

REVIEW AND SYNTHESIS

Applying population and community ecology theory to advance understanding of belowground biogeochemistry

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Abstract

Approaches to quantifying and predicting soil biogeochemical cycles mostly consider microbial biomass and community composition as products of the abiotic environment. Current numerical approaches then primarily emphasise the importance of microbe–environment interactions and physiology as controls on biogeochemical cycles. Decidedly less attention has been paid to understanding control exerted by community dynamics and biotic interactions. Yet a rich literature of theoretical and empirical contributions highlights the importance of considering how variation in microbial population ecology, especially biotic interactions, is related to variation in key biogeochemical processes like soil carbon formation. We demonstrate how a population and community ecology perspective can be used to (1) understand the impact of microbial communities on biogeochemical cycles and (2) reframe current theory and models to include more detailed microbial ecology. Through a series of simulations we illustrate how density dependence and key biotic interactions, such as competition and predation, can determine the degree to which microbes regulate soil biogeochemical cycles. The ecological perspective and model simulations we present lay the foundation for developing empirical research and complementary models that explore the diversity of ecological mechanisms that operate in microbial communities to regulate biogeochemical processes.

Keywords

Competition, microbial biomass, microbial physiology, nitrogen mineralisation, predation, soil carbon, soil respiration.

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INTRODUCTION

Greenhouse gas exchanges with the atmosphere and terrestrial primary productivity are strongly influenced by the decomposition of soil organic matter (SOM) and nutrient fluxes within and among ecosystems. Clarifying mechanisms governing the size and rate of soil biogeochemical pools and processes is critical to projecting likely terrestrial responses to global change (Schmidt *et al.* 2011; Luo *et al.* 2015). Notably, recent experimental evidence shows the potential for soil microbial physiology, biomass, and community composition to regulate soil biogeochemical cycles (Grandy & Neff 2008; Bradford *et al.* 2013; Cotrufo *et al.* 2015; Kallenbach *et al.* 2015; Lehmann & Kleber 2015). Such work has stimulated the explicit representation of microbial processes in several biogeochemical models (e.g., Lawrence *et al.* 2009; Allison 2012; Sulman *et al.* 2014; Wieder *et al.* 2014). These developments in soil biogeochemical theory and models have advanced our understanding of how microbe–environment interactions shape biogeochemistry (Sistla *et al.* 2014; Sulman *et al.* 2014; Wieder *et al.* 2015b),

but in a manner largely separate from our extensive knowledge on population modeling and microbial ecology.

While biotic interactions clearly shape the composition and function of microbial communities (Rønn *et al.* 2002; Lenoir *et al.* 2007; Rosenberg *et al.* 2009; Crowther *et al.* 2015), models typically assume that soil microbial biomass and activity scales with abiotic variables and so can be excluded by implicitly representing microbial processes (Coleman & Jenkinson 1996; Parton *et al.* 1998; Schimel 2001). Even with the explicit representation of microbial processes in models, abiotic variables still act as the prominent drivers of microbial biomass, cell turnover, cell dormancy, and biogeochemical fluxes (Lawrence *et al.* 2009; Manzoni & Porporato 2009; Wang *et al.* 2014a; He *et al.* 2015). Hence, even when microbial communities are explicitly considered as a control on biogeochemistry, an upper bound on microbial biomass or activity arising from ecological interactions is typically not invoked (but see Tang & Riley 2015); and when it is, the mechanisms remain uncertain and therefore difficult to evaluate empirically.

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In reality, population-level processes regulate soil microbial abundance, community composition and ecosystem process rates (Ruiter *et al.* 1993; Rønn *et al.* 2002; Crowther *et al.* 2015; Leff *et al.* 2015; Pelini *et al.* 2015). In particular, microbial ecological interactions such as competition, predation, and facilitation can explain variation in biogeochemical process rates (Couteaux & Bottner 1994; Alpehi *et al.* 1996; Bradford *et al.* 2014). For example, soil animals such as mites, spiders, springtails, and isopods may alter microbial biomass and community structure through selective predation, in turn altering biogeochemical rates (Sitvarin & Rypstra 2014; Crowther *et al.* 2015; Grandy *et al.* 2016; Soong *et al.* 2016). In one case, the composition of soil animal communities in forests explained variation in heterotrophic soil respiration rates better than temperature (Pelini *et al.* 2015). Further, territorial interactions between mycorrhizal and saprotrophic fungi can slow the decomposition of leaf litter (Bödeker *et al.* 2016). Thus, microbe-microbe and microbe-animal interactions can act as important controls of soil biogeochemical process rates (Lehmann & Kleber 2015; Soong *et al.* 2016). It is feasible that such biotic interactions are more important than abiotic controls at regulating process rates, at least at local- to regional-scales. There is a rich empirical literature supporting the importance of biotic interactions in soils as regulators of decomposition dynamics (Santos & Whitford 1981; Bardgett & Chan 1999; Daufresne & Loreau 2001; Lenoir *et al.* 2007; Bardgett & Wardle 2010; Holtkamp *et al.* 2011; Soong *et al.* 2016). Yet, efforts to formalise such empirical knowledge into theory for representation in modern decomposition models remains in its infancy (see Zheng *et al.* 1997; Zelenev *et al.* 2006 as early examples; and Buchkowski 2016; Grandy *et al.* 2016; Soong & Nielsen 2016 for justification). Incorporating insights from developments in population ecology into biogeochemical models represents a new frontier for development of biogeochemical theory and prediction.

Here, we attempt to identify the aspects of population ecology that will most meaningfully inform soil biogeochemical theory. To facilitate efficient integration of this knowledge, we assess the current assumptions concerning population and community dynamics in microbial-explicit biogeochemical models, identify deficiencies, and suggest ways to enhance their realism and predictive capability. We focus on ecological factors that determine microbial community size and structure, as a means to reach a balance between the complexity of microbial community dynamics and the need to keep model structures tractable (Schimel 2001). Specifically we:

- (1) Reframe microbial processes in terms of per capita rates and ecological theory;
- (2) Apply theory from population and community ecology to document the assumptions being made by current soil biogeochemical theory and models about microbial community ecology;
- (3) Summarise the ecological assumptions made by the equations commonly used in microbial-explicit decomposition models; and
- (4) Examine the impact of altering these equations and assumptions in representative model simulations.

SECTION 1: MICROBIAL PROCESSES, COMMUNITIES AND ECOLOGICAL THEORY

Microbes play a central role in biogeochemical cycles by decomposing and forming organic matter, thus mobilising and storing carbon and nutrients (Six *et al.* 2006). Many biogeochemical models implicitly represent microbial activity by assuming that biotic responses to the same environmental change are invariant over space and time (Coleman & Jenkinson 1996; Parton *et al.* 1998; Schimel 2001; Bradford & Fierer 2012). By contrast, models that explicitly represent microbial activity directly link the activity of microbial communities to biogeochemical fluxes, expressing how the rate at which microbial communities feed and grow on organic matter determines the amount and fate of the released nutrients (Wieder *et al.* 2015b). Thus, factors influencing the size and activity of the microbial biomass in these models strongly influence projected biogeochemical outcomes (Fig. 1). By explicitly representing mechanisms responsible for SOM decomposition and formation through microbial activity, these models present opportunities to evaluate the consequences of inclusion of a more detailed microbial ecology.

