ECOSPHERE

SPECIAL FEATURE: DATA ASSIMILATION

Improvement of global litter turnover rate predictions using a Bayesian MCMC approach

Oleksandra Hararuk $^{1,} \dagger$ and Yiqi Luo 1,2

¹Department of Microbiology and Plant Biology, University of Oklahoma, Norman, Oklahoma 73019 USA ²Center for Earth System Science, Tsinghua University, Beijing 100084 China

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Abstract. Global terrestrial carbon (C) cycle has a strong influence on atmospheric CO_2 concentrations and temperatures. Litter mass is relatively small in comparison to soil and plant pools but its turnover rate is fast. Litter dynamics is important part of the global terrestrial carbon cycle as it is a critical stage in the soil organic matter formation and nutrient mineralization. Litter turnover rates have been observed on site, regional, and global levels, however little effort has been put into validating and calibrating litter decay models against the observations. In this study, we used a Bayesian Markov Chain Monte Carlo data assimilation technique and globally observed leaf litter turnover rates to calibrate a first order litter decay model with different assumptions about litter quality limitations of decomposition. The first order decay model with original parameters and a commonly-used litter quality limitation function explained 15% of the spatial variation in the observed leaf litter turnover rates, and parameter calibration increased the explained variation in the observations to 44%. When litter quality limitation of decomposition was determined by litter lignin-to-nitrogen ratio rather than structural lignin content the performance of the calibrated first order decay model was further improved, explaining 62% of variation in the observations. Litter feedbacks to changing climate differed between the original and best-fitting models: original model predicted a 16% decrease in leaf litter pool after 95 years of climate change (2006–2100), whereas the bestfitting model predicted a 2% increase. Furthermore, assuming that litter quality decreased with increasing CO_2 concentrations resulted in a 28% decrease in leaf litter pool predicted by the original model, and a 15% increase predicted by the best-fitting model. Thus, assimilating observed leaf litter turnover rates into a first-order decay model improved model fit and reversed leaf litter feedbacks to changing climate.

Key words: carbon dynamics; model calibration.

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† E-mail: ohararuk@ou.edu

INTRODUCTION

Global carbon (C) cycle is tightly coupled with climate: climate regulates the ecosystem C storage capacity (Fung et al. 2005, Xia et al. 2013), and carbon released from or sequestered by ecosystems impacts climate (Falkowski et al. 2000, Houghton et al. 2001). Terrestrial ecosystems, in particular, have been shown to significantly affect temperature (Foley et al. 2003), therefore it is important to accurately represent the feedbacks between terrestrial carbon cycle and climate. Accurate prediction of these feedbacks will facilitate reliable assessments of the



global change effects on the ecosystems as well as development of the mitigation strategies for these effects.

Global terrestrial C pool is estimated at around 2000 Pg C (Falkowski et al. 2000), and although litter pool constitutes a small fraction of the global terrestrial C pool (68-97 Pg C [Matthews 1997]) litter decomposition is a critical stage in soil organic matter formation and nutrient mineralization (Austin and Ballaré 2010). Multiple studies show that litter decomposition is controlled by climate (Hobbie 1996, Gholz et al. 2000, Hobbie et al. 2000, Zhang et al. 2008), litter quality (e.g., initial litter lignin content or lignin to nitrogen [lignin:N] ratio [Melillo et al. 1982, Shaw and Harte 2001, Zhang et al. 2008]), and the origin of litter ("home-field advantage effect" [Gholz et al. 2000, Ayres et al. 2009]), however little effort has been put into calibrating those relationships against the observations to represent litter decomposition rates for various points around the globe.

With increase in the available ecological data, implementation of data-model fusion techniques for model improvement and uncertainty assessments of model predictions have been gaining momentum (Luo et al. 2009, Luo et al. 2011). Particularly, calibration of the litter decomposition models was carried out on site and regional levels: Williams et al. (2005) used Ensemble Kalman Filter to calibrate litter decomposition (among other model components) against the observations in central Oregon; Keenan et al. (2012) and Xu et al. (2006) used Bayesian inversion to calibrate an ecosystem carbon cycle model for Harvard forest and Duke forest respectively; and Adair et al. (2008) calibrated several litter decomposition model formulations with the observations from North and Central America.

Model calibration at the site level is useful for representing environmental effects on decomposition processes and their uncertainties for a particular set of environmental conditions, but it is unlikely that the obtained parameters will represent large-scale variability of turnover rates. Gholz et al. (2000) and Zhang et al. (2008) conducted analyses on the regional and global scales to identify spatial controls of the observed litter turnover rates. However these two studies used multiple regressions to characterize the relationships between turnover rates and environmental factors and/or litter chemistry—a rarely used approach in the global carbon cycle modeling. Adair et al. (2008), on the other hand, used regionally observed litter turnover rates to estimate parameters of a commonly used litter decay model formulation, and thus informing the existing modeling framework with observations. To our knowledge no studies have been conducted to inform the models of litter carbon dynamics with observations on a global scale.

In this study we used leaf litter turnover rates observed across the globe to (1) calibrate first order decay model formulations commonly used to represent leaf litter decomposition; (2) evaluate the causes of errors of the modeled estimates; (3) evaluate the impacts of model calibration on predictive ability of litter pools; and (4) assess global litter feedbacks to a climate change scenario along with the uncertainty of those feedbacks.

