation, even though there were strong community compositional responses to *L. humile* invasion.

The influence of invasive earthworms depends on whether the particular invaded environment has a history of earthworm presence (Migge-Kleian et al., 2006). In areas of North America that have a native earthworm presence, impacts of invasive earthworms may range from neutral to positive. These effects are often dependent upon other, soil profile disrupting disturbances such as agricultural or urban development (Hendrix et al., 2008; James, 2004; Stebbings, 1962), and it is frequently observed that when non-native species become established, they often reach higher population densities, and have different functional/behavioral traits than natives, further affecting the variability of their impacts (Kalisz and Dotson, 1989; Callahan et al., 2003b; Snyder et al., 2011). In general, invasive earthworms decrease abundance - often through competition for food resources (Schlaghamersky et al., 2014; Snyder et al., 2013) - and alter community structure of other soil fauna in areas where earthworms did not previously exist (also see Migge-Kleian et al., 2006). Species richness and density of millipedes was lower in the presence of invasive earthworms in a field study (Snyder et al., 2011). However, when incubated together in laboratory microcosms growth and mortality of one millipede species was unaffected, but the amount of litter-derived C within millipedes decreased in the presence of invasive earthworms (Snyder et al., 2009). In a similar incubation using a different millipede species, invasive earthworms induced early

mortality in the millipedes, but earthworms failed to reproduce when the two were incubated together, suggesting food resource competition (Snyder et al., 2013). McLean and Parkinson (2000b) and Burke et al. (2011) showed greater abundance of oribatid mites and significant decreases in mite diversity and species richness in the presence of invasive earthworms. Burtis et al. (2014) showed a significant decline in litter-dwelling arthropods, although taxonomic resolution in this study was low.

3.2.2. Effects on endogeic and anecic organisms

It is unclear how endogeic species that have invaded North American soils have influenced populations of native endogeic species. In one study that explicitly examined competitive interactions between native and introduced endogeic earthworms, Winsome et al. (2006) found that invasive earthworms were superior competitors to native earthworms in the Pacific Northwest, but this effect was only true in highly productive grassland systems, and native earthworms persisted in lower fertility soils. In parts of the Great Lakes Region of North America, several species of invasive root-feeding weevils were numerically dominant, accounting for >99% of all weevils, and >74% of all root-feeding fauna (Coyle et al., 2012; Pinski et al., 2005); these data suggest possible displacement of native rhizophagous species.

3.3. Interactions between invasive flora and fauna

There have been numerous studies on the interactions between invasive plants and invasive earthworms; primarily addressing if invasive earthworms benefit plant invasion. Nonnative earthworms have been linked to decreased native plant species and soil organic matter, and increased pH (Hopfensperger et al., 2011), and these alterations could degrade the stability of native systems and thus aid in plant invasion. Results regarding the relationship between invasive plants and invasive invertebrates are thus far mixed. For instance, Zelles (2012) found no relationship between invasive earthworms and garlic mustard, and Belote and Jones (2009) used a mesocosm experiment to show invasive earthworms did not aid in non-native plant invasion. Conversely, Nuzzo et al. (2009) and Wurst et al. (2011) both saw a positive relationship between earthworm invasion and plant invasion. In another greenhouse study, Whitfield et al. (2014) examined potential mechanisms behind "co-invasion" by non-native earthworms and non-native plants into ecosystems of varying native plant diversity. They found that non-native earthworms had a direct and positive effect on germination, establishment, and biomass of invasive plants, and this effect was not influenced by the diversity of the native plant communities examined. These studies, with variable results regarding interactions between non-native earthworms and non-native plants, illustrate the spatio-temporal variability of interactions among invasive groups, and the difficulty associated with making generalizations regarding their impacts.

