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Burning Questions: How do soil microbes shape ecosystem biogeochemistry in the context of global change?

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Earth system models disagree on the future of global soil carbon (C), with projections ranging from losses of 70 Pg to gains of 250 Pg by the year 2100 (Todd-Brown et al. 2014). This disagreement is due, in part, to the high degree of uncertainty in the mechanisms that control soil C (Sulman et al. 2018), the largest dynamic pool of organic C on Earth. It remains unclear how climate change, rising atmospheric CO_2 levels, and other environmental changes will combine to affect global soil C. As key engineers of biogeochemical cycling, microbes play a crucial role in soil C responses to these environmental changes. Yet the path toward representing microbes in soil models remains uncertain. Therefore, we address four burning questions relevant for modeling microbial ecological, evolutionary, and biogeochemical processes in soils: (1) What is the role of soil microbes in biogeochemical cycling? (2) Does microbial community composition matter for soil carbon cycling? (3) Which ecological and evolutionary processes contribute to functional changes? (4) How should we model microbial eco-evolutionary mechanisms in soil C models?

Question: Do microbes matter for soil biogeochemical cycling?
Answer: Yes.

As the key drivers of biogeochemical cycles, microbes are the "engines of life on Earth" (Falkowski, Fenchel, and Delong 2008). Soil microbes decompose soil organic matter (SOM), with respiration responsible for over 50% of soil CO_2 emissions (Jia et al. 2016). Priming effects, whereby adding fresh carbon to soil results in the respiration of existing carbon, are impossible to explain without invoking microbial mechanisms (Kuzyakov 2010). In addition to their role in soil carbon turnover, microbes also promote soil carbon storage. The byproducts of microbial decomposition have a high affinity for minerals, which helps to form stable soil C (Miltner et al. 2012). Consequently, soil C storage by microbes is a prospective mechanism to mitigate the effects of anthropogenic global change.

Knowledge Gaps: It's clear that microbial biomass matters for biogeochemistry, but the magnitude of impact depends on both abiotic and biotic factors. While microbial biomass is a primary driver of decomposition in litter and the rhizosphere, other factors may dominate soil C dynamics in mineral soils, where access to substrate may limit decomposition (Schimel and Schaeffer 2012). The identity of microbes, their traits, and their relative abundances within the community (i.e., composition) could also be important. Wieder and collaborators (William R. Wieder, Bonan, and

Allison 2013) revealed the extreme sensitivity of soil C predictions to microbial parameters that can reflect both historical selection (phylogeny) and contemporary selection (demography) by new climatic conditions (Jennifer B. Hughes Martiny et al. 2006; Hanson et al. 2012). Given that environmental selection varies between locations and over time, microbial parameters should reflect spatiotemporal variation. An early attempt to integrate spatio-temporal variation in microbial composition demonstrated that projections of C loss by 2100 nearly doubled (Abs, Saleska, and Ferriere 2022), highlighting the need to better understand what environmental factors determine microbial properties, especially within a community context.

Does community composition matter for soil carbon cycling?
Answer: Yes, in some cases.
There are now many studies showing that biogeochemical functions, including carbon cycling, depend on microbial community composition. Based on a reciprocal transplant along a climate gradient, Glassman et al. found that rates of litter decomposition varied across different microbial communities even under the same climate and substrate conditions (Glassman et al. 2018). In laboratory microcosms, cumulative respiration of plant litter depended on microbial community composition, with the greatest respiration rates observed when microbial communities decomposed their native litter (Strickland et al. 2009). This result, and other examples of so-called "home-field advantage," provide compelling evidence that microbial composition can influence soil carbon cycling (Bradford et al. 2017). Over long timescales (e.g. centuries), processes of soil C stabilization may also be controlled by specific microbes (Schimel and Schaeffer 2012).

