RESEARCH ARTICLE SUMMARY

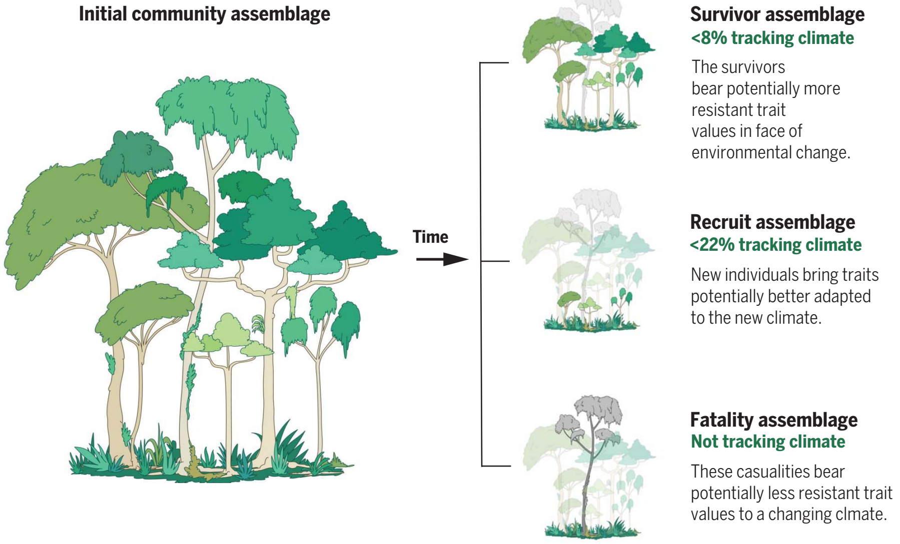
FOREST CHANGE

# Tropical forests in the Americas are changing too slowly to track climate change

**Jesús Aguirre-Gutiérrez*** ***et al.***

**INTRODUCTION:** Tropical land regions are experiencing rapid climate change, with some scenarios for the tropical Americas projecting temperature increases of up to ~4°C and precipitation reductions of close to 20% by 2100. This would expose current species assemblages to climates that they have never experienced before, potentially selecting for future plant communities adapted to such climates but unlike those currently observed. Community responses to climate change will thus likely depend on underlying mechanisms and geographical context. In the face of threats from climate change, it is both critical and urgent to understand the ability of these complex systems to adapt to change and survive. The relationships among environmental conditions, plant performance, and distribution are mediated by species' functional traits. Therefore, a trait-based approach provides a promising framework for predicting the impacts of climate change and resilience across forest ecosystems.

**RATIONALE:** Climate change is already affecting the survival and distribution of tropical American plant communities. If species respond to climate change through migration, then we would expect montane communities to track changes in climate better than those in the lowland forests because mountains have different climate conditions occurring at shorter distances and thus are potentially easier to migrate across than lowlands. Given exposure to a drying and warming climate, we could expect increased abundance of species exhibiting more drought-tolerance traits. Drought-avoidance traits, notably deciduousness, could also become more prominent in the future as an adaptation to increasing drought.



**Mechanisms driving changes in community trait composition and climate tracking.** Changes in climatic conditions significantly influence tropical forest tree community dynamics, including survival (survivor assemblages), recruitment (recruit assemblages), and mortality (fatality assemblages). Quantifying these community dynamics is crucial for understanding how tropical forests adapt to and track a changing climate. Survivor assemblages consist of trees with traits potentially suited to existing climatic conditions, aiding in incremental climate tracking. Conversely, recruit assemblages are composed of individuals with traits potentially better adapted to emerging climatic conditions, enhancing their ability to thrive under new environmental conditions. By contrast, fatality assemblages represent individuals with less resilient traits, leading to their inability to cope with climatic shifts. Our analysis reveals that survivor assemblages are tracking climate changes at <8% of the expected rate given current climate shifts. Recruit assemblages demonstrate a higher tracking rate, ~22% of the expectation. However, fatality assemblages by definition do not track climate because they consist of individuals that have already perished, likely due to their inadequate adaptation to changing climatic conditions.

It is as yet unclear how shifts in the abundance and distribution of species translate into changes in functional composition and what functional changes have occurred as a response to the onset of a warmer, drier, and more variable climate across the tropical Americas. It is uncertain if these functional shifts match the direction of climate change and, if so, whether the rate of functional trait change keeps pace with climate change or lags behind. Here, we address these knowledge gaps by analyzing tree community trait shifts that have occurred across the past 40 years in tropical forests of the Americas due to the dynamics of survivor, recruit, and fatality tree assemblages. The survivor tree assemblages consist of trees with traits potentially better suited to existing climatic conditions, and the recruit assemblages are composed of individuals with traits adapted to emerging climatic conditions. The fatality assemblages could represent individuals with less resilient traits that cause their inability to cope with climatic shifts. We also quantify if the observed changes in trait composition have been enough to track climate change to date.

**RESULTS:** Overall, we found that lowland forests show significant and larger changes in more community traits than montane forests. Across forests and for the survivor assemblages, the abundance of deciduous species is increasing, with accompanying increases in leaf photosynthetic capacity and decreases in leaf area and leaf thickness, perhaps as an adaptation to a warmer and dryer climate. However, the recruiting communities in the lowland forests have, on average, exhibited decreases in their abundance of deciduous species, in leaf carbon and nitrogen content, and in wood density. Crucially, most of these traits are changing at only a fraction of the rate required to maintain equilibrium with climate in the full tree community and survivor assemblages. The recruiting communities show the best tracking of a changing climate.

**CONCLUSION:** Our analysis demonstrates that tree community composition is shifting to track climate change, but tree species composition and functional properties of tropical American forests (and possibly all tropical forests) are increasingly out of equilibrium with local climate. Such disequilibrium likely increases vulnerability to climate change. ■

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RESEARCH ARTICLE

FOREST CHANGE

# Tropical forests in the Americas are changing too slowly to track climate change

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**Understanding the capacity of forests to adapt to climate change is of pivotal importance for conservation science, yet this is still widely unknown. This knowledge gap is particularly acute in high-biodiversity tropical forests. Here, we examined how tropical forests of the Americas have shifted community trait composition in recent decades as a response to changes in climate. Based on historical trait-climate relationships, we found that, overall, the studied functional traits show shifts of less than 8% of what would be expected given the observed changes in climate. However, the recruit assemblage shows shifts of 21% relative to climate change expectation. The most diverse forests on Earth are changing in functional trait composition but at a rate that is fundamentally insufficient to track climate change.**

Forest responses to human-driven perturbations such as climate change will largely determine the diversity and function of the terrestrial biosphere through this century and beyond. The Americas host the greatest concentration of tree species in the world (*1*), including six key biodiversity hotspots (*2*) and half of Earth's most intact tropical forests (*3*). In the face of threats from climate change and continuing loss in area and integrity (*3*–*6*), it is both critical and urgent to understand the ability of these complex systems to adapt to change and survive.

