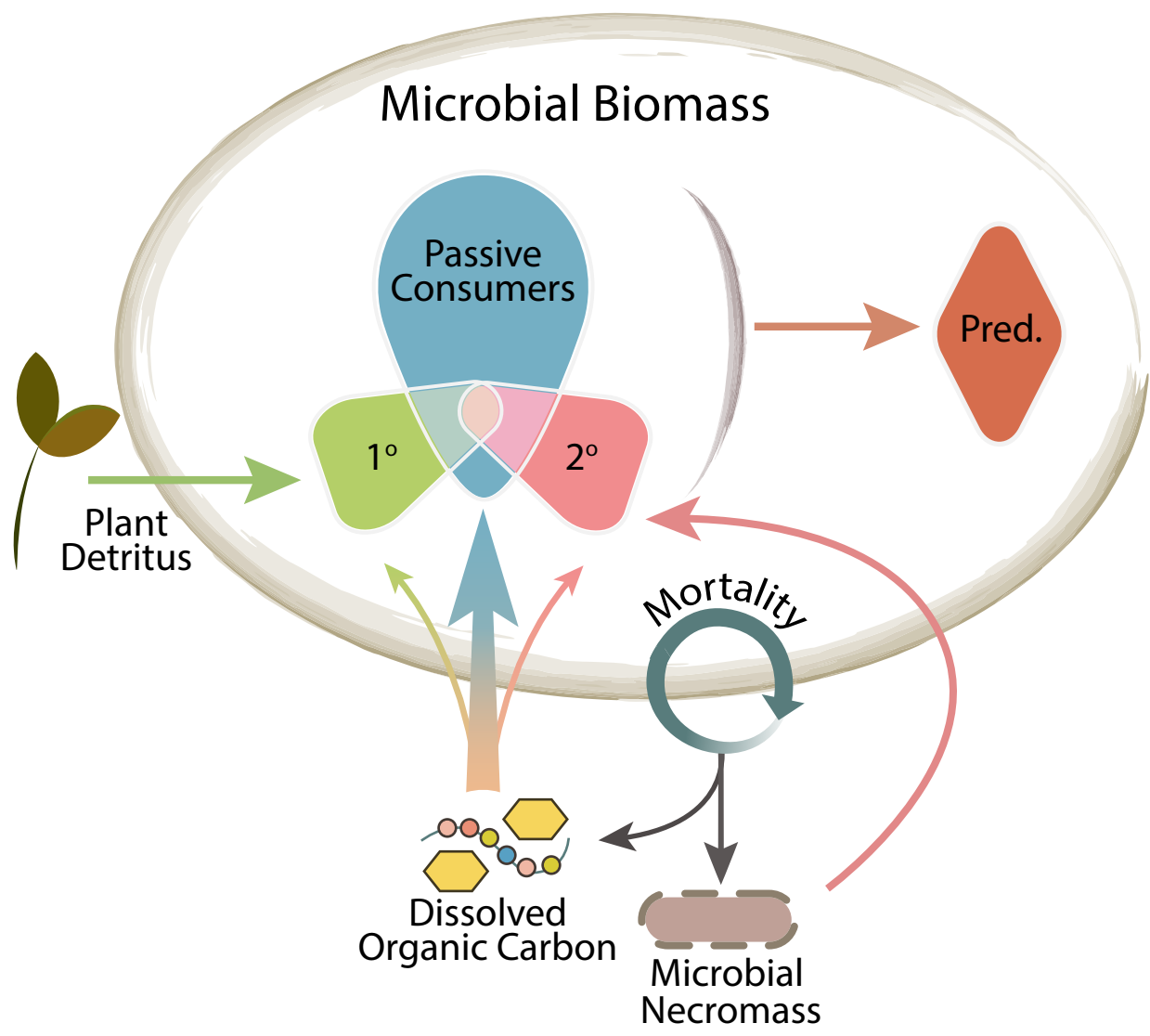


Carbon Acquisition Ecological Strategies



Ecological Strategy	Carbon Pool
• 1° Decomposer	Complex Plant Detritus
• 2° Decomposer	Complex Microbial Necromass
• Passive Consumer	Dissolved Organic Carbon
• Predator	Live Microbial Biomass

Highlights

- Microbes have specialized traits to use distinct pools of soil organic carbon
- Carbon acquisition traits may serve as a strong foundation for ecological strategies
- Ecological strategies can help condense microbial diversity for inclusion in models

Carbon acquisition ecological strategies to connect soil microbial biodiversity and carbon cycling

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Abstract

Soil carbon feedbacks to global change are uncertain, and the biological processes that govern soil organic matter decomposition are not resolved in current ecosystem models. Though it is recognized that microbial biodiversity influences decomposition rates, incorporating this relationship into ecosystem models is challenging because microbial communities are prohibitively diverse. It is likely necessary to distill microbial biodiversity by focusing on functional groups or ecological strategies. The ecological strategies that currently dominate the microbial ecology literature derive from macroecological theory, have clear weaknesses, and have had limited success when applied to predict soil carbon dynamics. Here, we present a new framework for soil microorganisms: Carbon Acquisition Ecological Strategies (CAES), and we outline a path toward incorporating microbial biodiversity into ecosystem models using this framework to enhance predictions of soil carbon feedbacks to global change. Because a microorganism's diet is central to its ecological niche and likely to covary with other ecologically significant traits, we posit that carbon acquisition may serve as a tractable foundation for developing ecological strategies. We describe four candidate ecological strategies for soil microorganisms: *1° decomposers* that assimilate complex plant polymers, *2° decomposers* that assimilate microbial necromass, *passive consumers* that assimilate dissolved organic C (DOC), and *predatory microbes* that assimilate live microbial biomass C. These strategies are directly linked to soil carbon pools currently represented in ecosystem models and may provide a foundation for greater integration of microbial community dynamics into ecosystem models.