In microbial-explicit decomposition models, hundreds to thousands of microbial taxa are generally summarised into one or more broad groups (Allison 2005; Waring *et al.* 2013; Wieder *et al.* 2014; Tang & Riley 2015). Therefore, these decomposition models are built at the microbial community scale, with very few models considering individual microbial populations (but see Allison 2012). However, much of the relevant ecological theory is framed at the population level and is best referred to as population ecology (Hastings 1997). We therefore use the term microbial community to refer to the groups of interacting microbial populations that are typically invoked in microbial-explicit decomposition models and population ecology to refer to the body of theory.

Biotic interactions and per capita rates

Abiotic and biotic factors drive microbial biomass and community composition. However, current models primarily emphasise the role of abiotic variables in determining

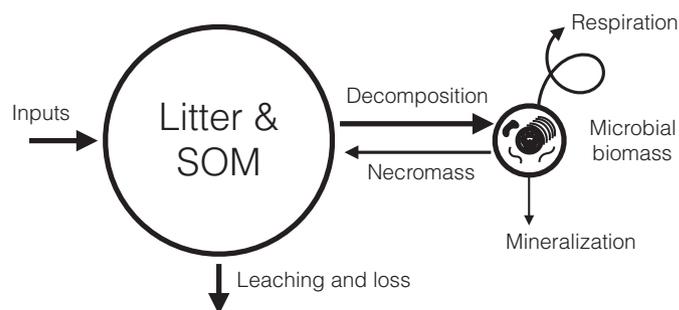


Figure 1 The major pathways of nutrient flow. The flow of nutrients from substrates such as litter and soil organic matter (SOM) through microbial biomass with possible fates including nutrient mineralisation, necromass and respiration.

microbial community dynamics (Allison *et al.* 2010; Davidson *et al.* 2012; Wieder *et al.* 2013), with a handful of models also considering exploitative competition for scarce resources (Allison 2005, 2012; Waring *et al.* 2013; Kaiser *et al.* 2014; Wieder *et al.* 2014). The models that do consider other biotic interactions, such as predation, tend to be built for a general case and evaluated qualitatively with empirical data, with a focus on biotic but often not other important controls (e.g. temperature, substrate quality) of decomposition and nutrient dynamics (Zheng *et al.* 1997, 1999; Daufresne & Loreau 2001; Louis *et al.* 2016). The generality makes these models very useful for developing conceptual theory into the potential influence of biotic interactions, but limits their applicability as predictive tools above the local or ecosystem scale where a critical set of modern decomposition models focus (Davidson *et al.* 2014; Wieder *et al.* 2015b). Our aim here is not to review these contributions, but to explore *how* their insights and techniques can inform the development of integrative biogeochemical models.

To test the relative importance of a much broader range of biotic interactions in microbial-explicit decomposition models, microbial community dynamics should be characterised in terms of a microbe's 'full' environment – i.e. both abiotic conditions and interactions with other organisms. A full environment characterisation of microbes in decomposition models would facilitate more quantitative model validation as is regularly applied to current microbial-explicit decomposition models (Waring *et al.* 2013; Wieder *et al.* 2013; He *et al.* 2015; Wang *et al.* 2015). To develop these models and make biotic interactions explicit, we suggest that it is necessary to define microbial community dynamics based on per capita or per biomass gain and loss rates that are determined by a microbe's abiotic and biotic environment.

Per capita rates change in three general ways, across population size and in response to environmental factors. The first is density dependence, in which the population per capita (or per biomass) growth rate decreases with density (Fig. 2; Hixon & Johnson 2009; Stevens 2009). The density-dependent

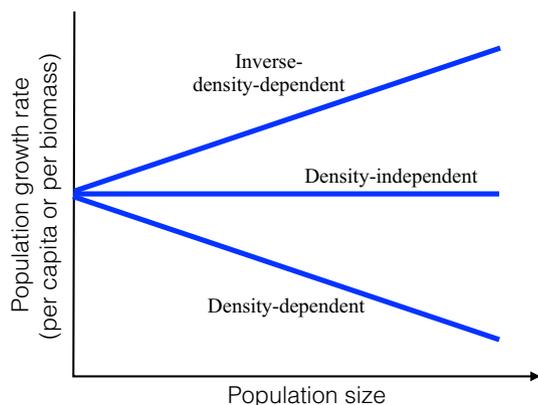


Figure 2 A graphical depiction of density dependence. The difference between density-dependent, inverse density-dependent, and density-independent population processes in graphical form. The relationships are depicted as straight lines, but both forms of density dependence can be nonlinear.

decrease in per capita growth rates can arise from processes affecting individual microbial growth and/or death, and additionally immigration and emigration (Hixon & Johnson 2009). An example occurs when microbial populations (e.g. fungi) experience declines in growth rate when they engage in interference competition for space or physical access to substrates (Boddy & Heilmann-Clausen 2008). In effect, they exert an increasingly negative feedback on each other with every incremental increase in population density. These negative feedbacks can lead to reduced per capita decomposition rates relative to scenarios where such competitive interactions are absent (Hiscox *et al.* 2015). Even though decomposition rates may remain high in the aggregate, the reduction in per capita decomposition rate is a critical factor influencing the projections of microbial models where decomposition rate is driven by microbial biomass (Manzoni & Porporato 2009).

The second form of per capita population change is inverse density dependence, where population growth rate increases with density (Fig. 2). Microbial populations can exhibit inverse density dependence when higher population densities allow decomposition products to accumulate in the surrounding soil matrix. For example, Allison (2005) identified a density threshold for negative versus positive population growth where higher microbial biomass promoted the necessary accumulation of decomposition products to overcome basal metabolic and enzyme production costs. Furthermore, the aggregation of microbes in social groups or biofilms can improve their ability to respond to adverse environmental conditions and increase population growth (Crespi 2001). Indeed, many more examples of cooperative or facilitative litter decomposition exist that could produce inverse density dependence (Gessner *et al.* 2010).

The final case is density independence, where per capita process rates are independent of population density. Even though density independence is commonly assumed in microbial models (Schimel & Weintraub 2003; Lawrence *et al.* 2009; Blagodatsky *et al.* 2010; Wieder *et al.* 2014), it is difficult to unambiguously classify a process as density independent because, at high or low population sizes, density will influence most processes. Basal respiration is perhaps the clearest example of a density-independent process for microbes because it occurs regardless of microbial density. However, total respiration may only be density independent over a certain range because changes in density can influence respiration rate by promoting overflow respiration or changing carbon-use efficiency (Schimel & Weintraub 2003). As for other taxa (Hixon & Johnson 2009), microbial processes likely have both density-independent (basal respiration) and density-dependent (overflow respiration) components.

The challenge in incorporating per capita effects into models is that they can be partitioned into a whole host of different population processes (e.g. birth, death, competition, predation, parasitism, dormancy, and immigration). Selecting which ones to include in biogeochemical models requires an understanding of the important drivers, given a particular scale or context, limiting population size or growth. We propose that to overcome such issues, we can begin by organising population processes into resource gains and losses.

SECTION 2: ECOLOGICAL ASSUMPTIONS INHERENT IN CURRENT BIOGEOCHEMICAL THEORY AND MODELS

Microbial community size and per capita resource consumption determine the rate of biogeochemical cycling. Consequently, density effects on microbial resource gain and loss influence both microbial population growth rates and SOM turnover – two critical components in microbial-explicit biogeochemical models (Moore *et al.* 1988; Manzoni & Porporato 2009; Crowther *et al.* 2015). Organising ecological effects into resource gains and losses is useful because these processes (1) directly influence microbial biomass and nutrient cycling and (2) simplify the myriad of population ecological processes in a manner that can be tractably modelled. The challenge then is to determine whether these resource gains and losses are density dependent or independent over realistic population sizes, and whether other taxa play an important role in regulating nutrient flows and microbial biomass.

