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Long-term measurements in a mixed-grass prairie reveal a change in soil organic carbon recalcitrance and its environmental sensitivity under warming

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Abstract

Soil respiration, the major pathway for ecosystem carbon (C) loss, has the potential to enter a positive feedback loop with the atmospheric CO_2 due to climate warming. For reliable projections of climate-carbon feedbacks, accurate quantification of soil respiration and identification of mechanisms that control its variability are essential. Process-based models simulate soil respiration as functions of belowground C input, organic matter quality, and sensitivity to environmental conditions. However, evaluation and calibration of process-based models against the long-term in situ measurements are rare. Here, we evaluate the performance of the Terrestrial ECOsystem (TECO) model in simulating total and heterotrophic soil respiration measured during a 16-year warming experiment in a mixed-grass prairie; calibrate model parameters against these and other measurements collected during the experiment; and explore whether the mechanisms of C dynamics have changed over the years. Calibrating model parameters against observations of individual years substantially improved model performance in comparison to pre-calibration simulations, explaining 79–86% of variability in observed soil respiration. Interannual variation of the calibrated model parameters indicated increasing recalcitrance of soil C and changing environmental sensitivity of microbes. Overall, we found that (1) soil organic C became more recalcitrant in intact soil compared to root-free soil; (2) warming offset the effects of increasing C recalcitrance in intact soil and changed microbial sensitivity to moisture conditions. These findings indicate that soil respiration may decrease in the future due to C quality, but this decrease may be offset by warming-induced changes in C cycling mechanisms and their responses to moisture conditions.

Keywords Soil respiration · Long-term warming experiment · Soil organic recalcitrance · Data-assimilation · Environmental sensitivity

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Introduction

Responses of the carbon (C) cycle to warming are associated with large uncertainty (Friedlingstein et al. 2006), indicating an insufficient understanding of the mechanisms controlling the storage and movement of C within ecosystems. A substantial portion of this uncertainty is attributed to the belowground C dynamics: the majority of ecosystem C is stored in litter and soil (Sun et al. 2004), and CO_2 emissions from root respiration and microbial decomposition of organic matter constitute a major C flux in terrestrial ecosystems. Therefore, improving our understanding of belowground C dynamics will likely reduce the uncertainty associated with model projections (Hanson et al. 2000; Heimann and Reichstein 2008; Subke et al. 2006; Wan et al. 2002). To accurately estimate belowground fluxes and their responses to climate change, it is important to improve our understanding of the processes regulating decay rates and their sensitivities to changing climate (Bond-Lamberty and Thomson 2010; Clark et al. 2001; Luo et al. 2011).

Field warming experiments are the primary approach for understanding the long-term temporal patterns in soil respiration and its response to elevated temperature (Carey et al. 2016; Luo et al. 2011; Melillo et al. 2017). Results from experimental studies reveal a wide range of responses to warming, but there is a unifying trend of a warming-induced increase in soil respiration (Lu et al. 2013; Rustad et al. 2001; Wu et al. 2011). Despite the uniform direction in this trend, the magnitudes of the warming effect on soil respiration are highly variable and depend on soil C quality and environmental conditions (Knorr et al. 2005; Melillo et al. 2002; Wan et al. 2007). Soil C quality is dependent on C input rates as well as stabilization/destabilization dynamics of soil organic C, which in turn is controlled by biotic activity (Torn et al. 2009). Changes in biotic activity are partly in ecosystem responses to environmental changes; thus, the dynamic of biological activity need to be examined over long-term periods due to the slowness of ecosystem responses to climate change (Luo et al. 2011; Post et al. 2008; Savage and Davidson 2001). While an analysis based on empirical observations is typically simpler, having mechanism implicit, the process-based model approach involves more comprehensive and mechanism explicit based on our knowledge and empirical observations (Adams et al. 2013). Therefore, to better understand ecosystem responses to the changing climate, the long-term empirical observations and their implicit mechanisms need to be incorporated into a process-based model.

C cycle models are mathematical implementations of theoretical knowledge about the mechanisms regulating C dynamics in the ecosystems. Simulated C dynamics depends on the model structure, driving variables (e.g., light, temperature, and water status), and model parameters. If the model structure and parameters accurately represent processes regulating C dynamics, forcing the model with the observed changes in the driving variables would result in an accurate representation of the observed changes in soil respiration (Luo et al. 2015; Trumbore 2006). However, simulations with constant parameters for different scenarios fail to include biological adjustments against climate change such as changes in carbon use efficiency (CUE) and C quality (Cox et al. 2000; Friedlingstein et al. 2006; Schmidt et al. 2011). Importantly, constant parameters of baseline turnover rates of SOC and their temperature sensitivities are impacting the accuracy of below-ground C loss under elevated temperature and various moisture conditions, leading to substantial differences in response to climate change (Liang et al. 2018; Post et al. 2008; Savage and Davidson 2001; Shi et al. 2015a). Therefore, process implicit C cycle models with optimally estimated parameters based on the status of the ecosystem can be a key to generate reasonable projections.

Biological adjustment of the C cycle to warming can be detected through data assimilation, or calibration of the model parameters. Data assimilation is a powerful tool for improving model performance because it minimizes the error between model output and observations (Fox et al. 2018; Keenan et al. 2013; Wang et al. 2009). The error is minimized through tuning model parameters and, as a result, the model performs to the best of its ability. This data assimilation property can be used to detect shifts in the mechanisms of C cycling in response to warming (Liang et al. 2018; Luo and Schuur 2020). Specifically, if the optimal parameters for the model calibrated against the observations from the warmed plots do not differ from those calibrated against the control plots, the mechanistic changes in C dynamics would be unlikely. Conversely, a significant shift in optimal parameter values would indicate the presence of the emergent biological adjustments that are not represented in the model structure (Luo and Schuur 2020). Such analysis has shown that elevated CO_2 increases foliage turnover rate and reduces the turnover rate of the recalcitrant fraction of the soil organic matter in a temperate forest (Xu et al. 2006b). A similar analysis revealed that warming increases biomass residence time and autotrophic respiration in a mixed-grass prairie (Shi et al. 2015b). Although changes in model parameters in response to environmental manipulation do not reveal the underlying mechanisms causing the change, they can expose a gap in the model structure and inform future experiments aimed at revealing these mechanisms.

Here, we used observations from a long-term (2002–2017) ecosystem warming experiment in the Great

Plains, U.S.A., to investigate the patterns in soil respiration responses to warming and explore the presence of emergent biological adjustments in C cycling. First, we calibrated the parameters in the Terrestrial ECOsystem (TECO) model against the field observations of soil total and heterotrophic respiration, aboveground net primary production (ANPP), below-ground net primary production (BNPP), and soil organic C. Following parameter calibration, we examined the changes in parameter values to test whether (1) there were significant emergent biological adjustments in soil organic C decay over 16 years of observations and (2) warming affected these adjustments.

Materials and methods

Descriptions of the study site and the experiment

The study was conducted at the Kessler Atmospheric and Ecological Field Station (KAEFS) in central Oklahoma in the Great Plains, U.S. (34° 58′ 31.8″ N, 97° 31′ 19.6″ W). The site had remained continuously uncultivated and ungrazed for 40 years before the experiment began in 1999. The dominant plant species were C_4 grasses (*Schizachyrium scoparium* and *Sorghastrum nutans*) and C_3 forbs (*Ambrosia psilostachya*, *Solidago nemoralis* and *Solidago rigida*).

In 1999, 12 square plots of 2×2 m were established. The experiment used a paired design with a clipping treatment nested within the main warming treatment. Continuous warming was carried out via infrared heaters (Kalglo Electronics, Bethlehem, PA, U.S.) located 1.5 m above the ground level with a radiation output of 100 W/m². Dummy heaters were installed in the control plots to create a similar shading effect. Each plot had four equal-sized subplots (1 m × 1 m). To avoid adjacent warming effects from the warming plots, the distance between the control and warmed plots was approximately 5 m. To mimic hay harvesting, plants in two diagonal subplots in each plot were clipped 10 cm above the ground once a year at peak biomass, while the other two subplots were left unclipped. Clipped biomass was removed from the plots permanently.

Field measurements and sample collection

Climatic data

The air temperature was measured by sheltered thermocouples at a height of 25 cm above the ground in the center of control and warmed plots. Soil temperature was measured by thermocouples at a depth of 2.5 cm in the center of unclipped and clipped subplots. Gaps due to mechanical issues of the data logger or the thermocouples were filled through regression between the available measurements and

the reference data from the Washington Station of Oklahoma Mesonet (Brock et al. 1995; McPherson et al. 2007), which was located 200 m away from the study site ($r^2 > 0.98$ and $P < 0.01$). Soil volumetric water content (VWC) was simulated by soil water dynamic module based on the bucket method from the Terrestrial ECOsystem (TECO) model (Weng and Luo 2008). Simulated soil VWC was validated ($r^2 > 0.71$ and $P < 0.01$) using the observed soil VWC which was measured manually at a 0–12 cm depth using time domain reflectometry (TDR) equipment (Soil Moisture Equipment Corp., CA, U.S.). VWCs in the intact soil collars and soil collars with root exclusion had similar seasonality and there was no significance between them (Zhou et al. 2018). Therefore, we forced the TECO model with the same soil VWC when simulating intact soils and soils with root exclusion treatment.

