TROPICAL FOREST

Long-term thermal sensitivity of Earth's tropical forests

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The sensitivity of tropical forest carbon to climate is a key uncertainty in predicting global climate change. Although short-term drying and warming are known to affect forests, it is unknown if such effects translate into long-term responses. Here, we analyze 590 permanent plots measured across the tropics to derive the equilibrium climate controls on forest carbon. Maximum temperature is the most important predictor of aboveground biomass (–9.1 megagrams of carbon per hectare per degree Celsius), primarily by reducing woody productivity, and has a greater impact per °C in the hottest forests (>32.2°C). Our results nevertheless reveal greater thermal resilience than observations of short-term variation imply. To realize the long-term climate adaptation potential of tropical forests requires both protecting them and stabilizing Earth's climate.

The response of tropical terrestrial carbon to environmental change is a critical component of global climate models (*1*). Land-atmosphere feedbacks depend on the balance of positive biomass growth stimulation by CO_2 fertilization (i.e., β) and negative responses to warmer temperatures and any change in precipitation (i.e., γ). Yet the climate response is so poorly constrained that it remains one of the largest uncertainties in Earth system models (*2*, *3*), with the temperature sensitivity of tropical land carbon stocks alone differing by >100 Pg C $°C^{-1}$ among models (*2*). Such uncertainty impedes our understanding of the global carbon cycle, limiting our ability to simulate the future of the Earth system under different long-term climate mitigation strategies. A critical long-term control on tropical land-atmosphere feedbacks is the sensitivity to climate of tropical forests (a key component of γ), where about 40% of the world's vegetation carbon resides (*4*).

The sensitivity to environmental change of tropical biomass carbon stocks, rates of production, and the persistence of fixed carbon can all be estimated by relating their short-term and interannual responses to variation in climate (*5*–*7*). These sensitivities are then used to constrain longer-term projections of climate responses (*2*). Such approaches typically find that higher minimum temperatures are strongly associated with slower tree growth and reduced forest carbon stocks, likely owing to increased respiration at higher temperatures (*7*–*9*). Tropical forest carbon is also sensitive to precipitation (*10*), with, for example, increased tree mortality occurring during drought events (*11*).

Yet the sensitivity of ecosystems to interannual fluctuations may be an unreliable guide to their longer-term responses to climate change. Such responses will also be influenced by physiological acclimation (*12*), changes in demographic rates (*13*), and shifts in species composition (*14*). For example, both respiration

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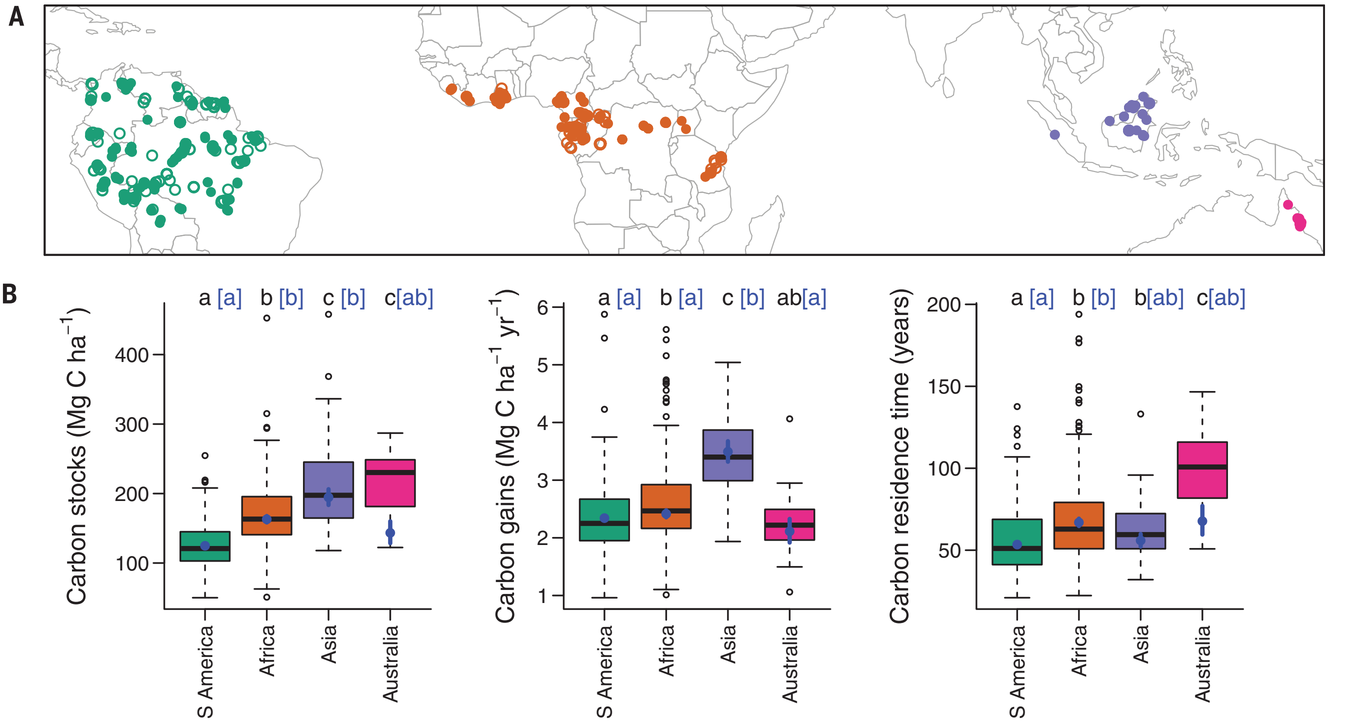

