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Aguirre-Gutiérrez, J, Berenguer, E, Oliveras Menor, I et al. (50 more authors) (2022) Functional susceptibility of tropical forests to climate change. Nature Ecology and Evolution, 6 (7). pp. 878-889. ISSN 2397-334X

https://doi.org/10.1038/s41559-022-01747-6

Functional susceptibility of tropical forests to climate change

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ABSTRACT

Tropical forests are some of the most biodiverse ecosystems in the world, yet their functioning is threatened by anthropogenic disturbances and climate change. Global actions to conserve tropical forests could be enhanced by having local knowledge on the forests functional diversity and functional redundancy as proxies for their capacity to respond to global environmental change. Here, we create estimates of plant functional diversity and redundancy across the tropics by combining a dataset of 16 morphological, chemical and photosynthetic plant traits sampled from 2461 individual trees from 74 sites distributed across four continents, together with local climate data for the last half century. Our findings suggest a strong link between climate and functional diversity and redundancy with the three trait groups responding similarly across the tropics and climate gradient. We show that drier tropical forests are overall less functionally diverse than wetter forests and that functional redundancy declines with increasing soil water and vapour pressure deficits. Areas with high functional diversity and high functional redundancy tend to better maintain ecosystem functioning, such as aboveground biomass, after extreme weather events. Our predictions suggest that the lower functional diversity and lower functional redundancy of drier tropical forests, in comparison to wetter forests, may leave them more at risk of shifting towards alternative states in face of further declines in water availability across tropical regions.

INTRODUCTION

Tropical forests are amongst the most biodiverse ecosystems on the planet [1], they harbour more than 50% of global biodiversity including between 67-88% of all tree species and are responsible for more than 30% of terrestrial productivity [2, 3]. Given the large distribution of tropical forests on earth, small but widespread changes in their tree community composition can have global impacts in the removal of CO_2 from the atmosphere [4]. Tropical forests are also essential to help mitigate the effects of climate change, as intact tropical forests are carbon sinks of around 1.26 Pg C yr^{-1} [5]. However, carbon storage can be negatively impacted by changes in water availability [6]. For example, the Amazon forest, which contains close to 123 Pg C of above and belowground biomass[7] lost 1.2-1.6 Pg C [8] – the equivalent of 1% of its total carbon stocks [9] – during the extreme drought of 2005 and it is now suggested to be a carbon source [10]. Besides impacting the carbon storage capacity of forests, changes in climate mean states and variability are key potential drivers of biodiversity declines around the world [11, 12]. Understanding how climate may affect tropical forests' capacity to store carbon thereby requires evaluation of how plants respond to drought stress. To do so, the Maximum Climatic Water Deficit (MCWD) and Vapour Pressure Deficit (VPD) are two fundamental proxies of hydric stress for plants [13, 14], with increases in VPD leading to greater plant transpiration stress [15, 16] (but see Costa et al.[17] for a review on the water table depth as another highly relevant metric under drought). Although it has been generally expected that communities historically adapted to high MCWD and VPD should be better adapted to increasing drier conditions, it could also be that such communities might already be at their climatic physiological limits and thus further droughts may increase water stress to such an extent that they are driven towards alternative states [18, 19]. To disentangle these two possibilities, evaluating functional trait composition may provide clues on their possible historical adaptations to water stress conditions [20, 21]. Although changes in MCWD and VPD are prominent features of climate change across tropical forests, detailed analyses that show their relationship with plant morphology/structure, leaf chemistry and photosynthesis related traits across climatic and elevation gradients at a pantropical scale remain scarce. Thus, understanding the functional-climatic gradients relationship is key to disentangling the long-term role of tropical forests for mitigating climate change and is crucial for deciphering the resilience of key ecosystem properties such as diversity and carbon stocks under a changing climate.

Ecosystem resilience may increase through different pathways, for example, by species having the same traits that affect a given ecosystem process, such as carbon capture, but different traits to respond to environmental changes, such as droughts. Arguably functional traits may respond differently to diverse drivers of change (e.g. temperature or precipitation change) which may be reflected in trait diversity but not necessarily in species richness [22] given that there is not always a tight relation between species richness and functional trait diversity [23, 24]. According to the biodiversity-ecosystem functioning insurance hypothesis [25], ecosystem functions should be less affected by a changing environment when 1) the ecosystem possesses both high functional diversity (e.g. large range of trait values; FD), 2) but also a wide set of species with similar functional characteristics [23] conferring the system with high functional redundancy (FRed) [26, 27]. Thus, in communities with high functional diversity and high functional redundancy, the loss of a given species is less likely to result in the disruption of the ecosystem function [28], as other species will probably continue carrying out the same functions, compensating the lost species [29, 30]. High FD and high FRed may enhance the temporal stability of ecosystem functions (e.g., biomass productivity) [31] and thus provide a buffering effect against environmental changes [25], conferring higher resilience. Nonetheless, these hypotheses have never been tested across the tropics, and the role of FD and FRed for maintaining the tropical forests ability to capture and store carbon remains to be tested and quantified at this global scale. Quantifying the FD and FRed is crucial to advancing our understanding of the resilience of these forests in the Anthropocene.