The annual precipitation data from 2002 to 2017 were retrieved from the Washington Station of Oklahoma Mesonet. To determine dryness, we used the standardized precipitation-evaporation index (SPEI), which was estimated using precipitation and potential evapotranspiration (PET) which was estimated by the Thornthwaite method (Beguería et al. 2014; Vicente-Serrano et al. 2010). Although the Penman-Monteith method estimates more realistic the atmospheric demand as affecting PET than the Thornthwaite method, there is no significant difference between calculations of SPEI based on either the Thornthwaite or the Penman-Monteith methods (McEvoy et al. 2013; Van der Schrier et al. 2011). Therefore, we used the Thornthwaite method for estimating PET to calculate SPEI at a 3-month time interval. SPEI was calculated by 'SPEI' package in R (Beguería et al. 2017). These monthly SPEI values were averaged annually to use for further analysis.

Soil respiration measurements

To measure soil respiration, we installed polyvinyl chloride (PVC) collars (10 cm in diameter) at a 2–3 cm depth in the center of each subplot for total soil respiration in 1999 and at about 70 cm depth for heterotrophic soil respiration in 2001 (Zhou et al. 2007). The insertion of the deep collars (70 cm) cut off existing plant roots and prevented the new growth of roots into the collars. To exclude the decomposition of the dead roots, the soil respiration rates in deep collars were measured after 5 months of insertions (Zhou et al. 2007). We removed small living plants at the soil surface inside the collars, whereas plant litter that fell into the collars were not removed. Soil respiration was measured once or twice a month between 10:00 and 15:00 using a LI-8100 portable soil CO_2 flux system with a 10 cm survey chamber (8100-102, LI-COR Inc., Lincoln, NE, U.S.). In this study, we considered the soil CO_2 flux measured from the collars installed down to 3 cm depth to be total soil respiration and

soil CO_2 flux measured from the deep collars – soil heterotrophic respiration.

Soil carbon content measurements

To measure soil carbon content, soil samples were taken from the outside (unclipped plots: 2002–2008, 2012, and 2015; clipped plots: 2012 and 2015) and inside of deep collars (unclipped plots: 2002 and 2009) using a soil core (4 cm in diameter, 0–15 cm in depth). Soil organic carbon (SOC) concentration and bulk density were used to estimate soil organic carbon stock. Inorganic C was removed by hydrochloric acid before measuring the concentration of C with a Shimadzu TC analyzer (Shimadzu Corporation, Kyoto, Japan) at the Soil, Water and Forage Analytical Laboratory at Oklahoma State University.

Above- and below-ground net primary production

ANPP was measured using two methods—direct measurements of clipped plants (the clipping treatment) and indirect estimates of unclipped plants with a pin-contact method (the unclipped treatment) as described in Frank and McNaughton (1990). To determine ANPP, the clipped plants were separated into C_3 and C_4 plants, dried in an oven (65 °C for 72 h) and weighed. The detailed procedures of the pin-contact method for estimating ANPP in unclipped plots was described in a previous study (Sherry et al. 2008). Briefly, we counted the numbers of C_3 and C_4 plants that touched pins. Then, we estimated ANPP from the unclipped plot through a linear regression with clipped ANPP ($r^2 > 0.6$).

To determine BNPP, we used the in-growth core method (Gao et al. 2008). We took soil samples from the following three depths: 0–15, 15–30, and 30-45 cm in both unclipped and clipped plots each year. We took the soil samples from each plot in the same place in the fall to estimate annual root growth. We backfilled the sampled spots using soils in similar layers from the adjacent area. Sampled roots were gently washed, dried at 70 °C for 48 h and weighed for calculating plot-level BNPP. In this study, summed BNPP of total depths were used. There were no root samples collected in the 2002–2004 period and in 2011.

Model description and parameterization

Model description

To estimate the annual total and heterotrophic soil respiration under different treatments, we used the modified Terrestrial ECOsystem (TECO) model with a 6-pool compartmental structure (Fig. 1). In the model, C enters
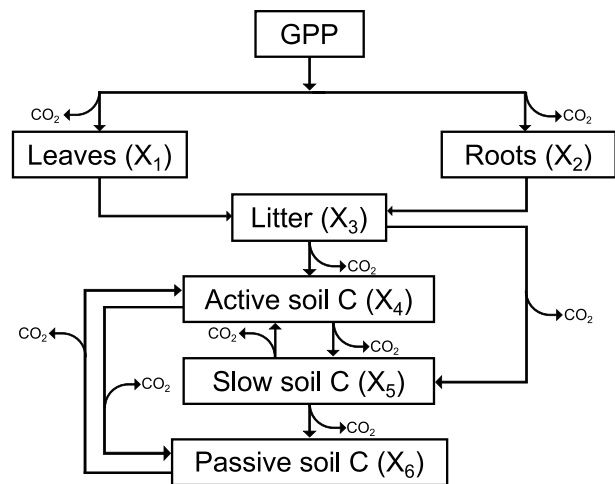

Fig. 1 Diagrams of carbon (C) pools and fluxes in the modified Terrestrial ECOsystem model (TECO). Soil respiration is the sum of fluxes from litter, active soil C, slow soil C, and passive soil C pools. GPP: gross primary production

the ecosystem through the canopy photosynthesis which is then allocated to leaves (X_1) and roots (X_2). When leaves and roots senesce and die, dead leaves and roots become litter (X_3) and a fraction of this litter is respired by microbes. Litter that was processed by microbes, but not respired was partitioned to active (X_4), slow (X_5), and passive (X_6) soil C pools. Despite the exclusion of C input via roots in the deep collars, litter that originated from the aboveground biomass of plants that grew outside of the collars might have dropped into the collars and eventually become soil carbon (C). Gross primary production (GPP)—the source of C input into the ecosystem—is generated for each of the four treatments (unclipped-ambient, unclipped-warming, clipped-ambient and clipped-warming) with a canopy photosynthetic sub-model which has been calibrated previously for the same site (Weng and Luo 2008). Briefly, the canopy photosynthesis sub-model is based on a two-leaf photosynthesis model, which is sensitive to leaf area index (LAI) (Wang and Leuning 1998). The LAI is derived by multiplying the leaf pool with a specific leaf area (SLA; 0.012 m^2 g^{-1}). The derived GPP was validated by available field observations before it was used for TECO simulations (Jung et al. 2019; Niu et al. 2013).

In the TECO model, change in the carbon pool is represented by the following first-order ordinary differential equation based on the matrix representation which has been validated by other earth system models (Huang et al. 2018a, b):

$$\frac{dX(t)}{dt} = A[\xi(t)K]X(t) + BU(t)$$

where A and K are 6×6 matrices, respectively given by

$$A = \begin{Bmatrix} -1 & 0 & 0 & 0 & 0 & 0 \\ 0 & -1 & 0 & 0 & 0 & 0 \\ 1 & 1 & -1 & 0 & 0 & 0 \\ 0 & 0 & a_{43} & -1 & a_{45} & a_{46} \\ 0 & 0 & a_{53} & a_{54} & -1 & 0 \\ 0 & 0 & 0 & a_{64} & a_{65} & -1 \end{Bmatrix}$$

$$K = \begin{Bmatrix} k_1 & 0 & 0 & 0 & 0 & 0 \\ 0 & k_2 & 0 & 0 & 0 & 0 \\ 0 & 0 & k_3 & 0 & 0 & 0 \\ 0 & 0 & 0 & k_4 & 0 & 0 \\ 0 & 0 & 0 & 0 & k_5 & 0 \\ 0 & 0 & 0 & 0 & 0 & k_6 \end{Bmatrix}$$

where a_{ij} in matrix A is the fraction of the decomposed jth pool entering ith pool. K is 6×6 diagonal matrix, the elements of which represent baseline turnover rates, or turnover rates when the temperature is 10 °C and soil water content is over 20%, of individual C pools. $X(t)$ is a vector of C pools at the time t; $B = (b_1, b_2, 0, 0, 0, 0)^T$ is a vector of partitioning coefficients that allocate fresh photosynthate to leaves and roots; $U(t)$ is C input, or gross primary production (GPP), at time t, which is simulated by a canopy photosynthetic model (Weng and Luo 2008); $\xi(t)$ is a diagonal matrix of values of a scaling function for temperature and moisture control on carbon decomposition: $\xi(t) = F_T(t)F_W(t)$. $F_T(t)$ describes temperature effects on plant respiration and decomposition of litter and SOC: $F_T(t) = Q_{10}^{(T(t)-10)/10}$, where Q_{10} represents the intrinsic temperature sensitivity of SOC decomposition. F_w represents the soil water stress based on soil water content (W) as follows (Rodríguez-Iturbe and Porporato 2007):

$$F_w(t) = \begin{cases} 1.0 - 5 \times (0.2 - W(t)) & W < 0.2 \\ 1 & W \geq 0.2 \end{cases}$$