Resource gains

The rate of microbial resource gain is largely determined by the rates of decomposition and nutrient uptake, which depends on the relationship between decomposition and substrate availability, enzyme concentration, and microbial biomass (Fig. 3a). Microbial implicit models assume that microbial catabolic capacity is large enough to maximise the rate of decomposition and, thus, show no relationship between microbial biomass (or enzyme concentration) and decomposition. In these first-order models, substrate availability alone determines decomposition rate (Parton *et al.* 1998; Schimel 2001). Alternatively, microbial biomass may influence decomposition rate, but through a constant per capita effect so that total rates scale with total biomass. This density-independent case corresponds to classic enzyme kinetics where any increase in the concentration of enzymes, which is sometimes assumed to be proportional to microbial biomass as in Allison *et al.* (2010), accelerates decomposition (Fig. 3a; Murray

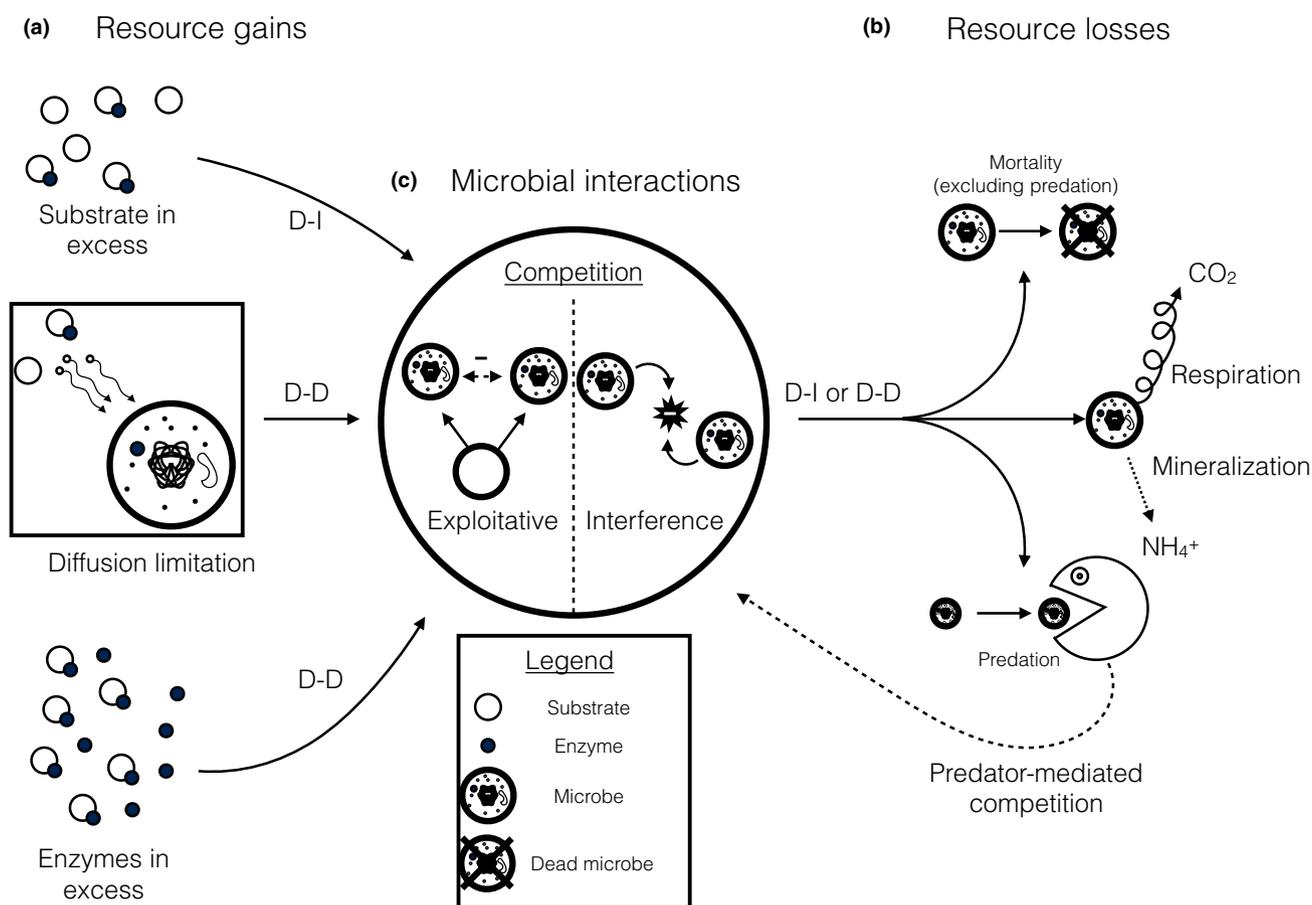


Figure 3 Conceptual diagram illustrating assumptions about microbial population ecology that are implicit in soil decomposition models related to microbial (a) resource gain, (b) resource losses, and (c) interactions. Microbial communities gain resources (a) through catabolic processes such as decomposition and then assimilation. These processes can be density independent (D-I) or density dependent (D-D; including inverse D-D) depending on our assumptions about microbial ecology. Microbial communities lose resources (b) through nutrient mineralisation and respiration, mortality, or predation. Microbial turnover, nutrient mineralisation, and respiration are commonly represented as density-independent processes (e.g. a fixed fraction of microbial biomass), however when losses are density dependent, these fluxes would accelerate with larger population sizes. (c) The size, structure, and function of microbial communities are partly determined by interactions. Exploitative competition over resources is more commonly considered in decomposition models, while direct combat, or interference competition, is not commonly considered.

1989). Finally, the rate of decomposition can be density dependent whenever an increase in microbial biomass decreases the per capita or per biomass rate of decomposition (Schimel & Weintraub 2003). For example, when enzymes exist at high concentrations relative to substrates, an increase in enzyme concentrations does not increase decomposition rate (Schimel & Weintraub 2003; Wang & Post 2013). Alternatively, density-dependent decomposition could occur if diffusion limitation of enzymes or decomposition products leads to longer diffusion distances, higher enzyme:substrate ratios, and more competition between microbes over diffusing products at higher biomass concentrations (Vetter *et al.* 1998; Allison 2005; Davidson *et al.* 2012). The rate of microbial resource gain is then likely often density independent at moderate to low densities and probably density dependent at high densities.

Diffusion as well as the spatial dynamics of substrates, microbes, and enzymes is critical for determining the per capita rate of resource gains (Davidson *et al.* 2012). Such phenomena underscore the importance of considering local-scale processes as factors affecting the relationship between microbial populations and biogeochemical fluxes (Blaud *et al.* 2014; Monga *et al.* 2014; Peth *et al.* 2014; Falconer *et al.* 2015; Vogel *et al.* 2015). For example, microbial clustering in aggregates or decomposition hotspots could promote the high enzyme:substrate ratios and/or long diffusion distances necessary for density dependence (Vetter *et al.* 1998). These dynamics are often represented in spatially explicit microbial decomposition models (Vetter *et al.* 1998; Allison 2005, 2012; Evans *et al.* 2016), which highlight the broad-scale impacts of density-dependent dynamics playing out in microsites. Where these types of density-dependent dynamics are important, microbial biomass and microbial-mediated decomposition rates cannot be predicted simply by total substrate availability as assumed in microbial-implicit models (Schimel 2001), or by models with density-independent decomposition rate (Allison *et al.* 2010). Two solutions available to modellers attempting to include changes in per capita resource gain are (1) to include density-dependent decomposition functions that implicitly account for local substrate depletion or enzyme competition (Schimel & Weintraub 2003; Sulman *et al.* 2014) or (2) to build a spatially explicit model that accounts for diffusion limitation and local substrate depletion (Vetter *et al.* 1998; Allison 2005).