Here, we address this knowledge gap by combining a new pantropical dataset of 16 plant traits related to morphology/structure (leaf area, leaf dry and fresh mass, leaf dry matter content, leaf water content, specific leaf area, leaf thickness, wood density), foliar nutrients (leaf calcium, potassium, magnesium, nitrogen and phosphorus content) and photosynthesis (photosynthetic rate, dark respiration). These plant traits are hypothesised to be of importance for tropical forests to adapt or respond to a drying climate (see Table S1 for a description of their hypothesised importance). The importance of such traits relies on their influence on the capacity of species to capture energy for growth and conserve resources (e.g. water) for survival under stressful environmental conditions, such as droughts, and have been shown to change in response to a changing climate [32, 33, 34]. The plant traits were collected from 2461 individual trees belonging to 1611 species distributed across 74 plots that contained 32,464 individual trees equal to or greater than 10 cm diameter at breast height from 2497 species (Fig. S1, Table S2, See Methods). The vegetation plots are free of obvious local anthropogenic disturbance (i.e., far from forest edges, and no evidence of logging or fires) and cover a wide range of the climatic conditions found across tropical and subtropical dry and moist broadleaf forests (Fig. S2; Fig. S3). This dataset was combined with estimates of MCWD and VPD from 1958-2017 and of soil chemistry (cation exchange capacity) and texture (clay content) (Fig. S3).

We address three fundamental questions: 1) Does the long-term mean ambient water stress environment (MCWD and VPD) or its changes (ΔMCWD and ΔVPD) over the last half-century determine current functional diversity (Fig. S3)? First, we examine the relationship between the functional diversity (here calculated as functional dispersion [35]) and redundancy levels across tropical regions. The relationship between changes in climate and long-term FD and FRed can be understood as a proxies of the effects of climate change on the functional diversity levels of the ecosystem given that we do not quantify their direct effect on changes in FD and FRed. 2) What is the spatial distribution of functional diversity and redundancy across tropical forests? 3) Is there a relationship between functional diversity or functional redundancy and one metric of ecosystem functioning (above ground biomass) during extreme drought events? We expect that: 1) Communities that are found in drier climate conditions and that have experienced stronger decreases in water availability across the last half century will be less functionally diverse but may be more functionally redundant as a result of climate filtering for better adapted traits than communities in less extreme conditions such as wetter forests; 2) Across the full spatial distribution of tropical forests, tropical wet forests communities, which are more species-rich than drier tropical forests, have higher functional diversity given a broader set of ecological strategies available as a result of more stable and favourable climate; 3) There is a positive relationship between functional diversity, functional redundancy and ecosystem functioning (i.e. above ground biomass) as more functionally diverse and redundant communities may attenuate the negative effects of a changing climate and may be therefore be considered to be more resilient.

Results

Functional diversity and redundancy across tropical forests as a proxy for their susceptibility to climate change

Fundamental knowledge on the climate-FD and climate-FRed relationships across tropical forest ecosystems has been missing. To fill this knowledge gap, we calculated, for vegetation plots distributed across the tropics, the FD and FRed for morphological/structural, leaf chemistry and photosynthetic traits that are hypothesised to be of importance for tropical forests to respond to a drying climate. The selected traits play a role in plant establishment, growth and/or survival [20, 21, 36] (Table S1). Then, we investigated variation in FD and FRed across tropical forests by modelling their relation with MCWD, VPD and their interaction, the ΔMCWD and ΔVPD and their interaction (see Methods section), where more positive values in MCWD and VPD reflect stronger water deficits. In our models, we also accounted for soil characteristics (see Methods) such as texture (Clay %) and chemistry (cation exchange capacity, CEC). Soils high in clay content may have high water holding capacity over longer periods of time which is important for vegetation under drought conditions [32]. Moreover, it is widely acknowledged that tropical forests in drier regions are generally associated with soils that are richer in nutrients in comparison to wet tropical forests [37]. The feedbacks between soil–rainfall and their effects on plant distributions could be disrupted under a changing climate and therefore have adverse effects on the functioning of tropical forest ecosystems. A principal component analysis (PCA) of climate conditions (long-term trends and recent changes) indicated that the first two axes explained 71.3% of the variation among plots (Fig. S4a) and the first two axes of the soil-based PCA (with soil chemistry and texture) account for 83% of the variation among plots (Fig. S4b).

