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Key Points:

- Model structure changes from carbon only to carbon-nitrogen coupling often result in lowered ecosystem carbon storage and lowered carbon sequestration, which may not reflect the reality in the real-world ecosystems
- Our study with data assimilation suggested that parameter values change with model structures whereas simulated ecosystem carbon dynamics are similar under either ambient and warning conditions
- Nitrogen (with other elements as well) regulates carbon cycle processes mainly through its influences on parameters in this study

Supporting Information:

Supporting Information may be found in the online version of this article.

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Reparameterization Required After Model Structure Changes From Carbon Only to Carbon-Nitrogen Coupling

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Abstract Prediction of carbon (C) sequestration in terrestrial ecosystems under climate change depends on C-nitrogen (N) interactions. While many newly developed C-N coupling models predict lower C storage than their C-only counterpart models, it has not been carefully examined whether or not such model predictions would be supported by real-world observations. This study is to retrieve knowledge on N cycle from one field warming experiment in an alpine meadow of China so that we can better predict land C sequestration. We estimated two sets of parameters with one C-only model and one C-N coupling model, respectively, with the data assimilation technique. Our results showed that estimated process rates (e.g., senescence and decomposition rates) of organic C from almost all pools except standing litter and leaf are higher with the C-N coupling model than those with the C-only model. The allocation coefficient of C to root estimated with the C-only model was 68.0% and 56.6% smaller than that with the C-N coupling model under the ambient and warming treatments, respectively. Both the C-only and C-N coupling models simulate similar C pool sizes as observed at either the ambient or warming treatment with their respective parameter estimates. Meanwhile, the warming treatment increased the slow soil organic matter (SOM) pool due to decrease in estimated decomposition rate of the slow SOM via parameter fitting and increase in the C input from surface litter. In general, our results suggest that reparameterization is required when we add N processes to a C cycle model to realistically predict the ecosystem dynamics in response to future changes in N availability.

Plain Language Summary Models with nitrogen (N) module usually predict lower carbon (C) storage than their C-only counterpart models, but the C storage in the real-world ecosystems won't change according to whether or not a model considers N processes. We estimated two sets of parameters with one C-only model and one C-N coupling model, respectively, from a field warming experiment in an alpine meadow of China with the data assimilation technique. The technique integrates observations with model via parameter estimation. We found that a model structure change from the C-only to C-N coupling influences model parameterization but doesn't influence the simulations. However, warming increased soil C storage due to the larger C input and the smaller decomposition rate than the control. We suggest when we add N processes to a C cycle model, the new models should be re-parameterized, ideally with data assimilation, to better predict the ecosystem C dynamics under chaing N availability.

1. Introduction

Terrestrial ecosystems sequester approximately one-third of anthropogenically emitted carbon (C) and thus play a critical role in mitigating climate change (Friedlingstein et al., 2020). Terrestrial C sequestration is strongly regulated by nitrogen (N) availability (Diaz et al., 1993; Hungate et al., 2003; Ineson et al., 1995; Luo et al., 2004; Raven et al., 2004; van Oijen and Levy, 2004). As a consequence, many of the Earth system models (ESMs) have incorporated N processes (Thornton et al., 2007; Zaehle & Friend, 2010). The C-N coupling models usually predict lower photosynthesis, lower C sequestration, and lower C storage in plant and soil pools than their counterpart, C-only models (Du et al., 2018; Zaehle & Friend, 2010). For example, Community Land Model version 4 (CLM4), which incorporates N processes, predicts soil C storage of 336 GtC, lower by 734 GtC than its precursor, CLM-CASA' (Thornton et al., 2007). Without N coupling, ecosystem C only model would overestimate ecosystem C inputs and sequestration, as potential N limitation can not be considered. While the predicted lower C storage might reflect the concept of N limitation in the C-N coupling models, it may not reflect the reality in the real world. In other words, the global terrestrial C storage in the real world, which is about 2,000 Gt (Houghton, 2007), would not change because we incorporate N processes into a C-only model. This paper is to explore how we can realistically model C and N interactions so that model predictions reflect real-world phenomena.

The formation of organic matter requires a certain amount of N in company with the processes of plant C assimilation (Hungate et al., 2003; Luo et al., 2004; Raven et al., 2004; van Oijen and Levy, 2004). Besides, the photosynthetic capacity is tightly related to the leaf N content because the proteins of the Calvin cycle represent the majority of leaf N (Evans, 1989). Furthermore, the conversion and decomposition of dry matter in terrestrial ecosystem are also accompanied by strongly coupled C and N cycle processes (Haynes, 1986; Prescott, 2005). Hence, there is a growing awareness that the terrestrial N cycle is crucial to accurately predict the C cycle by ESMs under different climate change scenarios, and more and more ESMs account for aspects of terrestrial N dynamics (Kyker-Snowman et al., 2020; Parton, 1996; Shi et al., 2016; Thornton et al., 2007; Zaehle & Friend, 2010).

To achieve these C-N interactions, ESMs usually simulate (a) N dependence of photosynthesis (Sokolov et al., 2008; Zaehle & Friend, 2010) and (b) C and N coupling via their stoichiometric relationships using either fixed or flexible C:N ratios in different pools of an ecosystem (Koven et al., 2013; Oleson et al., 2013; Zaehle & Friend, 2010). The C:N ratios of organic matter in different pools, in turn, affect rate processes, such as leaf senescence and litter decomposition (Parton et al., 1993; Zaehle & Friend, 2010). These ESMs that consider N cycle generally attenuate responses of terrestrial C storage to increasing atmospheric CO_2 concentration and associated climate changes (Meyerholt et al., 2020; Thornton et al., 2007; Wårlind et al., 2014; Zaehle & Friend, 2010; Zhang et al., 2014). ESMs with the N cycle usually predict 18%–43% lower total C storage than the C-only models. The reduction is greater for soil organic matter (SOM; 18%–61%) than for vegetation C (0%–36%), with intermediate reductions for litter and coarse woody debris pools (Asaadi & Arora, 2021; Meyerholt et al., 2020; Thornton et al., 2007; Wårlind et al., 2014; Zhang et al., 2014). Meanwhile, the C-N coupling models predict 33%–43% lower gross primary production (GPP) than the C-only models (Thornton et al., 2007; Zaehle & Friend, 2010).

The predicted lower GPP and lower C storage by the C-N coupling models than their C-only counterpart models all make sense in the modeling world as the C-N coupling models simulate N limitation whereas the C-only models do not. However, would the C storage in the real-world ecosystems change according to whether or not a model considers N processes? The C-N interactions (with other elements as well) always exist in the real-world ecosystems no matter whether or not there is a N module to constrain the C cycle in the modeling world. When we use a C-only model simulates ecosystem responses to climate change, N processes are considered to be unresolved in the model (Luo & Schuur, 2020). The N influences on C processes are usually represented in parameterization, especially when parameters are calibrated to optimize model performance according to observations. For example, when data assimilation is used to estimate parameters in a C-only model, the N-related information contained in the observation is implicitly represented in the estimated parameters. However, when a C-N coupling model is calibrated using the same observations, the N-related information is no longer implicitly represented in the C-related parameters. Thus, estimated parameters vis data assimilation are expected to differ between the C-only and C-N coupling models. It is important to examine the relationship among model structures, parameterization, and observations.

In this study, we used data assimilation to estimate parameters of a C-only model and C-N coupling model from 17 data sets collectd at a field warming experiment in an alpine meadow of Qinghai-Tibet Plateau. The estimated parameters were used in their respective models to simulate C and N dynamics during the experimental period from 2015 to 2018. The specific questions we addressed in this study are: (a) how do model structures influence parameter retrieval between a C-only and C-N coupling models? And (b) how does experimental warming influence model parameterization and predictions of ecosystem C dynamic with the C-only and C-N coupling models?

