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Title: *Microbial carbon limitation - the need for integrating microorganisms into our understanding of ecosystem carbon cycling*

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Abstract

Numerous studies have demonstrated that fertilization with nutrients such as nitrogen, phosphorus, and potassium increase plant productivity in both natural and managed ecosystems, demonstrating that primary productivity is nutrient limited in most terrestrial ecosystems. In contrast, it has been demonstrated that heterotrophic microbial communities in soil are primarily limited by organic carbon or energy. While this concept of contrasting limitations, i.e., microbial carbon and plant nutrient limitation, is based on strong evidence that we review in this paper, it is often ignored in discussions of ecosystem response to global environment changes. The plant-centric perspective has equated plant-nutrient limitations with those of whole ecosystems, thereby ignoring the important role of the heterotrophs responsible for soil decomposition in driving ecosystem carbon storage. In order to truly integrate carbon and nutrient cycles in ecosystem science, we must account for the fact that while plant productivity may be nutrient-limited, the secondary productivity by heterotrophic communities is inherently carbon-limited. Ecosystem carbon cycling integrates the independent physiological responses of its individual components, as well as tightly coupled exchanges between autotrophs and heterotrophs. To the extent that the interacting autotrophic and heterotrophic processes are controlled by organisms that are limited by nutrient versus carbon accessibility, respectively, we propose that ecosystems by definition cannot be 'limited' by nutrients or carbon alone. Here, we outline how models aimed at predicting non-steady state ecosystem responses can benefit from dissecting ecosystems into the organismal components and their inherent limitations to better represent plant-microbe interactions in coupled carbon and nutrient models.

Introduction

Industrialization, land use changes, and intensive agriculture have led to globally elevated atmospheric CO_2 levels and to greater availability of nitrogen (N) in many areas, altering the stoichiometry and functioning of natural ecosystems (Peñuelas et al., 2013; Peñuelas et al., 2012). Currently, terrestrial ecosystems take up more CO_2 from the atmosphere through photosynthesis, than is respired back to the atmosphere by autotrophs and heterotrophs. Terrestrial ecosystems globally sequester the equivalent of roughly 30% of the CO_2 that humans emit to the atmosphere (Le Quéré et al., 2017) and thereby mitigate climate warming, yet the future sequestration potential of land is uncertain (Liu et al., 2019; Penuelas et al., 2017). Environmental stoichiometry can be used to explain the differences in carbon and nutrient demands of plants and microorganisms in the soil, rhizosphere and litter layer and meet the grand challenges of the 21st century- to resolve uncertainty in ecosystem responses to non-steady state conditions (UN, 2019). For this to happen, we must recognize the basic concept that microbial carbon limitation in the soil feeds-back to plant nutrient demands from the soil to explain whole ecosystem responses to non-steady state conditions such as elevated CO_2 and N enrichment.

One characteristic of ecosystems that is rarely ever embedded in earth system or land surface models, yet may be crucial for predicting ecosystem responses to climate change, is the the role of nutrient and carbon limitation of plants and soil microorganisms in controling biogeochemical cycles. Our understanding of nutrient limitations to plant growth is well established after centuries of agricultural fertilization experiments focused on increasing crop yields. Recent advances in methods to measure microbial growth responses now provides better evidence that soil heterotrophic microorganisms are primarily limited by carbon, and only secondarily by nutrients. Plants depend on the activity of heterotrophic soil organisms for their nutrient supply and can stimulate heterotrophic decomposition of dead organic matter by providing decomposers with energy-rich substrates (*i.e.* priming). Heterotrophs in turn require plant-derived organic compounds for energy and enhance plant productivity by making nutrients available for uptake. Thus, within natural ecosystems, plants will essentially be nutrient limited, while decomposers in the soil will be carbon limited, and ecosystems as a whole are limited by neither.

This concept of simultaneous plant nutrient limitation and microbial carbon (energy) limitation is contradicting any "ecosystem limitation" by nutrients, as it is currently found in many textbooks. First, ecosystems are not organisms and thus cannot be limited themselves. Second, since ecosystems must be composed of autotrophic and heterotrophic organisms and because autotrophs and heterotrophs are inherently limited by different factors, a limitation of an ecosystem *per se* is not possible. Reports on nitrogen- or phosphorus-limited ecosystems in the scientific literature usually refer to ecosystems in which primary production is either nitrogen or phosphorus limited; such studies thus ignore that heterotrophic organisms play essential roles in nutrient cycling.