Methods

Litter decay rate

Litter mass loss is usually represented as an exponential decay process (Olson 1963, Aber et al. 1990, Harmon et al. 2009):

$$X_t = X_o e^{-kt} \tag{1}$$

where X_t is the litter pool size at the time t, X_o is the initial litter pool size, and k is the decay rate. The decay rate is dependent on climate and litter quality:

$$k = k_{\text{base}} \times f(T) \times f_n(Q) \tag{2}$$

where k_{base} is litter turnover rate under no climate or litter quality limitation, f(T) is temperature limitation, and $f_n(Q)$ is litter quality limitation (n = 1 or 2 depending on assumption about limitation). Temperature limitation is modeled as a Q10 function:

$$f(T) = Q_{10}^{(0.1 \times (T-30))} \tag{3}$$

where Q_{10} is temperature sensitivity of heterotrophic respiration and *T* is temperature. For litter quality limitation we used two assumptions: (1) litter quality limitation was determined by structural lignin carbon as in Parton et al. (1987); and (2) litter quality limitation was a function of lignin:N ratio in leaf litter as illustrated in Melillo et al. (1982), Stump and Binkley (1993), and Shaw and Harte (2001). Parton et al. (1987) modeled litter quality limitation as:

$$f_1(Q) = \exp(-a \times L_S) \tag{4}$$

where a = 3, and L_S is fraction of lignin-C in organic matter and was calculated as:

$$L_{S} = \frac{0.65 \times L}{0.45 \times (1 - F_{L})}$$
(5)

where 0.65 was the approximated fraction of C in a lignin molecule, 0.45 was the C content in the surface leaf litter, F_L was the fraction of labile C in the surface leaf litter, and following Parton et al. (1987) was calculated as:

$$F_L = 0.85 - 0.018 \times \text{LN} \tag{6}$$

where LN was the lignin:N ratio of the surface leaf litter. We represented the second assumption in litter quality limitation as a power function of lignin:N ratio:

$$f_2(Q) = \mathrm{LN}^{-b} \tag{7}$$

where b was an estimated parameter with initial value of 0, representing no litter quality limitation.

Observed data

We used the global database of leaf litter turnover rates (*k*'s) compiled by Zhang et al. (2008). This study calculated the *k*'s by fitting equation 1 to the litter decay data from 110 sites distributed from 38°S to 69°N. The database also provided data on temperature, precipitation, litter lignin content, and nitrogen content, which allowed us to simulate *k*'s at each given site. We randomly separated 141 globally distributed data points into two groups: for model calibration (n = 79), and for model validation (n = 62). The fit statistics in the results and discussion section will be provided for the model performance on validation dataset.

Parameter estimation

We calibrated k_{baser} , Q_{10} , a, and b using a Bayesian Markov Chain Monte Carlo (MCMC) technique. Mosegaard and Sambridge (2002) summarize Bayesian inversion as

$$p(c|Z) = v_c \times p(Z|c) \times p(c)$$
(8)

where p(c|Z) is posterior probability density function of model parameters c; p(Z|c) is a likelihood function of parameters c; p(c) is prior probability density function of parameters c; and v_c is a normalization constant. We assumed that the prediction errors were normally distributed and uncorrelated, and calculated the likelihood function, p(Z|c), as

$$p(Z|c) = v_L \times \exp\left\{-\sum_{i=1}^k \frac{(z_i - x_i)^2}{2\sigma_i^2}\right\}$$
(9)

where z_i is k reported in Zhang et al. (2008) at *i*th site, x_i is simulated k for the *i*th site; σ_i^2 is the associated with *i*th observation; k is the total number of sites (n = 79); and v_L is a constant. In their database, Zhang et al. (2008) did not report the uncertainties associated with litter turnover rates; therefore, we followed the approach used in Harmon and Challenor (1997) and Hararuk et al. (2014) and assumed a standard deviation of 30% for each observation, which we then used to calculate the variance.

We assigned minimum and maximum values to the parameters and used adaptive Metropolis (AM) algorithm (Haario et al. 2001) to sample from the posterior parameter distributions. We generated a parameter chain by running AM algorithm in two steps: a proposing step and a moving step. In the proposing step a new parameter set c^{new} was generated from a previously accepted parameter set c^{k-1} with a proposal distribution ($c^{\text{new}}|c^{k-1}$). In the moving step a probability of acceptance $P(c^{k-1}|c^{\text{new}})$ was calculated as in Marshall et al. (2004):

$$P(c^{k-1}|c^{\text{new}}) = \min\left\{1, \frac{p(Z|c^{\text{new}})p(c^{\text{new}})}{p(Z|c^{k-1})p(c^{k-1})}\right\}.$$
 (10)

The value of $P(c^{k-1}|c^{\text{new}})$ was then compared with a random number *U* from 0 to 1. Parameter set c^{new} was accepted if $P(c^{k-1}|c^{\text{new}}) \ge U$, otherwise c^k was set to c^{k-1} .

