CHAPTER

Assessing soil biological health in forest soils

16

T.H. DeLuca[a,*], M.R.A. Pingree[b], S. Gao[a]

[a]*W.A. Franke College of Forestry and Conservation, University of Montana, Missoula, MT, United States,*

[b]*Swedish University of Agricultural Sciences, Umeå, Sweden*

[*]*Corresponding Author.*

ABSTRACT

The sustainability of the world's forest ecosystems is greatly dependent upon the health and function of soils, unfortunately, there is ambiguity in the term "soil health" and only limited understanding of biotic function in soils. This discord leaves land managers and policy makers to formulate decisions without adequate consideration of the soil as a living resource. The following chapter is structured to provide an overview of the unique qualities and characteristics of forest soils followed by a synthesis of knowledge on functional roles of soil organisms, soil carbon (C) as the currency for microbial abundance and activity, and assessing biotic abundance and diversity in forest soils.

Introduction

Numerous review articles exist on the biological health of agricultural soils; however, far fewer syntheses exist for biota of forest soils. As a discipline, soil science has its origins in agricultural sciences, which has led to frequent misinterpretation and misapplication of agricultural principles and findings to far more heterogeneous forest soils. Agricultural ecosystems are anthropogenic constructs: greatly altered from their native state with a specific purpose of facilitating the growth and yield of individual crop species. Surface soils in agricultural ecosystems experience repeated disturbances with mixing or ploughing followed by amendment with fertilizers to re-establish nutrient pools that are depleted by the frequent removal of agricultural products and by-products. The result is an open-ended system that is dependent on artificial inputs to retain productivity. In contrast, the vast majority of forest soils are subject to occasional or intermittent disturbances (Boyle, 2005) that can be avnthropogenic (timber harvest) or natural (windthrow or fire). With the exception of plantation forests, forest soils are rarely ploughed and thus typically retain their natural morphology. We focus our discussion in this chapter on natural and seminatural temperate and boreal forest soils (as opposed to plantation forest soils) in a relatively closed system with timber harvested on a multi-decade interval. The purpose of this chapter is to summarize the unique structure and function of temperate boreal forest soils related specifically to the biotic activity in these systems with the intention of creating more meaningful definition of soil health (NRC, 1993; Doran and Zeiss, 2000). For the purposes of this article, we define forest soil health as *a collection of soil physical and biochemical properties that sustain the native biodiversity, processes and activity of soil biota and the proliferation of roots of forest species*. To adequately address forest soil health or assessment of the biotic component of forest soils, one needs to understand the unique characteristics and function of forest soils.

Global Change and Forest Soils. https://doi.org/10.1016/B978-0-444-63998-1.00016-1

Forest soil architecture, carbon storage, and biotic activity

It is impossible to discuss forest soil biota without considering the unique architecture of forest soils. When an individual envisions soil, they often imagine a prairie soil or agricultural soil with a thick A horizon underlain by a high chroma B horizon. Forest ecosystems represent a broad grouping of soils spanning multiple orders of US Soil Taxonomy (Buol et al., 2003), but rarely possess the morphology of the vast majority of agricultural soils. By far the majority of temperate (Chapter 6) and boreal (Chapter 5) forest soils fall within four orders: Alfisols, Inceptisols, Spodosols and Ultisols with tropical (Chapters 7 & 8) forest soils dominated by Ultisols and Oxisols. Alfisols represent soils of moderate maturity, relatively cold, wet conditions with the clear development of an argillic horizon (silicate clay accumulation in the B horizon). Inceptisols are developmentally young soils limited in their development by topography, climate or time. They have weakly developed cambic or calcic B horizons. Spodosols are far more common in boreal regions and are characterized by the formation of a strong albic E horizon and the accumulation of sesquioxides and potentially humus in the B horizon. Ultisols are relatively developmentally mature forest soils, characterized by a strong argillic or kandic (partially desilicated, kaolinite clay accumulation) B horizon. In all four cases, these soils normally have a well-developed O horizon, in the case of deciduous forests generally possess an A horizon, or in the case of Spodosols or Inceptisols may completely lack an A horizon (Buol et al., 2003; Nave et al., 2010).

Forest soils usually possess surface horizons that are dominated by presence of woody, perennial roots, which turnover far less frequently than the perennial or annual roots of prairie or agricultural ecosystems. This results in surface soils with far less carbon (C) accumulation, directly influences the biotic activity, and effects the balance of bacterial and fungal activity. Forest soils tend to have pH values that are neutral to strongly acidic partly as a result of the climatic conditions under which they form and partly as a result of the chemical composition of litter deposition in these systems. The acidic conditions that exist in forest soils tend to inhibit the presence of fauna known for mixing organic matter to depth in temperate prairie soils (Buol et al., 2003). This results in the accumulation of litter on the forest floor, which decomposes slowly in place and from the bottom up. Of course, there are exceptions to this and certain types of hardwood forests (e.g., *Acer* spp. forests) growing in parent material that is relatively high in limestone tend to be neutral to slightly alkaline and possess a deep A horizon more similar to prairie soils (Buol et al., 2003). Depending on the nature of the forest system, the O horizon may include a litter layer (Oi or L), partially decomposed or fermentation layer (Oe, F), and a highly decomposed or humus layer (Oa, H), and which tends to be a zone of highest microbial activity (Boyle, 2005).

The microbial community structure of forest soils is one that is generally dominated by fungi (Fisher and Binkley, 2000; Paul, 2015). In primary successional forest systems, soils are initially bacterial-dominated shortly following glacial retreat or after volcanic deposition, but quickly become fungal-dominated as forest cover and litter layers are established (Schmidt et al., 2016). This fungal dominance in litter layers once again separates forest soils from temperate agricultural or prairie soils in which fungal:bacterial ratios tend to decrease with level of disturbance (Bardgett et al., 1996; Paul, 2015). Forest litter layers are often exposed to extreme wetting and drying events as a function of their position in the forest environment and the loose-knit nature of litter. By contrast, humus layers underlying fungal dominated litter layers can be dominated by bacterial biomass (Berg et al., 1998). The dry

conditions of organic layers in forest soils generally favor fungi that tolerate desiccation better than bacteria and accommodate the hyphal morphology of fungi, wherein the organism can span wet and dry litter and soil allowing transverse movement of moisture, nutrients and C (Boyle, 2005; Paul, 2015).

Forest soils possess highly diverse microbial communities with functional representation from bacteria, archaea, fungi, and animals with all four possessing keystone organisms in a complex and dynamic food web (Fig. 16.1). The term food web does not do justice to the dynamic interplay between this diverse group of organisms that includes microorganisms (bacteria, fungi and viral phage), microfauna (including nematodes and protozoans), mesofauna (collembolan, oribatida, tardigrada), and macrofauna (spiders, beetles, worms, gophers). Rather than a two dimensional hierarchy of trophic levels presented in most introductory ecology books, one must envision a system that flows in multiple directions with a complex combination of producers, consumers, parasites, predators, and detritivores contributing across scales of time and space (Helmberger et al., 2017). In a classic cascade this would

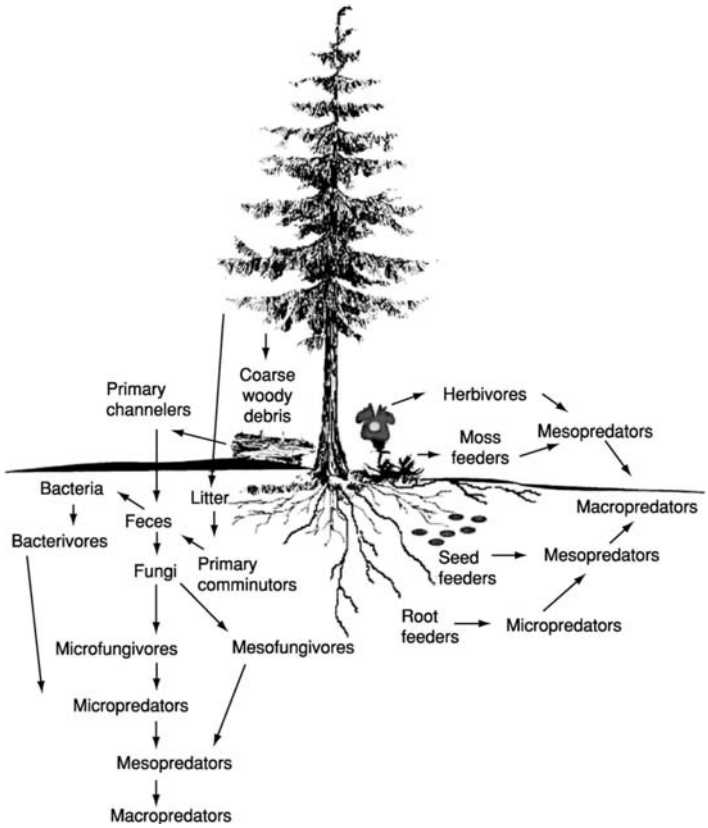

FIG. 16.1

A simplified foodweb for forest soils.

Reprinted from Boyle, J. R. 2005. Forest soils. in: Hillel, D., editor. Encyclopedia of Soils in the Environment. Elsevier, New York, pp. 73–79 permission obtained from publisher.

culminate with consumption by an apex predator (e.g., killer whale, eagle, or lion). But, the fact is that higher organisms such as predatory nematodes are subject to fungal traps (e.g., nematode trapping fungi), bacterial or viral infection, and attack by mesostigmatid mites creating an intricate foodweb with resources flowing horizontally and vertically (Fig. 16.1).

Functional roles of forest soil organisms

Dynamic and complex in nature, forest soils are fundamentally different from agriculture soils. Soil health in these systems is defined by the variety of relationships and interactions between soil physical parameters, chemical components, and biological communities. Soil organisms are, arguably, the most mutable and dynamic of these components and while they are organized by functional categories, it is important to consider these functions as spatially and temporally distinct and in no way static.

Decomposition and cycling of organic matter

The incorporation of organic matter into forest soils largely sets the stage for the retention and release of energy and nutrients in the form of biotic-derived, C-rich compounds such as plant and animal detritus, litterfall, throughfall, plant roots, and plant and microbial exudates. In most temperate forests, organic matter resides on the forest floor, but some temperate forest canopies also provide a substantial pool of organic matter (900−6800 kg ha^{-1}) as epiphytic mats on the tops of tree branches (Pike et al., 1977; Nadkarni, 1984). Soil organic matter (SOM) includes living, recently dead, partially decomposed, highly decomposed and stabilized reduced C compounds. Soil organic matter has long been recognized as beneficial to numerous soil properties and processes including soil water holding capacity, soil aeration, cation exchange capacity, plant root proliferation, soil biotic activity, nutrient transformations, and plant nutrient acquisition. Turnover rates of SOM in upland temperate, upland boreal and lowland tropical forests span from less than one year to over 6000 years and, in addition to climate constraints, are also driven by bulk density (i.e., mass/volume) and the ability for complex compounds to be hydrolyzed into more easily decomposed compounds (Table 16.1). These data exhibit where C is predominantly stored in soil profiles in these three forest biomes and provide a sense of turnover rates (yr^{-1}) as consolidated or loose material in different depths in the soil profile (Trumbore, 2000).

Highly decomposed or passive SOM has long been described as humic material in terrestrial and aquatic systems (Stevenson, 1994). Until recently, the model of humification has largely been defined by a chemical fractionation scheme resulting in humus, a large and recalcitrant group of polymers, as a relic of solubility in alkaline extractions. The traditional view is now being challenged with evidence from radiocarbon ages and techniques based on water solubility and accessibility to microorganisms (Lehmann and Kleber, 2015). Clearly, the role of microorganisms in SOM turnover has been greatly underestimated and this new paradigm requires further development as so much of SOM theory is defined by the formation of humus. Soil organic matter altered by microorganisms has recently been shown to convert pre-existing C and added simple C to lipids and proteins (34% across all treatments) and diversify the chemistry of SOM over an 18-month model soil systems incubation (Kallenbach et al., 2016).

Decomposition of organic matter is predominantly a biotic process carried out by soil biota and regulated by environmental conditions (i.e., temperature and moisture). Physical breakdown or

Table 16.1 Predicted organic matter fractions and turnover times in a mixed deciduous temperate forest, coniferous boreal forest and a lowland tropical forest. Annual C input = 0.95 Mg C ha^{-1} (See Trumbore 2000).

Horizon	Carbon (g C m^{-2})	Turnover time (yrs)
Temperate		
Oe leaves & roots	400	3–8
Oe + Oa humic	1300	30–40
Ap low bulk density	100	3–8
Ap low bulk density humus	2600	50–160
Ap high bulk density	600	160–400
B1 low bulk density	1200	800–1000
Total to 40 cm	6200	200–310
Boreal		
Moss/detritus	5800	60
Humic layer	9400	1000–1500
Total mineral to 40 cm	15,200	650–1250
Tropical		
Oe leaves	325	< 1.0
A 0–40 cm low bulk density	830	1–3
A high bulk density hydrolyzable	3110	10–30
A high bulk nonhydrolyzable	1190	> 6000
Total to 40 cm	5460	1040

'disintegration' of animal or plant organic matter (i.e., substrate) occurs through bioturbation, biotic shredding, freezing/thawing cycles, wetting/drying events, heating/cooling events, wind abrasion. The chemical breakdown or 'decomposition' of organic matter is mediated by soil microbes to produce smaller organic metabolites (including peptides, free amino acids, monosaccharides, and simple phenolics), CO_2 or CH_4 (aerobic or anaerobic, respectively), water, nutrients, soil humic matter, and eventually inorganic compounds. The biochemical process of decomposition combines the enzymatic cleavage of compounds that are then metabolized and oxidized to liberate electrons from reduced C compounds. In the tightly-coupled system of forest soils, much of the immediately available C is consumed and utilized by fast-growing opportunistic bacteria and fungi, leaving behind more recalcitrant compounds that are decomposed more slowly. In northern forest soils, 20%−30% of SOM remains after initial decomposition processes, the decomposition of which is then limited by substrate quality, soil invertebrate activity, and N availability to microbes (Edmonds, 1990).

Forest succession and carbon accumulation

Establishment of forest soils in primary successional gradients has been studied extensively (Bormann and Sidle, 1990; Whelan and Bach, 2016; Buma et al., 2017). A famous primary succession gradient following glacial retreat in Glacier Bay Alaska was used to assess plant community shifts and

ultimately soil development (Cooper, 1923). The contemporary soil profile is one that expresses inherited and acquired characteristics. The inherited characteristics are geogenic in origin and manifest themselves as a function of the parent material in which soils form. Acquired characteristics are those features that were established in the profile as a result of pedogenic processes. Key among these characteristics is soil C accumulation. This is one of the first features that differentiates soils from parent material. As C accumulates from the activity of producers (CO_2 conversion to reduced C compounds by higher plants, bryophytes, algae, cyanobacteria and chemolithoautotrohs) it serves as the currency for microbial activity and creates a positive feedback loop for soil development.

Moisture limitations in forests of semi-arid climates result in slowed decomposition during summer months when temperatures are otherwise sufficiently high to drive rapid decomposition. Forest soils of drier regions may have more rapid decomposition in the winter under snowpack in spite of subzero monthly temperatures. This 'subnivian' space where the snow melts up from the soil surface has a higher temperature than ambient air temperature, with moisture from the melting of snow resulting in adequate conditions for decomposition to occur (Massman et al., 1995; Jones, 1999). Moist, warmer conditions and subnivian nutrient deposition imparted by snow cover can be exploited by litter decomposing fungi that have previously infected needles or leaves (Stark, 1972). The snowpack serves as an important hydrologic and nutrient reservoir for winter decomposition greatly influencing annual decomposition rates in dry climates (Jones, 1999). For these reasons, a reduction in snowpack associated with climate change could adversely impact decomposition rates due to lower temperatures and moisture loss (Tucker et al., 2016).

Excessively wet soil conditions are another strong down-regulator of decomposition rates. Soils may become saturated or nearly saturated during periods of excess rainfall, snow melt, physical impediments to drainage (hard pans, fragipan or other impeding layers), and the wet soil conditions result in anaerobic or microaerophilic environments that slow decomposition rates (Wickland and Neff, 2008) and increase C accumulation (Sahrawat, 2003). Saturated conditions initially slow O_2 diffusion to soil microbes thereby forcing the microbial community to conduct oxidative decomposition using alternative electron acceptors (such as NO_3^- or SO_4^{-2}), but only slightly reducing the efficiency of decomposition. Ultimately saturated conditions result in anoxic conditions under which fermentation pathways are emphasized and decomposition rates slow dramatically as decomposition halts with the formation of acids and alcohols, which further slow decomposition rates by inhibiting microbial activity (Sahrawat, 2003). This partially explains the great degree of C accumulation in low lying wetlands and forest bogs (Tarnocai et al., 2009; Ping et al., 2010).

Soil disturbance and carbon mineralization

Natural and anthropogenic disturbances can reduce total ecosystem soil C storage by stimulating net C mineralization. Timber harvest of second growth forests generally reduces C storage in the O horizon and reduces total ecosystem C through biomass extraction, but generally harvests have little or no effect on mineral soil C (Nave et al., 2010). Timber harvest has been shown to influence total soil C stocks in the long-term by altering C input rates, mixing surface litter into mineral soils (Das Gupta and DeLuca, 2012), and exposing surface soils to warmer conditions thereby accelerating decomposition rates (Nave et al., 2010). Harvest of native or old growth forests greatly reduces total ecosystem C by removing the large accumulation of overstory biomass, reducing the potential for soil wood deposition, and reducing system insolation, but impacts to mineral soil C remain small or undetectable (Harmon et al., 1990; Bisbing et al., 2010).

Fire is a naturally occurring disturbance in temperate forest ecosystems with the recurrence of fire being dictated by climate, regeneration, and anthropogenic influences. Natural fire return intervals are difficult to assess given the long-term influence of humans on forest landscapes, but range from as short as a few years in pinon-juniper forests of the southwestern US to several hundred years in temperate rainforests of the Pacific Northwest (Agee, 1998). Accumulation of fine and coarse fuels on the forest floor, fuel moisture, and wind speed dictate the severity of the fire which in turn determine the magnitude of forest biomass consumed in a given fire event. In a "normal" mixed severity fire of the inland northwestern US one might expect fire to consume 40%−60% of the forest floor, 40%−80% of surface shrub cover, and 20%−30% of overstory biomass with most of that being needles, twigs, and branches leaving the main part of the forest bole intact (Agee, 1998). Although an individual fire rarely reduces mineral soil C to any degree, recurrent fire (Gundale et al., 2006b) and high severity fire (Bormann et al., 2008) can significantly reduce mineral soil C. Charcoal that is generated during fire events represents the 'short-cut' creation of a highly decay resistant form of C can also directly influence soil microbial processes through its uniquely adsorptive surfaces (Gundale et al., 2006b; Pingree et al., 2016). Wildfires and prescribed fires are also considered to create biogeochemical hot spots in forest ecosystems, where ignition, oxygen, and fuel combine to oxidize organic matter on the forest floor and release heat, CO_2 and other gasses into the atmosphere, and deposit pyrogenic C (PyC) which has a notable effect on soil properties and processes and serves as a form of passive soil C (DeLuca and Aplet, 2008).

Forest soils are prone to recurrent disturbances that alter decomposition and mineralization rates by directly or indirectly reducing substrate concentrations. Freezing events, droughts, and fires alter the stability of soil aggregates, adsorption interactions, water availability, can add hydrophobic compounds, and volatilize organic matter. In concert, these events and the complex molecular compounds present in heterogeneous forest soils create difficult challenges for the modeling of soil C stocks in future climate scenarios (Davidson and Janssens, 2006).

Mycorrhizae and nutrient acquisition

A discussion of forest soil health could not be complete without considering mycorrhizal fungi. Unfortunately, the topic is too large and well-studied to provide a thorough treatment here, rather we provide a brief summary and recommend the reader consider one of several articles for a more detailed review (Fahey, 1992; Mohan et al., 2014; Shantz et al., 2016). Mycorrhiza represent a group of fungi that live in a symbiotic relationship with higher plants and generally increase plants nutrient acquisition in trade for plant C resources. There are several types of mycorrhiza including those that infect plant root tissue, such as arbuscular mycorrhiza (most commonly associated with herbaceous plants, Fig. 16.2) and ericoid mycorrhiza (associated with ericaceous plants) and those that create a mantle around the root surface, but do not actually infect root cells, which are the ectomycorrhiza (most commonly associated with trees). All three of these forms of mycorrhiza exist in forest systems (Bücking et al., 2012) and greatly influence the nutrient dynamics and interplant relationships found in forest ecosystems (Fig. 16.2). Given the importance of ectomycorrhiza to trees, forest soil health has been related to the diversity and density of ectomycorrhiza in forest soils (Fahey, 1992).

Mycorrhizal fungi greatly expand the total surface area of plant roots through mycelial growth into the soil environment (Bücking et al., 2012). The greater root-soil contact increases the potential for nutrient interception (Fahey, 1992), facilitates solubilization of minerals (Finlay, 2008) and

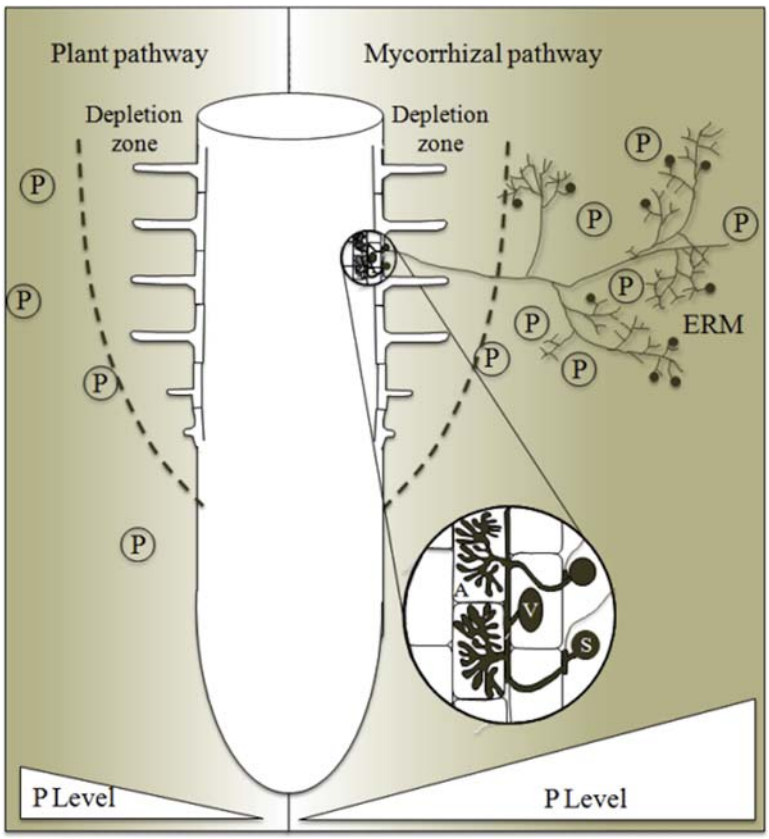

FIG. 16.2

Phosphorus uptake via the plant pathway or mycorrhizal pathway. Abbreviations: ERM - extraradical mycelium of the fungus, V — vesicles, S — spores of the arbuscular mycorrhizal fungi.

Reprinted from Bücking, H., E. Liepold, and P. Ambilwade. 2012. The role of the mycorrhizal symbiosis in nutrient uptake of plants and the regulatory mechanisms underlying these transport processes. IntechOpen. In: Dhal, N. K. and Sahu, S. C., (Ed.), Plant Science. InTech Open, London. Creative Commons License: https://creativecommons.org/licenses/by/3.0/).

decomposition of organic compounds (Talbot et al., 2008). Phosphorus availability to plants is limited by the insoluble nature of P and its propensity to adsorb to a variety of clay minerals. Mycorrhizal associations with roots can increase P uptake in the plant host via root/hyphal interception of P, which exhibits limited diffusion in soil (Lambers et al., 2008). Mycorrhiza increase uptake of a variety of nutrients through the solubilization of resident minerals (Finlay, 2007) and release of phosphatase enzymes (Lambers et al., 2008). Higher surface area associated with mycorrhiza also increases plant water uptake and thus reduces plant drought stress (Shantz et al., 2016). Furthermore, mycorrhizal associations can protect plants from soil borne pathogenic fungi (Liang et al., 2015) and increase fine root survival (Fahey, 1992). These characteristics make mycorrhiza incredibly important in plant community response to climate change (Mohan et al., 2014).

Forest soils with strong mycorrhizal associations afford ecosystem traits that may limit or reduce the deleterious impacts of global climate change. Networks of mycorrhizal fungi in forest soils connect plants and afford translocation of nutrients and C resources from one plant to another. While this could be viewed as a parasitic or pathogenic effect of the fungi on at least one of the host species, some researchers have investigated this as a mechanism of community integration and communication (Simard and Durall, 2004). Forest management and global change drivers including increasing seasonal temperatures, moisture stress, and nutrient deposition threaten to modify these relationships and again may serve as indicators of ecosystem health and function (Shantz et al., 2016).

Nitrogen fixation

Nitrogen accumulation in temperate forest ecosystems primarily originates from biological N_2 fixation with smaller amounts coming from resident sedimentary rocks (see above) and atmospheric deposition of NO_3^- and NH_4^+. Nitrogen accumulation is essential to the establishment of higher plant communities, therefore the role of N_2 fixing plant species in primary and secondary succession has been studied in great detail (Chapin et al., 1994; Vitousek et al., 2002; Sorensen et al., 2004; Zackrisson et al., 2004; Rousk et al., 2013). Biological N_2 fixation is accomplished by bacteria and archaea as free-living soil organisms or in association with plant and fungal partners. Free-living soil bacteria and archaea normally contribute roughly 0.5 kg N ha^{-1} yr^{-1} to temperate forest ecosystems (Cleveland et al., 1999; Burgoyne, 2006); however, much higher levels of N_2 fixation have been reported for free-living bacteria in association with decaying roots (Chen and Hicks, 2003). Nitrogen fixing lichen are particularly important in early succession on bare rock or sediments and represent symbioses between cyanobacteria, fungi and yeasts (Spribille et al., 2016). These organisms are capable of fixing N at relatively high rates (Crittenden and Kershaw, 1978), but their limited biomass in most forest systems restricts them to contributing less than 1 kg N ha^{-1} yr^{-1} to the larger ecosystem. Legumes and actinorhizal plants represent a symbiotic relationship between bacteria or archaea and herbaceous and woody plants. These leguminous and actinorhizal plant species have the capacity to build soil organic N stocks, a process that is uniquely important in early primary succession (Chapin et al., 1994; Schmidt et al., 2016; Buma et al., 2017). For example, red alder (*Alnus rubra*) as an early successional species that persists as a subdominant species well into late secondary succession has been reported to fix between 3.5 and 35 g N m^{-2} yr^{-1} (Binkley et al., 1994) in dense stands in the Pacific Northwest resulting in rapid accumulation of N in a relatively short period of time. Litter accumulation under red alder results in rapid N cycling and turnover (Perakis et al., 2012), which enhances N uptake by neighboring species.

