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Forests play a major role in the global carbon cycle. Previous studies on the capacity of forests to sequester atmospheric CO_2 have mostly focused on carbon uptake, but the roles of carbon turnover time 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 CO_2 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.

carbon cycle | carbon turnover | forest carbon stocks | forest productivity | tree mortality

Forests cover ~33% of the terrestrial surface area and play a prominent role in the global carbon cycle, sequestering roughly 25% of anthropogenic carbon emissions each year. Forests thus have the potential—via carbon–climate feedbacks—to either amplify or dampen the increasing trend in atmospheric CO_2 concentrations, and affect future climates (1, 2). The capacity of forests to sequester atmospheric CO_2 in a changing climate depends not only on the response of carbon uptake (plant productivity) but also on the timescale over which the accumulated carbon stock would theoretically be depleted by outflux (hereafter, carbon turnover time) (3–6). When considering aboveground living vegetation carbon in forests, outflux is largely dominated by tree mortality (7, 8). While decomposition dynamics influence the rate at which dead vegetation carbon enters the atmosphere, tree mortality directly affects the living vegetation carbon turnover time and thus mediates the net exchange of CO_2 between land and the atmosphere over the long term. Spatiotemporal trends of living vegetation carbon turnover time and the underlying drivers remain poorly understood (7–10), thus limiting our ability to predict forest carbon sinks and their feedbacks to climate.

Previous studies of carbon turnover time have primarily relied on the steady-state assumption that carbon stock on the land surface is not changing with time. Thus, carbon turnover time has been approximated as the ratio of the averaged carbon stock to the averaged carbon flux such as net primary productivity (NPP) (7, 9, 10). This steady-state approach has been applied to ecosystems across large spatial and temporal scales and allows for an understanding of the spatial variation of average carbon turnover time in different vegetation types/biomes and its spatial correlations with climate (7, 9, 10). However, a steady-state approach fails to capture any temporal variations in carbon turnover time that underlie forest–climate feedbacks.

Predicting future changes in the forest carbon sink requires a fundamental understanding of the drivers and mechanisms governing the changes in carbon turnover time across time and space. Ongoing environmental changes are expected to alter plant growth and mortality, carbon allocation, and species composition, all of which will affect plant carbon pools and carbon loss from

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 CO_2 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 CO_2, 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 CO_2 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.
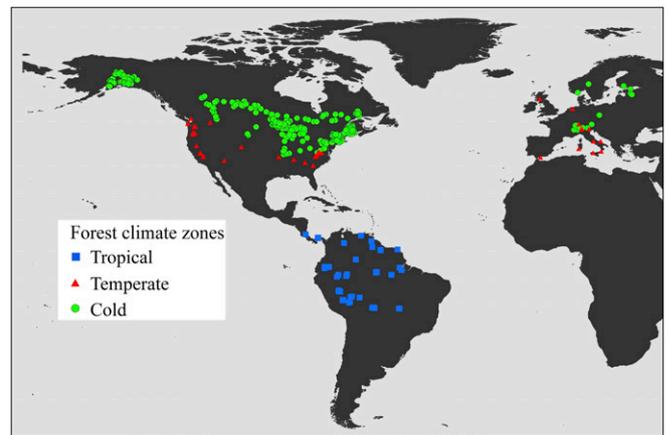
Fig. 1. Long-term forest plot data ranging from 1955 to 2018 over at least 3 censuses across tropical ($n = 128$), temperate ($n = 87$), and cold climate zones ($n = 480$) in South and North America and Europe. The forest climate zones are defined based on Köppen–Geiger climate classification.

