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

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Abstract: Understanding ecosystem responses to climate change is among the greatest challenges in biosphere science. This challenge is particularly acute in high biodiversity tropical forests. Here we examine how the functional composition of tropical forests of the Americas has shifted in recent decades. We found that functional shifts in the tree assemblages are insufficient to keep track with what would be expected given observed climate change, typically changing less than 8% of the required amount because of intrinsic inertia in tree demography. However, recruiting assemblages show stronger shifts of 21% of the proportional climate change expectation. Overall, trees of the most diverse forests on Earth are changing in functional trait composition, but at a rate that is insufficient to track climate change.

One-Sentence Summary: The composition of tropical forests in the Americas is changing but not fast enough to keep track of climate change.

Main Text

Forest responses to human-driven perturbations like climate change will determine the diversity and function of the terrestrial biosphere through this century and beyond. Here we focus on tropical American forests (henceforth referring to all forests encompassing continental areas from Brazil to Mexico). These 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, 4, 5*), it is both critical and urgent to understand the ability of these complex systems to adapt to change and survive.

The relationships between environmental conditions, plant performance, and distribution is mediated by species' functional traits (*6, 7, 8*). These morphological, structural, chemical, and phenological characteristics show consistent relationships with climate and other drivers, such as soil conditions and biotic interactions (*9*). Notably, recent work has shown positive relationships between mean annual temperature and leaf area, specific leaf area, leaf nitrogen, wood density, seed mass (*10*), and leaf thickness (*11*). Other work has detected a negative relationship with elevation for specific leaf area, and leaf nitrogen (11). Hence, a traits-based approach provides a promising framework for predicting the impacts of climate change and resilience across forest ecosystems (*7, 12, 13*). Such a framework can be used to understand responses of key ecosystem functions, such as forest carbon storage responses to climate change and extreme events (*14, 15*).

Tropical land regions are experiencing rapid climate change (*16*), which is already affecting tropical American plant communities. In Amazonia, changes in precipitation patterns and more frequent droughts have led to an increase in the recruitment of dry-affiliated species (xerophilization) (*17*). In the Andes, rising temperatures have led to increasing abundances of species tolerant to higher temperature (thermophilization) (*18*). Across Mesoamerica it is expected that climate change will cause an expansion of tropical dry forests to higher elevations (over 200 m above current average elevation) (*19*). However, tree species may be unable to shift their distribution fast enough to track their climatic niche, given their slow demography and the prevalence of dispersal limitation and competitive abilities (*20*), with such responses also being determined by environmental tolerances at different life stages (2*1*). Moreover, recent work has shown large range contractions of tree species rather than range shifts (*22*). 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 of close to 20% by 2100 (*23, 24, 25*). This would expose current species assemblages to climates they have not previously experienced (*26*), potentially selecting for future plant communities adapted to such climates but unlike those currently observed (*27*). Community responses to climate change will thus likely depend on underlying mechanisms and geographical context.

If species respond to climate change via migration, we would expect montane communities to track climate change better than those in the lowland forests because different climate conditions occur at shorter distances and hence are potentially easier to migrate to than in the lowlands (*28, 29, 30, 31*). Given exposure to a drying and warming climate, we could reasonably expect increased abundance of species exhibiting more drought-tolerance traits (i.e. in the 'slow' plant economics spectrum) (*32*), such as high wood density (e.g. to prevent cavitation) (*33*) and smaller, thicker leaves (e.g. for lower evapotranspiration and reduced radiation exposure) *(34)*. Other drought-avoidance traits, notably deciduousness (often associated with more acquisitive leaves), could also become more prominent in the future as an adaptation to increasing drought conditions and to past disturbances (*35, 36*). Seed traits play a pivotal role in the reproduction and dispersal, or migration capacity of species (*37*). Under a warming and drying climate we might expect species with smaller seeds to increase in abundance *(38)*. This is because wind-dispersed seeds, most frequent in drier and more seasonal biomes, tend to be smaller than animal-dispersed seeds (*39*). However, other factors, such as defaunation of frugivorous seed-dispersing large mammals and birds, may more strongly drive their shifts at short time scales (*40*). We would also expect montane forests to show stronger functional responses to climate change than lowland forests given their more varied climatic conditions at shorter distances (*18, 41*) and due to differences in soil nutrient availability (e.g., N:P ratios) across elevation gradients (*42*).

It is still unclear how shifts in the abundance and distribution of species translate into changes in functional composition, and what functional changes have occurred through the last half century as a response to the onset of a warmer, drier and more variable climate across the tropical Americas. Moreover, it is unknown if forest level functional shifts are more attributable to the surviving tree individuals or 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.

Here, we address these knowledge gaps by monitoring and analysing 415 long-term forest plot sites spanning more than 40 years (1980 - 2021) and encompassing >250,000 individual trees across the tropics from Mexico to southern Brazil. In these sites, tree diversity, structure and function were observed on the ground over the long term. Our effort spans structurally intact forests from the lowland tropics (hereafter forest plots <700 m elevation, see methods) to pre-montane and montane forests (>700 m elevation; henceforth referred to as montane) from the Andes to subtropical fringes (Fig. 1; Table S1). We combine this monitoring and analysis of changes in the plant community composition dataset with measurements and detailed assessment of 12 plant functional traits involved in responses to a changing climate. These include photosynthetic capacity (A_{sat}), leaf chemistry (content of carbon: C, nitrogen: N and phosphorus: P), leaf area (Area), specific leaf area (SLA), leaf fresh mass (FM), leaf thickness (Thickness), abundance of deciduous species (DE), maximum species tree height (H_{max}), wood density (WD) and seed mass (SM) (Table S2). We first investigate current plant trait-environment relationships for lowland and montane forests. We examine how and where these ecosystems have shifted in their functional trait composition due to changes in the plant community taxonomic composition. Because of the long lifespan of tropical trees (*43*) and their slow turnover, we performed this analysis at the whole community level, for survivors, and for the recruiting and mortality assemblages, with the last two expected to show faster change. We also analysed if observed changes in trait composition have been enough to track climate change to date. This climate change tracking analysis was carried out for the full community, survivors and the recruitment assemblages and not for mortality because these individuals will not contribute to future change. We hypothesise that for most traits there will be a consistent trait-climate relationship but this will vary according to functional trait and forest type, and that lowland and montane forests will differ in their functional responses to climate change given their different exposures to climatic conditions with spatial distance. We expect that, given the long lifespan of tropical trees and rapid pace of recent climate change, forests will demonstrate ecological inertia, so that changes in functional composition lag behind changes in climate.

