Pervasive decreases in living vegetation carbon turnover time across forest climate zones

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Forests play a major role in the global carbon cycle. Previous studies on the capacity of forests to sequester atmospheric CO2 have mostly focused on the role of carbon turnover and its spatiotemporal changes remain poorly understood. Here, we used long-term inventory data (1955 to 2018) from 695 mature forest plots to quantify temporal trends in living vegetation carbon turnover time across tropical, temperate, and cold climate zones, and compared plot data to 8 Earth system models (ESMs). Long-term plots consistently showed decreases in living vegetation carbon turnover time, likely driven by increased tree mortality across all major climate zones. Changes in living vegetation carbon turnover time were negatively correlated with CO2 enrichment in both forest plot data and ESM simulations. However, plot-based correlations between living vegetation carbon turnover time and climate drivers such as precipitation and temperature diverged from those of ESM simulations. Our analyses suggest that forest carbon sinks are likely to be constrained by a decrease in living vegetation carbon turnover time, and accurate projections of forest carbon sink dynamics will require an improved representation of tree mortality processes and their sensitivity to climate in ESMs.

Significance

With a limited understanding of spatiotemporal trends of carbon turnover time and its drivers, we are unable to quantify future changes in the forest carbon sink strength. By comparing long-term forest plot data and Earth system model (ESM) projections, we found a pervasive increase in carbon loss from tree mortality, likely driving declines in living aboveground vegetation carbon turnover time across forest climate zones. The climate correlations between temperature or precipitation and temporal trends of living vegetation carbon turnover time differed between forest plots and ESMs. Our results indicate that a mechanistic representation of tree mortality in ESMs and its sensitivity to climate is a crucial uncertainty in predicting the future forest carbon sink.
mortality and thus influence aboveground living vegetation carbon turnover time (see Eq. 3 in Materials and Methods) (8, 11). However, the large-scale effects of these environmental drivers on living vegetation carbon turnover time are poorly quantified. Studies in tropical forests suggest that CO₂ fertilization not only favors tree growth and productivity but also might accelerate rates of tree mortality, which may thus lead to shorter turnover time of vegetation carbon (12). Earth system models (ESMs) were found to consistently underestimate the spatial correlations of the hydrological cycle (i.e., precipitation) with carbon turnover time (7). Critically, however, climatic correlations in space do not necessarily indicate climate change-induced temporal changes in carbon turnover (9, 13).

We applied a dynamic approach to calculate instantaneous living vegetation carbon turnover time (Materials and Methods) and used linear mixed-effects models to quantify temporal trends and correlations with atmospheric CO₂, precipitation, and temperature across forest climate zones. Using this dynamic approach (8), a previous study reported divergent predictions of temporal trends of vegetation carbon turnover time across global vegetation models, and indicated that vegetation carbon turnover time is a major uncertainty for carbon sinks in terrestrial ecosystems with climate change. However, because long-term data for vegetation carbon stocks and NPP are scarce in continental-scale forest inventories (10), studies of temporal changes in the turnover time of vegetation carbon using a dynamic approach have not been estimated using observational data. To this end, we compiled a long-term dataset of mature, largely unmanaged (SI Appendix) forest plots spanning from 1955 to 2018 that contained at least 3 censuses across tropical (n = 128), temperate (n = 87), and cold climate zones (n = 480) in South and North America and Europe that have been minimally disturbed by humans (Fig. 1 and SI Appendix, Table S1, and Dataset S1). We further compared the emergent patterns of aboveground living vegetation carbon turnover time from the forest plots to estimates of living vegetation carbon turnover time from long-term remote sensing data of NPP and aboveground vegetation carbon stock from 1993 to 2011 (14, 15), as well as from 8 ESMs from phase 5 of the Coupled Model Intercomparison Project (CMIP5).

