



Representing life in the Earth system with soil microbial functional traits in the MIMICS model

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Representing life in the Earth system with soil microbial functional traits in the MIMICS model

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Abstract

Projecting biogeochemical responses to global environmental change requires multi-scaled perspectives that consider organismal diversity, ecosystem processes and global fluxes. However, microbes, the drivers of soil organic matter decomposition and stabilization, remain notably absent from models used to project carbon cycle–climate feedbacks. We used a microbial trait-based soil carbon (C) model, with two physiologically distinct microbial communities to improve current estimates of soil C storage and their likely response to perturbations. Drawing from the application of functional traits used to model other ecosystems, we incorporate copiotrophic and oligotrophic microbial functional groups in the Microbial-Mineral Carbon Stabilization (MIMICS) model, which incorporates oligotrophic and copiotrophic functional groups, akin to “gleaner” vs. “opportunistic” plankton in the ocean, or *r* vs. *K* strategists in plant and animals communities. Here we compare MIMICS to a conventional soil C model, DAYCENT, in cross-site comparisons of nitrogen (N) enrichment effects on soil C dynamics. MIMICS more accurately simulates C responses to N enrichment; moreover, it raises important hypotheses involving the roles of substrate availability, community-level enzyme induction, and microbial physiological responses in explaining various soil biogeochemical responses to N enrichment. In global-scale analyses, we show that current projections from Earth system models likely overestimate the strength of the land C sink in response to increasing C inputs with elevated carbon dioxide (CO₂). Our findings illustrate that tradeoffs between theory and utility can be overcome to develop soil biogeochemistry models that evaluate and advance our theoretical understanding of microbial dynamics and soil biogeochemical responses to environmental change.

1 Introduction

Soil contains the largest terrestrial pool of carbon (C) on Earth, and it is susceptible to environmental change. Earth system models (ESMs) show high uncertainty in their

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representation of current stocks and projected changes of soil C dynamics, and inadequately capture soil C cycle–climate change feedbacks (Todd-Brown et al., 2013, 2014). This uncertainty reflects, in part, the mismatch between model assumptions and our contemporary understanding of soil C processes – notably, the explicit representation of soil microbial activity and metabolic traits (Schmidt et al., 2011; Treseder et al., 2012). Recent research demonstrates that microbial explicit model structures can improve estimates of present-day soil C stocks, and may enhance our ability to predict its response to global change factors (Sulman et al., 2014; Tang and Riley, 2014; Wieder et al., 2013). Yet these models largely ignore metabolic tradeoffs and life history strategies of microbial communities in soil systems, as well as their interactions with the physicochemical soil environment (Dungait et al., 2012; Miltner et al., 2012; Schimel and Schaeffer, 2012). A functional trait-based approach that broadly captures ecologically relevant niches can simplify microbial metabolic diversity and provide a way to examine its role in soil C dynamics under global change across scales. In terrestrial and marine systems, functional traits provide a tractable means to represent the effects of biodiversity on ecosystem function and biogeochemical cycles across scales (Barton et al., 2013; Reich, 2014), but to date analogous approaches below-ground are less well developed.

Resource economic theory provides a framework to understand how tradeoffs in life history strategies result in growth trait variation among life forms. The theory posits that growth traits develop from the allocation of limited resources to competing metabolic purposes – namely growth, reproduction, or maintenance functions (Litchman and Klausmeier, 2008). In the ocean, for example, plankton communities are comprised of many functional groups (Barton et al., 2013), where “gleaners” grow slowly and efficiently use and store resources, whereas “opportunists” grow and acquire nutrients quickly though usually have short lifespans (Dutkiewicz et al., 2013; Litchman et al., 2013). The distribution of these functional groups and their diversity helps explain patterns in ocean productivity (Vallina et al., 2014). Similar gradients of trait tradeoffs are observed in terrestrial plants, animals, and aquatic bacteria, described as the “fast-

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slow” plant economic spectrum (Reich, 2014), r vs. K life-history strategies (Pianka, 1970; Sommer, 1981; Wilbur et al., 1974), and copiotrophic vs. oligotrophic growth strategies (Koch, 2001), respectively. Functional groups based on these life history traits are instrumental in determining the relative abundances of certain organisms in a given environment, influencing the outcome of many ecosystem processes depending on which growth strategy dominates (Follows et al., 2007). Application of functional traits, such as those used to classify plants, provides a tractable means to scale from organismal traits, ecosystem processes, and global fluxes (Reichstein et al., 2014; van Bodegom et al., 2014).

A trait-based framework for soil microbes does not yet exist within an ESM. Instead, current representations of microbial diversity in soil models primarily serve to explore microbial community ecology in the context of leaf litter decomposition studies (Allison, 2012; Kaiser et al., 2014) or plant-soil feedbacks (Fontaine and Barot, 2005; Miki et al., 2010). Thus, trait-based microbial explicit models that simulate soil C stabilization and decomposition are not currently integrated with ecosystem or Earth system models. This is partially the result of inadequate methods to quantify and identify ecologically meaningful traits. However, recent advances in microbial community analyses are creating new opportunities to examine resource controls on the microbial functional trait diversity and abundance (Berg and Smalla, 2009; Fierer et al., 2007, 2012a, b; Krause et al., 2014; Mendes et al., 2014).

In two previously published studies, we documented the feasibility and impact of explicitly representing microbial activity at global scales (Wieder et al., 2013), and introduced Microbial-Mineral Carbon Stabilization model (MIMICS) (Wieder et al., 2014c). Building on this work, in this study we: (1) evaluate litter decomposition dynamics with long-term observations across continental-scale climate gradients, extending the analysis from two (Wieder et al., 2014c) to fourteen sites; (2) compare simulated and observed steady state soil C pools and simulated soil C response to nitrogen (N) enrichment; (3) validate global steady-state soil C projections with observationally derived estimates; and (4) quantify uncertainty in terrestrial C storage projections with alter-

native model structures. Our previous efforts to explicitly consider effects of microbial activity at global scales were not similarly validated by cross-site analyses (Wieder et al., 2013). Moreover, simultaneous considerations of litter quality, microbial physiological tradeoffs, and physicochemical protection, key features of MIMICS, were absent from previously published microbial explicit soil biogeochemical models that are run at global scales (Sulman et al., 2014; Wieder et al., 2013). Moreover, here we explore how MIMICS refines soil C theory and improves soil C predictions under global change scenarios, compared to conventional models that do not explicitly account for microbial physiology and functional diversity.

2 Modelling approach

2.1 Model description

MIMICS is a soil biogeochemical model that explicitly considers relationships among litter quality, functional tradeoffs in microbial physiology, and the physical protection of microbial byproducts in forming stable soil organic matter (SOM). In MIMICS, microbial biomass pools govern litter and SOM turnover and correspond to microbial functional types that exhibit copiotrophic (i.e., r selected) and oligotrophic (i.e., K selected) growth strategies (Fig. 1, Appendix A). The incorporation of these two groups is a first step towards incorporating microbial functional diversity in a process-based model, which allows us to test recent observations and new theoretical understandings linking microbial functional traits to soil biogeochemical processes (Fierer et al., 2007; Krause et al., 2014; Molenaar et al., 2009). Key functional traits that define microbial growth strategies for copiotrophic and oligotrophic microbial communities include microbial kinetics (based on Michaelis–Menten kinetics; V_{\max} and K_m), growth efficiency (MGE), and turnover (τ).