Wildfire in temperate forests reduces total ecosystem N stocks through combustion of live biomass as well as forest floor and humus layer N (Neary et al., 1999). Wildfires may result in losses of 200−500 kg N ha^{-1} during a single fire event (Boby et al., 2010), a loss that must be rebuilt by biological N_2 fixation and N deposition. Legumes and actinorhizal species are favored by the reduced N and high light conditions created in post fire landscapes (Newland and DeLuca, 2000; Johnson et al., 2005) thereby rebuilding fire induced N losses (Hart et al., 2005). The role of disturbance in retaining symbiotic N_2 fixing species is supported by the observed increase in their presence in Douglas-fir forests of the Pacific Northwest that had been exposed to severe wildfire or logging (Perakis et al., 2015).

Bryophytes, soil crusts and lichen have been shown to play an important role early in succession (Arróniz-Crespo et al., 2014) and in arid environments as they aid in stabilizing surface sediments, altering surface hydrology, increasing soil C and fixing atmospheric N_2 into a plant useable form

(Ferrenberg et al., 2017). Mosses and the underlying humus layer act as a thermal buffer between mineral soil and the atmosphere (Turetsky et al., 2012) and are important in influencing soil characteristics such as soil temperature, moisture, pH, and nutrient availability (Lindo and Gonzalez, 2010; Lindo et al., 2013). Feather mosses can harbor N_2 fixing cyanobacterial associates (DeLuca et al., 2002; Zackrisson et al. 2004, 2009) and can account for the majority of N input to pristine (N deposition < 2 kg ha^{-1}) boreal ecosystems. Nitrogen deposition, fertilization and N from canopy throughfall down regulate N_2 fixation (DeLuca et al., 2008; Gundale et al., 2011) resulting in reduced or undetectable N_2 fixation rates in areas of high N deposition (Zackrisson et al., 2009). Rates of N_2 fixation in these ecosystems is relatively low (2−3 kg N ha^{-1} yr^{-1}), but fits well with rates of N loss and fire return intervals for this region (Zackrisson et al., 2004; Carcaillet et al., 2007). Recently, researchers have demonstrated significant rates of N_2 fixation in what have been historically considered non-N_2 fixing species (Bal and Chanway, 2012; Doty et al., 2016). The relative importance of endophytic N_2 fixation in accumulating N in forest soils has yet to be determined. Similar to feather mosses, increasing N accumulation in forest ecosystems likely down regulates endophytic N_2 fixation in trees.

Autotrophic activity

The N and C cycles rely heavily on heterotrophic microorganisms that are capable of utilizing organic and inorganic energy sources to conduct metabolic oxidation, but organic C sources must first be supplied by autotrophs, which conduct the most important reaction on Earth by utilizing CO_2 (and carbonates) as a C source to produce organic C. Autotrophs can be categorized as photoautotrophs, which use light as an energy source (e.g., green plants, algae, purple and green bacteria, and cyanobacteria), and chemolithotrophs, which use chemical energy from reduced minerals (e.g., nitrifiers, S oxidizers, methanotrophs, and anammox bacteria). Photoautotrophs are capable of growing with CO_2 as the sole source of C and convert light energy to sugars through light-sensitive pigments called chlorophylls, which are present in plants, algae, and cyanobacteria, or by bacteriochlorophylls, which are present in purple and green bacteria.

Cyanobacteria display a range of morphological diversity including unicellular and filamentous forms and contain two photosynthetic structures (PSI and PSII), which gives some cyanobacteria the ability to switch from oxygenic to anoxygenic photosynthesis if necessary. Cyanobacteria are important symbionts that fix N_2 as free living soil organisms or in symbiosis with fungi (as lichen) and mosses (DeLuca et al., 2002; Matzek and Vitousek, 2003; Lindo et al., 2013).

Chemoautolithotrophs in terrestrial systems utilize alternative electron donors such as S^{-2}, elemental S, NH_4^+, NO_2^-, and Fe^{+2} as a primary energy source. These organisms are key to the cycling and subsequent release of essential, often limiting nutrients: N, S, and Fe. Nitrifying bacteria and archaea are responsible for the oxidation of NH_4^+ to NO_3^-. Autotrophic organisms that oxidize N, S, and Fe, do so at a high energetic cost. The oxidation of S compounds occurs in multiple species of colorless sulfur bacteria (e.g. *Thiobacillus* spp.) by first oxidizing S^{-2} to elemental sulfur (S^0), where it can be stored or further oxidized to thiosulfate, sulfite and ultimately to sulfate thereby producing protons which can acidify soils.

Anaerobes and the role of microsites

In unsaturated soils, upland forest soils or ephemerally dry forest soils in lowlands, available soil C is the major limiting factor to denitrification by facultative or obligate anaerobes. Highly variable

denitrification rates by orders of magnitude, have been found associated with particular organic matter and clay aggregates, which provide essential hot spots for denitrification and anaerobic decomposition (Sexstone et al., 1985; Parkin, 1987). Anaerobic microsites can also produce CH_4, a potent greenhouse gas biochemically produced in forest soils (Yavitt et al., 1995). Across multiple ecosystems in Wisconsin over a two-year period, a planted conifer forests evolved the second highest total N_2O (1.5 kg N_2O—N ha^{-1} $year^{-1}$) when compared to a drained marsh, wet meadow, deciduous forest, prairie, and undrained marsh (Goodroad and Keeney, 1984). These high rates of N_2O production were likely a function of anaerobic microsites (Parkin, 1987). A simulated forest floor consisting of Douglas-fir monoculture samples showed anoxic sites were more likely to occur in larger (>0.25 mm dia.) organic particles in the less decomposed layers (upper 5 cm) even at low moisture contents (2 g g^{-1}) (van der Lee et al., 1999). Across the OM moisture gradients (2—3.9 g g^{-1}), the study did not find an effect on oxygen diffusion inside organic particles, which shows the possibility of denitrification and anaerobic processes even in low-water content OM (van der Lee et al., 1999).

The heterogeneous physical, chemical, and biological nature of soils lends to the existence of spatiotemporal 'hot spots' where biogeochemical reactants coincide and chemical reactions occur at disproportionally higher rates than surrounding areas (spatial hot spots) or occur in short periods of time (temporal hot spots) (Parkin, 1987; McClain et al., 2003). For example, denitrification rates tend to be higher where anoxic conditions and C substrate are abundant, such as wetlands (Johnston, 1991) and also occur at multiple scales, such as within a soil aggregate or earthworm cast and where allochthonous NO_3^- is delivered from uplands to anoxic areas (Parkin, 1987; McClain et al., 2003). The volume of anoxic microsites is heavily influenced by clay content in soils where clay is present, in some cases more so than organic matter, however, OM availability is strongly related to the supply of O_2 through microbial activity (Keiluweit et al., 2018). On a larger scale, bioturbation induced by geomorphic events or tree windthrow are particularly common in forest soils where slopes can be steep and variable, vegetation may be sparse, and other disturbances (heavy rains and fires) may facilitate microsites by adding to the heterogeneity of forest soils (Beatty and Stone, 1986; Peterson et al., 1990).

Soil fauna and organic matter turnover

Soil fauna help facilitate decomposition of organic matter through physical and chemical processes and aid in the activity and community assemblage of soil fungi and bacteria (Paul, 2015). These heterotrophic organisms are often classified by size, which spans from < 0.1 mm to over 20 mm (Fig. 16.3), but can also be grouped by functional group, both categorical systems exist across spatiotemporal scales in soil systems (Veresoglou et al., 2015). Functionally, soil fauna can be described as (1) ecosystem engineers that alter the physical structure of soil; (2) litter transformers that fragment decomposing litter; and (3) micro-food webs, which consist of microbial groups and microfauna predators (Wardle, 2002; Edwards, 2004; Coleman and Wall, 2007).

Soil microfauna (<0.1 mm in size or diameter) consist of free-living protozoans, nematodes and rotiphers in organic and mineral soil horizons. These organisms feed on bacteria and live in water films or water-filled spaces in soil. Protozoa are classified as flagellates, naked amebae, testate amebae, and ciliates. Traditional methods of quantifying microfauna likely discriminate against rare populations, those with unique substrate and growth conditions, and less active populations, which makes comparisons of abundance difficult across methodology (Foissner, 1999; Coleman and Wall, 2007). Rotifers and nematodes can exist in a desiccate-resistant state in order to survive through dry periods. Unlike

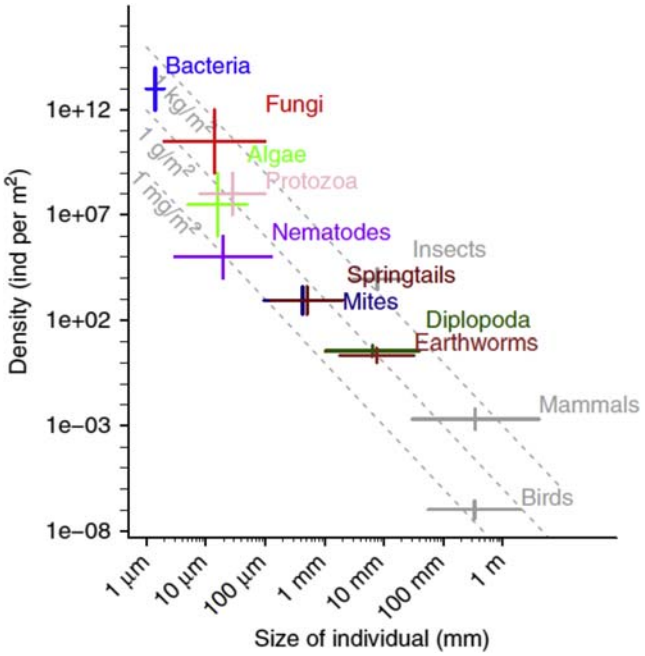

FIG. 16.3

Size-density relationships in representative above and belowground organisms.

Reprinted from Veresoglou, S. D., Halley, J. M., Rillig, M. C., 2015. Extinction risk of soil biota. Nature Communications 6:8862, Creative Commons License: http://creativecommons.org/licenses/by/4.0/.

protozoans and rotifers, nematodes have a much wider range of prey including fungi and roots, and are thus identified by their specialized anterior structures. Predatory nematodes that feed on parasites or other fauna may carry symbiotic bacteria, which can infect, kill, and allow nematodes to utilize hosts as substrate and habitat for larvae (Strong et al., 1996; Helmberger et al., 2017). Nematodes, however, have an earlier phylogenetic origin and are the most numerous and diverse group of microfauna in terrestrial systems (Blaxter et al., 1998).

Mesofauna range in size from 0.1 to 2 mm and consist of microarthropods such as Acari (mites), Collembola (springtails), Protura (coneheads), Diplura (two-prong bristletails), Symphyla (centipedes), Chelonethida (pseudoscorpions), Ttardigrada (water bears), and Enchytraeidea (potworms). These organisms are a more abundant group in forest soils compared to the microfauna groups (Petersen and Luxton, 1982). Mesofauna prey on fungi and nematodes and are prey for macrofauna, thus providing a link between micro- and macrofauna. Enchytraeids are particularly important in forest soils with abundance reported highest for acid soils with high organic matter, for example, 20,000−30,000 individuals m^{-2} in temperate deciduous forests (Coleman and Wall, 2007). Soil macrofauna are classified as organisms that are 2 mm−20 mm in size making them easy to observe and measure. The soil macrofauna are exceptionally diverse in size, shape and function and include Oligochaeta (earthworms), Formidacea (ants), Termitidae (termites), Coleoptera (beetles), Diplopoda (millipedes), Arachnida (spiders), and Gastropoda (slugs and snails). These organisms are large

enough to be measured on a square meter basis. For example, the abundance of macrofauna in a conifer forest soil in southern Finland (acidic podzol/spodosol) held 2.1×10^6 nematodes m^{-2}, 38,700 potworms m^{-2}, 7700 collembola m^{-2}, 3300 mites m^{-2}, 780 centipedes m^{-2}, 450 beetles m^{-2}, and 30 earthworms m^{-2} (Huhta et al., 1986).

For a holistic approach to soil biotic health, it is important to pair soil fauna population dynamics, abundance, and community with soil nutrient processes. A simulation of extreme precipitation patterns was enacted over an 18-week period and soil fauna residing in spruce (*Picea abies*) litter collected from a monoculture site in Germany in order to test the effects of changing moisture to the decomposer community (Taylor et al., 2004). Using mesh sizes to exclude macrofauna and mesofauna, the study showed the community abundance of mesofauna (low or high) did not influence the response of microfauna or microorganisms (bacterial and fungi) to regular and irregular precipitation patterns, nor did mesofauna abundance change. However, the presence of mesofauna did impact the total extractable inorganic N (NH_4^+ & NO_3^-) under different precipitation patterns (without mesofauna) suggesting a top-down control in trophic interactions with extreme precipitation patterns possibly via excretion or enhanced decomposition. The community structure of decomposers may enhance or diminish other functional parameters, such as N cycling, with changes in precipitation patterns. Trophic interactions and community structure of forest soils are complex with some components regulated by top-down controls (predation and physical alterations of soil) and bottom-up controls (substrate availability) (Wardle et al., 1998).

Given the intimate relationship between soil fauna and soil organic matter, it is often assumed that fire disturbance, which combusts and results in some loss of organic matter on the forest floor, will result in a reduction of soil fauna activity. In an early investigation of longleaf pine, fire-prone south-eastern US forests, Heyward and Tissot (1936) found a general reduction, but not an elimination, of meso- and macrofauna and in the specific case of Hymenoptera (mostly ants), an increase in abundance with recurrent fire was observed. More recent studies show the importance of soil fauna shifts after fire events, the ephemeral activity of pyrophilous insects, and the greater impact on soil fauna from higher severity fire events (Wikars and Schimmel, 2001; Malmström, 2010; Korobushkin et al., 2017). Post-fire recovery studies generally lack more than one year of pre-fire data and do not adequately compare population dynamics before and after a fire treatment, thus, these should not be considered a proxy for population dynamics with the treatment of fire (Malmström, 2010). In addition to fire severity, the structure of burned and unburned fuels also affects the abundance and recolonization of soil fauna where more mobile fauna can recolonize faster (Zaitsev et al., 2014), showing the importance of soil fauna life history in recovery after fire disturbances.

Assessing biotic abundance and diversity in forest soils

Historical methods

Soil microbiology is a relatively young science which started with our ability to sense soil microbial world using ever improving techniques in microscopy and molecular biology (Paul, 2015). Rough estimates of soil microbial biomass and diversity were generated based on what could be set in resin and observed at 200−400X. German microbiologist Robert Koch initiated the use of solid vegetative matter (potato or apple slices) to grow bacteria and successfully isolated pure cultures in the late 1800s. This approach was greatly improved with the advent of solid media (agarose gel) opening a new world

in terms of ability to grow bacteria and fungi in culture and actually observe and numerate soil microorganisms. It wasn't until 1935 that Danish ecologist Lars Romell successfully applied Winograskii's culture and direct observation methods to forest soils (Ackert, 2013). For the next seventy years, culture-based studies would be the standard for assessing forest microbial communities. Culture studies of microbial community relied on the assumption that the majority of soil microorganisms can grow on solid media. Using such a simple process inadvertently selected for organisms adapted to mesotrophic conditions, capable of growing on a solid surface or in liquid media, and capable of proliferating using the specific nutrient and C form in the media. The result was that the diversity of soil microorganisms was grossly underestimated using cultural techniques (Hill et al., 2000). A noted benefit of culture-based approaches include the fact that specific soil microorganisms could be isolated from a wide range of soils, availing the living organisms to deliberate experimentation. Recent advances in molecular approaches (discussed below) demonstrated that culture-based techniques capture less than 1% of soil bacterial diversity and even less is known regarding the capacity of culture techniques to assess the diversity of soil fungi (Vieira and Nahas, 2005).

Measuring soil microbial biomass

Soil microbial biomass, the total mass of all organisms in soil, is commonly used to give an estimate of the response of soil microbiota to changing environmental conditions. Microbial biomass is most commonly measured using chloroform fumigation-extraction method in which microorganisms are first killed by exposing fresh soil to ethanol-free chloroform for a certain period of time (usually 24 h), extracting the C released from the lysed microbial cells with a salt solution, analysis of the net increase in soluble C multiplied by a conversion factor to determine microbial biomass C. Other common methods of microbial biomass determination include use of fatty acid profiles, substrate induced respiration (SIR) (Beare et al., 1990) or biochemical indicators such as the measurement of ATP production (Jenkinson and Oades, 1979) or fungal ergosterol production (Hagenbo et al., 2017).

Global estimates of the soil microbial biomass pool based on both chloroform fumigation-extraction and fumigation-incubation methods were estimated to vary widely from 13.9, 14.6, and 23.2 to 26 Pg C (Wardle, 1992; Whitman et al., 1998; Serna-Chavez et al., 2013; Xu et al., 2013) with tropical forests exhibiting the highest total soil microbial biomass C and boreal forests having the lowest total microbial biomass of the forested biomes (Serna-Chavez et al., 2013). While temperature could serve as an indirect factor influencing microbial biomass on global scale, moisture availability was shown to be the primary driver shaping the global pattern of soil microbial biomass (Serna-Chavez et al., 2013).

Forest composition has been demonstrated to influence microbial activity in temperate forests, where soil microbial biomass, as estimated by using SIR, was found to be higher under beech trees than under oak and pine trees (Gartzia-Bengoetxea et al., 2016). Restoration of historically bottomland hardwood forests has been shown to shift catabolic profiles of the soil microbial community. Sites restored by direct-seeding of hardwood trees had higher rates of cellulose respiration compared to remnant forests which had a greater proportional respiration for glucose and citric acid (Strickland et al., 2017). Combining SIR with specific enzyme activities involved in organic matter or nutrient turnover can be used as more targeted approach to measuring microbial activities in forest ecosystems (Meier et al., 2017; Schimel et al., 2017).

Ergosterol is a sterol found in cell membranes of fungi and protozoans, thus its content can serve as a potential indicator of fungal biomass. Fungal biomass estimated by ergosterol has been reported to

decline with increasing age of boreal forest, and the trend was highly correlated with a drastic temporal decline of mycelial turnover, suggesting that change in turnover is the main factor regulating fungal biomass across a *Pinus sylvestris* chronosequence (Hagenbo et al., 2017). Total extracted ergosterol was reported to be higher and highly correlated with soil organic P availability, soil phosphatase activity, and total biomass in forest sites dominated by ectomycorrhizal trees compared to sites dominated by trees associated with arbuscular fungi, highlighting the importance of host trees and associated fungal communities in P acquisition strategies and cycling features in hardwood forests (Rosling et al., 2016).

Direct counts of soil fauna

Soil fauna represent an important group of heterotrophic organisms in forest soils; however, this group has been greatly ignored and compared to the more overt interest in bacteria, archaea, and fungi (Huhta, 2007). One square meter of temperate coniferous forest soil of O horizons contains approximately 2400 mg of soil invertebrates, and this total biomass is estimated as 8000 mg m^{-2} for deciduous forests (Shaw et al., 1991). Soil fauna regulate soil nutrient cycling by directly consuming organic matter, accelerating organic matter decomposition by fragmentation, or distributing nutrients by grazing on or transporting microbes with adhesion (Coleman and Wall, 2015). Thus, their populations and diversity are typically considered to be good indicators of soil quality in forest soils (van Straalen, 1998). As a gross example of this proxy for soil health, conversion of forests to agricultural land has been shown to greatly reduce the abundance and diversity of soil microarthropods (Begum et al., 2014; Martins da Silva et al., 2016).

Nematodes, collembolans, mites, and earthworms are the most commonly studied of the soil fauna. Nematodes non-segmented round worms that typically live in water films or water-filled pore spaces in soils. Nematodes are extracted from soil samples using the classic Baermann funnel method (Baermann, 1917). The abundance and biomass of nematodes have been reported to be consistent before and after a fire disturbance in forest ecosystems (Matlack, 2001; Butenko et al., 2017); however, its community diversity was found to shift with disturbance, where those bacteria-feeding nematodes were increased while hyphal- and plant-feeding nematodes were decreased following a forest fire (Butenko et al., 2017), further suggesting that nematodes community diversity could potentially serve as an indicator of ecological disturbance (Bongers, 1990).

Collembolans and mites are microarthropods and are commonly extracted by using a Tullgren funnel method (Tullgren, 1918) which simply uses a heat source to cause gradual drying of the soil forcing arthropods to descend through a filter into a container with of preservative liquid (Tullgren, 1918). The abundance, composition and species traits of Collembolan community has been reported to be sensitive to microclimate, such as forest SOM content and forms, soil acidity and moisture (Salmon et al., 2014). In addition, plant functional groups were also reported to have strong influence on Collembolan communities (Hasegawa and Okabe, 2017). For example, removal of feather moss (*Pleurozium schreberi* and *Hylocomium splendens*) ground cover resulted in a 64%−76% decrease in Collembolan abundance (Bokhorst et al., 2014).

Earthworms may be the most commonly studied organism among soil fauna perhaps owing to their morphology and size which facilitate their observation in forest soils. The population or biomass of earthworms can be directly examined by hand-digging and sorting in field; however, it is time-consuming and labour-intensive (Singh et al., 2016). Chemical extraction methods commonly employ

mustard solutions that are allowed to percolate into the soil, the mustard solution irritates the skin of the earthworms, forcing them to come to the surface for collection (Gunn, 1992). Alternatively an electrical octet method where voltage through soil provides the irritant, which works better in saturated soils or soils on steep slopes (Singh et al., 2016). In temperate and subboreal mixed forest, earthworm density/biomass were found to be higher in spring and autumn and lower in summer (Bayranvand et al., 2017). Site disturbance typically reduces earthworm populations. Soil tillage has been reported to reduce earthworm abundance by 2–9 times across a variety of tillage operations (Chan, 2001). Earthworm density and biomass also tended to be higher in forest sites with small canopy gaps (Kooch and Haghverdi, 2014; Marichal et al., 2014). Notably, high abundance of invasive earthworms have been shown to significantly increase the loss of forest floor C in a northern temperate forest soils (Bohlen et al., 2004; Gundale et al., 2006a; Fisk et al., 2015).

Enzyme activities

Soil enzymes are proteins that act with specific substrates to catalyze soil biochemical reactions necessary for microbial life functions. Enzymes increase the reaction rate at which organic matter decomposes and releases nutrients into soil environment. Soil enzymes can be constitutive (constantly produced) or induced and can originate from both living and dead microorganisms (Fig. 16.4), soil animals and plant roots (Tabatabai, 1994). Therefore, enzyme activity can serve as a sensitive indicator of ecological or microclimatic change (Kandeler, 2015). Due to high input of organic matter from plant litter, enzymes participating in the decomposition process play an important role in forest soil morphology and function (Sinsabaugh et al., 1991).

Enzyme activities of forest soils typically decrease with soil depth in a profile, and are more widely spatially varied compared to agricultural or grassland soils (Šnajdr et al., 2008). This vertical gradient and spatial variability of enzyme activities are commonly reported to be associated with litter quantity and quality (Saetre, 1999). In addition, soil enzyme activities were widely documented to be regulated by a variety of factors, such as microclimate factors (warming, drying, freezing and thawing) or soil biochemical factors such as litter chemistry, or indirect factors such as change in land-use. In temperate zones, higher enzyme activities are usually detected in warm summer period as compared to the winter; and forest soils were reported to exhibit reduced enzyme activities in dry seasons (Ren et al., 2017). Nitrogen additions have been reported to be associated with a reduction of soil enzyme activity in many forest ecosystems, particularly the activity of oxidative extracellular enzymes involved in plant litter degradation, such as peroxidase (Sun et al., 2016; Xia et al., 2017). This response might indicate a down-regulation of enzyme production from plant roots and a reduction in ectomycorrhizal fungal associated enzymes (Corrales et al., 2017). In addition, the quantity of plant secondary compounds such as tannins from decomposition processes have been reported to have various effects on the enzyme activities and thus catalytic activities of boreal forest soils (Adamczyk et al., 2017).

Phospholipid fatty acid profiles

Phospholipid fatty acid (PLFA) profiling is a technique for assessing soil biotic diversity based on the variability of fatty acids present in cell membranes of different organisms, this allows for phenotypic fingerprinting of soil microbial communities and provides a snapshot of the soil microbial community

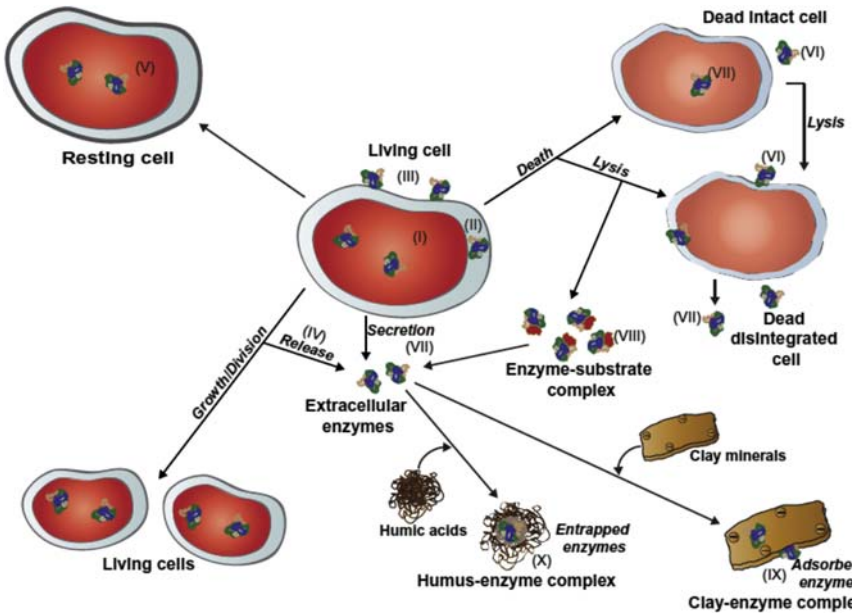

FIG. 16.4

Locations of soil enzymes. I, Intracellular enzymes; II, Periplasmatic enzymes; III, Enzymes attached to outer surface of cell membranes; IV, Enzymes released during cell growth and division; V, Enzymes within nonproliferating cells (spores, cysts, seeds, endospores); VI, Enzymes attached to dead cells and cell debris; VII, Enzymes leaking from intact cells or released from lysed cells; VIII, Enzymes temporarily associated in enzyme-substrate complexes; IX, Enzyme absorbed to surfaces of clay minerals; X, Enzymes complexed with humic colloids.

Reprinted from Kandeler, E. 2015. Physiological and biochemical methods for studying soil biota and their functions. In: Paul, E. A., (Ed.), Soil Microbiology, Ecology, and Biochemistry Academic Press, Cambridge, MA, pp. 187–222 permission obtained from publisher.

structure and an estimate of microbial biomass (Frostegård et al., 1993). Since phospholipids degrade rapidly in soils upon cell death, thus are considered excellent signature molecules for living organisms (Jenkinson and Ladd, 1981). Lipids are extracted from soil with organic solvents followed by separation of phospholipids from other lipids based on their polarity using a solid phase extraction (Bligh and Dyer, 1959). The PFLAs are then converted to fatty acid methyl esters (FAMEs) that can be analyzed by gas chromatography (GC) to determine the types and quantities of each (Bardgett et al., 1996). Ratios of certain PLFAs can be used as indexes or indicators for certain ecosystems, for instance, the ratio of monoenoic precursors to cyclopropane PFLA and trans/cis ratio of monoenoic PLFA are both indicators of microbial stress in soils (Fierer et al., 2003).

The PLFA technique has been widely used to study the change or difference in forest soil microbial community structure across a range of soil properties or tree species (Frostegård et al., 1993; Chodak et al., 2016; Khlifa et al., 2017), management practices or amendments (Gundale et al., 2015; Pluchon et al., 2016; Bastida et al., 2017), perturbations or land-use change (DeGrood et al., 2005; Gundale et al., 2005; Bischoff et al., 2016), and climatic origins (Rinnan et al., 2007; De Long

et al., 2016). Typically, forest soils have relatively higher total PLFA content and richness compared to agricultural soils, and the practice of afforestation has been reported to significantly increase both soil bacterial and fungal PLFA (Gunina et al., 2017). The PLFA technique is versatile and has been used to assess the influence of disturbance on forest soils including assessing the effect of clear cutting on bacterial, fungal, and other selected PLFAs compared to old-growth forest stands (Moore-Kucera and Dick, 2008) or warming effects on the compositional and functional structure of forest soil microbial communities (Zhang et al., 2005). Profiles of PLFAs are generally compared using multivariate analyses such as principal component analysis or canonical correspondence analysis; and such structure patterns can be related to underlying environment factors. While the PLFA technique can provide a broad-scale diversity index of the soil microbial community, such as the number of bacterial families present in the samples, it does not represent a higher resolution of microbial diversity where it is necessary to identify key microbial species at the community level or to elucidate their role in the ecosystem (Singh et al., 2004). Further, only a small number of fatty acids are truly characteristic for certain groups, as some may be derived from other soil organisms (Jandl et al., 2005) and very few main fungal markers are used in PLFA (Klamer and Bååth, 2004). All of these would yield uncertainties when trying to answer associated environmental questions, therefore, care should be taken when selecting a PLFA technique and interpreting PLFA results (Frostegård et al., 2010).

Molecular methods

While traditional culture-based methods are considered important for isolating soil microorganisms, they provide extreme bias in the evaluation of microbial genetic diversity by selecting for those populations of mesotrophic microorganisms that can be cultured. Recent advances in molecular analyses of environmental microbial communities are helping us better understand the structure of microbial communities and functional role of microbial processes in forest ecosystems.

Nucleic acids extraction, amplification, and sequencing

Nucleic acids such as deoxyribonucleic acid (DNA) and ribonucleic acids (RNA) from cells contained within soil samples are widely selected as target molecules in most molecular analyses for characterizing a vast diversity of microorganisms that are non-culturable (Knight, 2000). Such molecular techniques usually rely on extracting DNA from soil organisms, followed by an amplification through polymerase chain reaction (PCR) to get copies of a particular DNA sequence of interest. 16s rRNA is a structurally and functionally conserved gene existing in all prokaryotes, and thus has been used extensively as the target gene in characterizing microbial communities at higher levels of taxonomic classification. In eucarya the 18s rRNA or internal transcribed spacer (ITS) region is also commonly chosen in amplification using specific primers to characterize fungal communities. The polymerase chain reaction (PCR) products that are amplified from environmental DNA are primarily analyzed by cloning and sequencing, fingerprinting, metagenomics, or a combination of techniques (Thies, 2015). For instance, advanced sequencing technologies have been developed to yield 'next-generation sequencing' (NGS) platforms (e.g. Roche 454 pyrosequencing; ion torrent by Life Technologies; Illunima MiSeq, HiSeq, NextSeq 500; single-molecule real-time sequencing by Pacific Biosciences) over the past decade and have been largely applied to evaluate the response of forest soil microbial communities following disturbance (Mikkelson et al., 2016; Cutler et al., 2017), forestry practice (Wilhelm et al., 2017), soil management (Klavina et al., 2016; Jenkins et al., 2017), or in comparing the diversity

of soil microbial communities from beneath different vegetation (Landesman et al., 2014; Colin et al., 2017), or along a temporal gradient such as soil warming and seasonal change (Žifčáková et al., 2016; Oliverio et al., 2017).

Although DNA analysis has been used most frequently in soil microbial ecology across multiple ecosystems because it is stable, easier and less costly to extract, the extracted DNA from a soil sample likely originates from both live and dead cells and thus might not accurately reflect the abundance or potential activity of an active organism in a given sample. In contrast, RNA is highly labile making it very difficult to extract from soil samples before it degrades but would thereby reduce the chance of extracting RNA from dead cells. Importantly, RNA-based approaches offer complementary information to the analyses of phylogenetic affiliation within microbial communities and are far more relevant to understanding metabolic processes (Blagodatskaya and Kuzyakov, 2013). RNA-based analyses require extraction of RNA from a given soil sample, followed by a reverse transcription polymerase chain reaction (RT-PCR) where a step of reverse transcription of RNA into a complementary DNA (cDNA) is involved before running PCR. Such RNA-based techniques are often selected to be used in the context of forest microbial ecology in characterizing the expression of functional genes involved in specific soil processes. For example, arbuscular mycorrhizal fungal phosphate transport genes encoding LePT1 proteins in mature tree roots were detected to a greater extent under elevated soil pH (Carrino-Kyker et al., 2017), while others have used RT-PCR and pyrosequencing to identify *cbhl* gene, which encodes cellobiohydrolase, an essential enzyme for cellulose decomposition in a *P. abies* dominated coniferous forest soil (Baldrian et al., 2012).

While metagenomics involves the large-scale analysis of microbial genomes extracted from soil (often associated with NGS), metatranscriptomics is the study of the genes being expressed by the active members of soil biotic community and is based on the analysis of RNA transcripts, namely RNA sequencing (RNA-seq), where cDNA is first constructed and then sequenced using one of the platforms described above (Wang et al., 2009; Thies, 2015). Using RNA-seq, Damon et al. (2012) did a global evaluation on soil eukaryotic functional roles in a European forest that dominated by beech and spruce. Taxonomic affiliation of cDNA sequences showed a dominance of sequences from fungi rather than protists; and many genes that were involved in producing enzymes participating in either nutrient acquisition or degradation of polymers and organic matter decomposition were widely identified from those massive sequences, suggesting a diverse gene expression by Eukaryotes in that given forest (Damon et al., 2012). Another study reported an over 50% contribution of fungal sequences to total soil microbial transcription in a coniferous forest, and the transcript profiles of fungi, archaea, and most bacterial phyla were significantly different by seasons (Žifčáková et al., 2016).

Genetic fingerprinting

Genetic fingerprinting can provide a profile of microbial communities based on direct analysis of PCR products amplified from environmental DNA. The most commonly used PCR fingerprinting techniques for characterizing soil microbial community composition currently are denaturing- or temperature-gradient gel electrophoresis (DGGE or TGGE), and terminal restriction fragment length polymorphism (T-RFLP) analysis (Muyzer and Smalla, 1998). These techniques distinguish differences in microbial communities among different samples, but do not provide direct taxonomic identities. Such fingerprinting techniques are considered rapid in comparison with sequencing methods, thus enabling high sample throughput and 'fingerprints' from multiple samples can be readily compared using cluster analysis (Mohammadi and Prasanna, 2003).

In DGGE, PCR products are separated by electrophoreses on a polyacrylamide gel containing a linear gradient of DNA denaturant such as formamide; amplicons with different sequences will stop migrating at different positions in the gel and thus form a number of bands that are then used for community comparisons. The TGGE method is based on the same principle of DGGE except that the gradient is temperature based. Both DGGE and TGGE have been widely used to assess the diversity of bacteria and fungi in forest soils (Fierer and Jackson, 2006). With T-RFLP analyses, the target gene (i.e., 16s rRNA) is amplified with fluorescent tagged primers, resulting in fluorescent labeled PCR products. The amplicons are then digested with restriction enzyme(s), and the terminal restriction fragments (T-RFs) are separated on an automated DNA sequencer and sized with the detection of the fluorescent label. Community diversity is then estimated by analyzing the size, numbers, and peak heights of the resulting T-RFs, commonly by use of similarity matrices and multivariate statistics. To examine the influence of time-after-management on the fungal community composition of intensively managed subtropical bamboo forests where mulching and fertilization occurred, T-RFLP has been used to assess the abundance of dominant T-RFs of soil samples across a management chronosequence (Li et al., 2017).

Other fingerprinting techniques commonly used recently in forest soil microbial ecology include: (1) amplified ribosomal DNA restriction analysis (ARDRA), in evaluating the effect of deforestation on forest microbiota (Cordero et al., 2017); (2) automated ribosomal intergenic spacer analysis (ARISA), in investigating ectomycorrhizal fungal richness of a boreal forest following wildfire (Hewitt et al., 2017).

Opportunities

Forest soils contain an incredibly diverse and dynamic body of living organisms. The complex interplay of individual plant roots, microorganisms, mesofauna, and macrofauna, yields a tightly coupled ecosystem that is highly effective in the recycling of energy and nutrients and highly resilient to human or natural disturbance events. However, a key question remains: How do we use this knowledge of the complexity and dynamism of forests soils to inform intelligent land management decisions that work with soil biota to achieve positive outcomes? Currently, there is limited capacity to transform soil biotic data into a useful form for land managers. Advanced techniques in soil microbial ecology remain costly and require specialized training for interpretation of results that limit its use by land managers. Simple and field-accessible approaches to measuring some key biotic processes (e.g. soil organic matter, soil respiration, and decomposition rates) exist and make possible assessment of soil health for management purposes (DeLuca and Archer, 2009), albeit these methods are a vague representation of soil biotic communities. The next step will be to convince land managers of the importance of soil biotic health to the short-term and long-term sustainability of managed forest ecosystems and provide cost-effective accessibility to advanced methods.

Techniques for assessing soil biota have advanced dramatically over the past 100 years resulting in an increasing understanding of the diversity, complexity interactions, and importance of soil biota. The advent of molecular techniques demonstrated the incredibly diversity of soil microorganisms, but these methods do not allow for the isolation and manipulation of organisms that is required to fully understand soil microbial ecology. Clearly, no single method can reveal the composition and interplay of the soil microbial community, but integration of modern molecular techniques along with improvements

in cultural and direct observation methods will help us achieve a better understanding of whole ecosystem processes. As an example, genetic fingerprinting estimating of soil microbial community composition is not only able to support the clone library analysis (Lynn et al., 2017), but also provide insights into the divergence of community structure and assessment of the selection of proper amplicons prior to sequencing. In addition, quantification of active microbial populations obtained by RNA analysis is now commonly paired with enzyme activities and sequencing data to provide sufficient information in understanding decomposition or nutrient cycling process (Baldrian et al., 2012; Žifčáková et al., 2016). Refinement of simple, real time assessments of soil biodiversity and activity (e.g. soil CO_2 efflux systems, field DNA barcoding systems, photometric soil enzyme activity test kits) combined with the application of common physical and biochemical indices of soil health (e.g. portable soil moisture, pH, and Eh sensors) could ultimately allow for widespread adoption of soil health methods that can be integrated into land management decision making.

References

Ackert, L., 2013. Sergei Vinogradskii and the Cycle of Life.

Adamczyk, B., Karonen, M., Adamczyk, S., Engström, M.T., Laakso, T., Saranpää, P., Kitunen, V., Smolander, A., Simon, J., 2017. Tannins can slow-down but also speed-up soil enzymatic activity in boreal forest. Soil Biology and Biochemistry 107, 60−67.

Agee, J.K., 1998. The landscape ecology of western forest fire regimes. Northwest Science 72, 24.

Arróniz-Crespo, M., Pérez-Ortega, S., De Los Ríos, A., Green, T.G.A., Ochoa-Hueso, R., Casermeiro, M.Á., De La Cruz, M.T., Pintado, A., Palacios, D., Rozzi, R., Tysklind, N., Sancho, L.G., 2014. Bryophyte-cyanobacteria associations during primary succession in recently deglaciated areas of Tierra del Fuego (Chile). PLoS One 9.

Baermann, G., 1917. A simple method for the detection of Ankylostomum (nematode) larvae in soil tests. In: Mededelingen Uit Het Geneeskundig Laboratorium Te Weltevreden, pp. 41−47.

Bal, A., Chanway, C.P., 2012. Evidence of nitrogen fixation in lodgepole pine inoculated with diazotrophic Paenibacillus polymyxa. Canadian Journal of Botany 90, 891−896.

Baldrian, P., Kolařík, M., Stursová, M., Kopecký, J., Valášková, V., Větrovský, T., Zifčáková, L., Snajdr, J., Rídl, J., Vlček, C., Voříšková, J., Tursová, M.Š., Kopeck, J., Valášková, V., Větrovsk, T., Ifčáková, L.Ž., Najdr, J.Š., Rídl, J., Vlček, Č.E., Voříšková, J., 2012. Active and total microbial communities in forest soil are largely different and highly stratified during decomposition. The ISME Journal 6, 248−258.

Bardgett, R.D., Hobbs, P.J., Frostegård, Å., 1996. Changes in soil fungal:bacterial biomass ratios following reductions in the intensity of management of an upland grassland. Biology and Fertility of Soils 22, 261−264.

Bastida, F., Torres, I.F., Andrés-Abellán, M., Baldrian, P., López-Mondéjar, R., Větrovský, T., Richnow, H.H., Starke, R., Ondoño, S., García, C., López-Serrano, F.R., Jehmlich, N., 2017. Differential sensitivity of total and active soil microbial communities to drought and forest management. Global Change Biology 23, 4185−4203.

Bayranvand, M., Kooch, Y., Rey, A., 2017. Earthworm population and microbial activity temporal dynamics in a Caspian Hyrcanian mixed forest. European Journal of Forest Research 136, 447−456.