Within tropical American forests (by which we mean all forests encompassing continental areas from Mexico to Brazil), lowland forests provide relatively homogeneous climatic conditions over large areas, potentially allowing the existence of common functional adaptations over large spatial extents. By contrast, across mountain forests, climatic conditions tend to change rapidly in space, potentially facilitating the rapid turnover of functional adaptations to local environmental conditions. In Amazonia, changes in precipitation patterns and more frequent droughts have led to an increase in the recruitment of dry-affiliated species (xerophilization) (*7*). In the Andes, rising temperatures have led to increasing abundances of species tolerant to higher temperature (thermophilization) (*8*). Across Mesoamerica, it is expected that climate change will cause an expansion of tropical dry forests to higher elevations (>200 m above current average elevation) (*9*). However, tree species may be unable to shift their distribution fast enough to track their climatic niche given their slow demography (e.g., growth and recruitment), the prevalence of dispersal limitation (*10*), and different environmental tolerances at different life stages (*11*). All of these limitations would increase the vulnerability of tree species to climate change across tropical American forests. For instance, in higher latitudes, recent work has shown large range contractions of tree species rather than range expansions or shifts (*12*). Changes in climate across the tropical Americas are expected to become stronger, with some scenarios projecting temperature increases of up to ~4°C and precipitation reductions close to 20% by 2100 (*13*–*15*). This would likely increase the vulnerability of current tree species assemblages because they would face climates that they have not previously experienced (*16*), potentially selecting for no-analog future plant communities (*17*).

Functional traits mediate species responses to environmental change, affecting plant performance and species distributions (*18*–*20*). These morphological, structural, chemical, and phenological characteristics tend to show consistent relationships with climate and soil conditions (*21*). Recent work has shown positive relationships between mean annual temperature and leaf area, specific leaf area (SLA), leaf N content, wood density (WD), and leaf thickness (*22*), depicting plant functional adaptations to local environmental conditions. Other work has detected a negative relationship with elevation for SLA and leaf N content, potentially as an adaptation to cooler environments with lower nutrient availability (*22*). Therefore, these traits are tightly linked to the capacity of plant species to respond to environmental changes. For instance, having large area (i.e., larger leaves) can increase leaf temperature due to higher solar absorption, whereas smaller leaves dissipate heat more effectively and help to prevent water loss. Plants with lower SLA, i.e., with thicker and tougher leaves, tend to be more resistant to drought because they can better resist water loss. High WD is tightly related to increased resistance to cavitation, which can increase the plant's capacity to survive droughts. Therefore, a trait-based approach provides a promising framework for predicting the impacts of climate change and resilience across forest ecosystems (*19*, *23*, *24*).

It is still unclear how shifts in the abundance and distribution of species translate into changes in the functional trait composition and what functional changes have occurred through the past half century as a response to the onset of a warmer, drier, and more variable climate across the tropical Americas. Moreover, it is unknown whether forest-level functional shifts are more attributable to differential growth among the surviving trees than to the addition (i.e., recruitment) or removal (i.e., mortality) of trees to the assemblage. It is also uncertain if these functional shifts match the direction of climate change and, if so, whether the rate of functional trait change keeps pace with climate change or lags behind it. Understanding the above will allow the quantification of the present, and likely future, capacity of forest to adapt to a changing climate and also to uncover which functional trait characteristics may confer forests with a higher adaptation capacity to a changing climate.

Here, we address these knowledge gaps by analyzing records from 415 long-term forest plot sites monitored over >40 years (1980 to 2021) by the RAINFOR and MONAFOR networks and contributors to the ForestPlots.net meta-network. This dataset includes information on the identity, size, recruitment, and mortality of >250,000 individual trees across the tropics from Mexico to southern Brazil. Our effort spans relatively undisturbed forests from the lowland tropics (hereafter forest plots <700 m elevation) to pre-montane and montane zones (>700 m elevation; hereafter referred to as montane) from the Andes to subtropical fringes (Fig. 1 and data S1). These forests are distributed along a wide range of climatic and soil conditions (Fig. 1B) and have experienced strong changes in climate over the past decades (Fig. 1C). We combined this monitoring and analysis of changes in the plant community composition

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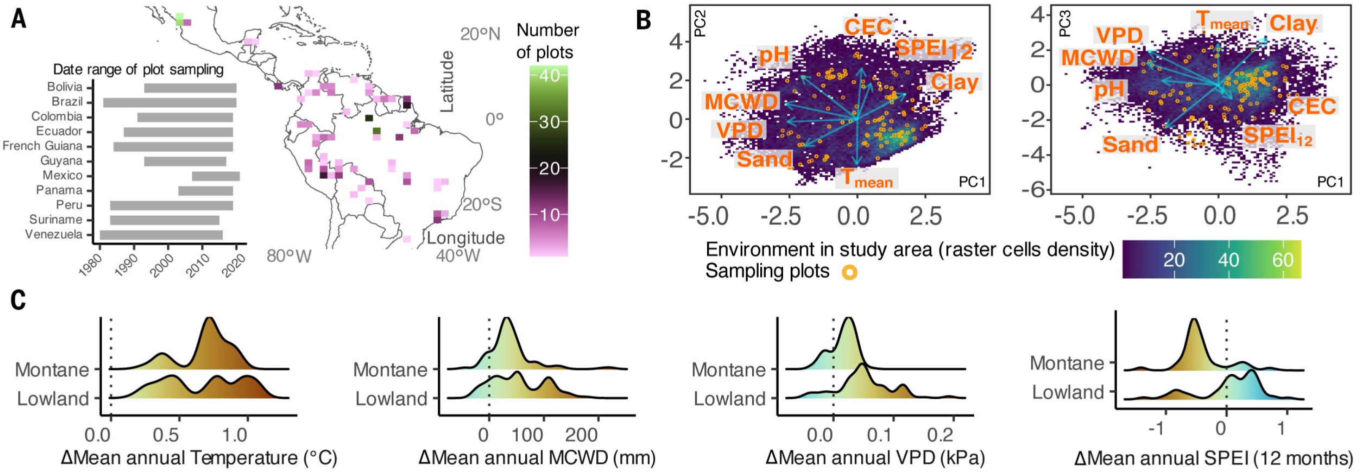

**Fig. 1. Study area showing the distribution and number of vegetation plots sampled across time, principal component analysis, location of sampling plots, and change in climate conditions (A).** (B) Principal component analysis (PC1, PC2, and PC3) depicting the climate and soil chemistry and texture space available in the study area. (**B** and **C**) Location of the sampling plots in the environmental space (B) and change in climate conditions (1980 to 1990 versus 2010 to 2020) in the plot network (C). In (B), PC1 is mainly loaded by the MCWD (−0.527) and VPD (−0.515), PC2 by $T_{mean}$ (−0.465) and soil CEC (0.524), and PC3 by soil clay percentage (−0.535) and soil sand percentage (0.486). In (C), the vertical dotted lines indicate zero change. Brown colors depict increases in temperature and drier conditions for MCWD and VPD or increased drought intensity for the SPEI. Blue colors depict an increase in water availability. In MCWD, larger positive values indicate higher water stress. Climate data were derived from the TerraClimate project (*48*) and soil data from SoilGrids (https://soilgrids.org/) (*49*).

with measurements of 12 plant functional traits that are potentially involved in responses to a changing climate. These include photosynthetic capacity ($A_{sat}$), leaf chemistry (content of leaf C, N, and P), leaf area, SLA, leaf fresh mass (FM), leaf thickness, abundance of deciduous species (DE), adult maximum height ($H_{max}$), WD, and seed mass (SM) (table S1). Tree functional trait data were obtained for several plots from local field collections carried out by collaborators (*25*–*27*), the Global Ecosystems Monitoring network (GEM) (*28*), and ForestPlots (www.ForestPlots.net) (*29*), in addition to databases from the Botanical Information and Ecology Network (BIEN; bien.nceas.ucsb.edu), the TRY Plant Trait Database (www.try-db.org) (*30*), and Díaz *et al.* (*19*, *31*).