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*A* 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*A* 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 for 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. 3*A*) and coefficient of variation (CV) (Fig. 3*B*) 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. 3 *A* 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. 3*B* 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
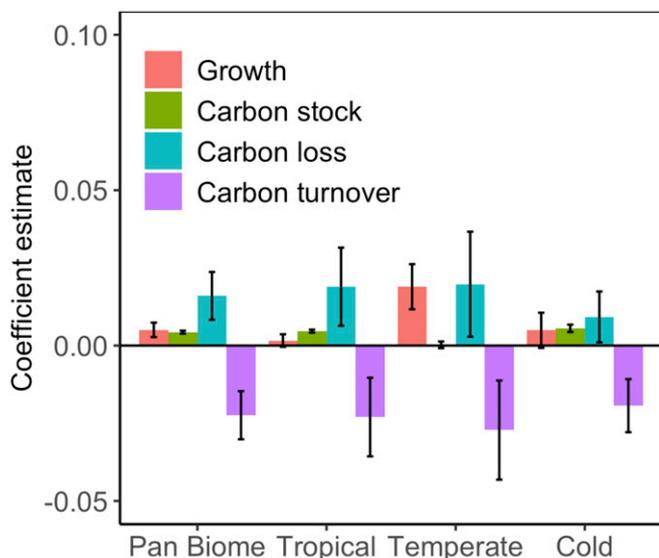
Fig. 2. Living vegetation carbon turnover time decreases across forest climate zones as observed by forest plot data. Temporal trend of growth (in kilograms per square meter per year), carbon stock (in kilograms per square meter), carbon loss (in kilograms per square meter per year), and aboveground 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) $\pm$ 95% CIs. Coefficient estimate of each variable refers to proportional change per year when data are log-transferred. Percent change per year in each variable was quantified as follows: $(\exp(\beta) - 1) * 100$, where β is the coefficient estimate.

(Fig. 3*A* and *SI Appendix*, Fig. S7). A sensitivity test that considered a historical period between 1971 and 2018 in ESMs, corresponding to the census period of the majority of forest plots (>95%) (*SI Appendix*, Fig. S9), showed very similar historical trends in simulated NPP, carbon loss, and living vegetation carbon turnover time across climate zones (*SI Appendix*, Fig. S10).

While there is generally consistency of the temporal trends in living vegetation carbon turnover time at scales of forest climate zones across forest plot data and models, we note that estimates of NPP and particularly carbon stocks used to calculate living vegetation carbon turnover time in ESMs have substantial uncertainty (13), which is reflected in our study by the large variation in temporal trends of carbon stocks across ESMs (*SI Appendix*, Fig. S6*D*), a result that is consistent with previous studies (4, 17). Forests in Africa generally showed decreasing (−2 to 0% per year) trends of living vegetation carbon turnover time, in contrast to Australian forests. Some locations showed increasing (even >2% per year) trends of living vegetation carbon turnover time, particularly in the Amazon, despite the general decreasing trends at pan biome scale. Moreover, the large spatial variations of trends in NPP, carbon stocks, carbon losses, and carbon turnover time from the remotely sensed data (*SI Appendix*, Fig. S11) were not identified by ESMs (Fig. 3*C* and *SI Appendix*, Figs. S6 and S12) and highlight key knowledge gaps in understanding the spatial patterns of changes in vegetation carbon turnover time that are essential to quantify the changes in the global forest carbon sink.

Carbon loss associated with widespread tree mortality has attracted much attention and has been documented in multiple regions in the last decade (18–20). As the dominant outflux of aboveground vegetation carbon (7, 8), increased tree mortality

likely drove the decreased living vegetation carbon turnover time across forests biomes, although changes in carbon allocation and/or species composition may play a role as well. The regrowth of human-disturbed forests could be another factor in affecting living vegetation carbon turnover time (21), but the forest plots used in this study were largely mature and unmanaged and we found no significant role of successional stages or forest age in living vegetation carbon turnover trends. Declines in living vegetation carbon turnover time associated with increased tree mortality have previously been suggested in Amazon rainforest (12). Our study compiles a dataset that spans a larger area of tropical forests but does not include tropical forests in Africa or Asia due to data limitations. With projected increases in tree mortality in a changing climate (i.e., drought and warming) (20, 22, 23), living vegetation carbon turnover time may decline further, potentially constraining forest carbon sinks under future climate scenarios.