2. Materials and Methods

2.1. Site Description

This study used data from the Hong Yuan field station, which was located on the eastern Qinghai-Tibet Plateau (32°84’N, 102°58’E) and has a continental plateau frigid temperate monsoon climate. The mean annual precipitation is 747 mm, the mean annual temperature is 1.5°C, the sunshine duration in a year is about 2,000–2,400 hr, the growing season lasts from April to October. The main vegetation type in the study site is alpine meadow, and the soil type is subalpine meadow soil and boggy soil (Song et al., 2014). This area is dominated by *Deschampsia*

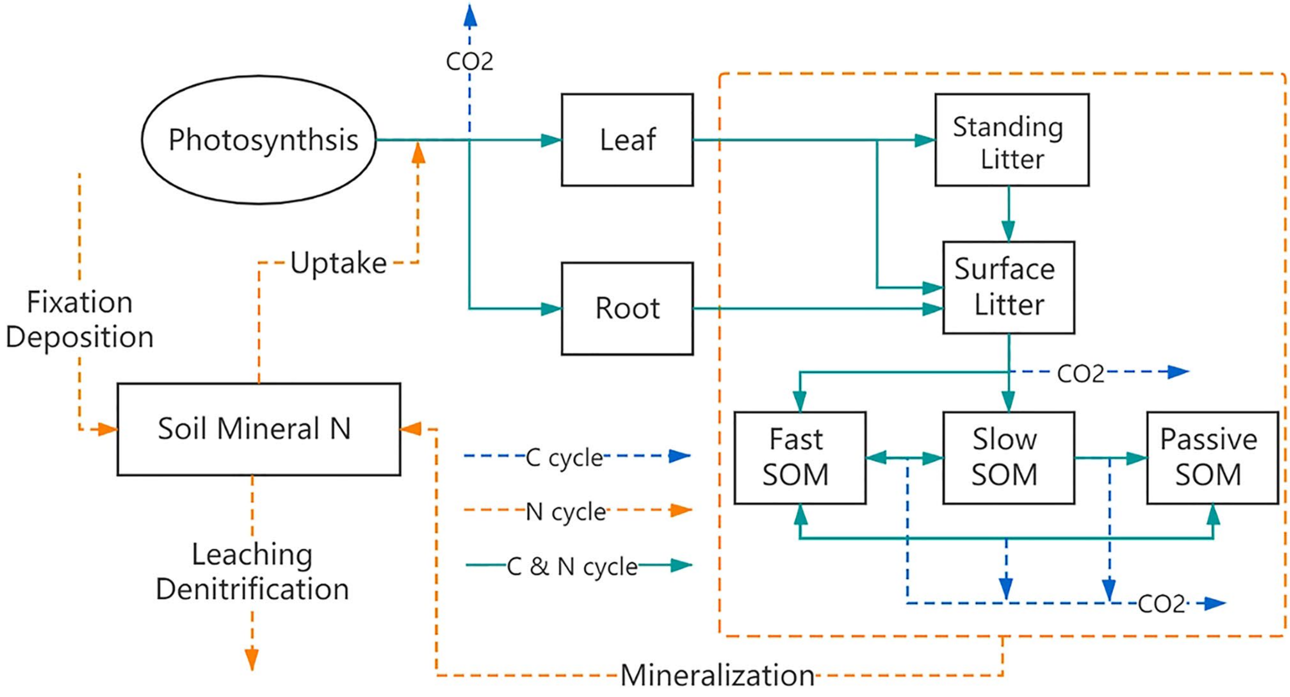

Figure 1. Carbon (C) and Nitrogen (N) pools and flux pathways in Grassland ECOsystem model. Blue arrows show C transfer processes, yellow arrows indicate N transfer processes, and green arrows represent C and N coupling processes. Soil organic matter.

caespitosa (Linn.) *Beauv., Koeleria cristata* (Linn.) Pers., *Gentiana sino-ornata* Balf. F., *Potentilla anserina* L., and *Anemone rivularis* Buch.-Ham (Quan et al., 2018).

2.2. Model

The Grassland ECOsystem (GECO) model was used in this study (Wang et al., 2021). GECO evolves from the Terrestrial ECOsystem (TECO) model (Xu et al., 2006, Shi et al., 2016) with a distinct standing litter pool for grassland. GECO has seven C and N pools and one more mineral N pool in this model. The pools are leaf (X1, N1), roots (X2, N2), standing litter (X3, N3), surface litter (X4, N4), fast (X5, N5), slow (X6, N6), passive (SOM, X7, N7) and mineral N pool (Figure 1). And the C-only model doesn't contain the N module whereas the C-N coupling model has the same C cycle module as in the C-only model. In the GECO model, measured GPP was used to drive the C cycle. Some of the GPP was used for plants' respiration, and the remaining was allocated in leaf (X1) and root (X2). The detritus of dead plants then flowed to the litter pool, which contained standing litter (X3) and surface litter (X4). And the underground litter was partly respired by microbes (X5) while the rest was converted to fast SOM (X5) and slow SOM (X6). The CO_2 released by the decomposition of soil C eventually returns to the atmosphere. Similarly, plants uptake N from mineral soil. Then, the uptaken N was distributed to plant pools and then transferred to litter and soil pools. Organic N in the seven pools returned to soils by microbial mineralization.

GECO model uses matrix-based first-order differential equations to describe the process of C transfer between ecosystem C pools as:

$$\frac{d}{dt}\boldsymbol{X}(t) = \boldsymbol{A}\xi(t)\boldsymbol{K}\boldsymbol{N}_s\boldsymbol{X}(t) + \boldsymbol{b}u(t) \tag{1}$$

$$\boldsymbol{X}(0) = \boldsymbol{X}_0$$

where $\boldsymbol{X} = (x_1\ x_2\ x_3\ x_4\ x_5\ x_6\ x_7)^T$, in which xi represents the C pools in leaves, roots, standing litter, surface litter, fast, slow and passive SOM at time t, respectively. Matrix **A** represents C transfer between pools (Xu et al., 2006). $\boldsymbol{K}$ is a 7×7 diagonal matrix with diagonal entries. The elements on the diagonal indicate the C decay rate from each of the pools ($i = 1, 2, ..., 7$). $\boldsymbol{N_s}$ is a 7×7 diagonal matrix with diagonal entries, elements on the diagonal indicate the N limitation effects to the pools decomposition rates, which is respresented $\boldsymbol{N_s(i)} = \exp((\mathrm{CN0}-\mathrm{CN}(i))/\mathrm{CN0})$ ($i = 1, 2, ..., 7$). u represents the C produced by canopy photosynthesis. $\boldsymbol{b}$ is a vector of partitioning coefficients of photosynthetic products to leaves and roots. $\xi(t)$ is an environmental scalar to account for temperature and moisture effects on decomposition (Luo et al., 2003).