We first investigated long-term plant trait-environment relationships to understand how climate drives trait distributions in tropical forests of the Americas and if these relationships are consistent across lowland and montane forests. We expected temperature and water availability to be the main drivers of plant trait distributions, with warmer and drier areas facilitating the dominance of more conservative trait syndromes (e.g., smaller and thicker leaves, higher WD, lower $A_{sat}$) compared with warm and wetter areas (*32*, *33*). Moreover, we expected trait-environment relationships to differ between lowland and montane forests given the different climatic ranges of these forest types.

We next studied how and where lowland and montane tropical American forests have shifted in their functional trait composition due to changes in the plant community taxonomic composition over the past four decades. We did this by analyzing the annual rate of change (Δ*r*) of the trait community-weighted mean (CWM) for all forests (lowland and montane together) and for lowland and montane forest separately. Because of the long lifespan of tropical trees (*34*) and their slow turnover, we performed this analysis at the full community level and separately for the recruiting (“recruit”), mortality (“fatality”), and surviving (hereafter “survivor”) assemblages (Fig. 2). Analyzing changes at the full community level [involving all trees >10 cm diameter at breast height (DBH) alive] allows us to understand how communities are changing in their trait CWM given tree growth, survival, and recruitment together. Analyzing the survivor (change in CWM given by growth) assemblage alone will provide insights into potentially more resistant trait values, whereas analyses for the fatality assemblages will identify potentially less resistant trait values. The recruit community will affect the full community-level trait composition dependent on their basal area. It will also provide information on potentially better-adapted trait values to the current climate that allow them to recruit into the community, as well as indicate the possible composition of future forests.

We further investigated whether observed changes in trait composition have been enough to track climate change to date by comparing observed and expected trait changes based on historical trait-environment relationships [see the materials and methods (*35*)]. This climate change tracking analysis was performed for the full community assemblage and for the survivor and recruit assemblages, but not for the fatality assemblage because these individuals will not contribute to future change (Fig. 2).

Given exposure to a drying and warming climate, we could reasonably expect an increased abundance of species exhibiting more drought-tolerance traits (i.e., in the “slow” section of the plant economics spectrum) (*36*), such as high WD (e.g., to prevent cavitation) (*37*) and smaller, thicker leaves (e.g., for lower evapotranspiration and reduced radiation exposure) (*38*). However, it is also possible that increasing drought will drive a shift toward drought-avoidance traits, notably DE (which is often associated with more acquisitive leaves) (*32*, *39*). Seed traits play a pivotal role in the reproduction and dispersal capacity of species (*10*). Under an unstable, warming, and drying climate, we might expect species with smaller wind-dispersed seeds to increase in abundance (*40*). This is because wind-dispersed seeds, which are more common in drier and more seasonal biomes, tend to be smaller than animal-dispersed seeds (*41*). However, other factors, such as wind and fire disturbance and defaunation of frugivorous seed-dispersing mammals and birds, may disrupt the expected trends in seed traits because these drive shifts more strongly at shorter time scales than a changing climate (*42*). If migration is an important component of species response to climate change, then we would also expect montane forests to show stronger functional responses than lowland forests given their more

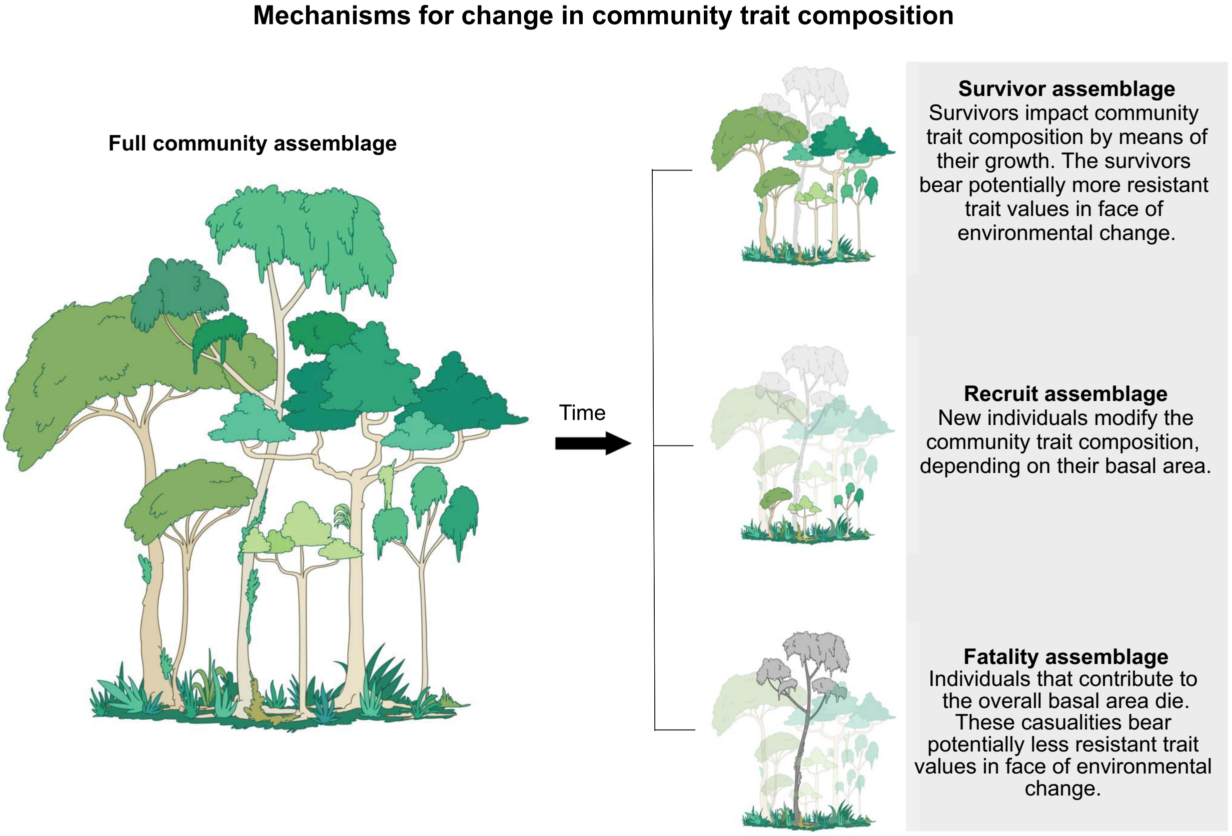

**Fig. 2. Conceptual figure depicting the analyzed mechanisms for change in community trait composition across the study area.** Tree individuals that are alive and have a DBH ≥10 cm are part of the full community assemblage. Across time, there can be changes in the community trait composition due to growth of the surviving tree individuals (survivor assemblage) given their increase in basal area (top right). Other mechanisms for changing community trait composition across time are the recruitment (recruit assemblage) of new individuals (middle right) and the death (fatality assemblage) of individuals in the community (bottom right).

varied climatic conditions at shorter distances (*8*, *33*) that make it potentially easier to migrate to a favorable climate than in the lowlands (*43*–*46*). In montane forests, nutrient availability (e.g., N:P ratios) can vary significantly along altitudinal gradients due to substantial changes in temperature and water availability (*47*). As a result, we expect strong functional responses to soil nutrient availability across these elevation gradients.

We expect that, given the long lifespan of tropical trees and the rapid pace of recent climate change, forests will show ecological inertia so that changes in functional composition will lag behind changes in climate. We expect the full community and survivor assemblages to show slower change given that their change is largely dependent on tree growth, which is a slow process among tropical forest trees. The recruit and fatality assemblages may show faster and larger community trait responses because they are less dependent on growth and more dependent on local climate conditions.