Parameter estimation

We calibrated model parameters using a Bayesian probabilistic inversion approach. Calibrated model parameters included allocation coefficients B, turnover rates K, transfer coefficients A, and temperature sensitivity of SOC decomposition (Q_{10}). The Bayes' theorem was described previously in (McCarthy 2007; Xu et al. 2006a; Zhou et al. 2010). In brief, we set the prior probability density function (PDF) $p(\theta)$ of parameters θ to be a uniform distribution with the ranges specified in Table 1. We assumed that errors between observed and simulated values followed Gaussian distributions, and approximated the likelihood function $p(Z|c)$ as

$$p(Z|c) \propto \exp \left\{ \frac{1}{2\sigma^2} \sum_{t \in \mathrm{obs}(Z_i)} \left[Z_i(t) - \varphi_i X(t) \right]^2 \right\}$$

where $Z_i(t)$ and $X(t)$ are observed and simulated values, respectively, and σ is the standard deviation for each measurement. φ is used for mapping the simulated state variables (soil C) and fluxes (soil respiration, ANPP and BNPP) to observational variables. ANPP (φ_1) = (1, 0, 0, 0, 0, 0); BNPP (φ_2) = (0, 1, 0, 0, 0, 0); heterotrophic soil respiration (φ_3) =

Table 1 Descriptions for model parameters in the Tettestrial ECO system (TECO) model and their prior ranges

Parameters	Ranges	Descriptions
b_1	0.1–0.5	Allocation coefficient of GPP to leaves
b_2	0.1–0.5	Allocation coefficient of GPP to root
k_1	1.00×10^{-6}–1.50×10^{-2}	Turnover rate of C from "leaves" pool (X1)
k_2	1.00×10^{-7}–8.70×10^{-4}	Turnover rate of C from "root" pool (X2)
k_3	0.50×10^{-5}–6.50×10^{-3}	Turnover rate of C from "litter" pool (X3)
k_4	0.10×10^{-4}–5.40×10^{-3}	Turnover rate of C from "active soil C" pool (X4)
k_5	0.10×10^{-6}–4.50×10^{-4}	Turnover rate of C from "slow soil C" pool (X5)
k_6	1.00×10^{-9}–1.00×10^{-5}	Turnover rate of C from "passive soil C" pool (X6)
a_{43}	0.3–0.7	Fraction of C in "litter pool" transferring to "active soil C pool"
a_{53}	0.05–0.15	Fraction of C in "litter pool" transferring to "slow soil C pool"
a_{54}	0.2–0.7	Fraction of C in "active soil C pool" transferring to "slow soil C pool"
a_{64}	0.10×10^{-3}–8.40×10^{-3}	Fraction of C in "active soil C pool" transferring to "passive soil C pool"
a_{45}	0.1–0.6	Fraction of C in "slow soil C pool" transferring to "active soil C pool"
a_{65}	1.00×10^{-2}–2.00×10^{-1}	Fraction of C in "slow soil C pool" transferring to "passive soil C pool"
a_{46}	0.3–0.7	Fraction of C in "passive soil C pool" transferring to "active soil C pool"
Q_{10}	0.6–5	Intrinsic temperature sensitivity of SOC decomposition

Fig. 2 Temporal variations of **a** soil temperature, **b** volumetric water contents (VWC), and **c** standardized precipitation-evaporation index (SPEI) from 2002 to 2017. Blue and orange colors in (**a**) and (**b**) indicate ambient and warming conditions of soils, respectively. Solid trend lines and gray shading denote a significant slope ($P < 0.01$) and 95% confidence interval. Standard error was used for error bar. Orange, gray, and blue colors in (**c**) represent drought (SPEI < -0.5), normal ($-0.5 <$ SPEI < 0.5), and wet (SPEI > 0.5) conditions

$(0, 0, 1 - a_{43} - a_{53}, 1 - a_{54} - a_{64}, 1 - a_{45} - a_{65}, 1 - a_{46})$; autotrophic soil respiration $= 0.25 \times (1 - b_1 - b_2) \times$ GPP(t); total soil respiration, the sum of heterotrophic and autotrophic soil respiration; and total soil carbon $(\varphi_4) = (0, 0, 0, 1, 1, 1)$ were used for mapping.

Posterior PDFs were obtained using the Metropolis–Hastings (M–H) algorithm and the Markov Chain Monte Carlo (MCMC) technique (Hastings 1970; Metropolis et al. 1953). The detailed processes of the M–H algorithm were described previously (Xu et al. 2006a). In brief, the M–H algorithm operates in three steps: proposing step, computing acceptance probability, and accepting or rejecting the candidate parameter. In the proposing step, θ^{new} is generated by previously accepted parameter set θ^{old} with a proposed distribution, which is uniform:

$$\theta^{\text{new}} = \theta^{\text{old}} + r(\theta_{\text{max}} - \theta_{\text{min}})/D$$

where θ_{max} and θ_{min} are the maximum and minimum values of a parameter, respectively (see Table 1); r is a random number between -0.5 and 0.5; and D is a controlling factor of the proposing step size. In this study, we set D to 7 so that the maximum step size is 7% of the range between the upper and lower limits of parameters. We discarded the first 3000 accepted parameters to account for the "burn-in" period and ensure the obtained posterior parameter distribution was stationary. We calculated maximum likelihood estimates (MLE) for the parameters using the obtained posterior parameter distributions.

We explored parameter stability by calibrating the parameters against (1) all observations at once and (2) observations grouped by individual years and treatment types (warming and clipping). The Bayesian inversion algorithm was implemented in MATLAB Release 2017b (The MathWorks, Inc., Natick, Massachusetts, USA). The simulation script is available on Github at https://github.com/eco-cgjung/Oecologia-simul.