We further investigated the degree to which atmospheric CO_2 concentrations and variations in precipitation and temperature were correlated with the temporal trends in carbon turnover time. Increased resource availability (e.g., resulting from increased CO_2) associated with global change can favor forest growth and productivity (3, 24, 25), but it may also accelerate the rate of tree mortality, reducing vegetation carbon turnover time (26, 27). This pattern of "faster growth–higher mortality–shorter carbon turnover time" has been suggested at local scales, particularly in tropical forests (12, 26, 27) and was recently demonstrated in boreal forests (28). We observed in the forest plot data that increasing
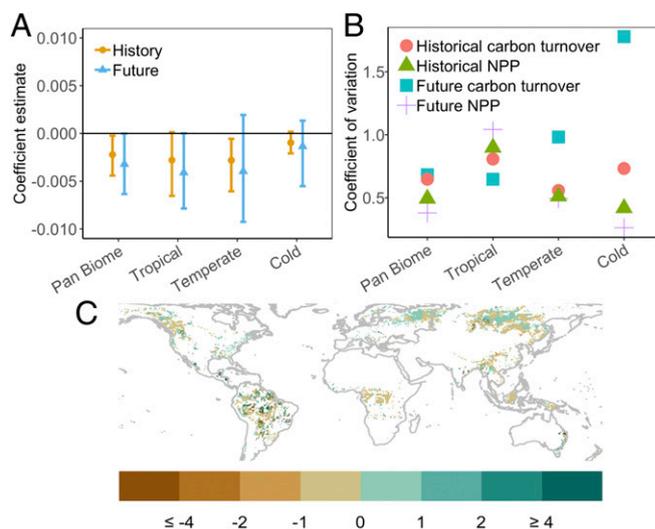
Fig. 3. ESMs show a pervasive decrease of historical living vegetation carbon turnover time across forest climate zones but with large cross-model differences. (*A*) Historical (1971 to 2005) and future (2006 to 2100) temporal trends in living vegetation carbon turnover time across forest climate zones 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 trends in the 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 $\log_e$-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 CO_2 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. 4 A and C) (26, 27, 29). We emphasize, however, that this correlation of living vegetation carbon turnover time and CO_2 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 (CO_2, 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 damping forest growth, increasing mortality, and thus decreasing carbon turnover are evident in temperate forests but not in cold forests (Fig. 4 A, 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 CO_2 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 CO_2 (Fig. 4 and *SI Appendix*, Fig. S15).

Positive relationships 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. 4 B, D, and F). Temperature damped 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
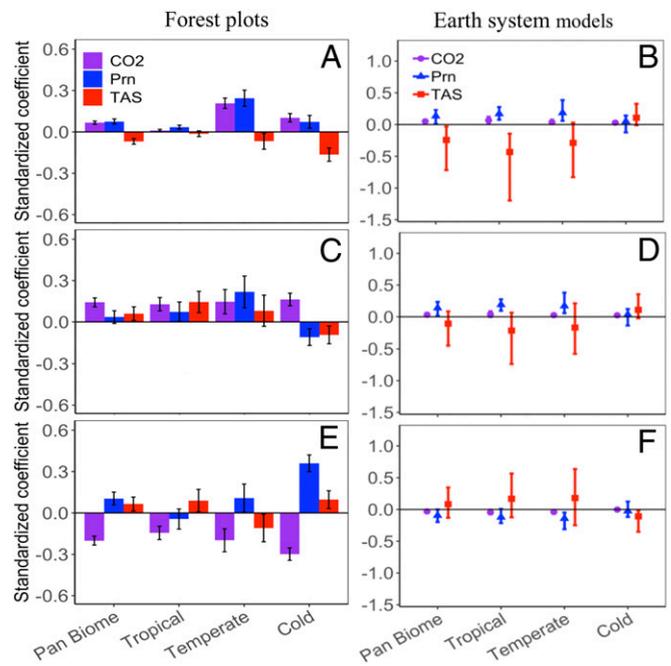
Fig. 4. The decrease in living vegetation carbon turnover time across forest climate zones is primarily associated with CO_2 fertilization. (*A, C,* and *E*) Standardized response coefficients between CO_2, precipitation (Prn), temperature (TAS), and growth (*A*), carbon loss (*C*), and aboveground living vegetation carbon turnover time (*E*) quantified for forest plot data using linear mixed models. The *y* axes are coefficients of each independent variable ± 95% CIs. (*B, D,* and *F*) Standardized response coefficients between CO_2, Prn, and TAS and NPP (*B*), carbon loss (*D*), and living vegetation carbon turnover time (*F*) for 8 ESMs using linear mixed models. The *y* axes are minimum, mean, and maximum coefficients of each independent variable in 8 ESMs. The data for NPP, carbon stock, carbon loss, and living vegetation carbon turnover time were natural log-transformed before analysis in both forest plot data and ESMs.

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 CO_2 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) over time (dt) is determined by changes in growth and the turnover time of carbon in living vegetation:

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

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 outflow (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., $\tau = CS/\text{growth}$) 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 by accounting for the random effect in each forest plot or grid cell. The Köppen–Geiger climate classification was used to determine the climate zones (i.e., tropical, temperate, and cold) of these forest plots or grid cells (37). More information on quantification of living vegetation carbon turnover time are provided in *SI Appendix*.