The AM algorithm required an initial parameter covariance matrix, which we generated from a test run of 40,000 simulations with uniform proposal distribution as in Xu et al. (2006):

$$c^{\text{new}} = c^{k-1} + r \times \frac{c^{\max} - c^{\min}}{D}$$
(11)

where c^{\max} and c^{\min} are upper and lower parameter limits, *r* is a random number between

		Prior					Lower	Upper
Parameter description	Abbreviation	Minimum	Maximum	Value	MLE	G-R	95% bounds	95% bounds
Model with $f_1(O)$								
Baseline turnover rate, year ^{-1}	k_{base}	0.50	24.00	7.00	0.93	1.00	0.87	1.03
Temperature sensitivity	Q_{10}	1.00	3.00	2.00	1.77	1.00	1.72	1.87
Litter quality limitation parameter	а	-5.00	5.00	3.00	-4.24	1.00	-4.88	-1.34
Model with $f_2(Q)$								
Baseline turnover rate, $vear^{-1}$	khase	0.50	24.00	7.00	2.37	1.00	2.18	2.73
Temperature sensitivity	Q_{10}	1.00	3.00	2.00	1.43	1.00	1.38	1.52
Litter quality limitation parameter	b	-1.00	1.00	0	0.36	1.00	0.34	0.40

Table 1. Parameter characteristics. MLE is maximum likelihood estimate, and G-R is the result of Gelman-Rubin chain convergence diagnostics.

-0.5 and 0.5, and D = 5. From the test run results we calculated the covariance matrix C_0 and modified the proposal step to be

$$c^{\text{new}} = N(c^{k-1}, C_k) \tag{12}$$

$$C_{k} = \begin{cases} C_{0} & k \le k_{0} \\ s_{d} \operatorname{cov}(c_{0}, ..., c_{k-1}) & k > k_{0} \end{cases}$$
(13)

where $k_0 = 2000$; $s_d = 2.38/\sqrt{3}$ (Gelman et al. 1996).

We made five parallel runs (each run containing 200,000 simulations) starting at dispersed initial points in the parameter space. We discarded the first half of the simulations (as burn-in phase) and tested the second half for convergence to stationary distributions with Gelman-Rubin diagnostics (Gelman and Rubin 1992).

We set the parameter boundaries (listed in Table 1) based on the literature and our assumptions. We varied temperature sensitivity, Q_{10} , between 1 (to assume that turnover rates insensitive to temperature changes) and 3, which was slightly higher than empirical values (Gholz et al. 2000, Zhou et al. 2008, Smyth et al. 2009). Baseline leaf litter turnover rate, k_{base}, varied between 0.5 years⁻¹ (2 years) to 24 years⁻¹ (\approx 2 weeks) to allow for a broad range of maximum leaf turnover rates. The lower boundary for parameter a was set to test whether model formulation would yield unrealistic responses of decomposition rates to litter quality, and the upper parameter boundary was reported to produce best model performance (Kirschbaum and Paul 2002). The upper boundary for parameter b was set slightly higher than the value reported in Melillo et al. (1982) (b = 0.78), and the value calculated from Shaw and Harte (2001) (b =(0.88); as for the parameter *a*, the lower boundary for the parameter b was set to test the model formulation for unrealistic dynamics.

Leaf litter feedbacks to climate change

We evaluated the uncertainties in surface leaf litter feedbacks to climate change by running the best-performing calibrated model forward, driving it with a climate change scenario (increasing CO₂ and temperatures) and sampling from the posterior parameter distributions. We used the Community Earth System Model (CESM) output for the Representative Concentration Pathway 8.5 (RCP8.5) experiment (specifically, the simulated temperature and C influx to leaves, which we assumed to be similar to leaf litter flux) to drive the leaf litter dynamics. The CESM model output was provided as a part of Coupled Model Intercomparison Project Phase 5 (CMIP5), and was available at http://pcmdi9.llnl.gov. Over 95 years CESM simulated a 3.5 K increase in mean global temperature and atmospheric CO_2 increase to 1150 ppm by the year 2100 (Keppel-Aleks et al. 2013). Before running the model forward in time we used global distributions of litter lignin content and CN ratios from the CESM model and the 2006–2010 temperature and C influx data to generate initial leaf litter pools:

$$X_{\text{Litter}} = \frac{\text{NPP}_{\text{L}}}{k} \tag{14}$$

where X_{Litter} was leaf litter pool, in g/m², and NPP_L was C influx to leaves, in g/m²/year. We then ran the litter dynamics model forward in time to the year 2100, generating litter feedbacks to the changing climate.

Increasing CO₂ has been reported to increase leaf litter lignin and decrease leaf litter nitrogen



Fig. 1. Posterior parameter distributions for two models with different assumptions of litter quality limitation of its turnover rate: $f_1(Q) = \exp(-a \times L_S)$ and $f_2(Q) = LN^{-b}$. Baseline leaf litter turnover rate was higher under the $f_2(Q)$ assumption, and leaf litter turnover was less sensitive to temperature under $f_2(Q)$ assumption than $f_1(Q)$ assumption

content (Norby et al. 2001, Liu et al. 2005) at a rate of 6.5% per \sim 300 ppm and 7.1% per \sim 300 ppm of increasing CO₂ respectively (Norby et al. 2001). We assumed the change in litter chemistry was linear and monotonic, applied the rates of change for lignin and nitrogen content to calculate new leaf litter quality parameters at each time step of a forward model run, and evaluated the effect of changing leaf litter chemistry on litter feedbacks to climate change.