Modeling experiment

We ran three TECO simulations using the calibrated model parameters: (1) a simulation forced with climatic variables under manipulated conditions (i.e., unclipped ambient, unclipped warming, clipped ambient and clipped warming) and annually calibrated parameters for each treatment, (2) a
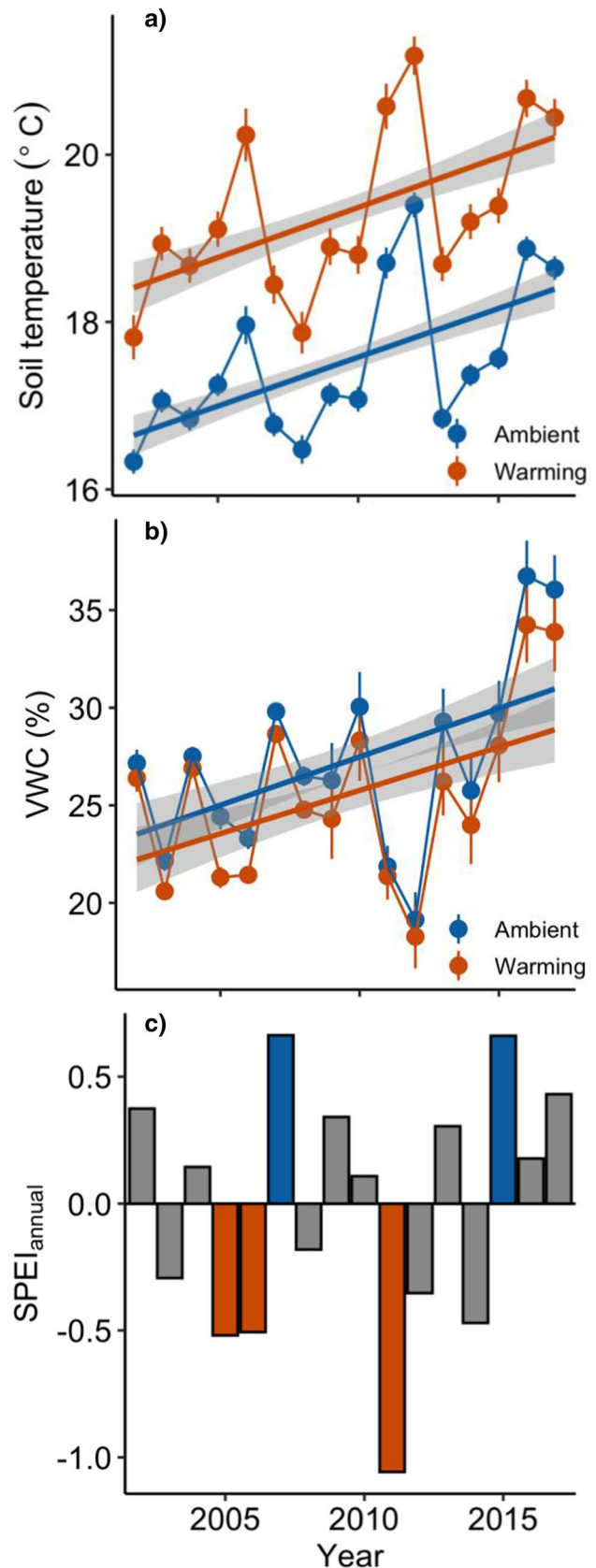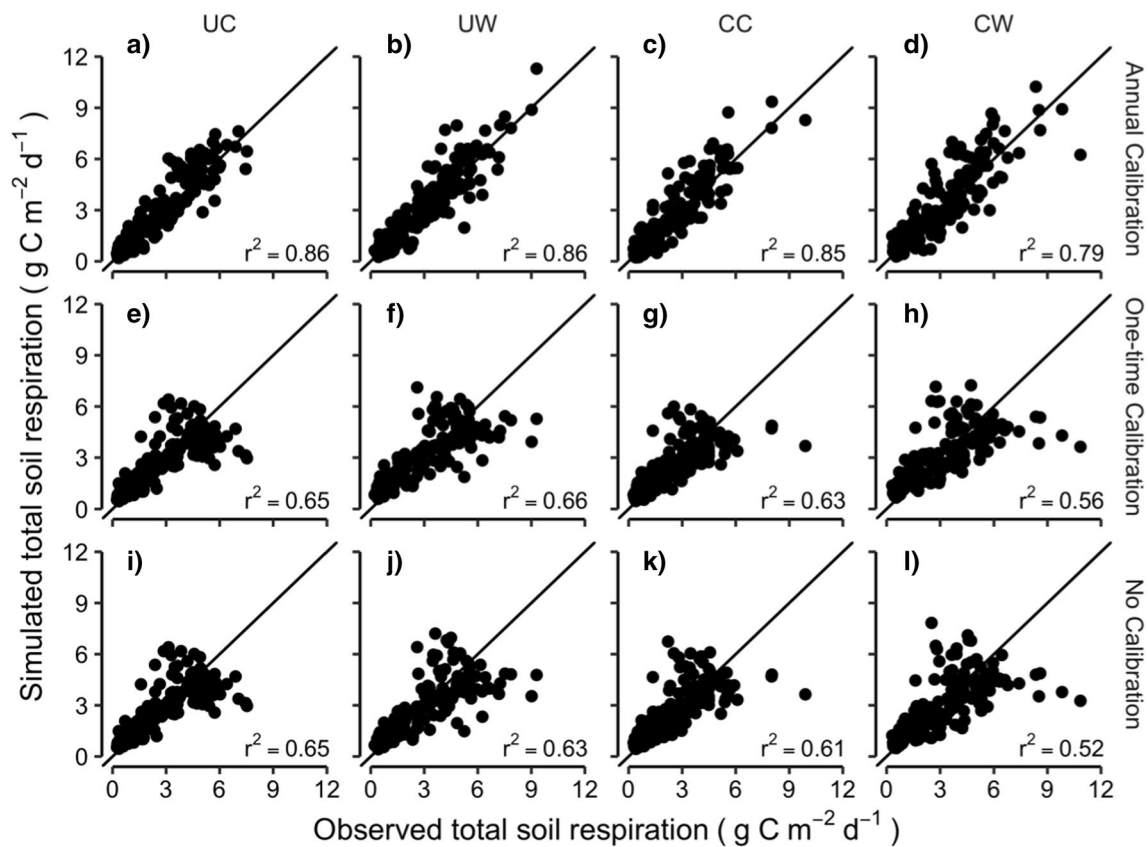
Fig. 3 Comparison of observed (*x*-axis) and model-simulated (*y*-axis) total soil respiration with **a–d** annual calibration, **e–h** one-time calibration, and **i–l** no calibration. *UC* unclipped-ambient, *UW* unclipped-warming, *CC* clipped-ambient, and *CW* clipped-warming

simulation forced with climatic variables under manipulated conditions and parameters calibrated using observations from all years for each treatment type, and (3) a simulation forced with the same climatic variables in the first and second simulations, but using one set of parameters that was estimated using the observations from the unwarmed and unclipped (control) plots. We compared the model performance in these three simulations (i.e., annual calibration, one-time calibration, and no calibration), and evaluated the presence biological adjustments, which would manifest as significant differences in posterior parameter distributions and improvement in model performance if forced with varying parameters.

Statistical analysis

In this study we focused on the temporal patterns and warming-mediated changes in environmental sensitivity, therefore clipping effects were not considered for further analysis. To examine the time-dependent effects and their interactions with environmental sensitivity (dryness index, SPEI) under warming on calibrated parameters, we used

the following structure of linear model: parameters ~ warming + soil temperature + $SPEI_{annual}$ + year + warming:soil temperature + warming:$SPEI_{annual}$ + warming:year. If there were significant effects on parameters, we calculated relative effects on year (relative to an effect at year = 2002) or $SPEI_{annual}$ (relative to an effect at $SPEI_{annual}$ = 0) with/without warming to examine the effects of time-dependent and moisture conditions, and how warming offsets single effects. Parameters were natural-log-transformed to satisfy normality assumptions. All analyses were performed using R version 3.6.3 (R-Core-Team 2019). The summary tables of the model fits are shown in Table S1 and S2.

Results

Long-term patterns in microclimate

Over the course of the 16-year experiment, we observed a wide variation in soil temperature and moisture conditions (Fig. 2). Long-term averages in soil temperature for ambient and warmed plots were 17.5 and 19.3 °C, respectively
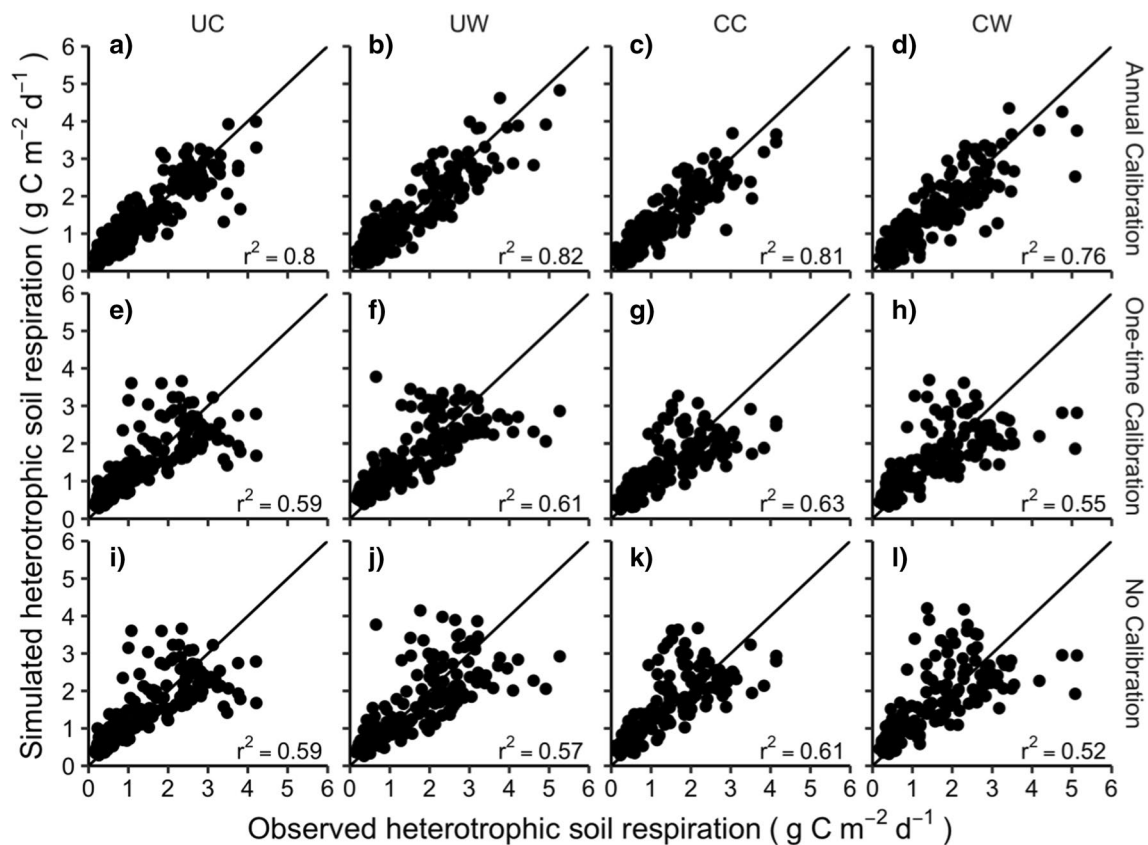
Fig. 4 Comparison of observed (*x*-axis) and model simulated (*y*-axis) heterotrophic soil respiration with **a–d** annual calibration, **e–h** one-time calibration, **i–l** and no calibration. For the abbreviations of treatment conditions, see the caption of Fig. 3