Based on the long-term mean MCWD, our results show that drier tropical forests are clearly morphologically less diverse (*slope*= -0.18 [-0.31, -0.05], median and 90% highest density intervals) than wet forests (Table S2). The effect of MCWD on morphological FD was modulated by atmospheric VPD, where the FD of communities with low VPD (blue fitted line in Fig. 1a) strongly decreased as MCWD increased, but FD tended to increase with MCWD in communities where VPD was high (red fitted line in Fig. 1a). Morphological/structural FD increased linearly with increases in clay content (*slope*= 0.08 [0.01, 0.16]; Fig. 1b). Foliar nutrients FD also tended to decrease towards drier forests (*slope*= -0.15 [-0.24, -0.05]; Fig. 1c). Overall, foliar nutrients FD increased towards communities with higher soil CEC (*slope*= 0.17 [0.12, 0.22]; Fig. 1d), while photosynthetic FD also increased towards areas that experienced stronger increases in MCWD (*slope*= 0.14 [0.02, 0.25]; Fig. 1e) but did not respond to the long-term mean MCWD. For the trait groups (morphology, nutrients, photosynthesis) for which a clear relationship with climate and soil was found (90% Highest Density Interval, HDI, of the posterior distribution does not overlap 0; Table S3), the models explained (R^2) 44%, 75% and 75% of the variation in morphology/structure, nutrients and photosynthetic FD, respectively.

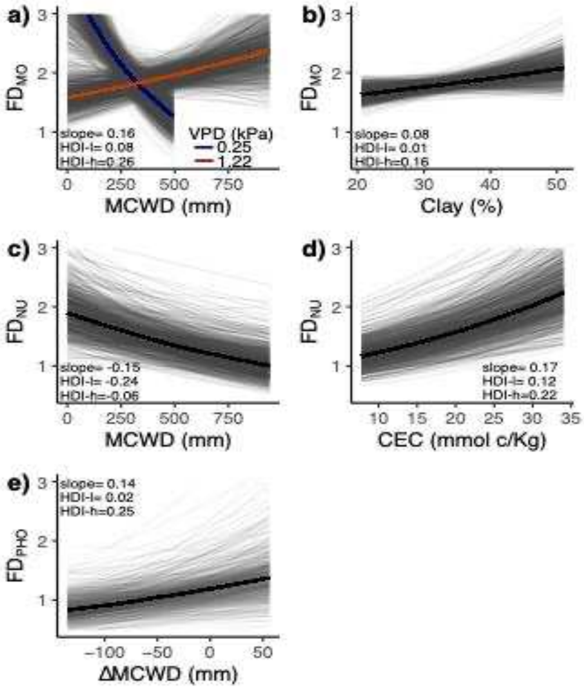


Figure 1. Long-term water availability and its recent changes and soil conditions drive functional diversity of morphological (a, b), leaf nutrients (c-d) and photosynthetic (e) plant traits across the tropics. Only climatic variables (X-axis) with a clearly important relationship (90% Highest Density Interval, HDI, of the posterior distribution does not overlap 0) with functional diversity (FD) are shown. Models for each group (morphology/structure, leaf nutrients, photosynthetic) were fitted as a function of long-term and recent changes

in climate and of soil chemistry (CEC) and texture (Clay). Thick black lines show the average response and shaded lines show 300 random draws from the model posterior distribution representing variability of the expected model fit. The blue fitted line in a) shows the effect of MCWD at the lowest value of VPD and the red fitted line at the highest values of VPD. Larger positive values in MCWD and VPD reflect stronger water deficits. MCWD: maximum climatic water deficit, VPD: vapour pressure deficit, CEC: cation exchange capacity. Δ: change. The Y-axis shows the FD of morphology/structure (FD_{MO}), leaf nutrients (FD_{NU}) and photosynthetic (FD_{PHO}) traits. For details about the single traits that form each of the groups (morphology/structure, leaf nutrients, photosynthetic) see Table S1. For full statistical results see Table S3.