The N processes can be described by this formula:

$$\frac{d}{dt}\boldsymbol{N}(t) = \boldsymbol{A}\xi(t)\boldsymbol{K}\boldsymbol{N}_s\boldsymbol{R}^{-1}\boldsymbol{X}(t) + \kappa_\mu N_{min}(t)\boldsymbol{\pi} \tag{2}$$

$$\mathbf{N}(0) = \boldsymbol{N}_0$$

where $\boldsymbol{N} = (\mathrm{n_1\ n_2\ n_3\ n_4\ n_5\ n_6\ n_7})^{\mathrm{T}}$, in which $\mathrm{n_i}$ represents the N pools in leaves, roots, standing litter, surface litter, fast, slow and passive SOM at time t, respectively. $\boldsymbol{R}$ is a 7×7 diagonal matrix with diagonal elements to indicate the C:N ratio of each pool. $\boldsymbol{\pi} = (\pi_1\ 1\text{-}\pi_1\ 0\ 0\ 0\ 0\ 0)^{\mathrm{T}}$ is an allocation coefficient vector of N from mineral soil to leaves and roots. $\kappa_\mu$is plants N uptake rate, N min (t) is the amount of soil available N at time t. The dynamic balance of mineral soil N is determined by the input of mineralization, biological fixation, atmospheric deposition and the output of plants input, leaching and gaseous N fluxes, which can be described by:

$$\frac{d}{dt}N_{min}(t) = -(\kappa_u + \kappa_L)\, N_{min}(t) + \boldsymbol{A}\xi(t)\boldsymbol{\varphi}_1^{*}\boldsymbol{K}\boldsymbol{N}_s\boldsymbol{R}^{-1}\boldsymbol{X}(t) + F(t) \tag{3}$$

$$N_{min}(0) = N_{min,0}$$

In Equation (3), $\kappa_\mu$and $\kappa_L$represent rates of N uptake and loss, respectively. $\boldsymbol{A}\xi(t)\boldsymbol{\varphi}_1^{*}\boldsymbol{K}\boldsymbol{N}_s\boldsymbol{R}^{-1}\boldsymbol{X}(t)$represents N mineralization, $\boldsymbol{\varphi}_1^{*}$is mineralization rate, and $F(t)$ is N input by biological fixation and atmospheric deposition.

In this study, the initial pool sizes of leaves, roots, standing litter, surface litter, fast soil, slow soil, and passive soil pools, were constrained using data in the ambient treatment. The initial pool sizes in the warming treatment used the same values that were used in the ambient treatment, assuming that no significant difference existed between the ambient and warming treatment before the treatment started.

This study was to estimate C exit rates (the proportion of C outflow to the total C pool) of seven pools, C allocation coefficients of NPP and C transfer coefficients with both the C-only and C-N coupling models. Meanwhile, N-related parameters, such as N partitioning coefficient, N uptake, N loss, external N input, the initial mineral N pool and C:N ratios of different ecosystem components, were estimated in the C-N coupling model.

2.3. Data Sources

Data sets that are used to drive the GECO model and data sets that are used to estimate parameters in this study both were from a co-located eddy-covariance measurement system and warming experiment. We used all 4 years of data to estimate parameters as it is a common practice for data assimilation research (Liang et al., 2018; Luo et al., 2011; Xu et al., 2006). Due to the photosynthesis module was not included in the GECO model for this study, the daily GPP data was collected from an eddy-covariance tower nearby our warming experiment. The warming experiment near the Eddy covariance tower used a random block design with two warming treatments (A, ambient temperature; W, warming treatment) with five replicates. The warmed plots were continuously heated by infrared radiators (MSR-2420, Kalglo Electronics Inc., Bethlehem, Pennsylvania, USA) suspended 1.5 m above the ground since June 2014. The output power was 2,000 W, increased soil temperature at 10 cm on average by 2.77°C (Quan et al., 2018). GPP and soil respiration (SR) were measured twice a month with static chambers (LI-6400XT, LI-COR Environmental, Lincoln, Nebraska, USA) in plots with different treatments in the growing season from 2015 to 2018. Biometric measurements were made once a year to quantify biomass of plant leaves and roots, standing litter, surface litter, and microbes, soil C content, total N content of microbe and soil, and soil inorganic N concentration in the ambient and warming plots.

The data to drive the model includes daily soil temperature, soil moisture, and GPP as C input from 2015 to 2018 as the GECO did not simulate photosynthesis. The measured GPP at the nearby eddy-covariance tower was used as GPP at ambient temperature (Chen et al., 2019). Daily GPP at the warming treatment was estimated from correlation analysis between eddy covariance measured GPP and static chamber GPP from the warming plot in the experiment. The static chamber GPP was calculated from directly measured ecosystem respiration (ER) and net ecosystem exchange (NEE) with Li 6,400 twice a month (Quan et al., 2018). The response ratio of GPP between the ambient and warming plots was used to interpolate daily GPP values for different warming treatments. CO_2 flux was measured by an eddy covariance measurement system installed at a height of 2 m above ground. Meteorological variables, such as soil volumetric water content (VWC) and soil temperature (T_{soil}) simultaneously measured with the eddy covariance system at a depth of 10 cm (Chen et al., 2019) were used to drive the GECO model at ambient temperature treatment. Daily VWC and T_{soil} at the warming treatments were similarly estimated from their response ratios between the ambient and warming plots (Quan et al., 2018) together with the measured values at the eddy-covariance site to drive GECO model.

The data that are assimilated into the GECO model for parameter estimation include C and N contents in leaf, root, standing litter, surface litter, microbial, soil, and autotrophic and heterotrophic respiration at both the ambient and warming treatments (Table S3 in Supporting Information S1).

2.4. Data Assimilation

We used Markov-Chain Monte-Carlo (MCMC) method to estimate parameters in the GECO following the method by Xu et al. (2006). The method considers the targeted parameters as random variables within a certain prior probability distribution. According to the Bayesian theorem, the prior knowledge of the parameter and information contained in data are fused to generate posterior distributions of parameters (Xu et al., 2006) as

$$\mathrm{P(p|Z) \propto P(Z|p)P(p)} \tag{4}$$

where $P(p)$ and $P(p|Z)$ represent the prior probability density function (PDF) and posterior probability density function (PPDF) of parameters, respectively. $P\,(Z \mid p)$ represents conditional probability density of observation under the prior parameters, which is also called the likelihood function of p. We assume that the random error is normally distributed with zero mean, so the likelihood function can be presented by:

$$P(Z|p) \propto \exp\left\{-\sum\nolimits_{i=1}^{17}\sum\nolimits_{t\in Z_i}\frac{[Z_i(t)-\varphi_i X(t)]^2}{2\sigma_i^2(t)}\right\} \tag{5}$$

where $Z_i\,(t)$ and $\varphi_i X(t)$represent measured and simulated values of variable i at time t, and $\sigma_i$is the standard deviation of measurements. In this study, i from 1 to 17 represents seventeen data sets, which are the C or N contents of leaf, root, standing litter, surface litter, microbe, soil, SR, soil inorganic N, soil mineralization, plant N uptake and external N input, respectively. $\varphi_i$is the mapping vector that maps the simulated variables to observations for each of the 17 data sets. And the observation operator $\varphi$is expressed as:

$$\text{Leaf C and N}:\ \varphi_1 = (1\,0\,0\,0\,0\,0\,0)$$

$$\text{Root C and N}:\ \varphi_2 = (0\,1\,0\,0\,0\,0\,0)$$

$$\text{Standing Litter C and N}:\ \varphi_3 = (0\,0\,1\,0\,0\,0\,0)$$

$$\text{Surface Litter C and N}:\ \varphi_4 = (0\,0\,0\,0.5\,0\,0\,0)$$

$$\text{Microbial C and N}:\ \varphi_5 = (0\,0\,0\,0\,1\,0\,0)$$

$$\text{Soil C and N}:\ \varphi_6 = (0\,0\,0\,0\,1\,1\,1)$$

$$\text{Soil mineralization}\ :\ \varphi_7 = (0\,0\,0\,m_4c_4m_5c_5m_6c_6m_7c_7),\ \text{in this formula}$$