4. Impacts of climate change

4.1. Increased atmospheric CO₂ and O₃

When compared to historical patterns, recent alterations in global climate characteristics - including increased atmospheric levels of carbon dioxide (CO₂) and ozone (O₃), amounts and spatial and temporal distribution of precipitation, and frequency of extreme weather events like tornadoes and hurricanes - are impossible to ignore. Recently, several major multi-national meetings (e.g., 2015 United Nations Conference on Climate Change - COP21, <http://www.cop21.gouv.fr/en/>; 2014 United Nations Climate Summit, <http://www.un.org/climatechange/summit/>)

have convened to discuss the impacts of climate change and come to agreements on ways to mitigate climate change impacts on the environment. While overwhelming evidence supports the existence of climate change, knowledge of climate change impacts on certain specific ecosystems – and faunal groups within these ecosystems – remains lacking. Belowground systems, in particular soil fauna, are an underrepresented group that may be greatly affected by climate change (McKenzie et al., 2013; Nielsen and Wall, 2013). In addition to a lack of knowledge regarding responses of certain faunal groups to climate change, we lack information pertaining to interactions among above and belowground taxa (García-Palacios et al., 2015; McKenzie et al., 2013). As global climate change occurs, the impacts of these changes on soil fauna will be increasingly important, yet there is a paucity of empirical data.

4.1.1. Effects on epigeic organisms

As with most factors discussed in this review, the available evidence suggests that impacts of increased CO₂ concentrations on soil invertebrates vary both temporally and spatially. Mite and collembolan abundance was unaffected after five years of elevated CO₂ treatments in Tennessee, USA (Kardol et al., 2011), but increased CO₂ resulted in >70% decreases in abundance of mites and collembolans at the Aspen FACE (Free Air CO₂ Enrichment) site in northern Wisconsin, USA (Loranger et al., 2004). After 7 years of treatments in a Swiss FACE experiment, increased CO₂ led to a decrease in collembolan abundance, an increase in individual body size, and did not impact community richness (Xu et al., 2013). Results from a German FACE site showed increased collembolan abundance and increased biodiversity with increased CO₂ concentrations (Sticht et al., 2006), while those from a New Zealand FACE site showed increased nematode and rotifer abundance with increased CO₂ (Yeates et al., 2003). However, results from this study showed invertebrates respond differently based on their trophic position and species. For example, abundance of plant-feeding *Longidorus* spp. nematodes was >4 times greater with elevated CO₂, while other nematode genera were unaffected (Yeates et al., 2003). Different taxonomic groups showed increased, decreased, or unchanged abundance in increased CO₂ conditions in the EucFACE experiment in Australia (Facey et al., 2017). Beyond changes in abundance and diversity, elevated CO₂ concentrations can impact decomposer food choices (Hättenschwiler and Bretscher, 2001) and palatability (Frouz et al., 2002), thereby potentially altering decomposition rates and biogeochemical cycles.

Increased O₃ concentrations led to decreases in mite abundance, but did not affect collembolans (Loranger et al., 2004), while another study at that same site (Aspen FACE) showed increased collembolan abundance under elevated O₃ concentrations (Meehan et al., 2010). These data support the notion that the impacts of global climate change can be highly variable, and may be taxon specific.

4.1.2. Effects on endogeic and anecic organisms

Impacts of both CO₂ and O₃ are highly variable on earthworm activity, though – as expected, these impacts vary among species (Zaller and Arnone, 1999). Meehan et al. (2010) showed decreased earthworm activity under elevated CO₂, while elevated O₃ had no impact on earthworm activity, but these authors did not indicate the earthworm species evaluated in their study. Impacts of elevated CO₂ and O₃ are commonly evaluated on *Lumbricus terrestris*, which generally exhibit reduced growth when fed elevated CO₂ foliage, especially *Alnus glutinosa* (Scullion et al., 2014).

