



Data-driven ENZYme (DENZY) model represents soil organic carbon dynamics in forests impacted by nitrogen deposition

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ABSTRACT

Soil microorganisms participate in almost all soil organic carbon (SOC) transformations, but they are not represented explicitly in the current generation of earth system models. This study used a data-driven approach to incorporate extracellular enzyme activity into the Terrestrial ECOsystem (TECO) model, and the updated version was named the Data-driven ENZYme (DENZY) model. DENZY is based on results from an extensive data synthesis, which show that the CN ratio is positively correlated with ligninase activity ($R^2 = 0.50$). The latter is inversely correlated to soil organic carbon storage. The DENZY model was parameterized using the revise database to information from a recent meta-analysis and tested for its ability to simulate SOC dynamics at Duke Forest (North Carolina, USA) from 1996 to 2007. DENZY can well simulate the observed negative relationship between ligninase activity and SOC under N deposition conditions (R^2 ranges from 0.61 to 0.89). Moreover, outputs from DENZY better matched the observed SOC than its prototype model with the same parameterization. This study provides a simple and straightforward approach to effectively use real-world observations to improve SOC projections in terrestrial biogeochemical models.

1. Introduction

Soil is the largest carbon (C) reservoir in the biosphere, and it stores more C than the vegetation and atmosphere combined (Falkowski et al., 2000). However, the difficulties associated with quantifying soil C storage and its long-term dynamics largely impede accurate projections of the global C cycle (Todd-Brown et al., 2013; Luo et al., 2015). The microbial-mediated decomposition process is usually assumed to be a first-order kinetic reaction in earth system models (ESMs). This assumption is suitable to estimate SOC storage across spatio-temporal scales, when models are properly calibrated and validated (Parton et al., 1993; Luo et al., 2016). Nevertheless, a first-order kinetic reaction may be too simplistic to represent decomposer-mediated processes in systems experiencing climate change (Blankinship et al., 2018). Increasing evidence across a range of scales (e.g., laboratory, cross-sites, and global) supports the notion that incorporating the microbial-mediated processes could potentially improve the SOC estimation (Fujita et al., 2014; Wieder et al., 2015; Bradford et al., 2017).

Many new models have been developed to explicitly integrate the microbial process into the terrestrial biogeochemical model (Schimel and Weintraub, 2003; Manzoni and Porporato, 2009; Wang et al., 2013; Wieder et al., 2013). A general approach is to consider the explicit microbial or enzymatic pools and fluxes in soil organic C modelling. Using this approach, a majority of microbial-mediated processes can be represented (Sulman et al., 2018), but challenges still exist in this model approach. For instance, it is unclear whether the response of microbial communities to specific climate change would function in the same way from the observational scale to the ecosystem or global scale (Bradford et al., 2017). Parameters related to microbial physiology are typically measured in laboratory studies and are difficult to interpret properly in ESMs (Wieder et al., 2015; Blankinship et al., 2018). The currently utilized models can exhibit unrealistic oscillatory behaviour due to the influence of small perturbations, illustrating the instability of the models (Wang et al., 2014; Hararuk et al., 2015). These issues reflect the gaps in both the theoretical understanding and observational limits of the C cycle and demonstrate the need to develop new models

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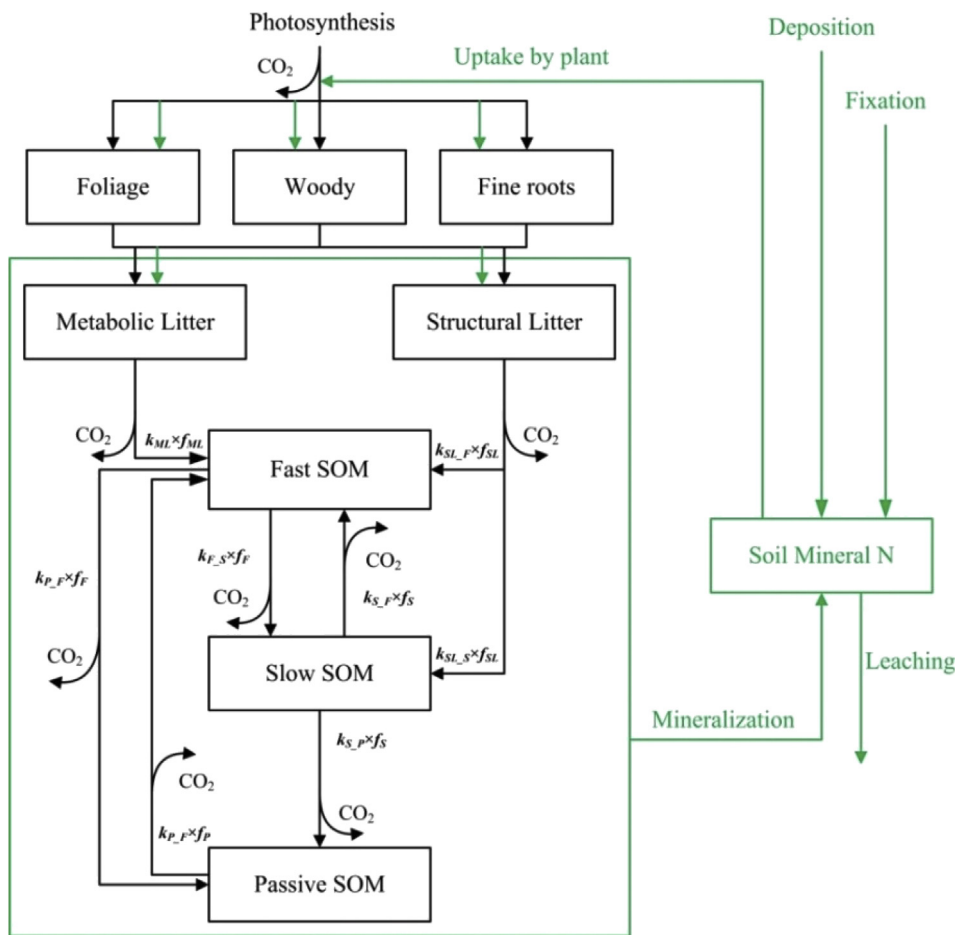