Resource losses

Microbial populations lose resources primarily through mineralisation, mortality, and predation (Fig. 3b). These loss rates are typically represented as density-independent processes (but see Zelenev *et al.* 2000; Tang & Riley 2015), because processes such as respiration are most conveniently modelled as a constant per capita rate (e.g. Schimel & Weintraub 2003; Blagodatsky *et al.* 2010; Wieder *et al.* 2014). However, empirical evidence supports density-dependent nutrient loss or death in microbial populations (Kumar *et al.* 2013; Phaiboun *et al.* 2015). Perhaps the most well studied example of density-dependent microbial death comes from the rhizosphere, where soil fauna prey more effectively on the high densities of

bacteria supported by resource-rich root exudates (Clarholm 1985; Moore *et al.* 2003). This density-dependent increase in predation rate releases large quantities of nutrients that become plant-available and increase plant growth rate (Elliott *et al.* 1979; Clarholm 1985; Wickings & Grandy 2011). Density-dependent microbial death can also be driven by predation in the litter layer. For example, at high nutrient levels wood rot fungi grow dense, conspicuous cords that are preferentially consumed by isopods leading to a density-dependent loss of hyphae (Crowther *et al.* 2015). Mortality, which includes cell death caused by viruses, and other pathways of resource loss such as mineralisation, can also be density dependent (Wiggins & Alexander 1985; Acea & Alexander 1988; Don *et al.* 2013). For example, dense colonies of wood rot fungi tend to have higher per capita respiration rates (Hiscox *et al.* 2015; D. Maynard person communication). While it may not always be necessary to consider density-dependent microbial death, it is likely that such biomass regulation will occur if resource gains do not limit microbial population size at sufficiently low densities to avoid increased respiration or predation.

Microbial interactions

Microorganisms exhibit a wide range of life histories involving cell dormancy, communication, and biofilm formation and participate in a wide range of ecological interactions, including disease, competition and predation (Wiggins & Alexander 1985; Crowther *et al.* 2011; He *et al.* 2015). While all these processes may have important ramifications for nutrient cycling, we focus on competition and predation because they are largely absent from microbial decomposition models and can be included, using the per capita approach discussed above.

Competition is an interaction that occurs within and among microbial populations and determines rates of resource gain or loss (Fig. 3c; Stevens 2009). Interactions between microbial populations can be classified as exploitative, interference, or predator-mediated completion. Explicitly defining microbe-microbe competitive interactions may help predict emergent nutrient cycling across environmental gradients because the different types of competition lead to different outcomes. First we review their functional differences.

Exploitative competition, involving indirect effects on the competitor through interception of a common resource, is, implicitly included in density-independent models of nutrient gain because resource availability ends up limiting microbial biomass (Tilman 1980). In models with multiple microbial taxa and therefore explicit exploitative competition, the objective has been to predict the abundance of large and broadly different groups of microbial taxa and how their functional differences drive nutrient cycling (Waring *et al.* 2013; Wieder *et al.* 2015a). These efforts have shown that accurately predicting competitive outcomes can significantly improve the utility of microbial models. Specifically, the models can predict spatial and temporal variation in microbial communities and microbial-mediated process rates that would be hidden and difficult to parameterise in models where the microbial biomass is implicit or treated as a single pool (Allison 2012).

Interference competition, in contrast, involves direct aggressive interactions between competitors to obtain space, and is a common mechanism behind density-dependent microbial death (Stevens 2009). Saprotrophic fungi engage in strong interference competition whose outcome determines the composition of the fungal community and decomposition rates (Boddy 2000). Although interference competition is less commonly considered in decomposition models, its inclusion in microbial-explicit models could facilitate a broader examination of how biogeochemical fluxes are driven by interactions among microbial taxa (Boddy 2000; Crowther *et al.* 2011; Hiscox *et al.* 2015).

Predator-mediated competition serves as a slightly more complex ecological process among microbial communities, which integrates microbial competition with the resource losses discussed above (Fig. 3b and c). Predators of microbes can structure the composition of microbial communities by altering the outcomes of both exploitative and interference competition (Couteaux & Bottner 1994; Rønn *et al.* 2002; Kreuzer *et al.* 2006; Crowther *et al.* 2011; Trap *et al.* 2016). For example, the introduction of amoebae into the rhizosphere of *Arabidopsis thaliana* consistently and rapidly shifted the composition of the bacterial community towards grazing tolerant species (Rosenberg *et al.* 2009). Moreover, fungal grazing can mediate microbial population densities, altering the competitive outcome from interference competition among fungi and leading to different rates of decomposition and nutrient release (Crowther *et al.* 2011). Furthermore, predator effects can interact with other important drivers such as nutrient availability and temperature, leading to context-specific competitive outcomes (Crowther *et al.* 2015). Explicitly considering the impact of selective predation on competitive outcomes may then help explain variation in microbial biomass, physiology, and community composition and improve carbon and nutrient cycling projections.

Microbial ecology and soil biogeochemistry

Consideration of microbial population ecology suggests that competition and predation can be important determinants of soil carbon and nutrient dynamics (Boddy 2000; Rosenberg *et al.* 2009; Averill *et al.* 2014; Hiscox *et al.* 2015; Bödeker *et al.* 2016), because they lead microbes to alter the cycling rate and fate of carbon and nutrients within the soil (*sensu* Schimel & Schaeffer 2012). However, accurately representing all the potential population processes in models would be a daunting and perhaps unnecessary exercise (Grandy *et al.* 2016). The important practical question to ask is which mechanisms are dominant determinants of microbial biomass, community composition, and/or physiological responses to environmental perturbations. The relevant mechanisms will likely change with scale and context (Levin 1992; Schmitz 2010; Hinckley *et al.* 2014). For example, microbial populations cycle dramatically in response to predation and resource pulses in the rhizosphere, while changes in the microbial biomass in the mineral soil are more subdued and largely controlled by substrate occlusion (Manzoni & Porporato 2009; Schimel & Schaeffer 2012; Blaud *et al.* 2014; Peth *et al.* 2014; Falconer *et al.* 2015). Consequently, predictions at the

rhizosphere scale may generally require more detailed models incorporating the interplay between root exudation and predation (Zelenev *et al.* 2006), whereas predictions at the scale of the entire soil profile may merely require consideration of mechanisms such as substrate occlusion augmented by simple or implicit predation and competition. However, these examples are clearly broad generalisations that may have many exceptions. The ability to predict where the combination of soil properties and community structure magnify the importance of biotic interactions is one of the most important justifications for developing decomposition models with more explicit population ecology (Zheng *et al.* 1999; Lenoir *et al.* 2007; Schmitz 2010; Crowther *et al.* 2015).