4.2. Indirect effects of a warmer climate

Although rising air temperatures and impacts on aboveground

flora and fauna have historically received a great deal of attention regarding climate change, belowground ecosystems are equally impacted by rising temperatures. This can, in turn, alter relationships among plants, soil microorganisms, and fauna. Numerous soil warming studies have been established from the tropics (e.g., TRACE, <http://forestwarming.org/>) to the arctic (e.g., ITEX, <http://ibis.geog.ubc.ca/itex/index.php>). In northern areas, warmer temperatures during winter months can set off an ecological cascade by leading to a reduction in snow cover, colder soils (because deep snow insulates the soil), and increased frequency and greater depth of soil freezing (Groffman et al., 2001; Hardy et al., 2001). Unfortunately, our knowledge of the impacts of changing soil dynamics on soil fauna is in its infancy, partially because few studies have undertaken this question, and partially because long-term data are necessary to generate meaningful results. Further complicating the issue, the impacts on soil fauna appear to be intricately tied to soil moisture, which, in turn, is often linked to the characteristics of the local flora. As such, many environmental factors interact and impact soil fauna community dynamics, and disentangling the influence of these inputs can be extremely challenging.

4.2.1. Effects on epigeic organisms

A recent meta-analysis indicated warmer and wetter conditions stimulated fungal (mycelial) growth, which contributed to increases in fungal-feeding soil biota (A'Bear et al., 2014). Acari and Collembola abundance was impacted little by experimental warming (i.e., –15 and –12% change, respectively) while increased precipitation resulted in 117% more Acari and 45% more Collembola (Wu et al., 2014). In this study, mite abundance was strongly correlated with plant abundance and cover. Likewise, nematode trophic groups were impacted little by soil warming treatments in a northern forest system, but exhibited altered community trophic structure under warmer soil temperatures; these changes were positively correlated with plant cover (Thakur et al., 2014). Smaller organisms (e.g., Acari) tend to be more sensitive to changes in soil temperature than larger organisms (e.g., Collembola), though even within a group there can be species-specific differences that result in a shift in community dominance from small-bodied to relatively larger-bodied individuals (Bokhorst et al., 2012). Other studies indicate a greater impact of warming soils on smaller bodied insects (Lindo, 2015), or simply that certain types of ecosystems (e.g., colder and drier) would be most impacted by warming soils (Blankinship et al., 2011). These results are seasonally-dependent, however, because warmer temperatures during summer interact with local flora to influence belowground fauna, while warmer temperatures in winter influence snowpack, which, in turn, creates a colder and harsher soil environment. These conditions generally result in a reduction of soil fauna, though there are some exceptions (Bokhorst et al., 2012; Templer et al., 2012). In these studies, smaller organisms were the most negatively impacted by harsh conditions (e.g., Acari, Pseudoscorpionida) while larger groups such as Chilopoda and Diplopoda were better able to withstand the changing soil conditions.

Our understanding of the impacts of climate change – and specifically soil warming – on soil fauna is continually challenged by species-specific and microscale differences. For instance, an open-top chamber experiment showed higher mite abundance in warmer soil, but higher insect and larval symphytan abundance in control chambers (Dollery et al., 2006). Abundance of most collembolan species was higher in control chambers, but one species (*Folsomia bisetosa*) had higher abundance in warmer chambers. Warmer soil temperatures positively influence soil mesofauna abundance and biomass during a cool, wet summer, but not during a warmer, drier summer (Harte et al., 1996). One study showed that the impacts of soil warming on soil microfauna depended upon

which peat layer (i.e., closer or further from the surface) was sampled (Krab et al., 2015). Finally, after two decades of experimental soil warming, collembolan species richness, effective number of species, total and individual species abundance were unaffected by the soil warming treatment, but these were greatly influenced by sampling site and microscale factors (Alatalo et al., 2015). These studies further demonstrate the interactivity and complexity involved when measuring the impacts of climate change on soil fauna.