Fig. 1. The model structure of DENZY. Black arrows show carbon cycling processes and the green arrows show nitrogen cycling processes. The variable k represents the potential decomposition rates for each carbon pool; the variable f represents the coefficient of ligninase activity. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

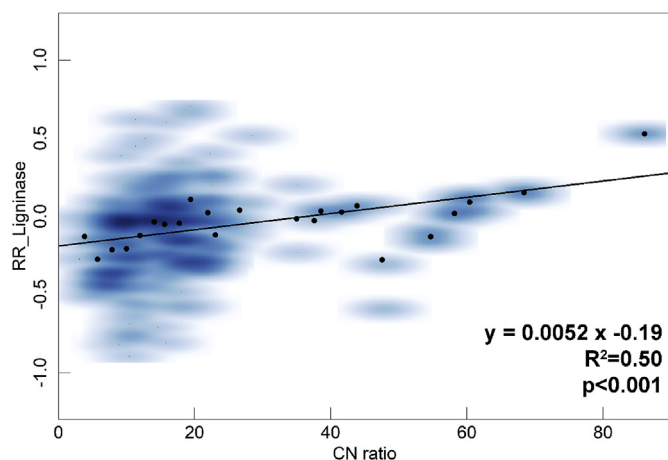


Fig. 2. The relationship between CN ratio and the response ratio of ligninase activity under N deposition. The blue color represents the data density of all the collected datasets. The color becomes deeper with higher data density. The black points represent the binned dataset. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

(Blankinship et al., 2018). Alternative approaches have been utilized to represent the microbial-mediated processes, including the multiplication of decomposition coefficients by microbial biomass (Fujita et al., 2014) or making decomposition a function of substrate chemistry (Moorhead and Sinsabaugh, 2006). These approaches can be calibrated, validated, and benchmarked under the same framework as the first-order models (Luo et al., 2016). However, the proper method of

representation of the microbial processes in terrestrial models is still under debate.

Global observations from various ecosystems offer important empirical evidence that can be used to interpret the responses of microbial communities to multiple global change variables and their underlying mechanisms. Global data synthesis or meta-analysis can reveal the general features of litter decomposition, N mineralization, CN interactions, and their potential environmental determiners (Knorr et al., 2005; Luo et al., 2006; Cornwell et al., 2008; Manzoni et al., 2012). These studies provide valuable empirical information to help determine which suitable microbial processes should be incorporated into SOC modelling. To date, observations and empirical data from these experiments have rarely been implemented in the development of models.

The unprecedented reactive N deposition processes and the N-related control of SOC dynamics are regarded as major mechanisms that drive future soil C dynamics (Reay et al., 2008; Liu and Greaver, 2010). Generally, N addition can benefit terrestrial C sequestration through two effects: enhancing NPP and repressing C decomposition. The underlying mechanisms and their relative contributions, however, are poorly understood and have not been well characterized (Nadelhoffer et al., 1999; Bragazza et al., 2006). Based on a global data synthesis, Chen et al. (2018) recently found that N deposition-mediated repressed ligninase activity rather than enhanced NPP plays the dominant role in driving soil C sequestration. This finding emphasizes the importance of incorporating this notable microbial feature in SOC predictions under N addition.

In this study, we proposed a data-driven microbial model for predicting SOC dynamics. Specifically, we developed the Data-driven ENZYmatic model (DENZY) based on the following: we incorporated the numerical relationships between ligninase activity and CN ratios