The usefulness of explicitly representing population ecology at a particular scale can be judged by developing competing models with different ecological assumptions, similar to those dealing with different biophysical assumptions (Davidson *et al.* 2014; Wieder *et al.* 2015b,c). Competing models may be separated on the basis of including a particular process (e.g. predation, cell dormancy, etc.) or by the per capita nature of that process (e.g. density dependent or density independent). In addition, developing research programmes that explicitly combine modeling and empirical testing of models (e.g. Allison 2012; Drake *et al.* 2013; Buchkowski *et al.* 2015) could help identify where microbial population ecology is a key driver of biogeochemical cycling. Doing this successfully requires identifying the limitations of existing microbial-explicit models (Wang *et al.* 2014b) and identifying how incorporating microbial ecology can improve them. The next two sections address these topics.

SECTION 3: ECOLOGICAL ASSUMPTIONS IN BIOGEOCHEMICAL MODELS: VARIATION IN THE DECOMPOSITION EQUATION

Recent microbial-explicit models that track biogeochemical flows through litter and SOM pools make a wide variety of assumptions about the factors limiting microbial communities and the nature of density effects. We consider the common assumptions across the range of these models by focusing on different representations of decomposition. Decomposition has received the largest degree of theoretical attention; resulting in many fundamental differences in the way SOM decomposition is characterised mathematically (Schimel & Weintraub 2003; Wang & Post 2013; Sihi *et al.* 2015; Tang 2015). These various decomposition equations implicitly include a wide variety of ecological assumptions (Schimel & Weintraub 2003). Consequently, the variety of different models and their biogeochemical and ecological assumptions can be largely categorised based on five interrelated forms of the decomposition equation (Fig. 4). The fifth form, where only enzyme concentration determines decomposition rate, is unrealistic and unstable because the enzyme pool promotes its own growth without any control imparted by the reduced availability of the substrate (see proof in Supporting Information). Consequently, we will not explore this fifth form in detail.

The most common modeling approach holds that substrate availability, and other abiotic drivers, are the primary

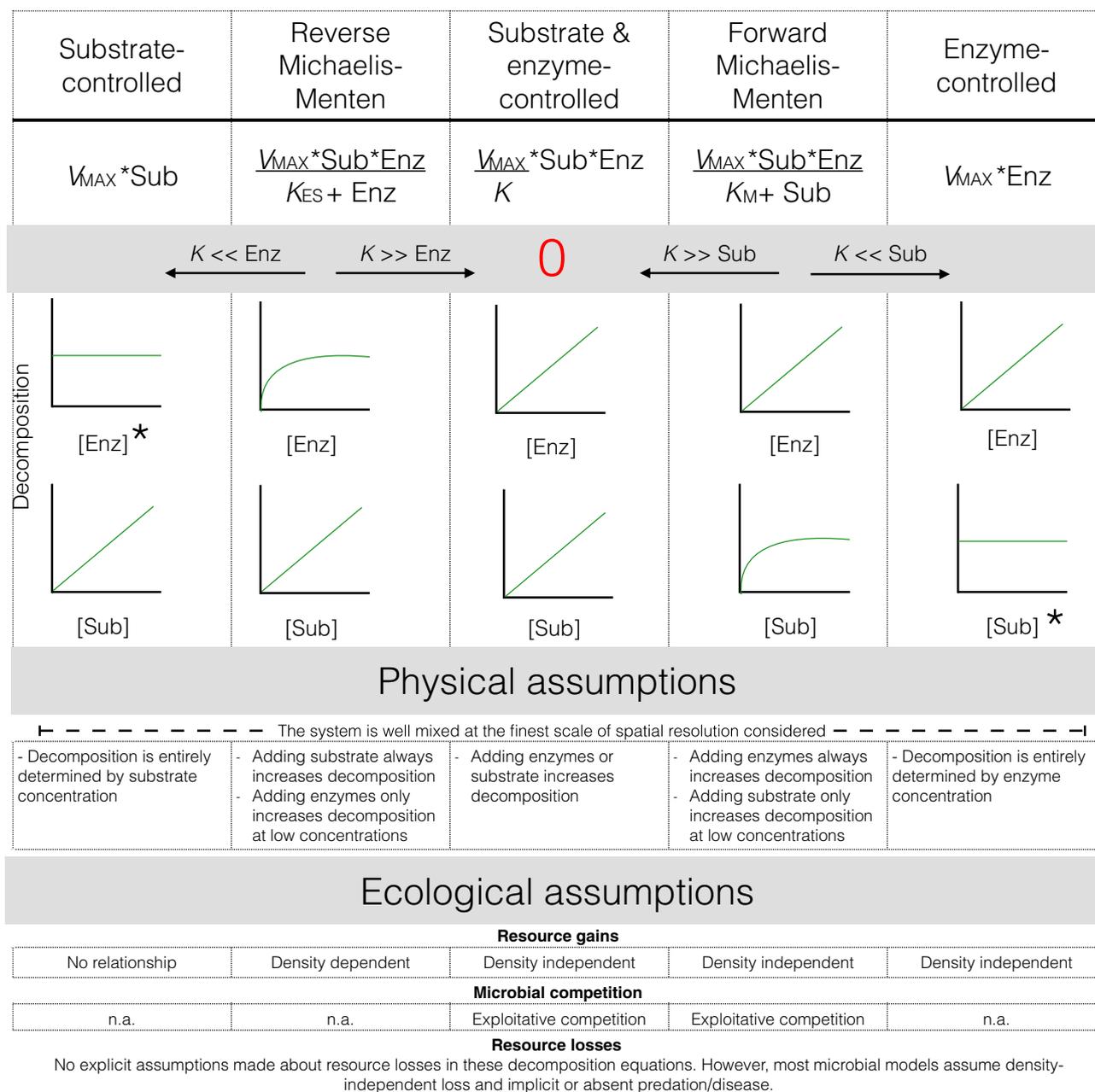


Figure 4 The continuum of decomposition equations considered in this paper from substrate- to enzyme-controlled models (left to right). From top to bottom the figure includes the name, equation, a graphical representation of the relationship between enzyme and substrate concentrations with rates of decomposition, and a summary of assumptions made by each decomposition equation. The red zero indicates that as K (i.e. the half saturation constant) is increased, decomposition approaches zero because the enzyme affinity approaches zero. V_{MAX} is the maximum rate of decomposition; K_M and K_{ES} are the half-saturation constants of the Michaelis-Menten function; Enz is enzyme concentration; Sub is substrate concentration. The asterisks on two of the sketched relationships indicate that $[Sub]$ or $[Enz]$ are implicit in the equation shown by being included in V_{MAX} .

determinants of decomposition rate (Coleman & Jenkinson 1996; Parton *et al.* 1998). This substrate-controlled approach assumes that microbial communities instantaneously achieve equilibrium with respect to available substrates and hence the microbial pool is represented implicitly in the decomposition equation. It is important to note that models using a substrate-controlled equation do not necessarily represent microbial pools implicitly (Parton *et al.* 1998; Daufresne & Loreau 2001; Lawrence *et al.* 2009; Zou *et al.* 2015). When using the

substrate-controlled equation, microbial density or community composition has no direct effect on biogeochemical cycling (Fig. 4), making this the simplest assumption about microbial effects on decomposition rates (Coleman & Jenkinson 1996; Parton *et al.* 1998).