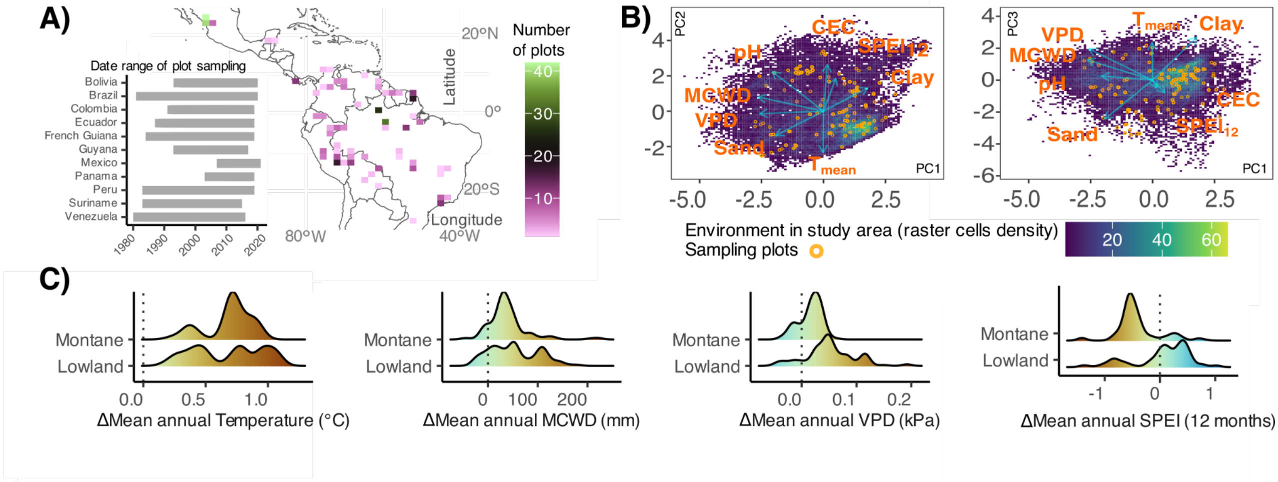


Fig. 1. Study area showing the distribution and number of vegetation plots sampled across time (A), principal component analysis (PC1, PC2 and PC3) depicting the climate and soil chemistry and texture space available in the study area (T_{mean}: mean air temperature, MCWD: maximum climatic water deficit, $SPEI_{12}$: standardised

precipitation-evapotranspiration index, VPD: vapour pressure deficit, CEC: soil cation exchange capacity, soil pH, sand and clay amount) and the location of the sampling plots in the environmental space (B), and change in climate conditions (1980-1990 vs 2010-2020) in the plot network (C). In B) PC1 is mainly loaded by the maximum climatic water deficit (MCWD: -0.527) and Vapour Pressure Deficit (VPD: -0.515), PC2 by air temperature (T_{mean}: -0.465) and soil cation exchange capacity (CEC: 0.524) and PC3 by soil clay % (-0.535) and soil sand % (0.486). In C) the vertical dotted lines indicate zero change. Brown colours depict increases in temperature, drier conditions (for MCWD and VPD) or increased drought intensity (for SPEI: standardised precipitation evapotranspiration index). Blue colours depict an increase in water availability. In MCWD larger positive values indicate higher water stress. Climate data was derived from the TerraClimate project (*44*) and soil data from SoilGrids.org.

Current trait-environment relationships

To evaluate contemporary trait-climate relationships across tropical American forests, we used data from 415 forest plots (mean plot size 0.88 [min: 0.12 , max: 25] ha and 5.7 [min: 2, max: 41] censuses per plot), for which we extracted climate (*44*) and soil (SoilGrids.org) data for their sampling years (1980-2021). As the most dominant species are expected to drive ecosystem processes (*45*), for each plot we calculated the community-weighted mean of each plant functional trait (Table S2; Methods) based on the relative basal area of the species and their trait value (hereafter "community functional traits"). We then modelled 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 (between 1980-2021) of temperature (T_{mean}), vapour pressure deficit (VPD_{mean}) (*46*), maximum climatic water deficit ($MCWD_{mean}$, here with positive values depicting higher water stress) (*47*) and standardised precipitation-evapotranspiration index ($SPEI_{12}$) (*48*), each one of these interacting with forest type (lowland or montane) (Methods). In order to control for possible soil effects which impact plant distributions (*13*), we included the additive effect of cation exchange capacity (CEC), pH, and the percentage of clay and sand for each plot location in the models (Methods).

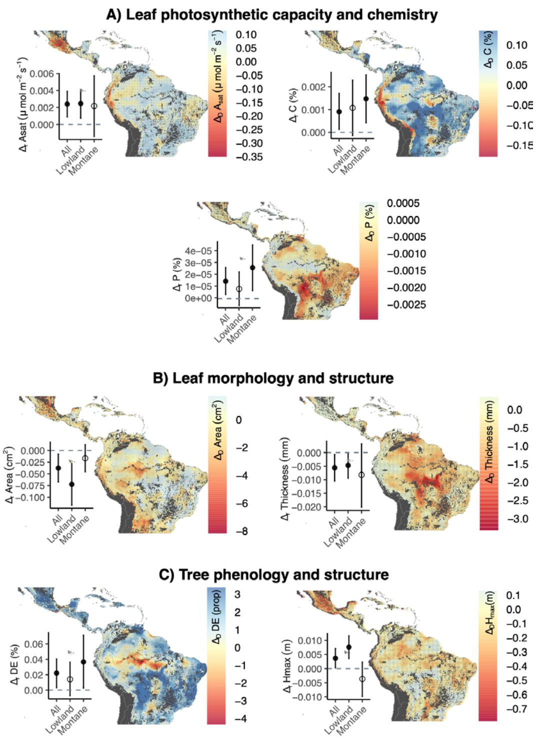
Several community functional traits show consistent relationships with climate, with temperature showing some of the strongest effects (Table S3; Fig. S2). For both lowland and montane forest types, an increase in temperature (T_{mean}) across space is associated with an increase in community-mean leaf area and seed mass, and a decrease in photosynthetic capacity, specific leaf area, and the proportion of deciduous species. However, the geographical relationship across lowland and montane forests is not consistent for leaf chemistry (leaf carbon, nitrogen and phosphorus content), wood density, maximum species tree height, leaf fresh mass or leaf thickness (Fig. S2). An increase in water stress ($MCWD_{mean}$) is associated with an increase in photosynthetic capacity, leaf nitrogen content, leaf area and wood density across lowland forests and decreases in montane forests, with decreases in specific leaf area and maximum species tree height for both forest types (Table S3; Fig. S2). The increase in these leaf traits in drier forests could be associated with the high photosynthetic rates generally attained by deciduous species over the growing season (*49, 50*) and the fact that lower maximum tree height and higher wood density tend to correlate with higher resistance to lethally low levels of soil moisture availability (*51*). However, consistent climatic relationships across both forest types are not apparent for the other traits analysed (Table S3; Fig. S2). One plausible explanation is that this reflects their different position along the climatic gradient (i.e. temperature and precipitation), with lowlands occupying areas with more homogeneous climate conditions across large spatial extents in comparison to montane forests, which span a large range of climates across smaller spatial extents. Alternatively, the differences between lowland and montane forests are potentially due to additional variables, such as cloud immersion effects in upper montane forests, which could shift the nature of trait-environment relationships given the lower radiation and temperature, and higher water availability across the year (*52, 53, 54*).