Fig. 1. Spatial variation in tropical forest carbon. (**A**) The RAINFOR (South America), AfriTRON (Africa), T-FORCES (Asia), and Australian plot networks. Filled symbols show 590 multicensus plots used in the main analysis; open symbols show 223 single-census plots used as an independent dataset. Symbol color indicates the region: green, South America; orange, Africa; purple, Asia; and pink, Australia. (**B**) Variation in carbon among continents. Boxplots show raw variation, whereas blue points show estimated mean values (±SE) after accounting for environmental variation. Letters denote statistically significant differences between continents (P < 0.05) based on raw data (black) or after accounting for environmental effects (blue in brackets).

and photosynthesis can acclimate under sustained temperature increases (*15–17*), tropical trees exhibit physiological plasticity (*18*), and shifts in species composition occur (*14*) under sustained drought. These processes could mean that tropical forests are less sensitive to climate than estimates derived from interannual variability imply. An alternative, complementary approach to assessing sensitivity to climate is to measure and analyze spatial variation in tropical ecosystems across climate gradients as a space-for-time substitution. Such biome-wide spatial variation in forest carbon stocks, fluxes, and persistence offers a distinctive and largely unexplored window into the potential equilibrium sensitivity of tropical forest vegetation to warming, because it captures real-world vegetation responses that allow for physiological and ecological adaptation (*12*).

To assess the long-term climate controls on tropical forest growth and carbon stocks, we assembled, measured, and analyzed a pantropical network of 590 permanent, long-term inventory plots (Fig. 1; see figs. S1 and S2 for ability to capture biome climate space). Our analysis combines standardized measurements from across South American, African, Asian, and Australian tropical lowland forests (273, 239, 61, and 17 plots, respectively). For every plot, we calculated aboveground carbon stocks (*19*). Then, to better assess the dynamic controls on aboveground carbon stocks, we also computed the rate of carbon gained by the system (aboveground woody carbon production, calculated as tree growth plus newly recruited trees, in Mg C ha^{-1} year^{-1}) and the carbon residence time in living biomass (calculated as the ratio of living carbon stocks to carbon gains, in years).

We found considerable variation in biomass carbon among continents, with lower stocks per unit area in South America compared with the Paleotropics, even after accounting for environmental variables (Fig. 1). Continents with high carbon stocks had either large carbon gains (Asia) or long carbon residence times (Africa) (Fig. 1). Because of these differences among continents, which are potentially due to differences in evolutionary history (*20*), we analyzed the environmental drivers of spatial variation in carbon stocks while accounting for biogeographical differences. We fitted linear models with explanatory variables representing hypothesized mechanistic controls of climate on tropical forest carbon (table S1). We also included soil covariates, continent intercepts, and eigenvectors describing spatial relationships among plots to account for other sources of variation (*21*).