$$m_4 = 1 - f_{5,4} - f_{6,4}$$

$$m_5 = 1 - f_{6,5} - f_{7,5}$$

$$m_6 = 1 - f_{5,6} - f_{7,6}$$

$$m_7 = 1 - f_{5,7}$$

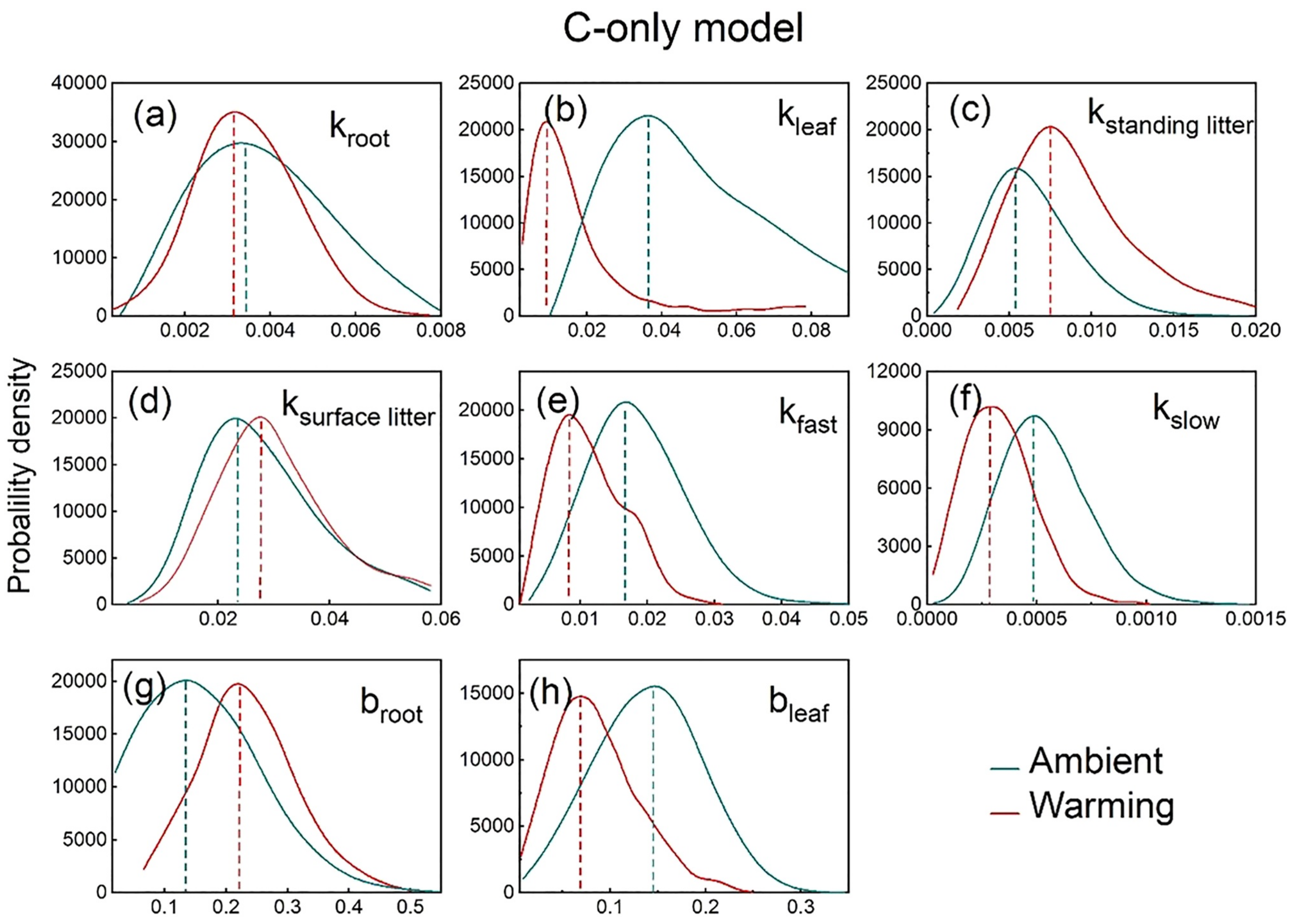

Figure 2. Posterior distributions of key parameters of the Carbon (C)-only model under the ambient and warming treatments. Baseline senescence rates of fine root (a) and leaf (b); baseline decomposition rates of standing litter (c), surface litter (d), fast soil organic matter (SOM) (e), and slow SOM (f); and C allocation coefficients to fine root (g) and leaf (h). The blue and red curves represent the estimated parameter distributions under ambient and warming treatments, respectively.

The Metropolis-Hastings (M-H) algorithm is used as the MCMC sampler (Hastings, 1970; Metropolis et al., 1953). The initial set of parameters was randomly selected within the priori parameter ranges. At each iteration, a set of new parameter values (p_{new}) is proposed based on the accepted parameters in the previous iteration ($p_{\mathrm{k-1}}$), and we accept the p_{new} only if $\mathrm{R} = \frac{\mathrm{P}(\mathrm{p}^{\mathrm{new}}|\mathrm{Z})}{\mathrm{P}(\mathrm{p}^{\mathrm{k-1}}|\mathrm{Z})} >$ a random number from 0 to 1. Otherwise, the p_{new} will be rejected and we let $p_{\mathrm{k}} = p_{\mathrm{k-1}}$ to start the next iteration. The M-H algorithm will be repeated until 300,000 sets of parameter values are accepted, and then all accepted parameter values will be used to construct the probability distribution functions (PDFs) (Weng & Luo, 2011; Xu et al., 2006).

3. Results

3.1. Parameters Estimated by Data Assimilation

Among 18 C-related parameters in both the C-only and C-N coupling models, eight were well constrained by observations according to their posterior PDFs. These eight well-constrained parameters are C exit rates of root, leaf, standing litter, surface litter, fast SOM, slow SOM, the allocation coefficients of C to root and leaf all under both the ambient and warming treatments (Figures 2 and 3). While the C exit rate of the passive SOM and the transfer coefficients among pools ($f_{i,j}$) were poorly constrained (Figures S1 and S2 in Supporting Information S1).

Among 12 N-related parameters in the C-N coupling model, eight were well constrained by observations as shown by their posterior PDFs. These eight well-constrained parameters are C:N ratios of root, leaf, standing litter, surface litter, fast SOM, slow SOM, the rate of plants N uptake and the rate of N input from deposition