The models of FRed as a function of climate and soil explained 53%, 73% and 33% of the variation in morphology/structure, nutrients and photosynthetic functional redundancy respectively across the tropical forest. The FRed models (Table S3) showed that redundancy of morphological/structural (*slope*= -0.06 [-0.11, -0.01]) traits declines with higher long-term mean MCWD and that photosynthetic FRed declines as long-term VPD increases (*slope*= -0.11 [-0.23, -0.01]; Fig. 2a and Fig. 2e respectively). While redundancy of morphological/structural and foliar nutrients traits decreased with increases in MCWD through time (ΔMCWD) in areas that also increased the most in VPD (ΔVPD; Fig. 2b and Fig. 2d red fitted line) the opposite was predicted for areas that experienced larger increases in MCWD but smallest increases in VPD (Fig. 2b and Fig. 2d blue fitted line). FRed of morphological/structural traits also tended to decrease with increases in soil clay content (*slope*= -0.04 [-0.07, -0.003]; Fig. 2c).

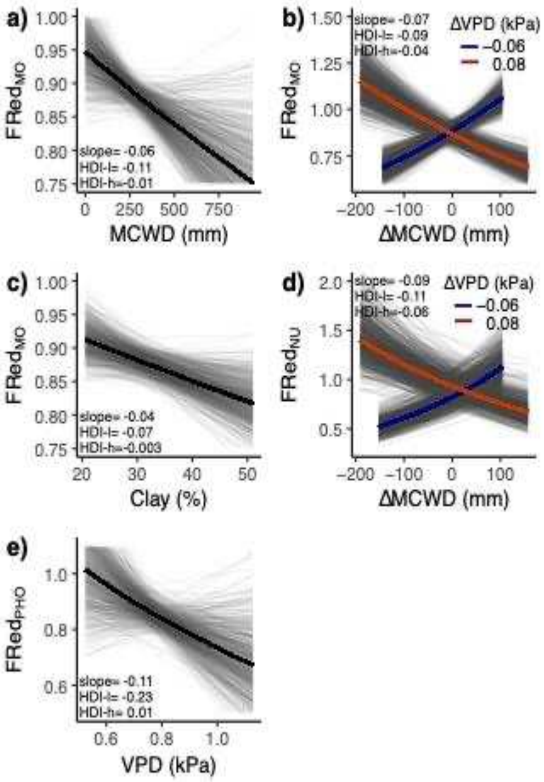


Figure 2. Long-term water availability and its recent changes and soil texture drive functional redundancy of morphological (a-c), leaf nutrients (d) and photosynthetic (e) plant traits across the tropics. Only climatic variables (X-axis) with a clearly important relationship (90% Highest Density Interval, HDI, of the posterior distribution does not overlap 0) with functional redundancy are shown but in e) where the effect of VPD on $FRed_{PHO}$ is marginal. Models for each group (morphology/structure, leaf nutrients, photosynthetic) were fitted as a function of long-term and changes in climate and of soil chemistry (CEC) and texture (Clay). Thick black lines show the average response and shaded lines show 300 random draws from the model posterior distribution representing variability of the expected model fit. The blue fitted line in b) and d) shows the effect of ΔMCWD at the largest