(Fig. 2a). Soil temperature ranged from 16.3 °C (2002) to 19.4 °C (2012) in the ambient plots and from 17.8 °C (2002) to 21.2 °C (2012) in the warmed plots. Soil moisture varied from 19.1 to 36.7% and 18.3 to 34.2% in the ambient and warming plots, respectively. The warming treatment increased soil temperature by approximately 1.8 ± 0.36 °C across the study period, whereas soil moisture was lowered by 1.7 ± 0.12% (Fig. 2a, b). Annual SPEIs (SPEI$_{annual}$) ranged from -1.06 (2011) to 0.66 (2007 and 2015) over the course of the study (Fig. 2c). The experimental site experienced multiple drought events (orange colored bars in Fig. 2c) when SPEI$_{annual}$ was less than -0.5 (i.e., 2005, 2006, and 2011) as well as high rainfall events (blue colored bars in Fig. 2c) when SPEI$_{annual}$ exceeded 0.5 (i.e., 2007 and 2015; SPEI$_{annual} > 0.5$).

Model performance

Calibrating parameters for each year and treatment type substantially improved model performance (Figs. 3 and 4). Before calibration, TECO explained 52–65% of temporal variation in total and heterotrophic soil respiration. Calibrating model parameters with 16-year time series of soil

respiration showed 2–4% improvements in the explained variation in the observations. The model with annually calibrated parameters explained 76–86% of the variation in the observed total and heterotrophic soil respiration, increasing the explained variation by 21–24% compared to the simulations from the non-calibrated TECO model. Importantly, the annually calibrated model captured higher rates of soil respiration in recent years (i.e., 2014–2017; Fig. S1 and S2).

Increasing recalcitrance of soil C pools

There was a marked negative trend in the turnover rates of the litter and three soil pools (i.e., active, slow, and passive) in intact soils, while in the root-free soils, this negative trend was significant only for litter and active soil C pool turnover rates (Table S1 and S2; Fig. 5). Temperature sensitivity of microbial organic matter decay (Q_{10}) had a significant positive trend in both intact and root-free soils. In the intact soils, the turnover rate of litter pool (k_3) had the largest negative trend, decreasing by about 32% in 2017 compared to 2002 (Fig. 5a). The turnover rates of active (k_4), slow (k_5), and passive (k_6) soil C pools exhibited decreases by 30, 28, and 23%, respectively, after 16 years of observations. In the
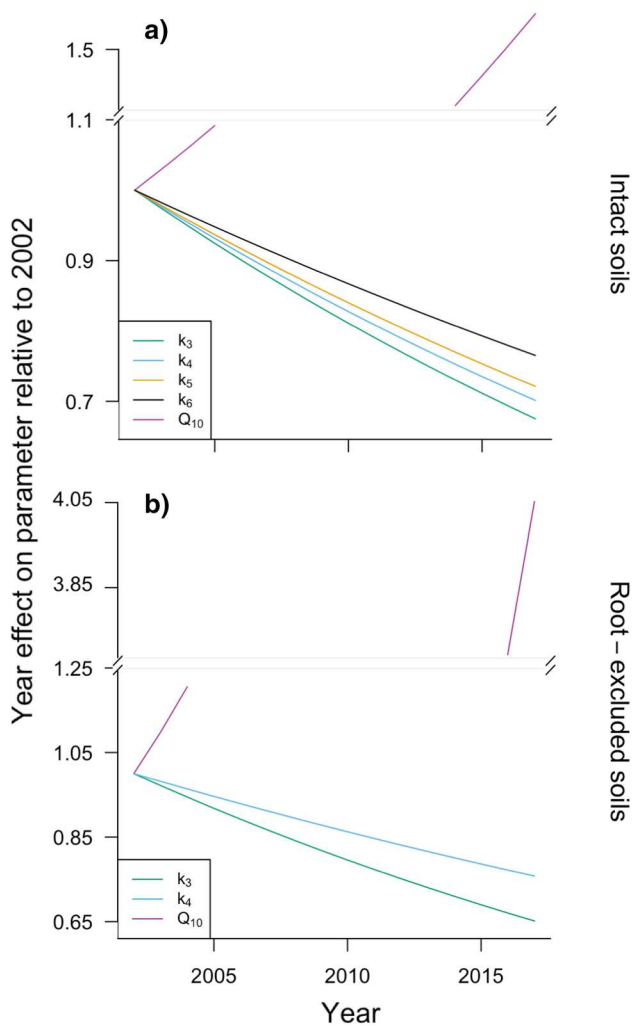
Fig. 5 Year effects on annually calibrated parameters of litter, soil C turnover rates, and temperature sensitivity of soil C for **a** intact soils and **b** root-excluded soils relative to 2002. Green, blue, orange, black, and purple colors indicate turnover rates of litter (k_3), active (k_4), slow (k_5), and passive (k_6) soil C, temperature sensitivity of soil C (Q_{10}), respectively

root-free soils, the turnover rate of litter (k_3) and active (k_4) soil C pool decreased by 35 and 24% after 16 years of observations, respectively (Fig. 5b). Q_{10} increased by 55% and 405% after 16 years of observations in intact and root-free soils, respectively. The significant decreases in the baseline turnover rates of these pools and increases in the temperature sensitivity indicate their increasing recalcitrance over the years.

Warming effects

Warming significantly affected baseline microbial turnover rates, carbon use efficiencies (CUEs) and their dependency on moisture conditions. Warming offset the negative trend in slow soil C turnover rate (k_5, $P < 0.1$, Table S1; Fig. 6a),

indicating that unlike in the control plots, the quality of the slow-decomposing organic matter did not decrease in the warmed plots. Warming treatment brought on marginally significant shifts in sensitivity of microbial CUEs in the active and slow pools (a_{65} for intact soils and a_{64} for the root-free soils) to moisture conditions; however, while slow pool CUE (a_{65}) increased with increasing moisture condition, the active pool CUE (a_{64}) was negatively affected by moisture conditions (Fig. 6b, c). Lastly, in the warmed root-free soils baseline decay rate of the passive pool, k_6, was significantly and positively related to SPEI, as opposed to k_6 in the control plots (Fig. 6d), indicating increased microbial sensitivity to moisture condition in the warmed plots with no fresh carbon input.

Discussion

Overall, forcing TECO with time-varying parameters obtained from the annual parameter calibrations led to substantial improvements in model performance, indicating that there were critical soil processes that were not accounted for in the model structure (Fig. 1). We discovered a clear increase in the recalcitrance of the dead organic matter, which manifested as a negative relationship between baseline turnover rates and the calendar years. Increasing recalcitrance is often associated with an increase in temperature sensitivity, Q_{10} (Fierer et al. 2005; Xu et al. 2010), which we also observed in this study (Fig. 5). Interestingly, the increase in C recalcitrance was more pronounced in plots that have not undergone fresh C exclusion (Fig. 5), which could indicate that an increase in dead organic matter recalcitrance could be caused by a shift in live biomass recalcitrance. In addition, the pattern of increase in temperature sensitivity is partly in line with results based on the previously demonstrated new theory—macromolecular rate theory (MMRT) (Hobbs et al. 2013). MMRT has proposed that temperature sensitivity varies in types of soil enzymes over time due to dynamics of the quality of C substrates (Alster et al. 2016a, b), which is another potential account for increasing C recalcitrant with Q_{10}.