Forest carbon stocks were most strongly related to maximum temperature [Fig. 2; –5.9% per 1°C increase in mean daily maximum temperature in the warmest month with a 95% confidence interval (CI) = –8.6 to –3.1%, which is equivalent to –9.1 Mg C ha^{-1} °C^{-1} for a stand with the mean carbon stock in our dataset, 154.6 Mg C ha^{-1}] followed by rainfall (Fig. 2; +2.4% per 100-mm increase in precipitation in the driest quarter with a 95% CI = 0.6 to 4.3%, equivalent to 0.04 Mg C ha^{-1} mm^{-1} for a stand with the mean carbon stocks in our dataset), with no statistically significant relationship with minimum temperature, wind speed, or cloud cover (Fig. 2). The effects of maximum temperature and precipitation are also evident in an analysis considering a wider suite of climate variables than those tied to hypothesized mechanisms (fig. S3) and in an additional independent pantropical dataset of 223 single-census plots (for which carbon gains and residence time cannot be assessed, fig. S4).

The negative effect of maximum temperature on aboveground carbon stocks mainly reflects reduced carbon gains with increasing temperature (–4.0% per 1°C, 95% CI = –6.2 to –1.8%; Fig. 2), whereas the positive effect of precipitation emerges through longer carbon residence times with increasing precipitation in the driest quarter (3.3% per 100 mm, 95% CI = 0.9 to 5.7%; Fig. 2). Carbon residence time also increased with the proportion of clay in the soil (Fig. 2). The additive effects of precipitation and temperature on carbon stocks were modified by an interaction between them [change in Akaike information criterion (ΔAIC) = 15.4 comparing the full linear model with or without interaction], with temperature effects more negative when precipitation is low (fig. S6). The interaction was through shortening carbon residence time (ΔAIC = 11.9) rather than reducing carbon gains (model without interaction performed better, ΔAIC = 1.4).

An alternative analysis using decision-tree algorithms (*22*) also showed maximum temperature and precipitation to be important (fig. S7). This decision-tree approach, which can capture complex nonlinear relationships (*22*), indicated potential nonlinearity in the relationships between carbon stocks and both temperature and precipitation, with the positive effect of increasing dry-season precipitation on residence times strengthening when precipitation was low and the negative effect of maximum temperature intensifying at high temperatures (fig. S7).

We further investigated nonlinearity in the temperature relationship using breakpoint regression (supported over linear regression based on lower AIC, ΔAIC = 15.0), which revealed that above 32.2°C (95% CI = 31.7° to 32.6°C), the relationship between carbon stocks and maximum temperature became more negative (cooler than breakpoint, −3.8% $°C^{-1}$, and warmer than breakpoint, −14.7% $°C^{-1}$; Fig. 3). By partitioning carbon stocks into their production and persistence, we found that this nonlinearity reflects changes to carbon residence time (ΔAIC = 10.6) rather than gains (ΔAIC = 1.7). Overall, our results thus indicate two separate climate controls on carbon stocks: a negative linear effect of maximum temperature through reduced carbon gains and a nonlinear negative effect of maximum temperature, ameliorated by high dry-season precipitation, through reduced carbon residence time.

The effect of temperature on carbon residence time only emerges when dry-season precipitation is low; this is consistent with theoretical expectations that negative effects of temperature on tree longevity are exacerbated by moisture limitation, rather than being independent of it and only due to increased respiration costs (*23*). This could occur through high vapor pressure deficits in hot and dry forests increasing mortality risk by causing hydraulic stress (*23*, *24*) or carbon starvation due to limited photosynthesis as a result of stomatal closure (*23*). Notably, the temperature-precipitation interaction we found for aboveground stocks is in the opposite direction to temperature-precipitation interactions reported for soil carbon (*25*). In soils, moisture limitation suppresses the temperature response of heterotrophic respiration, whereas in trees, moisture limitation increases the mortality risks of high temperatures.

The negative effects of temperature on biomass carbon stocks and gains are primarily due to maximum rather than minimum temperature. This is consistent with high daytime temperatures reducing CO_2 assimilation rates, for example, owing to increased photorespiration or longer duration of stomatal closure (*26*, *27*), whereas if negative temperature effects were to have increased respiration rates, there should be a stronger relationship with minimum (i.e., nighttime) temperature. Critically, minimum temperature is unrelated to aboveground carbon stocks both pantropically and in one continent, South America, where maximum and minimum temperature are largely decoupled [correlation coefficient (r) = 0.33; fig. S8]. Although carbon gains are negatively related to minimum temperature (fig. S9), this bivariate relationship is weaker than with maximum temperature and disappears once the effects of other variables are accounted for (Fig. 2). Finally, in Asia, the tropical region that experiences the warmest minimum temperatures of all, both carbon stocks and carbon gains are highest (Fig. 1 and fig. S11).