Results and Discussion

Estimated parameters

Most estimated parameters were well constrained within their prior ranges (Fig. 1, Table 1). Litter quality limitation parameter *a* from Eq. 4 was skewed against its minimum value, reversing the effect of lignin on litter decomposition: increase in litter structural lignin increased its turnover rate exponentially. Such effect of lignin on decomposition is unrealistic, therefore litter quality limitation function presented in Eq. 4 does not reflect the observed patterns. Parameter b, however, from Eq. 7 was constrained within a range producing realistic dynamics with the maximum likelihood value of 0.36 and a 95% confidence interval (CI) of 0.34–0.40, yielding a negative relationship between litter quality and decomposition rate.

The maximum likelihood effect of lignin:N ratio on litter decomposition was weaker than the one reported in Melillo ([1982], b = 0.78), as well as the ones calculated from the data in Shaw and Harte ([2001], b = 0.88), Taylor et al. ([1989], b = 0.41), and Wieder et al. ([2009], b = 0.54). Such spread in litter quality effect on decomposition rate could be due to differences in the microbial communities. Decomposition of the passive litter fraction is associated with higher fungi-to-bacteria ratio in the decompose passive litter fraction



Fig. 2. Comparison of the leaf litter turnover rates produced by CENTURY (a), calibrated CENTURY (b), and the model with different assumption about litter quality limitation on its turnover rate (c). Calibration improved performance of CENTURY, however, changing the assumption about litter quality limitation of its turnover rate improved model performance.

better than bacteria (Beare et al. 1992). Additionally, complex decomposer communities have been shown to increase turnover rate of the passive litter fraction (Coûteaux et al. 1991, O'Neill and Norby 1996), therefore sites with low values of b may have higher fungal biomass or more complex decomposer communities than the sites with high values of b. However, the studies with observed b's did not have the data on microbial community composition, therefore the reason for such variability in the observed effects of lignin:N ratio on decomposition requires further investigation.

Baseline litter residence time, k_{base} , was lower in the model with litter quality limitation function $f_1(Q)$, than in the model with the function $f_2(Q)$ (Table 1), and both estimates were higher than the value reported in Adair et al. (2008) ($k_{\text{base}} = 0.53$). One-pool litter decay model in Adair et al. (2008) did not include litter quality effect on decomposition, which was likely the reason for low k_{base} value as it was implicitly corrected for the litter quality effect. Similarly, there was no agreement in temperature sensitivities (Q_{10}) between the two models, however both estimates fell within the wide range of the values reported in the literature (from 1.17 to 2.7 [Gholz et al. 2000, Zhou et al. 2008, Smyth et al. 2009, Wang et al. 2012]).

Calibrated model performance

Original model formulation for leaf litter turnover, k, explained 15% of variance in the observed k's from Zhang et al. (2008) with the root-mean-square error (RMSE) of prediction equal to 0.39 (Fig. 2a). Calibration of the model with the original litter quality limitation function improved its performance, increasing the r^2 to 0.44, and decreasing RMSE by 41% (Fig. 2b). Changing the litter quality limitation function increased r^2 to 0.62, and reduced RMSE by 49% (Fig. 2c). Convergence of the parameter a to an unrealistic value and better fit statistics for the model with litter quality limitation $f_2(Q)$ than for the model with $f_1(Q)$ led us to the conclusion that litter lignin:N ratio was a better predictor of litter quality limitation of decomposition than litter structural lignin content.

Global leaf litter distribution

We calculated the global distribution of the surface leaf litter pools as in Eq. 14 using CESM leaf litter flux and the best fitting model for the leaf litter turnover rates (Eqs. 2 and 7). The best-fitting model predicted smaller litter pools than the original model in all regions except the tropical regions (Fig. 3), where the calibrated model predicted higher C storage than the original model. Comparison of our aboveground litter estimates to the ones provided in Vogt et al. (1986) revealed that calibration of the turnover rates did not improve model's predictive ability



Fig. 3. Global distribution of aboveground litter (excluding woody debris) before (a, c) and after (b, d) calibration of the turnover rates, and their comparisons to the observations from Vogt et al. (1986) (error bars represent standard deviations calculated for the observations per given latitude). Litter pool sizes are determined not only by litter turnover rates, but also by the input rate, therefore we compared modeled litter input rates to the observations (e) reported in Vogt et al. (1986).

for the aboveground litter pools in the lowtemperature regions (Fig. 3c, d). Since C pools were determined by C influx rates and C pool turnover rates (Xia et al. 2013) the mismatches between the modeled litter pool estimates and the observations were caused either by errors in the litterfall or errors in turnover rate predictions. Comparison of modeled and observed litterfall (Fig. 3e) revealed that most modeled estimates were within the range of the observed estimates with the largest mismatches (underpredictions) located in the tropical regions. Because there was general agreement between observed and modeled litter input estimates, the errors in modeled litter pools were caused by the errors in the litter turnover rates.

Errors in the modeled turnover rate estimates could be caused by errors in the model input data, such as inaccurate temperature and global lignin:N ratio distributions assumed in the CESM, or the issues with the data that were used to calibrate the model. CESM assessment showed that the model simulated the land surface temperatures well (Lawrence et al. 2011), however there was no global observed lignin:N ratio data product to validate CESM lignin:N distribution. Therefore lignin:N ratios remained a source of uncertainty for the global leaf litter turnover rates distribution. Long-term (10-year) litter decomposition rates have been reported to be lower than short term (1-year) decay rates on average by 22–30% (Harmon et al. 2009). The longest observation period for litter decomposition in Zhang et al. (2008) that was used in our study was three years, therefore litter decomposition rates might have been overestimated, causing underestimation of the litter pools. However, for the northern latitudes, where the model residuals were the largest (Fig. 3d), even a 30% decrease in the litter turnover rates would lead to approximately a 43% increase in the litter pools, which would not be enough to compensate for ~6-fold underprediction of litter pools. To address a potential issue with the data used for model calibration we used the leaf litter turnover rates from the Long-term Intersite Decomposition Experiment Team (LIDET) observed across multiple biomes and substrates (Harmon et al. 2009) for additional model validation. We calculated the leaf litter turnover rates from the temperatures and lignin:N ratios at the 27 LIDET sites distributed across North and Central America using the original and our best-fitting model, and compared them to the turnover rates from Harmon et al. (2009).