On the other hand, there are conditions under which microbial community composition may have little effect on soil biogeochemistry. Some researchers initially assumed that high microbial diversity equated to high functional redundancy among community members (Lawton and Brown 1994). Over the years, this idea has been tested, refined, and informed by trait-based theory (Allison and Martiny 2008; Jennifer B. H. Martiny et al. 2015). For example, many microbes can be considered redundant for "broad" functions such as respiration (Louca et al. 2018; Schimel and Schaeffer 2012) but possibly not for "narrow" functions such as methane production (McCalley et al. 2014). Microbial community composition may determine C flows in litter and in the rhizosphere, but not always in mineral soil where the limiting factor is access to substrate (Schimel and Schaeffer 2012; Dungait et al. 2012).

Knowledge Gaps: There is still work to be done to understand when and how microbial diversity is relevant for predicting biogeochemical processes. With high-throughput sequencing, characterizing who is present within a given soil microbial community is readily possible across large scales (Earth Microbiome Project). Yet functional metrics are still often aggregated at the community level, limiting our ability to link functional observations directly to taxonomic members and mechanistically link changes in abundance to function. For example, broad genetic characterizations of microbial communities (e.g.,16S rRNA gene amplicons) mask a high degree of variation in ecologically relevant traits among closely related strains, such as the temperature sensitivity of carbohydrate degradation (Chase et al. 2017; Johnson et al. 2006). Ultimately, there is a pressing need to understand which functions are conserved at which

taxonomic depth to better understand microbial genome-to-function relationships. By elucidating the degree of trait variation among co-occurring soil microbes, and the influence of ecological processes, we can better apply trait-based frameworks to understand the impact of both taxonomic and functional variation within soil microbial communities (Malik et al. 2020).

What ecological and evolutionary processes drive functional changes?
Answer: Environmental selection, dispersal, phenotypic plasticity, mutation, horizontal gene transfer, and stochasticity may all contribute to functional changes.

Ecological processes are largely associated with demography (shifts in abundance), while evolutionary processes can introduce entirely new alleles and traits into communities (Figure 1) (Chase et al. 2018). Field experiments demonstrate that microbial community composition can respond rapidly to environmental change (Matulich et al. 2015). Concurrently, recent evidence suggests that intra-species trait variation also influences compositional changes on similar timescales (Garud and Pollard 2020; Chase, Weihe, and Martiny 2021). Disentangling these processes provides essential information on the different mechanisms facilitating a microbiome's response to climate change.

Both taxonomic and functional changes are driven by deterministic (e.g., trait selection) and stochastic processes (Hanson et al. 2012). Deterministic processes combine more or less random sources of variation (physiological plasticity, dispersal, mutation, horizontal gene transfer) with environmental selection (sorting of species or alleles). Dispersal can stabilize or shift microbiomes through the immigration of novel and extant taxa. Stochastic processes, such as ecological and genetic drift, are non-selective and have been shown to play a major role in community assembly and functioning (Albright and Martiny 2018; Albright, Chase, and Martiny 2019). Ultimately, a microbiome's response to environmental change involves a continuum of these processes ranging from broad taxonomic shifts to the emergence of de novo mutations (Chase et al 2021).

<u>Knowledge Gaps:</u> While it is becoming increasingly clear that microbiomes respond to changing environments through ecological and evolutionary mechanisms, the timescales and relative contributions of each process remain unclear. For instance, we have a limited understanding of where microbial migrants come from (vegetation, soil, air) and whether dispersal should be viewed as an active or passive mechanism of a microbiome (Walters and Martiny 2020)). In a 30-year long climate manipulation experiment, (Melillo et al. 2017) found distinct phases of microbial community response to long-term warming. The fastest responses may result from changes in demography, whereas evolutionary responses may play out over years to decades. Additionally, given that past evolutionary divergence can frequently impact contemporary ecological patterns (J. B. Martiny et al. 2017), we need to assess when and where the outcomes of evolution affect ecological processes.