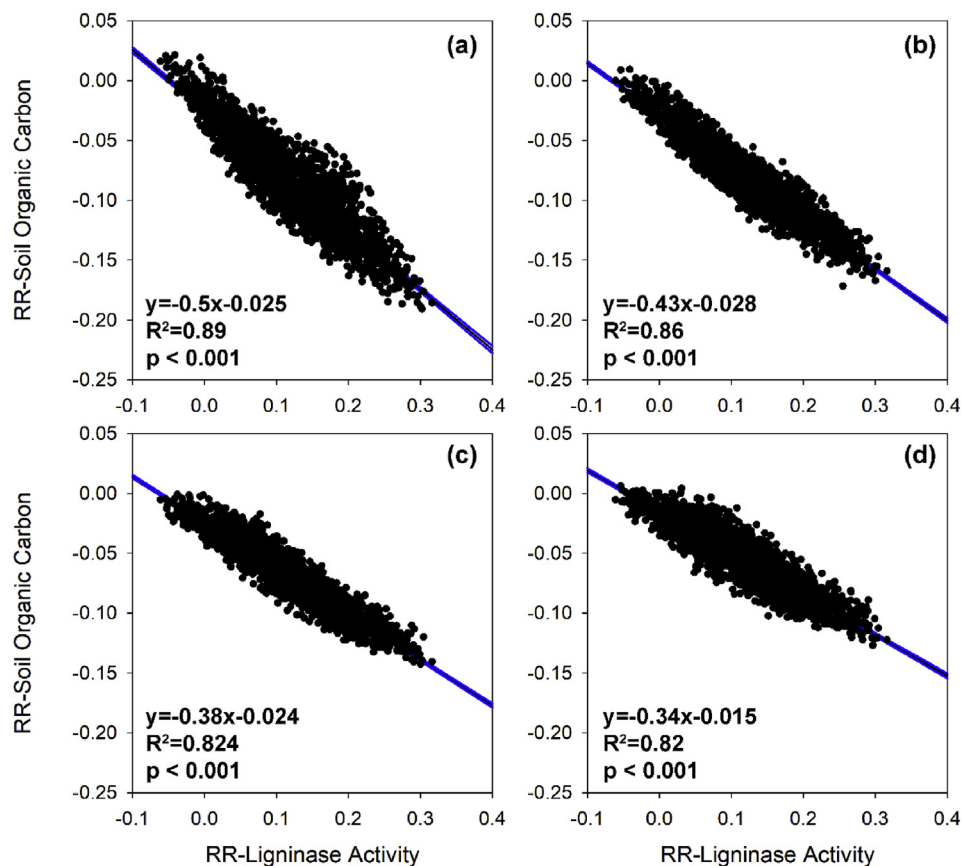


Fig. 3. Relationships between the response ratios of soil organic carbon and the response ratios of ligninase activity under N deposition with static CN ratios from site-based sampling. The sensitivity of ligninase activity is represented separately: (a) full, (b) high, (c) medium, and (d) low.

from a global data synthesis based on experiments in Duke Forest from 1996 to 2007; we compared the SOC predictions from DENZY and its prototype model, TECO-CN, against the observations. The aims of this study were to test: (1) if DENZY could well project the observed relationship between ligninase activity and SOC under N deposition; and (2) if DENZY could enhance the prediction accuracy of SOC dynamics under N deposition.

2. Materials and methods

2.1. Study site

We used data from the Duke Forest at Blackwood Division, Duke Forest, Orange County, NC (35°58'N, 79°5'W). The site is a loblolly pine forest planted in 1983 after the harvest of similar vegetation and has not been managed since planting. Daily climate variables from observations at Duke Forest were used to drive the model, including air temperature, soil temperature, vapor-pressure deficits, relative humidity, precipitation, and incident photosynthetically active radiation. Data used in this study was collected from 1996 to 2007.

2.2. DENZY development

2.2.1. TECO-CN

The prototype model we used in this study was the Terrestrial Ecosystem model with CN coupling (TECO-CN) (Fig. 1). The model had a multi-pool structure with eight C and N pools and a mineral N pool. It had been widely applied to study the responses of ecosystems to various global change phenomena, including CO₂ elevation, warming, disturbances, and N deposition (Zhou et al., 2008; Weng et al., 2012; Shi et al., 2015; Du et al., 2017).

TECO-CN employs a donor pool-dominated transfer and first-order decay scheme (Luo et al., 2003):

$$\frac{dX(t)}{dt} = BU(t) - A\xi CX(t) \quad (1)$$

The left side of the equation represents the change in each C pool per unit time, t . In TECO-CN, there were 8 pools (3 vegetation pools: foliage, woody, and root; 2 litter pools: metabolic and structural litter; and 3 soil pools: fast, slow, and passive SOM); therefore, $X(t) = (x_1, x_2, x_3, x_4, x_5, x_6, x_7, x_8)^T$ is a 8×1 vector that represents one pool size at a specific time. $BU(t)$ represents the C influx into the system and its allocation per unit time.

$A\xi CX(t)$ represents the C outflow from the system. Matrix A is the C transfer matrix among different pools. Matrix ξ is an 8×8 diagonal matrix that quantifies the environmental scalars for the carbon decomposition of each pool. Matrix C is an 8×8 diagonal matrix with diagonal input by vector $c = (c_1, c_2, c_3, c_4, c_5, c_6, c_7, c_8)^T$, which defines the potential turnover rate for each pool.

A more detailed introduction of TECO-CN can be found in the Supplementary Material.