1. Introduction

Soil contains the second largest reservoir of carbon (C) on earth, surpassed only by the oceans (Ciais et al., 2013). Soil C cycling is highly sensitive to environmental changes, such as shifts in temperature and moisture (Hursh et al., 2017; Melillo et al., 2017). In addition, soil microbial community composition can alter C cycling processes such as decomposition (via anabolism and extracellular enzyme production; Allison et al., 2013; Don et al., 2017) and C sequestration (by producing microbial necromass, metabolites, and external polymeric substances that adsorb onto soil particles; Buckeridge et al., 2020; Raczka et al., 2021).

As climate change continues, rising temperature and altered precipitation coupled with changes in above-ground communities, can influence soil microbial biodiversity (Fierer, 2017), which may feedback to regulate the balance of C decomposition and stabilization. However, many questions remain regarding the extent to which changes in microbial biodiversity and function may exacerbate or mitigate the impacts of global change on soil C stocks.

Microbial ecologists and ecosystem scientists struggle to make meaningful connections between microbial biodiversity and soil C, often leading to the omission of microbial biodiversity from soil C models (Bradford et al., 2016; Denman et al., 2007; Hutchins et al., 2019). There have been some efforts to represent microbial biodiversity using functional groups that differ in key traits; these have relied on assumptions from theoretical frameworks that are difficult to measure and, thus, difficult to parameterize (Moorhead and Sinsabaugh, 2006; Wieder et al., 2014). A promising approach is to build a bridge from microbial biodiversity to soil C cycling using ecological theory. Building this bridge is necessary to enhance our predictive understanding of the extent to which microbial biodiversity drives the response of soil C to global change.

Aboveground, the species composition of plant and animal communities influences ecosystem fluxes (e.g., Melvin et al., 2015; Wardle et al., 2012; Ylänne et al., 2015). Functional trait variation across species produces differences in resource use and interactions with the abiotic environment; consequently, community composition shapes ecosystem processes (Hooper and Vitousek, 1997; Verville et al., 1998). Increasing evidence suggests a similarly strong link between community composition and ecosystem function exists below ground. For example, carefully controlled manipulations of microbial community composition have been found to alter leaf litter decomposition (Allison et al., 2013), soil respiration (Don et al., 2017; Reed and Martiny, 2013), and nitrogen cycling (Delgado-Baquerizo et al., 2018; Philippot et al., 2013; Wagg et al., 2014). The composition of microbial communities belowground can also impact plant performance, creating another link to above-ground processes and drivers. Specifically, soil microbes can influence ecologically-important traits like flowering time and manipulate plant fitness under competition and during drought (Fitzpatrick et al., 2019; Lau and Lennon, 2011; Lu et al., 2018; Wagner et al., 2014). Despite clear experimental evidence that the “species” (or phylotype) composition of microbial communities influences ecosystem process rates, determining the impact of individual microbial taxa on community-level functioning remains challenging.

2. Ecological Strategies in Microbial Ecology

One path toward connecting the composition of microbial communities with ecosystem function is by classifying species based on ecological strategies. Ecological strategies describe traits that covary due to physiological and evolutionary tradeoffs, enabling species to be particularly successful under certain conditions. One such framework posits that animal species

fall on an r- to K- selection continuum. In this framework, natural selection favors species with the potential for rapid population growth in ecosystems with fluctuations in resource availability (r-strategists) and favors highly efficient and competitive organisms when resource availability is steady, and populations are near carrying capacity (K-strategists; MacArthur and Wilson, 2001; Pianka, 1970). Microbial ecologists adapted this framework, placing microbial species on a continuum from oligotrophic to copiotrophic. Oligotrophs are adapted to survive and compete in low nutrient conditions. They grow slowly and efficiently scavenge resources. Copiotrophs occupy the opposite trait space, growing rapidly when nutrient concentrations are high (Chen et al., 2021; Fierer et al., 2007; Lauro et al., 2009). A second well-known framework utilized by plant ecologists argues that plants adapt to maximize their ability to compete under steady and favorable conditions (competitors, “C”), withstand stressful conditions (stress tolerators, “S”), or thrive in high disturbance environments (ruderal, “R”; Grime, 2006, 1977). The C-S-R framework has helped enable the incorporation of plant community composition into dynamic vegetation models by developing trait distributions based on leaf longevity, resource investment, and photosynthesis rates (Berzaghi et al., 2020; Reich et al., 1997; Wright et al., 2004) (Berzaghi et al., 2020; Reich et al., 1997; Wright et al., 2004). Here again, microbial ecologists have attempted to adapt this framework to microorganisms (e.g., Fierer, 2017; Ho et al., 2017; Prosser et al., 2007); for instance, the Y-A-S framework proposes that microbes evolve to maximize growth yield (“Y”), resource acquisition (“A”), or stress tolerance (“S”, Malik et al., 2020). The application of these and other ecological strategies, originally developed for macro-organisms, to microbial systems has provided some insight into community dynamics and function; however, these ecological strategies have not yielded a robust framework for predicting

relationships between taxonomic composition and ecosystem function for heterotrophic soil microorganisms.