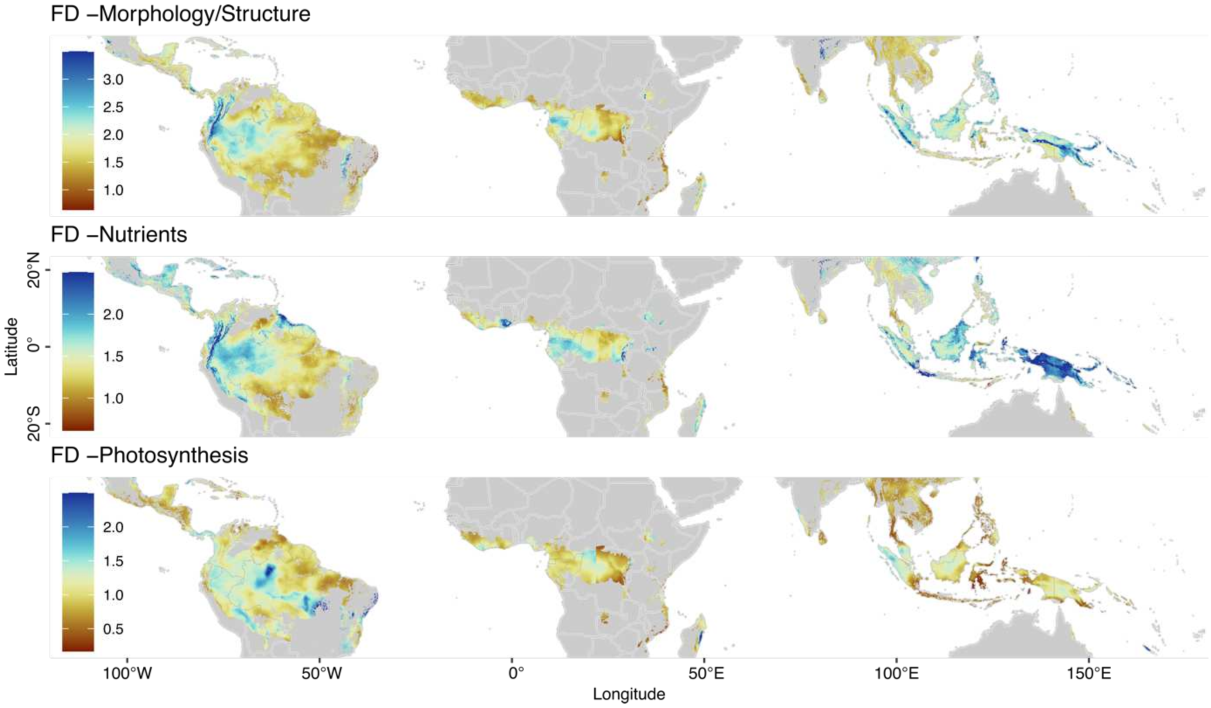
decrease in ΔVPD and the red fitted line at the larger increase in ΔVPD. Larger positive values in MCWD reflect stronger water deficits. MCWD: maximum climatic water deficit, VPD: vapour pressure deficit, Δ: change. The Y-axis shows the FRed of morphology/structure (FRed$_{MO}$), leaf nutrients (FRed$_{NU}$) and photosynthetic (FRed$_{PHO}$) traits. For details about the single traits that form each of the groups (morphology/structure, leaf nutrients, photosynthetic) see Table S1. For full statistical results see Table S3.

Mapping functional diversity and functional redundancy across tropical forests

Based on our understanding of the relation of FD and FRed of morphological/structural, leaf nutrients and photosynthetic trait groups with climate and soil (Fig. 1 and Fig. 2), and to fill the knowledge gap on the pantropical distribution of functional diversity and redundancy we created pantropical maps of both FD (Fig. 3) and FRed (Fig. 4) distribution. With our map predictions we aim to uncover the locations of forests with potentially higher and lower resilience to a changing climate. To this end, we used the statistical models built above (Table S3) to predict FD and FRed across the pantropical dry and moist broadleaf forests, for which our field sampling locations have a wide representation of the climatic conditions across those tropical forests (Fig. S2; Fig. S5 and Fig. S6). Based on the FD and FRed predictions, we calculated the percent area that had ‘low’, ‘intermediate’ and ‘high’ diversity and redundancy for each trait group (see methods). We also created bivariate maps that combine the FD and FRed scores in a single map to visualise where FD and FRed are both maximized and minimized across the tropics (Fig. 5). We further developed the same statistical models as described above but by removing from the analysis all plots from each continent (Asia and Australia out at the same time) to determine which regions have higher contribution to determining the observed spatial predictions (those of Fig. 5). For morphology/structure, foliar nutrients and photosynthesis we found high correlations between the bivariate maps developed with the full dataset and when Asia and Australia were left out (*r*= 0.96, 0.82 and 0.94; Fig. S7, Fig. S8, and Fig. S9 respectively; Also Fig. S10). For morphology/structure and photosynthesis there were also high correlations between the patterns based on the full dataset and those based on the one where Africa was removed (*r*= 0.92 and 0.93 respectively; Fig. S7 and Fig. S9 respectively). Low correlations between the maps generated with the full dataset and those based on smaller datasets depict those regions contributed significantly for the full model predictions (Fig. S10), which is also correlated to the number of observations available for each continent (Table S2 and Table S4).

As predicted, our results show that wetter tropical forests tend to be more functionally diverse than drier tropical forests, especially for morphological/ structural traits and foliar nutrients traits, but also more functionally redundant for foliar nutrients and photosynthetic traits than drier tropical forests (Fig. 3 and Fig. 4). While FD levels across our sampling locations are not significantly related to their taxonomic diversity (number of species, genera and families; *P-val* > 0.05), FRed$_{NU}$ appears to be positively correlated to taxonomic diversity (*P-val* < 0.05; Table S5). Our results suggest that given the lower FD (Fig. 3) and FRed (Fig. 4) of drier tropical forests for most of the analysed trait groups, these forests may be more at risk in the face of further water availability reductions.