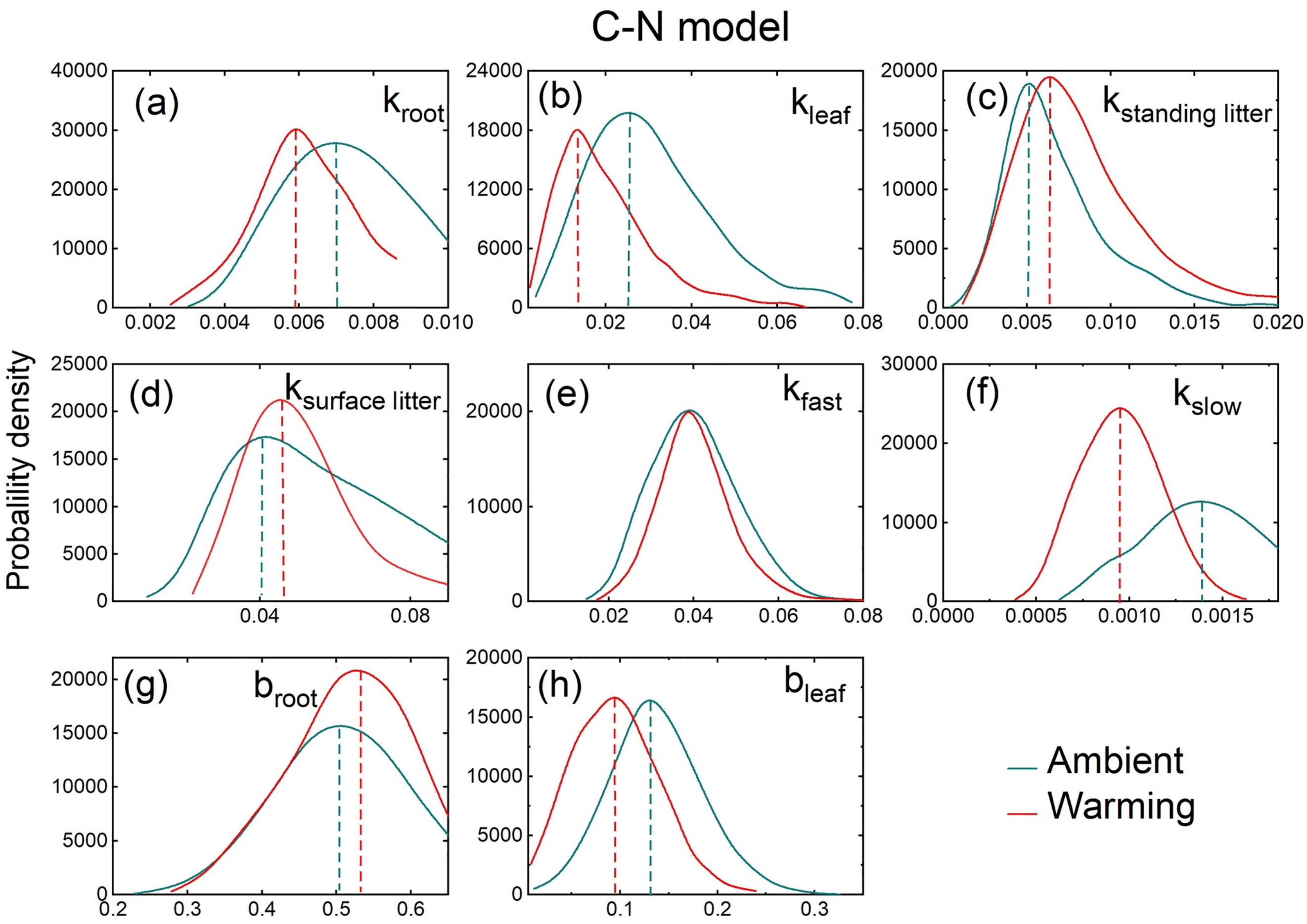

Figure 3. Posterior distributions of key parameters of the Carbon (C)-Nitrogen coupling model under the ambient and warming treatments. Baseline senescence rates of fine root (a) and leaf (b); baseline decomposition rates of standing litter (c), surface litter (d), fast soil organic matter (SOM) (e), and slow SOM (f); and C allocation coefficients to fine root (g) and leaf (h). The blue and red curves represent the estimated parameter distributions under ambient and warming treatments, respectively.

under both the ambient and warming treatments (Figures S3 and S4 in Supporting Information S1). While the C:N ratio of passive SOM, the allocation coefficient of N from soil to root, the N loss by leaching and denitrification, and the initial value of available N pool were poorly constrained (Figures S3 and S4 in Supporting Information S1).

3.2. Differences in Estimated Parameters Between the C-Only and C-N Coupling Models

The two structures of the C-only and C-N coupling models led to different posterior PDFs of these well-constrained parameters under either the ambient or warming treatments (Figures 4 and 5). In general, C exit rates of all the pools except the standing litter and leaf pools were higher in the C-N coupling model than the C-only model (Figures 4b, 4f and 5b, 5f). The maximum likelihood estimators (MLEs) of the C allocation coefficient from NPP to the leaf pool was smaller in the C-N coupling model than in the C-only model. Meanwhile, the allocation coefficient of NPP to the root pool in the C-only model was 68.0% and 56.6% smaller than that in the C-N coupling model under the ambient and warming treatments, respectively (Table S1 in Supporting Information S1). However, adding the N module to the C-only model had little influence on the allocation coefficient of C to leaf and the exit rate of leaf under both the ambient and warming treatments.

Changes in estimated parameters between the C-only and C-N coupling models differ with warming treatments. For example, the estimated root exit rate increased by 134% in the C-N coupling model in comparison to that in the C-only model under the ambient treatment but only 87% under the warming treatment (Table S1 in Supporting Information S1). In contrast, the estimated GPP allocation to leaf did not change much in the C-N coupling

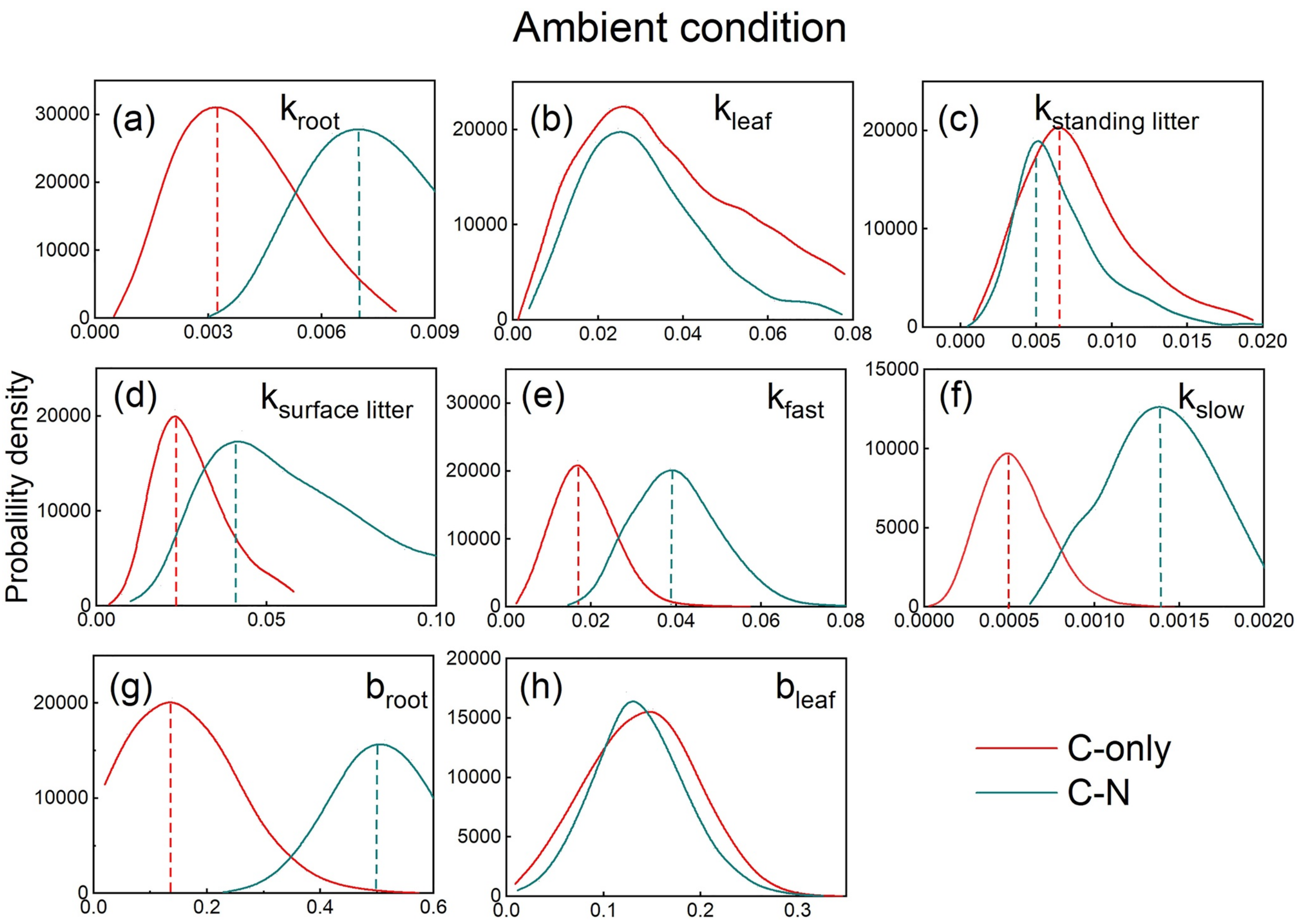

Figure 4. Posterior distributions of estimated key parameters of the Carbon (C)-only and C-Nitrogen (N) coupling models under the ambient treatment. Baseline senescence rates of fine root (a) and leaf (b); baseline decomposition rates of standing litter (c), surface litter (d), fast soil organic matter (SOM) (e), and slow SOM (f); and C allocation coefficients to fine root (g) and leaf (h). The blue and red curves represent the distributions of estimated parameters of the C-only and C-N coupling models, respectively.

model in comparison to that in the C-only model under the ambient treatment but increased by 28% under the warming treatment.