Changes in trait composition across time

We next analysed if and how the functional trait composition of tropical American forests has shifted, and how much of this can be explained by observed changes in climate over the past 40 years (Methods). We first calculated the community-weighted mean (CWM) of each plant functional trait for each vegetation census available for the full live tree community (i.e. including all trees alive in a given census), henceforth 'full community assemblage', and separately for the survivor tree assemblage (individuals that are alive in two subsequent censuses, e.g. from census one to census two), tree recruitment (individuals not present in the previous census and recruited in the subsequent census) and tree mortality (individuals alive in previous census but dead in the subsequent census) assemblages. We define the recruiting assemblage as individuals that passed the threshold of 10 cm DBH in a given census and were not present in the previous census. Then we calculated their yearly rate of change across time (Methods). We tested if the changes in trait CWM differed from zero when using all vegetation plots together and when 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 (Methods). 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 out of the 12 traits analysed exhibited significant changes in their CWM values (insets in Fig. 2). Only leaf nitrogen, fresh mass, specific leaf area, seed mass and wood density did not show significant shifts across time (Table S4; Fig. S3). The survivors assemblage showed the same pattern of community trait changes (Table S4; Fig. S4) as the full community assemblage with the main differences being a significant decrease in leaf fresh mass in the lowlands for the survivors assemblage. Hence, hereafter we focus on the results from the full community, recruiting and mortality assemblages. From the community traits with significant changes, we found an average increase in photosynthetic capacity of 0.0024 μmol m^{-2} s^{-1} year^{-1} (HDI-low and HDI-high: 0.0009, 0.0039), leaf carbon content 0.0009% year^{-1}(0.0001, 0.0017), phosphorus 1.5×10^{-5}% year^{-1} (3.58×10^{-6}, 2.63×10^{-5}), the abundance of deciduous species 0.02 % year^{-1} (0.003, 0.04) and species maximum height 0.0037 m year^{-1} (0.0002, 0.007), while community leaf area decreased on average -0.03 cm^2 year^{-1} (-0.06, -0.007) and leaf thickness decreased -0.005 mm year^{-1} (-0.01, -0.0007) (insets in Fig. 2; Table S4). In the lowland forests, we detected significant trait changes for four (increasing: photosynthetic capacity and species maximum height; decreasing: leaf area and thickness) out of the 12 traits analysed (Table S4; insets in Fig. 2). Montane forests showed significant increases in leaf carbon, phosphorus and the abundance of deciduous species (Table S4; Fig. 2 insets).

Fig. 2. Estimated changes in mean community functional trait values across time for tropical American forests. Only traits with significant changes are shown, with others shown in Fig. S3. A) Changes in trait community-weighted mean (CWM) for leaf photosynthetic capacity and leaf chemistry traits, B) for leaf morphology and structural traits and C) for tree phenology and structural traits. The insets in the left-hand side of each map show the observed yearly rate of change, obtained from sampled vegetation plots, from the statistical models in Table S4 for all forests together and only for lowland or montane forests. In the A-C insets, significant shifts are shown as filled circles and non-significant as empty circles. The vertical lines depict the Highest Density Intervals (95% HDI), and the horizontal grey dotted line indicates zero change. Maps show the decadal predicted changes (ΔD) in trait CWM across tropical American forests given changes in climate derived from the statistical model fits with R-squared values ranging between 0.21 and 0.34 (Table S5). In the maps, warmer colours represent decreases in the trait CWM, and cooler colours increase in the trait CWM, with yellow-white colours representing slight or no change. The grey mask on the background of each map represents all predominately non-forested areas (e.g., crop fields, swamps, open woodland, areas with small patches of trees, deserts and alpine regions) and was derived from the European Space Agency Land Cover CCI Product (*81*). A_{sat}: photosynthetic capacity at light saturation, C: leaf carbon content, P: leaf phosphorus content, Area: leaf area, Thickness: leaf thickness, DE:



deciduousness, H_{max}: adult maximum height. R-squared values of community functional trait model predictions range from 21%-34% and are shown in Table S5.

The recruitment assemblage experienced significant changes for seven traits, with six showing decreases, i.e. leaf carbon content -0.014% year^{-1} (-0.02, -0.001; in montane forests), leaf nitrogen content -0.002% year^{-1} (-0.004, -0.0002), leaf thickness -0.04 mm year^{-1}(-0.08, -0.01), deciduousness -0.17 % year^{-1} (-0.33, -0.02), tree adult maximum height (-0.03 m year^{-1} [-0.07, -0.003], and WD: -0.0007 g cm^{3} year^{-1}). The leaf fresh mass of recruits increased on average 0.04 g year^{-1} (0.006, 0.08; all but leaf carbon in lowland forests; insets in Fig. 3; Table S4).