The assumption of a constant decomposition rate under common environmental conditions can be relaxed by assuming that changes in microbial biomass or enzyme activities affect rates of biogeochemical transformations at low

microbial biomass densities and saturate at higher densities. This process is captured mathematically by the reverse Michaelis–Menten equation, where a half saturation constant (K_{ES}) determines the point where microbial or enzyme biomass reaches half its maximum decomposition potential. The reverse Michaelis–Menten equation imparts a density-dependent control on microbial biomass by decreasing the per biomass decomposition rate with increasing microbial density (Schimel & Weintraub 2003; Wang & Post 2013; Sihi *et al.* 2015). At low values of K_{ES} , the reverse equation maintains the microbial population at maximum density and behaves as a substrate-controlled equation (Sihi *et al.* 2015).

Alternatively models may assume that biogeochemical rates do not saturate with respect to microbial or enzyme biomass, but rather microbes maintain constant per biomass rates, where increased availability of substrates and enzymes is necessary to increase total decomposition rates. This substrate-enzyme controlled model (Fig. 4) is a very common form used by population ecologists to model microbial processes (Lotka 1925; Daufresne & Loreau 2001; Zou *et al.* 2015), although it is not commonly used in microbial-explicit biogeochemical models.

The final form of the decomposition equation assumes that increasing microbial biomass always increases decomposition rate, but when the concentrations of substrates are already high, the addition of more substrates has a diminishing effect. This is the basis of the forward Michaelis–Menten equation, where K_M determines the point where substrates are half way to saturating enzyme capacity (Murray 1989). The forward Michaelis–Menten equation is based on traditional enzyme kinetics, wherein substrates can saturate the available enzymes and consequently limit decomposition and microbial resource gains (Allison *et al.* 2010). The equation is density independent because the per biomass microbial decomposition rate is constant across varying levels of biomass. Instead, the decomposition rate changes nonlinearly across substrate concentrations for any given value of the biomass.

The five decomposition equations are expressed in Fig. 4. They all share a common feature that the value of K (i.e. half saturation constant K_M or K_{ES}) determines their behaviour over a range of substrate and enzyme concentrations. The constant K effectively controls the degree of nonlinearity (Wang *et al.* 2013). At one extreme K is vanishingly small (Fig. 4). This is called a substrate-controlled or enzyme-controlled equation wherein decomposition rate is completely saturated across the entire substrate or enzyme gradient. Increasing K produces more curvature and hence more variable responses leading to saturation. These conditions are represented by reverse and forward Michaelis–Menten equations. Finally, under high K values, saturation of substrates or enzymes never occurs over a biologically realistic range – leading to the substrate-enzyme controlled equation.

These alternative models offer a basis for considering the implications of population ecology on biogeochemical fluxes, given that changes in the half saturation constant influence both physical and ecological assumptions made by the decomposition equation (Fig. 4). For example models using the reverse Michaelis–Menten equation with relatively low values of K_{ES} limit or nullify the relationship between microbial

biomass and decomposition, leading to predictions similar to first-order, substrate-controlled models by increasing the strength of density dependence (Sihi *et al.* 2015). Next, we integrate the implications of considering the ecological assumptions about microbial resource gains (i.e. the decomposition equation), losses, and interactions (Fig. 3), and examine how various assumptions might interact to determine rates of biogeochemical processes.

SECTION 4: INTEGRATING MICROBIAL POPULATION ECOLOGICAL PROCESSES INTO BIOGEOCHEMICAL MODELS

Building new microbial-explicit models that are richer in microbial population ecology requires an explicit consideration of the mechanisms that determine microbial biomass and activity. An extensive review of all the potential mechanisms is beyond the scope of the paper. We instead explore some common, representative mechanisms that cover variation in competition and predation both implicitly and explicitly. We incorporate these mechanisms into models that embody the decomposition equations introduced above and vary the value of the half saturation constant K to capture differences in model behaviour. In soils, the value of K could vary with temperature, soil texture, and the specific microbial taxa involved in decomposition (Wieder *et al.* 2014). Overall, our modeling exercise considers three key variables identified in our review: the *decomposition equation*, *half saturation constant (K)*, and *model structure*. Model structure determines the types of ecological interactions (e.g. competition and predation) captured by the model and some of the associated assumptions. The ecological assumptions within the model are modified by differences in both the *decomposition equation* and the *model structure*. The former refers to ecological assumptions about microbial resource gain (see Sections 2 and 3 for details), while the latter influences assumptions regarding resource losses and microbial interactions (see Section 2 for details). By evaluating a variety of models that make different assumptions concerning the decomposition equation, K , and overall structure, we demonstrate that explicitly representing ecological processes expands range of dynamics captured by simple decomposition models and increases our ability to empirically validating model results using experiments or measurements of key ecological processes such as variation in competition, community composition, or predation rates.

Model methods

We used a simple microbial-substrate model to explore the impact of different ecological assumptions. The base model contains an available substrate pool and microbial pool, with a resource (e.g. carbon) entering the substrate pool, leaching, and passing to the microbial pool based on the rate of decomposition (Fig. 5; see Supporting Information for model equations). The substrate pool excludes any unavailable substrates which can make up a large fraction of the SOM pool, as incorporating these compounds would require detailed biogeochemistry beyond the scope of this paper (Lehmann & Kleber 2015). Resources enter the substrate pool(s) at a constant rate and