Likewise, changes in estimated parameters under the warming treatment in comparison with these under the ambient treatment vary with model structures. For example, the estimated root exit rate decreased by 23% in the warming treatment in comparison to that in the ambient treatment under the C-N coupling model but only 3% under the C-only model (Table S2 in Supporting Information S1). In contrast, the estimated GPP allocation to leaf decreased by 31% in the warming treatment in comparison to that in the ambient treatment under the C-N coupling model but 50% under the C-only model.

3.3. Simulations of C Dynamics With the C-Only and C-N Coupling Models

We chose 100 sets of parameter values from the PPDFs to ran GECO model and simulate the C dynamics from 2015 to 2018 by the C-only and C-N coupling models, respectively. The two models both well simulated C pools in leaf, standing litter, surface litter, microbe, soil and SR in comparison with the observations in the ambient and warming treatments (Figure 6 and Figure S5 in Supporting Information S1). However, the simulations of root C under either the ambient or warming treatments (Figures 6a, 6b) did not match the observations well, probably due to uncertainty in difficult root biomass measurements. In addition, the simulations of the C-only and C-N coupling models were consistent although their model structures were different (Figures 6 and 7).

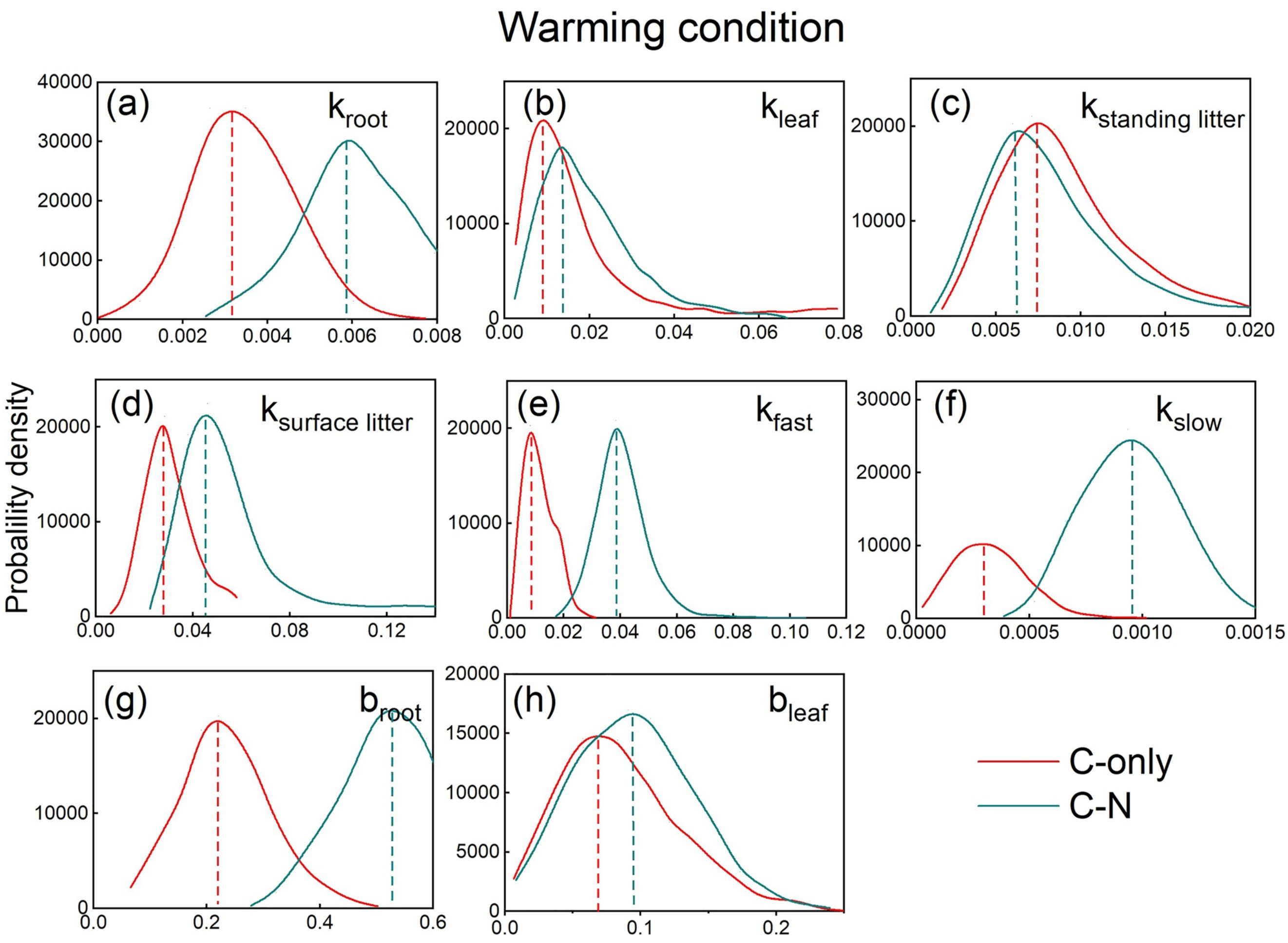

Figure 5. Posterior distributions of estimated key parameters of the Carbon (C)-only and C-Nitrogen (N) coupling models under the warming treatment. Baseline senescence rates of fine root (a) and leaf (b); baseline decomposition rates of standing litter (c), surface litter (d), fast soil organic matter (SOM) (e), and slow SOM (f); and C allocation coefficients to fine root (g) and leaf (h). The blue and red curves represent the distributions of estimated parameters of the C-only and C-N coupling models, respectively.

The different ecosystem C pools exhibited divergent responses to warming in the simulations by both the C-only and C-N coupling models. Simulated leaf C and passive SOM pools showed no warming effects (Figures 7b, 7f). Simulated standing litter and surface litter C pools decreased by 50.2% and 68.0%, respectively, under the warming treatment in comparison with these under the ambient treatment (Figures 7d, 7e). Simulated fine roots, fast and slow SOM C pools all increased under the warming treatment relative to that under the ambient treatment. Because the slow SOM C accounts for about 90% of the total soil C, total soil C pool responded similarly with slow SOM under the warming treatment (Figure 7h).

To further elucidate the N effects in the C only model, we tested the response of the C-N coupling model without retuning parameters to compare the N limitation of ecosystem carbon pools due to the addition of N coupling components. The results showed that the simulated ecosystem C storage increased if we ran the C-N coupling model with the parameters estimated by the C-only model (Figures S8a, S8b in Supporting Information S1). In contrast, the ecosystem C storage simulated by the C-only model with the parameters estimated by the C-N coupling model was smaller than that simulated by the C-only model with its counterpart parameters (Figures S8a, S8b in Supporting Information S1).