The ecological strategies currently dominating microbial ecology have limited ability to explain soil C cycling because they do not adequately reflect variation in the C acquisition traits of microorganisms. For example, the copiotroph-oligotroph framework emerged from measurements of microbial growth and substrate affinity in culture using low molecular weight dissolved organic carbon (DOC) substrates (Semenov, 1991). As most environmental microbes are not culturable, more recent work has inferred the ecological strategies of microbes based on changes in relative abundance, determined by DNA sequence data, following the addition of simple DOC substrates to soil (e.g., Fierer et al., 2007; Ho et al., 2017). Consequently, the copiotroph-oligotroph framework has two implicit assumptions. First, it assumes that all heterotrophs rely primarily on simple DOC compounds. Second, it assumes that copiotrophs compete well at high concentrations while oligotrophs are most competitive at low concentrations. This premise of reliance on DOC is clearly flawed. Many fungi and bacteria present in soil are not easily categorized as either copiotrophs or oligotrophs because they can degrade large and insoluble substrates. For instance, *Cytophagaceae* have novel enzymes for cellulose digestion (Xie et al., 2007) that are membrane bound (McBride et al., 2014). Since the small soluble products of cellulose degradation are produced and consumed at the cell membrane where other microbes cannot access them, *Cytophagaceae* avoid competition for DOC. A recent study using stable isotope probing confirmed that saprotrophic bacteria effectively competing for and assimilating polymeric substrates like cellulose (e.g., *Cytophagaceae*, *Caulobacteraceae*) do not assimilate appreciable amounts of simple DOC substrates such as glucose and amino acids (Dang et al., 2022a). Specialization in large insoluble polymers is even more common among

fungi (Algora Gallardo et al., 2021; Bhatnagar et al., 2018; López-Mondéjar et al., 2020) which have evolved suites of enzymes to support distinct saprotrophic lifestyles (e.g., lignocellulose decay by *Polyporales* and *Agaricales*; Ruiz-Dueñas et al., 2021).

The focus on DOC is a long-recognized flaw in the copiotroph-oligotroph framework, and other trophic classifications have been developed that attempt to further divide heterotrophs based on their ability to produce degradative enzymes (Semenov, 1991). The recent adaptation of the C-S-R framework proposed by Malik et al. (2020) is stronger in this regard as it acknowledges traits related to C acquisition from soil polymers are significant to the ecology of soil microorganisms. In this framework, *Cytophagaceae* would be classified under the resource acquisition strategy because they are motile and produces enzymes that degrade complex substrates (Malik et al., 2020). While the Y-A-S framework is more inclusive, some microbial taxa could fall into multiple categories based on their traits. For instance, many *Bacillus* species have a high growth rate (yield strategy) and also produce spores (stress tolerance strategy) (Sella et al., 2014). Further, this framework fails to encompass the diversity of microbial lifestyles in the soil environment. For instance, *Bdellovibrio* and like organisms (abbrev. BALOs), are motile, obligately predatory bacteria (Rotem et al., 2014) common in soil environments (Davidov et al., 2006; Williams and Piñeiro, 2006). Given their predatory lifestyle, these organisms are unlikely to compete for DOC or polymeric substrates like cellulose. While they could arguably be placed in the ‘acquisition’ strategy because they expend energy to acquire resources, they are likely to have a very different influence on soil C cycling than ‘acquisition’ bacteria that degrade complex plant-derived organic substrates. For example, past works suggest that predation by BALOs reduces microbial biomass and activity (Davidov et al., 2006; Williams and Piñeiro, 2006), while the decomposition of complex plant substrates by “acquisition” bacteria has the opposite effect

of stimulating microbial biomass and activity (Xiao et al., 2015). In summary, many soil saprotrophic microorganisms do not fit neatly into the ecological strategies stipulated by current frameworks, perhaps because these frameworks were originally developed using a community ecology lens for macro-organisms. We propose a more effective framework can be built “from the bottom up,” by instead focusing on the diverse traits, lifestyles, and functions of microbial taxa. When integrated, these attributes represent distinct strategies that drive soil C cycling at the ecosystem scale. We believe this novel framework for conceptualizing saprotrophic microbial communities may be especially useful in ecosystem models and could facilitate enhanced predictions of soil C feedbacks to global change.

3. Carbon Acquisition Ecological Strategies (CAES) for Soil Microorganisms

We propose that microbial ecologists draw inspiration from soil C biochemistry and ecosystem models to re-conceptualize the ecological strategies of soil saprotrophic microorganisms. Models of soil C mineralization and accumulation that distinguish chemically and functionally distinct soil organic C pools (Robertson et al., 2019; Sulman et al., 2018; Wieder et al., 2013) and explicitly represent microbial physiology (see Wieder et al., 2013) can outperform traditional first order decomposition models (Abramoff et al., 2022; Sulman et al., 2018; Wieder et al., 2013). While this is a step in the right direction, most of these “microbially explicit” models neglect microbial biodiversity and only simulate one microbial biomass pool. Some models (Moorhead and Sinsabaugh, 2006; Wieder et al., 2014) have integrated diversity using frameworks based on theoretical assumptions of how copiotrophs and oligotrophs differ in substrate use, activity, and growth. However, owing to methodological challenges in classifying copiotrophic or oligotrophic microbes and mapping differences between them in traits or

function, few studies have tested the assumptions or benchmarked the trait parameters underlying these models.

The classification of microorganisms into ecological strategies that clearly connect to soil C pools may facilitate the incorporation of microbial biodiversity into soil C models. To start simply, microbial saprotrophs could be partitioned into four ecological strategies based on the C pool or pools they utilize (Fig. 1): *1° decomposers* that assimilate complex plant derived C, *2° decomposers* that assimilate microbial necromass, *passive consumers* that assimilate labile DOC, and microbial *predators* that assimilate live microbial biomass. Unlike the ecological strategies that currently dominate the soil microbiology literature, these strategies are intimately associated with the pools and fluxes of C in soil (Fig. 1). As most bacteria can use DOC, many if not most of the *1°* and *2° decomposers* are also likely to consume DOC. However, we expect the majority of DOC will be taken up by *passive consumers* that are specialized for the rapid consumption of low molecular weight organic compounds (as reflected by arrow size in Fig. 1). Although *1° and 2° decomposers* are similar in that they both specialize on complex, polymeric detritus that may have a long turnover time (Clemmensen et al., 2013), the differences between plant and microbial detritus are likely to favor consumers with distinct traits. First, plant litter and microbial necromass are biochemically distinct; for instance, plant litter is more nitrogen poor (consisting of primarily cellulose and lignin) while microbial necromass is nitrogen rich (aminosugars, proteins; Kögel-Knabner, 2002). Consequently, *1° decomposers*, well suited to decompose plant litter (such as fungi), may have comparatively low biomass N requirements. Second, microbial necromass may be less susceptible to lysis by hydrolytic enzymes as it is more closely associated with soil minerals than plant detritus (Cotrufo et al., 2013) and gram negative cell wall membranes and fungal hyphae can be hydrophobic (Fernandez et al., 2016; Jørgensen et