Results and Discussion

The forest plot data provide cross-climate zone estimates of the temporal trends in growth (mainly aboveground wood production), carbon loss from mortality, and carbon turnover time of aboveground living vegetation of undisturbed forests. We found an increase in both carbon losses (1.9%, 2%, 0.9% per year) and a decrease of aboveground living vegetation carbon turnover time (~2.3%, ~2.7%, ~2% per year) across tropical, temperate, and cold climate zones, respectively (Fig. 2 and SI Appendix, Fig. S1). Decreases in aboveground living vegetation carbon turnover time were significant even when accounting for differences in stand density (forest basal area) and forest successional status or age (16) (SI Appendix, Figs. S2 and S3). As an exploratory analysis, we calculated living vegetation carbon turnover time using satellite remote sensing estimates of growth (NPP) and carbon stocks (Materials and Methods) (14, 15) and found the decreasing trends in living vegetation carbon turnover time that were generally consistent with forest plot data in most but not all analyses (SI Appendix, Figs. S4 and S5). However, given the limitations in current estimates of living vegetation carbon turnover time from satellite remote-sensing data, including a relatively short time range, uncertainty in productivity and carbon stocks trends, and challenges in accounting for the potential effects of CO₂ fertilization on productivity (see Materials and Methods and SI Appendix for details), we primarily focus on estimating the emergent patterns from forest plot data and comparing these observational estimates to simulations in 8 ESMs from CMIP5.

Comparing temporal trends in plot data to ESMs, ESMs displayed generally consistent trends with forest plot data, with both datasets showing positive trends in carbon loss from mortality, and negative trends in living vegetation carbon turnover time across climate zones (Figs. 2 and 3 and SI Appendix, Figs. S6 and S7). The estimated temporal trends (mean ± 1 SE after a natural log transformation: ~2.2 ± 0.4% per year) in living vegetation carbon turnover time at pan biome scale, however, were greater in forest plot data, compared to ESMs with mean values of negative trends ranging across the 8 models from ~0.5 to 0% per year after the same natural log transformation (Figs. 2 and 3 and SI Appendix, Figs. S1 and S7). This suggests that ESMs likely underestimate the negative trends of living vegetation carbon turnover time, although we note that our forest plots are not spatially comprehensive across the globe. Furthermore, it is important to note that forest plot data and ESM-estimated growth are not completely analogous. Growth was quantified as increment of mainly aboveground wood vegetation carbon including components of recruitment of new trees and growth of surviving trees in forest plot data; in the ESMs, growth (NPP) was calculated as total vegetation carbon (all plant tissues and aboveground plus belowground components), and thus living vegetation carbon turnover refers to all vegetation carbon. However, a sensitivity test using ESM estimates of aboveground NPP and vegetation carbon stocks (available in IPSL-CM5A-MR) showed no meaningful difference with estimates of total NPP and vegetation carbon stocks (SI Appendix, Fig. S8).

While ESM trends were generally consistent with those of forest plot data, we further sought to quantify the variation among ESMs. To this end, range (Fig. 3A) and coefficient of variation (CV) (Fig. 3B) were used to quantify the variations among ESMs in predictions of temporal changes in NPP, carbon loss, and living vegetation carbon turnover time. ESMs generally indicated a negative trend and a relatively low value (~1) of CV in living vegetation carbon turnover time across all forest climate zones except cold forests (Fig. 3A and B and SI Appendix, Fig. S7). ESM-simulated NPP exhibited an increasing trend and a relatively low CV (<0.6) across all forest climate zones except tropical forests (Fig. 3B and SI Appendix, Figs. S6 and S7). Collectively, these results suggest that ESM simulations differ in projections of temporal changes in living vegetation carbon turnover in cold forests and NPP in tropical forests. Temporal trends in living vegetation carbon turnover time for future climatic scenarios (2006 to 2100) showed similar signs as historical simulations (1971 to 2005) but were more uncertain, particularly for temperate and cold climate zones.
Figure 2. Living vegetation carbon turnover time decreases across forest climate zones as observed by forest plot data. Temporal trend of growth (in kilograms per square meter per year), carbon stock (in kilograms per square meter), carbon loss (in kilograms per square meter per year), and aboveground living vegetation carbon turnover time (in years) quantified by forest plot data ranging from 1955 to 2018 over at least 3 censuses across tropical (n = 128), temperate (n = 87), and cold (n = 480) climate zones. Data were natural log-transformed before analysis. Temporal trends were quantified by linear mixed-effect models accounting for each plot in each forest climate zone as a random effect. The y axes are coefficients of the independent variable (time) ± 95% CIs. Coefficient estimate of each variable refers to proportional change per year when data are log-transformed. Percent change per year in each variable was quantified as follows: \( \exp (\beta - 1) \times 100 \), where \( \beta \) is the coefficient estimate.