We also ran the model under warming treatment with and without data assimilation, separately, to examine how much the warming-induced changes are due to model prediction and how much is due to the fitting to the observed change (Figure S9 in Supporting Information S1). The simulated fine roots, leaf, fast, slow SOM C and total soil C pools without data assimilation all decreased under the warming treatment relative to that under

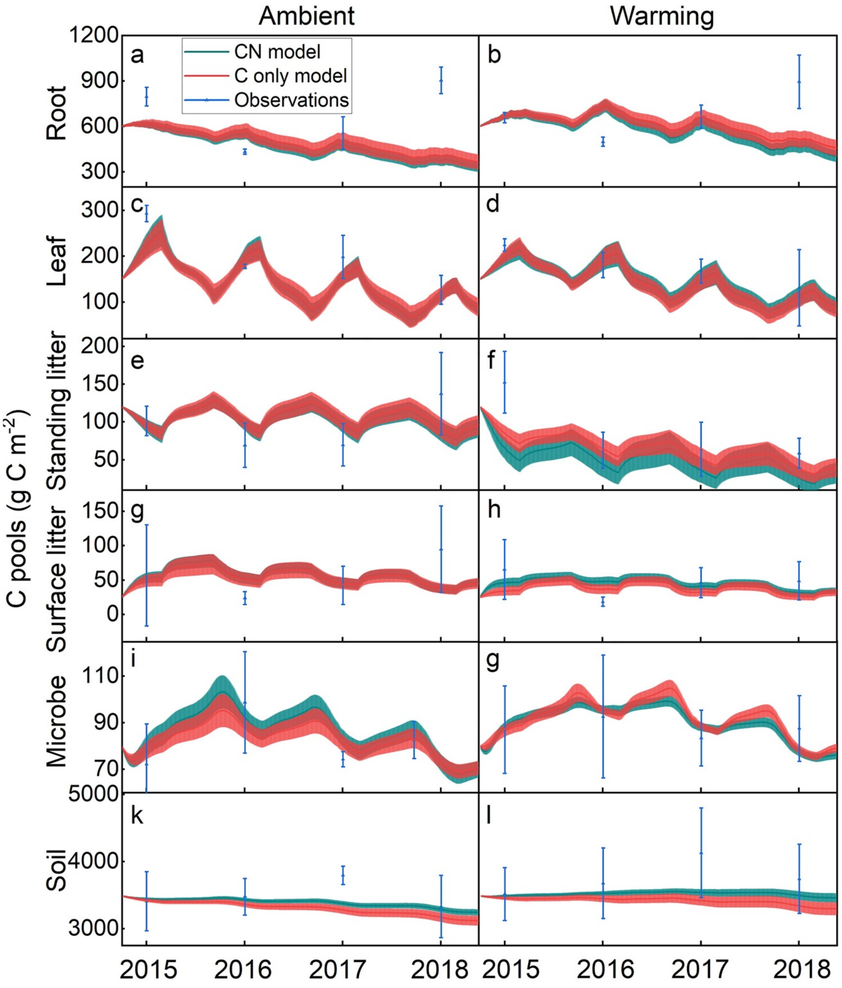

Figure 6. Modeled and observed pool size changes from 2015 to 2018. The modeled (shaded areas) and measured Carbon (C) pools (points with error bars) are compared for root (a) and (b), leaf (c) and (d), standing litter (e) and (f), surface litter (g) and (h), microbe (i) and (g), and soil (k) and (i) simulated by the C-only (red shaded areas) and C-Nitrogen coupling model (green shaded areas) under ambient (left column) and warming treatments (right column). The shaded areas represent the range of 25 and 75 percent quantiles of model simulations.

the ambient treatment (Figure S9 in Supporting Information S1), which was different from the results with data assimilation (Figure 7).

4. Discussion

4.1. Model Structures Influence Parameter Retrieval Between the C-Only and C-N Coupling Models

In the early days, researchers developed the ecosystem models based on their understanding of the ecosystem C cycle (Friend et al., 1997; Parton, 1996). But under the background of global change, people found that the model without N limitation will overestimate the GPP, which is not consistent with inorganic N supply (Hungate et al., 2003; Luo et al., 2004). Hence, more and more researchers incorporate an N module to consider the interactions of C and N cycles in their models (Lawrence et al., 2018; Thornton et al., 2009; Zaehle & Friend, 2010). These newly developed C-N coupling models predict lower GPP and C storage than their C-only counterpart models. But the interactions of C and N cycles always exist in the real-world ecosystems no matter whether ESMs incorporate N processes or not. However, how to retrieve information of the C-N interactions from ecosystem observations with models has not been explored before. This study uses two models: the C-only and C-N coupling models, to retrieve knowledge on C-N interactions. Our results show that all exit rates of C pools (i.e., senescence rates from plant tissues and decomposition rates of litter and SOC) and the allocation coefficients of GPP

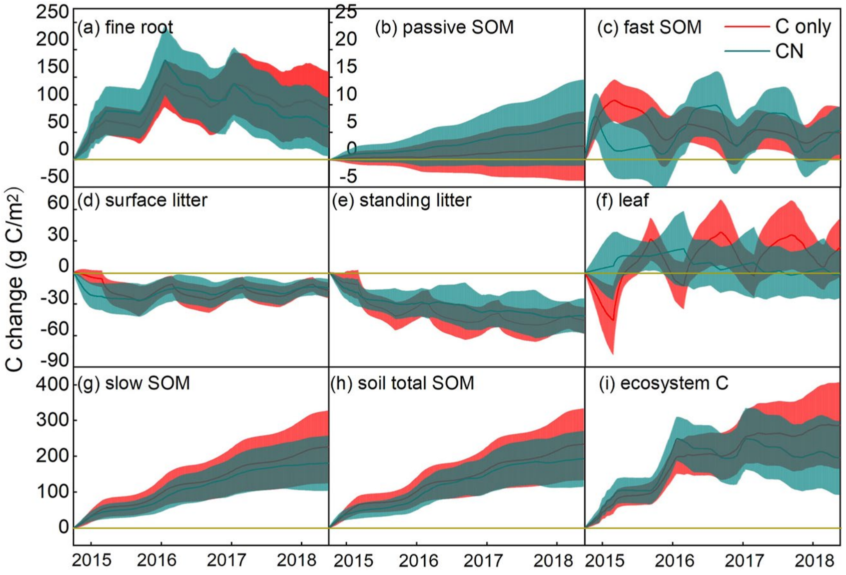

Figure 7. Warming-induced changes in simulated ecosystem Carbon (C) pools with the C-only (red shaded areas) and C-Nitrogen coupling models (blue shaded areas) from 2015 to 2018. The blue-red lines are the mean model simulations, and blue-red shaded areas represent the range of 25 percent and 75 percent quantiles of model simulation.

to root and leaf were higher in the C-N model than these in the C-only model except standing litter (Figure 5). Note that we did not retrieve the information of N limitation of C input as the GECO model in this study did not explicitly simulate but used observed photosynthesis. Even so, we hope that this study can make a clear point that model developers can consider because the N constraint on the C cycle not only in photosynthesis, but also in the decompositions of litter and soil (Hungate et al., 2003; Luo et al., 2004; Raven et al., 2004). Despite changes in C exit rates and allocation coefficients, the two models simulated similar dynamics of pool sizes during the experimental period from 2015 to 2018 (Figure 7). Differences in estimated parameters yet similarity in simulated pool dynamics occurred in both the ambient and warming treatments.

When we use a model to simulate ecosystem C dynamics, we usually calibrate (or often tune in practice) model parameters in such a way to match simulated state variables (e.g., C pool sizes) with observations. In this case, the N regulations of C cycle processes are not explicitly simulated and, thus, considered be unresolved in the C-only model. Influences of the unresolved processes (i.e., N regulation in this case) on explicitly simulated or resolved processes (i.e., C cycle processes) are usually accounted by calibrated parameter values (Luo & Schuur, 2020).