The seven C pools are considered in MIMICS (Fig. 1) include: metabolic and structural litter (LIT_m and LIT_s, respectively); copiotrophic and oligotrophic microbial biomass

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and observations of litter mass loss from the Long-Term Inter-site Decomposition Experiment Team (LIDET) study (Adair et al., 2008; Harmon et al., 2009). Expanding on our previous efforts to evaluate soil biogeochemical models with observational data (Bonan et al., 2013; Wieder et al., 2014c), this comparison evaluates the ability of both models to capture climate and litter quality effects on litter decomposition dynamics across continental-scale gradients. Here we summarize important details for the MIMICS simulations.

In contrast to conventional soil biogeochemistry models, MIMICS must first be spun up to steady-state conditions before beginning litter decomposition simulations. To facilitate model parameterization we calculated steady-state C pools in MIMICS using the stode function in the rootSolve package in R (Soetaert, 2009; R Team, 2014; sensu Wieder et al., 2014c). This requires site level information on climate (Harmon, 2013), edaphic properties (Zak et al., 1994), plant productivity (Knapp and Smith, 2001), and plant litter quality – here using biome level estimates from the TRY database (Brovkin et al., 2012; sensu Wieder et al., 2014a) (Table B1). Previous work shows no difference between simulations using seasonally varying temperature and mean annual temperature (W. Wieder, unpublished data), thus from steady-state conditions we ran parallel simulations with control and experimental settings using proscribed litter inputs and mean annual temperature. In six different experimental simulations we added an additional 100 gC to litter pools, portioned according to the lignin : N ratio of leaf litter used in the LIDET experiment. Since substrate and microbial biomass pools sizes determine rates of litter decomposition in MIMICS (Appendix A) we held microbial biomass pools constant in experimental simulations to avoid introducing unintended treatment effects from “litterbag” additions into our analysis. Using the difference between experimental and control litter pools we calculated the percent mass remaining of six litter types at 14 experimental sites over decade long simulations. Litter mass loss projections from DAYCENT (results from Bonan et al., 2013) and MIMICS were sampled at the same time points at LIDET results to compare model output with observational data.

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In MIMICS the size of microbial biomass pools are proportional to the quantity of litter inputs, in agreement with observations (Bradford et al., 2013; Fierer et al., 2009). Thus, our original parameterization of MIMICS produced biased results, where rates of mass loss were more rapid than LIDET observations at higher productivity sites (deciduous forests, conifer forests, and humid grasslands), and too slow in lower productivity sites (tundra, boreal forests, and arid grasslands). To alleviate this bias we normalized microbial turnover rates (τ) in MIMICS with an empirical relationship based on site level productivity (Appendix A).

Second, we evaluate the steady-state soil C pool projected by MIMICS and DAYCENT at the 14 LTER sites. DAYCENT represents C turnover above- and below-ground, emphasizing the importance of separately considering surface and sub-surface dynamics in soil biogeochemical models (Schmidt et al., 2011). Presently, MIMICS lacks this vertical resolution, thus we modified the microbial turnover and growth efficiency parameters from those used in the LIDET comparison. Such modifications seem justified given uncertainties generated because the processes regulating surface litter turnover differ from the C stabilization mechanisms that occur in mineral soils (Sollins et al., 1996). We estimated steady-state litter, microbial biomass, and soil C pools for MIMICS, again using the stode function in the rootSolve package in R (Soetaert, 2009; R Team, 2014). Similarly, we used an analytical approach to calculate steady-state pools with DAYCENT, modified to simulate 0–30 cm depth (Wieder et al., 2014a) (Table B1).

Third, we compared projections from both DAYCENT and MIMICS to increasing leaf litter inputs from a simulated N enrichment. In a recent meta-analysis, Liu and Greaver (2010) reported that across 111 published N enrichment studies mean leaf litter inputs increased 23%. We used this as the forced response of above-ground net primary productivity (ANPP) in cross-site simulations with both models. Although the temporal dynamics of soil C responses to environmental perturbations are critical, here we simplify our analysis by focusing on the steady-state response of soil C stocks to N enrichment. We calculated the change in steady-state litter, microbial biomass, and soil C

pools in response to this perturbation and compared simulated and observed results. We calculated the response ratio (treatment/control) for both model results and observations, and estimate uncertainty using a bootstrap analysis with the boot package in R (Canty and Ripley, 2013). Given observed changes in the microbial and biogeochemical response to N enrichment, we explored the parameter modifications that would have to be made to MIMICS to match these observations (Appendix A).

2.3 Global simulations

First, we compared the steady-state soil C stocks from MIMICS to field-derived soil C distributions, and then examined the response of soil C storage to rising CO₂ over the 21st century. Steady-state soil C estimates from MIMICS were generated using globally gridded estimates of mean annual NPP and soil temperature from an offline CLM4.5 simulation (D. Lawrence and C. Koven, unpublished data) as well as soil texture from the Harmonized World Soils Database (FAO et al., 2012) and litter quality (Brovkin et al., 2012) that were modified to the CLM grid (Wieder et al., 2014a, b). Using the stode function in the R rootSolve package (Soetaert, 2009) we calculated steady-state litter, microbial biomass, and soil C pools in MIMICS. We resolved uncertainties generated in applying MIMICS at global scales and to a depth of one-meter by adjusting parameter values τ , f_{met} , and P_{scalar} (Appendix A). All other parameter values were the same as in the LIDET experiment (Table B1). We compared soil C pools simulated by CLM4.5 and MIMICS (both 0–100 cm) to observationally-derived soil C estimates reported in the Harmonized World Soils Database (FAO et al., 2012) for the same depth interval (Wieder et al., 2014a, b, 2013).

Subsequently, we compared soil C projections from CLM4.5 and MIMICS to changing litter inputs under a simulation with elevated [CO₂] and constant climate. Mean annual NPP and soil temperature from CLM4.5 simulations were similarly used to force MIMICS. We did not modify our parameterization of MIMICS in transient global simulations because we lack the process-level understanding to guide potential microbial responses to elevated [CO₂]. Instead, our aim was to illustrate the potential effects of

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applying a microbial explicit approach in global C cycle projections. In our simulations we assume increases in $[\text{CO}_2]$ under Representative Concentration Pathway (RCP) 8.5 from 2006–2100 with a constant climate scenario (1850–1870), thus isolating the effects of increased productivity on soil C storage. We calculated the change in soil C pools simulated by CLM4.5 and MIMICS over the 21st century; however, differences in soil C accumulation between the models are likely conservative estimates because of discrepancies in how C substrates entered soil pools. The absolute C fluxes in MIMICS simulations are greater than CLM4.5, because we assume that changes in NPP immediately produce litterfall fluxes that enter LIT and SOM pools represented in MIMICS. Soils in CLM4.5 experience a longer temporal lag when “new” NPP enters litter pools, especially in forested regions where increasing NPP builds woodier biomass and augments coarse woody debris pools. These wood pools must first decompose before C substrates enter litter, and eventually SOM pools.