Beare, M.H., Neely, C.L., Coleman, D.C., Hargrove, W.L., 1990. A substrate induced respiration (SIR) method for measurement of fungal and bacterial biomass on plant residues. Soil Biology and Biochemistry 22 (5), 585−594.

Beatty, S.W., Stone, E.L., 1986. The variety of soil microsites created by tree falls. Canadian Journal of Forest Research 16, 539−548.

Begum, F., Bajracharya, R.M., Sitaula, B.K., Sharma, S., Ali, S., Ali, H., 2014. Seasonal dynamics and land use effect on soil microarthropod communities in the Mid-hills of Nepal, 5, pp. 114−123.

Berg, M.P., Kniese, J.P., Verhoef, H.A., 1998. Dynamics and stratification of bacteria and fungi in the organic layers of a Scots pine forest soil. Biology and Fertility of Soils 26, 313–322.
Binkley, D., Cromack, K.J., Baker, D.D., 1994. Nitrogen fixation by red alder: biology, rates, and controls. Pages 57–72. In: Hibbs, D.E., DeBell, D.S., Tarrant, R.F. (Eds.), The Biology and Management of Red Alder. Oregon State University Press, Corvallis, OR.
Bisbing, S., Alaback, P.B., DeLuca, T.H., 2010. Carbon storage in old-growth and second growth fire-dependent western larch (Larix occidentalis Nutt.) forests of the Inland Northwest, USA. Forest Ecology and Management 259, 1041–1049.
Bischoff, N., Mikutta, R., Shibistova, O., Puzanov, A., Reichert, E., Silanteva, M., Grebennikova, A., Schaarschmidt, F., Heinicke, S., Guggenberger, G., 2016. Land-use change under different climatic conditions: consequences for organic matter and microbial communities in Siberian steppe soils. Agriculture, Ecosystems & Environment 235, 253–264.
Blagodatskaya, E., Kuzyakov, Y., 2013. Active microorganisms in soil: critical review of estimation criteria and approaches. Soil Biology and Biochemistry 192–211 (Pergamon).
Blaxter, M.L., De Ley, P., Garey, J.R., Liu, L.X., Scheldeman, P., Vierstraete, A., Vanfleteren, J.R., Mackey, L.Y., Dorris, M., Frisse, L.M., Vida, J.T., Thomas, W.K., 1998. A molecular evolutionary framework for the phylum Nematoda. Nature 392, 71.
Bligh, E.G., Dyer, W.J., 1959. A rapid method of total lipid extraction and purification. Canadian Journal of Biochemistry and Physiology 37, 911–917.
Boby, L.A., Schuur, E.A.G., Mack, M., Verbyla, D.L., Johnstone, J.F., 2010. Quantifying fire severity, carbon, and nitrogen emissions in Alaska's boreal forest. Ecological Applications 20, 1633–1647.
Bohlen, P.J., Pelletier, D.M., Groffman, P.M., Fahey, T.J., Fisk, M.C., 2004. Influence of earthworm invasion on redistribution and retention of soil carbon and nitrogen in northern temperate forests. Ecosystems 7, 13–27.
Bokhorst, S., Wardle, D.A., Nilsson, M.C., Gundale, M.J., 2014. Impact of understory mosses and dwarf shrubs on soil micro-arthropods in a boreal forest chronosequence. Plant and Soil 379, 121–133.
Bongers, T., 1990. The maturity index: an ecological measure of environmental disturbance based on nematode species composition. October 83, 14–19.
Bormann, B.T., Homann, P.S., Darbyshire, R.L., Morrissette, B.A., 2008. Intense forest wildfire sharply reduces mineral soil C and N: the first direct evidence. Canadian Journal of Forest Research 38, 2771–2783.
Bormann, B.T., Sidle, R.C., 1990. Changes in productivity and distribution of nutrients in a chronosequence at Glacier Bay National Park, Alaska. Journal of Ecology 78, 561–578.
Boyle, J.R., 2005. Forest soils. In: Hillel, D. (Ed.), Encyclopedia of Soils in the Environment. Elsevier, New York, pp. 73–79.
Bücking, H., Liepold, E., Ambilwade, P., 2012. The role of the mycorrhizal symbiosis in nutrient uptake of plants and the regulatory mechanisms underlying these transport processes. IntechOpen. In: Dhal, N.K., Sahu, S.C. (Eds.), Plant Science. InTech Open, London. https://doi.org/10.5772/52570.
Buma, B., Bisbing, S., Krapek, J., Wright, G., 2017. A foundation of ecology rediscovered: 100 years of succession on the William S. Cooper plots in Glacier Bay, Alaska. Ecology 98, 1513–1523.
Buol, S.W., Southard, R.J., Graham, R.C., McDaniel, P.A., 2003. Soil Genesis and Classification. Iowa State Press, Ames, IA.
Burgoyne, T.A., 2006. Free-living Nitrogen-Fixation in Pondeosa pine/Douglas-fir Forests of Western Montana. Masters Thesis. The University of Montana, Missoula.
Butenko, K.O., Gongalsky, K.B., Korobushkin, D.I., Ekschmitt, K., Zaitsev, A.S., 2017. Forest fires alter the trophic structure of soil nematode communities. Soil Biology and Biochemistry 109, 107–117.
Carcaillet, C., Bergman, I., Delorme, S.E., Hörnberg, G., Zackrisson, O., 2007. Long-term fire frequency not linked to prehistoric occupations in northern Swedish boreal forest. Ecology 88, 465–477.

Carrino-Kyker, S.R., Kluber, L.A., Coyle, K.P., Burke, D.J., 2017. Detection of phosphate transporter genes from arbuscular mycorrhizal fungi in mature tree roots under experimental soil pH manipulation. Symbiosis 72, 123−133.

Chan, K.Y., 2001. An overview of some tillage impacts on earthworm population abundance and diversity — implications for functioning in soils. Soil and Tillage Research 57, 179−191.

Chapin, F.S., Walker, L.R., Fastie, C.L., Sharman, L.C., 1994. Mechanisms of primary succession following deglaciation at Glacier Bay, Alaska. Ecological Monographs 64, 149−175.

Chen, H., Hicks, W., 2003. High asymbiotic N_2 fixation rates in woody roots after six years of decomposition: controls and implications. Basic and Applied Ecology 4, 479−486.

Chodak, M., Klimek, B., Niklińska, M., 2016. Composition and activity of soil microbial communities in different types of temperate forests. Biology and Fertility of Soils 52, 1093−1104.

Cleveland, C.C., Townsend, A.R., Schimel, D.S., Fisher, H., Howarth, R.H., Hedin, L.O., Perakis, S.S., Latty, E.F., Von Fischer, J.C., Elseroad, A., Wasson, M.F., 1999. Global patterns of terrestrial biological nitrogen (N2) fixation. Global Biogeochemical Cycles 13, 623−645.

Coleman, D.C., Wall, D.H., 2007. Fauna: the engine for microbial activity and transport. In: Paul, E.A. (Ed.), Soil Microbiology, Ecology, and Biochemistry. Elsevier, San Franscisco, p. 532.

Coleman, D.C., Wall, D.H., 2015. Soil fauna: occurrence, biodiversity, and roles in ecosystem function. Soil Microbiology, Ecology and Biochemistry 111−149.

Colin, Y., Nicolitch, O., Turpault, M.-P., Uroz, S., 2017. Mineral types and tree species determine the functional and taxonomic structures of forest soil bacterial communities. Applied and Environmental Microbiology 83 e02684-02616.

Cooper, W.S., 1923. The recent ecological history of Glacier Bay, Alaska: the interglacial forests of Glacier Bay. Ecology 4, 93−128.

Cordero, I., Ruiz-Díez, B., Balaguer, L., Richter, A., Pueyo, J.J., Rincón, A., 2017. Rhizospheric microbial community of Caesalpinia spinosa (Mol.) Kuntze in conserved and deforested zones of the Atiquipa fog forest in Peru. Applied Soil Ecology 114, 132−141.

Corrales, A., Turner, B.L., Tedersoo, L., 2017. Nitrogen addition alters ectomycorrhizal fungal communities and soil enzyme activities in a tropical montane forest. Fungal Ecology 27, 14−23.

Crittenden, P.D., Kershaw, K.A., 1978. Discovering the role of lichens in the nitrogen cycle in boreal-Arctic ecosystems. The Bryologist 81, 258−267.

Cutler, N.A., Arróniz-Crespo, M., Street, L.E., Jones, D.L., Chaput, D.L., DeLuca, T.H., 2017. Long-term recovery of microbial communities in the boreal bryosphere following fire disturbance. Microbial Ecology 73, 75−90.

Damon, C., Lehembre, F.d. r., Oger-Desfeux, C., Luis, P., Ranger, J., Fraissinet-Tachet, L., Marmeisse, R., 2012. Metatranscriptomics reveals the diversity of genes expressed by eukaryotes in forest soils. PLoS One 7.

Das Gupta, S., DeLuca, T.H., 2012. Short-term changes in belowground C, N stocks in recently clear felled Sitka spruce plantations on podzolic soils of North Wales. Forest Ecology and Management 281, 48−58.

Davidson, E.A., Janssens, I.A., 2006. Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. Nature 440, 165.

De Long, J.R., Dorrepaal, E., Kardol, P., Nilsson, M.-C., Teuber, L.M., Wardle, D.A., 2016. Contrasting responses of soil microbial and nematode communities to warming and plant functional group removal across a post-fire boreal forest successional gradient. Ecosystems 19, 339−355.

DeGrood, S.H., Claassen, V.P., Scow, K.M., 2005. Microbial community composition on native and drastically disturbed serpentine soils. Soil Biology and Biochemistry 37, 1427−1435.

DeLuca, T.H., Aplet, G.H., 2008. Charcoal and carbon storage in forest soils of the Rocky Mountain West. Frontiers in Ecology and the Environment 6, 1−7.

DeLuca, T.H., Archer, V., 2009. Forest soil quality standards should be quantifiable. Journal of Soil and Water Conservation 26, 117−123.

DeLuca, T.H., Zackrisson, O., Nilsson, M.-C., Gundale, M.J., 2008. Ecosystem feedbacks and nitrogen fixation in boreal forests. Science 320, 1181.

DeLuca, T.H., Zackrisson, O., Nilsson, M.-C., Sellstedt, A., 2002. Quantifying nitrogen-fixation in feather moss carpets of boreal forests. Nature 419, 917−920.

Doran, J.W., Zeiss, M.R., 2000. Soil health and sustainability: managing the biotic component of soil quality. Applied Soil Ecology 15, 3−11.

Doty, S.L., Sher, A.W., Fleck, N.D., Khorasani, M., Bumgarner, R.E., Khan, Z., Ko, A.K.W., Kim, S.H., DeLuca, T.H., 2016. Variable nitrogen fixation in wild populus. PLoS One 11, e0155979.

Edmonds, R.L., 1990. Organic matter decomposition in western United States forests. In: Harvey, A.E., Neuenschwander, L.F. (Eds.), Proceedings— Management and Productivity of Western-Montane Forest Soils (GTR INT-280). USDA Forest Service, Intermountain Research Station, pp. 116−128.

Edwards, C.A. (Ed.), 2004. Earthworm Ecology, second ed. CRC Press, New York.

Fahey, T.J., 1992. Mycorrhiza in forest ecosystems. Mycorrhiza 1, 83−89.

Ferrenberg, S., Tucker, C.L., Reed, S.C., 2017. Biological soil crusts: diminutive communities of potential global importance. Frontiers in Ecology and the Environment 15, 160−167.

Fierer, N., Jackson, R.B., 2006. The diversity and biogeography of soil bacterial communities. Proceedings of the National Academy of Sciences of the United States of America 103, 626−631.

Fierer, N., Schimel, J.P., Holden, P.A., 2003. Influence of drying-rewetting frequency on soil bacterial community structure. Microbial Ecology 45, 63−71.

Finlay, R.D., 2007. Ecological aspects of mycorrhizal symbiosis: with special emphasis on the functional diversity of interactions involving the extraradical mycelium. Journal of Experimental Botany 59, 1115−1126.

Finlay, R.D., 2008. Ecological aspects of mycorrhizal symbiosis: with special emphasis on the functional diversity of interactions involving the extraradical mycelium. Journal of experimental botany 59 (5), 1115−1126.

Fisher, R.F., Binkley, D., 2000. Ecology and Management of Forest Soils, third ed. John Wiley and Sons, New York, USA.

Fisk, M.C., Yavitt, J.B., Sherman, R.E., Bohlen, P.J., Groffman, P.M., Fahey, T.J., Fisk, M.C., Yavitt, J.B., Sherman, R.E., Bohlen, P.J., Maerz, J.C., 2015. Earthworms increase soil microbial biomass carrying capacity and nitrogen retention in northern hardwood forests. Soil Biology and Biochemistry 87, 51−58.

Foissner, W., 1999. Soil protozoa as bioindicators: pros and cons, methods, diversity, representative examples. Agriculture, Ecosystems & Environment 74, 95−112.

Frostegård, A., Tunlid, A., Bååth, E., 1993. Phospholipid fatty acid composition, biomass, and activity of microbial communities from two soil types experimentally exposed to different heavy metals. Applied and Environmental Microbiology 59, 3605−3617.

Frostegård, Å., Tunlid, A., Bååth, E., 2010. Use and misuse of PLFA measurements in soils. Soil Biology and Biochemistry 43, 1621−1625.

Gartzia-Bengoetxea, N., Kandeler, E., Martínez De Arano, I., Arias-González, A., 2016. Soil microbial functional activity is governed by a combination of tree species composition and soil properties in temperate forests. Applied Soil Ecology 100, 57−64.

Goodroad, L.L., Keeney, D.R., 1984. Nitrous emission from forest, marsh, and prairie ecosystems. Journal of Environmental Quality 13, 448−452.