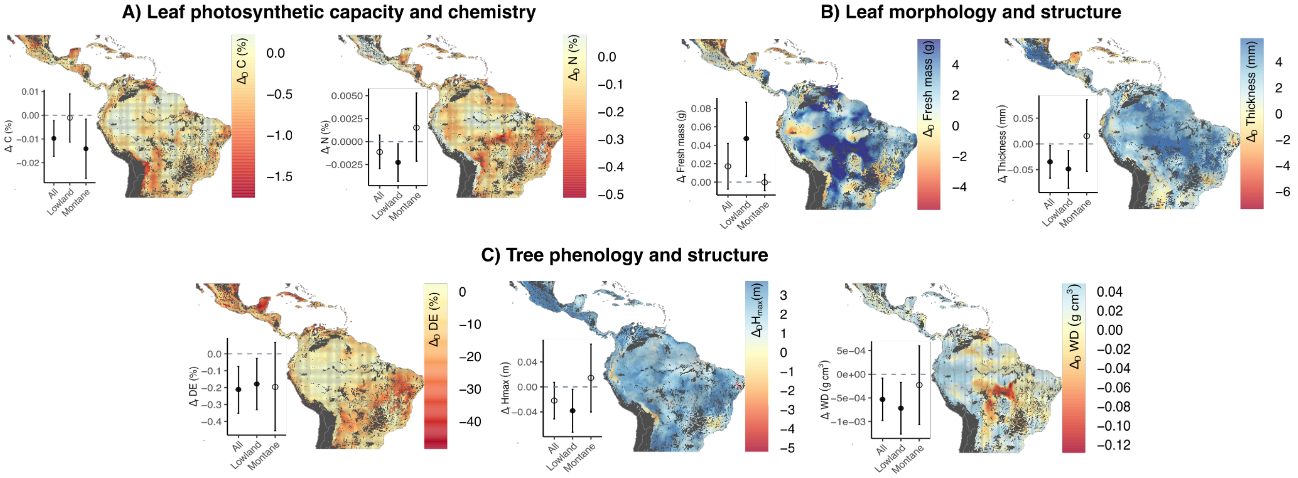


Fig. 3. Estimated changes in mean community functional trait values across time for tropical American forests for the recruitment assemblage. Only traits with significant changes are shown, with others shown in Fig. S5. A) Changes in trait community-weighted mean (CWM) for the recruitment assemblage for leaf chemistry traits, B) for leaf morphology and structural traits, and C) for tree phenology and structural traits. There were no significant changes recorded for dispersal traits. The insets in the left-hand side of each map show the observed yearly rate of change, obtained from sampled vegetation plots, from the statistical models in Table S4 for all forests together and only for lowland or montane forests. In the A-C insets, significant shifts are shown as filled circles and non-significant as empty circles. The vertical lines depict the Highest Density Intervals (95% HDI), and the horizontal grey dotted line indicates zero change. Maps show the decadal predicted changes (ΔD) in trait CWM across tropical American forests given changes in climate as a result of the statistical model fits with R-squared values ranging between 0.43 and 0.65 (Table S5). In the maps, warmer colours represent decreases in the trait CWM, and cooler colours increase in the trait CWM, with yellow-white colours representing slight or no change. The grey mask on the background of each map represents all predominately non-forested areas (e.g.,

crop fields, swamps, open woodland, areas with small patches of trees, deserts and alpine regions) and was derived from the European Space Agency Land Cover CCI Product (*81*). C: leaf carbon content, N: leaf nitrogen content, Fresh mass: leaf fresh mass, Thickness: leaf thickness, DE: deciduousness, H_{max}: adult maximum height, WD: wood density.

For the mortality assemblage, only the CWM of leaf nitrogen content -0.004 % year^{-1} (-0.007, -0.001; montane forests), leaf fresh mass, -0.02 g year^{-1} (-0.05, -0.0003) and seed mass -17.7mg year^{-1} (-29.9, -5.7) in lowland forests experienced significant declines (insets in Fig. 4; Table S4).

To help identify the underlying climatic drivers of forest functional change, we used multivariate linear models to estimate the yearly change (Δr; i.e. from first to last census), in the trait values (Δ_r trait CWM) as a function of the yearly rate of change in temperature (ΔT_r), maximum climatic water deficit ($\Delta MCWD_r$), standardised precipitation-evapotranspiration index ($\Delta SPEI_r$) and vapour pressure deficit (ΔVPD_r), each one of these interacting with forest type, and accounted for soil characteristics by including in the models the CEC, pH, clay and sand content (Methods; maps in Fig. 2, Fig. 3 and Fig. 4). Our results for the full community assemblage, survivors and for recruitment and mortality assemblages (Table S5) 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 S5). Our mapped model predictions (Fig. 2, Fig. 3 and Fig. 4 maps) depict in a spatially explicit way areas where stable CWM trait values (light yellow and light blue), 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.

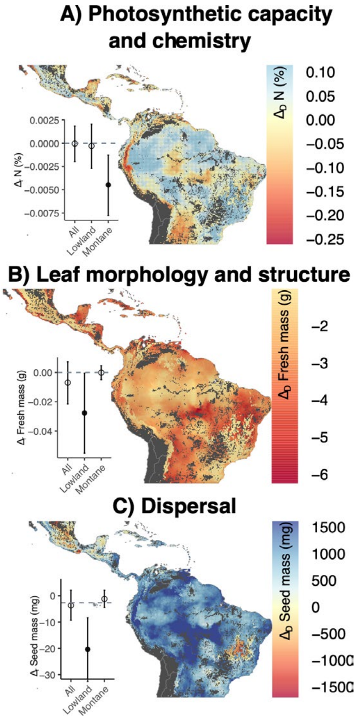


Fig. 4. Estimated changes in mean community functional trait values across time for tropical American forests for the mortality assemblage. Only traits with significant changes are shown, with others shown in Fig. S6. A) Changes in trait community-weighted mean (CWM) for the mortality assemblage for leaf chemistry traits, B) for leaf morphology and structural traits, and C) for dispersal traits. There were no significant changes recorded for tree phenology and structural traits. The insets in the left-hand side of each map show the observed yearly rate of change, obtained from sampled vegetation plots, from the statistical models in Table S4 for all forests together and only for lowland or montane forests. In the A-C insets, significant shifts are shown as filled circles and non-significant as empty circles. The vertical lines depict the Highest Density Intervals (95% HDI), and the horizontal grey dotted line indicates zero change. Maps show the decadal predicted changes (ΔD) in trait CWM across tropical American forests given changes in climate as a result of the statistical model fits with R-squared values ranging between 0.43 and 0.65 (Table S5). In the maps, warmer colours represent decreases in the trait CWM, and cooler colours increase in the trait CWM, with yellow-white colours representing slight or no change. The grey mask on the background of each map represents all predominately non-forested areas (e.g., crop fields, swamps, open woodland, areas with small patches of trees, deserts and alpine regions) and was derived from the