al., 2003). Adsorption, occlusion in soil aggregates, and hydrophobicity present unique challenges that *2° decomposers* would need to overcome. It is also possible that some bacteria may be true generalists and have the capability to use DOC as well as decompose and assimilate complex C of both plant and microbial origin. While some microbial taxa may have the ability to use more than one C pool, eco-evolutionary tradeoffs and intense competition for resources have likely driven most microorganisms to specialize and become highly competitive on a relatively narrow range of substrates. Consequently, we expect true generalists to be rare (limited overlap in Fig. 1), and we hypothesize that the majority of microbes exhibit substrate specialization, where organisms that are highly effective at decomposing complex plant or microbial detritus will be relatively poor competitors for DOC and vice versa.

Substrate specialization during the decomposition of both simple and complex soil organic matter constituents has been observed in enrichment (Algora Gallardo et al., 2021) and stable isotope probing experiments in soil (Drigo et al., 2012; López-Mondéjar et al., 2020; Wilhelm et al., 2019). For instance, a recent DNA qSIP-based study of forest soil found little overlap between the dominant consumers of labile DOC (glucose and amino acids) and insoluble plant material (cellulose; Dang et al., 2022b). Likewise, consumers of bacterial necromass were distinct from glucose consumers across 27 grassland soils as determined by PLFA SIP (Buckeridge et al., 2020). Such substrate specialization has led researchers to construct and discuss decomposer guilds (e.g., Allison, 2005; Barnett et al., 2021; Bhatnagar et al., 2018; Moore et al., 2004). Notable work includes the detrital dynamics model wherein saprotrophs are split into fungi that specialize on recalcitrant organic matter, and bacteria that utilize only labile organic matter (Moore et al., 2004). Another two-guild model was proposed by Allison (2005) that included enzyme ‘producers’ that depolymerize complex detritus and compete with

‘cheaters’ that scavenge for DOC. These groupings are somewhat analogous to the *1° decomposer* and *passive consumer* strategies we propose. More recently, empirical studies have made strides connecting microbial biodiversity with substrate preferences and have proposed decomposer guilds, but these have been too specific (i.e., focusing on a single substrate; Algora Gallardo et al., 2021; Bhatnagar et al., 2018) and/or numerous (e.g., Barnett et al. (2021) has 28 guilds) for straightforward incorporation into soil C models. CAES builds upon this past work and attempts to connect microbial diversity and ecology to our evolving understanding of soil organic matter while striking a balance between simplicity and veracity.

Because ecological strategies are defined as suites of traits that covary, one could argue that classification based solely on C acquisition is not enough to constitute an ecological strategy. However, because the CAES framework focuses on substrate assimilation, which is central to the niche of saprotrophic microorganisms and their position in the soil food web, differences in the C acquisition traits are likely to covary with several other ecologically significant traits such as motility, extracellular enzyme production, and growth rate. Similar extrapolation is common in macroecology. For example, growth rate is a key indicator of ecological strategy in plants (Poorter and Garnier, 1999), which is fundamentally tied to the rate at which organisms assimilate, transform, and release elements, thus making it innately connected to ecosystem biogeochemistry.

The CAES of soil microorganisms may help explain and describe functional traits for soil microorganisms, including growth rates (Fig. 2), C use efficiency, enzyme production, and motility (Table 1). For instance, motility is likely to be highly beneficial for degraders of insoluble substrates (*1°* and *2° decomposers*) and *predators*, but less prevalent among *passive*

consumers of DOC. Indeed, most *Arthrobacter* are non-motile (Busse et al., 2012), and members of this group can rapidly assimilate labile DOC in soil (Dang et al., 2022b; Mau et al., 2015).

Primary and secondary *decomposers* that consume complex plant- and microbe-derived organic C often invest energy into motility and enzyme production for resource acquisition (Allison et al., 2010), which may lead to a lower growth rate (Schmidt and Konopka, 2009) and C use efficiency (Fierer et al., 2007; Roller and Schmidt, 2015). Indeed, recent culture-based work supports a tradeoff between extracellular enzyme production and growth rate in soil bacteria (Ramin and Allison, 2019). Consequently, we hypothesize that 1° and 2° *decomposers* have higher motility and enzyme production, but lower growth rates and C use efficiencies than *passive consumers* (Fig. 2, Table 1).

While similar in some respects, 1° and 2° *decomposers* are likely to have important differences. For instance, 2° *decomposers* may produce antimicrobial secondary compounds to kill neighboring cells. Actinobacteria are likely to be 2° *decomposers*, as they exude a wide variety of antibiotic metabolites (Vijayakumar et al., 2015), produce chitinolytic enzymes (Bai et al., 2016) and were especially enriched following the addition of ^{13}C bacterial necromass to soil (Buckeridge et al., 2020). Additionally, while both 1° and 2° *decomposers* must produce exoenzymes to degrade polymers, we expect 2° *decomposers* will have lower rates of extracellular enzyme production than 1° *decomposers* for the following reasons. First, microbial necromass is often tightly adhered to soil minerals, which could produce a lower return on investment for enzyme production (Wutzler et al., 2017). Second, 2° *decomposers* may be able to efficiently uptake and directly assimilate necromass constituents, such as such as muropeptides (cell wall oligomers; Fernandez et al., 2016; Hu et al., 2020) reducing the need for extracellular depolymerization. Exoenzymes are metabolically costly (Calabrese et al., 2022), and lower

exoenzyme production may allow *2° decomposers* to have higher C use efficiencies than *1° decomposers* (Table 1).