3 Results

3.1 Cross-site simulations

MIMICS and DAYCENT both capture climate effects on mean rates of leaf litter mass loss across sites and can replicate within site variation driven by litter quality ($r^2 = 0.66$ and 0.68 , respectively, $p < 0.001$; Fig. 2, Table 1). Notably, these process-based models are able to explain roughly the same amount of variation in LIDET observations as simpler statistical models (Adair et al., 2008). Similarly, both MIMICS and DAYCENT can adequately capture the ecoclimatological effects and continental-scale variation in steady-state soil C pools among the 14 LTER sites studied here (Pearson’s correlation $r = 0.77$ and 0.47 , $P = 0.001$ and 0.09 , respectively; Table B1). This indicates that the parameterizations of both models adequately describe litter decomposition dynamics; thus, we examined soil C projections from MIMICS and DAYCENT and contrast their potential response to environmental perturbations.

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From these steady-state conditions, we considered the potential soil C storage response to N enrichment. While N enrichment may drive increases in plant productivity, meta-analyses consistently demonstrate that N fertilization studies result in declining microbial biomass pools and modest to negligible changes in soil C storage (Fig. 3, open circles) (Janssens et al., 2010; Liu and Greaver, 2010; Lu et al., 2011). DAYCENT does not simulate microbial biomass pools, and the modifications that would be necessary to match observational data could include faster turnover of SOM pools (van Groenigen et al., 2014) and/or decreased MGE (Frey et al., 2013). Both of these modifications contradict current empirical and theoretical understanding of soil microbial responses to N enrichment (Janssens et al., 2010; Manzoni et al., 2012) (discussed below); thus, we made no changes to DAYCENT parameterizations. Consequently, steady-state litter and SOM pools simulated by DAYCENT increased proportionally to changes in litter inputs, in excess of observations (Fig. 3, filled squares).

Without modifications MIMICS underestimates litter C accumulation and builds excessive amounts of microbial biomass, but projects reasonable changes in soil C pools in response to increasing litter inputs (Fig. 3, open triangles). Observed declines in microbial biomass pools present important information to guide the parameterization of potential microbial response to N enrichment in MIMICS. Microbial biomass in MIMICS could decline via modifications to MGE, microbial kinetics, and/or microbial turnover. Given the diversity of microbial physiological responses we could explore with MIMICS, we investigate these scenarios by separately modifying MGE, microbial kinetics (V_{\max}), and microbial turnover (τ) in response to N enrichment.

We assume inherent physiological traits of the copiotrophic microbial community generate greater N demands and a lower microbial C:N ratio relative to their oligotrophic counterparts (Kaiser et al., 2014). As N enrichment may alleviate this N limitation, we increase the MGE of the copiotrophic community in the first scenario. This increased the relative abundance of copiotrophs, summarized by the copiotrophic:oligotrophic (C:O) ratio, which increased from 12.6 ± 3.2 (mean $\pm 1\sigma$) to $39.6 \pm 8.8\%$ following modifications to MGE parameters. Because the copiotrophic microbes have

relation ($r = 0.42$) and comparable RMSE (13.7 kgC m^{-2}) as the fully coupled ESMs represented in the Coupled Model Intercomparison Project, phase 5 (CMIP5) archive (Todd-Brown et al., 2013). Using the same NPP and mean annual soil temperature, steady-state litter, microbial biomass and SOM pools simulated by MIMICS totaled 218, 16.3 and 1530 PgC, respectively (Fig. 4c). MIMICS SOM estimates show a higher spatial correlation with the Harmonized World Soils Database ($r = 0.46$) and have a smaller RMSE (6.8 kgC m^{-2}) than the CLM4.5 results shown here, the CLM microbial model (Wieder et al., 2013) forced with the same data (W. Wieder, unpublished data), or any of the models represented in the CMIP5 archive (Todd-Brown et al., 2013).

Steady-state litter pool estimates from MIMICS are inversely related to mean annual soil temperature ($r = -0.89$), and largest in high latitude systems. Given its slower turnover, structural litter pools made up the bulk of total litter pools ($79 \pm 4.6\%$) and show a fairly even spatial distribution (Fig. S2a). Estimates of microbial biomass from MIMICS were strongly related to NPP estimates ($r = 0.99$), in accordance with observations (Bradford et al., 2013; Fierer et al., 2009). The C:O ratio in soils was 0.46 ± 0.13 , and was positively correlated with the chemical quality of litter inputs ($r = 0.80$; Fig. S2b). Physically protected SOM comprised $15 \pm 15\%$ of total SOM pools; but in clay rich soils, especially across the tropics, over half of total soil C was found in physically protected pools (Fig. S2c). Chemically protected and available SOM comprised $28 \pm 10\%$ and $57 \pm 12\%$ of total SOM pools, respectively, and were generally higher in high latitude ecosystems (Fig. S2d and e). Finally, total microbial biomass pools comprise $2.5 \pm 9.6\%$ of total SOM pools, within observational bounds (Serna-Chavez et al., 2013; Xu et al., 2013), although this high variability is largely driven by the 2% of grid cell around desert regions that have significantly higher microbial biomass: SOM ratios (Fig. S2f).

Elevated $[\text{CO}_2]$ increases global NPP estimates from CLM4.5 27% percent over 2005 levels, totaling 63.6 PgC yr^{-1} by 2100. Global litter and SOM pools in CLM4.5 increase linearly throughout the 21st century, gaining 22 and 88 PgC, respectively, by 2100, resulting in 110 PgC of terrestrial C storage in the top meter of soils (Fig. 5a).

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MIMICS projects less optimistic gains in soil C storage with increased terrestrial productivity: global litter, microbial biomass, and SOM pools simulated by MIMICS increased 10, 3.8, 51 PgC, respectively, with terrestrial soil C storage increasing 65 PgC by the end of the 21st century. Thus, with the same experimental forcing, total soil C changes projected by MIMICS are nearly half of those from CLM4.5. With MIMICS, litter and microbial biomass pools clearly respond to inter-annual variation in soil temperature (Fig. 5), although the magnitude of this variation is less than two percent of global pools. Litter, microbial biomass, and physically protected SOM pools demonstrate a linear increase with increasing NPP throughout the 21st century, similar to the CLM4.5 response.

The spatial distribution of soil C changes projected by CLM4.5 and MIMICS in response to increasing NPP strongly diverge (Fig. 6). Total soil C gains projected by CLM4.5 are large across the vegetated land surface, and positively correlated with NPP ($r = 0.61$). By contrast, MIMICS projects more modest soil C gains that are largely driven by C accumulation in physically protected SOM pools (53 Pg globally by 2100) concentrated in tropical and mid-latitude ecosystems (Figs. 6 and S3). MIMICS also projects small increases in chemically protected SOM pools (2.3 Pg), and modest C losses from available SOM pools (-5.0 Pg, globally by 2100), with the greatest declines in high latitude systems.