### Long-term trait-environment relationships

To evaluate long-term (1980 to 2021) trait-climate relationships across tropical American forests, we used data from 415 forest plots [mean plot size 0.88 ha (minimum: 0.12, maximum: 25) and 5.7 censuses per plot (minimum: 2, maximum: 41)], for which we extracted climate (*48*) and soil (*49*) data for their sampling years. Because species' contributions to ecosystem processes likely depend on their relative abundances (*50*), we calculated the CWM of each plant functional trait (table S1) for each plot based on the relative basal area of the species and their trait value (hereafter "community functional traits"). The trait values were obtained from the sources mentioned above (*19*, *25*–*31*). We then modeled each community functional trait as a function of the additive effects of relevant and largely uncorrelated climatic drivers of species distributions (fig. S1), i.e., the mean annual values of temperature ($T_{mean}$), vapor pressure deficit ($VPD_{mean}$) (*51*), maximum climatic water deficit ($MCWD_{mean}$) (*52*), and the standardized precipitation-evapotranspiration index ($SPEI_{12}$) (*53*), with each of these interacting with forest type (lowland or montane). Because soil characteristics can affect plant distributions (*24*), we included cation exchange capacity (CEC), pH, and the percentage of clay and sand for each plot location in the models [see the materials and methods (*35*)]. We accounted for differences in the number of censuses, plot size, and census time per vegetation plot and for the potential spatial autocorrelation.

Several community functional traits show consistent relationships with climate across forest type (table S2 and fig. S2), with $T_{mean}$ showing some of the strongest effects driving plant trait distributions across lowland and montane forests (Fig. 3). As expected, an increase in $T_{mean}$ across space is associated with an increase in community-mean leaf area and SM and a decrease in $A_{sat}$, SLA, and the proportion of DE across lowland and montane forests. Moreover, an increase in water stress ($MCWD_{mean}$) is associated with decreases in SLA and $H_{max}$ for both forest types (table S2 and fig. S2). This represents an increase in the conservative trait strategy linked to more extreme conditions.

The relationship with $T_{mean}$ is not, however, consistent across lowland and montane forests for leaf chemistry (C, N, and P content), WD, $H_{max}$, leaf FM, or leaf thickness (Fig. 3). An increase in water stress ($MCWD_{mean}$) is associated with an increase in $A_{sat}$, leaf N content,

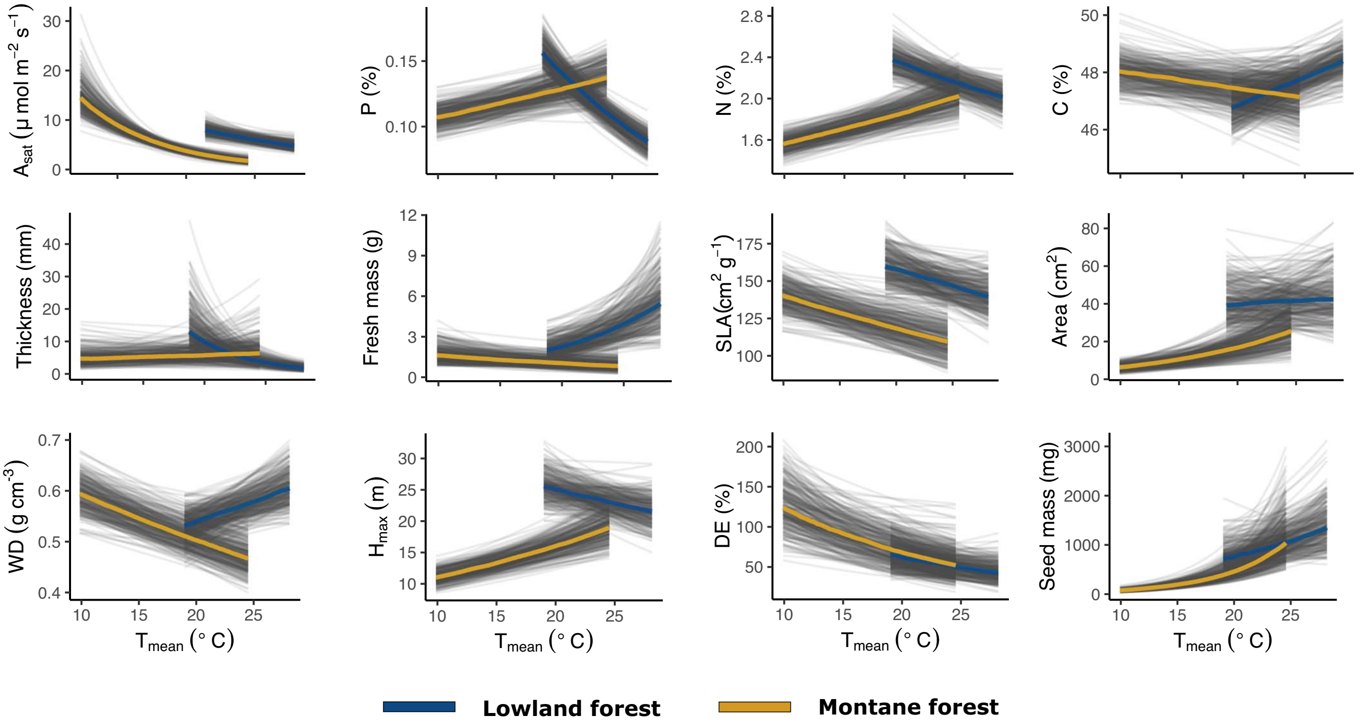

**Fig. 3. Relationship between community-mean plant traits and temperature.** Trait-environment relationships for $T_{mean}$ across the vegetation plots. Thick blue lines (for lowland forests) and yellow lines (for montane forests) show the average trait response to the climatic variable, with gray-shaded lines show 700 random draws from the model posterior distribution representing the variability of the expected model fit. Trait-environment relationships for mean maximum MCWD, VPD, and SPEI ($MCWD_{mean}$, $VPD_{mean}$, and $SPEI_{mean}$, respectively) are shown in fig. S2. For full statistical multivariate model results, see table S2.

leaf area, and WD across lowland forests but decreases in montane forests (table S2 and fig. S2). The increase in these leaf traits in drier forests could be associated with the high photosynthetic rates generally attained by DE over the growing season (*54*, *55*) and the fact that lower $H_{max}$ and higher WD tend to correlate with higher resistance to lethally low levels of soil moisture availability (*37*). However, consistent climatic relationships across both forest types are not apparent for the other traits analyzed (table S2 and fig. S2). One plausible explanation is that this reflects their different position along the climatic gradient (i.e., $T_{mean}$ and precipitation), with lowlands occupying areas with more homogeneous climate conditions across large spatial extents compared with montane forests, which span a large range of climates across smaller spatial extents.

## Changes in trait composition across time

We next investigated whether and how the functional trait composition of tropical American forests has shifted and how much of this can be explained by the observed changes in climate over the past 40 years. We first calculated the CWM of each plant functional trait for each vegetation census available for full community assemblage and separately for the survivor assemblage (individuals that are alive in two subsequent censuses, e.g., from census one to census two), recruit assemblage (individuals not present in the previous census and recruited in the subsequent census), and fatality assemblage (individuals alive in previous census but dead in the subsequent census). We defined the recruit assemblage as individuals that passed the threshold of 10 cm DBH between one census and the next. We then calculated their yearly rate of change across time. We tested whether the changes in trait CWM differed from zero across all vegetation plots, with plots separated into lowland and montane forests. We calculated the highest density interval (HDI) containing the 95% most probable effect values and considered it significant when the HDI did not overlap 0. We then investigated whether the observed shifts in trait CWM differed significantly between lowland and montane forests. For shorthand and readability, all mention of mean traits and shifts below refer to CWM trait values.