Overall, our results suggest that tropical forests have considerable potential to acclimate and adapt to the effects of nighttime minimum temperatures but are clearly sensitive to the effects of daytime maximum temperature. This is consistent with ecophysiological observations suggesting that the acclimation potential of respiration (*15*) is greater than that of photosynthesis (*17*). The temperature sensitivity revealed by our analysis is also considerably weaker than short-term sensitivities associated with interannual climate variation (*7*–*9*). For example, by relating short-term annual climate anomalies to responses in plots, the effect of a 1°C increase in temperature on carbon gains has been estimated as more than threefold our long-term, pantropical result (*28*). This stronger, long-term thermal resilience is likely due to a combination of individual acclimation and plasticity (*15*–*17*), differences in species' climate responses (*29*) leading to shifts in community composition due to changing demographic rates (*12*), and the immigration of species with higher performance at high temperatures (*12*).

Our pantropical analysis of the sensitivity to climate of aboveground forest carbon stocks, gains, and persistence shows that warming reduces carbon stocks and woody productivity. Using a reference carbon stock map (*30*) and applying our estimated temperature sensitivity (including nonlinearity) while holding other variables constant leads to an eventual biome-wide reduction of 14.1 Pg C in live biomass (including scaling to estimate carbon in roots) for a 1°C increase in mean daily maximum temperature in the warmest month (95% CI = 6.9 to 20.7 Pg). This compares with a large range of projected sensitivities in coupled climate carbon cycle models that report vegetation carbon (1 to 58 Pg C $°C^{-1}$), although these models have not been run to equilibrium (see supplementary methods).

Our results suggest that stabilizing global surface temperatures at 2°C above preindustrial levels will cause a potential long-term biome-wide loss of 35.3 Pg C (95% CI = 20.9 to 49.0 Pg, estimates with alternative baseline biomass maps of 24.0 to 28.4 Pg; fig. S12). The greatest long-term reductions in carbon stocks are projected in South America, where baseline temperatures and future warming are both highest (Fig. 4 and fig. S13). This warming would push 71% of the biome beyond

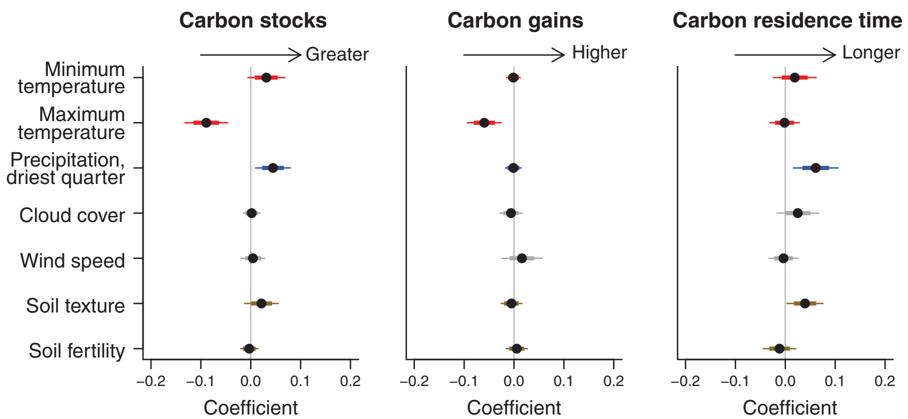

Fig. 2. Correlates of spatial variation in tropical forest carbon. Points show coefficients from model-averaged general linear models. Variables that did not occur in well-supported models are shrinkage-adjusted toward zero. Coefficients are standardized so that they represent change in the response variable for one standard deviation change in the explanatory variable. Error bars show standard errors (thick lines) and 95% confidence intervals (thin lines); error bar color is for illustrative purposes to reflect the category of variable. Soil texture is represented by the percentage clay and soil fertility by cation exchange capacity. The full models explained 44.1, 31.4, and 30.9% of spatial variation in carbon stocks, gains, and residence time, respectively. Coefficients are shown in table S2. Results are robust to using an alternative allometry to estimate tree biomass (fig. S5).