The bivariate predictions maps combining FD and FRed (Fig. 5) highlight how wet tropical regions, such as the Western Amazon, Central Africa, and several regions in South East Asia maintain high functional diversity and high functional redundancy of morphological/structural (FD_{MO} max=3.5, $FRed_{MO}$ max=1.5) and leaf nutrients traits (FD_{NU} max=2.5, $FRed_{NU}$ max=1.5), and also in several wet regions for leaf photosynthetic traits (FD_{PHO} max=2.5, $FRed_{PHO}$ max=1.5). We expect these wet tropical regions to be more resilient to a changing climate given their large combined FD (Fig. 3) and FRed (Fig. 4). To evaluate which are the different levels FD and FRed across tropical and subtropical dry and moist broadleaf forests, we distinguished low, intermediate and high scores based on the range of the spatial predictions (Table S6; see methods section). We predicted that only 2.4% of the tropical and subtropical dry and moist broadleaf forests have high morphological FD and 2.3% high morphological FRed. In contrast, the drier tropical forests show a functional diversity of morphological/structural traits that reach only about half of that in the wet tropics (FD_{MO} min=~1.5) and some of the lowest FRed (<0.6). From the total area of tropical and subtropical dry and moist broadleaf forests, 30.4% shows low morphological/structural FD and 5.5% have low morphological/structural FRed. Moreover, FD and FRed of leaf nutrients traits are lowest to intermediate across the tropical dry forest regions, such as the southernmost parts of the forests in Brazil, in parts of Mexico, and West Africa (Fig. 3 and Fig. 4).



FD –Morphology/Structure

FD –Nutrients

FD –Photosynthesis

Figure 3. Global predictions of functional diversity (FD) for morphological/structural (top panel), leaf nutrients (middle panel) and photosynthetic (bottom panel) traits across the tropical and subtropical dry and moist broadleaf forests. Dark brown colours depict areas where FD is lowest, light brown and light blue where FD is intermediate and dark blue where FD is predicted to be highest. Functional diversity predictions across the tropics were made using the statistical models for which details are shown in Table S3. The location of field sites whose data informed this analysis is shown in Figure S5.