Predators that consume live microbes in soil include both prokaryotes (e.g., BALOs) and eukaryotic organisms like protists (Schulz-Bohm et al., 2017). BALOs have very small cells and can reproduce rapidly, generating multiple progenies (~5-30) per prey cell (Rotem et al., 2014; Stolp and Starr, 1963). Consequently, these organisms are likely to grow rapidly when prey populations (gram negative bacteria) are stimulated and have high C use efficiency if they directly assimilate the cellular building blocks from their prey. In support of this hypothesis, BALOs have been observed to exhibit high relative C assimilation rates and growth rates in soil (Dang et al., 2022b; Hungate et al., 2021). In contrast, eukaryotic predators have longer generation times, consume many prey cells prior to reproduction (Friman et al., 2008; Gallet et al., 2007), and thus may have comparatively low growth and C assimilation rates (Kramer et al., 2016) and C use efficiencies.

Within *passive consumers*, a wide variety of maximum growth rates are likely to be observed if *passive consumers* fall on a spectrum from relatively oligotrophic to relatively copiotrophic (Fig 2) due to tradeoffs between substrate affinity and growth rate (Fierer et al., 2007; Roller and Schmidt, 2015). Past work shows that organisms assimilating simple DOC display a wide range of growth rates (Morrissey et al., 2019, 2017). Further, research from aquatic systems reveals that the oligotroph-copiotroph framework explains the distribution (Lauro et al., 2009) and C acquisition patterns of bacterioplankton, which rely solely on DOC (Nelson and Carlson, 2012). For these reasons, applying the principles of the oligotroph-copiotroph within the *passive consumer* strategy is likely of value in predicting the fate of DOC.

Much research is needed to determine if and how the CAES framework described here could be used to describe the lifestyles of heterotrophic soil microbes. A clear weakness of the CAES framework is that it does not readily encompass microbial responses to stress, which are undoubtedly an essential part of structuring microbial community composition (Manzoni et al., 2012; Schimel, 2018) and determining community level functioning (Feckler et al., 2018). All ecological frameworks have strengths and weaknesses, and no ecological strategy can explain or predict the entirety of a species' traits. Despite the weaknesses mentioned above, the oligotrophic-copiotrophic framework is clearly useful for understanding and modeling microorganisms in aquatic systems (Giovannoni and Stingl, 2007; Nelson and Carlson, 2012). Similarly, derivatives of the C-S-R framework may be effective in explaining the distribution of soil organisms (Nelson and Carlson, 2012) and may covary with ecosystem functions (Malik et al., 2020). Though new and untested, our CAES framework has the potential to be even more effective because it is built upon measurable microbial traits. Moreover, the fact that it can be so easily integrated with soil C models makes it potentially very powerful way to connect microbial biodiversity with soil C cycling.

4. Measuring microbial traits relevant to CAES

Due to the inherent challenges of studying tiny organisms in highly diverse communities, a suite of methodological approaches is needed to assign ecological strategies to individual microbial taxa (i.e., phylotypes, genera) and to characterize their traits. Identifying functional genes associated with the acquisition of a specific C pool (e.g., catabolic enzymes, transporters, motility, etc.) using gene-centric metagenomic approaches can aid in determining the ecological strategies of microbes. These utilize databases that store information on enzyme families

(Carbohydrate-Active enzyme (CAZy)) and biological pathways (Clusters of Orthologous Genes (COG), Kyoto Encyclopedia of Genes and Genomes (KEGG), Gene Ontology (GO)). For example, Taş et al. (2018) identified genes encoding specific classes of enzymes involved in the decomposition of soil organic C (e.g., chitin, cellulose, hemi-cellulose, and cellobiose degradation). Similarly, Li et al. (2022) proposed a list of KEGG orthologies for inferring the microbial life history strategies (growth yield, resource acquisition and stress tolerance) in soil metagenomes. These functional genes can also be taxonomically annotated to identify the microbial lineages that carry out a specific process (Boyd et al., 2018). However, gene-centric metagenomics does not allow reconstruction of metabolic pathways for individual microbial lineages, as genes originating from a single genome are distributed on highly fragmented sequence data and cannot be linked. Alternatively, genome-centric metagenomics approaches reconstruct metagenome assembled genomes (MAGs), which allow linking metabolic pathways to specific populations and can provide useful information to study how specific microbial lineages transform soil organic C (Woodcroft et al., 2018). However, a major caveat of both gene- and genome-centric metagenomic approaches is that these only provide information on potential functions and metabolic pathways employed by microorganisms. Gene and genome centric metagenomic approaches could be combined with metatranscriptomics and metaproteomics approaches (Woodcroft et al., 2018) as well as taxon-specific functional measurements to provide a more complete understanding of an organism's traits.

Microbial C assimilation and growth in soil can be measured using stable isotope probing (SIP) which can track heavy isotopes (i.e., ^{13}C , ^{18}O) from target substrates into the lipids (phospholipid fatty acids, PLFA-SIP; Neufeld et al., 2007) or nucleic acids (DNA-SIP; Radajewski et al., 2000) of microorganisms. Quantitative stable isotope probing (qSIP) is more

sensitive than traditional DNA-SIP and enables the detection of quantitative variation in the functional traits of microbial taxa within natural communities (Hungate et al., 2015; Morrissey et al., 2019). The functional traits that can be measured via qSIP include relative growth rate (Li et al., 2022) and relative C assimilation rate from various ^{13}C enriched substrates (Dang et al., 2022b; Morrissey et al., 2019). These traits are analogous to the phenotypic traits used to assess the ecological strategies of plants and animals, such as reproduction rate (Pianka, 1970) and photosynthetic capacity (Berzaghi et al., 2020; Bussotti, 2008), and can be directly compared to pools and transformation rates in microbial-explicit model simulations.

