Functional shifts of Neotropical lowland and montane forests are too slow to track climate change

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Understanding how ecosystems are responding to climate change is probably the biggest challenge in biosphere science. This challenge is particularly acute for tropical forests because of their high biodiversity, importance for global biogeochemical cycles, poorly understood ecophysiological function and chronic undersampling in field studies. Here we examine how the functional composition of the Neotropical forest biome, the most biodiverse and extensive of the tropical forest regions, has shifted in recent decades compared to climate change expectations. We combine long-term forest inventory data from more than 400 permanent forest plots with a functional traits dataset and Earth Observation to track and map functional change expected from observed changes in species composition. We found remarkable differences in trait-climate relationships for some traits between lowland and montane forest types across the Neotropics. Most of the observed change in trait composition over time is consistent with adaptation to a changing climate: a general increase in the abundance of deciduous species, decreases in leaf size, increases in photosynthetic capacity in lowland forests, and increases in leaf phosphorus in montane forests. Lowland forests show shifts for more community traits in comparison to montane forests. However, such functional shifts associated with changes in community composition do not appear sufficient to keep track with what would be expected given observed climate change, typically shifting around 10% of the required amount. It is unlikely that within-species variability and plasticity can make up the deficit, and hence Neotropical forests, and probably all tropical forests, are likely to be increasingly out of equilibrium with local climate, and hence increasingly vulnerable to climate change.

How forests respond to human-driven changes, and in particular climate change, will have a major bearing on the diversity and function of the biosphere throughout this century and beyond. Here we focus on Neotropical forests, which host the highest number of tree species in the world [1], including six key biodiversity hotspots [2] and half of Earth's most intact tropical forests [3]. At the same time, they are highly threatened by climate change having experienced some of the strongest climate and largest forest area changes over the last decade [3], as well as other anthropogenic drivers [4, 5].

One frequent and fundamental assumption in ecology is that plant species are adapted to the environmental conditions they inhabit by means of sets of functional strategies or syndromes [6, 7]. Functional traits are defined as morphological, structural, chemical or phenological characteristics that affect plant performance [6], and therefore their distribution along environmental gradients. Because functional traits underpin plant ecological strategies along the fundamental axes of growth, survival and reproduction [7], species distributed across different environmental conditions tend to have a different set of functional traits [8]. Moreover, it has been suggested that such plant functional traits show consistent relationships with climate across environmental gradients [9]. Therefore, plant functional traits provide a robust framework for predicting the impacts of climate change and resilience across forest ecosystems [7, 10]. Across the Neotropics, climate change is already affecting plant communities. For example, in the Amazon, changes in precipitation patterns and the occurrence of more frequent droughts have led to an increase in the recruitment of dry-affiliated species (xerophilization) [11]. In the Andes, increases in temperature have led to a higher abundance of heat-tolerant species (thermophilization) [12]. Across Mesoamerican forests, it is expected that climate change will cause the decline of temperate forest by 13% and the shift of tropical dry forests to higher elevations (over 200 m above current average elevation) [13].

Changes in Neotropical climate are expected to become stronger, with some scenarios projecting temperature increases of up to ~4°C and precipitation reductions of close to 20% [14-16]. Such changes would expose current species assemblages to climates they never experienced before [17]. Community responses to climate change will thus likely depend on underlying mechanisms and geographical context. For example, if species track climate change via migration, we would expect montane communities to track climate change better than those in the lowland forests [18] given the much sharper climate gradients across shorter distances in mountains [19]. Given past exposure to a drying and warming climate, we expect that species with more conservative trait syndromes, such as smaller, thicker leaves with higher wood density and lower photosynthetic capacity, increase in abundance, and that different forest types (i.e. lowland and montane) diverge in responses given their differences in climate change exposure [12, 20]. Other drought-tolerance syndromes, notably deciduousness (often associated with more acquisitive leaves), could also become more prominent in the future as an adaptation to increasing drought conditions [21, 22]. Fruit and seed traits play a pivotal role in the reproduction and dispersal capacity of species, and under a warming and drying climate we might expect them to decrease in size as has been observed in deep time studies [23], although other factors such as defaunation of frugivorous seed-dispersing large mammals and birds may more strongly drive their shifts at short time scales [24].

It is yet unclear how shifts in species composition translate into changes in functional composition and what functional changes have occurred through the last half a century as a response to the onset of a warmer, drier and more variable climate across the Neotropics. Moreover, it is unclear if the functional trait composition of such plant communities is tracking the observed changes in climate or lagging behind.

Here, we address these knowledge gaps by analysing a set of 415 long-term forest plot sites covering the last 40 years, encompassing >250,000 individual trees across 11 countries in the Neotropics where tree biodiversity, structure and function are being observed, spanning structurally intact forests from the lowland tropical core (<650m elevation) to pre-montane and montane forests (>650m elevation; here onwards referred to as montane) in the high Andes and subtropical fringes (Fig. 1; Supplementary Table 1). By combining this unprecedented monitoring and analysis of changes in plant community composition with measurements and detailed assessment of 13 plant traits involved in plant response to a changing climate (Supplementary Table 2), we investigate current plant trait-environment relationships and whether there are any climatic thresholds that underpin differences in responses between lowland and montane forests. We also examine how and where these ecosystems have shifted in their functional trait composition because of changes in the plant community taxonomic composition, and how well the tree communities have been able to track climate change to date**.** We hypothesise that for most traits there will be a consistent trait-climate relationship but this would vary per functional trait and per forest type, and that lowland and montane forests will differ in their functional responses to climate change given their different exposure to climatic conditions. We expect that, given their slow dynamics, Neotropical forests will demonstrate ecological inertia so that changes in functional composition lag changes in climate.

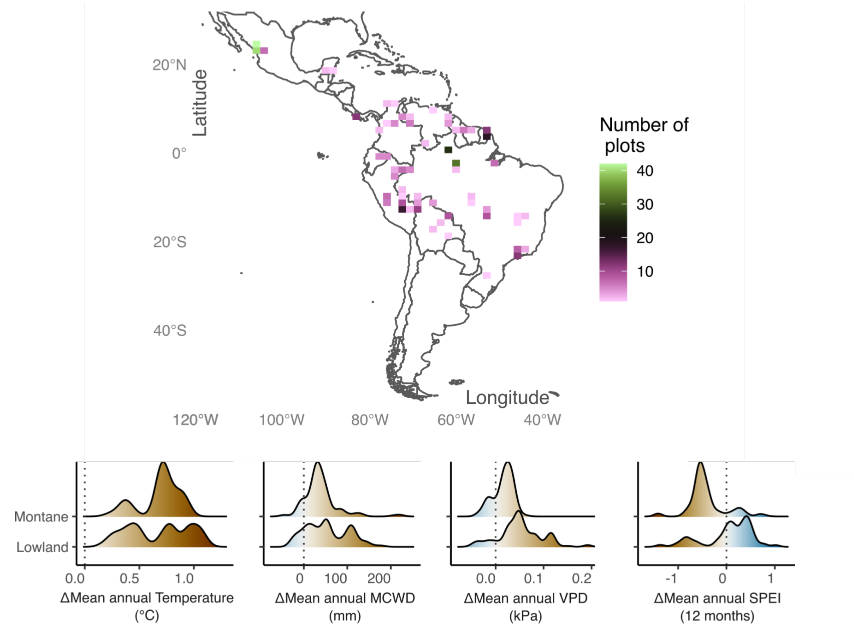


Figure 1. Study area showing the distribution and number of vegetation plots (top panel) and changes in climate conditions over the past 30 years (1980-1990 vs 2010-2020) that occurred across the sampled vegetation plots (bottom panel). In the bottom panel the vertical dotted lines indicate zero change. Brown colours depict increases in temperature, drier conditions (for MCWD and VPD) or increased drought intensity (for SPEI). Blue colours depict an increase in water availability. MCWD: maximum climatic water deficit here with larger positive values indicating higher water stress, VPD: vapour pressure deficit, SPEI: standardised precipitation-evapotranspiration index. The climate data was derived from the TerraClimate project [25].

Current Trait-Environment relationships

To evaluate current trait-climate relationships across Neotropical forests, we used data from 398 out of the total 415 forest plots for the current climatic conditions (i.e. 2000-2021), excluding those which did not have census data between 2000-2021 (mean plot size 0.97 ha). As the most dominant species are expected to drive ecosystem processes [26], for each plot, we calculated the community-weighted mean of each plant functional trait (Supplementary Table 2; Methods) based on the relative basal area of the species and their trait value (hereafter "community functional traits"). We then modelled, in multivariate linear models, each community functional trait as a function of the additive effects of relevant and largely independent (Extended Data Fig. 1) climatic drivers of species distributions, i.e., the mean annual values (between 2000-2021) of temperature (T_{mean}), vapour pressure deficit (VPD_{mean}) [27], and the maximum climatic water deficit ($MCWD_{mean}$)[28] and standardised precipitation-evapotranspiration index ($SPEI_{12}$) [29], each one of these interacting with forest type (lowland or montane) (Methods).

Most community functional traits show consistent relationships with climate gradients (Table 2; Figure 2; Extended Data Fig. 2). For both lowland and montane forest types, an increase in temperature (T_{mean}) along a spatial gradient is associated with an increase in leaf area (Area), maximum species tree height (H_{max}), wood density (WD), fruit length (FL) and seed mass (SM) and a decrease in leaf thickness (Thickness) and the proportion of deciduous species (DE). An increase in $MCWD_{mean}$ is associated with an increase in photosynthetic capacity (A_{sat}), DE, WD, and FL and a decrease in leaf area, fresh mass (FM), and leaf phosphorus (P) (Supplementary Table 3). The increase in these leaf traits in drier forests could be associated to the high photosynthetic rates generally attained by deciduous species over the growing season [30, 31] and the fact that higher WD tends to relate to higher resistance to lethal water potential [32]. Across forests, atmospheric water stress (VPD_{mean}) reduces WD, FL, and SM across forest types. Thickness, H_{max}, and SM tend to be higher in areas that experience stronger and more prolonged droughts ($SPEI_{12}$), but the opposite occurs for WD. However, consistent climatic relationships across both forest types are not apparent for leaf nitrogen (N), leaf carbon (C) and specific leaf area (SLA) (Supplementary Table 3).

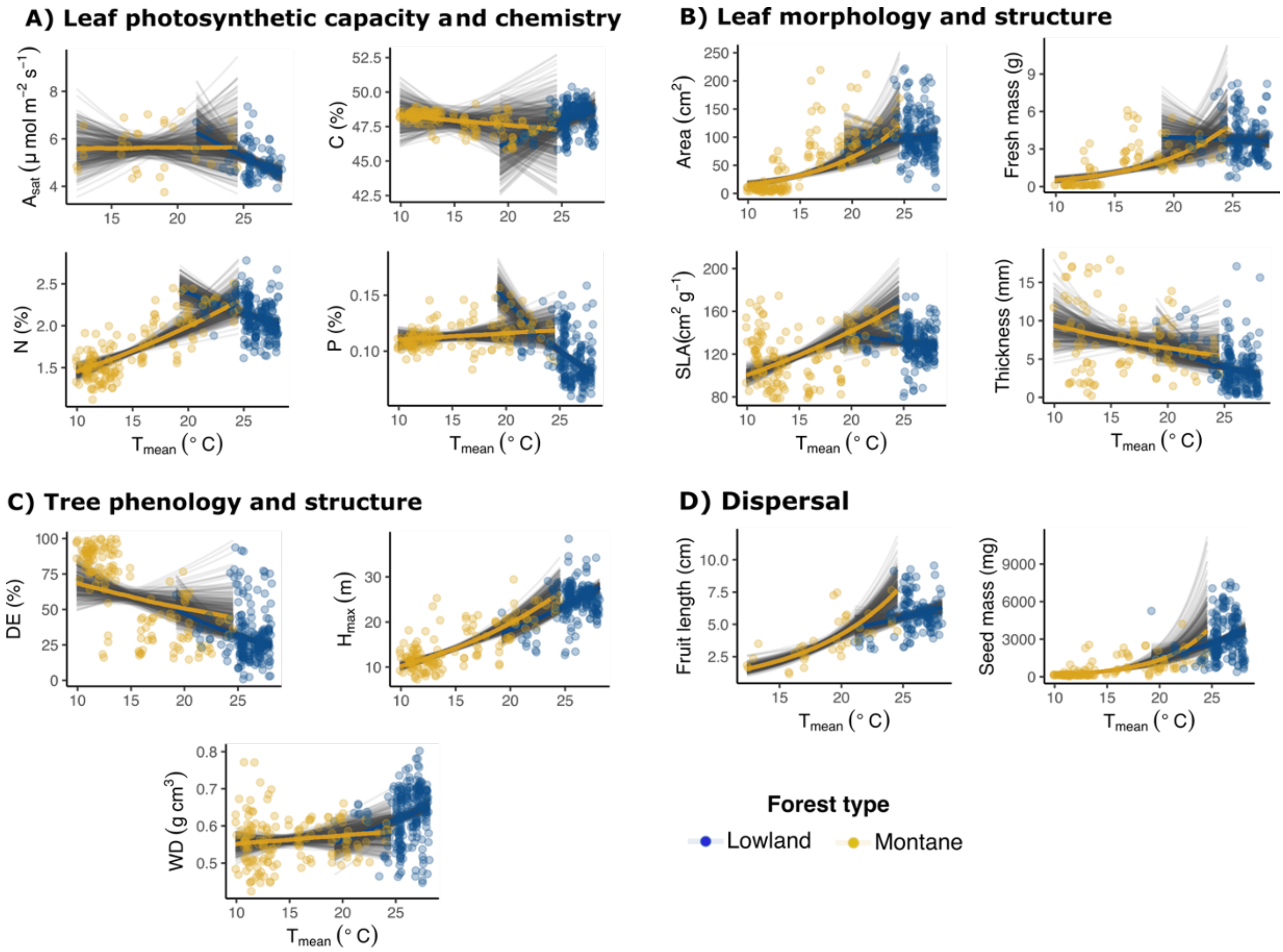


Figure 2. The relationship between canopy traits and climate. Trait-environment relationships for temperature (T_{mean}) across the vegetation plots with graphs for the other climatic variables used in the multivariate models shown in Extended Data Fig. 2 (also including the break point results). Filled dots represent vegetation plots for lowland (<650 m elevation, blue) and montane (>650 m elevation, yellow) forests across the Neotropics. Thick blue and yellow lines show the average trait response to the climatic variable for lowland and montane forests, respectively, and grey-shaded lines show 700 random draws from the model posterior distribution representing the variability of the expected model fit. For full statistical multivariate model results see Supplementary Table 3 and Supplementary Table 4**.** 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}: adult maximum height, WD: wood density, Fruit length: length of the fruit, Seed mass: mass of the seed.

Climatic thresholds of trait-environment relationships

Because lowland and montane forests might have different trait-environment relationships and given the expected strong effect of climate change on community functional traits across altitudinal gradients, we conducted a breakpoint analysis (Methods). This analysis detects, across the climatic gradient, the point at which the functional communities differ the most. We found that for several traits, lowland and montane forests have divergent relationships with climate (Supplementary Table 4; Extended Data Fig. 2).The point where we detected more differences in the average Trait-T_{mean} relationship varies between 16.1°C to 27.2°C depending on the trait, with an average of ~21°C (mean std. error = 1.18°C) (Extended Data Fig. 2; Supplementary Table 4). For the $MCWD_{mean}$ this is on average 343 mm (min= 36.1, max=722.5, mean std. error = 81.8), for VPD_{mean} the average threshold is 0.7 kPa (0.3, 1.1, 0.1) and for $SPEI_{12}$ this is -0.59 (-1.41, 0.08, 0.3).

Changes in trait composition across time

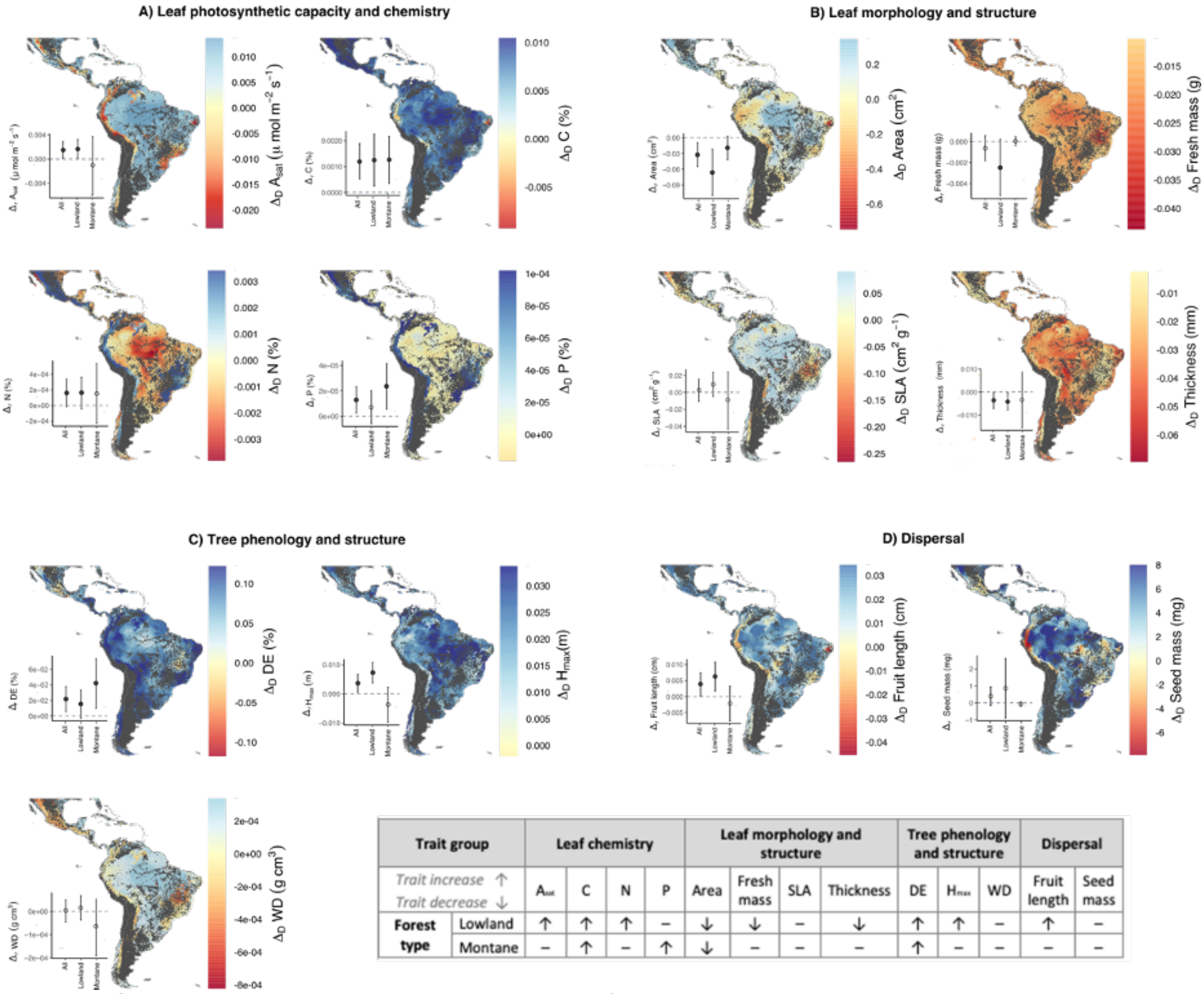
We next analysed if and to what extent the functional trait composition of Neotropical forests has shifted given observed changes in climate over the past 40 years (Methods). To this end, we used the full dataset containing 415 vegetation plots (mean plot size 0.88ha) which contained at least two censuses (mean 5.8 censuses) (Supplementary Table 1). We first calculated the community-weighted mean (CWM) and variance (CWV) of each plant functional trait for each vegetation census available and calculated its yearly rate of change across time (Methods). Using a Bayesian estimation approach, we tested if the changes in trait CWM and CWV were significantly different from zero when using all vegetation plots together and when divided into lowland and montane forests. We then investigated whether the observed shifts in trait CWM and CWV significantly differed between lowland and montane forests (Methods). For shorthand and readability, all mention of mean trait properties and shifts below refer to CWM trait values.

When including all plots together, we found that, out of the 13 traits analysed, nine underwent significant changes in their CWM traits (HDI: 90% highest density interval does not overlap zero). Only leaf FM, SLA, SM, and WD did not show significant shifts across time (Supplementary Table 5). Of the traits with significant changes across time, all leaf chemistry (N, P, C) and photosynthetic capacity-related traits (A_{sat}), tree structure (H_{max}, WD), deciduousness, and fruit length showed increases in trait values, while leaf area and thickness tended to show substantial declines (insets in Fig. 3).

In the lowland forests, we detected significant trait changes for nine (increasing: A_{sat}, N, C, DE, H_{max} and FL; decreasing: Area, FM, Thickness) out of the 13 traits analysed, spanning leaf chemistry, morphology, structure, and dispersal traits (Supplementary Table 5; insets in Fig. 3). Montane forests only showed significant increases in leaf C, P, Area, and DE (Supplementary Table 5 and Supplementary Table 6; Fig. 3 insets). Moreover, we found that the variance in community traits also increased for A_{sat}, SLA, H_{max} and FL in lowland forests, while in the case of montane forests only Area variance increased significantly (Supplementary Table 7 and Supplementary Table 8; Extended Data Fig. 3).

To help identify the underlying climatic drivers of forest functional change, we also modelled, using multivariate linear models, the full-term (ΔFT; i.e. from first to last census) change in the trait values as a function of the full-term changes in temperature (ΔT_{FT}), maximum climatic water deficit ($\Delta MCWD_{FT}$), standardised precipitation-evapotranspiration index ($\Delta SPEI_{FT}$), and vapour pressure deficit (ΔVPD_{FT}), each one of these interacting with forest type under a Bayesian modelling approach (Methods). We then used this ΔFT trait CWM model to spatially predict the temporal changes in trait composition across Neotropical forests over the past 40 years (Fig. 3).

Our results depict the role of climate, specifically temperature and water availability, as a determinant of trait shifts across Neotropical forests, and the differences in response between lowland and montane forests (Supplementary Table 9). We found that climate changes can partially explain the changes in traits across time and that lowland and montane forests have responded in different ways to climate changes (Extended Data Fig. 4). By building spatial predictions from our models of observed trait changes across time, we show that some forests are predicted to have increased in A_{sat} (up to 0.015 µmol m^{-2} s^{-1} $decade^{-1}$), C (0.01% $decade^{-1}$), SLA (0.8 cm^2 g^{-1} $decade^{-1}$), WD (0.0003 g cm^3 $decade^{-1}$), DE (0.11 % $decade^{-1}$), H_{max} (0.035 m $decade^{-1}$), FL (0.03 cm $decade^{-1}$) and SM (8 mg $decade^{-1}$), especially around the Caribbean and Amazonia (maps in Fig. 3). However, other forests are predicted to have experienced slight to large declines in most of these traits, especially across Mexico and the Andes (Fig. 3). FM and Thickness are predicted to have declined by up to -0.043 g $decade^{-1}$ and -0.07 $decade^{-1}$ mm respectively per decade over the last 40 years in some in central and southern Amazonian forests.



Trait group		Leaf chemistry				Leaf morphology and structure				Tree phenology and structure			Dispersal	
Trait increase ↑ *Trait decrease* ↓		A_{sat}	C	N	P	Area	Fresh mass	SLA	Thickness	DE	H_{max}	WD	Fruit length	Seed mass
Forest type	Lowland	↑	↑	↑	–	↓	↓	–	↓	↑	↑	–	↑	–
	Montane	–	↑	–	↑	↓	–	–	–	↑	–	–	–	–

Figure 3. Observed changes in the mean community functional trait values over the past 40 years across Neotropical forests. A) Changes in trait community-weighted mean (CWM) traits of vegetation plots for leaf photosynthetic capacity and leaf chemistry traits, B) for leaf morphology and structural traits, C) for tree phenology and structural traits, and D) 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 Supplementary Table 5 and Supplementary Table 6 for all forests together and only for lowland or montane forests. In the A-D insets significant differences from zero are shown as filled circles and non-significant differences as empty circles. The vertical lines depict the Highest Density Intervals (90% HDI), and the horizontal grey dotted line indicates zero change. Maps show the observed changes in trait CWM as a result of the statistical models (shown in Supplementary Table 9) for the community trait changes across the full time period, expressed as changes per decade (ΔD) and predicted across the Neotropics. 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 changes. The grey mask represents all predominately non-forested areas (e.g. crop fields, swamps, savannas, open forests, areas with small patches of forest) and was derived from the European Space Agency Land Cover CCI Product [33]. The inset table at the bottom summarises the observed trait changes across lowland and montane forests, with arrows either describing trait increases (up) or decreases (down) and dashes (—) showing no significant changes. 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}: adult maximum height, WD: wood density, Fruit length: length of the fruit, Seed mass: weight of the seed.

Changes in functional syndromes across time

Species exhibit functional traits that together shape functional syndromes or strategies, which allows species to respond to their environment [34]. A principal component analysis (PCA) of the spatial predictions of changes (as mapped in Fig. 3) in trait values across time reveals that the first three axes explained 80% of the variation in trait changes among plots (Supplementary Table 10). PC1 (explaining 41% of the variation) integrates changes related to resource acquisition, depicting predicted overall increases in leaf photosynthetic capacity (A_{max}) across lowland Amazonian forests accompanied by slight decreases in leaf N (possibly because much of the N is not used for Rubisco but for instance for defence) and P, and generally large increases in N and P at higher elevations ranging from Mexico to the tropical Andes (Fig. 4). PC2 (explaining 27% of the variation) depicts changes in syndromes related to water loss avoidance (phenology) and leaf economics (carbon, fresh mass), with large increases in the abundance of deciduous species (DE) and declines in leaf carbon (C; perhaps because of less lignin in deciduous leaves) across most forests but increases in northern Mexico and southeastern Brazil (Fig. 4). PC3 (explaining 12% of the variation) summarises changes in dispersal and resource acquisition (fruit length, seed mass and leaf area), with overall increases in the contribution of leaf area but decreases in fruit length (FL) and seed mass (SM) across Mesoamerican and Andean mountain ranges and central and eastern Amazonia, but increases in fruit and seed size in western Amazonia (Extended Data Fig. 5).

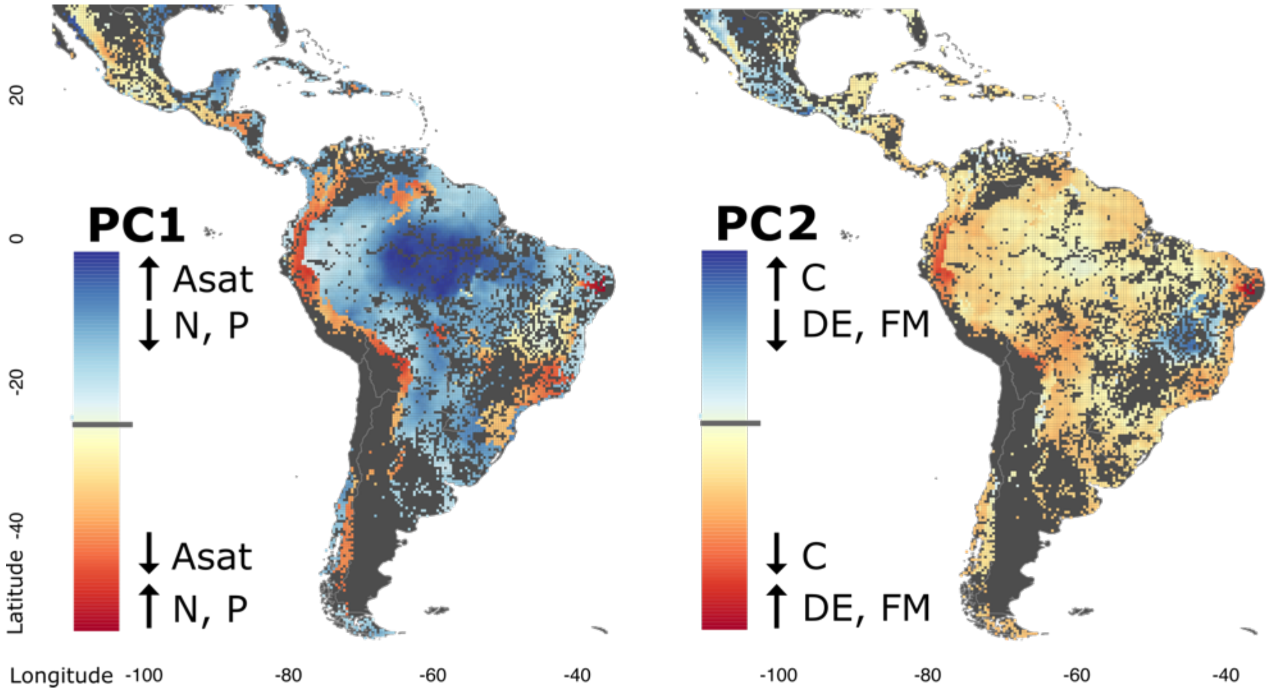


Figure 4. Maps of predicted changes in plant functional syndromes based on principal component analysis (PCA) of the observed trait changes across Neotropical forests. The maps depict the changes in functional syndromes across time (see full statistical results in Supplementary Table 10). The first two axes, shown as the two maps, explain 68% of the variation in trait CWM changes. Principal component 1 (PC1) explains 41% of the variation in trait changes, integrating syndromes related to resource acquisition such as leaf photosynthetic capacity (A_{max}), leaf N and P. PC2 explains 27% of the variation showing changes in syndromes related to water loss avoidance (DE: deciduousness) and leaf economics (C: carbon, and FM: fresh mass). The grey mask represents all predominately non-forested areas (e.g. crop fields, swamps, savannas, open forests, areas with small patches of forest) and was derived from the European Space Agency Land Cover CCI Product [33].

Has Neotropical forest functional composition shifted enough to track climate change?

We next examine whether the observed changes in traits are sufficient to maintain expected trait-environment relationships, the latter derived from the spatial trait-environmental relationships reported above. There is some potential for entanglement in using the same data for spatial and temporal analysis (temporal changes might already be affecting our spatial relationships), but the spatial environmental gradients are much greater than the temporal changes over 40 years, so this entanglement is likely to be small. Here, we took the current observed trait-climate models (Supplementary Table 3) and predicted the expected change in mean trait values per unit increase in T_{mean}. In the same way, we used the full-term trait change models (Supplementary Table 5) and obtained the observed traits change per unit change in temperature (Methods). This allowed us to understand the expected shift in mean trait values based on the current trait-climate relationship (Fig. 5 insets). We then mapped the observed (across time) and expected (current trait-climate relationships) trait changes across the Neotropics and calculated their ratio (observed/expected) expressed as a percentage (Methods; Fig. 5).

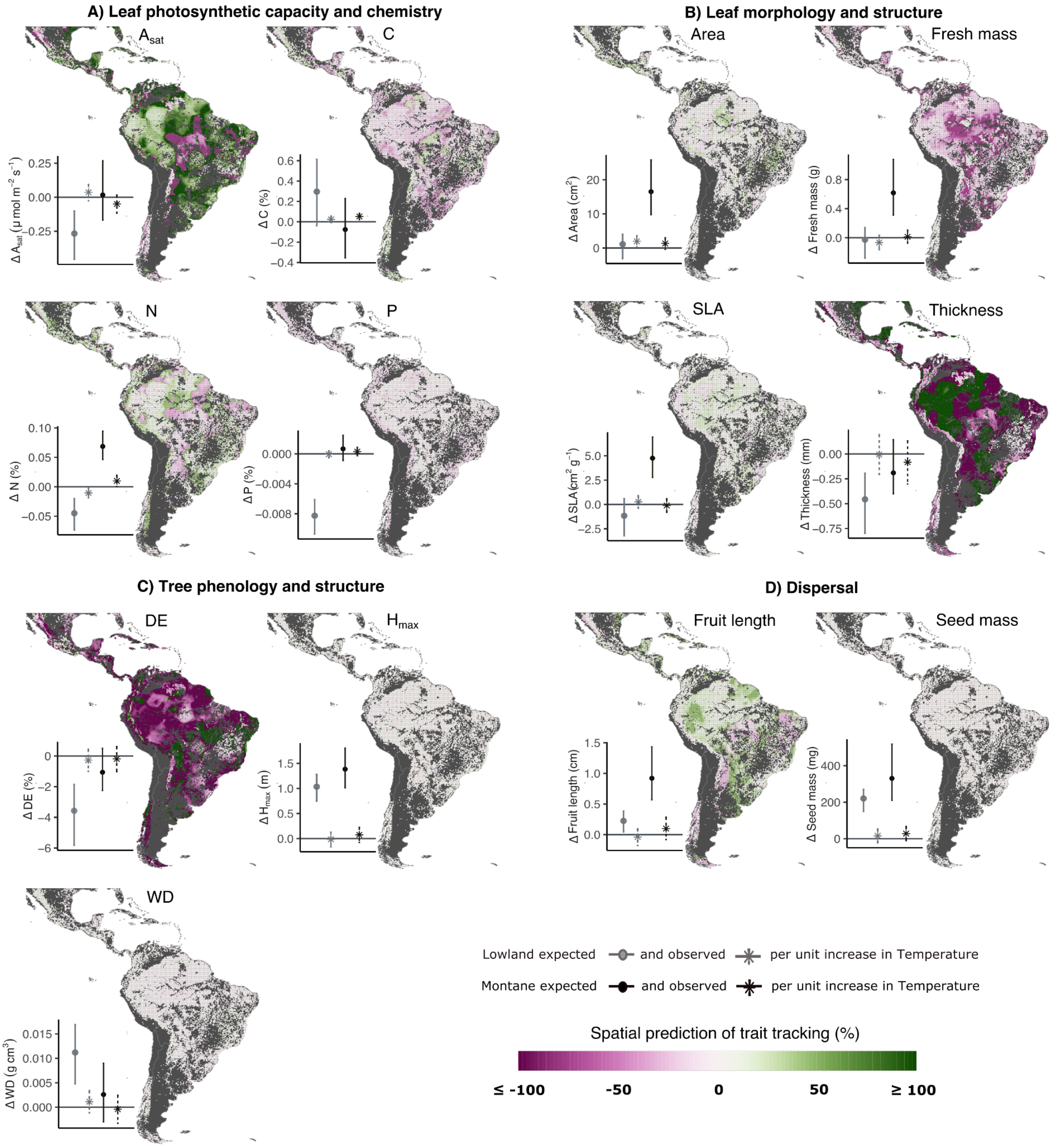


Figure 5. Relation between the expected changes in the traits (based on spatial traits-climate relationships) and observed changes across time for A) leaf photosynthetic capacity and leaf chemistry traits, B) leaf morphology and leaf structural traits, C) tree phenology and structural traits and D) for dispersal traits. The insets in the left-hand side of each map show the observed and expected change, obtained from sampled vegetation plots, for lowland and montane forests given a unit increase in temperature (see full statistical details in Supplementary Table 11 and Supplementary Table 12), relative to zero change (horizontal grey line). The vertical lines depict the Highest Density Intervals (90% HDI), while circles and stars show the mean expected and observed values respectively. Maps show the extent to which community traits are tracking the expected trait values as a percentage (% tracking). Cooler colours represent positive trait tracking, white represents slight or no trait shifts and warmer colours show predicted trait shifts in opposite direction than expected. Values above 100% or below -100% are classified as 100% or -100% respectively for clarity purposes, the original values are shown in the Extended Data Fig. 6. The grey mask represents all predominately non-forested areas (e.g. crop fields, swamps, savannas, open forests, areas with small patches of forest) and was derived from the European Space Agency Land Cover CCI Product [33]. 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}: adult maximum height, WD: wood density, Fruit length: length of the fruit, Seed mass: weight of the seed.

Our results show strong mismatches between the observed and expected changes in lowland and montane forests for most traits (Fig. 5 insets; Supplementary Table 11 and Supplementary Table 12). Overall, there is a larger lag between observed and expected changes in montane forests in comparison to lowland forests for leaf morphology and structure traits such as leaf area (mean change observed over the last 40 years: 1.3 cm^2; expected: 16.5 cm^2), FM (0.01 g; 0.61 g), SLA (-0.1 cm^2 g^{-1}; 4.7 cm^2 g^{-1}), H_{max} (0.07 m; 1.3 m), but also for leaf N (0.009 %; 0.06 %), and dispersal traits such as FL (0.09 cm; 0.92 cm) and SM (28 mg; 330 mg). For the lowlands differences between observed and expected changes are stronger than for montane forest for A_{sat} where there are on average smaller declines than expected (0.03 μmol m^{-2} s^{-1}; -0.26 μmol m^{-2} s^{-1}), P (-0.5^{e-05} %; -0.008 %), N (-0.01 %; -0.04 %), leaf thickness (-0.006 mm; -0.45 mm), deciduous species abundance (-0.2 %; -3 %), and smaller increases than expected for H_{max} (-0.01 m; 1.03 m), WD (0.001 g cm^3; 0.01 g cm^3) and SM (15.8 mg; 220.4 mg).

The spatial predictions show that most forest communities across the Neotropics are lagging behind the changes in trait composition required for tree communities to keep pace with climate change (maps in Fig. 5). The spatial predictions show that many areas around central-southern Amazonia are either not tracking (i.e. values close to zero) or shifting in the opposite direction than expected for leaf photosynthetic capacity and chemistry (e.g. Amax up to -50%, N up to -30%, leaf C up to -35% and P up to -15% of required rates of change). Some traits show large trends in directions opposite from those expected: for leaf morphology, these include leaf fresh mass (up to -70%) and thickness (up to -400%), and for tree phenology and structure, abundance of deciduous species (-300%). All other traits show weak positive or negative shifts in community traits for most of the extent of Neotropical forests, with especially little tracking for the montane forests regarding leaf P, SLA, deciduousness, fruit length and seed mass (Fig. 5).

Overall, we find that 1) trait-environment relationships are consistent for most but not all traits across lowland and montane Neotropical forests; 2) more traits show significant changes in lowland (nine out of 13) than montane forests (only four); 3) the abundance of deciduous species is increasing across forest types, with accompanying decreases in leaf mass and leaf thickness, especially in lowland forests; and 4) most of these traits are changing at only a fraction (typically 10%) of the rate required to maintain equilibrium with the climate.

Lowland and montane forests show different trait-climate relationships for some traits. One possibility is that this reflects their different position along the climatic gradient (i.e. temperature and precipitation), with lowlands occupying areas with more homogeneous climate across large spatial extent in comparison to montane forests which span a large range of climates across smaller spatial extents. We detected that such shifts in responses occur on average at mean annual temperatures ~21 °C. This temperature threshold may indicate a Neotropics-wide fundamental community functional phase shift in climate regime and also underline differential responses to a changing climate. Alternatively, such differences between lowland and montane forests are potentially due to additional variables, such as cloud immersion effects in upper montane, which could shift the nature of trait-environment relationships given the lower radiation and temperature, and the high water availability across the year [35, 36]. In an extensively studied transect in the Peruvian Andes, 21 °C corresponds closely to mean cloud base height and abrupt changes in many ecosystem functions and functional traits [36].

More traits are shifting in lowland than montane forests. There has been a larger increase in atmospheric dryness (VPD) in lowland than in montane forests, caused by 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. Recently it has been suggested that increases in VPD do not necessarily have to negatively impact photosynthesis and biomass, showing how some of the wettest parts of Amazonia increase photosynthesis with increases in VPD despite reductions in canopy conductance to CO_2 [37]. Larger increases in droughts and VPD 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, for instance by means of mortality of more vulnerable species [27]. We suggest the increase in photosynthetic capacity and other chemistry (such as N) and structural traits through time in lowland forests is more likely driven by a shift in the community composition towards a higher abundance of deciduous species. Increases in the abundance of deciduous species was also detected for montane forests. Overall, deciduous species tend to have acquisitive leaf syndromes with higher leaf nitrogen and phosphorus, photosynthetic capacity and photosynthetic nitrogen-use efficiency, especially under hydric stress [38]. The pattern observed across Neotropical forests could be due to leguminous species being nitrogen fixers, often deciduous and with higher photosynthetic nitrogen-use efficiency, that dominate in dry forests [39]. As the forests have become more deciduous over the last 40 years their community-level leaf thickness and fresh mass has also declined, especially across lowland forest in the Neotropics. The increase in deciduousness across Neotropical forests is remarkable, with only few regions in central Mexico and southeast Brazil showing opposite trends. The increase in deciduousness is accompanied by decreases in fresh mass and leaf thickness, as leaves from deciduous species tend to be thinner and lighter than those of evergreen species [40, 41]. This is consistent with what has been reported for West African tropical forests where increasing drought stress increased the abundance of deciduous species, and these changes in deciduousness explained changes in other morphological, structural and leaf chemistry traits [31]. Thus, increases in deciduousness is expected to be one process undertaken by forest communities as they track a drying environment, though it may be limited in infertile contexts, such as southeastern Amazonia, where new leaf construction is costly.

Leaf size is potentially important for the resilience of forests given their role in light capture but also for water loss and gas exchange [42, 43]. Given the current trait-environment relationship we expected a decline in individual leaf area with increases in water stress. We find an overall decrease in individual leaf area across lowland and montane forests over the last 40 years with concomitant increases in water stress. Thus, it is likely that forest communities across the Neotropics are experiencing increases in species with smaller leaves as an adaptive response to increasing temperature and atmospheric and soil hydric stress. Moreover, our analyses show significant increases in fruit length in lowland forests associated with climate change and slight decreases for montane forests, the latter as might be expected under a warming and drying climate [23]. Some wetter regions (e.g. western Amazonia) do show better tracking of climate, but other regions (e.g southern and eastern fringes of Amazonia) show a decline in fruit length, which may be an indicator of heavy defaunation pressure [44] instead of a direct climate effect. More widely, such defaunation effects may be exacerbating climate change effects. Our predictions of decreases in fruit length and seed mass broadly match spatial predictions of high defaunation [45], especially in those more accessible areas of Mesoamerica, the Andes and eastern Brazil, which could thus be important drivers of the observed dispersal trait changes across time.

In some cases the changes in single traits do not behave as expected from theory, for instance it would mechanistically be expected that increasing drought would cause plant communities to shift to lower H_{max}, higher WD and thicker leaves. However, such coordinated changes may not readily happen in the community as what is changing in abundance are whole phenotypes, particular combinations of traits, rather than isolated traits. Moreover, not all trait combinations may be present in any given regional species pool, even in this mega-rich biome, which may limit the shifts in community traits that can occur at any given time, for instance as a response to environmental change.

We find that taxonomic community composition changes in Neotropical forests are driving shifts in the community traits composition, but not quickly enough to keep in equilibrium with climate, with most traits only changing at a low percentage (e.g. ~10%) of the expected change. Trees are long-lived organisms with slow turnover rates compared to the rate of climate change and this may partly explain the slow changes observed. Such lags in response to climate changes are especially important in forests, such as the Maya forest in Mesoamerica [46], the Atlantic and the southern Amazon forests in Brazil [47], which have become increasingly fragmented and which may be already facing strong edge effects affecting the capacity of communities to adapt to the new climate conditions. These forests face a double challenge from fragmentation and climate change as they try to track their suitable climate across forests with diminished landscape connectivity [48]. Furthermore, there are other factors besides climate that may further explain trait shifts or a lack of shifts across forest communities, such as soil conditions [49], biotic interactions (e.g. animal-plant interactions; [50] and wind disturbance [51]. An important point to consider is that our analysis assumes traits are fixed at species-level, and traits may be showing intra-specific 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 play an important role for adaptation to a changing climate [52, 53]. Our analysis clearly demonstrates that community changes are insufficient to track climate change, and the overwhelming onus would be on within-species variability and traits plasticity to track climate change. Given the scale of the tracking deficit we observe, it is very unlikely that such traits plasticity is sufficient to track climate change, and hence it is likely that tree species composition and functional properties of Neotropical forests, and all other tropical forests, are increasingly out of equilibrium with local climate. Such disequilibrium almost certainly increases vulnerability to climate change.

METHODS

Plot data

Our study focuses on Neotropical forests. We gathered tree-by-tree vegetation census data for 254,307 individual trees from 415 vegetation old-growth forest plots across 11 countries across the Neotropics, spanning a wide range of environmental conditions and elevations from sea level to >3000m elevation, with at least two census recorded (on average 5.7 census per plot) between the years of 1980 and 2021 and with at least ten years interval between the first and the last census with exception of the DUK plots which had only six years available (Supplementary Table 1). The plot modal size was 1 ha (mean 0.88 ha); all plots are located in structurally intact forests with no signs of direct anthropogenic impacts. Data were obtained through the ForestPlots network (www.ForestPlots.net) [54, 55]. We classified vegetation plots as either lowland (<650 metres above sea level (masl)) and montane forests (>650 masl) following other recent studies [56], which also included premontane 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 (e.g. [57-59]), from the Global Ecosystems Monitoring network (GEM; gem.tropicalforests.ox.ac.uk)[60], and the ForestPlots network (www.ForestPlots.net)[54] and also from the BIEN (bien.nceas.ucsb.edu), TRY (www.try-db.org)[61] networks and Diaz et al. [62]. The plant traits are related to the leaf chemistry, photosynthetic capacity, leaf morphology, maximum plant height, phenology, seed mass, and seed length (Supplementary Table 2). When species trait data was unavailable from the GEM and ForestPlots we also used the TRY plant trait database (www.try-db.org) and BIEN (bien.nceas.ucsb.edu) network data. We aimed to cover at least 70% of the basal area of each plot with trait data, often covering more than that (Extended Data Fig. 7). When species-level trait data were unavailable, we used the mean genus-level data. 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 investigate the role that long-term climate and its changes play on determining the trait community composition across Neotropical forests by gathering climatic data on the mean annual temperature (T_{mean}), mean maximum climatic water deficit (MCWD) [28], vapour pressure deficit (VPD_{mean}) [27], standardised precipitation-evapotranspiration index for a 12 month window ($SPEI_{12}$) [29] 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. All climatic variables were derived from the TerraClimate dataset [25] and had an original spatial resolution of ~4 × 4 km at the Equator. The dry season length was calculated as the average annual number of consecutive months with rainfall below 100 mm [63]. The MCWD was included as it is a metric for drought intensity and severity that has been shown to impact vegetation growth and survival [31]. 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 severities [64]. VPD is an indicator of atmospheric aridity, acts as a key environmental driver of plant transpiration and reduces plant water use efficiency [65]. We then tested the correlation between all pairs of climatic variables (full-term and their changes) and all had Pearson's correlation coefficients |<0.70| apart from dry season length which was highly correlated to MCWD (Extended Data Fig. 1), and we thus dropped dry season length and its change to avoid distorting model coefficients [66]. We also calculated the change in the climatic variables (ΔT_{FT}, $\Delta MCWD_{FT}$, $\Delta VPD_{FT,}$ and $\Delta SPEI_{FT}$) between a first period corresponding to a climatology of 30 years encompassing 1958–1987 and a second period encompassing the years 1988–2017 and which represents the climatic conditions across the period under analysis and for which vegetation data is available. Furthermore, we calculated the yearly rate of change of the climatic variables 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).

The study area in the Neotropics used to extract the climatic data and to make spatial predictions was delineated using the European Space Agency Land Cover CCI Product [33] using all land use classes defined as tree or shrub cover classification.

Soil variables are relevant predictors of vegetation distribution and are related to the functional trait composition [67]. Variation in soil properties could modify the rate of change in response to environmental change [68]. However, in our models, we did not include soil characteristics such as texture (clay percentage) and chemistry (cation exchange capacity, CEC) given that for the time frame analysed they are not expected to change and because our focus is on the climate change effect on vegetation.

Trait CWM calculation

The most dominant species are expected to drive ecosystem processes using their traits as described by the mass ratio hypothesis [26]. 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: $CWM_{xp} = \sum_{i-1}^{s} BA_{ip} \times x_i$. Here BA_{xp} 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, we averaged the trait values at the species level; when the species had no trait values, we averaged the trait values at the genus level. We calculated in the same way the weighted variance (CWV). Although species show some degree of intraspecific trait variation, work suggests it is relatively small compared to the trait variation found across forest tree species [69]. 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 Latin America. 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 [70]. 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

To understand the current trait-climate relationships across Neotropical forests, for each plant trait we modelled the trait CWM as a function of the T_{mean}, VPD_{mean}, $MCWD_{mean}$ and the $SPEI_{12}$, each one of these interacting with forest type (lowland or montane) (here onwards referred to these models as M1).

We observed that across the T_{mean} gradient, there was often a breakpoint where the slopes of the lowland and montane forests crossed, so we decided to investigate the specific T_{mean} at which this breakpoint occurred. To this end, we carried out a multivariate breakpoint regression analysis with the trait CWM values as a function of the four climatic variables, T_{mean}, $MCWD_{mean}$, VPD_{mean} and the $SPEI_{12}$, without separating by forest type. For the break point models we used a starting value centred at a temperature of 18 °C, 250 mm for $MCWD_{mean}$, 0.5 kPa for VPD_{mean} and -0.5 for the $SPEI_{12}$, which were often the values at which the lowland and mountain forests crossed. For the breakpoint analysis we used the 'segmented' package for R [71].

We next analysed the climatic drivers of shifts in each functional trait given observed changes in climate over the past 40 years. To this end we modelled the full term (ΔFT; i.e. from first to last census) change in the trait CWM as a function of ΔT_{FT}, $\Delta MCWD_{FT}$, $\Delta SPEI_{FT}$ and ΔVPD_{FT} each one of these interacting with forest type (hereafter referred to these models as M2). We used the M2 models to predict and spatialise the changes in trait composition across Neotropical forests over the past half-century.

All linear models were fitted under a Bayesian modelling framework with the 'rstanarm' R package. All numeric explanatory variables were centred before analysis. All models were run with normal diffuse priors with mean 0 and 2.5 standard deviations (sd) to adjust the scale of coefficients and ten sd to adjust the scale of the intercept. The models were run with three chains and 2,000 iterations. We computed the HDI (highest density interval), resulting in the range containing the 90% most probable effect values, and calculated the region of practical equivalence (ROPE) values using such HDI as in Makowski et al. [72]. The 95% HDI was not used as this range is unstable with effective sample size <10,000 [73]. If the score of a climatic variable at 90% HDI did not overlap 0, we considered it had an important (significant) effect on the response variable. 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 plot size [74]. The trait CWM change models (a separated model per trait) used a Gaussian distribution, weighting the observations by the time between the first and last census and by the size of the plots, this is we weighted by the cubic root of census interval length plus the fourth root of sampled area minus one [74].

Understanding shifts in trait CWM

We calculated the temporal changes in trait CWM at the plot level as the annual rate of change (Δr 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 (Δr). To investigate if the rate of trait changes for the overall forests (lowland and montane together), for the lowland forests alone and the highland forest alone, was significantly different from 0, and also if there were important differences between the rate of change between lowland and highland forests we carried out a Bayesian version of a typical T-test analysis using Bayesian estimation [73, 75, 76]. 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 rendering the range containing the 90% most probable effect values.

Principal component analysis of trait changes to understand shifts in functional strategies

We carried out a PCA of the trait CWM changes mapped predictions from the full term changes specified above (i.e. those from M2 and shown in maps of Fig. 3) to investigate the changes in functional strategies that have occurred across Neotropical forests and time. To this end we took the maps of mean changes in each CWM trait (M2 models) and used the 'rasterPCA' function from the RStoolbox package in R to create a Neotropics wide PCA prediction. The PCA results describe how much of such changes in strategies can be explained by the changes in each functional trait. The PCA analysis was carried out with centred and scaled trait CWM change values (mapped predictions from Fig. 3).

Understanding if forest community traits are tracking climate changes.

We used the statistical models constructed above for the current trait-climate relationships (M1) and for the observed change in trait CWM across time (M2). We took the current observed Trait-Climate (2000-2021) models (M1) and predicted the expected change in mean trait values per unit increase in T_{mean}. In the same way, we used the full-term trait change models (M2) and predicted the expected change per unit change in Temperature. We applied the same protocol mentioned above for each of the covariates in the models, for which we assumed a change in MCWD of 10mm, 1kPa for VPD and -1 unit for SPEI. While making the predictions for each covariate we kept all others constant.

This allowed us to understand the expected shift in mean trait values based on the current trait-climate relationship and that based on the observed trait changes across time (i.e., from 1980-2021). This is, the current 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.

Then, we predicted (mapped) the current trait-climate model across the Neotropics by increasing the climate values by the amount observed across the last 40 years, spatialised this model (made a map) and subtracted the original predictions (those without changes in climate conditions) as to obtain the expected changes at the pixel level (in the map) for across the Neotropics based on current trait-climate relationships. Then we calculated the ratio of the observed, i.e. spatial predictions of the trait changes observed across time, versus expected (described above) and converted to percentage 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 even 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 to the study area. The study area in the Neotropics was delineated using the European Space Agency Land Cover CCI Product [33] 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 values inherent to the climate data, we allowed 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 using the packages raster, sf, tidyverse, rgdal, rnaturalearth, rasterVis and RStoolbox.

Acknowledgements

J.A.-G. was funded by the Natural Environment Research Council under the Independent Research Fellowship (NERC; NE/T011084/1) and the Oxford University John Fell Fund (10667). This paper is a product of the NERC funded projects NE/T011084/1, 'Arboles' lead by D.G. (NE/S011811/1) and the Global Ecosystems Monitoring (GEM) network (gem.tropicalforests.ox.ac.uk). Global traits collection and traits analyses under the GEM were funded by ERC Advanced Investigator Award (GEM-TRAIT: 321131) to Y.M. under the European Union's Seventh Framework Programme (FP7/2007–2013) with additional support from NERC grant NE/D014174/1 and NE/J022616/1 for traits work in Peru, NERC grant ECOFOR (NE/K016385/1) for traits work in Santarem. Plot inventories in Peru were supported by funding from the US National Science Foundation Long-Term Research in Environmental Biology program (LTREB; DEB 1754647) and the Gordon and Betty Moore Foundation Andes–Amazon Program. Plots inventories in Nova Xavantina (Brazil) were supported by the National Council for Scientific and Technological Development (CNPq), Long Term Ecological Research Program (PELD), process 441244/2016–5 and the Foundation of Research Support of Mato Grosso (FAPEMAT), Project ReFlor, process 589267/2016. C.A.J. acknowledges support from the Brazilian National Research Council/CNPq (PELD process 403710/2012–0), NERC and the State of São Paulo Research Foundation/FAPESP as part of the projects Functional Gradient, PELD/BIOTA and ECOFOR (processes 2003/12595-7, 2012/51509-8 and 2012/51872-5, within the BIOTA/FAPESP Program—The Biodiversity Virtual Institute (www.biota.org.br); COTEC/IF 002.766/2013 and 010.631/2013 permits. B.S.M. was supported by the CNPq/PELD projects (number 441244/2016-5 and number 441572/2020-0) and CAPES (number 136277/2017-0). M.S. acknowledges funding for Andes Biodiversity and Ecosystem Research Group (ABERG) plot network from the US National Science Foundation (NSF) Long-Term Research in Environmental Biology (LTREB) 1754647, the Gordon and Betty Moore Foundation's Andes to Amazon Initiative and RAINFOR. E.B, J.B. and Y.M. acknowledge the support from NERC under projects NE/K016431/1 and NE/S01084X/1. Y.M. is supported by the Frank Jackson Foundation. The authors also thank the next contributors: Abel Monteagudo-Mendoza, Alberto Vicentini, Alejandro Araujo-Murakami, Alexander Parada Gutierrez, Antonio Peña Cruz, Antonio S. Lima, Armando Torres-Lezama, Aurélie Dourdain, Benoit Burban, Casimiro Mendoza, Damien Catchpole, Darcy

Galiano Cabrera, David Howard Neill Asanza, Douglas Morton, Eduardo Hase, Ezequiel Chavez, Freddy Ramirez Arevalo, Gabriel Damasco, Gabriela Lopez-Gonzalez, Guillermo Bañares de Dios, Hans Buttgenbach Verde, Irina Mendoza Polo, James Richardson, James Singh, John Lleigue, José Luís Camargo, Juliana Stropp, Julien Engel, Julio Serrano, Karina Melgaço, Leandro Ferreira, Luis Gustavo Canesi Ferreira, Luisa Fernanda Duque, Luzmila Arroyo, Marc Steininger, Marcos Salgado Vital, Maria Carmozina Araújo, Marisol Toledo, Massiel Corrales Medina, Mathias Tobler, Michel Baisie, Natalino Silva, Pascal Petronelli, Patricia Alvarez Loayza, Percy Núñez Vargas, Peter van der Hout, Pétrus Naisso, Raimunda Oliveira de Araújo, Terry Erwin*, Raquel Thomas, Rene Boot, René Guillén Villaroel, Roderick Zagt, Samaria Murakami, Timothy Killeen, Victor Chama Moscoso, Vincent Bezard, Wemo Betian, Wendeson Castro, Yhan Soto Shareva, Yuri Tomas Huilca Aedo.

*We thank these contributors who are no longer with us.

Contributions

J.A.-G. conceived the study, designed and carried out the analysis and wrote the first draft of the paper. Y.M. and S.D. conceived the study and discussed the analysis framework and commented on earlier versions of the manuscript. D.G. lead the general 'Arboles' project. Y.M. conceived and implemented the GEM Network, obtained funding for most of the GEM traits field campaigns. O.P. leads the ForestPlots network. All co-authors participated in or coordinated vegetation and/or trait data collection or processed field data and commented on and approved the manuscript.

Competing interests

The authors declare no competing interests.

Data availability

The vegetation census and plant functional traits data that support the findings of this study are available from the gem.tropicalforests.ox.ac.uk and www.ForestPlots.net 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.

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