4.2.2. Effects on endogeic and anecic organisms

Little is known regarding the impacts of soil warming on endogeic or anecic organisms. Exceptions include work on Enchytraeidae in peat soils under experimental warming (Cole et al., 2002), where enchytraeid numbers were found to be depressed by warmer soil conditions. These authors also found that warming disrupted the role of enchytraeids in terms of dissolved organic carbon release, but with no apparent effect on total ecosystem function (assessed as plant growth). Holmstrup et al. (2015) indicated that drier soil was more influential than warmer soil, as temperatures alone did not impact enchytraeid abundance or bio-volume. Similar to epigeic fauna, disentangling the impacts of soil warming and soil moisture are very difficult. Earthworms are known to become more abundant in wetter soil (Eggleton et al., 2009) and have been shown to decrease under increasing soil temperature (Zaller et al., 2009) – although this study did not record soil moisture. A study by Eisenhauer et al. (2014) demonstrated the complex interactions that can occur between environmental factors and soil fauna population dynamics. They showed a decrease in earthworm (described as primarily *L. rubellus*, *A. caliginosa*, *D. rubidus*, and *D. octaedra*, with a small number of *Aporrectodea rosea*, *A. chlorotica*, and *Octolasion lacteum*) densities with an increase in soil temperature, unless there was increased rainfall; these results varied depending on which of their two research sites or three sampling dates were analyzed. Further, canopy coverage of the plots impacted earthworm densities during the summer (June) sampling period when deciduous trees had leaves.

5. Future directions

Soil faunal responses to disturbance are characterized by complex interactions, and can vary greatly by taxonomic and functional identity and disturbance type. As such, the dynamics of the belowground ecosystem are rarely straightforward. The impact of any given disturbance is dependent not only on the faunal group considered and disturbance type, but also on interacting impacts from the local and regional biota (e.g., plant community, invertebrate and vertebrate community composition), soil characteristics (e.g., chemistry, structure, composition), weather and other abiotic factors, and other macro- and micro-site influencing factors. In spite of the tremendous effort put forward by generations of scientists to accumulate the findings cited within this text, our search for general patterns has been frustrating. We hope to provide suggestions for future research by highlighting several observations, our concerns with these observations, and identifying areas that we think would greatly benefit from future studies.

5.1. Spatial and temporal heterogeneity matters ... a lot!

Most soil habitats are inherently heterogeneous, making the interaction of disturbance with spatial and temporal heterogeneity unavoidable. Soils are frequently characterized by the formation of microhabitats, and these microhabitats influence essentially every chemical parameter as well as plant community, organic matter

content, and subsequently, fauna (Frouz et al., 2011). For example, abiotic variables (pH, soil moisture, temperature), vegetation, and soil macrofauna all varied greatly among microhabitats (in this case, a 1 m² quadrat or dead stump or log) in ash-maple and conifer woodlands (Burton and Eggleton, 2016). Even smaller microhabitats such as earthworm middens can harbor significantly greater abundance of several fauna (Stroud et al., 2016). This heterogeneity has no doubt led to the evolution of diverse communities capable of functioning under different conditions (of temperature, moisture of plant cover) than those which currently dominate at any given site. In practice, the products of such extensive adaptation within the soil biota are only revealed when we modify habitats with large-scale (anthropogenic) disturbances that generate conditions that would otherwise be seen only on a microhabitat scale. For example, a few taxa might be dominant in soils in a forest clear-cut, but these same taxa might only occur in small blowdown areas in the “natural” landscape. Temporally, faunal responses to disturbance are likely impacted by season and life stage of the faunal group considered. We encourage the incorporation of spatial and temporal heterogeneity of faunal communities when designing future experiments. In a similar vein, explicit tests of spatial and temporal heterogeneity in faunal communities would be a valuable contribution to the field (i.e., Chust et al., 2003).

5.2. Taxonomy is important, and we need more of it!

Total abundance is perhaps the most common metric reported for faunal studies, but this information is not always indicative of the most important trends in faunal responses, and in some cases may be misleading. Taxonomic and functional trait-based approaches are far more useful, but seldom accomplished. This is likely because we generally know taxonomic specificity is important, but it is lacking for many groups. As an example, an excellent review of the soil fauna of South Africa by Janion-Scheepers et al. (2016) highlights this issue. Through this comprehensive work, the authors detailed known taxonomic information for 26 soil-dwelling groups, ranging from bacteria to vertebrates. From their review, it is apparent that certain groups (e.g., earthworms, ants) are much more thoroughly sampled, known, and understood than others (e.g., proturans, enchytraeids). Certainly, this pattern is not restricted to South Africa, and is applicable to the entirety of the global terrestrial ecosystem.