Pure culture-based characterizations of microbial functions and traits can also help facilitate ecological classification of soil microorganisms. For example, taxa closely related to microbial groups known to prey on live bacteria and fungi in culture may be putatively classified as *predators* (Hungate et al., 2021). These would include the prokaryotic BALOs (Rotem et al., 2014) as well as eukaryotic phagotrophic protists (Murase, 2017). If microbial specialization on soil C pools covaries with other ecologically significant traits (as predicted in Table 1 and Fig 3), CAES may provide a useful lens through which to understand and model the impact of microbial community composition on ecosystem function.

5. Integrating CAES into a microbially explicit model

The Carbon Acquisition Ecological Strategies (CAES) proposed in Fig. 1 may be well suited for integration into soil C cycling models, which are structured based on stocks and transformation rates of specific C pools that can be classified under this framework. By way of example, the Carbon Organisms and Rhizosphere Processes in the Soil Environment (CORPSE) model (Sulman et al., 2017, 2014) divides SOM into three pools, representing rapidly-decomposing “labile” DOC, complex plant-derived substrates that are resistant to decomposition,

and microbial necromass. Ecological strategies encompassing groups of microorganisms that utilize these SOM pools and their corresponding traits may be a tractable conceptual advance toward integrating microbial biodiversity using data, rather than theoretical assumptions, into existing modeling frameworks like CORPSE. In this way, the CAES we propose are more conceptually aligned with current models of soil carbon cycling than other ecological stagey frameworks. For instance, because the oligotroph-copiotroph framework is built upon microbial responses to DOC, is not well suited to represent the influence of microbial biodiversity on exoenzyme production and the decomposition of complex soil organic matter. Further, neither the copiotroph-oligotroph nor the YAS frameworks yield insights into connections between microbial biodiversity and the decomposition of microbial necromass in soil. As mounting evidence suggests that microbial necromass accounts for a sizable fraction (Angst et al. 2021), if not the majority (Liang et al. 2019, Wang et al. 2021) of soil organic matter in many ecosystems, accurately modeling this pool is a high priority.

By directly linking microbial strategies with the soil C pools commonly represented in models, CAES provides a potential roadmap for integrating empirical data on microbial community diversity and function into soil C models and beyond. Using the CORPSE model as a case study, the CAES framework suggests a strategy to move beyond the current model, which uses one microbial biomass pool to represent the aggregate ability of the entire community to degrade all three soil C pools, into the four microbial groups that capture the strategies hypothesized by CAES. This could be accomplished by explicitly modeling three microbial groups that vary in their ability to decompose and assimilate DOC, primary plant material, and necromass. Currently, CORPSE models the decomposition of each pool based upon the following equation:

$$D_i = V_{max,i} \cdot f_i(T, \theta) \cdot C_{U,i} \frac{C_M/C_{U,i}}{\frac{C_M}{C_{U,i}} + k_M} \quad (1)$$

where the decomposition rate (D_i) of a given unprotected C substrate class ($C_{U,i}$) is a function of the maximum decomposition rate of the C substrate ($V_{max,i}$) scaled by its temperature (T), moisture sensitivity $f_i(T, \theta)$, and a saturating function of the ratio of microbial biomass (C_M), C substrate pool ($C_{U,i}$), and microbial substrate affinity (k_M). Decomposed C is partitioned into microbial biomass (B) and CO₂ production based on a substrate-specific carbon use efficiency (CUE_i), which could also be altered for different microbial functional groups. Microbial biomass turns over at a fixed lifetime (τ_B) which integrates maintenance respiration and mortality:

$$\frac{dB}{dt} = \sum_i CUE_i D_i - \frac{B}{\tau_B} \quad (2)$$

Using the measurement approaches outlined above, it may be possible to establish empirically grounded V_{max} , CUE , and k_M parameters controlling the ability of each functional group to decompose each substrate class. For example, 2° *decomposers*' preference for necromass would be represented by a higher V_{max} and CUE coupled with a comparatively lower k_M for that functional group decomposing necromass than for DOC or primary plant material. Because decomposition in the CORPSE model is a saturating function of the microbial biomass and the C substrate pool size, competition between microbial functional groups would be an emergent property of the model. In addition, predation in the model can be represented within the same framework by treating microbial biomass of another microbial functional group as the substrate for decomposition in Equation (1) (i.e., replacing $C_{U,i}$ with B of another functional group) and by adding an additional predation term to the mortality of the prey group in Equation (2). Different *predator* functional groups could be distinguished in turn using various maximum substrate acquisition rate (V_{max}), prey affinity (k_M), CUE , and mean lifetime (τ_B) parameters.

The empirical data needed to ground the $V_{\max}$, CUE, and k_M parameters for the CAES functional groups are likely to derive from laboratory microcosm experiments, and scaling from laboratory measurements to ecosystem processes is challenging. However, process-based models are a valuable platform for applying laboratory process measurements to ecosystem-level predictions (McGuire and Treseder, 2010). For example, Wang and Allison (2019) showed that microbial decomposition kinetics can be effectively scaled to ecosystem processes across heterogeneous soils, and Wang et al. (2013) used a suite of measurements to constrain key microbial parameters in a microbial-explicit soil C model. In many cases, parameter values measured at laboratory scales cannot be directly integrated into ecosystem-scale models due to differences in definitions or contrasting laboratory and field conditions (e.g., Steinweg et al., 2012). However, tractable approaches for bridging scales from the microbially-relevant microscale to the soil profile or ecosystem level have been developed (Davidson et al., 2014), and measured relative differences across microbial functional groups or environmental conditions can be valuable constraints on the variations in model parameters even when exact values may not be directly transferable (Wang et al., 2022).