2.2.2. Meta-analysis of soil extracellular enzyme activities (EEAs) and soil C storage

To incorporate the concept of enzyme-mediated soil C dynamics into model simulations, we performed a meta-analysis to investigate how soil C-degrading EEAs related to soil C dynamics with enhanced N deposition. The dataset was firstly limited to studies that simultaneously reported soil C-degrading EEAs and soil C storage. Our results indicated that the suppression of ligninase activity was closely related to an increase in soil C sequestration under N deposition (i.e., the significant negative correlation between ligninase activity and SOC) over a

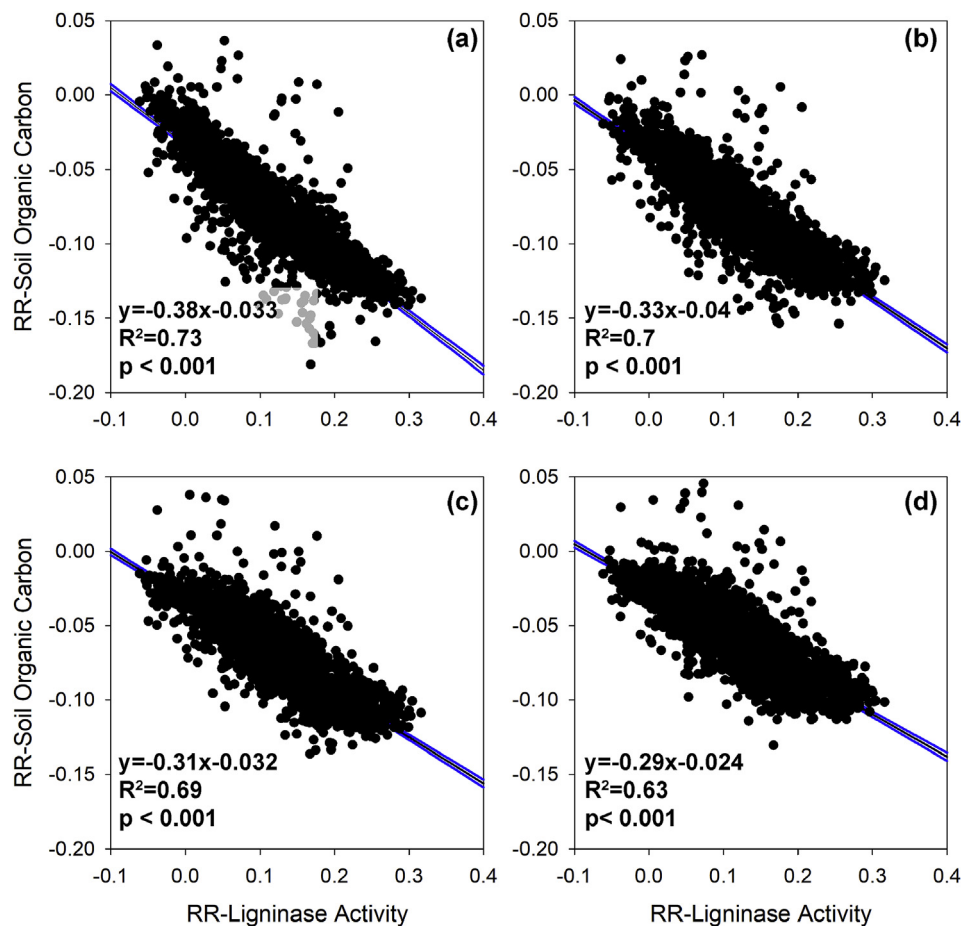


Fig. 4. Relationships between the response ratios of soil organic carbon and the response ratios of ligninase activity under N deposition with varied CN ratios generated from site-based sampling. The sensitivity of ligninase activity is represented separately: (a) full, (b) high, (c) medium, and (d) low.

wide range of climate conditions, ecosystem types, and N addition methods (Chen et al., 2018).

Based on the published dataset (<https://figshare.com/s/37aa98b76a7ef51da2e2>) by Chen et al. (2018), we updated almost all journal articles that reported the effects of N addition on ligninase activity. In this study, we focused on how the soil CN ratio influenced ligninase activity. The effects of N addition on ligninase activity were evaluated by meta-analysis following the method outline by Chen et al. (2018). The datasets were binned intervals of every 2 CN ratios. All data associated with the soil CN ratio and SOC are available from the published dataset mentioned above.

2.2.3. Incorporation of ligninase activity into TECO-CN

To incorporate enzymatic factors into the SOC modelling, we used the relationship between the CN ratio and ligninase activity derived from the meta-analysis and considered the effect of ligninase activity as an adjusted coefficient of the potential decomposition rate (c_i) in each carbon pool. A function representing the relationship from the meta-analysis, $f(CN_i)$, was added to represent the influence of ligninase activity on the decomposition in the carbon pool i , where CN_i is the CN ratio in the carbon pool i (Fig. 1).

Another coefficient, p , was explicitly added to represent the proportion of lignin-related decomposition in each C pool. In this study, we assumed four sensitivity levels of ligninase activity in each C pool (i.e., Low, Medium, High, Full) (Table S1).

Therefore, in DENZY, the vector $c = (c_1, c_2, c_3, c_4 \times f(CN_4) \times p_4, c_5 \times f(CN_5) \times p_5, c_6 \times f(CN_6) \times p_6, c_7 \times f(CN_7) \times p_7, c_8 \times f(CN_8) \times p_8)^T$ was used.