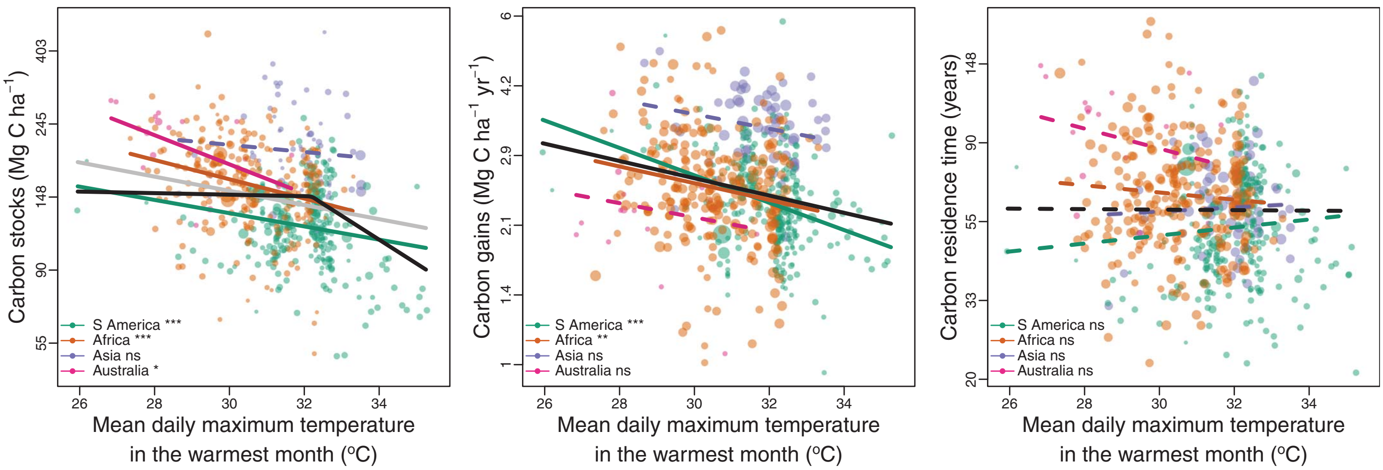

Fig. 3. Temperature effects on tropical forest carbon stocks, carbon gains, and carbon residence time. Black lines show the best pantropical relationships accounting for environmental covariates. The gray line additionally shows the linear pantropical relationship for carbon stocks. Colored lines show bivariate relationships within each continent, as identified in the legend. Statistically significant relationships are shown with solid lines; nonsignificant relationships are shown with dashed lines. The *y* axis is on a log scale. Symbol point size is proportional to weights used in model fitting based on plot size and monitoring length; see supplementary materials and methods. For stocks and gains, linear and breakpoint pantropical relationships are all statistically significant ($P < 0.001$) as are better-sampled continents. For carbon residence time, relationships with temperature are nonsignificant (ns), but there is a statistically significant interaction between maximum temperature and precipitation in the driest quarter (fig. S6). Relationships with other variables are shown in figs. S8 to S10. ***$P < 0.001$; **$P < 0.01$; *$P < 0.05$; ns, $P \geq 0.05$.