The calibrated model performed better than the original model (Fig. 4a, b), however it overpredicted low turnover rates, underpredicted high turnover rates, and overall had a much lower predictive ability compared to that of the data from Zhang et al. (2008) (Fig. 2c). Most of the turnover rates from the LIDET data were obtained from 10-year decomposition records, whereas the maximum length of decomposition records included in the Zhang et al. (2008) dataset was three years. Some studies argue that leaf litter turnover rates are best represented by two or three turnover rate components: fast, slow, and passive (Adair et al. 2008, Harmon et al. 2009) with the impact of slower components on the total leaf litter turnover rates dependent on litter quality (Adair et al. 2008). Comparison of the LIDET turnover rates with the estimates from our calibrated best-fitting model revealed no significant relationships neither between the model's residuals and lignin:N ratios (Fig. 4c) nor between the residuals and litter lignin content (Fig. 4d), therefore the model errors were not caused by the absence of explicitly modeled slow pools' turnover rates.

At the site level, fraction of the explained variance in the observed turnover rates was dependent on annual precipitation: our bestfitting model had higher predictive ability in humid climate than in arid regions (Fig. 4e). Precipitation affects soil moisture, which is an important factor in determining litter decay (Cortez 1998, Riutta et al. 2012, Lee et al. 2014). However, due to absence of soil moisture data in the database used for model calibration, we did not include moisture limitation in the litter decay model formulation (Eq. 2). Furthermore, in the arid regions moisture limitation of litter decomposition may be countered by photo degradation, which tends to increase litter decay rate with decreasing precipitation, latitude and leaf area index (Smith et al. 2010, King et al. 2012), introducing additional source of uncertainty to litter decay predictions.

The predictability of the leaf litter turnover rates was also dependent on temperature: sitelevel RMSE's increased with increasing mean annual temperatures (Fig. 4f). Dependency of the turnover rate predictability on temperature and precipitation indicates the need for more research of litter C dynamics in the high-temperature arid regions, and in addition to including moisture and irradiance effect on litter decay, may point at the need to explicitly model microbial biomass dynamics in the litter pool. For instance the effect



Fig. 4. Comparison of modeled turnover rates to the observed turnover rates from Harmon et al. (2009) before (a) and after (b) calibration. The explained variability of the observations was correlated with annual precipitation (e), site-level RMSE's were correlated with mean annual temperatures (f), and there were no significant relationships between litter:N ratio and model residuals (c) or between model residuals and litter lignin content (d).

of moisture on organic matter decomposition in the arid regions is represented better by microbial models than by the first order decay models (Lawrence et al. 2009). Additionally, because LIDET experiment identified turnover rates for litter transplants decrease in turnover rate predictability with increasing temperatures might be due to maladaptation of the microbial communities to the foreign substrates (Gholz et al. 2000). The importance of modeling photo degradation, moisture limitation of litter decay, and explicit representation of microbial dynamics can be assessed with the approach used in this study coupled with the databases containing soil moisture, irradiance, litter decay rates, or time series of litterfall and pool observations.

Litter feedbacks to climate change

Global leaf litter pool size simulated by the best performing model was 26.3 Pg C with a 95%



Fig. 5. Global leaf litter pool (a), and its response to changing climate with (c) and without (b) the assumption of changing litter quality with increasing CO_2 .

CI of 25.6–27.5 Pg C, which was lower than the original model estimate of 29.3 Pg C (Fig. 5a). The calibrated estimate was higher than the observed global leaf litter pool (13 Pg C [Matthews 1997]), but lower than the previous model estimates (60 Pg C [Esser et al. 1982] and

51 Pg C [Potter et al. 1993]).

Changing the litter quality limitation function along with model calibration resulted in the opposite direction of litter pool feedback to 95 years of increasing temperatures and CO₂ concentrations. The original model predicted a 16%decrease in leaf litter pool, whereas the calibrated model simulated a 2% increase (with the range of a 2% decrease to an 8% increase) in the leaf litter pool after 95 years of climate change (Fig. 5b). Including the assumption about decreasing leaf litter quality with increasing CO₂ resulted in a 28% decrease in the leaf litter pool predicted by the original model in response to 95 years of climate change, and a 16% increase (with the range of a 10% to a 23% increase) in the leaf litter pool predicted by the calibrated model (Fig. 5c). The counter-intuitive response of the leaf litter pool to decreasing litter quality in the original model was due to a larger rate of change in the numerator of the Eq. 5 than in its denominator. Overall, unlike the original model, the calibrated model simulated a negative feedback of leaf litter to changing climate, which was amplified by CO₂-induced decrease in litter quality.