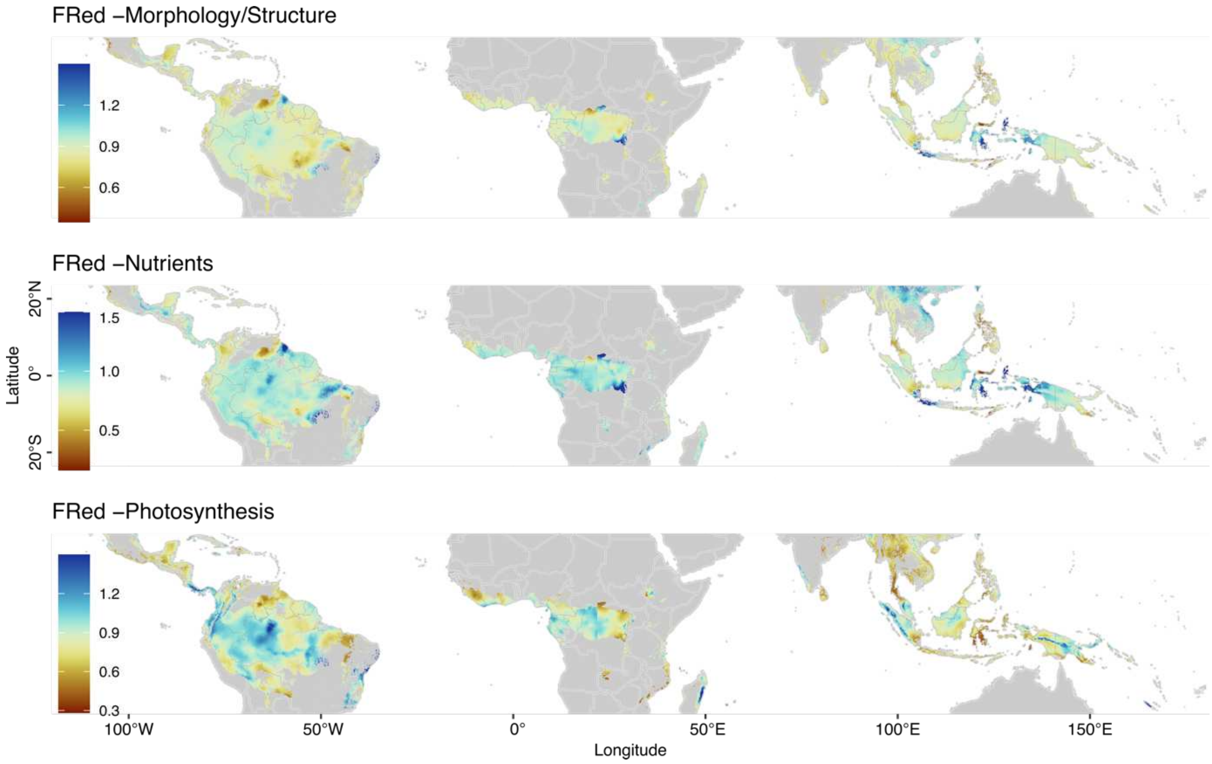


Figure 4. Global predictions of functional redundancy (FRed) for morphological/structural (top panel), leaf nutrients (middle panel) and photosynthetic (bottom panel) traits across the tropical and subtropical dry and moist broadleaf forests. Dark brown colours depict areas where FRed is lowest, light brown and light blue where FRed is intermediate and dark blue where FRed is predicted to be highest. Functional redundancy predictions across the tropics were made using the statistical models for which details are shown in Table S3.

While 14.8% of the forest area has low foliar nutrients FD and 3.7% low FRed, 14.1% shows high nutrients FD and 7% high FRed. Drier tropical forests in Western Mexico, the southern forest portion of Brazil and parts of central and West Africa show intermediate to high photosynthetic FD (max=2.5) but they also tend to show intermediate to low levels of FRed ($\mathrm{FRed_{Pho}}$ min=0.3). However, photosynthesis FD and FRed do not seem to have a clear difference between wetter and drier forests. About 36.8% of the tropical and subtropical dry and moist broadleaf forest area is predicted to have low photosynthetic FD and 16.9% to have low photosynthetic FRed, while only 2.4% is expected to have high photosynthetic FD and 6.8% high photosynthetic FRed. Overall, a large amount of forest area has intermediate photosynthetic FD and/or FRed levels (60.7% and 76.3% respectively). The bivariate FD-FRed predictions show that most tropical forests across West Amazon and Central Africa reach some of the highest predicted morphological and photosynthesis FD and FRed, while a smaller area of western South America reaches some of the highest predicted nutrients FD and FRed (Fig. 5). In general forests in drier areas show lower FD and FRed combined scores (grey colour; Fig. 5 bottom panel) for the three functional groups (morphology/structure, nutrients and photosynthesis) but this is more evident for the photosynthesis traits (Fig. 5).