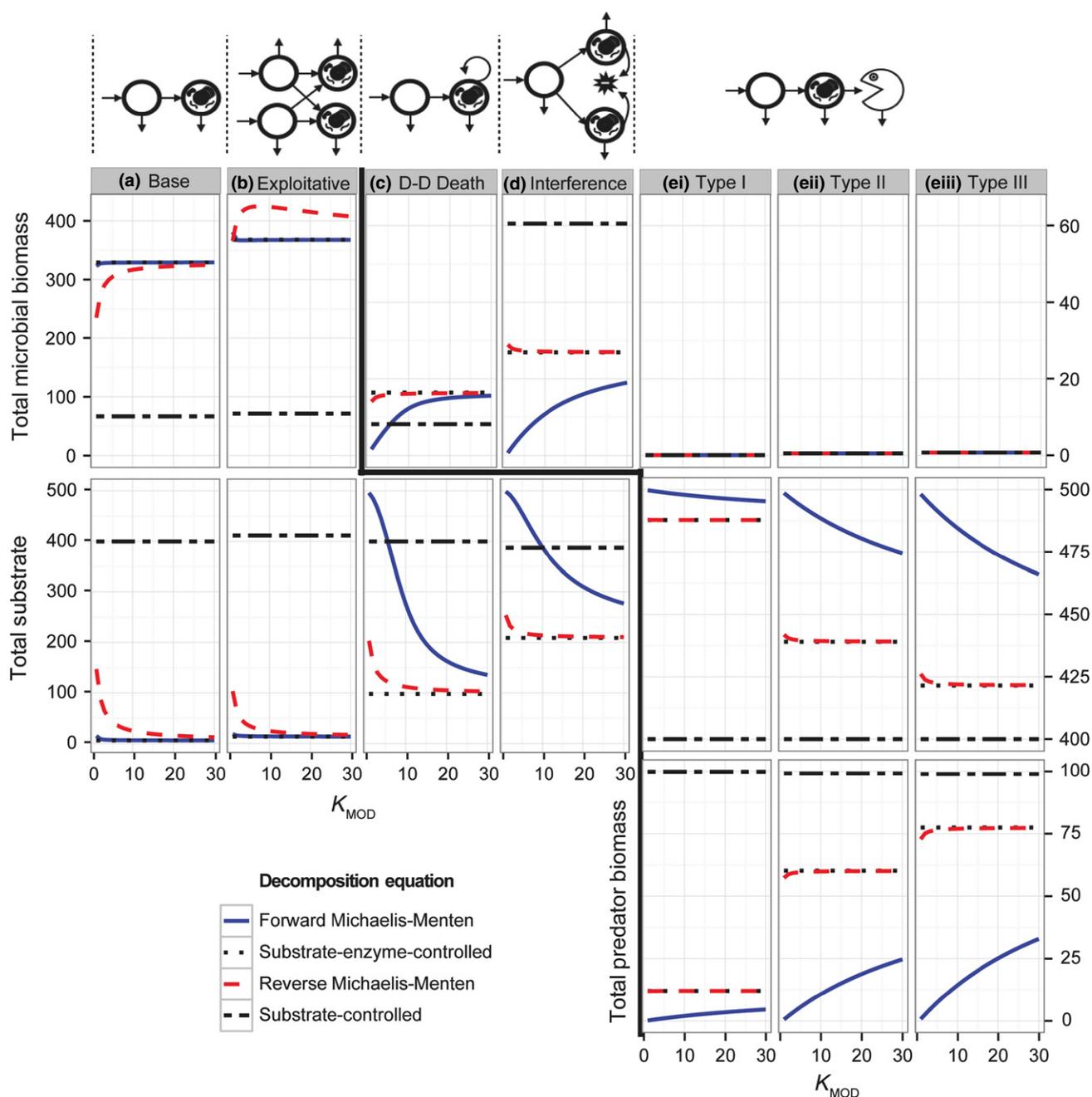


Figure 5 Results of idealised simulations showing the effect of different decomposition equations and ecological assumptions on equilibrium microbial, predator, and substrate biomass. The simulations are carried out across a range of the half-saturation constants of the decomposition equation ($K_z = K_{MOD,z} \times K$), while maintaining a constant ratio between the parameters K and V_{MAX} to aid equation comparisons. The decomposition equations are summarised in Fig. 4, and include substrate controlled (black dashed line), reverse Michaelis–Menten (red line), substrate-enzyme-controlled (black dotted line), and forward Michaelis–Menten (blue line). The models are: (a) the base model with only substrate and microbes, (b) exploitative competition between two microbes for two substrates, (c) density dependent (D-D) microbial death, (d) interference competition between two microbes, and (e) three different types of predation (Type I, Type II, and Type III). The base model results demonstrate the expected relationship between the value K and the decomposition equations. Modifying the other ecological assumptions influences the model behaviour in a manner that interactions with the assumptions in the decomposition equation. Model parameters and a full description can be found in the supporting information along with simulations, using other parameter values. The thick black line separates panels plotted on the left and right vertical axes, which have different scales.

leach as a constant fraction of the available pool. We assume that microbial biomass pools have access to the entire substrate pool(s), with resource gains described by different decomposition equations (Fig. 4) across a 30-fold range of K (half saturation constant) values. We maintain a constant ratio between

V_{MAX} and K in all our simulations to ensure that decomposition rates do not tend to zero as K increases (Fig. 4). Consequently, the substrate-control and substrate-enzyme control models remain constant across all values of K , but do respond to the different model structures (Fig. 5). Microbial losses

(respiration and mortality) are assumed to be linear functions of microbial biomass in the base model, but become nonlinear in the density-dependent model and are based on the biomass of other groups in the interference competition and predation models. The model does not include the microbial formation of SOM, because the substrate is assumed to be fresh organic inputs, and only considers a single resource (e.g. carbon). The primary goal of the model is to explore the influence of different ecological assumptions on relative outcomes rather than to predict soil biogeochemical cycling *per se*.

We examine five variations in model structure with different ecological assumptions: (A) base model, (B) exploitative competition between distinct populations or communities, (C) density-dependent microbial death, (D) interference competition between distinct populations or communities, and (E) predation (Fig. 5). We note that microbial-explicit biogeochemical models tend not to consider interference competition, density-dependent death rates, and predation (but see Zelenev *et al.* 2000, 2006; Tang & Riley 2015). Models A, D, & E, only consider a single microbial pool, whereas the competition models (B & C) necessarily include two microbial populations. In the competition models, we parameterised individual microbial populations as exhibiting rapid vs. slow growth strategies for resource gains and losses (*sensu* Wieder *et al.* 2014). Interference competition is represented as a resource loss proportional to the rate of interaction between competing populations (i.e. constant \times Biomass 1 \times Biomass 2). The exploitative competition model has two substrate pools to prevent global competitive exclusion. Finally, in model E we consider three common equations for modeling predation called Type I, Type II, and Type III that represent linear, saturating and sigmoidal responses of predators to prey density or biomass respectively (Holling 1969).

Model equilibria were calculated in Mathematica using the function NSolve (version 9.0.1.0) using parameter values that allowed all versions of the model across all decomposition equations to produce positive equilibrium. We display results for parameter values where microbial biomass is larger than the substrate pool in some cases in order to compare different models in the same parameter space and clearly display the relative effects of different model structures and decomposition equations. To demonstrate the generality of our results we replicated the same simulations in a different, but still stable, parameter space where microbial biomass tends to be smaller than the substrate pool. We ran further simulations of the base and exploitative competition models because they required parameters outside of the stable range of other models to reduce microbial biomass below the substrate pool size (Supporting Information). Models B and C had multiple equilibria, corresponding to competitive exclusion scenarios, but we focus only on equilibria where there was coexistence of both microbial populations. Model results were summarised and plotted in R (version 3.1.3).

Model results and discussion

Examining the results of the base model provides a clear picture of the impact of different decomposition equations – and hence

ecological assumptions – across variation in the half saturation constant (Fig. 5a; Figs S2 and S3a). As K increases both the forward and reverse equations approached the substrate-enzyme controlled model as anticipated by the continuum presented in Fig. 4. Furthermore, at low values of K the reverse equation approaches the substrate-controlled model (Fig. 5a), whereas the forward equation becomes unstable (not presented). These results at extreme values of K were consistent across different model structures with their different ecological assumptions. However, the transition between these two extremes, which is arguably the most relevant region to biogeochemical models, was highly dependent on the model structure and its inherent ecological assumptions. The behaviour of the models with forward and reverse Michaelis–Menten equations at intermediate values of K therefore highlights the impact of different ecological assumptions on substrate dynamics and microbial biomass in our simulations (Fig. 5).

Exploitative competition is the most common model structure modification currently being implemented in microbial models (Allison 2012; Waring *et al.* 2013; Wieder *et al.* 2014). The well-known benefit of adding exploitative competition between microbial taxa is the ability to predict variation in microbial community composition across relevant gradients (Allison 2012; Wieder *et al.* 2015a). Our modeling results show an additional, unexpected property of exploitative competition models that arises when either Michaelis–Menten equation is used (Fig. 5b; Figs S2 and S3b). At low values of K where uptake is relatively slow, the total microbial biomass increases above the substrate-enzyme-controlled line that it should approach based on the predictions in Fig. 4 and the base model behaviour (Fig. 5a; Fig. S3b). As K increases further, microbial biomass falls back towards the substrate-enzyme-controlled line, as expected. The slow growing, conservative microbial population drives this unexpected model behaviour, because they benefit from the low rate of resource uptake imposed by density-dependence or enzyme saturation in the reverse and forward equations, respectively. Their strategy of low rates of resource loss paired with slower resource uptake causes their biomass to increase until the rapidly growing microbes are released from density-dependent control or enzyme saturation at higher values of K (Figs S1 and S3b).