4 Discussion

The incorporation of microbial functional diversity in MIMICS enhanced both the prediction and understanding of potential feedbacks between microbial traits and soil C cycle dynamics, relative to models that lack explicit representation of microbial diversity such as DAYCENT or CLM. Though we already know that conventional and microbial models provide divergent predictions of soil C dynamics in transient simulations (Wieder et al., 2013), previous models used to predict C cycle–climate feedbacks fail to represent the metabolic tradeoffs within microbial communities, physiological traits, or interactions

with the physicochemical environment. Such deficiencies limit their capacity to inform our theoretical and mechanistic understanding of how soil microbial activity and diversity may ultimately affect soil C storage (Perveen et al., 2014) under various global perturbations. Using a trait-based model structure, MIMICS enhances both prediction and understanding of feedbacks between microbial diversity and soil biogeochemical function.

4.1 Cross-site simulations

The absolute and relative abundance of microbial functional types strongly regulates rates of C turnover in MIMICS. At sites spanning continental-scale gradients, MIMICS and DAYCENT can both adequately replicate observations from the LIDET study (Fig. 2, Tables 1 and B1), providing robust validation for climate and litter quality effects on simulated rates of leaf litter decomposition. By applying contemporary understanding of soil biogeochemical theory and providing greater process-level representation, particularly the inclusion of different microbial communities, MIMICS also generates a host of testable hypotheses that can motivate synergistic data collection – model development activities. Specifically, MIMICS responds more accurately to regional-scale perturbations, as illustrated by the cross-site response to N enrichment.

Potential effects of N enrichment on soil microbial activity, microbial community composition, and biogeochemical responses illustrate one example where such synergy may be found. Nitrogen enrichment commonly depresses oxidative enzyme activity (Saiya-Cork et al., 2002; Waldrop et al., 2004) and shifts microbial community structure (Fierer et al., 2012a; Frey et al., 2004; Gallo et al., 2004; Ramirez et al., 2012). As a result, N enrichment typically decreases rates of leaf litter decomposition (Fog, 1988; Hobbie, 2008; Knorr et al., 2005), reduces total microbial biomass pools and results in modest to negligible changes in soil C storage (Janssens et al., 2010; Liu and Greaver, 2010; Lu et al., 2011). These responses present significant modeling challenges because, as commonly parameterized, the quantity of litter inputs are proportional to the size of SOM and microbial biomass pools in conventional and microbial explicit mod-

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els, respectively (Todd-Brown et al., 2013; Wang et al., 2014; Wieder et al., 2013). By comparison, MIMICS also considers the physiological attributes of microbial functional types. This provides a means to capture the nuanced changes in inputs, microbial biomass, and SOM changes following N enrichment.

5 Theory and observations suggest that MGE should increase with nutrient availability, although data are sparse from soil systems (Manzoni et al., 2012). Theoretically, N enrichment may increase the MGE of the copiotrophic microbial community by decreasing the energy spilling (Bradford, 2013) associated with their intrinsically high N demand (Kaiser et al., 2014). By increasing copiotrophic growth efficiency with N enrichment,
10 this community builds more biomass, better competes for C substrates, and increases in relative abundance; results that are consistent with observational findings from N enrichment manipulations (Fierer et al., 2012a; Ramirez et al., 2012). Thus, microbial community shifts driven by changes in MGE may provide a mechanism that explains soil biogeochemical responses to N enrichment (Fig. 3) (Chen et al., 2014). Assuming
15 the oligotrophic community produces more oxidative enzymes, decreasing their absolute abundance would elicit declines in oxidative enzyme activity (Saiya-Cork et al., 2002; Waldrop et al., 2004). Our results suggest this is more likely through changes in community structure that are driven by MGE or microbial turnover than through direct enzyme inhibition (Fig. S1a). These examples broadly illustrate how consideration
20 of microbial functional traits in MIMICS can simultaneously advance predictions and theory, producing testable hypotheses that can help guide future experimental work.

The interplay between microbial community composition and soil biogeochemical response in MIMICS depends on assumptions made about how physiological differences between microbial functional types affect the ultimate fate of C (Schimel and Schaeffer,
25 2012; Wieder et al., 2014c). However, microbial allocation strategies remain poorly understood, emphasizing the need for better theoretical and quantitative understanding microbial physiological traits, including microbial efficiency and turnover (Hagerty et al., 2014), the partitioning of microbial residues into different SOM pools, and microbial C : O ratios. Moreover, we also lack adequate data and understanding of how microbial

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tion with increasing productivity, thus showing no long-term soil C accumulation (Wang et al., 2014; Wieder et al., 2013). Results from MIMICS present a middle ground between these two approaches, where increasing litter inputs accelerates rates of soil C turnover, but also builds stable SOM (Figs. 5 and 6). These findings result from the implementation of microbial traits and their interactions with the physicochemical soil environment in MIMICS.

Strikingly different spatial patterns of soil C changes emerge from our global simulations. Whereas CLM4.5 presents nearly uniform increases in soil C accumulation across vegetated land surfaces, MIMICS projects a much more nuanced and heterogeneous response of soil C response to increasing NPP (Fig. 6). Low-latitude and some temperate ecosystems provide a moderate C sink, while high latitude systems become a weak source of C to the atmosphere. These spatial differences are driven by the response of microbial biomass and SOM pools to increasing litter inputs in MIMICS. Globally, increasing litter inputs builds more microbial biomass (Fig. 5). Subsequent effects of larger microbial biomass pools on soil C storage, or loss, depend on interactions between microbial functional traits, community composition, and the physicochemical soil environment.

Microbial residues build SOM, especially in clay rich soils that physically protect inherently labile microbial residues. At low latitudes the high chemical quality of litter inputs increases the relative abundance of copiotrophs, which also have faster turnover rates and produce residues that are physically protected in clay rich soils common across the tropics (Fig. S2d). Accordingly, we see the largest soil C gains in physically protected SOM pools across the tropics in response to elevated $[\text{CO}_2]$ (Figs. 6b and S3a), illustrating how interactions between microbial functional traits and the physicochemical soil environment may influence soil C responses to perturbations. By contrast, low litter quality characteristic in high latitude systems favors an oligotrophic dominated community. The coarsely textured soils common at high latitudes also afford little physical protection of SOM. These factors result in large SOM pools that are not protected by mineral-association and are vulnerable to microbial degradation and loss.

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Thus, increasing NPP and microbial biomass accelerates the decomposition of litter and SOM, with significant losses from available SOM pools evident across arctic and boreal ecosystems (Figs. 6b and S3c). By incorporating a trait-based framework, spatial variability in soil C projections from MIMICS generate testable hypotheses that can be evaluated with future experimental work. These results emphasize the importance of interactions between litter quality, microbial community dynamics, and soil texture in mediating soil C response to environmental change at regional- to global-scales.

Although direct experimental tests to evaluate these results are scant, results from leaf litter manipulations indicate that augmenting litter C inputs may drive soil C accumulation on high clay soils (e.g., tropical forests; Leff et al., 2012; cf. Sayer et al., 2011), whereas coarsely textured soils (e.g., temperate forests) show less dramatic soil C accumulation, and some evidence for net soil C losses (Bowden et al., 2014; Lajtha et al., 2014). Moreover, empirical data shows CO₂ enrichment may stimulate plant productivity, but without proportional increases in soil C storage (Hungate et al., 2009; van Groenigen et al., 2014). Thus, we find little experimental evidence to support the large and ubiquitous soil C gains projected by CLM4.5 and other conventional soil biogeochemistry models in response to increasing C inputs. Although projections from MIMICS seem to better agree with observations, greater attention should be given to evaluating the models' process-level representation and temporal dynamics across ecoclimatological gradients. Key uncertainties in the parameterization of MIMICS include the partitioning of microbial residues to different SOM pools as well as understanding factors controlling C fluxes between protected and available pools. In particular, these fluxes are critical in regulating the size and turnover of physically protected SOM pools in MIMICS, which largely determine the soil C response (Figs. 5, 6 and S3).

Beyond differences in total soil C accumulation, MIMICS also shows stronger sensitivity to inter-annual variability than conventional models. For example, effects of inter-annual temperature variability on litter and microbial biomass pools are clearly evident (Fig. 5). Following perturbations, microbial explicit models can also exhibit an oscillatory behavior (Li et al., 2014; Wang et al., 2014). Our global simulation provides some

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insight into the magnitude of these responses in the context of a realistic, global environmental perturbation. Together, inter-annual variability and the oscillatory response in MIMICS show less than two percent variation in litter and microbial biomass pools, significantly less than in other microbial models (Wang et al., 2014; sensu Wieder et al., 2014c). Future application of non-linear models, however, should be aware of these characteristics, especially in climate change simulations. The temperature sensitivity and oscillations in litter and microbial biomass pools, however, are dwarfed by large, sustained changes in SOM pools throughout the 21st century driven by increasing NPP (Figs. 5 and 6); therefore, testing the accuracy of projections and their underlying mechanisms in MIMICS is more important than concern over potential oscillations in litter and microbial biomass pools.

5 Conclusions

Our study shows that the incorporation of soil microbial functional traits in MIMICS improves representation of soil C dynamics in an ESM. Moreover, MIMICS offers a platform to develop new understanding of the relationships between microbial communities and SOM dynamics by addressing ecological questions surrounding microbial community composition and soil biogeochemical function. By grouping microbial diversity into simplified functional groups, we demonstrate how community differences can have strong influence over soil C projections, and show that understanding how functional traits and groups organize across environmental gradients and reorganize following perturbations is needed to parameterize and accurately simulate soil biogeochemical function in ESMs.

Appendix A: Model description

A1 Model structure, assumptions and equations

The temperature sensitivity of microbial kinetics (described in Table B1) are derived from observational data (German et al., 2012; sensu Wieder et al., 2013, 2014c), with modifications based on assumptions regarding microbial functional types (Beardmore et al., 2011; Dethlefsen and Schmidt, 2007; Molenaar et al., 2009), litter chemical quality and soil texture effects (V_{mod} and K_{mod} ; Table B1). Other parameter values broadly rely on our theoretical understanding of how physiological tradeoffs produce life-history strategies that are optimized for different resource environments (Beardmore et al., 2011; Resat et al., 2012; Russell and Cook, 1995). For example, fast-growing r strategists (copiotrophs) are typically characterized by a lower MGE, but higher growth and turnover rates, relative to slower-growing K strategists (oligotrophs) (Fierer et al., 2007, 2012a; Klappenbach et al., 2000; Pianka, 1970; Ramirez et al., 2012). Given that physiological traits in MIMICS are also sensitive to environmental factors, including temperature and resource chemistry (Frey et al., 2013; Keiblinger et al., 2010; Manzoni et al., 2012; Rousk and Bååth, 2007; Sinsabaugh et al., 2013; Steinweg et al., 2008; Thiet et al., 2006) the physical and chemical resource environment determines the relative abundance of these microbial functional types. Here we assume that the production of microbial biomass will be more rapid and more efficient using substrates from metabolic litter and available SOM pools, and that for a given substrate oligotrophic microbial communities will have a higher MGE than copiotrophs (Kaiser et al., 2014; Wieder et al., 2014c).

Turnover of microbial residues (Eqs. A4 and A8) provides inputs to SOM pools that are considered microbial available, chemically protected, or physically protected, with the latter determined by soil clay content in different soil environments. We assume that finely textured soils will restrict enzyme access to available C substrates, which is represented by increasing the half saturation constant (K_m) of available SOM with increasing clay content. We assume the size and composition of microbial biomass

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pools influences the decomposition of chemically protected SOM into simpler substrates (available SOM, Eq. A10) that can be assimilated into microbial biomass. The size of the microbial biomass pool has no influence on the transfer of physically protected SOM to available SOM pools (Eq. A9). This flux is intended to represent the physical desorption of SOM from mineral surfaces and/or the breakdown of aggregates, with flux rates inversely related to soil clay content. There are no soil respiration losses associated with movement of chemically or physically protected SOM into the available SOM pool. The fluxes ($\text{mg C cm}^{-3} \text{ h}^{-1}$) numbered on Fig. 1, are calculated as:

$$A_1 = \text{MIC}_r \times V_{\text{max}[r1]} \times \text{LIT}_m / (K_{m[r1]} + \text{LIT}_m) \quad (\text{A1})$$

$$10 \quad A_2 = \text{MIC}_r \times V_{\text{max}[r2]} \times \text{LIT}_s / (K_{m[r2]} + \text{LIT}_s) \quad (\text{A2})$$

$$A_3 = \text{MIC}_r \times V_{\text{max}[r3]} \times \text{SOM}_a / (K_{m[r3]} + \text{SOM}_a) \quad (\text{A3})$$

$$A_4 = \text{MIC}_r \times \tau_{[r]} \quad (\text{A4})$$

$$A_5 = \text{MIC}_K \times V_{\text{max}[K1]} \times \text{LIT}_m / (K_{m[K1]} + \text{LIT}_m) \quad (\text{A5})$$

$$A_6 = \text{MIC}_K \times V_{\text{max}[K2]} \times \text{LIT}_s / (K_{m[K2]} + \text{LIT}_s) \quad (\text{A6})$$

$$15 \quad A_7 = \text{MIC}_K \times V_{\text{max}[K3]} \times \text{SOM}_a / (K_{m[K3]} + \text{SOM}_a) \quad (\text{A7})$$

$$A_8 = \text{MIC}_K \times \tau_{[K]} \quad (\text{A8})$$

$$A_9 = \text{SOM}_p \times D \quad (\text{A9})$$

$$A_{10} = (\text{MIC}_r \times V_{\text{max}[r2]} \times \text{SOM}_c / (\text{KO}_{[r]} \times K_{m[r2]} + \text{SOM}_c)) + (\text{MIC}_K \times V_{\text{max}[K2]} \times \text{SOM}_c / (\text{KO}_{[K]} \times K_{m[K2]} + \text{SOM}_c)) \quad (\text{A10})$$

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Thus, changes in C pools (mg C cm^{-3}) can be described using the following equations:

$$\frac{d\text{LIT}_m}{dt} = I_{[\text{LIT}_m]} \times (1 - f_{i,\text{met}}) - A_1 - A_5 \quad (\text{A11})$$

$$\frac{d\text{LIT}_s}{dt} = I_{[\text{LIT}_s]} \times (1 - f_{i,\text{struc}}) - A_2 - A_6 \quad (\text{A12})$$

$$\frac{d\text{MIC}_r}{dt} = (\text{MGE}_{[1]} \times A_1) + (\text{MGE}_{[2]} \times A_2) + (\text{MGE}_{[1]} \times A_3) - A_4 \quad (\text{A13})$$

$$\frac{d\text{MIC}_K}{dt} = (\text{MGE}_{[3]} \times A_5) + (\text{MGE}_{[4]} \times A_6) + (\text{MGE}_{[3]} \times A_7) - A_8 \quad (\text{A14})$$

$$\frac{d\text{SOM}_p}{dt} = I_{[\text{LIT}_m]} \times f_{i,\text{met}} + (f_{p[r]} \times A_4) + (f_{p[K]} \times A_8) - A_9 \quad (\text{A15})$$

$$\frac{d\text{SOM}_c}{dt} = I_{[\text{LIT}_s]} \times f_{i,\text{struc}} + (f_{c[r]} \times A_4) + (f_{c[K]} \times A_8) - A_{10} \quad (\text{A16})$$

$$\frac{d\text{SOM}_a}{dt} = (f_{a[r]} \times A_4) + (f_{a[K]} \times A_8) + A_9 + A_{10} - A_3 - A_7 \quad (\text{A17})$$

A2 Cross-site simulations

To simulate steady state SOC pools with MIMICS (Table C1) we modified parameters relating to microbial growth efficiency (MGE) and turnover (τ). Specifically, we decreased the MGE of the copiotrophic community (to 0.5 and 0.2 for metabolic and structural substrates, respectively), and increased the sensitivity of MIC_r turnover to litter quality ($5.2 \times 10^{-4} \times e^{0.6(f_{\text{met}})}$). We also increased microbial turnover three-fold over values listed in Appendix A.

To match observed changes in the microbial and biogeochemical response to N enrichment we further modified potential changes to microbial physiology following N enrichment. These included modifications to MGE, microbial kinetics, and microbial turnover. Modifications to MGE following N enrichment and their effect on steady-state

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C pools simulated by MIMICS are described in the main text (Fig. 3). We also explored the likelihood of matching observed soil C response to N enrichment by modifying microbial kinetics and turnover (V_{\max} and τ , respectively). In both of these simulations MGE values were the same as in the LIDET experiment (0.55 and 0.25, for metabolic and structural substrates entering MIC_r). To represent N inhibition of oxidative enzyme activity (Fog, 1988; Knorr et al., 2005) we decreased the V_{\max} parameter associated with oligotrophic community turnover of structural litter pools and chemically protected SOM in MIMICS by 15 % (Fig. S1a, filled triangles). To explore how change in microbial turnover may alter steady-state C pools simulated by MIMICS we show results following modifications to τ . Data in Fig. S1b (filled triangles) show results following a six percent increase in the turnover of MIC_K in response in N enrichment.

A3 Global simulations

We resolved uncertainties generated in applying MIMICS at global scales and to a depth of one-meter by adjusting parameter values τ , f_{met} , and P_{scalar} . Specifically, we increased the sensitivity of MIC_r turnover to litter quality ($5.2 \times 10^{-4} \times e^{0.4(f_{\text{met}})}$). We used the same equation to partition litter inputs into metabolic and structural pools, but reduced total allocation to metabolic pools 15 %. Finally, we modified the physical protection scalar ($P_{\text{scalar}} = (0.8 \times e^{-3\sqrt{f_{\text{clay}}}})^{-1}$).

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Table B1. MIMICS parameters, values, and units used for LIDET simulations.

Parameter	Description	Value	Units
f_{met}	Partitioning of litter inputs to LIT_m	0.85–0.013 (lignin/N)	–
f_i	Fraction of litter inputs transferred to SOM	0.05, 0.05 ^a	–
V_{slope}	Regression coefficient (Eq. 1)	0.063 ^b	$\ln(\text{mg C}_s (\text{mg MIC})^{-1} \text{h}^{-1}) \text{ } ^\circ\text{C}^{-1}$
V_{int}	Regression intercept (Eq. 1)	5.47 ^b	$\ln(\text{mg C}_s (\text{mg MIC})^{-1} \text{h}^{-1})$
a_V	Tuning coefficient (Eq. 1)	8×10^{-6} b	–
V_{mod-r}	Modifies V_{max} for fluxes into MIC_r	10, 2, 10 ^c	–
V_{mod-K}	Modifies V_{max} for fluxes into MIC_K	3, 3, 2 ^d	–
K_{slope}	Regression coefficient (Eq. 2)	0.017, 0.027, 0.017 ^{c,d}	$\ln(\text{mg C cm}^{-3}) \text{ } ^\circ\text{C}^{-1}$
K_{int}	Regression intercept (Eq. 2)	3.19 ^b	$\ln(\text{mg C cm}^{-3})$
a_K	Tuning coefficient (Eq. 2)	10 ^b	–
K_{mod-r}	Modifies K_m for fluxes into MIC_r	0.125, 0.5, $0.25 \times P_{scalar}$ c	–
K_{mod-K}	Modifies K_m for fluxes into MIC_K	0.5, 0.25, $0.167 \times P_{scalar}$ d	–
P_{scalar}	Physical protection scalar used in K_{mod}	$(2.0 \times e^{-2\sqrt{f_{clay}}})^{-1}$	–
MGE	Microbial growth efficiency	0.55, 0.25, 0.75, 0.35 ^e	mg mg^{-1}
τ	Microbial biomass turnover rate	$5.2 \times 10^{-4} \times e^{0.3(f_{met})} \times \tau_{mod}$, $2.4 \times 10^{-4} \times e^{0.1(f_{met})} \times \tau_{mod}$ f	h^{-1}
τ_{mod}	Modifies microbial turnover rate	$0.8 < \sqrt{\text{NPP}/100} < 1.2$ g	–
f_p	Fraction of τ partitioned to SOM_p	$0.3 \times e^{1.3(f_{clay})}$, $0.2 \times e^{0.8(f_{clay})}$ f	–
f_c	Fraction of τ partitioned to SOM_c	$0.1 \times e^{-3(f_{met})}$, $0.3 \times e^{-3(f_{met})}$ f	–
f_a	Fraction of τ partitioned to SOM_a	$1 - (f_p + f_c)$ f	–
D	Desorption rate from SOM_p to SOM_a	$1.5 \times 10^{-5} \times e^{-1.5(f_{clay})}$	h^{-1}
KO	Further modifies K_m for oxidation of SOM_c	4, 4 ^f	–

^a For metabolic litter inputs entering SOM_p and structural litter inputs entering SOM_c , respectively.

^b From observations in (German et al., 2012), as used in (Wieder et al., 2013, 2014c).

^c For LIT_m , LIT_s , and SOM_a , fluxes entering MIC_r , respectively.

^d For LIT_m , LIT_s , and SOM_a , fluxes entering MIC_K , respectively.

^e The first two values correspond to C fluxes into MIC_r , the second two values correspond to C fluxes into MIC_K (see Eqs. A13 and A14).

^f For MIC_r and MIC_K , respectively.

^g NPP units = $\text{g C m}^{-2} \text{yr}^{-1}$.

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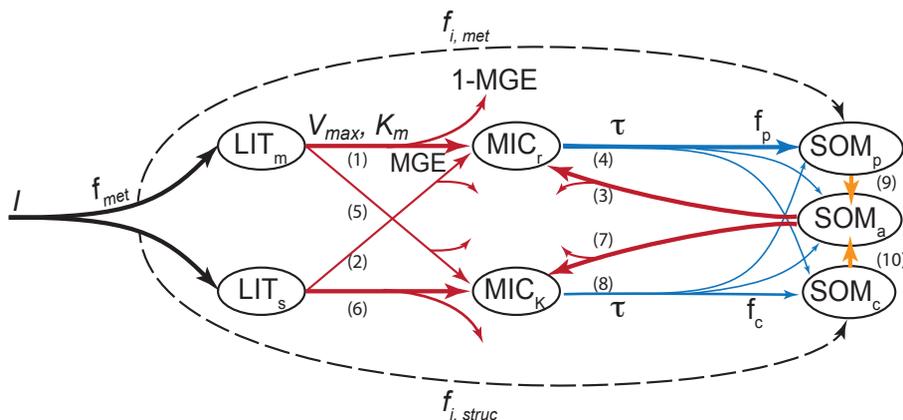


Figure 1. Soil C pools and fluxes represented in MIMICS. Litter inputs (I) are partitioned into metabolic and structural litter pools (LIT_m and LIT_s) based on litter quality (f_{met}). Microbial growth efficiency (MGE) determines the partitioning of C fluxes entering microbial biomass pools vs. heterotrophic respiration. Turnover of the microbial biomass (τ , blue) depends on microbial functional type (MIC_r and MIC_k), and is partitioned into available, physically protected, and chemically protected SOM pools (SOM_a , SOM_p , and SOM_c , respectively).

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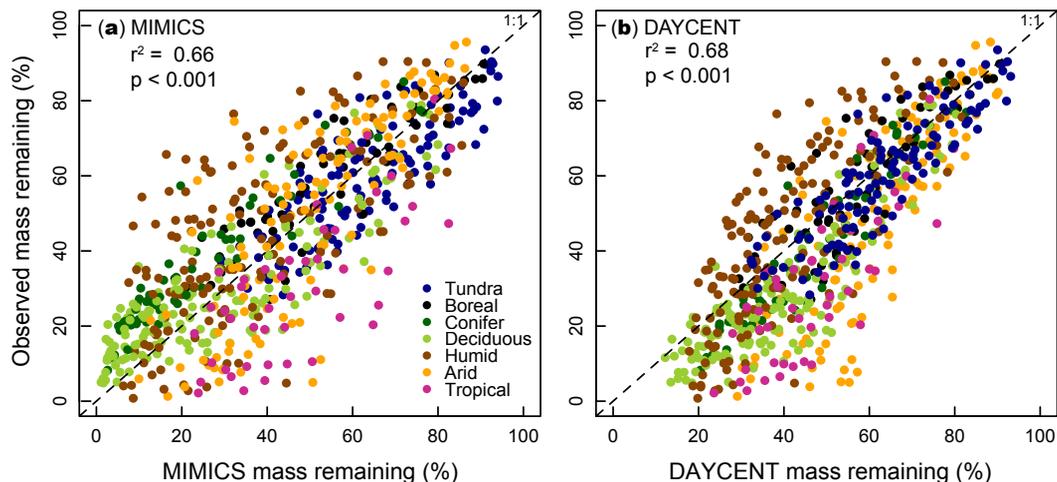


Figure 2. Litter decomposition results from observation and models. Points show the percent leaf litter mass remaining of six different litter types that decomposed over a decade long experiment across 14 different LTER sites, which correspond to seven different biomes. Simulations from **(a)** MIMICS and **(b)** DAYCENT were sampled at the same time points as LIDET observations. Dashed line shows the 1 : 1 line (see also Table 1).

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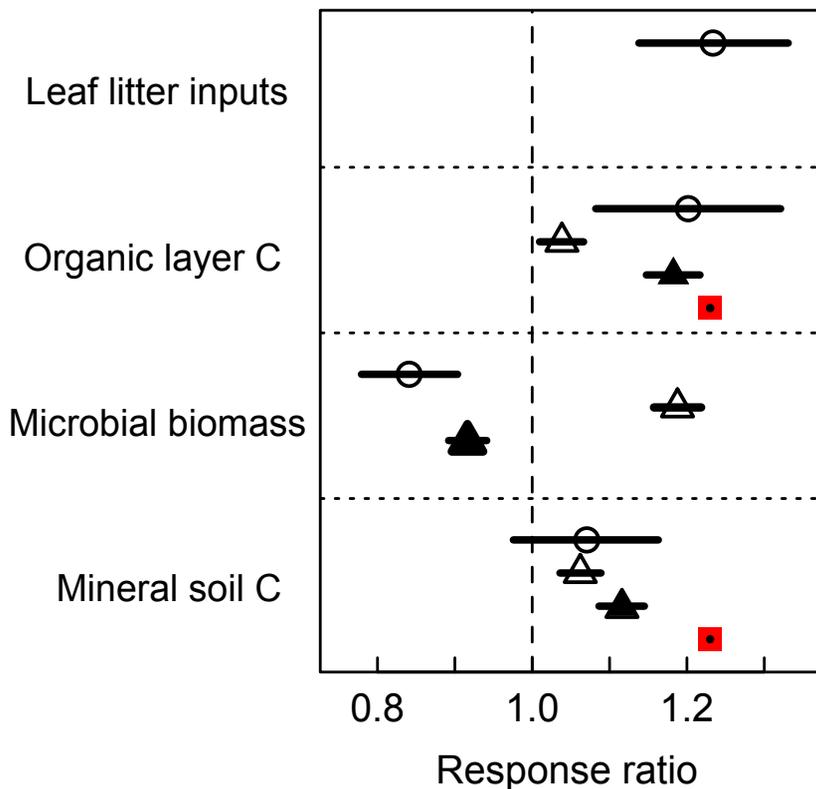


Figure 3. Observed and modeled C response ratio (treatment/control) to experimental N enrichment. Open circles show observed mean and 95 % confidence interval of leaf litter inputs, organic layer C, microbial biomass, and mineral soil C (Liu and Greaver, 2010). Modeled results show the steady-state changes in pools following increases in leaf litter inputs projected by MIMICS (open triangles), MIMICS (with increasing MGE in response to N enrichment; filled triangles) and DAYCENT (filled squares; see also Fig. S1).