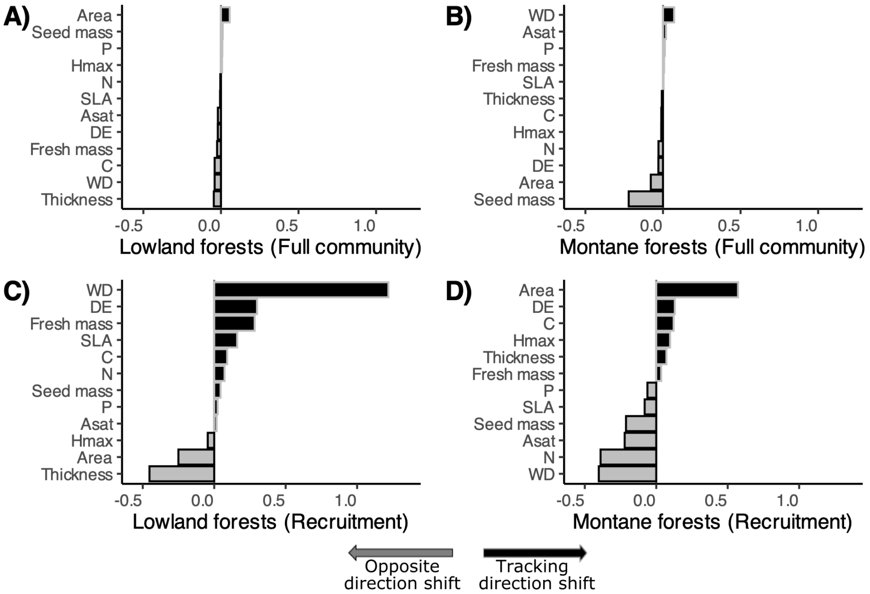
European Space Agency Land Cover CCI Product (*81*). N: leaf nitrogen content, Fresh mass: leaf fresh mass, Seed mass: seed mass weight.

Can tropical American forest functional composition track climate change?

We next examined whether the observed community trait changes are sufficient to maintain expected trait-environment relationships for the full community, the survivors, and the recruiting assemblages. We expected recruitment to be more sensitive to climate change as 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 (1980-2005; i.e., as baseline CWM trait-environment relationships). We took our observed trait-climate relationships (built with the 1980-2005 period data; Table S6) and used them to predict the trait CWM to the 1980-2005 climate conditions plus the observed changes in climate across the study sites for the full time period (the last 40 years; Methods; Table S4). This allowed us to predict the CWM trait values that the forests should have if they fully tracked recent climate change (Tables S7 and S8). The ratio between the observed and the expected changes (for the full and the recruiting assemblages) indicates how well these forest traits are tracking these climate equilibrium predictions based on community changes alone (Methods; Fig. 5).

Our results show that for all measured traits of the full community and survivor assemblages, tree species community composition is not changing sufficiently to track climate change but that the recruiting community shows the largest shifts (Fig 5; results for survivors and mortality assemblages in Fig. S7). At the region-wide scale for the full community assemblage, all traits show less than 6% (average of 1.9% of positive shifts) for lowland forests and 7% (average of 2% of positive shifts) for montane forest of the change required. Several traits show very little change or even modest changes in the opposite direction to those expected (Fig. 5A and Fig. 5B; Table S7 and Table S8). For the survivor assemblages, all traits show less than 8% (average of 2.8% of positive shifts) for lowland forests and 4% (average of 1.7% of positive shifts) for montane forest of the change required (Fig. S7). We detect larger community trait shifts in the recruiting assemblages of an average 21.8% of the change required for lowland forests and 17.5% for montane forests when only positive tracking traits are considered. When both positive and negative tracking is considered, the recruitment assemblage shows an average tracking of 11.4% for lowland and -0.67% for mountain forests (Fig. 5C and Fig. 5D; Table S7 and Table S8). In lowland forests, community mean wood density appears to be changing fast enough in the recruiting assemblages to track climate change expectation. Overall, we see some evidence of how the recruiting 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 recruiting community does not seem to be changing quickly enough to track climate change. More significant community trait shifts have occurred in lowland than in montane forests, which is consistent with a more rapidly drying climate in lowland forests (Fig. 2, Fig. 3 and Fig. 4; Table S4).

Fig. 5. Tracking of trait community weighted mean (CWM) for the full live (A, B) and recruiting (C, D) assemblages in lowland (A, C) and montane (B, 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, hence, are going into the same direction, whereas negative values (grey 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 Table S7 and Table S8). Values of zero and close to zero represent no or slight trait shifts. A_{sat}: photosynthetic capacity at light saturation, C: leaf carbon content, N: leaf



nitrogen content, P: leaf phosphorus content, Area: leaf area, Fresh mass: leaf fresh mass, SLA: Specific leaf area, Thickness: leaf thickness, DE: deciduousness, H_{max}: maximum height, WD: wood density, Seed mass: weight of the seed.

Overall, we find that 1) trait-environment relationships are similar for most traits across lowland and montane tropical American forests; 2) lowland forests show significant and larger changes in more community traits than montane forests; 3) across the forests and for the full community and survivor assemblages, the abundance of deciduous species is increasing, with accompanying increases in leaf photosynthetic capacity and decreases in leaf area and leaf thickness. However, the recruiting communities in the lowland forests have on average decreased in the abundance of deciduous species, leaf carbon and nitrogen content and wood density; and 4) crucially, for the full tree community and survivors assemblages most of these traits are changing at only a fraction of the rate required to maintain equilibrium with climate. Notably, the recruiting communities show the best tracking of a changing climate.