Ambient environmental changes, such as rising atmospheric CO_2 concentrations, increasing temperature, and changing moisture regime can cause a shift in the plant functional types. For instance, an area dominated by plants with a C_3 photosynthetic pathway may transition into an ecosystem dominated by plants with a more efficient C_4 photosynthetic pathway (Loladze 2002; Shi et al. 2018). Species with the C_4 photosynthetic pathway tend to have higher C:N biomass ratios compared to those in C_3 species (Baer et al. 2002; Wedin and Tilman 1990), and tissues with the higher C:N ratios are more resistant to microbial decay (Silver and Miya 2001). Therefore, an increase in belowground

Fig. 6 Warming offset/amplifies year and standardized precipitation-evaporation index (SPEI) effect on **a** turnover rate of slow soil C (k_5) and **b** transfer coefficient from slow to passive soil C pools (a_{65}) for intact soils; **c** transfer coefficient from active to passive soil C pools (a_{64}) and **d** a turnover rate of passive soil C (k_6) for root-excluded soils. Black and red colors represent year/SPEI only and year/SPEI with warming effects, respectively. Solid, dashed, dotted lines, respectively represent $P < 0.05$, $P < 0.1$, and $P > 0.1$
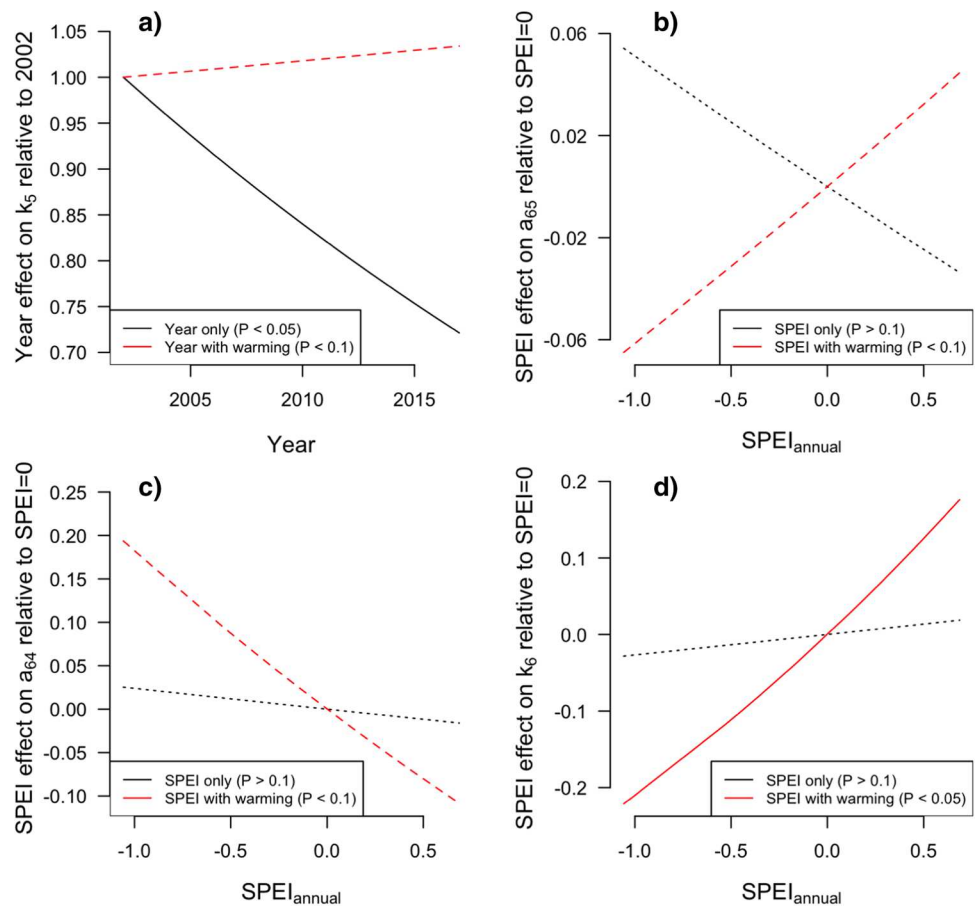
C recalcitrance may have been caused by a shift in species composition in this area (Shi et al. 2018). Alternatively, root C input may have caused an increase in the apparent C recalcitrance through the formation of aggregates, which protect belowground C from decay (Cheng et al. 2014; Cotrufo et al. 2013; Fontaine et al. 2007).

Mounting evidence suggests that climate warming plays an important role in soil C loss by increasing the rate of microbial decomposition of soil organic matter (Stocker 2014). The effect of temperature on microbe-driven decay of organic matter is represented in TECO as an exponential relationship between temperature and decay rate (Zhou et al. 2008). However, our results showed an additional effect of the warming treatment, which offset the increasing recalcitrance trend in slow soil C pool in the presence of fresh C input (Table S1 and S2; Fig. 6a) that was unaccounted for in the model. Such effects could be the result of a shift in the microbial community, as indicated by a recent incubation study performed with soils from our experimental site (Feng et al. 2017). In absence of limitation of the fresh C supply warming stimulated the abundance of microbial genes associated with complex compound degradation; however, under limitation of fresh C supply (i.e., root exclusion treatment), warming did not have such effect (Feng et al. 2017).

We also found a warming-mediated relationship between C transfer coefficients and moisture conditions. Transfer coefficients in the TECO model are conceptually similar to C use efficiency (CUE) (Allison 2014; Geyer et al. 2016; Manzoni et al. 2012) and are represented as constant fractions of decomposed C in the upstream (donor) pool that is transferred to the downstream (recipient) pool. Our results showed that some CUEs became dependent on moisture conditions under warming (Fig. 6). Temperature and moisture are key factors that can stimulate or suppress CUE; thus, decreasing or increasing soil respiration fluxes, respectively (Allison and Treseder 2008; Allison et al. 2010; Li et al. 2019). Prior results from the same experimental site reported that under drought conditions, warming created an unfavorable environment for microbes, reducing microbial populations by 50–80%, whereas under wet conditions warming increased microbial abundance (Sheik et al. 2011). While it is unclear whether community-level microbial CUE shifted in Sheik et al.'s study, positive relationship between slow pool CUE and moisture conditions uncovered here was consistent with their findings.

In absence of fresh C input, we saw that CUE in the active pool decreased with increasing SPEI (Fig. 6c). Such contrasting response may indicate an increasing

consumption of slow soil C: moist conditions increase reaction rates and microbial energy demand, but lack of labile C to meet this demand in the root-free soils forces microbes to consume a more recalcitrant C which is associated with low CUE (Agren and Bosatta 1987). Alternatively, increased rainfall may flush the available nitrogen (N) out of soils, forcing microbes to mine for N by decomposing complex organic compounds in order to maintain the C:N stoichiometry at the cost of biomass growth (Manzoni et al. 2012). This pattern is partly explained by the birch effect—increasing rainfall stimulates microbes to utilize mineral SOM-N complex (Birch 1958; Lado-Monserrat et al. 2014). Furthermore, especially warming under lower moist condition potentially exhibited slow diffusions of enzymes and substrates as shifts in microbial community and associated metabolic products (Fuchslueger et al. 2016; Or et al. 2007; Suseela et al. 2012). This response to changing environments is perhaps the innate function of microbes aimed at surviving under harsh conditions by enhancing their local environments (Schimel 2018).

In summary, we used a data assimilation approach to inform a process-based TECO model with the long-term in situ observations of C dynamics and gain understanding about the temporal changes in soil C dynamics as well as its response to warming. We demonstrated that model performance was substantially improved after accounting for interannual parameter variability. Variations in model parameters indicated presence of processes that significantly affected C dynamics, but were not reflected in the TECO model structure. These unrepresented mechanisms manifested as the increase in organic matter recalcitrance and dependency of turnover rates and CUEs on moisture conditions, partly supported by MMRT (Alster et al. 2016a, b). Consistent temporal trends in model parameters (i.e., time-varying parameters) uncover a potential issue in simulating C dynamics under unprecedented environmental conditions if the processes underlying these trends are not incorporated into the model structure as recently reported by Luo and Schuur (2020). Future research should explore the potential mechanisms that cause parameter variation, namely the long-term trends in plant traits and the mechanistic pathways of microbe-mediated organic matter decay.

Compliance with ethical standards

References

Adams HD, Williams AP, Xu C, Rauscher SA, Jiang X, McDowell NG (2013) Empirical and process-based approaches to climate-induced forest mortality models. Front Plant Sci 4:438. https://doi.org/10.3389/fpls.2013.00438

Agren GI, Bosatta N (1987) Theoretical analysis of the long-term dynamics of carbon and nitrogen in soils. Ecology 68:1181–1189. https://doi.org/10.2307/1939202

Allison SD (2014) Modeling adaptation of carbon use efficiency in microbial communities. Front Microbiol 5:571. https://doi.org/10.3389/fmicb.2014.00571

Allison SD, Treseder KK (2008) Warming and drying suppress microbial activity and carbon cycling in boreal forest soils. Glob Change Biol 14:2898–2909. https://doi.org/10.1111/j.1365-2486.2008.01716.x

Allison SD, Wallenstein MD, Bradford MA (2010) Soil-carbon response to warming dependent on microbial physiology. Nat Geosci 3:336–340. https://doi.org/10.1038/ngeo846

Alster CJ, Baas P, Wallenstein MD, Johnson NG, von Fischer JC (2016a) Temperature sensitivity as a microbial trait using parameters from macromolecular rate theory. Front Microbiol 7:1821. https://doi.org/10.3389/fmicb.2016.01821

Alster CJ, Koyama A, Johnson NG, Wallenstein MD, von Fischer JC (2016b) Temperature sensitivity of soil microbial communities: an application of macromolecular rate theory to microbial respiration. J Geophys Res Biogeosci 121:1420–1433. https://doi.org/10.1002/2016JG003343

Baer S, Kitchen D, Blair J, Rice C (2002) Changes in ecosystem structure and function along a chronosequence of restored grasslands. Ecol Appl 12:1688–1701. https://doi.org/10.1890/1051-0761(2002)012[1688:CIESAF]2.0.CO;2

Beguería S, Vicente-Serrano SM, Reig F, Latorre B (2014) Standardized precipitation evapotranspiration index (SPEI) revisited: parameter fitting, evapotranspiration models, tools, datasets and drought monitoring. Int J Climatol 34:3001–3023. https://doi.org/10.1002/joc.3887

Beguería S, Vicente-Serrano SM, Beguería MS (2017) Package 'SPEI'.