Further, there are many examples of fine resolution responses that would have been interpreted differently had a higher order taxonomic approach been taken. For example, Čerevková et al. (2013) identified collembolans to the species level, as well as divided them into functional groups (e.g., detritivores). The species-level data make comparisons among species within functional groups possible, and show how different species respond to environmental factors. Conversely, if only the functional groupings were used in the analysis, much less information could be inferred from this study. In contrast, Griegel (2008) simply reported “Collembola” responses to flooding, which precludes the examination of the several likely species-specific responses, and Facey et al. (2017) grouped taxa into Order and ecological guilds, masking potentially important species-level responses.

The scholarship of soil ecology within the realm of interpreting effects of disturbances – especially regarding most meso- and macrofauna – has so far focused much effort on “what’s there, and under which conditions” but few have made the next step of describing functionality and relevance to the ecosystem. Notable exceptions include our ever-growing understanding of non-native earthworms in North American forests (Bohlen et al., 2004; Hendrix, 2006; Hopfensperger et al., 2011; Huang et al., 2010; Richardson et al., 2016; Snyder et al., 2009) and soil microbial

functionality (e.g., Bell et al., 2009; Fajardo et al., 2012; Gleeson et al., 2016; Pérez-de-Mora et al., 2006).

5.3. Function may be more important for certain groups

Microbial ecology has advanced far more rapidly than faunal ecology, and this advance is likely due to our capacity to identify the diversity of microbial communities in ways that have been impossible in the past. Identifying microbial species is neither necessary to answer questions related to ecology or function nor possible given the rules of biological nomenclature (Hibbett, 2016). Researchers of soil faunal ecology may be in need of a similar method in which we no longer need to know the name of an organism, but can assign operational taxonomic units (OTUs) and then direct our focus on function. However, this approach should be taken with caution, as there is evidence that using functional rather than taxonomic groups can significantly impact the data interpretation (Sechi et al., 2015). Further, this approach would likely not be practicable for diverse taxonomic groups that encompass multiple trophic levels, such as Acari or Formicidae.

Perhaps nowhere is there more potential for discovery and importance for soil fauna than in soil food webs and biogeochemical cycles. A recent special issue in this journal (Vol. 102, November 2016) featured several papers that covered these topics, highlighting our current knowledge and posing additional hypotheses. Grandy et al. (2016) and Soong and Nielsen (2016) make the case for greater representation of soil fauna in food webs and biogeochemical models, and a better understanding of the function of and interactions among different soil fauna groups. King (2016) highlights and recognizes the importance of eusocial insects (in this case, ants and termites) in soil food webs, and emphasizes their impact on soil structure and as food for other organisms. It is clear that relative to other belowground organisms – particularly microbes – soil invertebrates are underrepresented in what is there, what they do, and how they interact with all components of the soil environment. Whatever the complexity of these interactions within food webs, we expect that these become more complex under the influence of environmental disturbances, but understanding such responses will be critical to predicting changes in ecosystem function when disturbances occur.

Soil fauna are acknowledged as key components of soil health, ecology, sustainability, and agriculture (Brussaard et al., 2007; Doran and Zeiss, 2000; Johnson and Murray, 2008; Pauli et al., 2016), yet are perpetually underrepresented in the literature (Hunter, 2001; Zaitsev et al., 2016). This is unfortunate considering their immense diversity, but not completely surprising considering the challenges associated with studying this group. Soil fauna's underrepresentation in the literature has, in our opinion, diminished the perceived importance of these organisms to both scientists and the public (i.e., the “out of sight, out of mind” mentality). In keeping with the rapid accumulation of information regarding microbial diversity in soils, we call for a renewed effort to document the taxonomic and functional diversity of soil fauna and to recognize the essential processes performed by these organisms. Our hope is that this culmination of previous work and encouragement for future studies will lead to an advanced understanding of faunal ecology in relation to disturbance, in general, and in the context of sustainability and global soil health.

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