When considering all plots together for the full community assemblage, we found that seven of the 12 traits analyzed exhibited significant changes in their CWM values (fig. S3; see Fig. 4 for trait changes across assemblages). Only leaf N, FM, SLA, SM, and WD did not show significant shifts across time (table S3 and fig. S4). The survivor assemblage showed the same pattern of community trait changes (table S3 and Fig. 5) as the full community assemblage, with the main differences being a significant decrease in leaf FM in the lowlands for the survivor assemblage. Thus, hereafter, we focus on the results from the survivor, recruit, and fatality assemblages. Overall, we found larger variation in trait CWM across space (i.e., with geographical variation in climate) than across time. For the community traits with significant changes for the survivor assemblage, we found an average increase in $A_{sat}$ of 0.0023 $\mu$mol m$^{-2}$ s$^{-1}$ year$^{-1}$ (HDI-low and HDI-high: 0.0007 and 0.0038, respectively), leaf C content 0.0011% year$^{-1}$ (0.0004 and 0.0019), leaf P content $1.6 \times 10^{-5}$% year$^{-1}$ ($5.7 \times 10^{-6}$ and $2.7 \times 10^{-5}$), abundance of DE 0.03% year$^{-1}$ (0.01 and 0.05), and $H_{max}$ 0.006 m year$^{-1}$ (0.002 and 0.009), whereas community leaf area decreased on average –0.03 cm$^2$ year$^{-1}$ (–0.06 and –0.007) and leaf thickness decreased –0.05 mm year$^{-1}$ (–0.08 and –0.02) (table S3 and Fig. 5). In the lowland forests, we detected significant trait changes for six (increasing: $A_{sat}$, leaf C content, $H_{max}$, and abundance of DE; decreasing: leaf area and FM) of the 12 traits analyzed (table S3 and Fig. 5). Montane forests showed significant, but rather small, increases in leaf C and P content, and the abundance of DE (table S3 and Fig. 5).

The recruit assemblage experienced significant changes for seven traits, with six showing decreases, i.e., leaf C content –0.014% year$^{-1}$

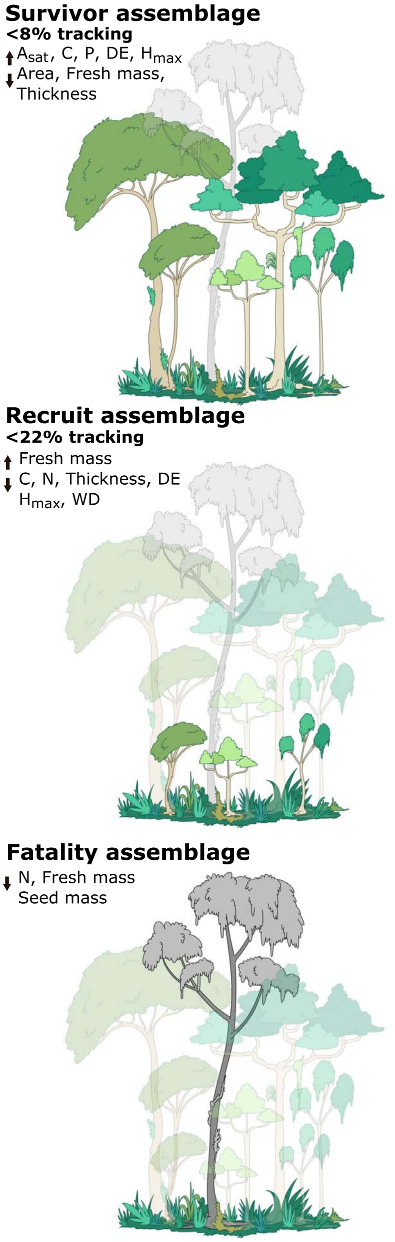

**Fig. 4. The analyzed survivor (top panel), recruit (middle panel), and fatality (bottom panel) assemblages in the study.** In each panel, the highlighted vegetation represents the specific assemblage under analysis. Each panel provides a summary of observed changes in community traits and the percentage of climate tracking by each assemblage, with exception of the fatality assemblage, for which climate tracking is not possible.

(HDI-low and HDI-high: −0.02 and −0.001, respectively, in montane forests), leaf N content −0.002% year$^{-1}$ (−0.004 and −0.0002), leaf thickness −0.04 mm year$^{-1}$(−0.08 and −0.01), DE −0.17% year$^{-1}$ (−0.33 and −0.02), $H_{max}$ −0.03 m year$^{-1}$ (−0.07 and −0.003), and WD −0.0007 g cm$^{3}$ year$^{-1}$. The leaf FM of recruits increased on average 0.04 g year$^{-1}$ (0.006 and 0.08; table S3 and Fig. 5). For the fatality assemblage, only the CWM of leaf N content −0.004% year$^{-1}$ (−0.007 and −0.001 in montane forests), leaf FM −0.02 g year$^{-1}$ (−0.05 and −0.0003) and SM −17.7 mg year$^{-1}$ (−29.9 and −5.7) in lowland forests experienced significant declines (table S3 and Fig. 5).

To help identify the underlying climatic drivers of forest functional change, we used multivariate linear models to estimate the $\Delta r$ (i.e., from the first to the last census) in the trait values ($\Delta_r$ trait CWM) as a function of the yearly rate of change in temperature $T_r$ ($\Delta T_r$), MCWD ($\Delta MCWD_r$), SPEI ($\Delta SPEI_r$), and VPD ($\Delta VPD_r$), each of these interacting with forest type, and accounted for soil characteristics by including in the models the CEC, pH, and clay and sand content (maps in figs. S3 to S8). Our results for the full community assemblage, the survivor assemblage, and the recruit and fatality assemblages (table S4) demonstrate the role of climate, specifically temperature and water availability, as a determinant of trait shifts across the forests and show the differences in response between lowland and montane forests (table S4). Our mapped model predictions (maps in figs. S3 to S8) depict in a spatially explicit way areas where stable CWM trait values (light yellow and light blue) and their increases (darker blue) or decreases (yellow to red) are predicted to have occurred across tropical American forests with some of the strongest CWM trait shifts predicted across forests in Amazonia.

### Can tropical American forest functional composition track climate change?

We next investigated whether the observed community trait changes are sufficient to maintain the expected trait-environment relationships for the full community, survivor, and recruit assemblages based on spatial relationships between traits and climate. We expected recruitment to be more sensitive to climate change because the full community is dominated by the demographic inertia of established adult trees. To quantify the trait changes that would be necessary for forest communities to track predicted climate change, we first quantified the relationship between community traits and environment before most anthropogenic climate changes occurred (1980 to 2005; i.e., as baseline CWM trait-environment relationships). We took our observed trait-climate relationships (built with the 1980 to 2005 period data; table S5) and used them to predict the trait CWM to the 1980 to 2005 climate conditions plus the observed changes in climate across the study sites for the full time period (the past 40 years). This allowed us to predict the CWM trait values that the forests would have if they fully tracked recent climate change, assuming that trait-climate relationships are similar across space and time (table S6 and table S7). The ratio between the observed and expected changes (for the full and the recruit assemblages) indicates how closely these forest traits are tracking our climate equilibrium predictions based on community changes alone (Fig. 6).