Birch H (1958) The effect of soil drying on humus decomposition and nitrogen availability. Plant Soil 10:9–31. https://doi.org/10.1007/BF01343734

Bond-Lamberty B, Thomson A (2010) A global database of soil respiration data. Biogeosciences 7:1915–1926. https://doi.org/10.5194/bg-7-1915-2010

Brock FV et al (1995) The Oklahoma Mesonet: a technical overview. J Atmos Ocean Technol 12:5–19. https://

doi.org/10.1175/1520-0426(1995)012%3c0005:TOMAT O%3e2.0.CO;2

Carey JC et al (2016) Temperature response of soil respiration largely unaltered with experimental warming. Proc Natl Acad Sci USA 113:13797–13802. https://doi.org/10.1073/pnas.1605365113

Cheng W et al (2014) Synthesis and modeling perspectives of rhizosphere priming. New Phytol 201:31–44. https://doi.org/10.1111/nph.12440

Clark JS et al (2001) Ecological forecasts: an emerging imperative. Science 293:657–660. https://doi.org/10.1126/science.293.5530.657

Cotrufo MF, Wallenstein MD, Boot CM, Denef K, Paul E (2013) The Microbial Efficiency-Matrix Stabilization (MEMS) framework integrates plant litter decomposition with soil organic matter stabilization: do labile plant inputs form stable soil organic matter? Glob Change Biol 19:988–995. https://doi.org/10.1111/gcb.12113

Cox PM, Betts RA, Jones CD, Spall SA, Totterdell IJ (2000) Acceleration of global warming due to carbon-cycle feedbacks in a coupled climate model. Nature 408:184–187. https://doi.org/10.1038/35041539

Feng W et al (2017) Enhanced decomposition of stable soil organic carbon and microbial catabolic potentials by long-term field warming. Glob Chang Biol 23:4765–4776. https://doi.org/10.1111/gcb.13755

Fierer N, Craine JM, McLauchlan K, Schimel JP (2005) Litter quality and the temperature sensitivity of decomposition. Ecology 86:320–326. https://doi.org/10.1890/04-1254

Fontaine S, Barot S, Barre P, Bdioui N, Mary B, Rumpel C (2007) Stability of organic carbon in deep soil layers controlled by fresh carbon supply. Nature 450:277–280. https://doi.org/10.1038/nature06275

Fox AM et al (2018) Evaluation of a data assimilation system for land surface models using CLM4. 5. J Adv Model Earth Syst 10:2471–2494. https://doi.org/10.1029/2018MS001362

Frank DA, McNaughton SJ (1990) Aboveground biomass estimation with the canopy intercept method: a plant growth form caveat. Oikos. https://doi.org/10.2307/3565736

Friedlingstein P et al (2006) Climate–carbon cycle feedback analysis: results from the C4MIP model intercomparison. J Clim 19:3337–3353. https://doi.org/10.1175/JCLI3800.1

Fuchslueger L et al (2016) Drought history affects grassland plant and microbial carbon turnover during and after a subsequent drought event. J Ecol 104:1453–1465. https://doi.org/10.1111/1365-2745.12593

Gao YZ, Giese M, Lin S, Sattelmacher B, Zhao Y, Brueck H (2008) Belowground net primary productivity and biomass allocation of a grassland in Inner Mongolia is affected by grazing intensity. Plant Soil 307:41–50. https://doi.org/10.1007/s11104-008-9579-3

Geyer KM, Kyker-Snowman E, Grandy AS, Frey SD (2016) Microbial carbon use efficiency: accounting for population, community, and ecosystem-scale controls over the fate of metabolized organic matter. Biogeochemistry 127:173–188. https://doi.org/10.1007/s10533-016-0191-y

Hanson PJ, Edwards NT, Garten CT, Andrews JA (2000) Separating root and soil microbial contributions to soil respiration: a review of methods and observations. Biogeochemistry 48:115–146. https://doi.org/10.1023/a:1006244819642

Hastings WK (1970) Monte Carlo sampling methods using Markov chains and their applications. Biometrika 57:97–109. https://doi.org/10.1093/biomet/57.1.97

Heimann M, Reichstein M (2008) Terrestrial ecosystem carbon dynamics and climate feedbacks. Nature 451:289–292. https://doi.org/10.1038/nature06591

Hobbs JK, Jiao W, Easter AD, Parker EJ, Schipper LA, Arcus VL (2013) Change in heat capacity for enzyme catalysis determines temperature dependence of enzyme catalyzed rates. ACS Chem Biol 8:2388–2393. https://doi.org/10.1021/cb4005029

Huang Y et al (2018a) Matrix approach to land carbon cycle modeling: a case study with the Community Land Model. Glob Chang Biol 24:1394–1404. https://doi.org/10.1111/gcb.13948

Huang Y et al (2018b) Matrix-based sensitivity assessment of soil organic carbon storage: a case study from the ORCHIDEE-MICT model. J Adv Model Earth Syst 10:1790–1808. https://doi.org/10.1029/2017MS001237

Jung CG et al (2019) Experimental warming amplified opposite impacts of drought vs. wet extremes on ecosystem carbon cycle in a tallgrass prairie. Agric For Meteorol 276:107635. https://doi.org/10.1016/j.agrformet.2019.107635

Keenan TF, Davidson EA, Munger JW, Richardson AD (2013) Rate my data: quantifying the value of ecological data for the development of models of the terrestrial carbon cycle. Ecol Appl 23:273–286. https://doi.org/10.1890/12-0747.1

Knorr W, Prentice IC, House JI, Holland EA (2005) Long-term sensitivity of soil carbon turnover to warming. Nature 433:298–301. https://doi.org/10.1038/nature03226

Lado-Monserrat L, Lull C, Bautista I, Lidón A, Herrera R (2014) Soil moisture increment as a controlling variable of the "Birch effect". Interactions with the pre-wetting soil moisture and litter addition. Plant Soil 379:21–34. https://doi.org/10.1007/s11104-014-2037-5

Li J et al (2019) Reduced carbon use efficiency and increased microbial turnover with soil warming. Glob Change Biol 25:900–910. https://doi.org/10.1111/gcb.14517

Liang J et al (2018) Biotic responses buffer warming-induced soil organic carbon loss in Arctic tundra. Glob Change Biol 24:4946–4959. https://doi.org/10.1111/gcb.14325

Loladze I (2002) Rising atmospheric CO2 and human nutrition: toward globally imbalanced plant stoichiometry? Trends Ecol Evol 17:457–461. https://doi.org/10.1016/S0169-5347(02)02587-9

Lu M et al (2013) Responses of ecosystem carbon cycle to experimental warming: a meta-analysis. Ecology 94:726–738. https://doi.org/10.1890/12-0279.1

Luo Y, Schuur EA (2020) Model parameterization to represent processes at unresolved scales and changing properties of evolving systems. Glob Change Biol 26:1109–1117. https://doi.org/10.1111/gcb.14939

Luo Y et al (2011) Coordinated approaches to quantify long-term ecosystem dynamics in response to global change. Glob Change Biol 17:843–854. https://doi.org/10.1111/j.1365-2486.2010.02265.x

Luo Y, Keenan TF, Smith M (2015) Predictability of the terrestrial carbon cycle. Glob Change Biol 21:1737–1751. https://doi.org/10.1111/gcb.12766

Manzoni S, Taylor P, Richter A, Porporato A, Agren GI (2012) Environmental and stoichiometric controls on microbial carbon-use efficiency in soils. New Phytol 196:79–91. https://doi.org/10.1111/j.1469-8137.2012.04225.x

McCarthy MA (2007) Bayesian methods for ecology. Cambridge University Press, Cambridge

McEvoy DJ, Huntington J, Abatzoglou J (2013) A comparison of the standardized precipitation evapotranspiration index using the penman-monteith and thornthwaite parameterizations for potential evapotranspiration. In: 93rd American meteorological society annual meeting

McPherson RA et al (2007) Statewide monitoring of the mesoscale environment: a technical update on the Oklahoma Mesonet. J Atmos Ocean Technol 24:301–321. https://doi.org/10.1175/JTECH1976.1