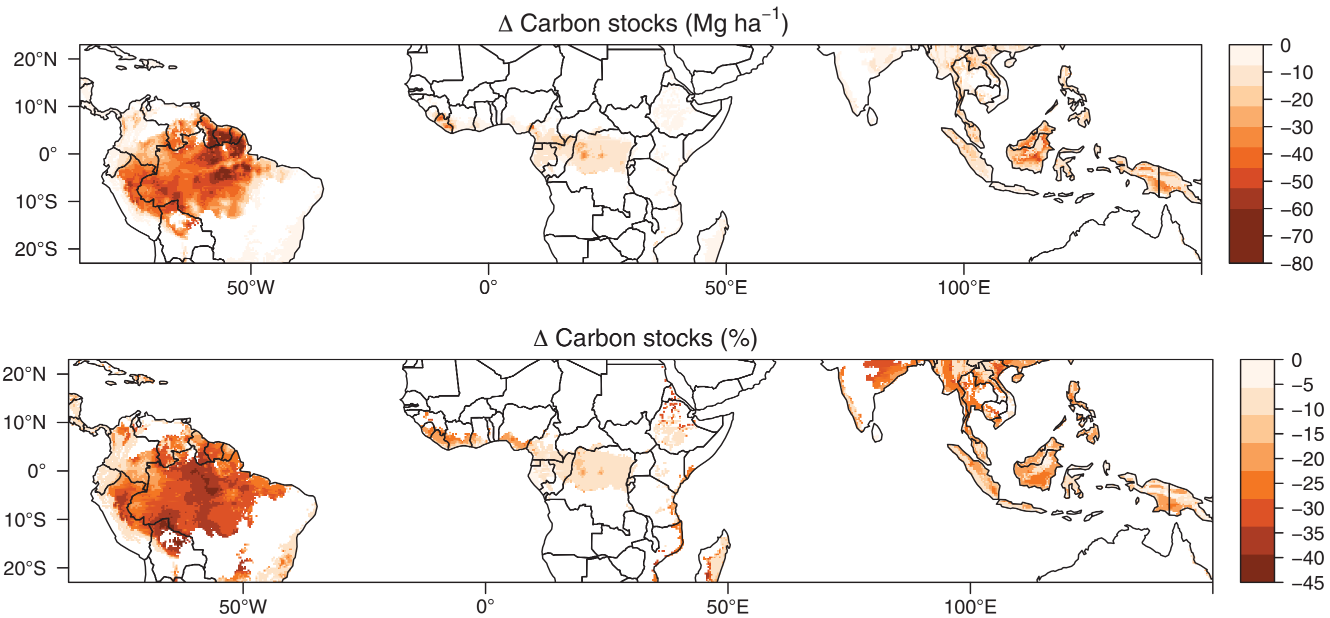

Fig. 4. Long-term change in carbon stocks due to temperature effects alone for global surface air temperature warming of 2°C. Maps show the predicted absolute and relative change in tropical forest carbon stocks. Parts of the biome become warmer than observed now in our dataset (fig. S14). See fig. S12 for predictions using alternative carbon reference maps. Predictions are based on temperature alone and do not include precipitation changes (for which future patterns of change are uncertain) or moderation by increased CO_2. (See fig. S15 for analysis incorporating this.)

the thermal threshold—a maximum temperature of 32.2°C—where larger long-term reductions in biomass are expected (fig. S14). Of course, growth stimulation by carbon dioxide (*31*) will partially or wholly offset the effect of this temperature increase, depending on both the level of atmospheric carbon dioxide that limits warming to 2°C above preindustrial levels and the fertilization effect of this carbon dioxide on tropical trees. Although CO_2 fertilization will reduce temperature-induced carbon losses from biomass across the tropics (table S3), our analysis indicates that CO_2 fertilization will not completely offset long-term temperature-induced carbon losses within Amazonia (fig. S15), consistent with a recent decadal-scale analysis of inventory data (*32*).

The long-term climate sensitivities derived from our pantropical field measurements incorporate ecophysiological and ecological adaptation and so provide an estimate of the long-term, quasi-equilibrium response of tropical vegetation to climate. This thermal adaptation potential may not be fully realized in future responses because (i) the speed of temperature rises may exceed species' adaptive capabilities, (ii) habitat fragmentation may limit species' ability to track changes in the environment, and (iii) other human impacts such as logging and fire can increase the vulnerability of forest carbon stocks to high temperatures. Although many tropical forests are under severe threat of conversion, our results show that, in the long run, tropical forests that remain intact can continue to store high levels of carbon under high temperatures. Achieving the biome-wide climate resilience potential that we document depends on limiting heating and on large-scale conservation and restoration to protect biodiversity and allow species to move.

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SUPPLEMENTARY MATERIALS

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Long-term thermal sensitivity of Earth's tropical forests

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Thermal sensitivity of tropical trees

A key uncertainty in climate change models is the thermal sensitivity of tropical forests and how this value might influence carbon fluxes. Sullivan *et al.* measured carbon stocks and fluxes in permanent forest plots distributed globally. This synthesis of plot networks across climatic and biogeographic gradients shows that forest thermal sensitivity is dominated by high daytime temperatures. This extreme condition depresses growth rates and shortens the time that carbon resides in the ecosystem by killing trees under hot, dry conditions. The effect of temperature is worse above 32°C, and a greater magnitude of climate change thus risks greater loss of tropical forest carbon stocks. Nevertheless, forest carbon stocks are likely to remain higher under moderate climate change if they are protected from direct impacts such as clearance, logging, or fires.

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