Here, we argue that understanding the interaction of heterotrophic and autotrophic communities within ecosystems and its implication for the regulation of ecosystem functioning

and carbon cycling is key to accurately project ecosystem carbon balance in response to nutrient availability and increasing atmospheric CO_2 concentrations. First, we define 'limitation' at the organismal level and provide evidence for microbial carbon limitation. Then we describe the empirical methods for determining microbial carbon limitation and how microbial carbon limitation can help to explain certain ecological phenomena. Finally, we discuss ways of integrating microbial carbon limitation into ecosystem models to improve predictions of ecosystem responses to global change drivers.

Concepts of limitation

While the concept of limitation is a key concept in ecology, it remains poorly defined in many studies, especially in the context of global change. One of the most widely used conceptual models of nutrient limitation is 'Liebig's Law of the Minimum', which states that biomass production is determined by the availability of the scarcest, or most limiting, resource (von Liebig, 1840). This model is based on centuries of agricultural research on fertilization with nitrogen (N), phosphorus (P), and potassium (K) to increase crop yield and has crossed over into ecological theory of how the availability of nutrients in ecosystems limit net primary production. Liebig's law is thus a concept of yield limitation, comparing biomass production of a single species to a situation where all environmental, competition, and resource constraints have been removed. In contrast, 'Blackman limitation' defintes limitation based on growth, rather than yield (Blackman, 1905). This is an important distinction since standing biomass (yield) is often not correlated to growth rate. An alternative model to single nutrient limitation models is the 'Multiple Limitation Hypothesis' (Gleeson & Tilman, 1992; Sperfeld et al., 2012), stating that biomass yield can be limited by more than one nutrient simultaneously, suggesting that nutrient demands of organisms or populations can be adjusted so that nutrients become co-limiting. This can occur for various reasons, such as physiological interactions within an organism (mostly between different resources, such as CO_2 and nutrients), the acquisition of one nutrient being dependent on the availability of another (e.g. nitrogen fixation depending on sufficient phosphorus supply), or uneven distribution of nutrients between species within a given population/community. Thus, additions of multiple nutrients at once can lead to an increase in community biomass because species with different nutrient demands respond to different nutrients in the mix (Saito et al., 2008; Vitousek et al., 2010).

Microbial ecologists recognize that labile carbon, a primary elemental energy source, is most limiting to the growth of heterotrophic soil microorganisms (Demoling et al., 2007; Ekblad & Nordgren, 2002; Hobbie & Hobbie, 2013; Kamble & BÅÅTh, 2018; Spohn & Schleuss, 2019). The carbon limitation to microbial growth is also evident from a stoichiometric point of view. The concept of a threshold element ratio (TER) was introduced to assess the C:N ratio of organisms and resources at which organisms are co-limited by carbon and nitrogen, under the assumption that no other element limits growth (Sterner & Elser, 2002).

$$TER \approx C{:}N_{org} \times \frac{NUE_{sub}}{CUE_{sub}}$$

Where TER can be estimated by multiplying the biomass C:N ratio of the target organism ($C{:}N_{org}$) with the ratio of nitrogen use efficiency (NUE_{sub}) over carbon use efficiency (CUE_{sub}) for a given substrate (Mooshammer et al., 2014a). Carbon and nitrogen use efficiencies are calculated as the partitioning of carbon or nitrogen between anabolic (growth and cellular regeneration) and catabolic processes (mineralization) (REF). Soil microbial biomass exhibits a global average C:N ratios of 8 (Xu et al., 2013), with an average carbon use efficiency of 0.3 (Sinsabaugh et al., 2013) and a nitrogen use efficiency of 0.9 (Mooshammer et al., 2014a; Mooshammer et al., 2014b). Thus, the global average TER of soil microbial biomass is 21. Since soils have an average C:N ratio of 16 (Xu et al., 2013), or even lower in the mineral soil, soil microorganisms are clearly carbon limited. Fresh leaf litter has an average C:N ratio of 53 (Yuan & Chen, 2009), thus microorganisms feeding on fresh leaf litter are instead limited by nitrogen, in this scenario. Similar calculations can also be done with phosphorus, showing the same prevailing carbon limitation in soil and nutrient limitation in litter for microbial community growth (Fanin et al., 2014; Nottingham et al., 2015; Zechmeister-Boltenstern et al., 2015).