2.3. Model experiments

Three experiments were designed to test the performance of DENZY. The first two experiments were used to test if the model was able to reproduce the relationship between ligninase activity and SOC dynamics and to determine if results were consistent and robust given various conditions (e.g., different sensitivity levels of ligninase activity and wider ranges of CN ratios). All model simulations used the same site-based climate data from 1996 to 2007.

2.3.1. Simulations based on CN ratios from the site-based parameterization

The site-based CN ratios were calibrated by Shi et al. (2015) using a data assimilation approach. First, we applied the results of the CN ratio parameterization from Shi et al. (2015) (i.e., mean values and standard deviations, Table S2). Thereafter, we used Monte Carlo sampling to generate groups of CN ratios by assuming normal distributions of the parameters (Xu et al., 2006). The algorithm was repeated 30,000 times, and we discarded the first 10,000 groups and accepted 2000 groups of parameters by interval sampling (one accepted from each ten sampled, Fig. S1).

Each group of CN ratios was used to drive the model. Simulations with and without N deposition were performed to calculate the response ratio of SOC. Both conditions with static and varied CN ratios were tested.

2.3.2. Simulation based on CN ratios from the global observed dataset

The observed CN ratios from the global synthesis were calculated as the weighted average of CN ratios of each litter and soil C pool:

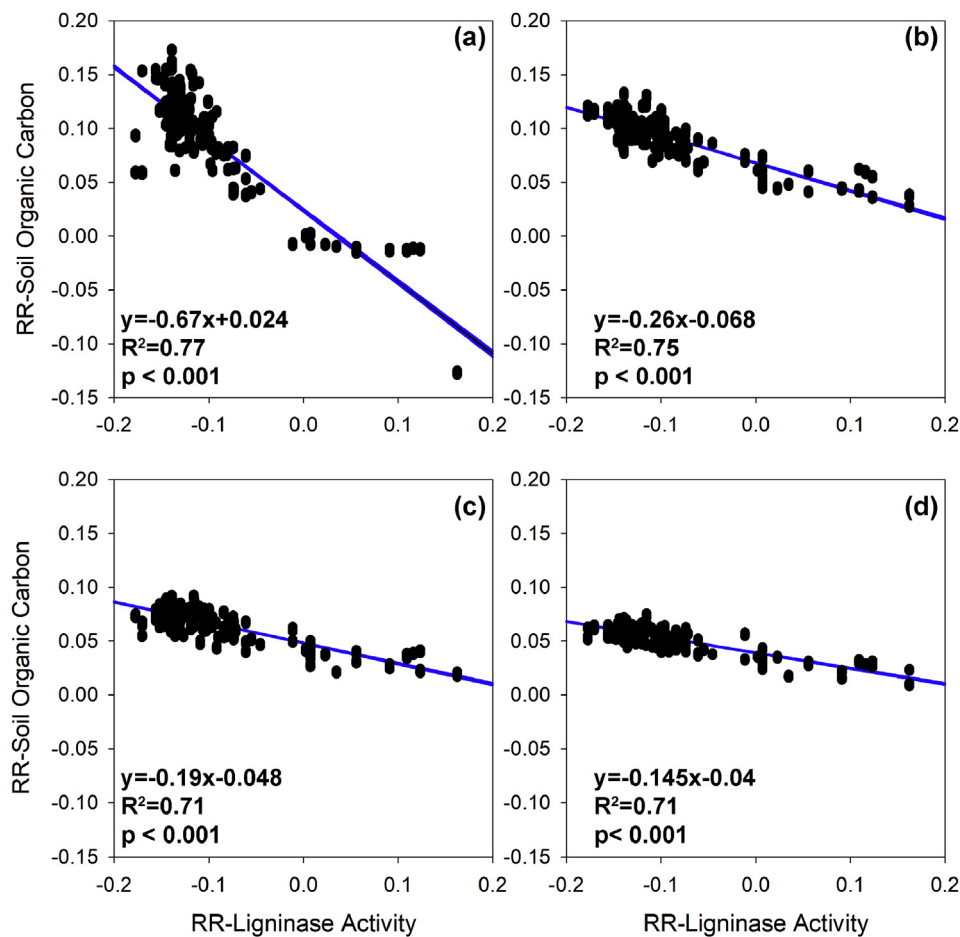


Fig. 5. Relationships between the response ratios of soil organic carbon and the response ratios of ligninase activity under N deposition with static CN ratios based on the global synthesis. The sensitivity of ligninase activity is represented separately: (a) full, (b) high, (c) medium, (d) low.

$$CN_{observed} = \frac{\sum CN_i \times C_i}{\sum C_i} \quad (2)$$

where CN_i was the CN ratio in the i pool and C_i was the soil organic C in pool i . The range of soil CN ratios were much larger due to the global CN ratio, so we varied the CN ratio of each pool to a wider scope than the local CN experiment (See Table S2). We generated 200 groups of CN ratio samples for each $CN_{observed}$. The same simulations as in 2.3.1 were performed in this section.

2.3.3. Model-data comparison

In this section of the model experiment, both the DENZY and its prototype model, TECO-CN, were run to simulate real-time SOC dynamics. Different sensitivities of ligninase activity were also considered in this model section. The model outputs were compared against site observations of litter, soil microbial C pools, and mineral C pools (Allen et al., 2000; Lichter et al., 2008).