The community trait shifts were similar for the full community and the survivor assemblages but generally differed from those of the recruitment and mortality assemblages. This is likely because the trait shift responses of the full community and survivor assemblages are dominated by large individuals that continued growing throughout the study period. Although large individuals would have the highest impact on ecosystem functioning (*45*) due to their size and long lifespans, the functional responses of the community to ongoing climate change may be more evident when analysing the functional traits of recruiting individuals. Moreover, it is the recruiting communities that will eventually dictate future community traits. There is a mismatch in trait responses to climate change between the recruiting assemblage and both the full community and survivor assemblages. This mismatch is most pronounced with respect to the abundance of deciduous species, leaf carbon, and maximum adult height. The recruiting assemblages select for lower leaf carbon, lower deciduousness, and species with shorter maximum heights. This finding suggests a decoupling in trait space between the functional trait characteristics of old forests we see in the present, and the possible future functional composition of tropical American forests. The selection for low leaf nitrogen in the mortality and recruitment assemblages raises the question of whether and to what extent such recruitment assemblages with low leaf nitrogen content will be able to survive to larger adult sizes (e.g. *55, 56*), especially across montane forests where there is a stronger mismatch (Fig. 3 and Fig. 4). Such a decoupling in trait space between the survivor and recruitment assemblages could potentially indicate the slow beginnings of forest level adaptation to new climatic conditions, which is likely to impact the functioning of tropical forest ecosystems (*57*).

The full community, survivor and recruiting assemblages often show more changes in traits in lowland than montane forest. Lowland forests are highly dynamic and harbour 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 last 40 years, which could partially explain the shift of a larger number of community functional traits in lowland than montane forests (*58*). Larger increases in VPD and more severe droughts appear to have modified the community composition of lowland forests more strongly than that of montane forest, towards a set of species better adapted to drier and hotter conditions, which could be due to the mortality of more vulnerable species (*46*). Recent work across sites in the Amazon and Andes also suggest an important impact of increasing temperatures and declines in water availability on changes in tree trait composition (*59*). A shift in community composition towards more deciduous species in both lowland and montane forests appears to have caused increases in photosynthetic capacity, leaf chemistry traits such as leaf carbon and phosphorous content, and species maximum height through time.

The abundance of deciduous tree species has generally increased in tropical American forests over the last 40 years (Fig. 2C). For the full-community and recruiting assemblages this was accompanied with a general decline in leaf thickness. Temporal increases in VPD have favoured increases in the proportion of deciduous species, especially across montane forests, and increases in MCWD have promoted decreases in leaf thickness. Overall, deciduous species tend to have acquisitive leaf traits with higher leaf nitrogen and phosphorus, photosynthetic capacity and photosynthetic nitrogen-use efficiency, especially under hydric stress [56], than evergreen species (*60, 61*). The pattern observed across tropical American forests could be attributable to leguminous nitrogen fixing species that dominate in dry forests which are often deciduous and with higher photosynthetic nitrogen-use efficiency (*62*). This is consistent with a previous report for West African tropical forests, where increasing drought stress co-occurred with an increased abundance of deciduous species, and where changes in deciduousness explained changes in other morphological, structural and leaf chemistry traits (*50*). However, the distribution of tree species with such trait syndromes may be limited by the spatial heterogeneity in essential soil nutrients, such as nitrogen and phosphorus (*63*). Thus, increase in deciduousness is expected to be one adaptation strategy, especially in dry tropical forests with more seasonal precipitation regimes than wetter tropical forests. Yet, increased deciduousness may be limited by soil fertility in some areas, such as in infertile south-eastern Amazonia, where short-lived deciduous leaf construction is a too-costly strategy.

With increasing temperatures and reduced water availability, we expected an increase in abundance of deciduous species to also be reflected in the recruitment assemblage (*50*). However, the decline in abundance of deciduous species in the recruits assemblage indicates potential shifts in phenological strategies towards more conservative strategies in response to increasing temperatures or altered precipitation patterns. However, we did not find a significant selection against deciduous species in the mortality assemblage. This suggests that a combination of drought avoidance and drought resistance strategies (*34*) could both be playing an important role as means of 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 defaunation, which could be an important driver of the observed changes in dispersal traits across time *(64)*. Some wetter regions (e.g., central Amazonia) show increases in seed mass for the full community, with the mortality assemblage showing significant declines in individuals with smaller seeds in the lowlands (Fig. 4C). However, drier regions (e.g., southern and eastern fringes of Amazonia) and montane forests show a slight predicted decline in seed mass (Fig. S3 D). These changes may be an indicator of strong defaunation pressure (*65*) as spatial predictions of decreases in seed mass broadly match spatial patterns of high defaunation (*66*), especially in those more accessible areas of Mesoamerica, and both south and eastern Brazil. They could also be driven by climatic factors as 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 *(39)*.

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 found under the forest canopy (*67*). This is of particular importance when investigating the effects of a changing climate, especially on the forest's recruiting assemblages, which tend to occupy the space below the canopies of the older larger trees. Ultimately, such microclimatic conditions may play an important role for determining the responses of below canopy plants to a changing climate (*68, 69, 70*) and therefore on the rate of change in community trait composition of the recruiting assemblages. Hence, microclimatic conditions at the plot level may partly explain the differences in trait shifts between the full community and survivors assemblages and the recruiting assemblages.

Changes in single traits do not always behave as expected from theory. For instance, it would mechanistically be expected that increasing drought would cause plant communities to shift to species with higher wood density and thicker leaves or that the abundance of deciduous species increases across time. Such coordinated changes may not readily happen in the community as 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 deciduousness combined with low wood density and thin leaves (drought avoidance), or evergreenness combined with high wood density and thicker leaves (drought tolerance). The favoured 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, such as 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)*.

In conclusion, we find that overall community composition changes are leading to small shifts, ~10% of the expectation given climate change, in the overall community trait composition. These shifts are primarily driven by variation in growth rates of existing trees, rather than by new recruitment or mortality. However, we observed larger changes for the recruiting 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 to the rate of climate change and this partly explains the differences observed in community trait shifts between the full community and those of the recruiting 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, across these regions, edge effects and in general a more constrained physical environment may be impacting the capacity of forests to adjust to new climate conditions (*28*, 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 track climate change. 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 (*79, 80*). Hence it is overwhelmingly likely that 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.

Materials and Methods

Plot data

Our study focuses primarily on tropical American forests, with some overflow into adjoining subtropical and warm temperate regions of Brazil and Mexico. We gathered tree-by-tree vegetation census data for 254,307 individual trees from 415 vegetation old-growth forest plots across 11 countries, spanning a wide range of environmental conditions and elevations from sea level to >3000 m elevation, with at least two censuses recorded (on average 5.7 censuses per plot) between the years of 1980 and 2021 (Table S1). The modal plot size was 1 ha (mean 0.88 ha); all plots were located in structurally intact forests with no signs of direct anthropogenic impacts. In each, all woody plants with a diameter ≥10 cm at breast height (DBH) or above buttress roots were measured.

Overall, identification rates of individuals exceeded 85% to the species level and 99% to the genus level (Fig. S8). Data were obtained through the ForestPlots network (www.ForestPlots.net) (*83*) and the MONAFOR Mexican plots network (forestales.ujed.mx/monafor). We classified vegetation plots as either lowland or montane forests. We based our classification on literature that uses 500-800 metres above sea level (masl) as the threshold between lowland and montane climatic conditions (*29, 83*). In our dataset there were two clear elevational groups, where plots <604 masl (261 plots) were classified as lowland forests, and plots >730 masl (154 plots) were classified as montane forests.

Trait data

Tree functional trait data were obtained for several plots from local field collections carried out by collaborators from where plots are located (*84, 85, 86*), the Global Ecosystems Monitoring network (GEM; gem.tropicalforests.ox.ac.uk) (*87*), and the ForestPlots network (www.ForestPlots.net) (*82*) in addition to databases from BIEN (bien.nceas.ucsb.edu), TRY (www.try-db.org) (*88*) and Diaz et al. (*89*). The plant traits are related to fundamental aspects of leaf chemistry, photosynthetic capacity, leaf morphology, plant and organ size, and phenology (Table S2). We gave priority to trait data from the GEM and ForestPlots networks; when these were not available, we used the databases from TRY (www.try-db.org), Diaz et al. (*89*), and the BIEN (bien.nceas.ucsb.edu) network's database. When more than one trait value per species was available, we used the trait mean at the species level for subsequent analysis. We aimed to cover at least 70% of the basal area of each plot with trait data at species or genus level, often covering more than that (Fig. S9). When species-level trait data were unavailable, we used the mean genus-level data. Hence, our analysis could be seen as more representative of the genus-level trait responses. When achieving at least 70% coverage was not possible for a given trait, such a plot was left out of the analysis for the specific trait. All species names were standardised following the Taxonomic Name Resolution Service (TNRS; https://tnrs.biendata.org).

Climate data

We investigated the role that long-term climate and its changes play on determining the trait community composition across tropical American forests by gathering climatic data on the mean annual values of temperature (T_{mean}), maximum climatic water deficit (MCWD) (*47*), vapour pressure deficit (VPD_{mean}) (*46*), standardised precipitation-evapotranspiration index for a 12-month window ($SPEI_{12}$) (*48*) and dry season length. We calculated the long-term climate conditions as the mean annual values for the metrics described above between the years 1980 to 2021 (i.e., full time period). All climatic variables were derived from the TerraClimate dataset (*31*) and had an original spatial resolution of ~4 × 4 km at the Equator. We selected the TerraClimate product because of its accuracy and coverage. TerraClimate has higher spatial resolution and greater accuracy when compared to other historical climatic datasets such as Climatic Research Unit data (*44*). The dry season length was calculated as the average annual number of consecutive months with rainfall below 100 mm (*88*). The MCWD was included as it is a metric for drought intensity and severity that has been shown to impact vegetation growth and survival (*50*). MCWD is thus defined as the most negative value of the climatological water deficit (CWD) each year. We converted the MCWD so that positive values indicate increases in water stress. Equally, the SPEI reflects drought severity, but its multi-scalar nature enables the identification of different drought types and severity (*91*). VPD is an indicator of atmospheric aridity, acts as a key environmental driver of plant transpiration, and reduces plant water use efficiency (*92*). We then tested the correlation between all pairs of climatic variables (full-term and their changes); all had Pearson's correlation coefficients |<0.70| apart from dry season length which was highly correlated to MCWD (Fig. S1), and we thus dropped dry season length and its change to avoid confounding model coefficients (*93*). We also obtained the same variables outlined above for a period covering 1980-2005 (see models below). We calculated the yearly rate of change of the climatic variables (Δr T, Δr MCWD, Δr VPD, and Δr $SPEI_{12}$) to standardise for a different time between censuses for different plots and avoid the bias due to inter-annual short-term variability that occurs in addition to the long-term change. To this end, we fitted a linear model predicting the climate variable value as a function of time (year) and used the slope as the predicted annual rate of change (Δr).

Soil variables are relevant predictors of vegetation distribution and are related to functional trait composition (*14*). Variation in soil properties could modify the rate of change in response to environmental change (*94*). Hence, in our models, we included soil clay (%), sand (%), cation exchange capacity (CEC; mmol) and pH information averaged from the first 30 cm of the soil surface. The soil data was derived from the SoilGrids global dataset (www.soilgrids.org).

All climatic and soil variables were numerically centred around the mean value before model fitting. The study area that was used to extract the climatic and soil data and to make spatial predictions was delineated using the European Space Agency Land Cover CCI Product (*81*) using all land use classes defined as tree or shrub cover classification.

Trait CWM calculation

The most dominant species are expected to drive ecosystem processes using their traits as described by the mass ratio hypothesis (*45*). Therefore, for each of the plant functional traits *t* and plots *p* per census time we calculated their community-level weighted mean (CWM) using the species basal area as the weighting factor: $CWM_{xp} = \sum_{i-1}^{s} \blacksquare \; BA_{ip} \times x_i$. Here BA_{ip} is the basal area of species *i* in plot *p* , with x_i representing the average trait value of species *i*. Before calculating the trait CWM, when more than one value per trait was available for a species we averaged the trait value at the species level; when the species had no trait values, we averaged the trait values at the genus level. Although species show some degree of intraspecific trait variation, research suggests it is relatively small compared to the trait variation found across forest tree species (*95*). Moreover, given the vast majority of functional trait data has only been collected in the last decade, it is not yet possible to evaluate the magnitude of intraspecific trait shifts across the spatial extent of the study area. The trait CWM is an indicator of mean canopy properties as basal area and crown area are highly related, and the latter indicates the amount of canopy area occupied by a specific trait (*96*). In the case of phenological strategy, as it was obtained as a categorical variable (deciduous or not deciduous), we calculated the percentage of basal area that is deciduous.

Understanding trait CWM-Climate relationships and the effects of climate change for driving trait CWM changes

All statistical models described below are linear models fitted under a Bayesian modelling framework with the ‘rstanarm’ R (*97*) package. All models were run with normal diffuse priors with a mean of 0 and 2.5 standard deviations (sd) to adjust the scale of coefficients and 10 sd to adjust the scale of the intercept. The models were run with three chains and 3,000 iterations. We computed the HDI (highest density interval), resulting in the range containing the 95% most probable effect values (*98, 99*), and considered a result significant when the HDI did not overlap 0. The CWM change models (a separated model per trait) used a Gaussian distribution, weighting the observations by the number of censuses, census time and plot size (*9*).

To understand the current trait-climate relationships across forests of the tropical Americas, for each plant trait we modelled the trait CWM as a function of the T_{mean}, VPD_{mean}, $MCWD_{mean}$, the $SPEI_{12}$ (from the full time period data) and the soil covariates, with each one of the climatic variables interacting with forest type (lowland or montane) (here onwards referred to these models as M1**).** Because the studied functional trait values are always positive and often have a long-tailed distribution, the current Trait-Climate relationship statistical models used a Gamma distribution and log link function, using a weighting given the number of censuses, plot size and census time. We tested the model predictions using a spatial K-fold cross-validation approach where the spatial groups were determined based on the group ID described below. All models were developed in the R language for statistical computing (*97*).

We next analysed the climatic drivers of shifts in each functional trait given observed changes in climate over the past 40 years for the full community and survivors assemblages (415 vegetation plots), for the recruiting community (377 plots) and mortality community (375 plots). We define the recruiting community as individuals that passed the threshold of 10 cm DBH in a given census and were not present in the past census for a given plot. The mortality community is defined as those individuals of a plot who 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 annual rate of change (Δ*r* of the trait CWM) to standardise for a different time between censuses for different plots. To this end, we fitted a linear model predicting the trait value as a function of time (year) and used the slope as the predicted annual rate of change (Δ*r*). We then modelled the Δ*r* CWM trait as a function of Δ*r* of the climatic variables described above, each one of these interacting with forest type and also included the soil characteristics to account for their possible effect on the observed CWM trait changes (hereafter referred to these models as M2). We weighted the observations by the number of censuses, census time and plot size. We used the M2 models to predict and spatially project the changes in trait composition across Latin American forests over the past half-century.

We tested for spatial autocorrelation effects in the CWM traits using the Moran's I test and found significant effects (P-value<0.05). Therefore, for each trait CWM we calculated the spatial distance at which the spatial effect decreased, finding that a distance of nine kilometres for the full community and survivors assemblages (1 km for recruitment and mortality) captured most of the spatial autocorrelation effect. Based on this we generated an identification (ID) for each group of plots that were at maximum nine kilometres away (or 1 km respectively) from each other and included such group ID as a random factor (*14*) in the statistical models to account for the spatial autocorrelation and visually checked the model residuals for any obvious patterns (*5*).

Understanding shifts in trait CWM

We used the annual rate of change (Δ*r*) of the trait CWM of the full, survivors, recruiting and mortality assemblages to investigate if the rate of trait changes for the overall forests (lowland and montane together), for the lowland forests alone and the montane forest alone, was significantly different from 0. We did the same to understand if there were important differences between the rate of change between lowland and montane forests. To this end we carried out a Bayesian version of a typical T-test analysis using Bayesian estimation (*99, 100*). The Bayesian estimation was done using the 'BEST' package for R, with normal priors with mean for μ (the mean of rate of change) of 0 and a standard deviation for μ of 10. We used broad uniform priors for σ (standard deviation), and a shifted-exponential prior for the parameter v which describes the normality of the data within the group. 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 if forest community traits are tracking climate changes.

The process outlined below was carried out for the full community, the survivors and recruiting assemblages only as the mortality ones are not tracking climate. We first built the same type of statistical models constructed above for the current trait-climate relationships (M1) but using only plot and climatic data from between 1980 and 2005, including also the soil variables described above (from now on called M1.1). This was done as there is potential for entanglement when using the same data for spatial and temporal analysis. The plot data up to year 2005 were still representative of the plot distributions across tropical Americas and helped separate the temporal effect from the spatial relationships.

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 1980-2005 climate plus the observed climate yearly rate of change across the study period (here onwards 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. Lastly we compared the expected trait CWM calculated above with the observed Δ*r* CWM trait (i.e., from section 'Understanding trait CWM-Climate relationships and the effects of climate change for driving trait CWM changes'). This allowed us to understand the expected shift in mean trait values given the 1980-2005 trait-climate relationship in comparison to the observed trait changes across time (i.e., from 1980-2021). Thus, the 1980-2005 trait-climate relationship shows how much the tree communities would need to change to keep up with climate changes, and the observed trait changes across time show how much they have actually changed. We compared the observed and expected average change trait CWM across the sampling vegetation plots to understand the magnitude of their difference for lowland and montane forests and calculated their change ratio. To understand if there was a significant difference between observed and expected community trait changes, we carried out a Bayesian version of a typical T-test analysis using Bayesian estimation as described above and considered significance when at least 95% of the HDI values were greater than zero (99*, 100*).

We also created map predictions of the 1980-2005 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 (1980-2005) plus the yearly rate change observed. We then subtracted the original map predictions (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. Then we calculated the ratio of the observed, i.e., spatial predictions of the trait changes observed across time (from M2 models), versus expected and converted to percentage change relative to the 1980-2005 condition to understand if 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). All statistical analyses were carried out in R.

Creating the spatial predictions (maps)

All maps were generated by predicting the focus model (i.e., M1, M1.1, M2) to the study area. The study area was delineated using the European Space Agency Land Cover CCI Product (*81*) using all classes having tree cover classification and numbered from class 50 to class 100 as suggested here: http://maps.elie.ucl.ac.be/CCI/viewer/index.php. To avoid extreme values in the maps, given some extreme climate and soil values inherent to the climate and soil data, we truncated the map predictions to contain the 90 percentile predicted value as the maximum instead of the 100% which allowed us to eliminate the outlier values. The maps were created in the R platform.

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Data availability

The vegetation census and plant functional traits data that support the findings of this study are available from gem.tropicalforests.ox.ac.uk, www.ForestPlots.net, forestales.ujed.mx/monafor and their other original sources. To comply with the original data owners' requirements, the processed community-level data used in this study can be accessed through the corresponding author upon request.

Supplementary Materials

Supplementary Text

Figs. S1 to S7

Tables S1 to S9