Our results show that for all measured traits of the survivor and full community assemblages, the community trait composition is not changing sufficiently to track climate change, with most changes being rather small and unlikely to represent important impacts on ecosystem functioning. However, the recruit community shows the largest shifts (Figs. 4 and 6; results for all assemblages are in fig. S9). At the region-wide scale for the survivor assemblages, all traits show <8% for lowland forests and <4% for montane forests of the change required to track climate. For the full community assemblage, all traits show <6% of the climate-predicted shifts in the expected direction for lowland forests and <7% for montane forests of the expected change (fig. S9 and tables S6 and S7). Several traits show very little change or even modest changes in the opposite direction from those expected (Fig. 6, A and B). We detected larger community trait shifts in the recruit assemblages of an average 21.8% of the change required for lowland forests and 17.5% for montane forests when only traits shifting in the expected direction are considered. When both shifts in the expected direction and those in the opposite direction are considered, the recruit assemblage shows an average shift of 11.4% for lowland forests and −0.67% for montane forests (Fig. 6, C and D, and tables S6 and S7). In lowland forests, community mean WD appears to be changing fast enough in the recruit assemblages to track climate change expectation. Overall, we see some evidence of how the recruit forest assemblages of lowland and montane forests are shifting their community traits, often for different sets of community mean trait values, in response to climate change. However, for most traits, even the recruit community does not seem to be changing quickly enough to track climate change. More significant community trait shifts have occurred in lowland forests than in montane forests, which is consistent with a more rapidly drying climate in the former (table S3 and Fig. 5).

### Discussion

Overall, we found that (i) trait-environment relationships are similar for most of the studied traits across lowland and montane tropical American forests; (ii) lowland forests show significant and larger changes in more community traits analyzed than do montane forests; (iii) across the forests and for the full community and survivor assemblages, the abundance of DE is increasing, with accompanying increases in leaf $A_{sat}$ and decreases

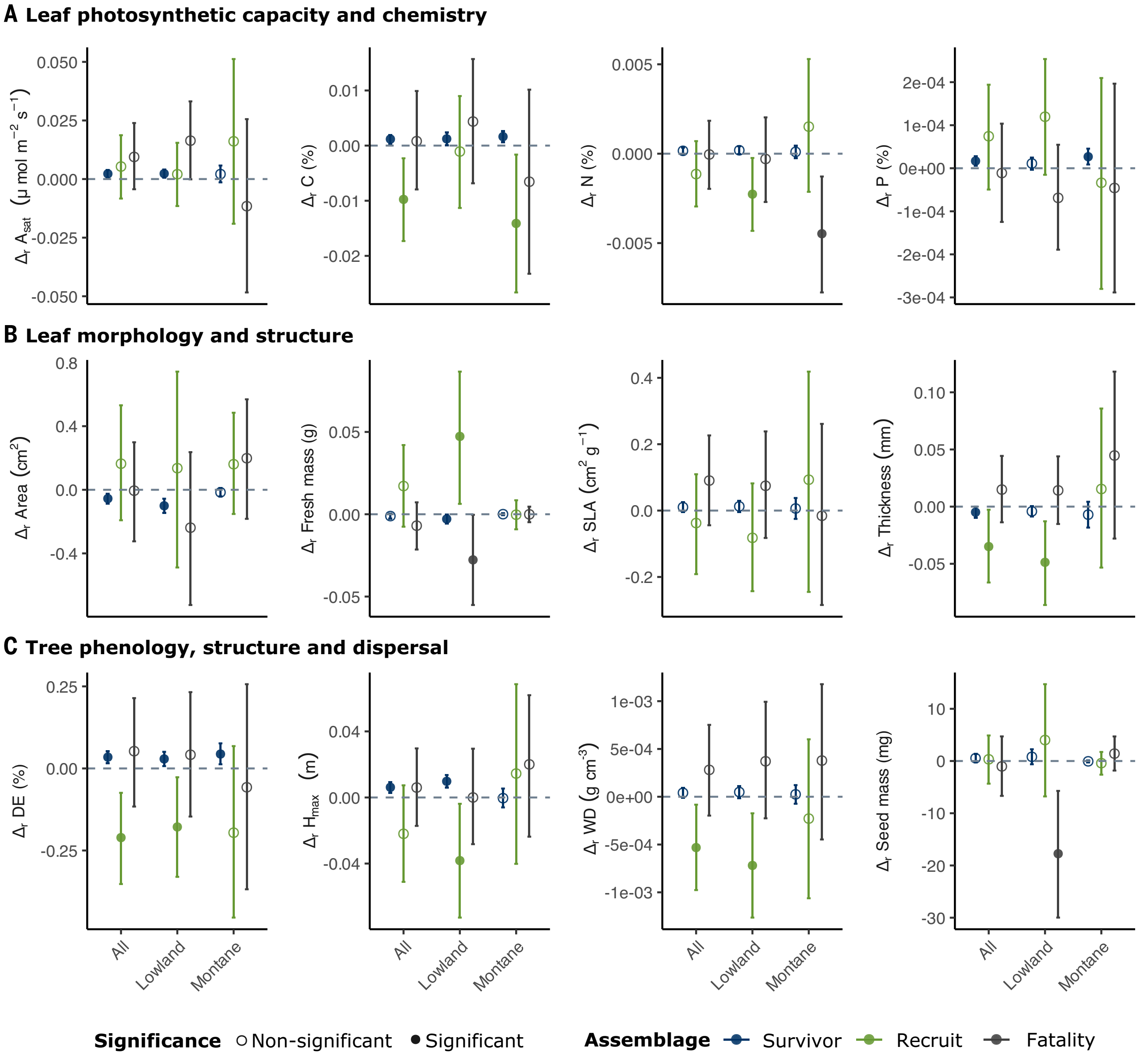

**Fig. 5. Estimated changes in mean community functional trait values across time for tropical American forests.** All traits with their spatial prediction maps are shown in figs. S3 to S8. (**A** to **C**) Changes in trait CWM for leaf $A_{sat}$ and leaf chemistry traits (A), for leaf morphology and structural traits (B), and tree phenology and structural traits (C). Each panel shows the observed yearly rate of change obtained from sampled vegetation plots from the statistical models in table S3 for all forests together and only for lowland or montane forests for the survivor (blue), recruit (green), and fatality (gray) assemblages. Significant shifts are shown as filled circles and nonsignificant as empty circles. The vertical lines depict the highest density interval (95% HDI), and the horizontal gray dotted line indicates zero change.

in leaf area and leaf thickness, yet the recruit communities in the lowland forests have on average decreased in the abundance of DE, leaf N content, and WD; and (iv) crucially, for the full tree community and survivor assemblages, most of these traits are changing at only a fraction of the rate required to maintain equilibrium with climate. The recruit communities show the best tracking of a changing climate.