Soil microorganisms need carbon to satisfy their energy demands for maintenance (i.e., respiration costs) and for the synthesis of structural molecules to build biomass. However, catabolic and anabolic pathways have divergent stoichiometric demands. For example, while carbon is the main fuel for the energy costs of microbial maintenance, biomass growth has relatively higher nutrient demands due to the synthesis of structural molecules (e.g., nitrogen for protein and enzyme synthesis, phosphorus for DNA and RNA synthesis and for energy storage). Soil microorganisms may therefore modulate their metabolic pathways according to the stoichiometry of substrates available in soil, leading to shifts in carbon use efficiency. This could provide a powerful approach for integrating shifts in microbioal metabolic pathways into models of ecosystem carbon and nutrient exchange.

The stoichiometric argument highlights the fact that heterotrophic carbon consumption by decomposers is fundamentally different from light-driven photosynthetic reactions that drive autotrophic acquisition of carbon from atmospheric CO_2. Nutrient limitations of whole ecosystems do not exist due to the fact that ecosystems are comprised of many organisms with varying physiological constraints and stoichiometric demands (Peñuelas et al., 2019; Sardans et al., 2012; Turner et al., 2018). The direct effect of a nutrient addition on increasing autotrophic growth can, however, indirectly impact heterotrophs that feed on the products of autotrophic activity, although it does not directly affect the heterotrophs. As decomposers degrade soil organic matter and utilize it for their growth, surplus nutrients not needed for microbial growth are mineralized and made available for plant uptake while mineralized carbon is respired to the atmosphere as CO_2 (Hodge et al., 2000; Mooshammer et al., 2014a; Spohn & Kuzyakov, 2013). This excess nutrient release by microorganisms is fundamental to ecosystem functioning (Capek et al., 2018). The fact that plants release an organic carbon surplus for soil microorganisms, and

159 microorganisms provide a nutrient surplus to plants, is a cornerstone property of ecosystem
160 functioning (Figure 1).
161 Unlike the growth of organisms or populations, ecosystem-scale carbon balance cannot
162 be explained by nutrient or carbon limitation concepts alone. Incorporation of nutrient-carbon
163 feedbacks between plants and decomposers with contrasting primary limitations should however
164 be used in models to better represent ecosystem response to elevated CO_2 and nitrogen
165 availability and to understand feedbacks between heterotrophic and autotrophic ecosystem
166 components that may drive carbon storage (Figure 1). As the black box of soil biogeochemistry
167 has opened in the past decades, the fundamental heterotrophic characteristic of carbon limitation
168 can now be leveraged to better understand whole-ecosystem responses to altered resource
169 availability.
170
171 *Empirical methods of determining microbial carbon limitation*
172 Measurements of soil microbial growth responses to carbon and nutrient additions is not
173 straightforward. Traditionally, an elemental limitation has been estimated for plant communities
174 as an increase in a biological process or pool by addition of a nutrient or element (Vitousek et al.,
175 2010). This has been done by direct measurements, e.g. of net primary productivity or
176 aboveground plant biomass (LeBauer & Treseder, 2008), or indirectly, by measuring changes in
177 available nutrients, by measurements of leaf stoichiometry (Hou et al., 2012) or comparison
178 across ecosystems (Vitousek & Farrington, 1997). For soil heterotrophs, resource limitations
179 have typically been estimated by measuring a net change in microbial biomass (standing stock)
180 or a change in respiration (interpreted as microbial activity) after carbon or nutrient amendment.
181 Measurements of net biomass changes have also been done by chloroform fumigation-extraction
182 in response to substrate addition (Vance et al., 1987), direct cell counts (Alexander, 1982),
183 membrane lipid concentrations (Balkwill et al., 1988), or substrate induced respiration methods
184 (Anderson & Domsch, 1978). Standing microbial biomass itself is, however, not an adequate
185 indication if the target question is substrate limitation of microbial growth.
186 Standing biomass indicates whether a certain nutrient addition can change the carrying
187 capacity of a soil, that is the microbial mass that can be supported by a specific soil under
188 specific environmental conditions. The microbial carrying capacity of a soil is dynamic because
189 it can depend on the occurrence and activity of predators (e.g., bacterial grazers or predatory
190 bacteria) or viruses (Fierer, 2017). Growth limitation of microbial communities has traditionally
191 been measured by changes in soil respiration in response to added substrates and nutrients.
192 However, microbial respiration is composed of respiration for maintenance, growth, enzyme
193 production and overflow as well as waste metabolism to overcome stoichiometric imbalances
194 (Manzoni et al., 2012). Therefore, respiration per definition cannot be an adequate metric of the
195 nutrient or carbon limitation of microbial growth (Mori et al., 2018). An increase in respiration
196 with nutrient or carbon additions can also be due to the revitalization of otherwise dormant
197 microorganisms (Blagodatskaya & Kuzyakov, 2013), stimulation of a selected portion of the
198 microbial population (Cleveland et al. 2007, Mori et al., 2018), or priming of native soil organic