Figure 3. ESMs show a pervasive decrease of historical living vegetation carbon turnover time across forest climate zones but with large cross-model differences. (A) Historical (1971 to 2005) and future (2006 to 2100) temporal trends in living vegetation carbon turnover time across forest climate zones quantified by the 8 ESMs (CanESM2, CCSM4, GFDL-ESM2G, HadGEM2-ES, IPSL-CM5A-MR, MIROC-ESM, MPI-ESM-LR, NorESM1-M) from phase 5 of the Coupled Model Intercomparison Project (CMIP5). Temporal trends were quantified by linear mixed-effect models accounting for pixel in each forest climate zone as a random effect. Data were natural log-transformed before analysis. The y axes are the minimum, mean, and maximum of the temporal trend of carbon turnover time across 8 ESMs. (B) Coefficient of variance quantified as the ratio of the SD to the absolute value of mean across the 8 ESMs in CMIP5 while predicting historical and future temporal trends in log-transformed values of NPP and living vegetation carbon turnover time across forest climate zones. (C) Global patterns of historical (1971 to 2005) percent change of living vegetation carbon turnover time quantified by the ensemble mean of the 8 ESMs in CMIP5. Percent change is quantified as an increase or reduction (percentage) per year relative to initial value at year 1971. The temporal trend was quantified by a linear regression model and expressed as coefficient of the independent variable (time).
atmospheric CO₂ concentrations were strongly and negatively correlated with living vegetation carbon turnover time across multiple climate zones (Fig. 4E) and positively correlated with growth and carbon loss associated with plant mortality (Fig. 4A and C) (26, 27, 29). We emphasize, however, that this correlation of living vegetation carbon turnover time and CO₂ does not necessarily imply causation, as it could arise from 2 concurrent trends. Thus, further research is needed to examine potential mechanistic links between faster growth and decreased living vegetation carbon turnover time.

Decreased precipitation was correlated with increased carbon loss (tree mortality), and thus decreased carbon turnover time is significant in cold forests in forest plot data (Fig. 4 C and E) when accounting for other potential drivers, consistent with previous studies (30, 31). At the plant community scale, increased growth under resource (CO₂, precipitation, or temperature) enrichment could potentially lead to biomass accumulation and higher water usage, thereby increasing drought stress and plant mortality associated with competition for limited soil water resources in drought years (32). Similarly, we observed the positive influences of rainfall variability on carbon loss, thereby decreasing living vegetation carbon turnover time in cold forests (SI Appendix, Fig. S13). These patterns related to precipitation are robust to considering an estimate of plant competition (i.e., basal area) (SI Appendix, Fig. S14) (33). At climate zone scale, the impacts of rising temperature on dampening forest growth, increasing mortality, and thus decreasing carbon turnover are evident in temperate forests but not in cold forests (Fig. 4A, C, and E), even when accounting for an estimate of competition (SI Appendix, Fig. S14).

Evaluating ESM climate correlations compared to those of forest plots, ESMs exhibited similar temporal trends in their simulated responses of living vegetation carbon turnover time to rising CO₂ concentrations (Fig. 4F and SI Appendix, Fig. S15). The order of magnitude in the standardized coefficients between climate variables (precipitation and temperature) and temporal trends of NPP, carbon loss from mortality, and living vegetation carbon turnover was comparable between forest plot data and ESMs (Fig. 4 and SI Appendix, Fig. S15). In contrast to the forest plot data, however, ESMs predicted much lower correlations in temporal trends of NPP, carbon loss from mortality, and living vegetation carbon turnover with CO₂ (Fig. 4 and SI Appendix, Fig. S15). Positive associations between precipitation and NPP and precipitation and carbon loss, leading to a negative relationship between living vegetation carbon turnover time and precipitation, were observed across tropical and temperate climate zones in ESMs, which was in contrast to the forest plot data (Fig. 4). In cold forests, the impacts of precipitation on NPP, carbon loss, and living vegetation carbon turnover time from forest plot data also largely diverged from those in ESMs (Fig. 4B, D, and F). Temperature dampened growth (Fig. 4B) and thus increased living vegetation carbon turnover time (Fig. 4F), except in cold forests with higher growth in a warmer climate (34). Collectively, these results appear to suggest that, in ESMs, the factors that favor growth also accelerate carbon loss, thus leading to the decrease in living vegetation carbon turnover time, whereas the climate influences on mortality are more complex and multifaceted in forest plot data. Indeed, our analysis shows strong and positive correlations between growth and mortality and carbon stock across climate zones in ESMs (SI Appendix, Fig. S16), which are not observed in forest plot data (SI Appendix, Fig. S17). This strong association is likely because ESMs poorly represent carbon loss (tree mortality), frequently as a static process via a background rate (10, 13) or function of forest growth or carbon stock.