When we incorporated a N module into the C-only model, N processes are explicitly simulated. N influences on C processes are no longer accounted by C-related parameter values. That is why the simulation in the C-N coupling model using the parameters that were fitted for the C-only model was larger than that simulated by the C-N coupling model with its counterpart parameters (Figure S8 in Supporting Information S1). When a C-N coupling model is calibrated with observations via data assimilation as done in this study, C-related parameter values in the C-N coupling model differ from these in the C-only model. Almost all exit rates of C pools and the allocation coefficients of GPP to root and leaf were higher in the C-N coupling model than these in the C-only model except standing litter (Figure 5). Because the N availability in the C-N coupling model will restrict the decomposition processes of litter and soil. To match the ecosystem C pools dynamic with the observations, the C-N coupling model must increase the exit rates to be downregulated by the limitation from the N module in comparison with the C-only model.

Nonetheless, the two models simulate similar pool dynamics when two sets of parameters are used in accordance with their different structures. This is reasonable as models with different structures are supposed to similarly simulate dynamics of the same ecosystem under the same conditions (at either ambient or warming treatment). It does make sense that both the C-only model and the C-N coupling model can well simulate the ecosystem C dynamic, but the ecological information behind estimated parameters are different. Estimated C-related parameters no longer contain N processes for the C-N coupling model but contain information on unresolved N processes with the C-only model.

4.2. Warming Effects on Parameters and Predictions of Ecosystem C Dynamics

The C only model and C-N coupling model simulated similar pool dynamics at either the ambient or warming treatment as long as two sets of parameters were used in accordance with their different structures. In the other words, the warming treatment effects were similar in models with or without considering N module. However, changes in estimated parameters under the warming treatment relative to these under ambient treatment reflected the impacts of the warming treatment on ecosystem C dynamic using either the C-only model or C-N coupling model. For example, the estimated C exit rates of fine roots, leaf, fast and slow SOM decreased in response to warming in comparison with these at the ambient temperature treatment (Figures 2 and 3). The decreased C exit rate of fine roots, together with increased NPP and increased allocation to roots, resulted in increased root biomass under the warming treatment relative to that under the ambient treatment. Warming increased NPP in this and other warming experiments by enhancing plant photosynthesis, increasing nutrient availability, and prolonging growing season length (Liang et al., 2018; Luo, 2007; Natali et al., 2012; Wang et al., 2012). Meanwhile, warming-induced drought promoted NPP allocation to root growth (Joslin et al., 2000; Quan et al., 2020).

Our results are consistent with findings from data-model integration studies in a warming experiment in US Great Plains that warming-induced acclimation strongly regulated predictions of ecosystem responses to climate change (Guo et al., 2020; Liang et al., 2018). However, warming-induced drought counteracted direct warming effects on microbial decomposition, resulting in no substantial change in fast SOM pool (Brockett et al., 2012; Sardans et al., 2008). The decreased C exit rate of slow SOM, together with increased C input from surface litter, resulted in increased slow SOM pool under the warming treatment relative to that under the ambient treatment. Furthermore, warming-induced biotic acclimation buffered the negative warming effects on soil C storage (Guo et al., 2020; Liang et al., 2018), and benefited the soil C accumulation. A previous study also found that warming promoted the ecosystem C accumulation by larger C fixation in the alpine meadow ecosystem (Wei et al., 2021).

In contrast, the warming treatment resuted in increases the estimated C exit rates in standing litter and surface litter via parameter fitting, which explain for the decreases in their C pools sizes, in comparison with these under the ambient treatment. The decrease of litter C pools was also partly because carbon input via senescence of both leaf and root decreased under the warming treatment. Meanwhile, warming increased the soil temperature and reduced the soil moisture in our field experiments (Figure S6 in Supporting Information S1). These warming-induced changes in soil temperature and moisture directly increased the ecosystem turnover rates via an environmental scalar (Figure S7 in Supporting Information S1). The increased environmental scalar value can partially offset the final decreases of some pools' turnover rates under the warming treatment. Furthermore, the plant and soil C storages decreased under the warming treatment relative to that under the ambient treatment if we ran the C-only and C-N coupling models without using data assimilation (Figure S9 in Supporting Information S1), which was contrary to their counterpart model simulations with data assimilation (Figure 7). These results indicated that most of the warming-induced changes in this study were due to fitting to the observed changes, rather than due to the model prediction.

It needs to be specifically pointed out that the passive SOM is long preserved and has a protracted turnover time. It means that it would take a longer time to change (Parton et al., 1993, 1994; Trumbore, 1997). Hence, data from short-term experiments may not have enough information to constrain the long turnover rate, and warming also has no significant influence on the pool size of the passive SOM over the experimental period. Other studies have also showed that parameters related to the passive SOM can not be well constrained (Shi et al., 2016; Wang et al., 2021; Xu et al., 2006). Data from long-term experiments are needed to constrain long-term parameters.

4.3. Implications for Developing ESMs to Predict Carbon and Nitrogen Interactions

More and more ESMs incorporate N processes to represent interactions of the N cycle with the C cycle (Eyring et al., 2016; O'Neill et al., 2016). However, how to re-parameterize the models once N processes are incorporated has not been carefully examined. Often, the parameter values in their original C-only models were kept or manually tuned for the new models with N processes (Koven et al., 2013; Sokolov et al., 2008; Zaehle & Friend, 2010). Predictions by these newly modified ESMs with the N modules mostly predict lower photosynthesis rates, lower

C sequestration, and lower ecosystem C storage than their C-only counterpart models. Our results in this study reveal that such predictions of lower C storage with the C-N coupling models than their original models may not reflect the reality. Our study suggests that re-parameterization is required once the model structure is modified to predict ecosystem carbon cycle dynamics in the real world. This re-parameterization is also likely required when ESMs incorporate phosphorus and other element processes in addition to the N processes.

Our study also highlights the need to use observations to constrain model parameterization or re-parameterization using data assimilation. Parameter tuning has been practiced by modelers for decades but did not help our learning much on the model structure-parameter relationships. To understand the model structure-parameter relationships, it is essential to use data assimilation, which is a statistically rigorous approach. When data assimilation is applied to integrate experimental data with models, we have learned that parameters vary with treatment levels of global change factors as in this and other studies (Liang et al., 2018; Luo et al., 2003; Shi et al., 2016; Xu et al., 2006). When data assimilation is applied to integrate model with observational data over space, estimated parameters must vary over space to match data well (Li et al., 2016; Tao et al., 2020). Moreover, predicted carbon sequestration in terrestrial ecosystems is substantially different in response to global change when different sets of parameter values are used in model predictions (Liang et al., 2018; Xu et al., 2006).

Interactions of C and N processes have been implemented into terrestrial ecosystem models so that C-N coupling models can realistically simulate C sequestration under the situations when N availability changes either due to changing N deposition or other global change factors (e.g., progressive N limitation, Luo et al., 2004). Without N processes incorporated, the C-only model unlikely simulates the C dynamic well when the N availability changes although the calibrated C-only model via data assimilation can simulate C dynamics well during the period of observation. This study was not to diminish the importance of developing C-N coupling models. Rather, we emphasize the importance of reparameterization after model structure changes from C only to C-N coupling before the C-N coupling model is used to simulate ecosystem carbon dynamics in response to changing N availability.

5. Conclusion

Based on a 4-year field warming experiment and data assimilation method, this study carried out an inverse analysis with the C-only model and the C-N coupling model. We found that model structures influenced model parameterization, and N regulated C cycle processes mainly through its influences on parameters. ESMs with N processes usually predicted lowered ecosystem C storage and lowered C sequestration than their counterpart models without N processes. But our study with data assimilation found that both the C-only and C-N coupling models simulated similar C pool sizes as observed at either the ambient or warming treatment with their respective parameter estimates. In addition, warming increased alpine meadow ecosystem C storage by larger C input and slower turnover rates in this study. In general, we suggested that doing reparameterization and retrieving the N limitation when adding N processes to a C cycle model was vital to realistically simulate the ecosystem dynamics.

Data Availability Statement

The data used in this study at https://doi.org/10.6084/m9.figshare.19524379.v1as an archival repository.

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