The information about the site observations are listed in Supplementary Material, Table S3.

3. Results

3.1. Relationship between soil CN ratios and ligninase activity

The correlation between CN ratios and the response ratio of ligninase activity under N deposition (RR-Lig) can be seen in Fig. 2. The results suggest a two-stage response pattern of ligninase activity to N deposition with varying CN ratios. With lower CN ratios, the RR-Lig ratio was negative. However, with higher CN ratios, the RR-Lig ratio

was positive. Overall, the RR-Lig ratio was positively correlated with the soil CN ratio ($y = 0.0052x - 0.19$, $R^2 = 0.50$) (Fig. 2). This equation was further used in the model simulations.

3.2. Model simulations

3.2.1. Simulations with the site-based parameterization

By linking the CN ratios to ligninase activity, DENZY was able to reproduce well the strong control of ligninase activity over SOC under N deposition. Both the results from static and varied CN ratios showed significant negative correlations ($p < 0.001$) between the response ratio of ligninase activity (RR-Lig) and the response ratio of SOC (RR-SOC) (Fig. 3 and Fig. 4). With different inputs for the sensitivity of ligninase activity, the outputs exhibited similar response patterns. The mean R^2 values were higher for the static CN results than for the varied CN results (mean $R^2 = 0.86$ vs. 0.69). The R^2 value from the CN varied experiment, which simulated the real site situation, was closer to the results from the global synthesis reported by Chen et al. (2018) ($R^2 = 0.404$).

3.2.2. Simulations based on the observed CN ratios from global synthesis

The CN ratios from the global synthesis showed a much larger range than the site-based CN ratios and better represented various soil quality conditions. Similar negative correlations between RR-Lig and RR-SOC were observed in both static and varied CN experiments (Fig. 5 and Fig. 6). With the minimized impact from the ligninase activity, the patterns became more consistent with the increasing of slopes. Nevertheless, significant negative correlations between RR-Lig and RR-SOC persisted ($p < 0.001$).

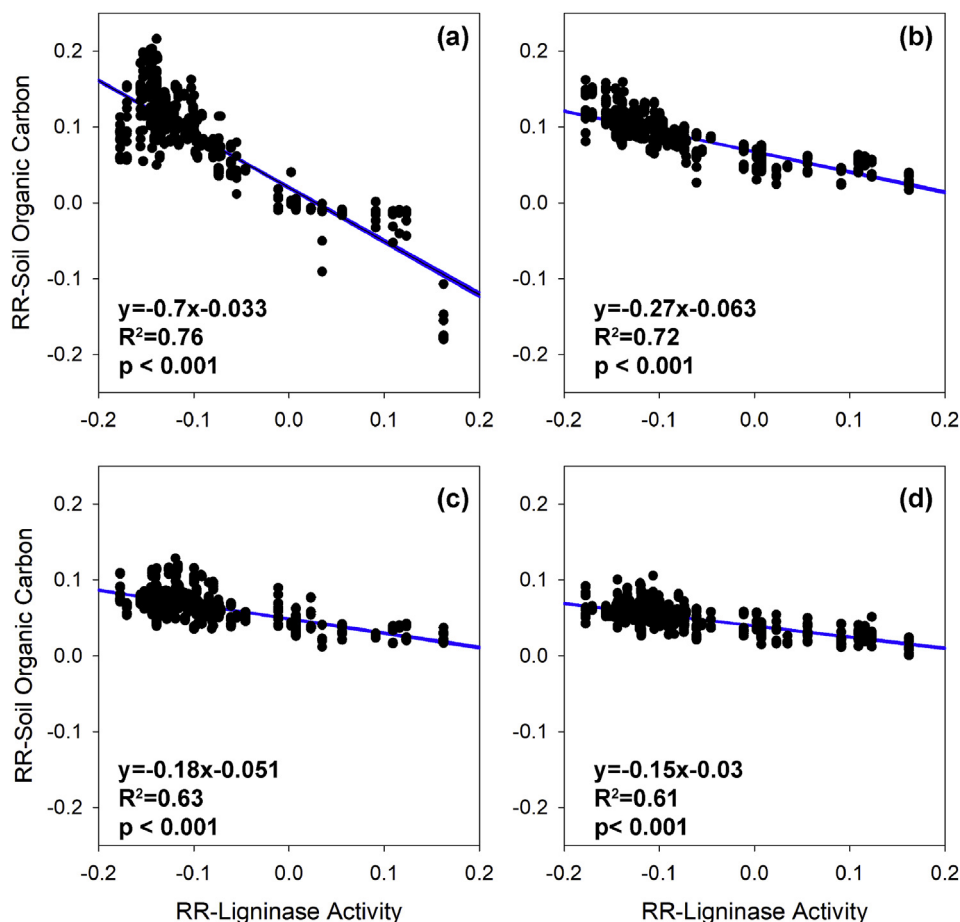


Fig. 6. Relationships between the response ratios of soil organic carbon and the response ratios of ligninase activity under N deposition with varied CN ratios based on the global synthesis. The sensitivity of ligninase activity is represented separately: (a) full, (b) high, (c) medium, (d) low.