Gundale, M.J., DeLuca, T.H., Feidler, C.E., Ramsey, P.W., Harrington, M.G., Gannon, J.E., 2005. Restoration treatments in a Montana ponderosa pine forest: effects on soil physical, chemical and biological properties. Forest Ecology and Management 213, 25−38.

Gundale, M.J., DeLuca, T.H., Nordin, A., 2011. Bryophytes attenuate anthropogenic nitrogen inputs in boreal forests. Global Change Biology 17, 2743−2753.

Gundale, M.J., Jolly, W.M., DeLuca, T.H., 2006a. The susceptability of a northern hardwood forest to exotic earthworm invasion. Conservation Biology 19, 1075−1083.

Gundale, M.J., Metlen, K.L., Fiedler, C.E., DeLuca, T.H., 2006b. Spatial nitrogen heterogeneity increases diversity following restoration in a ponderosa pine forest, Montana. Ecological Applications 16, 479−489.

Gundale, M.J., Nilsson, M.-C.M.C.M.-C., Pluchon, N., Wardle, D.A., 2015. The effect of biochar management on soil and plant community properties in a boreal forest. GCB Bioenergy 8, 777−789.

Gunina, A., Smith, A.R., Godbold, D.L., Jones, D.L., Kuzyakov, Y., 2017. Response of soil microbial community to afforestation with pure and mixed species. Plant and Soil 412, 357−368.

Gunn, A., 1992. The use of mustard to estimate earthworm populations. Pedobiologia 36, 65−67.

Hagenbo, A., Clemmensen, K.E., Finlay, R.D., Kyaschenko, J., Lindahl, B.D., Fransson, P., Ekblad, A., 2017. Changes in turnover rather than production regulate biomass of ectomycorrhizal fungal mycelium across a *Pinus sylvestris* chronosequence. New Phytologist 214, 424−431.

Harmon, M.E., Ferrell, W.K., Franklin, J.F., 1990. Effects on carbon storage of conversion of old-growth forests to young forests. Science 247, 699−702.

Hart, S.C., DeLuca, T.H., Newman, G.S., MacKenzie, M.D., Boyle, S.I., 2005. Post-fire vegetative dynamics as drivers of microbial community structure and function in forest soils. Forest Ecology and Management 220, 166−184.

Hasegawa, M., Okabe, K., 2017. Assessment of the effects of soil and the site environment on collembolan community structure in deciduous forest and coniferous plantations using soil monolith transfer. European Journal of Soil Biology 81, 11−18.

Helmberger, M.S., Shields, E.J., Wickings, K.G., 2017. Ecology of belowground biological control: entomopathogenic nematode interactions with soil biota. Applied Soil Ecology 121, 201−213.

Hewitt, R.E., Chapin, F.S., Hollingsworth, T.N., Taylor, D.L., 2017. The potential for mycobiont sharing between shrubs and seedlings to facilitate tree establishment after wildfire at Alaska arctic treeline. Molecular Ecology 26, 3826−3838.

Heyward, F., Tissot, A.N., 1936. Some changes in the soil fauna associated with forest fires in the longleaf pine region. Ecology 17, 659−666.

Hill, G.T.T., Mitkowski, N.A.A., Aldrich-Wolfe, L., Emele, L.R.R., Jurkonie, D.D.D., Ficke, A., Maldonado-Ramirez, S., Lynch, S.T.T., Nelson, E.B.B., 2000. Methods for assessing the composition and diversity of soil microbial communities. Applied Soil Ecology 15, 25−36.

Huhta, V., 2007. The role of soil fauna in ecosystems: a historical review. Pedobiologia 50, 489−495.

Huhta, V., Hyvönen, R., Kaasalainen, P., Koskenniemi, A., Muona, J., Mäkelä, I., Sulander, M., Vilkamaa, P., 1986. Soil fauna of Finnish coniferous forests. Annales Zoologici Fennici 23, 345−360.

Jandl, G., Leinweber, P., Schulten, H.R., Ekschmitt, K., 2005. Contribution of primary organic matter to the fatty acid pool in agricultural soils. Soil Biology and Biochemistry 37, 1033−1041.

Jenkins, J.R., Viger, M., Arnold, E.C., Harris, Z.M., Ventura, M., Miglietta, F., Girardin, C., Edwards, R.J., Rumpel, C., Fornasier, F., Zavalloni, C., Tonon, G., Alberti, G., Taylor, G., 2017. Biochar alters the soil microbiome and soil function: results of next-generation amplicon sequencing across Europe. GCB Bioenergy 9, 591−612.

Jenkinson, D.S., Ladd, J.N., 1981. Microbial biomass in soil: measurement and turnover, In: Paul, E.A., Ladd, J.N. (Eds.), Soil Biochemistry, 5, 415−471.

Jenkinson, D.S., Oades, J.M., 1979. A method for measuring adenosine triphosphate in soil. Soil Biology and Biochemistry 11, 193−199.

Johnson, D.W., Murphy, J.D., Susfalk, R.B., Caldwell, T.G., Miller, W.W., Walker, R.F., Powers, R.F., 2005. The effects of wildfire, salvage logging, and post-fire N fixation on the nutrient budgets of a Sierran forest. Forest Ecology and Management 220, 155−165.

Johnston, C.A., 1991. Sediment and nutrient retention by freshwater wetlands: effects on surface water quality. Critical Reviews in Environmental Control 21, 491−565.
Jones, H.G., 1999. The ecology of snow-covered systems: a brief overview of nutrient cycling and life in the cold. Hydrological Processes 13, 2135−2147.
Kallenbach, C.M., Frey, S.D., Grandy, A.S., 2016. Direct evidence for microbial-derived soil organic matter formation and its ecophysiological controls, 7, 13630.
Kandeler, E., 2015. Physiological and biochemical methods for studying soil biota and their functions. In: Paul, E.A. (Ed.), Soil Microbiology, Ecology, and Biochemistry. Academic Press, Cambridge, MA, pp. 187−222.
Keiluweit, M., Gee, K., Denney, A., Fendorf, S., 2018. Anoxic microsites in upland soils dominantly controlled by clay content. Soil Biology and Biochemistry 118, 42−50.
Khlifa, R., Paquette, A., Messier, C., Reich, P.B., Munson, A.D., 2017. Do temperate tree species diversity and identity influence soil microbial community function and composition? Ecology and Evolution 7965−7974.
Klamer, M., Bååth, E., 2004. Estimation of conversion factors for fungal biomass determination in compost using ergosterol and PLFA 18:2ω6,9. Soil Biology and Biochemistry 36, 57−65.
Klavina, D., Pennanen, T., Gaitnieks, T., Velmala, S., Lazdins, A., Lazdina, D., Menkis, A., 2016. The ectomycorrhizal community of conifer stands on peat soils 12 years after fertilization with wood ash. Mycorrhiza 26, 153−160.
Knight, I.T., 2000. Molecular genetic methods for detection and identification of viable but nonculturable microorganisms. In: Nonculturable Microorganisms in the Environment. Springer, US, Boston, MA, pp. 77−85.
Kooch, Y., Haghverdi, K., 2014. Earthworms − good indicators for forest disturbance. Journal of Bioscience and Biotechnology 3, 155−162.
Korobushkin, D.I., Gorbunova, A.Y., Zaitsev, A.S., Gongalsky, K.B., 2017. Trait-specific response of soil macrofauna to forest burning along a macrogeographic gradient. Applied Soil Ecology 112, 97−100.
Lambers, H., Raven, J.A., Shaver, G.R., Smith, S.E., 2008. Plant nutrient-acquisition strategies change with soil age. Trends in Ecology & Evolution 23, 95−103.
Landesman, W.J., Nelson, D.M., Fitzpatrick, M.C., 2014. Soil properties and tree species drive ß-diversity of soil bacterial communities. Soil Biology and Biochemistry 76, 201−209.
Lehmann, J., Kleber, M., 2015. The contentious nature of soil organic matter. Nature 528, 60−68.
Li, Y., Li, Y., Chang, S.X., Liang, X., Qin, H., Chen, J., Xu, Q., 2017. Linking soil fungal community structure and function to soil organic carbon chemical composition in intensively managed subtropical bamboo forests. Soil Biology and Biochemistry 107, 19−31.
Liang, M., Liu, X., Etienne, R.S., Huang, F., Wang, Y., Yu, S., 2015. Arbuscular mycorrhizal fungi counteract the Janzen-Connell effect of soil pathogens. Ecology 96, 562−574.
Lindo, Z., Gonzalez, A., 2010. The bryosphere: an integral and influential component of the Earth's biosphere. Ecosystems. https://doi.org/10.1007/s10021-010-9336-3.
Lindo, Z., Nilsson, M.-C., Gundale, M.J., 2013. Bryophyte-cyanobacteria associations as regulators of the northern latitude carbon balance in response to global change. Global Change Biology 19, 2022−2035.
Lynn, T.M., Liu, Q., Hu, Y., Yuan, H., Wu, X., Khai, A.A., Wu, J., Ge, T., 2017. Influence of land use on bacterial and archaeal diversity and community structures in three natural ecosystems and one agricultural soil. Archives of Microbiology 199, 711−721.
Malmström, A., 2010. The importance of measuring fire severity—evidence from microarthropod studies. Forest Ecology and Management 260, 62−70.
Marichal, R., Grimaldi, M., Feijoo, M.A., Oszwald, J., Praxedes, C., Ruiz Cobo, D.H., del Pilar Hurtado, M., Desjardins, T., da Silva Junior, M.L., da Silva Costa, L.G., Miranda, I.S., Delgado Oliveira, M.N., Brown, G.G., Tsélouiko, S., Martins, M.B., Decaëns, T., Velasquez, E., Lavelle, P., 2014. Soil macroinvertebrate communities and ecosystem services in deforested landscapes of Amazonia. Applied Soil Ecology 83, 177−185.

Martins da Silva, P., Carvalho, F., Dirilgen, T., Stone, D., Creamer, R., Bolger, T., Sousa, J.P., 2016. Traits of collembolan life-form indicate land use types and soil properties across an European transect. Applied Soil Ecology 97, 69–77.

Massman, W., Sommerfeld, R., Zeller, K., Hehn, T.E.D., Hudnell, L., Rochelle, S., 1995. CO2 flux through a Wyoming seasonal snowpack: diffusional and pressure pumping effects. In: Tonnessen, K., Williams, M., Tranter, M. (Eds.), Biogeochemistry of Seasonally Snow-Covered Catchments. IAHS Publication, pp. 71–80.

Matlack, G., 2001. Factors determining the distribution of soil nematodes in a commercial forest landscape. Forest Ecology and Management 146, 129–143.

Matzek, V., Vitousek, P.M., 2003. Nitrogen fixation in bryophytes, lichens, and decaying wood along a soil-age gradient in Hawaiian montane rainforest. Biotropica 35, 12–19.

McClain, M.E., Boyer, E.W., Dent, C.L., Gergel, S.E., Grimm, N.B., Groffman, P.M., Hart, S.C., Harvey, J.W., Johnston, C.A., Mayorga, E., McDowell, W.H., Pinay, G., 2003. Biogeochemical hot spots and hot moments at the interface of terrestrial and aquatic ecosystems. Ecosystems 6, 301–312.

Meier, I.C., Finzi, A.C., Phillips, R.P., 2017. Root exudates increase N availability by stimulating microbial turnover of fast-cycling N pools. Soil Biology and Biochemistry 106, 119–128.

Mikkelson, K.M., Lozupone, C.A., Sharp, J.O., 2016. Altered edaphic parameters couple to shifts in terrestrial bacterial community structure associated with insect-induced tree mortality. Soil Biology and Biochemistry 95, 19–29.

Mohammadi, S.A., Prasanna, B.M., 2003. Analysis of genetic diversity in crop plants—salient statistical tools and considerations. Crop Science 43, 1235.

Mohan, J.E., Cowden, C.C., Baas, P., Dawadi, A., Frankson, P.T., Helmick, K., Hughes, E., Khan, S., Lang, A., Machmuller, M., Taylor, M., Witt, C.A., 2014. Mycorrhizal fungi mediation of terrestrial ecosystem responses to global change: mini-review. Fungal Ecology 10, 3–19.

Moore-Kucera, J., Dick, R.P., 2008. PLFA profiling of microbial community structure and seasonal shifts in soils of a douglas-fir chronosequence. Microbial Ecology 55, 500–511.

Muyzer, G., Smalla, K., 1998. Application of denaturing gradient gel electrophoresis (DGGE) and temperature gradient gel electrophoresis (TGGE) in microbial ecology. Antonie Van Leeuwenhoek 127–141.

Nadkarni, N.M., 1984. Biomass and mineral capital of epiphytes in an Acer macrophyllum community of a temperate moist coniferous forest, Olympic Peninsula, Washington State. Canadian Journal of Botany 62, 2223–2228.

Nave, L.E., Vance, E.D., Swanston, C.W., Curtis, P.S., 2010. Harvest impacts on soil carbon storage in temperate forests. Forest Ecology and Management 259, 857–866.

Neary, D.G., Klopatek, C.C., DeBano, L.F., Ffolliott, P.F., 1999. Fire effects on belowground sustainability: a review and synthesis. Forest Ecology and Management 122, 51–71.

Newland, J.A., DeLuca, T.H., 2000. Influence of fire on native nitrogen-fixing plants and soil nitrogen status in ponderosa pine - Douglas-fir forests in western Montana. Can. J. For. Res. 30, 274–282.

NRC, N.R.C., 1993. Soil and Water Quality. National Academy Press, Washington, DC.

Oliverio, A.M., Bradford, M.A., Fierer, N., 2017. Identifying the microbial taxa that consistently respond to soil warming across time and space. Global Change Biology 23, 2117–2129.