Our study quantifies the temporal changes in living vegetation carbon turnover time, which are highly relevant to evaluate the impacts of climate change. Previous studies using a steady-state approach that examined the spatial relationships of carbon turnover time with climate found that ESMs consistently underestimated the impacts of the hydrological cycle (precipitation) (7). Our forest plot data suggest that living vegetation carbon turnover strongly increases with precipitation in cold forests, potentially because of lower rates of tree mortality in wetter regions (30, 31). ESMs, however, predict an opposite pattern, likely because of the simplified processes of carbon loss (tree mortality and other disturbances) (13, 24). Our forest plot data, however, show the weak dependence of temporal trends in living vegetation carbon turnover time on temperature in cold forests or show a negative correlation between these 2 in temperate forests, which is generally not observed in ESMs.

By analyzing long-term forest plot data and ESMs, we documented pervasive declines in living vegetation carbon turnover time across multiple climate zones. Given that we consider only living vegetation carbon here, we note that disturbance and decomposition dynamics will be critical in quantifying the net exchange of carbon between the biosphere and atmosphere on the scale of years to decades. Our study also found little spatial coherence among models and observations, highlighting a key knowledge gap in understanding the spatial patterns of changes in living vegetation carbon turnover time. Our results further highlight that the beneficial effects of CO₂ fertilization on the terrestrial carbon sink may be transitory due to the accelerating mortality, particularly in a changing climate with increased risks of drought. Collectively, our findings suggest that a better understanding and representation of tree mortality processes in ESMs is central to constrain future forest carbon sinks and their feedbacks to climate in the 21st century.
Materials and Methods

Quantification of Living Vegetation Carbon Turnover Time. We quantified living vegetation carbon turnover time (τ) across forest climate zones based on a previously established approach (8, 11), where changing vegetation carbon stock (dCS/dt) over time (dt) is determined by changes in growth and the turnover time of carbon in living vegetation:

\[
\frac{dCS}{dt} = \text{Growth} \cdot CS - \tau. \quad [1]
\]

Changes in vegetation carbon stock (CS) can equivalently be modeled as follows:

\[
\frac{dCS}{dt} = \text{Growth} - \text{carbon loss}, \quad [2]
\]

where carbon loss is flux of vegetation carbon out of living vegetation pools. Assuming no human disturbance, aboveground living vegetation carbon loss is primarily associated with tree mortality.

By rearranging Eqs. 1 and 2, we have the following:

\[
\tau = \frac{CS}{\text{carbon loss}}. \quad [3]
\]

Thus, Eq. 3 divides a time-varying stock over a time-varying outflux (woody mortality flux) to quantify the instantaneous living vegetation carbon turnover time (35). We note that growth refers to mainly aboveground wood production in forest plots and thus τ represents the aboveground living vegetation carbon turnover time, while in ESMs growth is NPP including belowground components and τ refers to carbon turnover time by total living vegetation. We also caution that one should not interpret τ quantified in this study as the amount of time carbon resides in terrestrial living vegetation at equilibrium state because the ecosystem is not indeed in a steady state (35). Rather, τ is an instantaneous rate of carbon loss normalized by the carbon stock (technically the inverse of the rate). It quantifies the timescale for the aboveground vegetation carbon stock to be depleted at the rate of woody mortality flux. This approach of using woody mortality flux does not include short-term phenological turnover (i.e., leaf and root turnover), since this study focuses on multiannual changes in aboveground vegetation. This dynamic approach considering carbon losses has advantages over using the input as the flux to calculate τ (13) because the growth-based vegetation carbon turnover time generated (i.e., τ = CS/growth) quantifies the timescale for replenishment of the current carbon pool, which includes leaves and roots, and because tree mortality rate and longevity are increasingly realized as critical controls of vegetation carbon stocks and turnover (12, 27, 28). The approach of using outflux is also a reasonable way to compare with forest plot observations, where woody mortality flux is directly measured. We note, however, that our study only quantified one of the key carbon turnover times, which is primarily affected by woody mortality flux. Indeed, turnover rate of leaves and roots, carbon allocation to leaves and roots, and decomposition of litterfall also influence the overall vegetation carbon turnover time when we consider the total vegetation pool including litterfall and belowground components.