matter decomposition (Kuzyakov et al., 2000). More generally, respiration is an estimate for catabolic reactions, while growth should be estimated by a measure for anabolic reaction. Some methods measure growth rates of microbial communities by the incorporation of radiolabeled substrates such as ^{14}C-acetate, ^{14}C-leucine or ^{3}H-thymidine in their respective biopolymers (ergosterol, proteins or nucleic acids, respectively) (Rousk & Bååth, 2011). However, since these substrates contain carbon and in part nitrogen, those methods need to be treated with care, when they are used to assess carbon and nutrient limitations.

Recent technical developments have now made it possible to measure microbial growth directly without adding carbon or nitrogen containing substrates, using ^{18}O-DNA labeling, finally allowing for a more rigorous exploration of what limits soil microbial growth in ecosystems under change (Geyer et al., 2019; Spohn et al., 2016b). This novel ^{18}O-DNA method estimates microbial growth by measuring the synthesis of DNA by the incorporation of ^{18}O from ^{18}O-enriched water into microbial DNA (Spohn et al., 2016a). This, in contrast to traditional methods, allows one to differentiate between new growth (gross growth rates), microbial biomass changes (net growth rates) or standing microbial biomass stocks, and to quantify microbial CUE within a given environment. Using the ^{18}O-DNA method, only investment in new growth (i.e., synthesis of ds-DNA) is assessed, thus investment in other cellular compounds not associated with growth, such as extracellular enzymes or extracellular polymeric substances that are exuded into the environment are not accounted for. Under an assumption of steady state, microbial biomass turnover could be calculated using the ^{18}O-DNA method, however since the microbial pool is not static, we caution this application. Instead, an independent assessment of microbial turnover is necessary to understand whether controls of biomass turnover rates (e.g., microbial death rates, predation, viral lysis, etc.) are limited by the same elements as growth rate, specifically under climate change. The ability to quantify new microbial growth directly and independent of substrate addition, rather than net biomass changes, using the ^{18}O-DNA method represents a new advancement in the field of microbial ecology that can be utilized to test the carbon and nutrient limitation of soil microbial communities.

How carbon limitation of soil decomposers drives ecosystem processes

Carbon and nutrient mineralization during litter decomposition and soil organic matter formation

Leaf litter decomposition studies are particularly illustrative of how the limitation of decomposers changes as carbon-rich plant material is progressively decomposed into lower C:N soil organic matter. During the early, high mass-loss, phase of litter decomposition, excess labile carbon availability leads to microbial nutrient limitation, and nitrogen is translocated from the soil to meet microbial stoichiometric needs as excess carbon is respired as CO_2 (Bonan et al., 2013; Frey et al., 2003; Soong et al., 2015). In later stages of litter decomposition, litter mass loss and microbial activity slow down progressively due to an increasing limitation of easily decomposable organic matter. As the C:N of decomposing material narrows, and approaches that of the microbial community, decomposers become carbon limited and nitrogen is mineralized

(Melillo et al., 1989). Litter in these later stages of decomposition is primarily comprised of less biochemically labile substrates, such as lignin and microbial products (McKee et al., 2016), and can exhibit a lower C:N ratio due to the presence of nitrogen-rich microbial biomass and imported N from the soil (Frey et al., 2003). Partially decomposed litter fragments that are difficult to decompose and low in labile carbon then enter the soil as particulate organic matter, contributing to soil organic matter formation (Cotrufo et al., 2015). The switch from nitrogen limitation to carbon limitation during litter decomposition explains why nitrogen additions stimulate the early stages of litter decomposition but in general do not affect longer term decomposition rates (Knorr et al., 2005).

Although soil is the larges reservoir of carbon in terrestrial ecosystems, microorganisms in the soil are carbon limited due to the relatively low concentration of organic matter in mineral soils, its low C:N ratio, the physical and chemical protection of organic matter within the soil mineral matrix (Lehmann & Kleber, 2015). During the decomposition continuum from high C:N plant litter to lower C:N soil organic matter, decomposers thus become progressively more carbon limited, initially conserving nutrients while losing carbon, but eventually mineralizing excess nutrients as ammonium or phosphate. The heterogeneous composition of soil often masks microbial carbon limitation, for example, although nitrogen additions can accelerate the decomposition of carbon-rich plant residues in the light fraction, it does not stimulate lower C:N mineral associated organic matter or bulk soil decomposition (Neff et al., 2002). Thus, perspective of soil microorganisms as primarily carbon limited explains the variation in their response to carbon and nitrogen availabilities across sites with varying degrees of labile carbon availability in the soil.