Parkin, T.B., 1987. Soil microsites as a source of denitrification variability. Soil Science Society of America Journal 51, 1194–1199.

Paul, E.A., 2015. Soil Microbiology and Biochemistry, fourth ed. Elsevier, London.

Perakis, S.S., Matkins, J.J., Hibbs, D.E., 2012. N2-fixing red alder indirectly accelerates ecosystem nitrogen cycling. Ecosystems 15, 1182–1193.

Perakis, S.S., Tepley, A.J., Compton, J.E., 2015. Disturbance and topography shape nitrogen availability and d15N over long-term forest succession. Ecosystems 18, 573–588.

Petersen, H., Luxton, M., 1982. A comparative analysis of soil fauna populations and their role in decomposition processes. Oikos 39, 288−388.

Peterson, C.J., Carson, W.P., McCarthy, B.C., Pickett, S.T.A., 1990. Microsite variation and soil dynamics within newly created treefall Pits and mounds. Oikos 58, 39−46.

Pike, L.H., Rydell, R.A., Denison, W.C., 1977. A 400-year-old Douglas fir tree and its epiphytes: biomass, surface area, and their distributions. Canadian Journal of Forest Research 7, 680−699.

Ping, C.L., Michaleson, G.J., Kane, E.S., Packee, E.C., Stiles, C.A., Swanson, D.K., Zaman, N.D., 2010. Carbon stores and biogeochemical properties of soils under black spruce forest, Alaska. Soil Science Society of America Journal 74, 969−978.

Pingree, M.R.A.A., DeLuca, E.E., Schwartz, D.T., DeLuca, T.H., 2016. Adsorption capacity of wildfire-produced charcoal from Pacific Northwest forests. Geoderma 283, 68−77.

Pluchon, N., Vincent, A.G., Gundale, M.J., Nilsson, M.-C., Kardol, P., Wardle, D.A., 2016. The impact of charcoal and soil mixtures on decomposition and soil microbial communities in boreal forest. Applied Soil Ecology 99, 40−50.

Ren, C., Zhao, F., Shi, Z., Chen, J., Han, X., 2017. Differential responses of soil microbial biomass and carbon-degrading enzyme activities to altered precipitation. Soil Biology and Biochemistry 115, 1−10.

Rinnan, R., MichelsenI, A., Bååth, E., Jonassen, S., 2007. Fifteen years of climate change manipulations alter soil microbial communities in a subarctic heath ecosystem. Global Change Biology 13, 28−39.

Rosling, A., Midgley, M.G., Cheeke, T., Urbina, H., Fransson, P., Phillips, R.P., 2016. Phosphorus cycling in deciduous forest soil differs between stands dominated by ecto- and arbuscular mycorrhizal trees. New Phytologist 209, 1184−1195.

Rousk, K., Jones, D.L., Deluca, T.H., 2013. Moss-cyanobacteria associations as biogenic sources of nitrogen in boreal forest ecosystems. Frontiers in Microbiology 4, 150.

Saetre, P., 1999. Spatial patterns of ground vegetation, soil microbial biomass and activity in a mixed spruce-birch stand. Ecography 22, 183−192.

Sahrawat, K.L., 2003. Organic matter accumulation in submerged soils. Advances in Agronomy 81, 169−201.

Salmon, S., Ponge, J.F., Gachet, S., Deharveng, L., Lefebvre, N., Delabrosse, F., 2014. Linking species, traits and habitat characteristics of Collembola at European scale. Soil Biology and Biochemistry 75, 73−85.

Schimel, J., Becerra, C.A., Blankinship, J., 2017. Estimating decay dynamics for enzyme activities in soils from different ecosystems. Soil Biology and Biochemistry 114, 5−11.

Schmidt, S.K., Porazinska, D., Concienne, B.L., Darcy, J.L., King, A.J., Nemergut, D.R., 2016. Biogeochemical stoichiometry reveals P and N limitation across the post-glacial landscape of Denali National Park. Alaska. Ecosystems 19, 1164−1177.

Serna-Chavez, H.M., Fierer, N., Van Bodegom, P.M., 2013. Global drivers and patterns of microbial abundance in soil. Global Ecology and Biogeography 22, 1162−1172.

Sexstone, A.J., Revsbech, N.P., Parkin, T.B., Tiedje, J.M., 1985. Direct measurement of oxygen profiles and denitrification rates in soil aggregates. Soil Science Society of America Journal 49, 645−651.

Shantz, A., Lemoine, N.P., Burkepile, D.E., 2016. Nutrient loading alters the performance of key nutrient exchange mutualisms. Ecology Letters 19, 20−28.

Shaw, C.H., Lundkvist, H., Moldenke, A., Boyle, J.R., 1991. The relationships of soil fauna to long-term forest production in temperate and boreal ecosystems: processes and research strategies.

Simard, S.W., Durall, D.M., 2004. Mycorrhizal networks: a review of their extent, function, and importance. Canadian Journal of Botany 82, 1140−1165.

Singh, B.K., Millard, P., Whiteley, A.S., Murrell, J.C., 2004. Unravelling rhizosphere−microbial interactions: opportunities and limitations. Trends in Microbiology 12, 386−393.

Singh, J., Singh, S., Vig, A.P., 2016. Extraction of earthworm from soil by different sampling methods: a review. Environment, Development and Sustainability 18, 1521−1539.

Sinsabaugh, R.L., Antibus, R.K., Linkins, A.E., 1991. An enzymic approach to the analysis of microbial activity during plant litter decomposition. Agriculture, Ecosystems & Environment 34, 43−54.

Šnajdr, J., Valášková, V., Merhautová, V., Herinková, J., Cajthaml, T., Baldrian, P., 2008. Spatial variability of enzyme activities and microbial biomass in the upper layers of Quercus petraea forest soil. Soil Biology and Biochemistry 40, 2068−2075.

Sorensen, P.L., Jonasson, S., Michelsen, A., 2004. Nitrogen fixation, denitrification, and ecosystem nitrogen pools in relation to vegetation development in the subarctic. Arctic Antarctic and Alpine Research 38, 263−272.

Spribille, T., Tuovinen, V., Resl, P., Vanderpool, D., Wolinski, H., Aime, M.C., Schneider, K., Stabentheiner, E., Toome-Heller, M., Thor, G., Mayrhofer, H., Johannesson, H., McCutcheon, J.P., 2016. Basidiomycete yeasts in the cortex of ascomycete macrolichens. Science 353, 488−492.

Stark, N., 1972. Nutrient cycling pathways and litter fungi. BioScience 22, 355−360.

Stevenson, F.J., 1994. Humus Chemistry. Wiley, New York.

Strickland, M.S., Callaham, M.A., Gardiner, E.S., Stanturf, J.A., Leff, J.W., Fierer, N., Bradford, M.A., 2017. Response of soil microbial community composition and function to a bottomland forest restoration intensity gradient. Applied Soil Ecology 119, 317−326.

Strong, D.R., Kaya, H.K., Whipple, A.V., Child, A.L., Kraig, S., Bondonno, M., Dyer, K., Maron, J.L., 1996. Entomopathogenic nematodes: natural enemies of root-feeding caterpillars on bush lupine. Oecologia 108, 167−173.

Sun, T., Dong, L., Wang, Z., Lü, X., Mao, Z., 2016. Effects of long-term nitrogen deposition on fine root decomposition and its extracellular enzyme activities in temperate forests. Soil Biology and Biochemistry 93, 50−59.

Tabatabai, M.A., 1994. Soil enzymes. In: Methods of Soil Analysis: Part 2 - Microbiological and Biochemical Properties. Soil Science Society of America, pp. 775−833.

Talbot, J.M., Allison, S.D., Treseder, K.K., 2008. Decomposers in disguise: mycorrhizal fungi as regulators of soil C dynamics in ecosystems under global change. Functional Ecology 22, 955−963.

Tarnocai, C., Schuur, E.A.G., Kuhry, P., Mazhitova, G., Zimov, S., 2009. Soil organic carbon pools in the northern circumpolar permafrost region. Global Biogeochemical Cycles 23, GB2023.

Taylor, A.R., Schröter, D., Pflug, A., Wolters, V., 2004. Response of different decomposer communities to the manipulation of moisture availability: potential effects of changing precipitation patterns. Global Change Biology 10, 1313−1324.

Thies, J.E., 2015. Molecular approaches to studying the soil biota. In: Paul, E.A. (Ed.), Soil Microbiology, Ecology and Biochemistry. Elsevier, pp. 151−186.

Trumbore, S.E., 2000. Age of soil organic matter and soil respiration: radiocarbon constraints on belowground C dynamics. Ecological Applications 10, 399−411.

Tucker, C.L., Tamang, S., Pendall, E., Ogle, K., 2016. Shallow snowpack inhibits soil respiration in sagebrush steppe through multiple biotic and abiotic mechanisms. Ecosphere 7, e01297.

Tullgren, A., 1918. Ein sehr einfacher Ausleseapparat Fur terricole Tierformen. Zeitschrift Fur Angewante Entomologie 4, 149−150.

Turetsky, M.R., Bond-Lamberty, B., Euskirchen, E., Talbot, J., Frolking, S., McGuire, A.D., Tuittila, E.-S., 2012. The resilience and functional role of moss in boreal and arctic ecosystems. New Phytologist 196, 49−67.

van der Lee, G.E.M., de Winder, B., Bouten, W., Tietema, A., 1999. Anoxic microsites in Douglas fir litter. Soil Biology and Biochemistry 31, 1295−1301.

van Straalen, N.M., 1998. Evaluation of bioindicator systems derived from soil arthropod communities. Applied Soil Ecology 9, 429−437.

Veresoglou, S.D., Halley, J.M., Rillig, M.C., 2015. Extinction risk of soil biota. Nature Communications 6, 8862.

Vieira, F.C.S., Nahas, E., 2005. Comparison of microbial numbers in soils by using various culture media and temperatures. Microbiological Research 160, 197−202.

Vitousek, P.M., Cassman, K., Cleveland, C., Crews, T., Grimm, N.B., Howarth, R.W., Marino, R., Martinelli, L., Rastetter, E.B., Sprent, J.I., 2002. Towards an ecological understanding of biological nitrogen fixation. Biogeochemistry 57/58, 1−45.

Wang, Z., Gerstein, M., Snyder, M., 2009. RNA-Seq: a revolutionary tool for transcriptomics. Nature Reviews Genetics 10, 57−63.

Wardle, D.A., 1992. A comparative assessment of factors which influence microbial biomass carbon and nitrogen levels in soil. Biological Reviews 67, 321−358.

Wardle, D.A., 2002. Communities and Ecosystems: Linking the Aboveground and Belowground Components. Princeton University Press.

Wardle, D.A., Verhoef, H.A., Clarholm, M., 1998. Trophic relationships in the soil microfood-web: predicting the responses to a changing global environment. Global Change Biology 4, 713−727.

Whelan, P., Bach, A.J., 2016. Retreating glaciers, incipient soils, emerging forests: 100 years of landscape change on Mount Baker, Washington, USA. Annals of the Association of American Geographers. https://doi.org/10.1080/24694452.2016.1235480.

Whitman, W.B., Coleman, D.C., Wiebe, W.J., 1998. Prokaryotes: the unseen majority. Proceedings of the National Academy of Sciences 95, 6578−6583.

Wickland, K.P., Neff, J.C., 2008. Decomposition of soil organic matter from boreal black spruce forest: environmental and chemical controls. Biogeochemistry 87, 29−47.

Wikars, L.-O., Schimmel, J., 2001. Immediate effects of fire-severity on soil invertebrates in cut and uncut pine forests. Forest Ecology and Management 141, 189−200.

Wilhelm, R.C., Cardenas, E., Maas, K.R., Leung, H., Mcneil, L., Berch, S., Chapman, W., Hope, G., Kranabetter, J., Dubé, S., Busse, M., Fleming, R., Hazlett, P., Webster, K.L., Morris, D., Scott, A., Mohn, W.W., 2017. Biogeography and Organic Matter Removal Shape Long-Term Effects of Timber Harvesting on Forest Soil Microbial Communities. Nature Publishing Group.

Xia, M., Talhelm, A.F., Pregitzer, K.S., 2017. Long-term simulated atmospheric nitrogen deposition alters leaf and fine root decomposition. Ecosystems 1−14.

Xu, X., Thornton, P.E., Post, W.M., 2013. A global analysis of soil microbial biomass carbon, nitrogen and phosphorus in terrestrial ecosystems. Global Ecology and Biogeography 22, 737−749.

Yavitt, J.B., Fahey, T.J., Simmons, J.A., 1995. Methane and carbon dioxide dynamics in a northern hardwood ecosystem. Soil Science Society of America Journal 59, 796−804.

Zackrisson, O., DeLuca, T.H., Gentili, F., Sellstedt, A., Jäderlund, A., 2009. Nitrogen fixation in mixed *Hylocomium splendens* moss communities. Oecologia 160, 309−319.

Zackrisson, O., DeLuca, T.H., Nilsson, M.-C., Sellstedt, A., Berglund, L., 2004. Nitrogen fixation increases with successional age in boreal forests. Ecology 85, 3327−3334.

Zaitsev, A.S., Gongalsky, K.B., Persson, T., Bengtsson, J., 2014. Connectivity of litter islands remaining after a fire and unburnt forest determines the recovery of soil fauna. Applied Soil Ecology 83, 101−108.

Zhang, W., Parker, K.M., Luo, Y., Wan, S., Wallace, L.L., Hu, S., 2005. Soil microbial responses to experimental warming and clipping in a tallgrass prairie. Global Change Biology 11, 266−277.

Žifčáková, L., Větrovský, T., Howe, A., Baldrian, P., 2016. Microbial activity in forest soil reflects the changes in ecosystem properties between summer and winter. Environmental Microbiology 18, 288−301.