Although long-term *in vitro* microbial evolution experiments have shown strong evidence for adaptation (Lenski 2017; Rodríguez-Verdugo 2021; Rainey and Travisano 1998; Travisano and Lenski 1996), it is unclear if these observations extend to natural systems (Koskella and Vos 2015). In the few examples investigating the impact of evolution within natural communities, it

appears that slow generation times (Caro et al. 2022) combined with high spatial heterogeneity may limit detection of genome evolution and result in different evolutionary dynamics than those observed in laboratory environments (Chase, Weihe, and Martiny 2021). Resolving the feedbacks between ecological and evolutionary processes will be essential for improving model predictions of biogeochemical functions, and might contradict the current belief that biodiversity inhibits evolutionary responses to changing environments (Loeuille and Leibold 2008; Johansson 2008; de Mazancourt, Johnson, and Barraclough 2008).
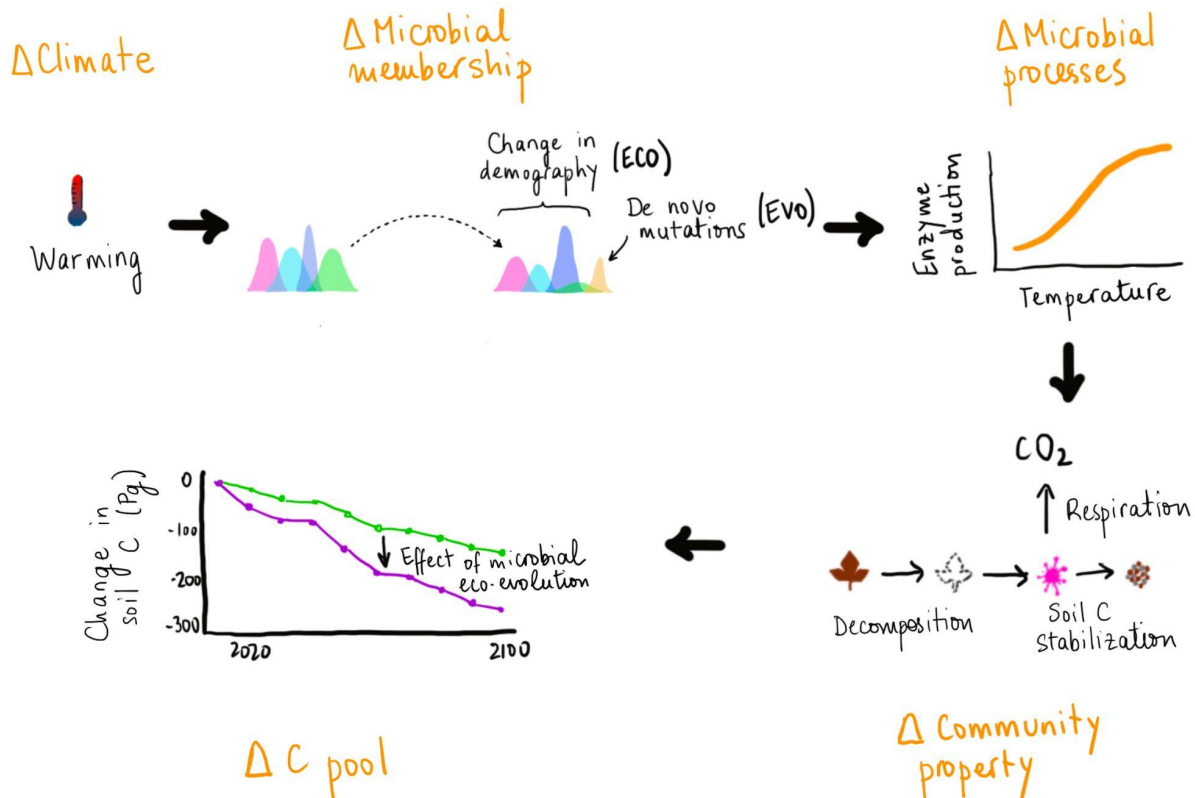

Figure 1: Conceptual diagram of microbial eco-evolutionary feedbacks to global change (here warming) and their implications for global soil C stocks.