3.2.3. Model-data comparisons

All of the model simulations were able to generate the temporal pattern of SOC dynamics, such as the increasing and decreasing trends in forest floor and mineral soil C pools (Fig. 7). DENZY was able to produce better predictions than TECO-CN over all three major C pools (i.e., forest floor, soil microbial and mineral C pools); it decreased the over-estimation of litter C content and largely compensated for the under-estimations of soil microbial and mineral C contents from TECO-CN. Since both models were well parameterized, the overall R^2 was 0.92 for TECO-CN and 0.97 for all simulations of DENZY. The results indicated that enhanced prediction capability was gained from the improved parametrization and process incorporation. However, the magnitudes of some observed variations were still not picked up by DENZY, such as the fast accumulation of mineral soil C from ~ 1900 gC/m² yr to ~ 2400 gC/m² yr during the period from 2000 to 2003. The fast increase of C input to SOC without a comparable input of extra soil organic N at the site is a possible reason for the model data mismatch (Lichter et al., 2008).

4. Discussion

DENZY was able to capture the significant response of ligninase activity to SOC through incorporation of a ligninase-CN ratio response pattern. More importantly, DENZY further improved the well-parameterized TECO-CN model to better fit observations, indicating this data driven incorporation was able to source extra useful information. Both results support the effectiveness of model development by introducing the data based process from the global synthesis into an ecosystem model. Based on our knowledge, DENZY is among the first

attempts to incorporate quantitative information from a meta-analysis into a land model to improve the prediction of SOC dynamics.

4.1. Ligninase activity regulated by soil CN ratio

The CN ratio is the key stoichiometry in soil and the indicator of substrate quality. Based on the output of our data synthesis, a two-stage relationship between ligninase activity and substrate quality was illustrated under N deposition (Fig. 2). Ligninase activity is closely related to N-containing molecules that are protected and cannot be accessed without specific types of extracellular enzyme (Jilling et al., 2018). With additional N input, the ligninase activity tends to be more active under conditions of soil organic matter (SOM) with low quality but less active in high quality SOM sites (Carreiro et al., 2000; Janssens et al., 2010). This mechanism helps explain the response pattern of ligninase activity to N additions over a wide range of CN ratios. Under conditions of significant nutrient deficiency, additional N promotes the growth of soil decomposer communities by alleviating the overall nutrient limitation (Grandy et al., 2013). With the increasing N availability in SOC, N addition further compensates the nutrient deficiency and reduces ligninase activity due to the diminished need for the release of nutrients protected by recalcitrant substrates (Manzoni et al., 2008). With further increased N availability, N addition can become a negative factor for ligninase activity, which has been extensively reported by previous studies (FOG, 1988; Higurashi, 1990; Zak et al., 2008). Under the situation of SOM with sufficient N sources, the effect of N addition further minimized. This mechanism also explained the high variability of the response pattern of ligninase activity to N addition at the end of high N availability (Fig. 2). Our results further suggest that the latter effect