Once the functional groups posited by the CAES are added to a process-based model like CORPSE, there may be challenges with the ability of the model to capture complex interactions between functional groups and, eventually, model stability. As structured, CAES would limit competition between functional groups because it assumes that distinct substrate preferences by each group would reduce competition for C substrates. However, we expect this assumption to be challenged by new empirical findings or emerge in the model as competition for shared resources like inorganic nitrogen. Previous theoretical modeling efforts may provide a roadmap for dealing with this type of emerging complexity. For example, Loreau (2001) showed that

assuming microbes were either substrate specialists or generalists modified the impact of microbial diversity on nutrient recycling. Also, lessons learned from food web models that explicitly represent detritus (e.g., Moore et al., 2004; Moore and Hunt, 1988) may also provide a roadmap for maintaining the stability of the groups when there is instability in the inputs, outputs, and pool size of their preferred substrate or when *predators* are introduced into a process-based model. Overall, these challenges in scaling and complexity are inherent to any effort to incorporate microbial functional groups into microbial-explicit soil models. As such, future efforts to integrate CAES into these models should assess whether representing multiple functional groups improves model performance or instead leads to more model uncertainty when compared to existing first order kinetic and single microbial pool models.

6. Conclusion

While the frameworks that currently dominate the microbial ecology literature have utility, over reliance on the application of ecological strategies originally developed for macro-organisms may stifle progress. We may be able to develop a more robust predictive framework if we instead focus on ways to generalize and synthesize our understanding of the functional diversity of soil microorganisms and the biochemical diversity of soil organic matter. The Carbon Acquisition Ecological Strategies (CAES) framework we have described here does this, and may help bridge the gap between microbial ecologists, biogeochemists, and ecosystem modelers. CAES offers a promising novel pathway to connect microbial biodiversity conceptually and quantitatively with soil C fluxes to predict feedbacks to global change.

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Figure Legends

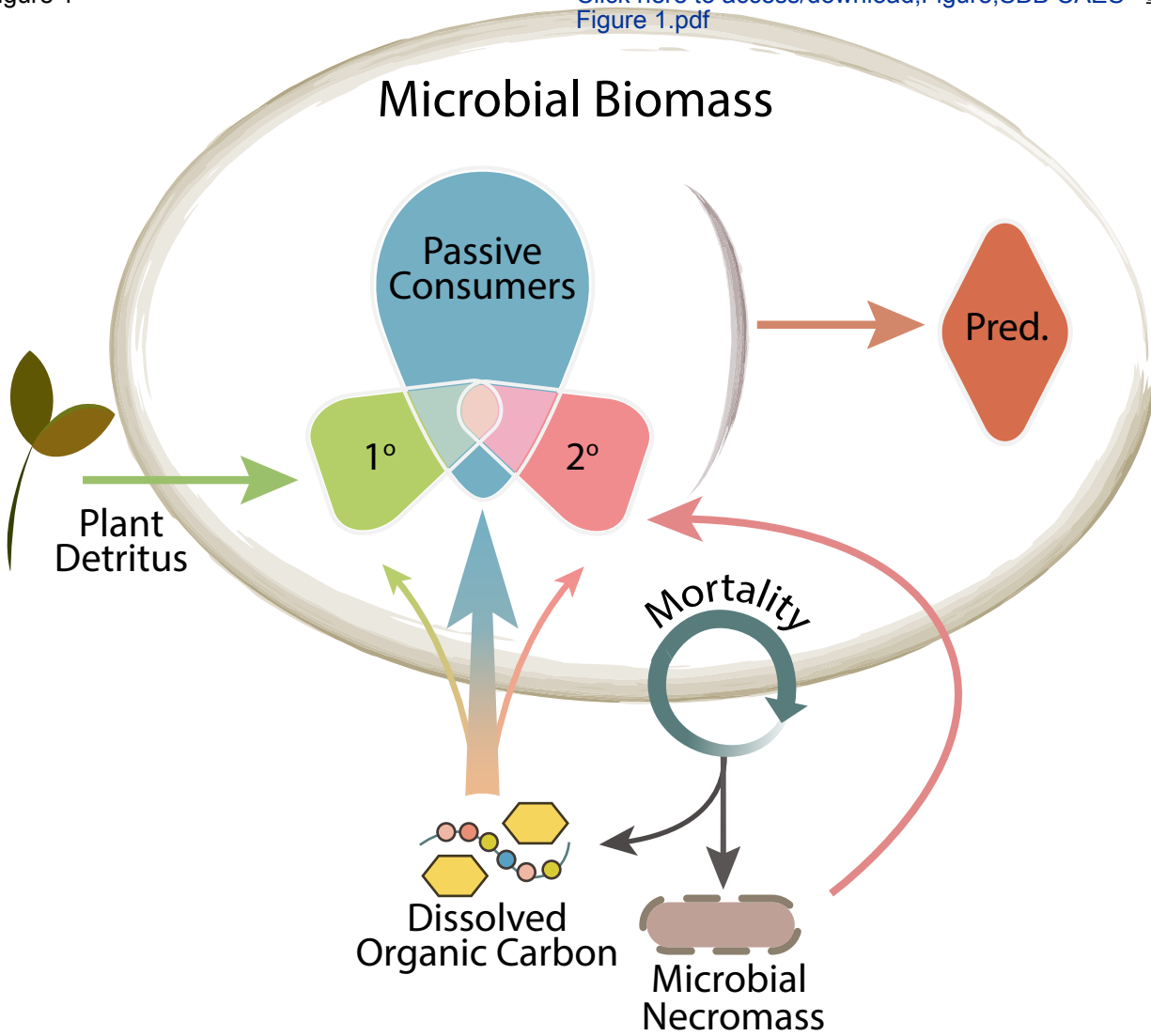
Fig. 1. Carbon acquisition ecological strategies (CAES) of soil microorganisms and associated carbon pools. In this framework, saprotrophic microbial taxa are categorized into an ecological strategy based on the soil carbon pool they predominantly consume and their role in the soil food web. Arrows reflect the assimilation of carbon from distinct soil organic matter pools into each of the CAES groups.