Carbon sequestration in deep soils and its vulnerability

The carbon limitation of microorganisms also helps to explain the increasing residence time and persistence of deep soil carbon (Fontaine et al., 2007; Torn et al., 2009). The median depth of new carbon incorporation into the mineral soil is 10 cm, while half of the soil carbon is located in soil layers deeper than 30 cm (Balesdent et al., 2018). This can be explained in part by the lack of fresh plant inputs, which are concentrated at or near the soil surface, and fuel higher microbial activity in top soil layers (Loeppmann et al., 2016).

Fresh carbon inputs from plants in the form of litter or root exudates can prime the decomposition of soil organic matter (Bingemann et al., 1953; Zhu et al., 2014). Input of these carbon-rich, labile plant materials in shallow soils and the rhizosphere alleviates microbial carbon limitation and leads to hot spots of microbial activity in the soil (Blagodatskaya & Kuzyakov, 2013; Cheng et al., 1996; Kuzyakov & Blagodatskaya, 2015). This can be seen in the linear scaling of the priming affect with microbial biomass along a litter addition gradient (Xiao et al., 2015) whereby as litter inputs from steppe vegetation increased, microbial biomass increased, along with the decomposition, or priming, of more nutrient-rich soil organic matter in order to meet the stoichiometric demands of their greater biomass (Chen et al., 2014). Inclusion of the priming effects on microbial biomass can improve predictions of global soil organic

carbon stocks and predictions of their change due to climate forcing over the 21st century (Guenet et al., 2018). The vulnerability of soil organic matter to increased decomposition with increased plant inputs that alleviate microbial carbon limitation indicates that deep soil carbon may be vulnerable to decomposition if elevated CO_2 and nitrogen enrichment change root exudation by plants (Phillips et al., 2009; Shahzad et al., 2018).

Although deep soil organic matter may have longer mean residence times in soils, it is as vulnerable to decomposition as shallow soils given a shift in conditions that favor microbial activity, such as warming temperatures (Hicks Pries et al., 2017) or labile carbon inputs (de Graaff et al., 2014; Fontaine et al., 2007). In an incubation of root litter at several depths along a 1 meter soil profile, initially the labile portion of root litter was decomposed at similar rates along the soil profile, but the later stages of decomposition slowed down much more in deep soils (Hicks Pries et al., 2018). This is likely due to the lack of labile carbon in deeper soils, which is needed to decompose the lower C:N material remaining at the later stages of decomposition (Knorr et al., 2005; Soong et al., 2015). Estimating the carbon sequestration potential from deeper root-carbon inputs to the soil due to land-use or climate change, must therefore account for both the direct inputs of root-carbon to deep soils, but also the potential priming effect of root exudates to stimulate microbes to decompose soil organic matter. This underscores how changes in deep soil carbon inputs due to land use or climate change could destabilize current carbon-climate feedbacks in natural ecosystems by alleviating deep soil microorganisms of their carbon limitations, which currently inhibit the decomposition of soil organic matter and contribute to vast soil carbon sequestration in deep soils.

Nutrient fertilization experiments

Nutrient fertilization experiments do not consistently demonstrate a stimulation of soil-carbon decomposition with nutrient additions because soil microorganisms are primarily carbon limited. Carbon limitation of micorroganisms can explain the lack of latitudinal trends in microbial nutrient responses (Capek et al., 2018; Wild et al., 2015), when aboveground primary productivity generally shifts from N-limitation in high latitudes or young soils to P-limitation in low latitudes and older soils (Vitousek & Farrington, 1997; Vitousek et al., 2010). While long-term nitrogen fertilization or warming leading to enhanced nitrogen availability led to a loss of soil carbon in one arctic tundra ecosystem (Mack et al., 2004), it is unclear whether this was caused by nitrogen directly stimulating microbial decomposition, or indirectly by shifting vegetation allocation, rooting structure, and inputs (Mack et al., 2004; Sistla et al., 2013; Weintraub & Schimel, 2003). In the Gigante fertilization experiment in the Panamanian tropics, even clear evidence of decreased phosphatase enzyme activity and microbial biomass after eight years of phosphorus fertilization (Turner & Wright, 2014) cannot rule out the possibility of increased carbon inputs from higher plant productivity (Wright et al., 2011) as a co-explanatory factor of the microbial responses (Mori et al., 2018). A review of over 20 experiments from tropical forests did not find evidence of phosphorus additions significantly affecting decomposition and microbial respiration (Camenzind et al., 2018), although phosphorus

additions can lead to desorption of organic compounds that are respired by microorganisms (Spohn & Schleuss, 2019).