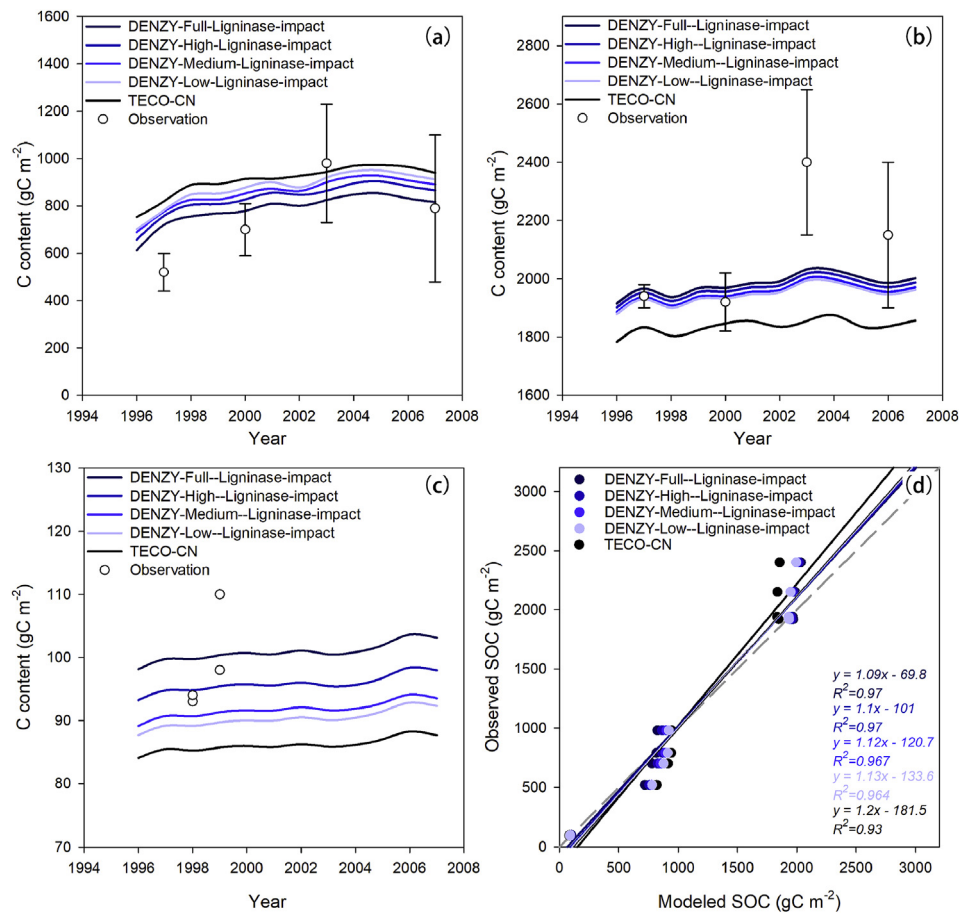


Fig. 7. Comparisons of modeled vs. measured results in (a) forest floor, (b) soil microbial and (c) mineral soil C pools, and (d) the linear correlation between modeled and measured results.

should dominate in this two-stage control pattern as the turning point of the CN ratio (37.2) was markedly higher than the soil CN ratio from this site observation (Shi et al., 2015) and the global scale average (Cleveland and Liptzin, 2007).

By incorporating this explicit relationship into the TECO-CN model, we were able to capture the significant response of SOC to ligninase activity under N deposition without creating additional pools and parameters. Similar responses from different impact fractions and different model protocols (i.e., static and varied CN ratios, site-based and global data-based CN ratios) also suggested the effectiveness and generality of the model performance under various conditions. Moreover, DENZY compensated for the under- or over-estimations of its first-order predecessor and better matched observations, indicating its potential for improving SOC predictions. We propose that the model can be further improved if local data based relationships can be used in future applications.

4.2. Data-driven modelling for SOC dynamics

Soil is a complex system and contains various biological, physical, and chemical processes, many of which influence SOC decomposition. However, different processes could only be detected or effective over certain scales. The response of microbe communities to specific climate change signals at the ecosystem level is, in fact, the result of various interactions among the microbial communities (so called emergent properties) (Gilbert and Henry, 2015). These properties can hardly be quantified as numerical sums of isolated components in the system (Casadevall et al., 2011). For example, the oscillations of microbial biomass from the microbial-substrate interactions would only be

detected on small spatiotemporal scales (Semenov et al., 1999; Zelenev et al., 2006). Although key features of emergent properties at the community level have been recently illustrated (Goldford et al., 2018), our understanding of the link between microbial behaviour and ecosystem phenomena is severely lacking due to the large scale differences and wide varieties of ecosystems involved. A determination of what microbial processes are responsible for ecosystem phenomena is critical for developing sufficient ecosystem level models.

To better project the responses of SOC to global changes, we need to better understand how to quantify an emergent worldwide environmental behaviour using a series of mathematical equations. Information from global data synthesis is highly instructive and using observational evidence from the global scale will help clarify which processes should be explicitly considered in the global models. The data-driven approach can help determine if a process should be considered and how to properly incorporate an essential process into models.

DENZY was constructed on an ecosystem level model (i.e., a first-order kinetic model), which was widely studied and applied over the last several decades (Giardina and Ryan, 2000; Kirschbaum and Paul, 2002; Cornwell et al., 2008; Weedon et al., 2009). Important parameters, such as C transfer coefficients (Xu et al., 2006), CN ratios (Shi et al., 2015), and environmental scalars (Williams et al., 2005; Zhou et al., 2009), have been well calibrated and constrained over both local and global scales. The model has been widely tested and validated for long-term simulations (Kirschbaum and Paul, 2002; Corbeels et al., 2005; Izaurralde et al., 2006; Stockmann et al., 2013). In this study, we conducted a site-based study to demonstrate how DENZY was developed to reproduce ecological patterns and SOC dynamics based on existing datasets.

4.3. Future improvements and perspective

Although DENZY showed its advantages and potential usage through the site-based model tests, future research is largely needed for its general application. Ligninase activity is the key variable in DENZY. We developed the current model version mainly based on a single relationship between substrate quality (i.e., CN ratios) and ligninase activity. However, this condition can hardly improve the temporal trend predictions due to the stability of soil stoichiometry (Cleveland and Liptzin, 2007; Sinsabaugh et al., 2009). Other internal (e.g., system properties and processes) and external factors (e.g., environmental scalars) that are closely related to the ligninase activities are necessary to be considered for the future improvement of the model. For example, soil pH has long been regarded as a primary external driver for extracellular enzyme production in the soil microbial communities. The strong control of pH values for oxidative enzymatic potential has been identified over the global scale (Sinsabaugh et al., 2008; Leifeld et al., 2013; Min et al., 2014). The utilization of this factor into the prediction model is regarded as a next task for the future development of DENZY. The statistical derivation (Reth et al., 2005), parameterization (Wang et al., 2013), and our data synthesis (Chen et al., 2018) may provide insights for the inclusion of additional modelling factors.

In this study, we set four impact levels of ligninase activity in different litter and soil C pools to represent the contrast importance of ligninase-mediated C (i.e., recalcitrant C) in different pools. As a result, the changes in ligninase activity influence the magnitude of the difference from the original model (Fig. 7). Future studies will need to explicitly consider the C composition of different chemical compositions and decomposition stages.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.soilbio.2019.107575>.

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