Melillo JM et al (2002) Soil warming and carbon-cycle feedbacks to the climate system. Science 298:2173–2176. https://doi.org/10.1126/science.1074153

Melillo JM et al (2017) Long-term pattern and magnitude of soil carbon feedback to the climate system in a warming world. Science 358:101–105. https://doi.org/10.1126/science.aan2874

Metropolis N, Rosenbluth AW, Rosenbluth MN, Teller AH, Teller E (1953) Equation of state calculations by fast computing machines. J Chem Phys 21:1087–1092. https://doi.org/10.1063/1.1699114

Niu S, Sherry RA, Zhou X, Luo Y (2013) Ecosystem carbon fluxes in response to warming and clipping in a tallgrass prairie. Ecosystems 16:948–961. https://doi.org/10.1007/s10021-013-9661-4

Or D, Smets BF, Wraith JM, Dechesne A, Friedman SP (2007) Physical constraints affecting bacterial habitats and activity in unsaturated porous media—a review. Adv Water Resour 30:1505–1527. https://doi.org/10.1016/j.advwatres.2006.05.025

Post J, Hattermann FF, Krysanova V, Suckow F (2008) Parameter and input data uncertainty estimation for the assessment of long-term soil organic carbon dynamics. Environ Model Softw 23:125–138. https://doi.org/10.1016/j.envsoft.2007.05.010

R-Core-Team (2019) R: A language and environment for statistical computing

Rodríguez-Iturbe I, Porporato A (2007) Ecohydrology of water-controlled ecosystems: soil moisture and plant dynamics. Cambridge University Press, Cambridge

Rustad L et al (2001) A meta-analysis of the response of soil respiration, net nitrogen mineralization, and aboveground plant growth to experimental ecosystem warming. Oecologia 126:543–562. https://doi.org/10.1007/s004420000544

Savage K, Davidson E (2001) Interannual variation of soil respiration in two New England forests. Global Biogeochem Cycles 15:337–350. https://doi.org/10.1029/1999GB001248

Schimel JP (2018) Life in dry soils: effects of drought on soil microbial communities and processes. Annu Rev Ecol Evol Syst 49:409–432. https://doi.org/10.1146/annurev-ecolsys-110617-062614

Schmidt MW et al (2011) Persistence of soil organic matter as an ecosystem property. Nature 478:49. https://doi.org/10.1038/nature10386

Sheik CS, Beasley WH, Elshahed MS, Zhou X, Luo Y, Krumholz LR (2011) Effect of warming and drought on grassland microbial communities. ISME J 5:1692–1700. https://doi.org/10.1038/ismej.2011.32

Sherry RA et al (2008) Lagged effects of experimental warming and doubled precipitation on annual and seasonal aboveground biomass production in a tallgrass prairie. Glob Change Biol 14:2923–2936. https://doi.org/10.1111/j.1365-2486.2008.01703.x

Shi Z et al (2015a) Evidence for long-term shift in plant community composition under decadal experimental warming. J Ecol 103:1131–1140. https://doi.org/10.1111/1365-2745.12449C

Shi Z et al (2015b) Experimental warming altered rates of carbon processes, allocation, and carbon storage in a tallgrass prairie. Ecosphere 6:1–16. https://doi.org/10.1890/ES14-00335.1

Shi Z et al (2018) Successional change in species composition alters climate sensitivity of grassland productivity. Glob Chang Biol 24:4993–5003. https://doi.org/10.1111/gcb.14333

Silver WL, Miya RK (2001) Global patterns in root decomposition: comparisons of climate and litter quality effects. Oecologia 129:407–419. https://doi.org/10.1007/s004420100740

Stocker TF (2014) Climate change 2013: the physical science basis: Working Group I contribution to the Fifth assessment report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge

Subke J-A, Inglima I, Francesca Cotrufo M (2006) Trends and methodological impacts in soil CO2 efflux partitioning: a metaanalytical review. Glob Change Biol 12:921–943. https://doi.org/10.1111/j.1365-2486.2006.01117.x

Sun OJ, Campbell J, Law BE, Wolf V (2004) Dynamics of carbon stocks in soils and detritus across chronosequences of different forest types in the Pacific Northwest, USA. Glob Change Biol 10:1470–1481. https://doi.org/10.1111/j.1365-2486.2004.00829.x

Suseela V, Conant RT, Wallenstein MD, Dukes JS (2012) Effects of soil moisture on the temperature sensitivity of heterotrophic respiration vary seasonally in an old-field climate change experiment. Glob Change Biol 18:336–348. https://doi.org/10.1111/j.1365-2486.2011.02516.x

Torn M, Swanston C, Castanha C, Trumbore S (2009) Storage and turnover of organic matter in soil. In: Biophysico-chemical processes involving natural nonliving organic matter in environmental systems. Wiley, Hoboken, pp 219–272. https://doi.org/10.1002/9780470494950.ch6

Trumbore S (2006) Carbon respired by terrestrial ecosystems–recent progress and challenges. Glob Change Biol 12:141–153. https://doi.org/10.1111/j.1365-2486.2006.01067.x

Van der Schrier G, Jones P, Briffa K (2011) The sensitivity of the PDSI to the Thornthwaite and Penman-Monteith parameterizations for potential evapotranspiration. J Geophys Res Atmos. https://doi.org/10.1029/2010JD015001

Vicente-Serrano SM, Beguería S, López-Moreno JI (2010) A multi-scalar drought index sensitive to global warming: the standardized precipitation evapotranspiration index. J Clim 23:1696–1718. https://doi.org/10.1175/2009JCLI2909.1

Wan S, Luo Y, Wallace LL (2002) Changes in microclimate induced by experimental warming and clipping in tallgrass prairie. Glob Change Biol 8:754–768. https://doi.org/10.1046/j.1365-2486.2002.00510.x

Wan S, Norby RJ, Ledford J, Weltzin JF (2007) Responses of soil respiration to elevated CO2, air warming, and changing soil water availability in a model old-field grassland. Glob Change Biol 13:2411–2424. https://doi.org/10.1111/j.1365-2486.2007.01433.x

Wang Y-P, Leuning R (1998) A two-leaf model for canopy conductance, photosynthesis and partitioning of available energy I: Model description and comparison with a multi-layered model. Agric For Meteorol 91:89–111. https://doi.org/10.1016/S0168-1923(98)00061-6

Wang Y-P, Trudinger CM, Enting IG (2009) A review of applications of model–data fusion to studies of terrestrial carbon fluxes at different scales. Agric For Meteorol 149:1829–1842. https://doi.org/10.1016/j.agrformet.2009.07.009

Wedin DA, Tilman D (1990) Species effects on nitrogen cycling: a test with perennial grasses. Oecologia 84:433–441. https://doi.org/10.1007/BF00328157

Weng E, Luo Y (2008) Soil hydrological properties regulate grassland ecosystem responses to multifactor global change: a modeling analysis. J Geophys Res Biogeosci. https://doi.org/10.1029/2007JG000539

Wu Z, Dijkstra P, Koch GW, Peñuelas J, Hungate BA (2011) Responses of terrestrial ecosystems to temperature and precipitation change: a meta-analysis of experimental manipulation. Glob Change Biol 17:927–942. https://doi.org/10.1111/j.1365-2486.2010.02302.x

Xu T, White L, Hui D, Luo Y (2006) Probabilistic inversion of a terrestrial ecosystem model: analysis of uncertainty in parameter estimation and model prediction. Glob Biogeochem Cycles. https://doi.org/10.1029/2005GB002468

Xu X, Zhou Y, Ruan H, Luo Y, Wang J (2010) Temperature sensitivity increases with soil organic carbon recalcitrance along an elevational gradient in the Wuyi Mountains, China. Soil Biol Biochem 42:1811–1815. https://doi.org/10.1016/j.soilbio.2010.06.021

Zhou X, Wan S, Luo Y (2007) Source components and interannual variability of soil CO2 efflux under experimental warming and

clipping in a grassland ecosystem. Glob Change Biol 13:761–775. https://doi.org/10.1111/j.1365-2486.2007.01333.x

Zhou X, Weng E, Luo Y (2008) Modeling patterns of nonlinearity in ecosystem responses to temperature, CO2, and precipitation changes. Ecol Appl 18:453–466. https://doi.org/10.1890/07-0626.1

Zhou X et al (2010) Concurrent and lagged impacts of an anomalously warm year on autotrophic and heterotrophic components of soil respiration: a deconvolution analysis. New Phytol 187:184–198. https://doi.org/10.1111/j.1469-8137.2010.03256.x

Zhou X, Xu X, Zhou G, Luo Y (2018) Temperature sensitivity of soil organic carbon decomposition increased with mean carbon residence time: field incubation and data assimilation. Glob Change Biol 24:810–822. https://doi.org/10.1111/gcb.13994