It is difficult to partition direct microbial responses to nutrient additions from indirect responses mediated by altered plant carbon inputs *in situ*. Results from laboratory soil incubations in the absence of plants demonstrate the primary limitation of microorganisms by carbon, and secondarily by nutrients across ecosystems from soils from the arctic (Jonasson et al., 1996; Wild et al., 2014), sub-arctic grasslands (Marañón-Jiménez et al., 2019), mangroves (Keuskamp et al., 2012), and tropical forests (Duah-Yentumi et al., 1998; Soong et al., 2018).

Water limitations

The stoichiometric explanation that soil microbial growth is primarily limited by carbon availability and plant growth is primarily limited by nutrient availability does not account for other environmental limitations, such as water availability. Under aird and semi-arid conditions, plants may restrict their photosynthetic capacity, limiting their carbon uptake to minimize water loss from open stomata (Peters et al., 2018). Reduced plant carbon uptake and allocation belowground, along with increased organo-mineral stabilization, can exacerbate soil microbial carbon limitation under dry conditions (W. Huang & Hall, 2017). Plant-microorganism, carbon-nutrient, mutualistic interactions could breakdown further under water-limited conditions if resources are invested in osmotic adjustment or osmoregulation, rather than growth.

Integrating carbon and nutrient limitations of organisms into conceptual and numerical models

We must move beyond the concept of ecosystem limitations as a whole and move away from plant-centric ecosystem thinking to recognize how the limitations of individual heterotrophic and autotrophic organisms balance one another out to maintain ecosystem functioning. New molecular techniques are now allowing for better measurements of growth responses of microbial communities, or even of specific microbial taxa, which allow for the limitations of decomposers to be better tested and quantified (Geyer et al., 2019; Hungate et al., 2015; Spohn et al., 2016b). In plants, shifts in carbon use efficiency (the fraction of carbon fixed allocated to growth) have been observed: managed trees growing on fertile soils allocated a greater fraction of their gross primary productivity to growth and thus exhibit higher carbon-use efficiency than trees on infertile soils (Campioli et al., 2015; Vicca et al., 2012). The carbon-use efficiency concept is also used for microbial communities, determining the proportion of carbon uptake that is allocated to growth (Geyer et al., 2019; Manzoni et al., 2012; Mooshammer et al., 2014b; Sinsabaugh et al., 2013). Since microbial necromass (mainly microbial cell walls) is essentially the building block of stable soil organic matter, the impact of microbial decomposition on an ecosystem's carbon balance is strongly dependent on anabolic processes (Liang et al., 2017), microbial growth, and carbon-use efficiency (Walker et al., 2018) and thus on carbon or nutrient limitations on microbial communities. Quantification of carbon- (and nutrient-) use efficiencies of organisms in relation to available resources is a promising tool to fully integrate the carbon and nutrient limitations of soil microorganisms and plants into models

of ecosystem carbon exchange (Y. Huang et al., 2018; Tang & Riley, 2013; G. Wang et al., 2015; Wieder et al., 2015).

Ecosystem models must continue to improve their representation of ecosystem responses to changing environmental conditions over time in order to better inform land use and climate-based decision-making. The feedbacks and interactive effects among nutrient ratios, climate, and the capacity of ecosystems to store and release CO_2 have only recently begun to be studied–in experiments and by introducing nitrogen and phosphorus cycles into carbon and climatic models (Fleischer et al., 2019; Goll et al., 2017; Peñuelas et al., 2013; Y. Wang et al., 2018). Recent advances in our ability to quantify the energy and nutrient limitations of heterotrophs and autotrophs within ecosystems and how they interact provide a powerful tool for improving predictions of ecosystem carbon balance in response to nutrient availability and increasing atmospheric CO_2 concentrations. The interaction between nutrient and carbon demands of plants and microorganisms represents an exciting new frontier in biogeochemistry that will allow for the integration of soil microbial communities, and their decisive role in nutrient recycling and ecosystem carbon storage, into models of ecosystems undergoing changes in resource availability.

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