The community trait shifts were similar for the survivor and full community assemblages and, although significant in several cases, these have been rather small over the past 40 years. In general, such community trait changes differ from those of the recruit and fatality assemblages. This is likely because the trait shift responses of the survivor and full community assemblages are dominated by large individuals that continued growing throughout the study period. Another potential explanation is that the survivor and full community assemblages, along with their concurrent functional trait composition, are still able to withstand the observed changes in climate. The survivor and full community assemblages have shifted toward more deciduous communities with higher $A_{sat}$, leaf chemistry, and $H_{max}$. At the same time, we uncovered a general decrease in leaf thickness for the survivor and recruit assemblages. Temporal increases in VPD have potentially favored increases in the proportion of DE, especially across montane forests, and increases in MCWD partially explain decreases in leaf thickness. Overall, DE tend to have acquisitive leaf traits with higher leaf N and P contents, $A_{sat}$, and photosynthetic N-use efficiency, especially under water stress (56), than do evergreen species (57, 58). The pattern

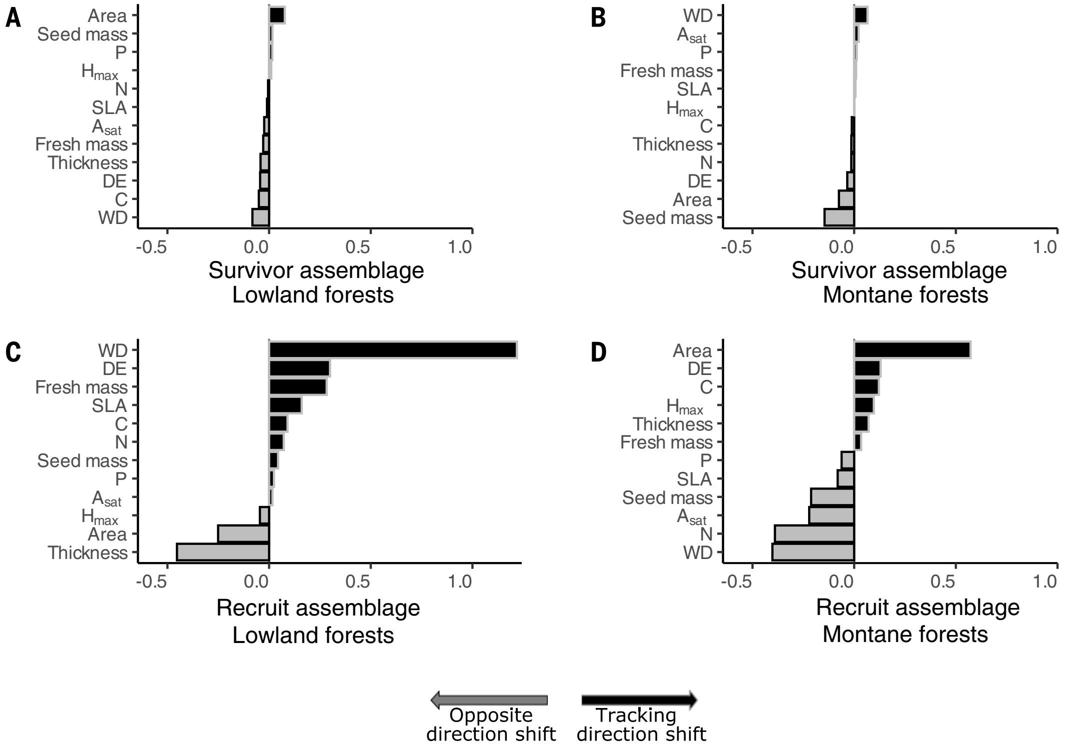

**Fig. 6. (A to D) Tracking of trait CWM for the survivor [(A) and (B)] and recruit [(C) and (D)] assemblages in lowland [(A) and (C)] and montane [(B) and (D)] forests given the observed changes in climate across the sampling plots.** The *x* axis shows the ratio of changes in trait CWM based on actual trait CWM changes observed at the plot level through time, versus expected changes in trait CWM based on spatial climate-trait relationships given observed changes in climate. Positive values (black bars) indicate that observed and predicted changes are both positive or both negative and thus are going into the same direction, whereas negative values (gray bars) indicate that observed and predicted changes are going in opposite directions. A ratio of change value of one would indicate perfect tracking. The *y* axis shows the traits sorted by the change ratio amount (see full statistical details in tables S6 and S7). Values of zero and close to zero represent no or slight trait shifts.

observed across tropical American forests could be attributable to leguminous N-fixing species that dominate in dry forests, which are often deciduous and have higher photosynthetic N-use efficiency (*59*). This is consistent with a previous report for West African tropical forests, where increasing drought stress co-occurred with an increased abundance of DE, and changes in DE explained changes in other morphological, structural, and leaf chemistry traits (*55*). The abundance of DE may be limited by soil fertility (*60*) in areas such as in southeastern Amazonia (more so the Guiana Shield), where short-lived deciduous leaf construction is too costly. Thus, increase in DE is expected to be one adaptation strategy, especially in dry tropical forests with more seasonal precipitation regimes and nutrient-rich soils than wetter tropical forests.

There is a mismatch in trait responses to climate change between the recruit assemblage and both the full community and survivor assemblages. This mismatch is most pronounced with respect to the abundance of DE, leaf C content, and $H_{max}$. With increasing temperatures and reduced water availability, we expected an increase in abundance of DE to also be reflected in the recruit assemblage (*55*). However, the decline in abundance of DE in the recruit assemblage indicates potential shifts in phenological strategies toward more conservative strategies in response to increasing temperatures or altered precipitation patterns. The recruit assemblages also select for lower leaf C content and species with shorter $H_{max}$. This finding suggests a decoupling in trait space between the functional trait characteristics of the mature forests that we see in the present and the possible future functional composition of tropical American forests. The selection for low leaf N content in the recruit and fatality assemblages raises the question of whether and to what extent such recruit assemblages will be able to survive to larger adult sizes (e.g., *56*, *61*), especially across montane forests, where there is a stronger mismatch. Such a decoupling in trait space between the recruit and survivor assemblages could potentially indicate the slow beginnings of forest-level adjustment to new climatic conditions, which is likely to affect the functioning of tropical forest ecosystems (*62*). We did not find a significant selection against DE in the fatality assemblage. This suggests that a combination of drought avoidance and drought resistance strategies (*38*) could both be playing an important role in adaptation to a warming climate across lowland and montane tropical forests.

Other factors may be promoting the observed change in community-mean traits, such as species interactions and defaunation, the latter being a potentially important driver of changes in dispersal traits across time (*63*). Some wetter regions (e.g., central Amazonia) show slight increases in SM for the full community (fig. S4D), with the fatality assemblage showing significant declines in individuals with smaller seeds in the lowlands (Fig. 5). However, drier regions (e.g., the southern and eastern fringes of Amazonia) and montane forests show a slight predicted decline in SM (fig. S4D). These changes may be an indicator of defaunation pressure (*64*), because spatial predictions of decreases in SM broadly match spatial patterns of high defaunation (*65*), especially in those more accessible areas of Mesoamerica and in both southern and eastern Brazil. They could also be driven by climatic factors because the observed changes are consistent with a shift from endozoochory (animal dispersal) to anemochory (wind dispersal), with the latter exhibiting smaller seeds than those dispersed by animals and being more prevalent in drier biomes (*41*). Including other relevant traits, such as those related to hydraulics and thermal tolerance, and considering ecological interactions could further bring new evidence of these potential forest adjustments to a changing climate.

The survivor, full community, and recruit assemblages often show more changes in traits in lowland than montane forest. Lowland forests are highly dynamic and harbor a high functional trait diversity that potentially allows for selection from a wider pool of trait values under climate stress. There has been a larger increase in atmospheric VPD in lowland forests than in montane forests caused by more pronounced increases in temperature over the past 40 years, which could partially explain the shift of a larger number of community functional traits in lowland forests than in montane forests (66). Larger increases in VPD and more severe droughts appear to have modified the community composition of lowland forests more strongly than that of montane forests toward a set of species better adapted to drier and hotter conditions, which could be due to the mortality of more vulnerable species (51). Recent work across sites in the Amazon and the Andes also suggest an important impact of increasing temperatures and declines in water availability on tree trait composition (67). We investigated the impact of macroclimate on the changes in functional trait composition of tropical forests. However, such macroclimate conditions may not directly mirror the microclimatic conditions, such as temperature, found under the forest canopy (68). This is of particular importance when investigating the effects of a changing climate, especially on the recruit assemblages, which tend to occupy the space below the canopies of the older, larger trees. Ultimately, such microclimatic conditions may play an important role in determining the responses of understory plants to a changing climate (45, 69, 70) and therefore the rate of change in community trait composition of the recruit assemblages. Therefore, microclimatic conditions at the plot level may partly explain the differences in trait shifts between the full community and survivor assemblages and the recruit assemblages.