Fig. 2. Hypothesized distribution of maximum growth rates for saprotrophic soil microbes within each of the proposed carbon acquisition ecological strategies. Predators include both prokaryotic Bdellovibrio and like organisms (“BALOs”) and eukaryotic organisms such as phagotrophic protists.

Table 1. Select traits predicted to covary with carbon acquisition ecological strategies and associated soil carbon pools.

Ecological Strategy	Soil Carbon Pool	Carbon Use Efficiency	Exoenzyme Production	Motility
<i>1° Decomposer</i>	Complex plant detritus	Low	High	High
<i>2° Decomposer</i>	Microbial necromass	Intermediate	Intermediate	Intermediate
<i>Passive Consumer</i>	Dissolved organic carbon	High	Low	Low
<i>Predator</i>	Live microbial biomass	Intermediate	Low	High

Figure 1



Ecological Strategy

Carbon Pool

- | | |
|--------------------|-----------------------------|
| • 1° Decomposer | Complex Plant Detritus |
| • 2° Decomposer | Complex Microbial Necromass |
| • Passive Consumer | Dissolved Organic Carbon |
| • Predator | Live Microbial Biomass |

Figure 2



Growth Rate

Passive Consumers

oligotrophic

copiotrophic

Predators

eukaryotic

BALOs

secondary

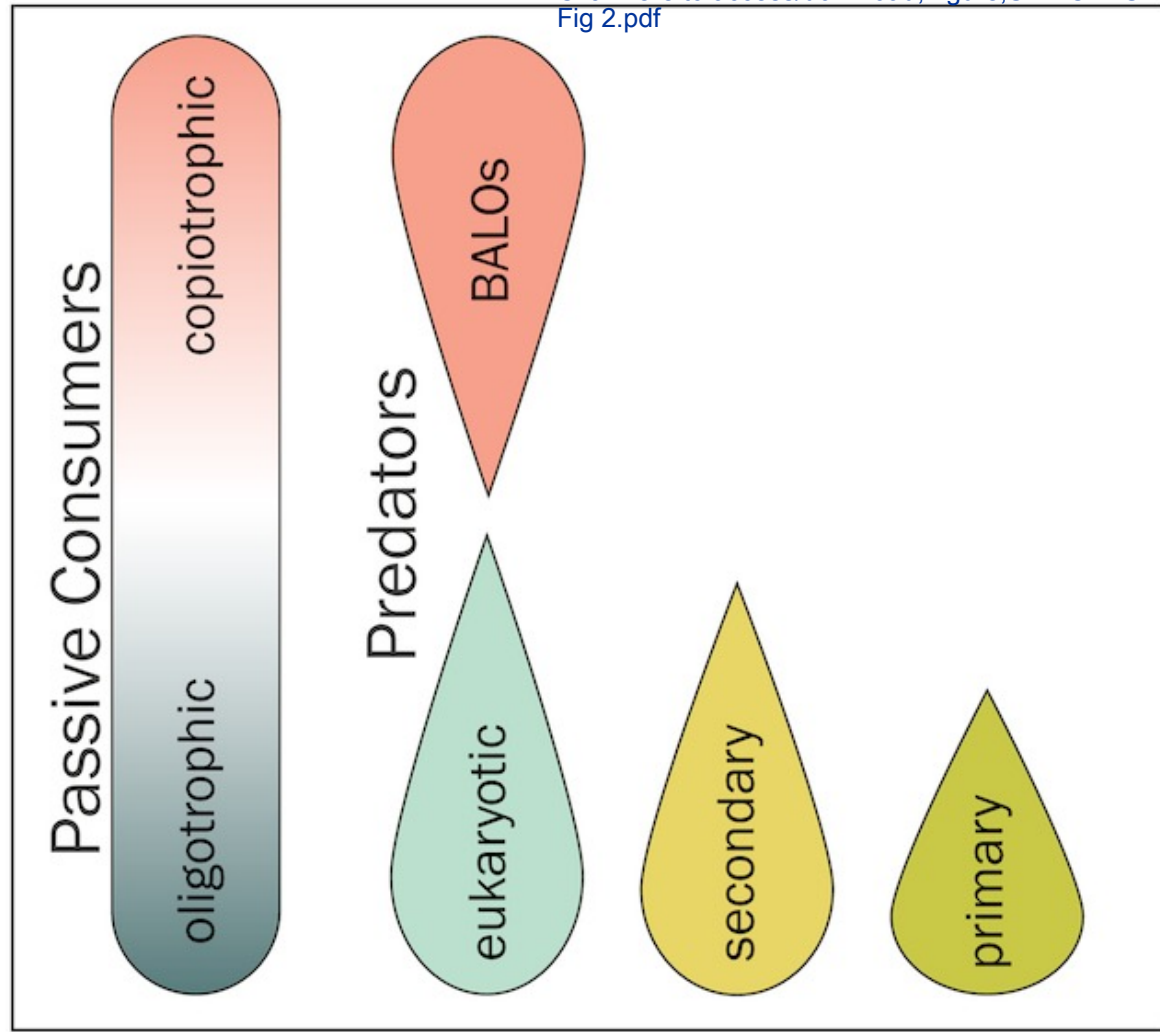
primary

DOC

*Live
Microbes*

*Dead
Microbes*

*Plant
Complex*



Declaration of interests

☒The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

☐The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: