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Decomposition by ectomycorrhizal fungi alters soil carbon storage in a simulation model

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Abstract. Carbon cycle models often lack explicit belowground organism activity, yet belowground organisms regulate carbon storage and release in soil. Ectomycorrhizal fungi are important players in the carbon cycle because they are a conduit into soil for carbon assimilated by the plant. It is hypothesized that ectomycorrhizal fungi can also be active decomposers when plant carbon allocation to fungi is low. Here, we reviewed the literature on ectomycorrhizal decomposition and we developed a simulation model of the plant-mycorrhizae interaction where a reduction in plant productivity stimulates ectomycorrhizal fungi to decompose soil organic matter. Our review highlights evidence demonstrating the potential for ectomycorrhizal fungi to decompose soil organic matter. Our model output suggests that ectomycorrhizal activity accounts for a portion of carbon decomposed in soil, but this portion varied with plant productivity and the mycorrhizal carbon uptake strategy simulated. Lower organic matter inputs to soil were largely responsible for reduced soil carbon storage. Using mathematical theory, we demonstrated that biotic interactions affect predictions of ecosystem functions. Specifically, we developed a simple function to model the mycorrhizal switch in function from plant symbiont to decomposer. We show that including mycorrhizal fungi with the flexibility of mutualistic and saprotrophic lifestyles alters predictions of ecosystem function.

Key words: carbon cycle; decomposition; ectomycorrhizae; extracellular enzyme activity; plant-soil interactions; simulation model; soil carbon sequestration.

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Introduction

While interactions among species shape community structure and ecosystem function, they also increase ecosystem complexity and thus model complexity. However, recent calls for improving soil decomposition models highlight the importance of incorporating biological mechanisms that lead to ecosystem fluxes (Treseder et al. 2012, Schimel 2013, Wieder et al. 2013, Xu et al. 2014). For example, decomposition of soil organic matter by microbes through extracellular enzymes and subsequent mineralization transforms carbon (C) stored in soil into atmospheric C, a flux that has ramifications for greenhouse gas levels and thus climate. Models linking soil and atmospheric pools of C have recently advanced because of our increased understanding of microbial ecology (Treseder et al. 2012). Field measurements of decomposition closely match model predictions when we explicitly model microbes with diverse traits (Allison

2012) and guilds growing at various rates and specializing on different types of organic matter (Moorhead and Sinsabaugh 2006). Functional groups of microbes, such as free-living and mycorrhizal fungi, respond differently to soil nutrient availability and modeling different groups of fungi changes predictions of ecosystem nutrient cycling (Orwin et al. 2011). However, most ecosystem models still do not incorporate distinct microbial groups, even though their roles in ecosystem processes are diverse.

Interactions among species can influence important ecosystem functions such as net primary productivity and decomposition (Bruno et al. 2003, van der Heijden et al. 2008). For example, mycorrhizal fungi form a mutualism with one or several plants (van der Heijden and Horton 2009, Philip et al. 2010) where soil nutrients are exchanged for plant-assimilated C. Mycorrhizal plants transfer 23% more assimilated C belowground compared to non-mycorrhizal plants (Rygiewicz and Andersen 1994) thus altering soil C storage. Carbon transfer to mycorrhizae varies with plant genotype and species (Hoeksema and Classen 2012), season (Apple et al. 2005, Courty et al. 2007), and soil nutrient availability (Olsson et al. 2010). Carbon transferred to mycorrhizal fungi can contribute to soil C storage if fungal tissues decompose more slowly than fine roots (Langley et al. 2006) or if their biological residues persist for decades to centuries (Clemmensen et al. 2013, Cotrufo et al. 2013). Mycorrhizal fungi can also slow decomposition by monopolizing humus layers and reducing activity and abundance of free-living decomposers (Lindahl et al. 2010, McGuire et al. 2010, Orwin et al. 2011). Finally, mycorrhizal fungi may increase soil organic matter stabilization by increasing soil aggregation (Daynes et al. 2012).

On the other hand, mycorrhizae may contribute to soil C release if fungal tissues decompose more quickly than fine roots (Fernandez and Koide 2011, Koide et al. 2011), if they are exuding labile carbon sources, or if they are actively decomposing organic matter (Read and Perez-Moreno 2003). In this paper we review mechanistic hypotheses of ectomycorrhizal (ECM) decomposition activity and then discuss which, where, and when mycorrhizae might decompose organic matter in soil. Because mycorrhizae are part of the soil microbial community and have some potential decomposition capabilities, we highlight the importance of recognizing mycorrhizal fungi as a distinct group in a conceptual C model. We present a conceptual model that demonstrates how ECM decomposition of soil carbon may influence soil carbon dynamics and then use the model to compare two alternative mechanistic scenarios of when mycorrhizal fungi may take part in soil carbon decomposition.

Evidence for saprotrophic activities of ECM

The morphology and enzymatic capabilities of ECM make them more likely to decompose organic matter than arbuscular mycorrhizal fungi (Chalot and Brun 1998, Read and Perez-Moreno 2003, Talbot et al. 2008). ECM produce prolific belowground structure of mycelium, thus ECM are more likely than arbuscular mycorrhizae to decompose organic matter. Additionally, ECM exude extracellular enzymes that AM fungi do not produce to decompose organic matter (Norkrans 1950, Abuzinadah and Read 1986, Smith and Read 2008, Bodeker et al. 2009) including cellulose (Chalot and Brun 1998, Vaario et al. 2012) and lignin (Read and Perez-Moreno 2003, Bodeker et al. 2009). Finally, ECM are commonly found proliferating in patches of organic matter such as decomposing nematode biomass (Perez-Moreno and Read 2001) and decaying logs (Austin 2013). While decomposition of soil C by ECM seems likely given observed enzyme activities and their abundance in patches of organic matter, we are still unable to predict which ECM species might act as decomposers.

ECM, even within a genus, vary in having genes that indicate the ability to decompose organic matter. This may be because the genes that code for decomposition, saprotrophy, have evolved and been lost several times across ECM phylogenies (Tedersoo et al. 2010). Having the genetic ability to degrade organic matter does not necessarily translate to using the function, however. For example, while some *Amanita* species lack genes coding for organic matter degradation (endoglucanase and cellobiohydrolase) others retain similar C-degrading genes (e.g., beta-glucosidase). Select *Amanita* species grown in culture cannot survive saprotrophically given organic nutrients (Wolfe et al. 2012); yet, other unculturable ECM genera are suspected of

decomposition including *Cortinarius* (Bodeker et al. 2009), *Suillus*, *Rhizopogon*, *Cennococcum*, *Lacarria* (Durall et al. 1994), *Lactarius* (Courty et al. 2007, Bodeker et al. 2009) *Paxillus* (Chalot and Brun 1998, Perez-Moreno and Read 2001, Rineau et al. 2012), *Russula* (Bodeker et al. 2009), and *Tomentella* (Courty et al. 2010). Clearly, research needs to target other species of ECM using functional gene assays to predict which mycorrhizal taxa are capable of decomposing organic matter.

Alternative mechanisms for ECM decomposition

In a provocative idea paper, Talbot and colleagues (2008) proposed mechanisms for ECM decomposition; we compare two of them here. On one hand, ECM may increase enzymatic activity in response to lower plant C assimilation. When plants allocate less C to ECM, either due to budbreak or dormancy, relative activity of C-degrading enzyme activity increases when mycorrhizae are present than absent (Courty et al. 2007, Cullings et al. 2008). Thus, mycorrhizal decomposition of soil C could be triggered by reduced total allocation of C from the plant to ECM during a prolonged suspension of photosynthesis. Alternative evidence from nitrogen fertilization studies, where relative C allocation to mycorrhizae is reduced with fertilization, shows the number of ECM root tips decreases (Pritchard et al. 2014) while tissues growing away from roots such as rhizomorphs are unaffected (Treseder et al. 2006). These combined results suggest that when fertilization limits C allocation, mycorrhizae are capable of continuing rhizomorph production via C from an alternative source. Upon regaining adequate supplies of photosynthate, mycorrhizae may stop decomposing soil C. On the other hand, ECM may decompose soil C continuously while breaking down organic matter to obtain nutrients like nitrogen or phosphorus (Rineau et al. 2012). As ECM decompose organic matter and acquire nutrients, which is widely accepted as the basis for the plant-mycorrhiza symbiosis, they could also acquire soil-derived C released during decomposition. It is unknown whether ECM use soil C as an energy source or if they coincidentally acquire C while acquiring N (e.g., from amino acids) (Talbot et al. 2008). Although it is recognized that plant-mycorrhizal interactions affect ecosystem soil C storage, the symbiosis is seldom included in soil decomposition or ecosystem models (but see Deckmyn et al. 2008, Meyer et al. 2010, Orwin et al. 2011).

Similar to ECM, free-living soil microbes decompose soil using extra-cellular enzymes and their activity has recently been made explicit in ecosystem models. While traditional C models account for microbial C mineralization indirectly (e.g., Parton et al. 1988, Thornton and Rosenbloom 2005), recent advances in C models use enzyme kinetics to describe decomposition (Moorhead and Sinsabaugh 2006, Lawrence et al. 2009, Allison 2012, Wang et al. 2012). In models utilizing enzyme kinetics theory, decomposition is described by a logarithmic curve that increases with substrate (i.e., reaction site) availability and plateaus at a maximal enzyme activity rate. Since mycorrhizal fungi and free-living microbes use extracellular enzymes to degrade organic matter, we took an approach similar to the microbial enzyme kinetics models to describe mycorrhizal enzyme activity. To our knowledge, our model is the first to focus on mycorrhizal C acquisition strategies and how these changes influence soil C dynamics. We simplified and focused our model on C dynamics so it could provide a straightforward framework for future experimental tests.

While ectomycorrhizal fungi have the enzyme capacity to degrade soil C (Read and Perez-Moreno 2003, Brzostek and Finzi 2011, Burke et al. 2011, Jones et al. 2012, Vaario et al. 2012), there have been few empirical studies to explore if mycorrhizal fungi directly increase soil C degradation. Theoretical models can be the first step in exploring how the presence of mycorrhizae might or might not alter soil C dynamics. Here, we developed a theoretical model to explore: (1) how ectomycorrhizal fungi alter soil C dynamics when they uptake C from the soil, (2) if changes in plant productivity alter ectomycorrhizal C uptake from the soil, and (3) if shifts in soil organic matter degradation are due to the direct uptake of C by mycorrhizae or to the response of other soil organisms to ectomycorrhizal activity.

We developed a simulation model to investigate impacts of mycorrhizal C acquisition strategies on soil C storage. We studied three strategies of mycorrhizal uptake of C that range from C uptake primarily from plants to uptake

Table 1. Description of parameters used in the model with sources providing a close approximation to the parameters.

Parameter	Description	Value	Range	Units	Reference
G	net primary productivity	1000.00	800–1300.000	g C·m^{-2}·yr^{-1}	Whittaker and Likens 1973
a_L	leaf litter allocation	0.05	0.014–0.100	yr^{-1}	Litton et al. 2007
k_L	litter turnover	0.50	0.032–0.624	yr^{-1}	Gholz et al. 2001
r_L	fraction of litter respired	0.90		...	
k_R	root turnover	0.30	0.036–0.501	yr^{-1}	Gholz et al. 2001
a_M	mycorrhizal allocation	0.02	0.008–0.060	yr^{-1}	Hobbie 2006
r_M	mycorrhizal respiration	1.00	0.400–1.500	yr^{-1}	Fenn et al. 2010
a_R	root allocation	0.03	0.120–0.070	yr^{-1}	Raich and Nadelhoffer 1989
k_M	mycorrhizal turnover	3.00	1.740–5.210	yr^{-1}	Rygiewicz et al. 1997, Treseder et al. 2006, McCormack et al. 2010, Orwin et al. 2011
k_B	microbial turnover	3.75	0.439–11.388	yr^{-1}	Wang et al. 2012
K_M	mycorrhizal half-saturation	5000.00		g C/m^2	
K_B	microbial half-saturation	5000.00		g C/m^2	Wang et al. 2012
$V_{\max,M}$	maximum mycorrhizal C uptake	200.00		g C·m^{-2}·yr^{-1}	
$V_{\max,B}$	maximum microbial C uptake	1600.00	400–5800.00	g C·m^{-2}·yr^{-1}	Wang et al. 2012
e_P	plant-acquisition efficiency	1.00		...	
e_S	soil-acquisition efficiency	0.30		...	
s	scales G	0–1.00		...	
u	specific mycorrhizal C uptake	2.50		g C·g^{-1} C of M·yr^{-1}	
r_B	microbial respiration	5.00	1.75–7.00		Hogberg et al. 2001

from plants and soil. In the first strategy, ECM only acquire C from a plant, assuming a constant allocation coefficient. In the second and third strategies they acquire additional C from soil. The second strategy simulates specific ectomycorrhizal enzyme activity rate (i.e., activity per unit mycorrhizal biomass) at a constant rate, whereas in the third strategy the activity rate from soil is variable and depends on substrate availability. We use the enzyme kinetic function (Michaelis-Menten 1913, as cited in Johnson and Goody 2011), which regulates extracellular enzyme activity based on the amount of available substrate. Parameter values are provided (Table 1).

Model description

Carbon moves from aboveground, where it is assimilated into plant biomass, to belowground, where it is decomposed (Fig. 1). Plants (P) acquire C from the atmosphere and assimilate it into biomass through net primary production (G) (Eq. 1).

$$dP/dt = Gs - p[a_M + a_R + a_L]. \quad (1)$$

The rate of production is scaled (s) from 0 to 100% as a way to reduce plant productivity, thus reducing the amount of C transported belowground. Environmental factors vary mechanistically in how they alter allocation patterns. We do not focus on mechanisms of abiotic factors that impact allocation patterns, but instead on whether alternative carbon uptake strategies of mycorrhizae can affect soil C storage. Some photosynthate is allocated to mycorrhizal fungi (a_M) and roots (a_R) while some contributes to leaf production (a_L). The remaining plant biomass can be considered woody tissue or C reserves that will be used during bud-break the following year. Leaf litter (L) accumulates and turns into humus as it enters soil at the rate k_L (Eq. 2):

$$dL/dt = a_L P - k_L L. \quad (2)$$

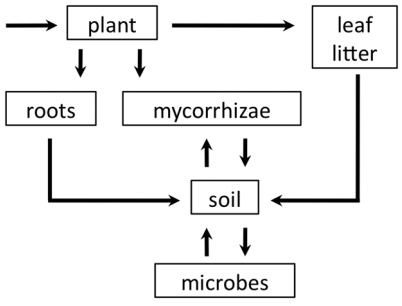

Fig. 1. Carbon fluxes (arrows) between pools (boxes) where it is stored in plant tissues, mycorrhizae, free-living microbial biomass and labile soil organic matter. Equations developed for the conceptual system are given in *Introduction: Model description*.

Similarly, roots (R) grow as plants allocate C to them, and when they turn over they contribute to soil organic matter (k_R) (Eq. 3).

$$dR/dt = a_R P - k_R R. \quad (3)$$

Soil organic matter accumulates as root litter, leaf litter, and decaying mycorrhizal (k_M) and free-living microbial biomass (k_B) enters soil. (Eq. 4).

$$dS/dt = k_L L(1 - r_L) + k_R R + k_M M + k_B B - V_i - V_B. \quad (4)$$

This pool contains labile organic C and is analogous to a "fast"-cycling pool (sensu Parton et al. 1988). We have not modeled a "slow"-cycling pool of C because it is likely that inputs from plants, whether high or low chemical quality, do not directly contribute to a stabilized pool of soil C (Schmidt et al. 2011, Cotrufo et al. 2013). Heterotrophic respiration (r_L) occurs as litter is consumed by litter detritivores. Mycorrhizae take up soil C (V_i), which we modeled in the three strategies as described below. V_B is soil C uptake by free-living (i.e., non-mycorrhizal) microbes.

We simulated mycorrhizal C uptake from soil using three different strategies. First we assumed mycorrhizae do not take up any C from soil (Eq. 5).

$$V_1 = 0. \quad (5)$$

In this model version, C gained by mycorrhizal fungi is only derived from plants, and C is only transferred out of soil through free-living microbial decomposition resulting in CO_2 release to the atmosphere. This is considered to be the null model, however, there is evidence mycorrhizal fungi use extracellular enzymes to decompose SOM similar to free-living decomposers in soil (Jones et al. 2012, Vaario et al. 2012). In the second model version ectomycorrhizal fungi (M) decompose SOM at a constant specific uptake rate (u_M) (Eq. 6).

$$V_2 = u_M M. \quad (6)$$

This function is used in place of V_i in the constant uptake model version. Third, we used the enzyme kinetics function applied to microbial activity to describe mycorrhizal activity. We assumed a maximum uptake rate independent of mycorrhizal biomass (Eq. 7).

$$V_3 = V_{\max,M} S/(S + K_M). \quad (7)$$

This function is used in place of V_i in the variable uptake model version. Mycorrhizal enzyme activity is regulated by the availability of substrate (S) with half-saturation coefficient (K_M) where activity is 50% of maximum. The third model implicates that the mycorrhizal fungal specific uptake rate increases when mycorrhizal biomass decreases with decreasing NPP. We chose $V_{\max,M}$ and K values based on model simulations that produced realistic levels of mycorrhizal and soil C at equilibrium that are within a reasonable range of microbial parameter values (Table 1). We selected u_M, $V_{\max,M}$, and K_M parameter values such that models V_2 and V_3 would produce similar amounts of mycorrhizal biomass compared to V_1, thus ensuring models V_2 and V_3 produce the same amount of soil carbon when plant productivity is 100%. We did this to have a common baseline against which to test changes in soil carbon in models V_2 and V_3 in response to reduction in plant productivity. While the simpler model V_2 may initially be more appealing than V_3, model V_3 contains an indirect link between plant productivity (NPP) and mycorrhizal fungal activity as the substrate consumed is derived from plant inputs. Therefore, model V_3 is more dynamic and may be more relevant to natural systems.

Mycorrhizae grow with inputs from plants ($a_M P$) and soil (V_i) (Eq. 8).

$$dM/dt = e_1 a_M P + e_2 V_i - k_M M - r_m M. \quad (8)$$

We assume an energy tradeoff: ectomycorrhizae can gain C more efficiently from plants, since it is relatively labile, and less efficiently from soil ($e_1 > e_2$), since it is relatively recalcitrant. We consider the C that is lost as V_i is scaled down as mycorrhizal growth respiration. Mycorrhizal maintenance respiration (r_M) also accounts for C lost from the system, while mycorrhizal turnover (k_M) contributes C to soil. While mycorrhizal growth and functions feed back to net primary productivity (NPP), the feedback is implicit in our model. Since mycorrhizal turnover rate is much faster than the turnover rate for plants, mycorrhizal biomass reaches quasi-equilibrium as a function of plant productivity. Thus, mycorrhizal feedback on NPP is equivalent to plant biomass feedback to itself, and reaches a

steady state.

The free-living microbial community uses soil C (V_B) for respiration (r_B) and C is returned to soil through microbial mortality (k_B):

$$dB/dt = V_{\max,B}S/(S + K_B) - k_B B - r_B B. \quad (9)$$

Free-living microbial enzyme activity is assumed to have a maximum uptake rate ($V_{\max,B}$) regulated by the availability of substrate (S) with a half-saturation coefficient (K_B). We assume that the free-living microbial community uptakes carbon from soil following enzyme kinetic dynamics, a Michaelis-Menten function. Thus, free-living microbes have a variable uptake of C in all three models and mycorrhizae have a variable uptake only in model V_3. In models V_2 and V_3 where mycorrhizae are decomposing, mycorrhizae and microbes are accessing the same soil C pool. This assumption is appropriate for the purposes of our model since we do not specify soil depth, even though we recognize that mycorrhizae and free-living microbes occupy spatially distinct niches defined by soil depth (Lindahl et al. 2007).

We made simplifying assumptions about the theoretical ecosystem in order to reduce model complexity. We are primarily interested in C cycling changes that occur on short ecological timescales, thus we only described pools that turn over rapidly. For example, because they are more labile we describe leaf litter and fine roots and not woody stems and coarse roots. While these assumptions limit the applicability of the model, they are appropriate for theoretical investigation of ectomycorrhizal activity responding to lower plant productivity. Since we made simplifying assumptions and have not attempted to produce a complex ecosystem model, we discuss results of models with mycorrhizal activity relative to one without mycorrhizal activity. This is appropriate for our questions given the theoretical nature of this work, but could be translated into absolute results for comparison with field observations after parameters are verified by experiments.

Parameterization and model simulations

Parameter values and ranges are mainly from previous studies on primary production, soil organic carbon degradation, and microbial physiology (references provided in Table 1). We estimated baseline parameter values based on steady-state mass balance. We assumed baseline net primary productivity (G) at 1000 g·m^{-2}·yr^{-1}, 50% of which passed to leaf litter fall, 30% of which passed to root litter, and the remains were allocated to mycorrhizae. With the baseline plant standing biomass assumed to be 10,000 g C/m^2 from literatures, we estimated a_L, a_R, and a_M at 0.05, 0.03 and 0.02, respectively. Leaf litter was partially decomposed at soil surface, thus, 45% of NPP was respired before entering soil C pool (450 g C·m^{-2}·yr^{-1}). Mycorrhizal turnover and respiration rates were estimated to be 3.0 and 1.0 yr^{-1}, so that mycorrhizae function as a C sink in V_1 with 150 g C·m^{-2}·yr^{-1} deposited in soil, and 50 g C·m^{-2}·yr^{-1} is released as CO_2. The rest of C fluxes out of the system by microbes at 500 g C·m^{-2}·yr^{-1} in V_1. The microbial turnover rate was estimated at 3.75 yr^{-1}, so that the carbon use efficiency was around 0.47 (Anderson and Domsch 1986, Six et al. 2006). The half-saturation coefficient was set at 5000 g C/m^2 to ensure the Michaelis-Menten kinetics were functional. There were no direct data available for estimation of maximum mycorrhizal C uptake, and half-saturation coefficient in V_3. We assumed the maximum uptake rate of mycorrhizae to be around 1/8 of microbial uptake rate (200 g C·m^{-2}·yr^{-1} mycorrhizae; 1600 g C·m^{-2}·yr^{-1} microbial). We compared two half-saturation coefficients for mycorrhizae, one assumed to be equal to microbial half-saturation ($K_M = 5000$ g C/m^2). The other coefficient assumed faster uptake rate at low substrate concentration ($K_M = 2000$ g C/m^2), which represents a trade-off between maximum uptake rate and substrate affinity. The parameter u in V_2 was adjusted to produce similar soil carbon storage between V_2 and V_3 at maximal plant productivity. Most estimated parameters and simulated C pools are within published ranges (Table 1).

We simulated C fluxes through plants, leaf litter, roots, ectomycorrhizal fungi, and soil. We solved the set of ordinary differential equations described above using the ode45 problem solver in MatLab (version R2011b; MathWorks, Natick, MA, USA). First, we used a Latin hypercube sampling (LHS) algorithm (McKay et al. 1979) to develop 1000 sets of parameters values. The LHS algorithm allows an un-biased estimate of the average model output, with the advantage that it

requires fewer samples than simple random sampling to achieve the same accuracy. Next, we conducted Monte Carlo (MC) simulations with the model using each of the 1000 sets of parameter under each of the three versions of the model, at monthly time steps until a steady state was reached (~1800 months). Monthly time steps were chosen based on the time scale of mycorrhizal turnover. Plant production was scaled randomly from 0% to 100% for each permutation. Only four permutations resulted in negative pool sizes and were excluded from model comparisons.

We compared changes of soil C storage at steady state in the constant uptake version (V_2) and the variable uptake version (V_3) as a percent of soil C storage predicted by the null model (V_1). We calculated C going to mycorrhizae from soil, which is zero in the null model, as a percentage of total C flux from plants and soil to mycorrhizae. Soil C is taken up by microbes and mycorrhizae, and we calculated the percentage of C flux from soil to mycorrhizae as a percent of total flux out of soil to mycorrhizae and microbes. In the null model, mycorrhizal C was stored in soil after maintenance respiration was deducted. When mycorrhizal decomposition was accounted for, we calculated net flux of C from mycorrhizae to soil.

We studied global sensitivity of parameters to soil carbon pool, using the estimated baseline parameters. Based on the MC ensemble simulations results above, we calculated a parameter sensitivity index using partial rank correlation coefficient (PRCC). PRCC is a robust sensitivity measure for nonlinear but monotonic relationships between parameters and model outputs (Marino et al. 2008), which performs a partial correlation between specific parameter and model outputs on rank-transformed data taking into account the remaining parameters.

Results

Declines in plant productivity reduced soil C storage across all strategies (V_1, V_2, V_3). When ECM function as decomposers (V_2 and V_3) their effect on soil C dynamics varied with plant productivity (Fig. 2, data shown relative to null model V_1). At zero productivity there are no fresh inputs of C to the system. However soil, mycorrhizal, and microbial C pools remain positive at steady state. This is because of a tight recycling of C that is taken up by mycorrhizae and microbes. Their necromass and waste products then regenerate soil organic matter, which may contribute to soil carbon buildup (Cotrufo et al. 2013). The effect of the two ECM decomposition strategies diverged as plant productivity was reduced. ECM with constant uptake rates (i.e., V_2) had less of an effect on soil C storage than ECM with variable uptake rates (i.e., V_3). Changes in mycorrhizal biomass were likely the mechanism for the difference between the two models. Less mycorrhizal biomass means lower

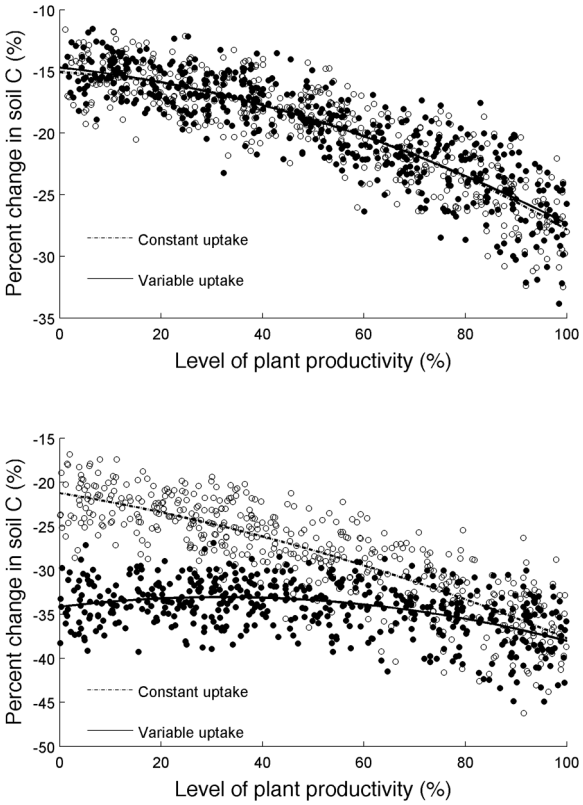

Fig. 2. Change in soil carbon storage with increasing plant productivity (parameter *s*) in the constant uptake model version (dashed line) and the variable uptake model version (solid line) as a percent of soil carbon storage predicted by the null model. Mycorrhizal fungal activity was simulated using parameters similar to microbial activity (top panel) and with a faster uptake rate (bottom panel; see *Introduction: Parameterization and model simulations* for details).

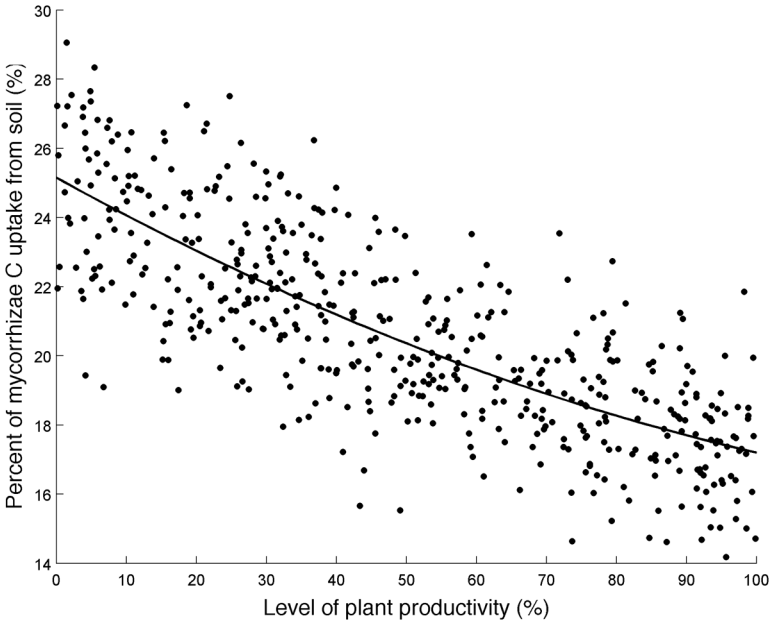

Fig. 3. Carbon flux to mycorrhizae from soil as a percent of total fluxes coming from soil and plants declines with plant productivity (parameter *s*) in the variable uptake model version.

total enzymes are exuded when mycorrhizal activity is modeled as constant. However, relatively more enzymes are exuded when mycorrhizal decomposition is modeled as variable with substrate availability.

In the variable uptake model (V_3) the level of plant productivity altered the amount of C taken up from soil by mycorrhizae. Mycorrhizae acquired C from two sources: plants and soil. The percent of C acquired by mycorrhizae from soil out of total C from soil and plants did not vary with plant productivity in the constant uptake model. The percent of C acquired by mycorrhizae from soil gradually increased in the variable uptake model (Fig. 3).

Mycorrhizae and the free-living soil microbial community simultaneously decomposed soil C and their combined activity decreased soil C storage in models V_2 and V_3. At the highest plant-productivity levels a small amount of C moving from soil to biotic pools went into mycorrhizal biomass rather than free-living microbial biomass (Fig. 4). This C pathway remained at the same level in the constant uptake model (*data not shown*). In the variable uptake model the amount of C moving from soil to mycorrhizae gradually increased. Thus, even at low plant productivity, free-living microbes acquired most of decomposable soil C. In addition to decomposing and assimilating C in soil, mycorrhizae contribute to C storage as their tissues decay. The net amount of C transferred from decaying mycorrhizal biomass to soil was similar for the constant and variable models when plant productivity was high (Fig. 5). However, when plant productivity was reduced, the effect of mycorrhizae on soil in the constant model deviated from the variable model. The net amount of C transferred to soil by mycorrhizae was greater under the constant uptake model compared to the variable uptake model. At low levels of plant productivity, the effect on soil storage became negative, meaning there was net loss of C from the soil to mycorrhizae.

Using soil C pool size as the response variable, our sensitivity analysis showed parameters related to microbial activity are important across all three models (Fig. 6). This is likely because microbes directly regulate decomposition. Soil C was also affected by plant C allocation patterns and soil respiration. The more C transferred to soil from plant and mycorrhizal litter, the higher soil respiration. Parameters related to mycorrhizal activity showed different sensitivities among

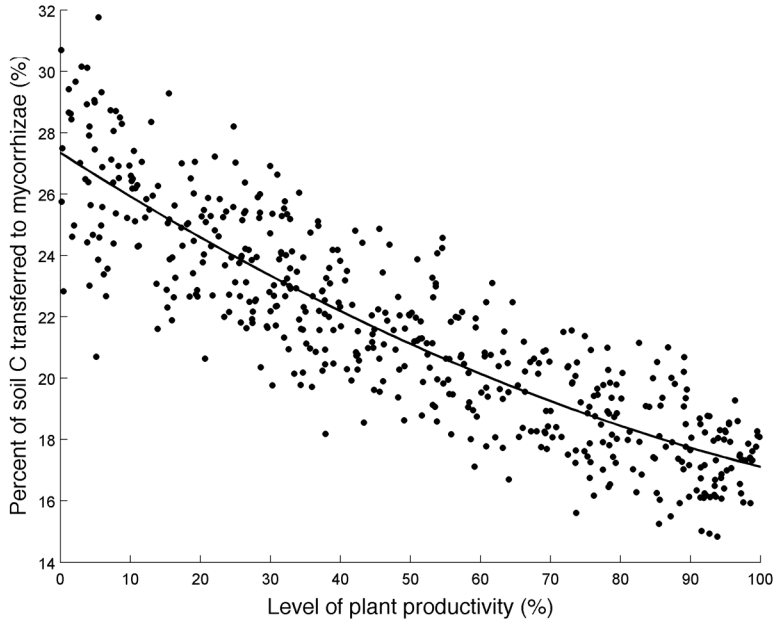

Fig. 4. Carbon flux to mycorrhizae from soil as a percent of total fluxes from soil to mycorrhizae and free-living microbes declines with plant productivity (parameter s) in the variable uptake model version.

the three models. In model V_1, mycorrhize are a source for soil C similar to plant litter. But plant C allocation to mycorrhizal biomass (a_M) and mycorrhizal respiration (r_M) are less important than plant litter in controlling soil C storage. On the other hand, model V_2 predicts a strong mycorrhizal uptake of C from soil and soil C therefore has a linear relationship to mycorrhizal biomass. Thus, a_M and u_M are important parameters that are negatively related to the soil C pool. The sensitivity index of mycorrhizal respiration (r_M) is positive, suggesting that soil carbon reductions in model V_2 are due to carbon stored in mycorrhizal biomass not respired to the atmosphere. Most parameters in model V_3 have sensitivity similar to model V_1, with a few exceptions unique to model V_3. The soil C pool in V_3 is not sensitive to plant allocation to mycorrhizal biomass, which means that mycorrhizae can adjust C uptake from soil depending on how much C they are allocated from plants.

Discussion

Biotic interactions that drive ecosystem functions such as decomposition and mycorrhizal-plant interactions contribute significantly to ecosystem functioning (van der Heijden et al. 1998). Yet, ecologists have only begun to consider how ectomycorrhizal utilization of plant assimilated C can affect soil C storage within a predictive framework (Orwin et al. 2011). To our knowledge this model is the first to

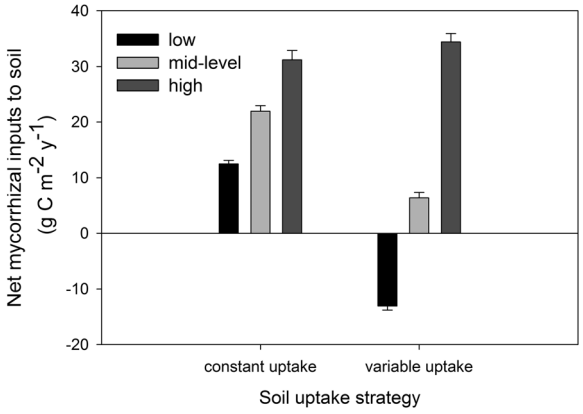

Fig. 5. Net flux of carbon from mycorrhizae to soil, after mycorrhizal decomposition is accounted for, in the constant and variable uptake model versions at three levels of plant productivity: low (40%), mid-level (70%), and high (100%). Bars show mean and SE of 500 permutations with parameters varied 10%.

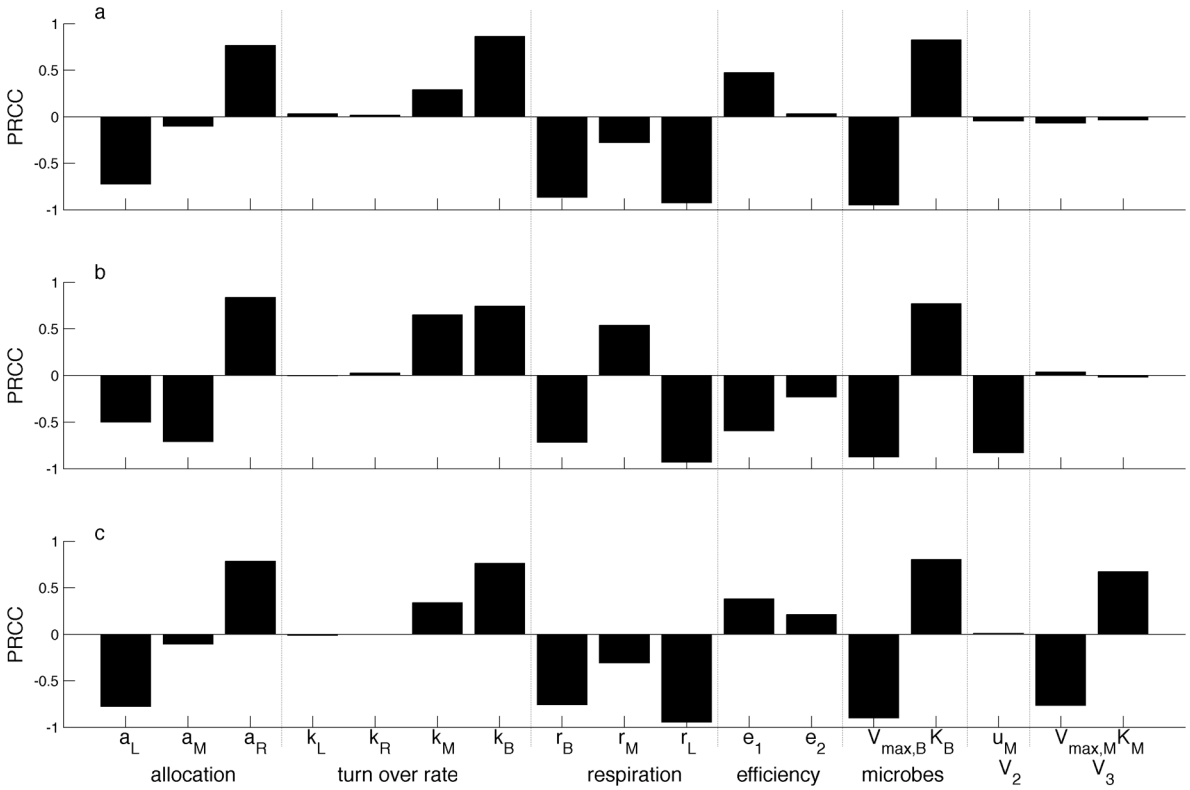

Fig. 6. Analysis of sensitivity of soil carbon pool to parameters for (a) model V_1, (b) model V_2, and (c) model V_3. We varied parameters by 10% and show the strength of that parameter's effect on predicted soil C (partial ranked correlation coefficient; PRCC). A higher absolute PRCC indicates that soil C predictions are sensitive to that parameter, and strong empirical support of that parameter is needed to produce reliable quantitative model predictions. Parameters are separated by vertical dash lines as categories of allocation, turn over rate, respiration, efficiency, microbes, and parameters unique to model V_2 and V_3.

incorporate decomposition of organic matter and subsequent C acquisition by ectomycorrhizal fungi. The work here leads to two primary conclusions: ectomycorrhizal fungi have a substantial effect on soil C storage, and the effect of ectomycorrhizae on C storage is markedly different depending on plant productivity, at least in the variable uptake model. We recognize that numerous biotic interactions within an ecosystem contribute to soil C storage. However, increasing the number of interactions in a model will not necessarily generate more reliable model predictions. Model efforts should focus on those interactions that have the capacity to significantly change model predictions. Plant-mycorrhizae-soil interactions play a pivotal role in ecosystem C dynamics and including them in models is both important and feasible.

Mycorrhizal activity alters soil C dynamics

The two strategies we modeled for mycorrhizal C uptake affected soil C storage differently. Soil C storage was reduced more when specific enzyme activity was variable with plant productivity and soil substrate availability compared to when mycorrhizal uptake was constant. The two models converged in their predictions of soil C storage at high levels of plant productivity; thus, in simulated ecosystems with high plant productivity the mechanism for mycorrhizal C acquisition from soil does not influence soil C storage differently than a simulated ecosystem lacking mycorrhizal activity.

Regardless of strategy, soil C storage was affected by mycorrhizae because they were an additional decomposer group. As plant production declined, fungal biomass declined, contrib-

uting to the relatively small effect of mycorrhizae on soil C storage at low plant productivity. In our model, productivity affects the absolute and relative amount of C transferred from plant to mycorrhizal fungi because the allocation parameter a_M is constant. Fertilization can shift allocation patterns, thus changing the relative amount of C transferred from plants to mycorrhizal fungi, which may affect mycorrhizal activity in the same way as reduced total productivity as modeled here. In this respect, our result corroborates several other studies where N fertilization reduces relative C allocation to mycorrhizae and leads to fewer mycorrhizal root tips and lower mycorrhizal production (Pritchard et al. 2014), mycorrhizal respiration, and sporocarp production (Hasselquist et al. 2012). Still, the mechanism remains unclear and we suggest experiments manipulate plant productivity or relative allocation patterns and measure ectomycorrhizal fungal specific enzyme activity in situ, or at least measure potential activity in a controlled setting in combination with ectomycorrhizal fungi biomass. Activity of plant cell wall-degrading enzymes in the mycorrhizsphere increases when relative allocation of C to mycorrhizae is reduced via nitrogen fertilization (Jones et al. 2012), but it is unclear whether this effect is directly attributable to mycorrhizal activity. While we are unaware of methods for measuring enzyme activity rates in situ, we think proteomic or metabolomic methods may be a useful tool to exploit. Others have used proteomic methods to suggest mycorrhizal genera rather than other microbial groups produce soil enzymes (Rineau et al. 2012). If we could target general ECM enzyme activity compared to free-living microbial activity, we could produce a validated range of expected mycorrhizal enzyme activity rates that would strengthen model predictions.

Plant productivity affected mycorrhizal C fluxes in the variable uptake model but not in the constant uptake model. In the variable uptake model, mycorrhizae acquired more C from soil than plants, simultaneously reducing the role of the free-living microbial community in decomposition. Mycorrhizae acquired more C from soil in a low productivity ecosystem compared to a highly productive ecosystem. The amount of C acquired by mycorrhizae was constrained by mycorrhizal C use efficiency, a parameter that remains to be experimentally evaluated. If ectomycorrhizae are efficient at using soil C, our model underestimated the amount of soil organic matter decomposed by mycorrhizae. Plant productivity was a key driver of mycorrhizal activity in the variable uptake model, but not in the constant uptake model. The constant uptake model assumed mycorrhizae acquire C as a secondary product while they mine organic matter for nutrients (Talbot et al. 2008). Plant productivity therefore alters the absolute amount of soil C decomposed by mycorrhizae because mycorrhizal biomass declines. However, the relative amount of soil C decomposed by mycorrhizae compared to the free-living microbial community does not change. To disentangle the effects of mycorrhizal from the effects of the free-living microbial community on soil C decomposition, future studies that manipulate plant productivity should measure mycorrhizal and free-living microbial biomass and partition decomposition measurements (litter mass loss, soil C turnover, soil C respiration) between the mycorrhizal and free-living pools. Although the pattern between ectomycorrhizal fungal enzyme activity and plant production was striking, the quantitative effects of ectomycorrhizal fungal enzyme activity on soil C are contingent upon experimental validation of mycorrhizal enzyme kinetics. Tedersoo and colleagues (2012) measured ectomycorrhizal enzyme activity in a tropical rainforest, but studies across different ecotypes are needed to produce a broadly applicable range of parameters.

Recommendations for improving future decomposition models

Our work demonstrates that incorporating microbial functional groups into soil decomposition models may improve our understating of soil C dynamics, especially when plant productivity varies. Plant productivity can alter soil C storage via altering the activity of the soil microbial community. Soil respiration increases when plant productivity is reduced through defoliation and this increase mirrors increases in enzyme activity within root tips, which may be indicate mycorrhizal activity (Cullings et al. 2008, Cullings and Hanely 2010). The amount of soil C mineralized by mycorrhizae could be quantified using stable C isotope techniques

(Heinemeyer et al. 2006, Heinemeyer et al. 2007). Increases in extracellular enzyme activity could also result from increased free-living microbial abundance feeding on decaying mycorrhizal tissue (Lindahl et al. 2010). While we have not explored this phenomenon here, we note that some types of mycorrhizae may enhance decomposition by increasing the activity of the free-living soil microbial community (Hodge et al. 2001). Still, field measurements that directly target the rate of soil C uptake and mineralization by ectomycorrhizal fungi are needed to improve our model predictions.

The flux of soil C to mycorrhizae compared to the total C flux from plants and soil to mycorrhizae seemed high relative to other empirical studies. Treseder et al. (2006) found 2% of C in mycorrhizal biomass was derived from recently decomposed leaf litter, suggesting mycorrhizae are responsible for decomposing a negligible fraction of soil C. However, this result can be interpreted in at least two ways. First, it may be a product of mycorrhizal C use efficiency. We have assumed that mycorrhizae are less efficient at assimilating soil-derived C due to soil C physicochemical complexity compared to photosynthate allocated to mycorrhizae. Treseder et al. (2006) did not measure the amount of soil C respired by mycorrhizae. It is possible that mycorrhizae break down a substantial amount of soil C but assimilate little of it into biomass and instead release the majority as CO_2. Field studies that isolate mycorrhizae and use isotopic tracers to track soil C into mycorrhizal biomass and respiration and laboratory C use efficiency studies are needed to confirm this idea. Secondly, the Treseder et al. (2006) result may indicate activity specific to mycorrhizal root tips rather than all mycorrhizal fungal tissues. Mycorrhizal tissues vary in expression of genes encoding different aspects of decomposition, such as enzyme production, nutrient assimilation, and transport (Wright et al. 2005). It may be that Treseder et al. (2006) targeted tissues not involved in the ecosystem processes they measured. We suggest testing the hypothesis that foraging hyphae exude a greater abundance or diversity of extracellular enzymes and assimilate more soil-derived C than tissues associating directly with plant roots by measuring enzyme activity at various distances away from roots.

The model we developed considers additional features that are significant to C cycling by adding an additional decomposer group with the flexibility to change its decomposition rate based on environmental change. Widely used C cycle models produce very different results for C pool estimates (Todd-Brown et al. 2012). Adding biological details such as microbial community changes, especially among functional groups, in response to nutrient availability and partitioning fluxes of C among roots and mycorrhizae could result in improved model predictions (Chapin et al. 2009, Todd-Brown et al. 2012, Treseder et al. 2012).

Many models have one or many soil compartments that turnover at constant rates and enzyme activity by microbes is assumed to be uniform across decomposer groups, but this is not an accurate representation of natural ecosystems (Sinsabaugh and Moorhead 1994, Hanson et al. 2008). Soil C dynamics are partly determined by microbial traits (Allison 2012), guilds that partition resource niches (de Boer et al. 2005, Moorhead and Sinsabaugh 2006), and microbial community structure with many functional groups (Orwin et al. 2011). Adding microbial enzymatic decomposition to C models resulted in increased prediction accuracy compared to field-measured responses (Lawrence et al. 2009). To our knowledge, only a few other models include mycorrhizal fungi as a unique guild (Deckmyn et al. 2008, Meyer et al. 2010, Orwin et al. 2011). In these, mycorrhizal fungi have the ability to take up nutrients from soil, exchange these for C from plants, and subsequently alter soil C storage. Mycorrhizal biomass, nutrient uptake rates (Meyer et al. 2010, Orwin et al. 2011), and C allocation from plants to mycorrhizae (Orwin et al. 2011) are important mycorrhizal parameters in simulated C dynamics. However, previous models lack the function of mycorrhizae to directly contribute to decomposition of soil C. Our study includes direct effects of mycorrhizae on soil C and indicates that ectomycorrhizal fungi can alter soil C storage through decomposition activity suggesting that pathway should be included in models.

Conclusions

Using mathematical theory we demonstrate that biotic interactions can affect predictions of

ecosystem functions. While biotic interactions are often complex, we developed a simple function to model the mycorrhizal switch in function from plant symbiont to decomposer. Mechanisms causing a switch need to be further parameterized using experiments before our model can confidently predict accurate fluxes and pools of C in an ecosystem. We suggest that mycorrhizal biomass, specific enzyme activity, and respiration be measured in decomposition experiments that manipulate plant productivity in order to increase the utility of this model. Other rhizosphere interactions could be modeled by manipulating external factors (e.g., plant productivity) and internal regulators (e.g., carbon use efficiency), which may depend upon the biomass of an interacting species.

Experiments and models also need to explore when and where ECM decompose soil organic matter. Given C allocation from plants to ECM varies with season, there is likely seasonal variation in when ECM decompose soil organic matter. ECM growth and enzyme activity is highest in the autumn (Wallander et al. 2001, Buee et al. 2005, Kaiser et al. 2010), when total C received from plants is low because of reduced photosynthesis. Similarly, mycorrhizae may access soil C in the spring during bud break when C allocation to belowground structures is low (Courty et al. 2007). Thus, decomposition by ECM could be highest in early spring and autumn. Soil organic matter decomposition by ECM may be higher in areas where nitrogen is limiting to plant and microbial growth. While ECM decomposition may be possible in nutrient-limiting ecosystems, it may not be the prevailing process that regulates C stocks in soil. For example, in N-limited and ECM dominated boreal systems C stocks are higher than in N-rich systems dominated by arbuscular mycorrhizal fungi (Averill et al. 2014), possibly owing to nutrient competition between plants and fungi. In order to acquire nitrogen for uptake and growth, the microbial community must mineralize C, thus C and nitrogen processes in soils are tightly coupled. When investigating how mycorrhizal fungi alter soil organic matter decomposition, we suggest that experimentalists target nitrogen-limited ecosystems during the fall and the spring. We also think temporal dynamics as well as the nutrient status of an ecosystem should be incorporated into modeling efforts. Mycorrhizal fungi clearly have the capacity to decompose organic matter and our theoretical model demonstrates they can be important in regulating processes pertinent to C cycling. Thus, we conclude that incorporating complex ecological interactions into C cycle models is feasible and could adjust model predictions significantly.

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Supplemental Material

Supplement

R code for simulating long-term soil carbon pools (*Ecological Archives*, http://dx.doi.org/10.1890/ES14-00301.1.sm)