Increasing atmospheric CO₂ concentration leads to the reduction of litter quality, however the effect of the latter on litter decomposition remains controversial (Norby et al. 2001). Some experiments revealed that CO₂-induced decrease in litter quality decreased litter turnover rates and caused litter mass accumulation (Cotrufo et al. 1994, Cotrufo and Ineson 1996), others showed that decrease in litter quality might increase or have no effect on litter decomposition rate (Coûteaux et al. 1999, Finzi and Schlesinger 2002). The neutral or even positive effect of decreasing litter quality on its turnover rate may be caused by increases in fungi-to-bacteria ratio in response to elevated CO₂ (Carney et al. 2007). The varying reports of CO₂ effect on litter turnover rates along with the evidence of significant effect of microbial community shifts on organic matter decomposition indicates the need of adjustments to the first-order decay models to account for microbial community dynamics.

We calibrated a leaf litter decomposition

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model against the global observed leaf litter turnover rate dataset using a Bayesian MCMC approach. Our results indicated that model calibration substantially improved model performance; lignin-to-nitrogen ratio was a better predictor of litter quality limitation of decomposition than litter lignin content; and that predictability of the leaf litter turnover rates decreased with decreasing annual precipitation and increasing temperatures. The posterior parameter uncertainties, when propagated in time under RCP8.5 scenario, resulted in a range of a 0.26 Pg C loss to a 1.99 Pg C gain in leaf litter pool in response to 95 years of climate change. Assuming that litter quality will decrease under increasing atmospheric CO₂ increased the leaf litter pool by 2.5 Pg C to 6.1 Pg C after 95 years of climate change.

As we show in this study, data assimilation is a useful tool for carbon cycle model improvement as well as for assigning uncertainties to the model projections. Complementing the existing databases of litter decay rates with irradiance and soil moisture data will facilitate constraining and assessing the importance of effects of these environmental factors on litter decay. More data is needed on the effects of climate on microbial community compositions around the globe, and the effect of the latter on organic matter turnover. Assimilating these data into carbon cycle models will constrain C cycle feedbacks to changing climate and provide confidence in the carbon budget predictions, facilitating effective management of the natural resources.

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LITERATURE CITED

- Aber, J. D., J. M. Melillo, and C. A. McClaugherty. 1990. Predicting long-term patterns of mass-loss, nitrogen dynamics, and soil organic matter formation from initial fine litter chemistry in temperate forest ecosystems. Canadian Journal of Botany 68:2201–2208.
- Adair, E. C., W. J. Parton, S. J. Del Grosso, W. L. Silver, M. E. Harmon, S. A. Hall, I. C. Burke, and S. C. Hart. 2008. Simple three-pool model accurately describes patterns of long-term litter decomposition in diverse climates. Global Change Biology 14:2636–2660.
- Austin, A. T., and C. L. Ballaré. 2010. Dual role of lignin in plant litter decomposition in terrestrial ecosystems. Proceedings of the National Academy of Sciences 107:4618–4622.
- Ayres, E., H. Steltzer, B. L. Simmons, R. T. Simpson, J. M. Steinweg, M. D. Wallenstein, N. Mellor, W. J. Parton, J. C. Moore, and D. H. Wall. 2009. Homefield advantage accelerates leaf litter decomposition in forests. Soil Biology and Biochemistry 41:606–610.
- Beare, M. H., R. W. Parmelee, P. F. Hendrix, W. Cheng, D. C. Coleman, and D. A. Crossley, Jr. 1992. Microbial and faunal interactions and effects on litter nitrogen and decomposition in agroecosystems. Ecological Monographs 62:569–591.
- Carney, K. M., B. A. Hungate, B. G. Drake, and J. P. Megonigal. 2007. Altered soil microbial community at elevated CO₂ leads to loss of soil carbon. Proceedings of the National Academy of Sciences 104:4990–4995.
- Cortez, J. 1998. Field decomposition of leaf litters: relationships between decomposition rates and soil moisture, soil temperature and earthworm activity. Soil Biology and Biochemistry 30:783–793.
- Cotrufo, M. F., and P. Ineson. 1996. Elevated CO₂ reduces field decomposition rates of *Betula pendula* (Roth.) leaf litter. Oecologia 106:525–530.
- Cotrufo, M. F., P. Ineson, and A. P. Rowland. 1994. Decomposition of tree leaf litters grown under elevated CO₂: Effect of litter quality. Plant and Soil 163:121–130.
- Coûteaux, M.-M., C. Kurz, P. Bottner, and A. Raschi. 1999. Influence of increased atmospheric CO₂ concentration on quality of plant material and litter decomposition. Tree Physiology 19:301–311.
- Coûteaux, M.-M., M. Mousseau, M.-L. Célérier, and P. Bottner. 1991. Increased atmospheric CO₂ and litter quality: decomposition of sweet chestnut leaf litter with animal food webs of different complexities. Oikos 61:54–64.
- Esser, G., I. Aselmann, and H. Lieth. 1982. Modelling the carbon reservoir in the system compartment 'litter'. Mitteilungen aus dem Geologisch-Palaonto-

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logischen Institut der Universitat at Hamburg, SCOPE/UNEP Sonderband Heft 52:39–58.

- Falkowski, P., R. J. Scholes, E. Boyle, J. Canadell, D. Canfield, J. Elser, N. Gruber, K. Hibbard, P. Högberg, S. Linder, F. T. Mackenzie, B. Moore III, T. Pedersen, Y. Rosenthal, S. Seitzinger, V. Smetacek, and W. Steffen. 2000. The global carbon cycle: a test of our knowledge of earth as a system. Science 290:291–296.
- Finzi, A. C., and W. H. Schlesinger. 2002. Species control variation in litter decomposition in a pine forest exposed to elevated CO₂. Global Change Biology 8:1217–1229.
- Foley, J. A., M. H. Costa, C. Delire, N. Ramankutty, and P. Snyder. 2003. Green surprise? How terrestrial ecosystems could affect earth's climate. Frontiers in Ecology and the Environment 1:38–44.
- Fung, I. Y., S. C. Doney, K. Lindsay, and J. John. 2005. Evolution of carbon sinks in a changing climate. Proceedings of the National Academy of Sciences USA 102:11201–11206.
- Gelman, A., G. Roberts, and W. Gilks. 1996. Efficient metropolis jumping hules. Bayesian Statistics 5:599–608.
- Gelman, A., and D. B. Rubin. 1992. Inference from iterative simulation using multiple sequences. Statistical Science 7:457–511.
- Gholz, H. L., D. A. Wedin, S. M. Smitherman, M. E. Harmon, and W. J. Parton. 2000. Long-term dynamics of pine and hardwood litter in contrasting environments: toward a global model of decomposition. Global Change Biology 6:751–765.
- Haario, H., E. Saksman, and J. Tamminen. 2001. An adaptive Metropolis algorithm. Bernoulli 7(2):223– 242.
- Hararuk, O., J. Xia, and Y. Luo. 2014. Evaluation and improvement of a global land model against soil carbon data using a Bayesian MCMC method. Journal of Geophysical Research: Biogeosciences 119:403–417.
- Harmon, M. E., W. L. Silver, B. Fasth, H. U. A. Chen, I. C. Burke, W. J. Parton, S. C. Hart, Currie, W. S. and Lidet.2009. Long-term patterns of mass loss during the decomposition of leaf and fine root litter: an intersite comparison. Global Change Biology 15:1320–1338.
- Harmon, R. and P. Challenor. 1997. A Markov chain Monte Carlo method for estimation and assimilation into models. Ecological Modelling 101:41–59.
- Hobbie, S. E. 1996. Temperature and plant species control over litter decomposition in Alaskan tundra. Ecological Monographs 66:503–522.
- Hobbie, S. E., J. P. Schimel, S. E. Trumbore, and J. R. Randerson. 2000. Controls over carbon storage and turnover in high-latitude soils. Global Change Biology 6:196–210.
- Houghton, J. T., Y. Ding, D. J. Griggs, M. Noguer, P. J.

van der LINDEN, X. Dai, K. Maskell, and C. Johnson. 2001. Climate change 2001: the scientific basis. Cambridge University Press, Cambridge, UK.

- Keenan, T. F., E. Davidson, A. M. Moffat, W. Munger, and A. D. Richardson. 2012. Using model-data fusion to interpret past trends, and quantify uncertainties in future projections, of terrestrial ecosystem carbon cycling. Global Change Biology 18:2555–2569.
- Keppel-Aleks, G., J. T. Randerson, K. Lindsay, B. B. Stephens, J. Keith Moore, S. C. Doney, P. E. Thornton, N. M. Mahowald, F. M. Hoffman, C. Sweeney, P. P. Tans, P. O. Wennberg, and S. C. Wofsy. 2013. Atmospheric carbon dioxide variability in the community earth system model: evaluation and transient dynamics during the twentieth and twenty-first centuries. Journal of Climate 26:4447–4475.
- King, J., L. Brandt, and E. C. Adair. 2012. Shedding light on plant litter decomposition: advances, implications and new directions in understanding the role of photodegradation. Biogeochemistry 111:57–81.
- Kirschbaum, M. U. F. and K. I. Paul. 2002. Modelling C and N dynamics in forest soils with a modified version of the CENTURY model. Soil Biology and Biochemistry 34:341–354.
- Lawrence, C. R., J. C. Neff, and J. P. Schimel. 2009. Does adding microbial mechanisms of decomposition improve soil organic matter models? A comparison of four models using data from a pulsed rewetting experiment. Soil Biology and Biochemistry 41:1923–1934.
- Lawrence, D. M., K. W. Oleson, M. G. Flanner, C. G. Fletcher, P. J. Lawrence, S. Levis, S. C. Swenson, and G. B. Bonan. 2011. The CCSM4 land simulation, 1850–2005: assessment of surface climate and new capabilities. Journal of Climate 25:2240–2260.
- Lee, H., J. Fitzgerald, D. B. Hewins, R. L. McCulley, S. R. Archer, T. Rahn, and H. L. Throop. 2014. Soil moisture and soil-litter mixing effects on surface litter decomposition: A controlled environment assessment. Soil Biology and Biochemistry 72:123– 132.
- Liu, L., J. S. King, and C. P. Giardina. 2005. Effects of elevated concentrations of atmospheric CO₂ and tropospheric O₃ on leaf litter production and chemistry in trembling aspen and paper birch communities. Tree Physiology 25:1511–1522.
- Luo, Y., K. Ogle, C. Tucker, S. Fei, C. Gao, S. LaDeau, J. S. Clark, and D. S. Schimel. 2011. Ecological forecasting and data assimilation in a data-rich era. Ecological Applications 21:1429–1442.
- Luo, Y., E. Weng, X. Wu, C. Gao, X. Zhou, and L. Zhang. 2009. Parameter identifiability, constraint, and equifinality in data assimilation with ecosys-

tem models. Ecological Applications 19:571-574.

- Marshall, L., D. Nott, and A. Sharma. 2004. A comparative study of Markov chain Monte Carlo methods for conceptual rainfall-runoff modeling. Water Resources Research 40:W02501.
- Matthews, E. 1997. Global litter production, pools, and turnover times: Estimates from measurement data and regression models. Journal of Geophysical Research: Atmospheres 102:18771–18800.
- Melillo, J. M., J. D. Aber, and J. F. Muratore. 1982. Nitrogen and lignin control of hardwood leaf litter decomposition dynamics. Ecology 63:626.
- Mosegaard, K., and M. Sambridge. 2002. Monte Carlo analysis of inverse problems. Inverse Problems 18:R29–R54.
- Norby, R. J., M. F. Cotrufo, P. Ineson, E. G. O'Neill, and J. G. Canadell. 2001. Elevated CO₂, litter chemistry, and decomposition: a synthesis. Oecologia 127:153–165.
- O'Neill, E. G., and R. J. Norby. 1996. Litter quality and decomposition rates of foliar litter produced under CO₂ enrichment. Pages 87–103 *in* G. W. Koch and H. A. Mooney, editors. Carbon dioxide and terrestrial ecosystems. Academic Press, San Diego, California, USA.
- Olson, J. S. 1963. Energy storage and balance of producers and decomposers in ecological systems. Ecology 44:322.
- Parton, W. J., D. S. Schimel, C. V. Cole, and D. S. Ojima. 1987. Analysis of factors controlling soil organic matter levels in Great Plains grasslands. Soil Science Society of America Journal 51:1173–1179.
- Potter, C. S., J. T. Randerson, C. B. Field, P. A. Matson, P. M. Vitousek, H. A. Mooney, and S. A. Klooster. 1993. Terrestrial ecosystem production: A process model based on global satellite and surface data. Global Biogeochemical Cycles 7:811–841.
- Riutta, T., E. M. Slade, D. P. Bebber, M. E. Taylor, Y. Malhi, P. Riordan, D. W. Macdonald, and M. D. Morecroft. 2012. Experimental evidence for the interacting effects of forest edge, moisture and soil macrofauna on leaf litter decomposition. Soil Biology and Biochemistry 49:124–131.
- Shaw, M. R., and J. Harte. 2001. Control of litter decomposition in a subalpine meadow-sagebrush steppe ecotone under climate change. Ecological Applications 11:1206–1223.
- Smith, W. K., W. E. I. Gao, H. Steltzer, M. D. Wallenstein, and R. Tree. 2010. Moisture availability influences the effect of ultraviolet-B radiation on leaf litter decomposition. Global Change Biology 16:484–495.

- Smyth, C., J. Trofymow, W. Kurz, and CIDET Working Group. 2009. Decreasing uncertainty in CBM-CFS3 estimates of forest soil C sources and sinks through use of long-term data from the Canadian Intersite Decomposition Experiment. Information Report BC-X-422. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Victoria, British Columbia, Canada. http://www.cfs.nrcan. gc.ca/publications/?id=31205
- Stump, L. M., and D. Binkley. 1993. Relationships between litter quality and nitrogen availability in Rocky Mountain forests. Canadian Journal of Forest Research 23:492–502.
- Taylor, B. R., D. Parkinson, and W. F. J. Parsons. 1989. Nitrogen and lignin content as predictors of litter decay rates: a microcosm test. Ecology 70:97–104.
- Vogt, K. A., C. C. Grier, and D. J. Vogt. 1986. Production, turnover, and nutrient dynamics of above- and belowground detritus of world forests. Pages 303–377 in A. MacFadyen and E. D. Ford, editors. Advances in ecological research. Academic Press, New York, New York, USA.
- Wang, C., G. Han, Y. Jia, X. Feng, and X. Tian. 2012. Insight into the temperature sensitivity of forest litter decomposition and soil enzymes in subtropical forest in China. Journal of Plant Ecology 5:279– 286.
- Wieder, W. R., C. C. Cleveland, and A. R. Townsend. 2009. Controls over leaf litter decomposition in wet tropical forests. Ecology 90:3333–3341.
- Williams, M., P. A. Schwarz, B. E. Law, J. Irvine, and M. R. Kurpius. 2005. An improved analysis of forest carbon dynamics using data assimilation. Global Change Biology 11:89–105.
- Xia, J., Y. Luo, Y. P. Wang, and O. Hararuk. 2013. Traceable components of terrestrial carbon storage capacity in biogeochemical models. Global Change Biology 19:2104–2116.
- Xu, T., L. White, D. Hui, and Y. Luo. 2006. Probabilistic inversion of a terrestrial ecosystem model: Analysis of uncertainty in parameter estimation and model prediction. Global Biogeochemical Cycles 20:GB2007.
- Zhang, D., D. Hui, Y. Luo, and G. Zhou. 2008. Rates of litter decomposition in terrestrial ecosystems: global patterns and controlling factors. Journal of Plant Ecology 1:85–93.
- Zhou, G., L. Guan, X. Wei, X. Tang, S. Liu, J. Liu, D. Zhang, and J. Yan. 2008. Factors influencing leaf litter decomposition: an intersite decomposition experiment across China. Plant and Soil 311:61– 72.