Eqs. 1–3 can be solved at different spatial scales. Previous studies have aggregated vegetation carbon stock and NPP on global scale to quantify vegetation carbon turnover time (8) (see SI Appendix for details). However, this method may misrepresent critical local scale processes that have been found to compensate locally and thus damp the patterns of carbon cycle observed on large (global) scale (36). Thus, we quantified carbon turnover time on local scale (in each forest plot or grid cell) and then used a linear mixed model to quantify the temporal trend of carbon turnover time in each forest climate zone (tropical, temperate, and cold) using linear mixed-effects models in which each plot or pixel in each forest climate zone was treated as a random effect: (tropical, temperate, and cold climate zones, respectively) to global scale was used as weighting coefficients (39). The temporal trends of growth, carbon loss, and vegetation carbon turnover time and its association with climate were not affected by other factors such as competition and forest succession and spatial autocorrelations. More information about testing the influences of these factors are provided in SI Appendix.

Statistical Analysis. We evaluated trends over time in growth, carbon stock, carbon loss, and living vegetation carbon turnover time in each forest climate zone (tropical, temperate, and cold) using linear mixed-effects models in which each plot or pixel in each forest climate zone was treated as a random effect:

\[
\log\{\text{Variable}_{ij}\} = \beta_0 + \beta_1 \tau_j + \beta_2 c_i + \epsilon_{ij}, \quad [4]
\]

where i refers to plot or pixel; j is census interval; the dependent “Variable” refers to either growth, carbon stock, carbon loss, or carbon turnover time; τj is the time of the jth plot and the jth census interval and quantified as mean value of time between consecutive time steps j and j + 1; β1 is the standardized fixed effect associated with an individual model parameter; β2 represent the random effect of the jth plot; and ε is random error, which is assumed to follow a normal distribution with mean zero and SD ε. For forest plot data, data of growth (mainly aboveground wood production), carbon stock, carbon loss, and aboveground living vegetation carbon turnover time were natural log-transformed to meet the requirement of normal distribution of residual in linear mixed models. For remote sensing and ESMs that had long-term and annual time series of data, we used 2 approaches (see SI Appendix for details).

We evaluated the association between growth, carbon stock, carbon loss, or carbon turnover time and CO2 concentration (CO2), total annual precipitation (P), and mean annual temperature (TAS) in forest plot data and ESMs. We have the following:

\[
\log\{\text{Variable}_{ij}\} = \beta_0 + \beta_1 \text{CO2}_i + \beta_2 \text{P}_i + \beta_3 \text{TAS}_i + b_i + \epsilon_{ij}, \quad [5]
\]

where parameters were identical to Eq. 4 and the dependent variables were natural log-transformed before analysis. Nitrogen deposition, which could influence forest growth at local and regional scales, is not expected to change the observed relationships between vegetation carbon turnover and climate over our entire plot sample because many of our forest plots (i.e., most all plots in tropical regions and much of the North American cold forest plots) are generally located in low nitrogen deposition zones (38).

In all of the analysis on temporal trends and their associations with climate variables, when investigating the patterns in global forests, the ratio of total aboveground vegetation carbon stock in each forest climate zone (0.55, 0.32, and 0.14 in tropical, temperate, and cold climate zone, respectively) to global scale was used as weighting coefficients (39). The temporal trends of growth, carbon loss, and vegetation carbon turnover time and its association with climate were not affected by other factors such as competition and forest succession and spatial autocorrelations. More information about testing the influences of these factors are provided in SI Appendix.

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