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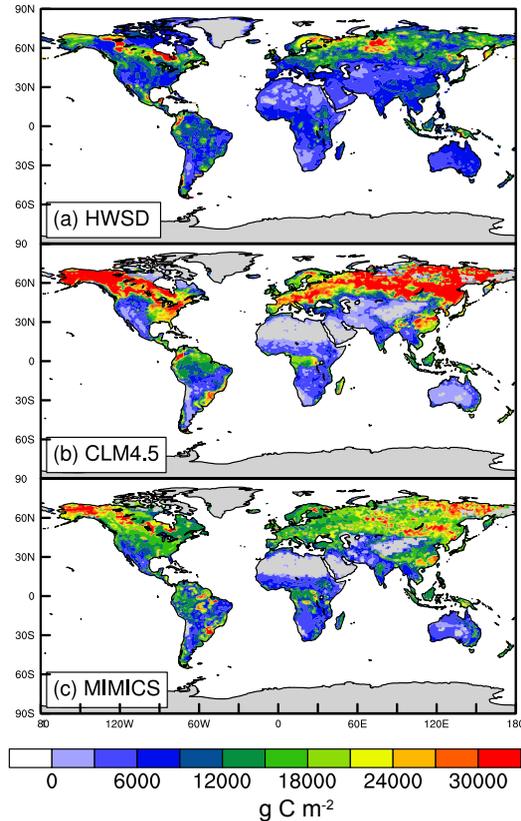


Figure 4. Global soil C pools (g C m^{-2} , 0–100 cm) from observations and models. **(a)** Observations from the Harmonized World Soils Database and global total = 1260 Pg C. **(b)** CLM4.5 global total = 1780 Pg C (spatial correlation with observations (r) = 0.42, model-weighted root mean square error (RMSE) = 13.7 kg C m^{-2}). **(c)** MIMICS global total = 1530 Pg C (r = 0.46, RMSE = 6.8 kg C m^{-2}).

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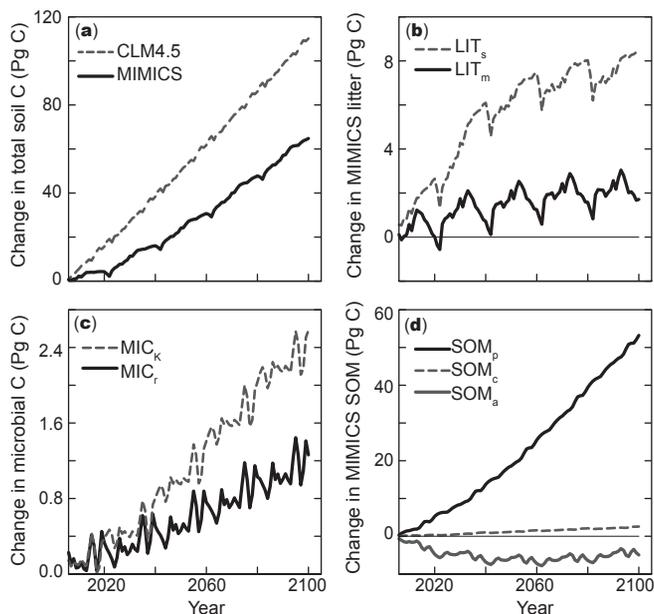


Figure 5. Temporal change in global soil C pools (Pg C; 0–100 cm) in response to elevated $[\text{CO}_2]$ and increasing plant productivity throughout the 21st century. **(a)** Changes in all litter, microbial biomass, and SOM pools simulated by CLM4.5 (dashed line) and MIMICS (black line), totaling 110 and 65 PgC globally, respectively, for simulations receiving the same C inputs and environmental conditions. Specific changes in individual MIMICS pools included: **(b)** Structural and metabolic litter pools (dashed and solid lines, respectively); **(c)** Oligotrophic and copiotrophic soil microbial biomass pools (dashed and solid lines, respectively); and **(d)** physically protected, chemically protected, and available SOM pools (solid black, dashed, and solid grey lines, respectively). Results are from offline (land-only), biogeochemically coupled simulations where terrestrial NPP increases from 50 Pg C yr^{-1} in 2005 to 64 Pg C yr^{-1} by 2100, without concurrent changes in climate. Note differences in the y axes scales among panels.

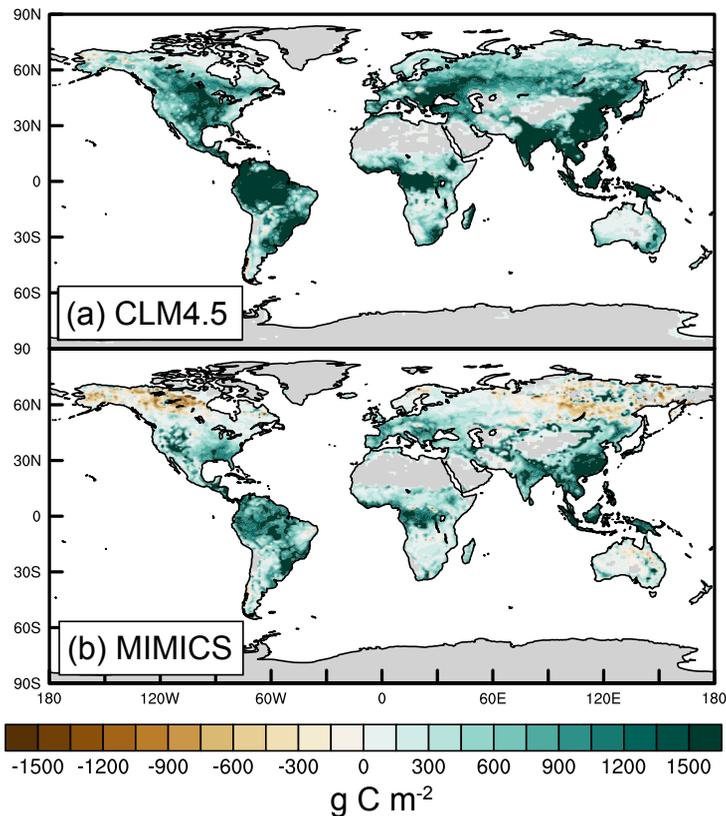


Figure 6. Spatial distribution of changes in soil C pools projected using **(a)** CLM4.5 and **(b)** MIMICS. Values (g C m^{-2}) were calculated by subtracting the sum of all soil C pools (0–100 cm) projected in 2100 under RCP 8.5 [CO_2] from those estimated in 2005. Positive values show regions of net soil C accumulation over the 21st century with increasing litter inputs from elevated [CO_2].