Data Availability. Three long-term datasets—forest plot, remote sensing, and ESMs—were used. The forest plot dataset, containing time series of growth, carbon stock, carbon loss from mortality, and aboveground living vegetation carbon turnover time at each plot, are archived on the Hive, the University of Utah's Open Access Institutional Data Repository. Satellite remote-sensing estimates of NPP and carbon stocks were derived from the previous publications (14, 15). NPP and carbon stocks of 8 ESMs from CMIP5 are publicly available at https://pcmdi.llnl.gov/mips/cmip5/data-portal.html. More information

on datasets of forest plot, remote sensing, and ESMs, CO_2, and climate data 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:

$$\text{Log}(\text{Variable}_{i,j}) = \beta\, t_{ij} + b_i + \varepsilon_{ij}, \quad [4]$$

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; t_{ij} is the time of the ith plot and the jth census interval and quantified as mean value of time between consecutive time steps j and $j + 1$; β is the standardized fixed effect associated with an individual model parameter; b_i represent the random effect of the ith plot; and ε_{ij} is random error, which is assumed to follow a normal distribution with mean zero and SD σ. 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 on CO_2 concentration (CO_2), total annual precipitation (Prn), and mean annual temperature (TAS) in forest plot data and ESMs. We have the following:

$$\text{Log}(\text{Variable}_{i,j}) = \beta_1\, CO_{2i,j} + \beta_2 Prn_{i,j} + \beta_3 TAS_{i,j} + b_i + \varepsilon_{ij}, \quad [5]$$

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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1. G. B. Bonan, Forests and climate change: Forcings, feedbacks, and the climate benefits of forests. *Science* **320**, 1444–1449 (2008).

2. M. Heimann, M. Reichstein, Terrestrial ecosystem carbon dynamics and climate feedbacks. *Nature* **451**, 289–292 (2008).

3. W. Cramer *et al*., Global response of terrestrial ecosystem structure and function to CO_2 and climate change: Results from six dynamic global vegetation models. *Glob. Change Biol.* **7**, 357–373 (2001).

4. P. Friedlingstein *et al*., Climate-carbon cycle feedback analysis: Results from the C4MIP model intercomparison. *J. Clim.* **19**, 3337–3353 (2006).

5. S. Sitch *et al*., Evaluation of the terrestrial carbon cycle, future plant geography and climate-carbon cycle feedbacks using five Dynamic Global Vegetation Models (DGVMs). *Glob. Change Biol.* **14**, 2015–2039 (2008).

6. C. Yizhao *et al*., The role of residence time in diagnostic models of global carbon storage capacity: Model decomposition based on a traceable scheme. *Sci. Rep.* **5**, 16155 (2015).

7. N. Carvalhais *et al*., Global covariation of carbon turnover times with climate in terrestrial ecosystems. *Nature* **514**, 213–217 (2014).

8. A. D. Friend *et al*., Carbon residence time dominates uncertainty in terrestrial vegetation responses to future climate and atmospheric CO_2. *Proc. Natl. Acad. Sci. U.S.A.* **111**, 3280–3285 (2014).

9. L. T. Berner, B. E. Law, T. W. Hudiburg, Water availability limits tree productivity, carbon stocks, and carbon residence time in mature forests across the western US. *Biogeosciences* **14**, 365–378 (2017).

10. M. Thurner *et al*., Evaluation of climate-related carbon turnover processes in global vegetation models for boreal and temperate forests. *Glob. Change Biol.* **23**, 3076–3091 (2017).

11. J. S. Olson, Gross and net production of terrestrial vegetation. *J. Anim. Ecol.* **33**, 99–118 (1964).

12. R. J. W. Brienen *et al*., Long-term decline of the Amazon carbon sink. *Nature* **519**, 344–348 (2015).

13. C. D. Koven *et al*., Controls on terrestrial carbon feedbacks by productivity versus turnover in the CMIP5 Earth system models. *Biogeosciences* **12**, 5211–5228 (2015).

14. Y. Y. Liu *et al*., Recent reversal in loss of global terrestrial biomass. *Nat. Clim. Chang.* **5**, 470–474 (2015).

15. W. Kolby Smith *et al*., Large divergence of satellite and Earth system model estimates of global terrestrial CO_2 fertilization. *Nat. Clim. Chang.* **6**, 306–310 (2016).

16. A. T. Trugman, D. Medvigy, W. R. L. Anderegg, S. W. Pacala, Differential declines in Alaskan boreal forest vitality related to climate and competition. *Glob. Change Biol.* **24**, 1097–1107 (2018).

17. S. L. Lewis, J. Lloyd, S. Sitch, E. T. A. Mitchard, W. F. Laurance, Changing ecology of tropical forests: Evidence and drivers. *Annu. Rev. Ecol. Evol. Syst.* **40**, 529–549 (2009).

18. N. McDowell *et al*., Mechanisms of plant survival and mortality during drought: Why do some plants survive while others succumb to drought? *New Phytol.* **178**, 719–739 (2008).

19. C. D. Allen *et al*., A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *For. Ecol. Manage.* **259**, 660–684 (2010).

20. W. R. L. Anderegg, J. M. Kane, L. D. L. Anderegg, Consequences of widespread tree mortality triggered by drought and temperature stress. *Nat. Clim. Chang.* **3**, 30–36 (2013).

21. T. A. M. Pugh *et al*., Role of forest regrowth in global carbon sink dynamics. *Proc. Natl. Acad. Sci. U.S.A.* **116**, 4382–4387 (2019).

22. N. G. McDowell *et al*., Multi-scale predictions of massive conifer mortality due to chronic temperature rise. *Nat. Clim. Chang.* **6**, 295–300 (2016).

23. H. D. Adams *et al*., A multi-species synthesis of physiological mechanisms in drought-induced tree mortality. *Nat. Ecol. Evol.* **1**, 1285–1291 (2017).

24. A. P. Walker *et al*., Predicting long-term carbon sequestration in response to CO_2 enrichment: How and why do current ecosystem models differ? *Global Biogeochem. Cycles* **29**, 476–495 (2015).

25. T. F. Keenan *et al*., Recent pause in the growth rate of atmospheric CO_2 due to enhanced terrestrial carbon uptake. *Nat. Commun.* **7**, 13428 (2016).

26. C. Körner, Through enhanced tree dynamics carbon dioxide enrichment may cause tropical forests to lose carbon. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **359**, 493–498 (2004).

27. C. Körner, A matter of tree longevity. *Science* **355**, 130–131 (2017).

28. U. Büntgen *et al*., Limited capacity of tree growth to mitigate the global greenhouse effect under predicted warming. *Nat. Commun.* **10**, 2171 (2019).

29. O. L. Phillips, A. H. Gentry, Increasing turnover through time in tropical forests. *Science* **263**, 954–958 (1994).

30. C. Peng *et al*., A drought-induced pervasive increase in tree mortality across Canada's boreal forests. *Nat. Clim. Chang.* **1**, 467–471 (2011).

31. R. A. Hember, W. A. Kurz, N. C. Coops, Increasing net ecosystem biomass production of Canada's boreal and temperate forests despite decline in dry climates. *Global Biogeochem. Cycles* **31**, 134–158 (2017).

32. A. S. Jump *et al*., Structural overshoot of tree growth with climate variability and the global spectrum of drought-induced forest dieback. *Glob. Change Biol.* **23**, 3742–3757 (2017).

33. J. Zhang, S. Huang, F. He, Half-century evidence from western Canada shows forest dynamics are primarily driven by competition followed by climate. *Proc. Natl. Acad. Sci. U.S.A.* **112**, 4009–4014 (2015).

34. H. Saxe, M. G. R. Cannell, Ø. Johnsen, M. G. Ryan, G. Vourlitis, Tree and forest functioning in response to global warming. *New Phytol.* **149**, 369–400 (2001).

35. C. A. Sierra, M. Müller, H. Metzler, S. Manzoni, S. E. Trumbore, The muddle of ages, turnover, transit, and residence times in the carbon cycle. *Glob. Change Biol.* **23**, 1763–1773 (2017).

36. M. Jung *et al*., Compensatory water effects link yearly global land CO_2 sink changes to temperature. *Nature* **541**, 516–520 (2017).

37. M. C. Peel, B. L. Finlayson, T. A. McMahon, Updated world map of the Köppen-Geiger climate classification. *Hydrol. Earth Syst. Sci.* **11**, 1633–1644 (2007).

38. J. F. Lamarque *et al*., Multi-model mean nitrogen and sulfur deposition from the Atmospheric Chemistry and Climate Model Intercomparison Project (ACCMIP): Evaluation of historical and projected future changes. *Atmos. Chem. Phys.* **13**, 7997–8018 (2013).

39. Y. Pan *et al*., A large and persistent carbon sink in the world's forests. *Science* **333**, 988–993 (2011).