How should we model microbial eco-evolutionary mechanisms in soil C models?
Answer: We need to represent observed mechanisms in models and develop approaches for scaling them up.

Thus far, microbial updates to soil biogeochemical models have involved very coarse representations of eco-evolutionary mechanisms. Several models have integrated the acceleration of microbial enzyme kinetics (degradation, uptake) with warming (biochemical response) (William R. Wieder, Bonan, and Allison 2013; Sulman et al. 2014; W. R. Wieder et al. 2014, 2015). A few models have also added a linear decrease in microbial carbon use efficiency (CUE) with warming (Li et al. 2014), which has been observed in short-term warming experiments and is the result of higher cellular maintenance needs (physiological response) (del Giorgio and Cole 1998; Manzoni et al. 2018; Geyer et al. 2019). Wieder et al's model assumed

that if microbes can adapt to warming, they will reduce or even cancel that loss in CUE (William R. Wieder, Bonan, and Allison 2013). They found that decreasing CUE (short-term physiological response) led to a slight soil C gain (5 Pg) by 2100, while constant CUE (long-term adaptation) led to a large soil C loss (300 Pg). However, there is no proof that evolutionary pressure will keep CUE constant.

More mechanistic modeling approaches are starting to emerge. Abs et al. proposed a mathematical method based on game theory to predict the microbial community eco-evolutionary response to warming (Abs, Saleska, and Ferriere 2022). This method accounts for progressive community trait change modifying the ecological environment (resources, competition), which initiates an eco-evolutionary feedback to modify selection of community traits. The model is agnostic to the ecological versus evolutionary mechanisms contributing to the trait change. The model predicted that microbes' C allocation to the production of C-targeting enzymes should non-linearly increase with warming, leading to greater soil C loss than in the non-adaptive model and with losses concentrated in cold regions.

<u>Knowledge Gaps</u>: Although there has been some recent progress in modeling microbial eco-evolutionary mechanisms, there are still many open questions. Do different mechanisms lead to different community functions, or do they converge functionally? Does it matter whether dispersal or mutation introduces new alleles, or can they be modeled as a combined process? Should the emergence of new variants be modeled as a constant rate or a variable dependent on each process? Empirical evidence suggests a complicated interaction between ecological and evolutionary processes (Chase, Weihe, and Martiny 2021). Consequently, eco-evolutionary theoretical models that predict the relative contribution of each process (e.g., demography vs mutations) will need to account for environmental selective pressures across different timescales. For instance, we predict that 1) new functions arising from de novo mutations might dominate in highly fluctuating, dispersal-limited environments; 2) dispersal could facilitate rapid functional turnover from regional species or population pools; and 3) demographic shifts could be more pronounced in isolated, functionally diverse communities and slow-oscillating environments (Loeuille and Leibold 2008).

Conclusion

We know that microbial communities respond to climate change through processes occurring at many spatiotemporal scales, ranging from physiological acclimation to entire community compositional shifts. Yet it remains unclear whether incorporating these processes into ecosystem models will reduce the current uncertainty in soil C predictions. The paradigm shift from modeling soil microbial communities as a "black box" to appreciating their role in soil formation has certainly propelled soil C modeling into a new, integrative frontier. With more local-scale empirical studies disentangling ecological and evolutionary processes, we can better understand whether and how adaptive processes influence predictions of microbial functioning. The integration of realistic soil spatial structure (pores, aggregates, rhizosphere vs bulk soil) is another necessary step towards reducing uncertainty in soil biogeochemical models. By taking these steps, we can build better mechanistic models of microbial community dynamics. With

these models in hand, we can predict the impact of microbes on soil C balance with applications for future climate prediction and greenhouse gas mitigation.

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