CHAPTER 11

Soil fauna and their potential responses to warmer soils

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Introduction

Most people who concern themselves with the study of soil will broadly agree that soil is a dynamic mixture of chemical, physical, and biological components. That there is a biological component to soil therefore suggests that soil, or at least “healthy” soil, is alive. But to say that soil is simply alive does not do justice to the multitude of organisms that occupy soil, ranging from the simplest forms, like bacteria, through most of the invertebrate phyla, and up to fossorial reptilian and mammalian vertebrates. In recent years, life in soil has been intensively studied mainly in terms of microbial

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organisms (archaea, bacteria, and fungi), with less emphasis on invertebrate animals (see Coyle et al., 2017). However, invertebrates are diverse and abundant in soils world-wide, and they are known to influence soil microbial communities and soil processes. In relation to warming, soil invertebrates (in general) are understudied, the majority of studies focus on microarthropods (mites and Collembola). This chapter will first give an overview of soil invertebrate distributions and functions and follow with a discussion of the potential responses of these organisms to a warming soil. Due to the limited amount of research in this area, the diversity of the fauna, and the diversity of the existing studies, our discussion centers on a framework for understanding observed and potential responses and a suite of themes interwoven through the literature.

Distribution of invertebrates in soil—General global patterns

Invertebrate communities can be generally thought of as being responsive to major global patterns of climate and the vegetation (or lack thereof) associated with general patterns of temperature and moisture (Coleman et al., 2018). One result of this is that in very cold and/or dry climates, such as those associated with the Antarctic or high alpine soils, the soil fauna consists of relatively species-poor communities of simple invertebrate forms, such as nematodes and tardigrades (Barrett et al., 2008; Convey and McInnes, 2005). As latitude decreases and precipitation increases, primary productivity and plant diversity increase and soil invertebrate communities respond with greater diversity, greater biomass, and greater complexity of trophic interactions. In very hot and dry desert ecosystems, where plant productivity and diversity are low, there is a concomitant pattern of generally lower diversity among soil invertebrates. Importantly, agricultural soils—covering up to 40% of Earth's land surface—typically have been significantly modified from their native physical and chemical states and are also used to produce only a few plant species. These intensively managed ecosystems usually have soils with distinct communities of soil invertebrates which are frequently lower in diversity, and are often characterized by nonnative, disturbance tolerant species (e.g., Callaham et al., 2006). The same pattern is typical of soils impacted by urban development. Thus on a global scale, one important general pattern emerges: when soils are relatively warm, wet, and undisturbed (e.g., not tilled and covered by native vegetation), the relative diversity and biomass of organisms within these soils is maximized. An excellent general discussion of global patterns of soil microbial and faunal diversity and abundance is given in Orgiazzi et al. (2016).

Distribution of invertebrates in soil—Regional patterns

Given that global patterns of climate can influence the overall diversity and biomass of soil invertebrate communities, it is possible to discern patterns of community composition within the invertebrate fauna at a regional or biome/ecosystem level of resolution. The dominant vegetation of any ecosystem is strongly influenced by the local patterns of temperature, precipitation, and disturbance regime. This dominant vegetation then interacts with the soil in more or less predictable ways, and therefore dictates the composition of the soil faunal community. One classic, well-understood example of this relationship is the dominance of microarthropods (and decreased importance of macrofauna, e.g., earthworms) in the soil fauna of evergreen forest vegetation (e.g., Wu et al., 2014; Coleman et al., 2018). This relationship is driven by the lower "quality" (best characterized by a high carbon to nitrogen ratio, or C:N ratio) of the evergreen litter inputs, which favors fungal dominance of microbial decomposers, which in turn favors those organisms that feed primarily on fungi (microarthropods, especially Collembola). Likewise, regional vegetation with higher quality litter (lower C:N ratio) will have soil fauna with many more macrofauna which feed on this more easily metabolized material.

Functions of invertebrates in soil

The functions that invertebrates perform in soils are quite diverse, as might be expected of such a biologically diverse set of organisms. However, generalizations are possible, and can be linked reasonably with the size of the organism in question. Microscopic invertebrates, like the nematodes and tardigrades, live entirely within water films surrounding soil particles and water-filled pores within soil aggregates. Yet functionally, these organisms operate in several domains with representatives that exclusively feed on roots, others that feed on fungi, yet others that feed on bacteria and archaea, and finally predators and parasites (Yeates et al., 1993). Small arthropods (mites, springtails, and others) occupy surface litter and air-filled pores within the mineral soil matrix. These so-called microarthropods are also trophically diverse with food webs containing as many as four trophic levels just within the mites alone (Klarner et al., 2013). Microarthropod activity has been demonstrated to influence the decomposition of leaf litter in many forested ecosystems (Heneghan et al., 1998). Larger bodied invertebrates, such as earthworms or insects that live in eusocial colonies of many thousands of individuals (ants and termites), can have profound impacts on ecosystems through their feeding, burrowing, and nest building. These three groups are often termed ecosystem engineers (Jones et al., 1994; Lavelle et al., 2016), due to their capacity to move tremendous volumes of soil and their construction of structures that offer habitats to organisms that would otherwise not inhabit a particular ecosystem. Earthworms, termites, and ants (and some larger immature insects) participate directly in soil bioturbation which can influence pedogenic processes over the long term, creating and/or obliterating soil horizons, and are strongly implicated in the incorporation of surface-derived plant materials into soil organic matter pools (Jouquet et al., 2011; Langmaid, 1964). Aside from bioturbation, soil and litter macroinvertebrates, such as millipedes and isopods, also participate in the decomposition of surface-deposited organic materials either through direct consumption of leaf material or through the process of comminution (literally, tearing large pieces of litter into smaller particles enhancing the surface area available for microbial attack). It seems clear that any changes in the abundances or activities of these important "engineering" organisms due to warming will have disproportionate effects on the processes that they influence. We are only aware of one explicit manipulation of soil ecosystem engineers (large warming chambers for aboveground and belowground ants; Pelini et al., 2011) which is in progress at the time of writing this chapter. To our knowledge there have not been any studies of changes in activity or behavior of soil ecosystem engineers relative to warming, although ants are thermophilic (Dunn et al., 2009) and might be expected to increase their activity.

Spatial scales influenced by soil invertebrates

Although smaller invertebrates like nematodes and microarthropods may have individual spheres of influence in the range of 1–10 cm^3 of soil volume, it is true that when populations of particular species (e.g., plant parasites or root feeders) reach high densities, their impacts can span over hectares, particularly in agricultural ecosystems (Blackshaw and Hicks, 2013; Wrather et al., 2001). Larger invertebrates have greater individual capacity to move through space (of the order of tens to hundreds of meters), and when their population densities are high they can influence ecosystem processes at the landscape scale (Bohlen et al., 2004) or even be responsible for the long-term persistence of certain landscape features (Zangerlé et al., 2016). Indeed, in extreme cases there are whole ecosystems that would cease to exist were it not for the casting activity of earthworms, like the Surales seasonal wetland ecosystems in the South American pampas of Colombia and Venezuela (Zangerlé et al., 2016).

What about warming?

How will soil fauna respond to warming manipulations?

Even in the absence of global change, temperature varies on multiple timescales: predictably at daily and seasonal scales and somewhat less predictably due to weather patterns at scales of weeks, months, and years. Temperature changes also occur at different rates. Unsurprisingly, organisms are adapted for a range of temperatures and for temperature changes over short and/or longer timescales. For terrestrial ectotherms, this temperature flexibility is generally greater at higher latitudes, but this may not mean increased upper thermal limits (Sunday et al., 2011). Additionally, the Southern Hemisphere has higher average temperatures than the Northern Hemisphere; species have adaptations specific to these climates (Dunn et al., 2009). The temperature buffering capacity of soil—due in large part to its water content—results in a smaller change in temperature than is observed in aboveground systems, with soils exhibiting dampened diurnal or seasonal oscillations relative to aboveground air temperature (Schaetzl and Anderson, 2005). Nevertheless, temperature does fluctuate in soils, especially near the surface where most of the biodiversity is found.

Complex interactions between temperature and soil present some challenges to experimentally assessing how long-term soil warming might affect soil fauna—both from a methodological standpoint and from the standpoint of potential responses. In terms of methodology, most studies in both the field and laboratory have warmed soil continuously throughout a given experiment, whereas some studies have only warmed at night (Song et al., 2014). The soil interface with the atmosphere and aboveground ecosystems creates a gradient of temperature through the soil profile; whether the experimental approach involves warming air, warming soil, or warming both can have important implications for how the increased temperature is experienced by soil organisms, and thus may dictate their responses to treatments. As an example, we consider organisms like root-chewing beetle larvae, that might move to deeper depths (Villani and Wright, 1990) in the soil profile in response to warmer surface temperatures (as in warmed air treatments), but how such organisms might respond to warming from below (as in warmed soil experiments) is not clear. Additionally, the installation of infrastructure for treatments may involve soil disturbance (Pelini et al., 2011) that can have its own effects, as described below.

Due to natural fluctuations in temperature and organism response, timing and amount of warming have the potential to cause different effects (but to our knowledge no studies have examined this). While many studies have warmed soil over extended periods of time (months to years), some studies have examined shorter, more rapid changes. For instance, Bokhorst et al. (2012) simulated extreme winter warming by altering the frequency of freeze-thaw cycles in subarctic heathland, finding that some microarthropod taxa were negatively affected but that changes were not observable at the community level. Furthermore, the irregularity of both temperature magnitude and rate of change can result in the community-level response to warming being nonlinear. Swift et al. (1998) suggested that Arctic warming likely leads to increased biodiversity of soil fauna, but variability and extreme events may reduce the rate at which species become and remain established. This is supported by evidence for large shifts in microarthropod communities due to extreme events (Barrett et al., 2008; Bokhorst et al., 2012; Perdomo et al., 2012). In any case, although the current trajectory of global temperature change is quite rapid relative to changes observed in the geologic record, it is clear that any experimental manipulation of soil or air temperature will occur over short timescales. Experimentally induced temperature change may not elicit the actual response of a soil invertebrate assemblage over decadal time. For example, it is possible that the more mobile members of the community will simply move to cooler soils adjacent to any experimentally warmed plots, when this will clearly not be an option for soils experiencing general warming over landscape scales. Unfortunately, it seems that only a temperature change at the landscape scale will allow for a full understanding of how adaptable (or unadaptable) a particular soil invertebrate assemblage might be.

Factors that covary with warming

One seriously confounding factor in evaluating temperature effects on soil organisms is that temperature and moisture are strongly linked in soil systems (and arguably in all ecosystems). In a review of soil insect behavioral responses to edaphic changes in agricultural systems, Villani and Wright (1990) found that it was uncommon for studies to consider warming independently (i.e., ignoring concomitant changes in moisture). In our review, it was true that most studies rarely considered temperature, moisture, and any interactive effects (but see Wu et al. (2014) for an important exception to this general trend). Aerts (2006), in a metaanalysis of decomposition rates in experimentally warmed cold biomes, found that moisture was not typically considered but was likely as limiting as temperature. At best, is it unrealistic to consider warming without the accompanying changes in moisture.

Additionally, in the current situation of global climate change, it is impossible to ignore the temperature-independent effects of changes in the concentrations of related atmospheric gasses. In short, carbon dioxide concentrations are increasing along with average temperature (Keeling et al., 2005). Although CO_2 concentrations are already fairly high in the gaseous component of soil systems (Schaetzl and Anderson, 2005), the influence of these elevated concentrations on plant physiology and plant tissue chemistry cannot be ignored. Research in this field has not yet teased out the interactive effects of changes in atmospheric gasses, plant physiology, and processes in soils. However, it is known that as the quality of the litter inputs change, not all soil fauna will react in the same way, and current theory predicts that those with smaller body sizes will avoid low-quality foods, while those with larger body sizes will eat more to get their necessary nutrients (compensatory feeding) (Ott et al., 2012).

Finally, we consider that the potential changes to actual weather events, that are predicted to be associated with a warming climate, may have a strong influence on extreme events, such as the incidence and severity of droughts (Allen et al., 2010) and damaging wind events (e.g., tornadoes and intense hurricanes) (Knutson et al., 2013), and may even change the risk of occurrence of wildfires or elicit wholesale changes in fire regimes (Liu et al., 2010). Clearly, the indirect effects of any of these disturbances to vegetation, or the soil environment itself, will have the potential to influence the composition and function of the soil biotic community, but these effects are difficult to predict. We present a conceptual model (Fig. 1) to depict some of the interrelated effects of changes associated with disturbance regimes and various components of soil ecosystems.

Indirect effects

Clearly, changes associated with warming and its covariates under global climate change can influence multiple ecosystem components. Changes in vegetation in particular can have indirect feedbacks on the diversity and function of invertebrates in soils. Shifts in plant communities are likely to shift associated soil fauna communities, as seen in the case of nematodes (Thakur et al., 2014). These indirect effects are in addition to any direct effects that warming might have on individual species or community structure within the invertebrate fauna, and so any attempt to describe or predict the overall influence of warming must be nuanced and cautious. In actual practice, there have been relatively few studies to address direct or indirect

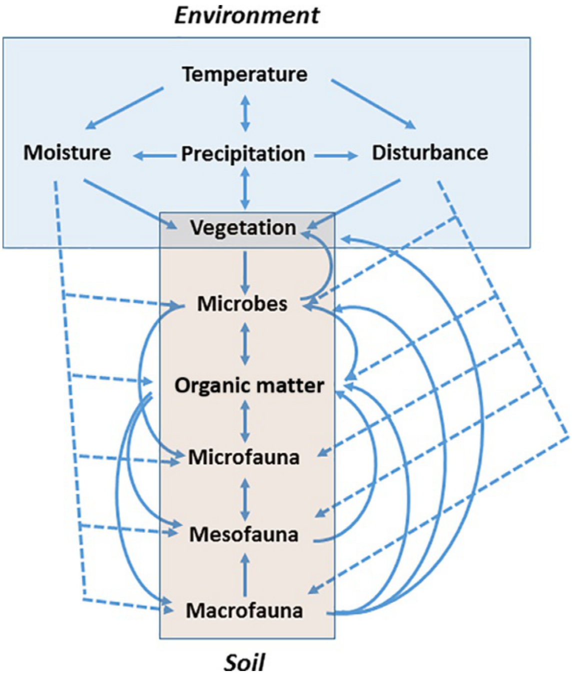

Fig. 1 Conceptual model of warming impacts on the soil environment and potential cascading effects within the soil biota. Warming induced perturbations of moisture, vegetation, or disturbance regime will have potential consequences throughout the detrital food web. Predicting these consequences and the resulting impacts on soil processes (such as decomposition, soil organic matter formation, and nutrient cycling), is likely not possible, given our current level of understanding. Each of the *arrows* represent either a known or predicted interaction. These interactions can be direct, indirect, or both. The *solid arrows* depict direct primary interactions, whereas the *dashed arrows* depict potential secondary effects of warming (e.g., changes in microbial community structure resulting from changes in moisture that are due to warming).

effects of warming on soil invertebrates per se, but the number is growing (Pelini et al. 2011). However, because of the complexity inherent in ecological interactions among the atmosphere, vegetation, and animal and microbial organisms, generalizations have been difficult to identify.

It is important to remember that soil organisms may themselves contribute to these interactions. The actions of earthworms have been documented to contribute to greenhouse gas emissions, including demonstrations that earthworm-inhabited soils produce more CO_2 than worm-free soils (Zhang and Hendrix, 1995) and that earthworms may even contribute to nitrous oxide production in some soils (Depkat-Jakob et al., 2013). However, Lubbers et al. (2013) found that the addition of plants made understanding earthworm contributions to greenhouse gas emissions more complicated. Decomposition can be strongly driven by litter-dwelling species, to the extent that differences in decomposition rates due to CO_2 and temperature disappeared with the presence of millipedes (Rouifed et al., 2010). In terms of feedbacks, soil fauna can modify plant (tree seedlings) responses to warming (Makoto et al., 2016).

Responses

A framework for potential responses

Given the context above, soil fauna will respond to temperature changes in extremely varied ways. Issues of scale are critically important in considering these responses, especially since soil organisms vary in size by five orders of magnitude and vary in life span by three orders of magnitude, from tens of days for quickly reproducing members of the nematodes and microarthropods to thousands of days for 17-year-old cicadas which spend all but a few days of their lives below ground (Coleman et al., 2018; Whiles et al., 2001). We have organized these responses primarily along temporal scales and secondarily across the level of biological hierarchy (individual—population—community—ecosystem) (Fig. 2).

Soil organism responses to warming (or temperature changes in general) begin with behavioral changes, including movement. Soil insects are known to respond by changing their vertical position in the soil profile (Villani and Wright, 1990). These changes occur over the shortest timescales of hours to days, and with seasonal changes may also occur over weeks to months.

Warming causes physiological changes in organisms. Over longer periods of time this may result in changes in abundance, density, biomass, reproduction, and fitness. These ultimately result in observable changes at the population and community level, which are likely to alter processes mediated (in part) by fauna (i.e., decomposition, nutrient cycling, and soil respiration). An example of the interaction between physiology and community structure can be found in the concept of community downsizing, in which warming favors smaller bodied organisms; this has been recently demonstrated to occur in mites (Lindo, 2015). Our framework includes these changes as occurring over years to decades (Fig. 2), however, depending on the rate and magnitude of temperature change they could happen more quickly. The rate of change at the community level results from the

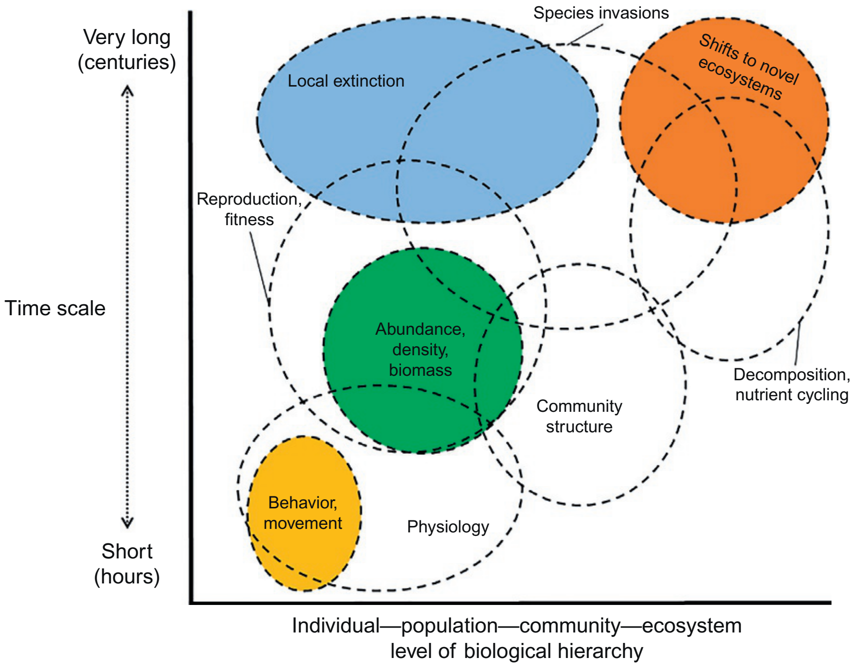

Fig. 2 A framework for potential responses to warming of soils. Each *oval* approximates the level of biological hierarchy and temporal scale at which responses to warming might be observed. Responses may be observed to be faster or slower than these generalizations, depending on the rate and magnitude of temperature change.

rate of change in populations combined with any changes to species interactions; variability in the rate of community-level change would be expected to be due primarily to the highly variable life spans across soil fauna.

As an example of how the variable life spans of individual species of invertebrates will influence the net response rate of these organisms to global change phenomena, we point to the relative response rates that have been observed for periodical cicadas of the Konza Prairie Long-Term Ecological Research Site in Kansas, United States. In these predominantly grassland systems there has been a trend of expanding woody vegetation along riparian corridors in the landscape. This is thought to be partly attributable to changes in local climate and disturbance regimes (particularly the absence of fire). When we sampled the emergence dynamics of periodical cicadas (*Magicicada* spp.) at this site in 2015 (Whiles, Snyder, Brock, Bonjour, Callaham, and Meyer, unpublished data), we observed very few individuals to emerge in sites where there was little or no woody vegetation during the previous (1998) emergence (Whiles et al., 2001). This pattern is directly related to the requirement of woody twigs and branches for the female cicadas to successfully oviposit eggs. So, although other soil fauna taking advantage of the incipient litter layer of expanding riparian woody vegetation may have been in place for many years (and possibly for dozens or even hundreds of generations), the opportunities for periodical cicadas to respond to changes in aboveground vegetation can only occur at discreet, widely separated points in time (every 13 or 17 years). This is an extreme example (in terms of soil faunal life span), but serves to illustrate how important the individual life history traits of soil organism species will be in terms of their capability to adapt and respond to direct or indirect changes in climate or vegetation.

The ecosystem-scale processes mentioned above are affected by soil fauna but are primarily driven by soil microbial communities (Coleman et al., 2018). Over these longer term temporal scales, it is important to note that changes in processes may not persist. For example, in a review paper, Romero-Olivares et al. (2017) found that soil respiration was similar in both warmed and control treatments after a decade. It is not known whether changes in other ecosystem processes or community structure will persist with long-term warming.

On very long timescales we predict that community-level and ecosystem-level shifts will lead to local extinctions, creation of unique niches, more species becoming established in new habitats, and/or more species invasions. Over longer temporal scales these might be observed as range shifts for native and invasive species. Little data currently exists for these long-term changes. Dunn et al. (2009) concluded that contemporary patterns in ant diversity were likely due to extinctions related to climate changes since the Eocene. However, it is important to note that this includes both soil-dwelling and arboreal ant species.

Due to shifts above ground as well, whole ecosystems may transition to different types, novel ecosystems (i.e., no-analog ecosystems, *sensu* Williams and Jackson, 2007), and/or alternate stable states (van de Leemput et al., 2015). There is some support for the possibility of major community changes occurring in the soil fauna. For example, Perdomo et al. (2012) established artificial landscapes of moss patches with microarthropod communities, some of which experienced extreme heating of 6°C. In this study it was observed that the combination of this warming and differing recolonization distances from the "mainland" led to the establishment of unique microarthropod communities. Physiological tolerances (discussed below) may play into which species are able to disperse and establish in new (to the species) or novel environments (Diamond et al., 2012). Physiology is linked closely to evolutionary history; ultimately, temperature is an important driver of evolution and this should be considered, however, a review of potential evolutionary changes is beyond the scope of this chapter.

General themes

Due to the paucity of publications in this area of study, and the multifaceted complexity of the soil fauna community and their responses, it was most valuable to focus on themes found within the literature. Themes tend to cross boundaries of scale, organization, and ecosystem type; this may be more useful for understanding soil fauna responses to warming than a classification system would.

A major factor in understanding each study was *context specificity*. Each study has a unique combination of initial temperature regime, altered temperature regime (s), soil(s), animal(s), and/or plants, and thus yielded unique results. What we know about the effects of warming cannot be disentangled from the context of the study, and thus generalities are hard to draw. Context specificity is the rule, rather than the exception. Even in considering only polar regions, there were many cases where site was an important factor (Nielsen and Wall, 2013). Soil type is an important factor as well (e.g., Makoto et al., 2016) and may be highly variable.

Research on community structure often examines the underlying changes at the population level to explain why a community did or did not change. Responses of individual species to warming are not always similar and are often discussed as seeming idiosyncratic (e.g., McGeoch et al., 2006). However, across studies, *species-specific responses* became a distinct theme. Villani and Wright (1990) found that even on short timescales, soil insect feeding responses are species-specific. Bokhorst et al. (2008) found changes due to one particular collembolan species and one particular mite taxon. Notably, even this change was only observed under lichen cover, not moss cover at this site—yet another example of context specificity. Species-specific responses may occur even if species are closely related: Makoto et al. (2014) found different feeding responses to warming in congeneric millipede species! All of these results underscore the importance of single-species responses to warming, and the idiosyncratic nature of soil invertebrate responses that may be expected (but not predicted) to result from warming.

On some level, this should be not be surprising. Species are different from each other, regardless of the species concept to which one subscribes.

In the context of responses to warming it is also important that their evolutionary history is also different, and with it their physiological tolerances, whether due to genotypic differences or plasticity. The physiological range of a species was a concern in several studies (Makoto et al., 2014; Sjursen et al., 2005) and was explicitly addressed as a potential predictor for ant species (Diamond et al., 2012). Species can tolerate a certain range of temperatures. If they are already living at the top of this range, additional warming may push that species beyond what they can handle. Indeed, Diamond et al. (2012) found that thermal tolerance was a good predictor of ant response to warming, but only near their physiological limit. Individuals used in experiments may also be adapted to a local climate, and thus may not reflect the responses that individuals from other populations might show.

In a diverse system, redundancy in ecosystem function exists across species with similar niches. Even if some species are near the edge of their physiological limit with regard to temperature, others with similar function may not be near their limit. If this is the case, it may provide some resiliency for ecosystem function in a changing world. However, challenges exist: many ecosystems are already impacted by other aspects of global change (e.g., agricultural development or invasive species) and thus may begin with less diverse communities. Additionally, the current rate of temperature change is relatively fast (compared to historic global change) and species may not be able to adapt or evolve fast enough to keep up with climate change.

Strong interlinking of temperature and moisture in soil systems, and importantly in soil fauna physiology, was another common theme across many studies. Many soil organisms live in the water films around soil particles or in open pore spaces with near 100% relative humidity. These faunas have a low tolerance for moisture loss and do poorly when soils dry (Makkonen et al., 2011; Nielsen and Wall, 2013). However, faunas are often able to tolerate higher temperatures if there is sufficient water available (Richardson et al., 2009; Sjursen et al., 2005). Contradicting this general pattern, Turnbull and Lindo (2015) found that a positive effect of decreased moisture was that there would be more open pore space, potentially benefitting organisms that inhabit this space.

Conclusion

Future research and management

It is clear there is a strong need to predict future changes in soil faunal populations, soil faunal communities, and soil faunal-driven ecosystem processes.

Unraveling the web of interactive effects across multiple taxa ultimately requires the use of multivariate approaches and creative experimental design. However, one challenge to achieving this is the current state of understanding of our soil systems. Nearly 15 years ago a special issue of *Science* was touting soils as the final frontier (Sugden et al., 2004). This has not changed much—there is still a tremendous need to understand these communities and processes. Even in the soil-warming literature, comparisons can be hard to draw because it is unknown how some fauna contribute to processes under current conditions (Swift et al., 1998). Without a better understanding of soil ecology, diversity, and distributions of fauna we do not have an effective reference point for future changes.

To study native species, or not to study native species: we found few studies on earthworms that examined responses to temperature change. Of these, two studied native species in the U.K. (Eggleton et al., 2009; Gerard, 1967) while the remaining three all focused on European species that had invaded other continents (Eisenhauer et al., 2014; Makoto et al., 2016; Zaller et al., 2009). While invasive species are a growing problem and soil warming will certainly increase their spread, native species are neglected.

One conservation management response to warming temperatures has been that of assisted migration of particularly vulnerable plant species into climates and environments where they are more likely to successfully grow and reproduce (McLachlan et al., 2007). Given that many soil invertebrates are quite slow moving, and capable of moving as a population front only on the order of 10 m yr^{-1} (Marinissen and van den Bosch, 1992; Snyder et al., 2011), it seems appropriate to also include soil organisms in this discussion. We are not aware of any such discussion to date, but we propose that future research in this area should consider the known preferences of certain species for particular soil chemical and physical characteristics (or to conduct trials to establish tolerances of species for varying soil conditions), to ensure maximum success and benefit of any assisted migrations attempted for soil invertebrates. Furthermore, we recommend that any such efforts should focus on transfers of species assemblages (including plants and associated soil invertebrates) that are native to a particular donor location and avoid moving species introduced from other continents. In short, species identity among soil invertebrates should be carefully evaluated prior to assisted migration, as movement of nonnative species of earthworms (for example) could ultimately prove to be counterproductive.

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