It would mechanistically be expected that increasing drought would cause plant communities to shift to species with higher WD and thicker leaves or that the abundance of DE would increase across time. Such coordinated changes may not readily happen in the community because it is whole phenotypes that are changing, i.e., particular combinations of traits rather than isolated traits. Moreover, coordination of different strategies could allow for alternative adaptations to the same drivers. For example, drier conditions might encourage DE combined with low WD and thin leaves (drought avoidance) or evergreenness combined with high WD and thicker leaves (drought tolerance). The favored combination(s) may depend on forest seasonality patterns and soil nutrients. Furthermore, not all trait combinations may be present in any given regional species pool, even in species-rich biomes, which may limit the shifts in community traits that can occur at any given time as a response to environmental change. Other factors may also contribute to trait shifts or a lack thereof across forest communities. These include soil conditions (71), biotic interactions (e.g., animal-plant interactions) (72), and wind disturbance (73). Our analyses represent community-wide responses mainly based on trait information at the species and genus level; traits may also express intraspecific plasticity that we are unable to assess here given the scale and multidecadal nature of the study. Some traits may show more or less plasticity than others, and species-intraspecific variation may contribute to adaptation to a changing climate (74, 75). Overall, there is a lack of knowledge and data on the extent to which intraspecific trait variation plays a role in the adaptation of tree communities to a changing climate across the tropics. Here, we analyzed only a set of relevant plant functional traits without adding information on intraspecific trait variation. Further research could focus on understanding responses of tree communities to climate change, including as much as possible information on intraspecific trait variation, and analyzing other relevant traits. These could be hydraulic and thermal tolerance traits, which at the moment are not widely available across tropical American forests.

In conclusion, we found that overall changes in community trait composition are leading to small shifts amounting to only ~10% of the expectation given climate change. These shifts are primarily driven by variation in growth rates of existing trees rather than by recruitment or tree mortality. However, we observed larger changes for the recruit assemblage, directionally tracking climate at an average of 21%, which can potentially contribute to keeping these forests closer to, although still far from, the equilibrium with climate. Trees are long-lived organisms with slow turnover rates compared with the rate of climate change, and this partly explains the differences observed in community trait shifts between the full community and those of the recruit assemblages. There are specific areas where there seems to be a larger lag in forest responses to climate changes, especially in the Maya Forest in Mesoamerica (76) and both the Atlantic Forest and the southern Amazon Forest in Brazil (77), which have become increasingly fragmented over time. Consequently, the impacts of other disturbances across these regions, such as habitat fragmentation and in general a more constrained physical environment, may be affecting the capacity of forests to adjust to new climate conditions (43, 78). Our analysis demonstrates that tree community composition is shifting to track climate change, but that the overwhelming onus would have to be on within-species variability and trait plasticity (79, 80) to adequately do so. However, the changes in climate are likely to be too fast for adaptive phenotypic plasticity to keep track, especially in environments with low climatic heterogeneity (70, 80). Thus, it is overwhelmingly likely that the tree species composition and functional properties of tropical American forests (and probably all tropical forests) are increasingly out of equilibrium with local climate. Such disequilibrium almost certainly increases vulnerability to a further changing climate.

## Methods summary

### Understanding trait CWM-climate relationships and the effects of climate change on driving trait CWM changes

To understand the current trait-climate relationships across forests of the tropical Americas, for each plant trait, we modeled the trait CWM as a function of climatic and soil covariates, with each one of the climatic variables interacting with forest type (lowland or montane) (hereafter referred to as M1). We next analyzed the climatic drivers of shifts in each functional trait given observed changes in climate over the past 40 years for the full community and survivor assemblages, for the recruit community, and for the fatality community. The fatality community is defined as those individuals of a plot that were alive in a previous census but dead in the following census. We calculated the temporal changes in trait CWM at the plot level as the $\Delta r$ to standardize for a different time between censuses for different plots. We then modeled the $\Delta r$ CWM trait as a function of $\Delta r$ of the climatic variables described above, with each of these interacting with forest type, and also included the soil characteristics (hereafter referred to as M2).

### Understanding shifts in trait CWM

We used the $\Delta r$ of the trait CWM of the full, survivor, recruit, and fatality community assemblages to investigate whether the rate of trait changes for the overall forests (lowland and montane together), for the lowland forests alone, and for the montane forest alone was significantly different from 0. We did the same to determine whether there were important differences between the rate of change between lowland and montane forests. To this end, we performed a version of a typical $t$ test analysis using Bayesian estimation (81, 82). As above, here, we calculated the HDI containing the 95% most probable effect values and considered a result significant when the HDI did not overlap 0.

### Understanding whether forest community traits are tracking climate changes

The process outlined below was performed only for the full community assemblage and the survivor and recruit assemblages because the fatality assemblages are not tracking climate. We first built the same type of statistical models as M1 but using only plot and climatic data from between 1980 and 2005, including also the soil variables (hereafter referred to as M1.1). We used the M1.1 trait-environment statistical models and obtained predictions of the trait CWM to a new set of climatic conditions composed of the 1980 to 2005 climate plus the observed climate yearly rate of change across the study period (hereafter referred to as M2). We then calculated the difference between the trait CWM obtained with the M1.1 and M2 models to obtain the expected trait CWM change. Finally, we compared the expected trait CWM calculated above with the observed $\Delta r$ CWM trait. This allowed us to understand the expected shift in mean trait values given the 1980 to 2005 trait-climate relationship compared with the observed trait changes across time (i.e., from 1980 to 2021). We tested for significant differences between observed and expected community trait changes using Bayesian estimation (*81*, *82*). We also created map predictions of the 1980 to 2005 M1.1 trait-climate model across tropical American forests by predicting this model to a climate change scenario that was composed of the observed climate (1980 to 2005) plus the yearly rate change observed. We then subtracted the original map predictions (i.e., those made with the M1.1 models without changes in climate conditions) to obtain the expected CWM trait changes at the pixel level (in the map) for across forests in tropical America. Next, we calculated the ratio of the observed, i.e., spatial predictions of the trait changes observed across time (from M2 models) versus the expected and converted to percentage change relative to the 1980 to 2005 condition to determine whether and to what extent the observed trait changes are tracking (values above zero) or not (values of zero) the expected changes given the observed changes in climate or shifting in opposite direction than expected (values below zero).

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Given data sovereignty from the original data owners, raw data on vegetation censuses across time are not publicly available but can be requested by contacting all researchers through the ForestPlots (*30*) data request protocol described in forestplots.net/en/join-forestplots/working-with-data. Raw climate data can be accessed through the TerraClimate database at https://www.climatologylab.org/terraclimate.html (*48*). The SPEI data can be obtained from the SPEI database at https://spei.csic.es/ (*83*). The computer code used to reproduce the main findings in this manuscript (*84*) and the plot-level processed data (*85*) are archived in the Zenodo repository at https://zenodo.org/.

## SUPPLEMENTARY MATERIALS

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Materials and Methods
Figs. S1 to S11
Tables S1 to S7
References (*86*–*95*)

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