Notably, these changes in community composition only occur if parameter space passes through the nonlinear range of the decomposition function. In Fig. 5, where substrate concentrations remain low, only the reverse Michaelis–Menten equation produces these dynamics because enzyme saturation does not occur (cf. Figs S1 and S3b). The implication here is that changes in the rate of resource gains can influence the strength and outcome of exploitative competition between microbial taxa with different life history strategies. Understanding how differences in model structure, reflecting disparate ecological assumptions, influence competitive outcomes may aid the development of broad-scale models with multiple microbial pools where coexistence can be problematic (Wieder *et al.* 2014). Furthermore, exploitative competition models may help explain nonlinear trends in microbial-mediated decomposition and population size by

combining nonlinear resource uptake with competitive dynamics.

While our model example includes only two microbial groups, the interaction between competitive outcomes and ecological assumptions such as density dependence is likely general. In models with more than two microbial groups or variable environmental conditions, resource competition theory could be used to summarise and interpret model predictions (Tilman 1980, 1992; e.g. Marleau *et al.* 2011). A clear understanding of the ecological assumptions governing exploitative competition combined with resource competition theory could facilitate the development and interpretation of more taxonomically diverse decomposition models (Louis *et al.* 2016).

Both density-dependent death and interference competition models invoke density-dependent resource losses from the microbial biomass. Adding density-dependent resource loss has the largest effect on the forward Michaelis–Menten model where no other density-dependent mechanism exists (Fig. 5c and d; Fig. S2). This is consistent with a previous observation that different mechanisms of density dependence should be redundant because only one ends up controlling microbial biomass (Schimel & Weintraub 2003). It also suggests that adding ecological mechanisms to microbial decomposition models can be simplified by summarising the various mechanisms of density dependence into a single function representing the dominant density-dependent force.

In our model results, the substrate and biomass are reduced and build-up, respectively, in a nonlinear fashion as microbes become more rapid decomposers at higher values of K . Decomposition rate increases at higher values of K because the strength of density dependence in the reverse equation or the level of enzyme saturation in the forward model are reduced by moving the half-saturation constant to higher levels of biomass or substrate, respectively. The nonlinear, almost sigmoidal substrate curve arises from the combination of the forward Michaelis–Menten nonlinearity across substrate concentrations (Fig. 4) paired with the nonlinear, density-dependent microbial death (Fig. 5c and d). These two density-dependent mechanisms could be important to capture the nonlinear population and decomposition dynamics that have been observed in microbial communities, especially in response to changes in resource abundance or environmental conditions (Kumar *et al.* 2013; Phaiboun *et al.* 2015). Notably, similar substrate dynamics – at least qualitatively – may arise from different trends in total microbial biomass depending on whether interference competition is handled explicitly or implicitly (Fig. 5c and d; Fig. S2). The benefit of the interference competition model (Fig. 5d) over a single population with density-dependent death (Fig. 5c) is the ability to predict community composition and microbial biomass over environmental or biotic gradients. For example, including interference competition may improve predicted changes in the composition and function of fungal communities, where the strength of interference competition is most apparent and can be readily measured (Boddy 2000).

Adding predation suppressed microbial biomass significantly relative to other model types; effectively nullifying the

differences across decomposition equations and the value of the half saturation constant K (Fig. 5e–eiii). In fact, microbial biomass is controlled entirely by predation rate so that all the biomass lines fall on top of each other in plates 4e–eiii. While other predator functions and different regions of state-space exist that would dampen the strength of predation, we show this extreme example to allow a clear demonstration. Furthermore, there are some environments, such as the rhizosphere, where predators might control certain microbial populations (Zelenev *et al.* 2006; Rosenberg *et al.* 2009). Substrate concentrations, in contrast to microbial biomass, change as expected across the range of decomposition equations and the value of K , but as in the density-dependent resource loss models, the forward equation yielded the most drastic differences. The reason for this difference is that the forward equation has no density-dependent control stemming the flow of resources from substrate to predators. Consequently, predator population size and therefore control change as decomposition rate increases with K (Fig. 5e–eiii).

One particularly interesting outcome of adding predators was that the reverse Michaelis–Menten and substrate-enzyme-controlled equation behaviours converged strongly across values of K , especially when predators had unlimited consumption ability (Type I functional response; Fig. 5e). The similarity between these decomposition equations under predation is a perfect example where models might be paired with experimental work to distill which mechanisms are controlling nutrient cycling. It may be that the substrate-enzyme-controlled equation is a sufficient representation of microbial decomposition when predation pressure is high enough to negate the importance of density-dependence via enzyme saturation. Adding more complex population ecology to models becomes much more tractable in such cases where the additional ecological detail constrains the model into a smaller state space and permits simple linear approximations (i.e. substrate-enzyme controlled decomposition) to replace more complex functions (i.e. reverse Michaelis–Menten; Schimel 2001). For these reasons, predation and density dependence might be more easily integrated into complex microbial explicit biogeochemical models than had been anticipated. Such integration would be most advantageous if we make models modular with mechanisms such as predation included in contexts where they are known to be a dominant control on the microbial community (Krome *et al.* 2009; Rosenberg *et al.* 2009; Louis *et al.* 2016).

The experiments necessary to test the results of competing models would likely be carried out at a small scale where the concurrent manipulation of abiotic and biotic conditions is possible (e.g. Buchkowski *et al.* 2015). Models that perform well in small-scale experiments could then be used to make larger-scale predictions to be tested against observational data. Larger-scale datasets examining the importance of microbial communities and soil organisms are also available to test models with more detailed ecological mechanisms (Wall *et al.* 2008; Bradford *et al.* 2014). Future models with more complete biogeochemical pathways could include these ecological mechanisms to make testable predictions about the importance of density dependence and predation on litter decay and SOM formation.

CONCLUSIONS

Empirical work is uncovering a richer and more detailed picture of microbial ecology. Paramount to our new understanding has been evidence that the response of microbial communities to variation in abiotic conditions is mediated by factors such as competition and predation (Bradford *et al.* 2014; Crowther *et al.* 2015). The resulting effects, mediated by changes in microbial communities, affect carbon and nutrient cycling in a manner that may be better understood and predicted by explicitly considering the discussed ecological mechanisms. We argue that the most parsimonious way to incorporate these mechanisms is to reframe the microbial components of soil biogeochemical models in terms of population and community ecology. In doing so, we can understand and tractably include the processes of competition and predation in candidate biogeochemical models to be tested against experiments and observations. Although the questions of scale that challenge the most basic microbial models will remain (Schimel 2001), models with richer ecological detail will provide predictions based on representing our best available understanding of soil community dynamics, which can then be tested at ecosystem and global scales.

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DATA ACCESSIBILITY STATEMENT

The model equations are provided in the Supporting Information and the code is available at <https://github.com/robertb1024/Community-ecology-and-soil-biogeochemistry.git>.

AUTHORSHIP

R.W.B., M.A.B., A.S.G., O.J.S. and W.R.W. developed the article content. R.W.B. and W.R.W. conducted the modelling work. R.W.B. wrote the first draft and all authors contributed substantially to the manuscript.

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