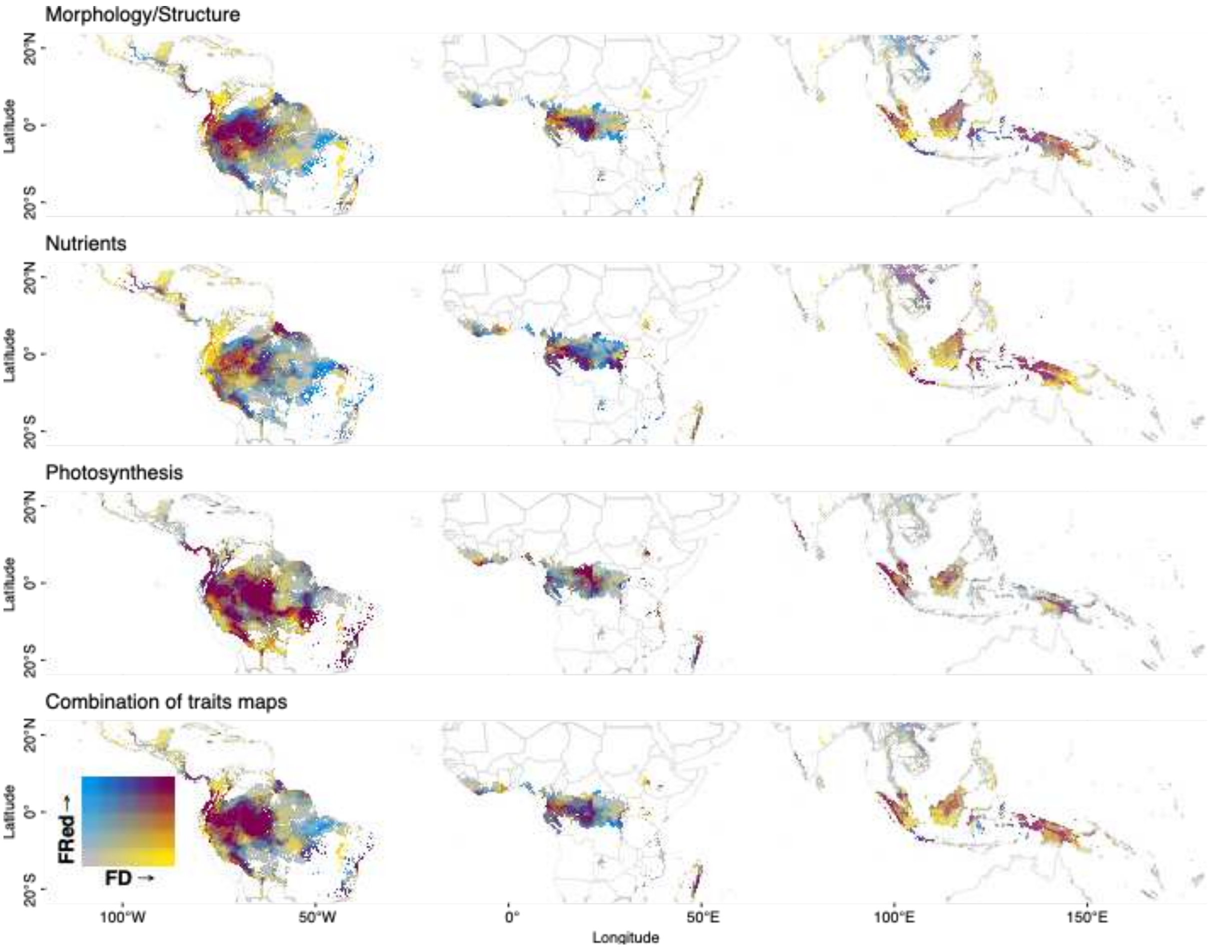


Figure 5. Global bivariate maps combining the scores of the Functional Diversity (FD) and Functional Redundancy (FRed) for morphological/structural (top panel), leaf nutrients (second panel) and photosynthetic (third panel) traits across the tropical and subtropical dry and moist broadleaf forests. The bottom panel shows the combination of the morphological/structural, nutrient and photosynthesis bivariate maps, after standardizing (with values 0 to 1) and summing them to obtain a general bivariate map of global functional diversity and functional redundancy. Purple-red colours depict areas where both FD and FRed are highest, while yellow points to areas with higher FD and blue to areas with higher FRed. Gray colours show areas where both FD and FRed are predicted to be lowest. See full details of the statistical models underlying these predictions in Table S3.

Testing the link between functional diversity, functional redundancy and resilience in ecosystem functions under climate change

We tested to what extent the long-term FD and FRed model predictions (Fig. 3 and Fig. 4), could capture the functioning of tropical forests after climatic disturbances such as El Niño events. By obtaining the above ground biomass data (AGB) from a set of 86 vegetation plots in tropical Africa before and after the 2015 El Niño event [38], we calculated the change in aboveground biomass (ΔAGB) and modelled it as a function of the predicted long-term FD and FRed map scores. Bennett et al. [38] did not detect a strong decline in AGB for most forests they analysed after the 2015 El Niño event. We show that, on average, smaller decreases or larger increases in AGB (Fig. 6; Table S7) can be found at locations that are predicted to have higher long-term FD and FRed of morphology/structure (*slope*= 1.97, [0.28, 3.65]; Fig. 6a) and nutrients traits (*slope*= 2.94, [0.25, 5.69]; Fig. 6b) and also higher FRed of photosynthesis traits (*slope*= 2.96, [0.94, 5.13]; Fig. 6d) (Table S9). The effect of $\mathrm{FD}_{\mathrm{NU}}$ on ΔAGB was mediated by recent changes in MCWD (ΔMCWD), with positive $\mathrm{FD}_{\mathrm{NU}}$ effects found in areas that experienced larger increases in mean MCWD (Fig. 6b). There was no strong effect of FD_{PHO} in areas where ΔVPD was smaller (blue fitted line in Fig. 6c) but the effect became negative for areas where ΔVPD was larger (becoming drier, red fitted line in Fig. 6c). The effect of $FRed_{NU}$ on ΔAGB was mediated by ΔMCWD with a positive effect only in regions that experienced increases in water availability (Fig. 6e blue fitted line; *slope*= 2.94 [0.25, 5.69]).

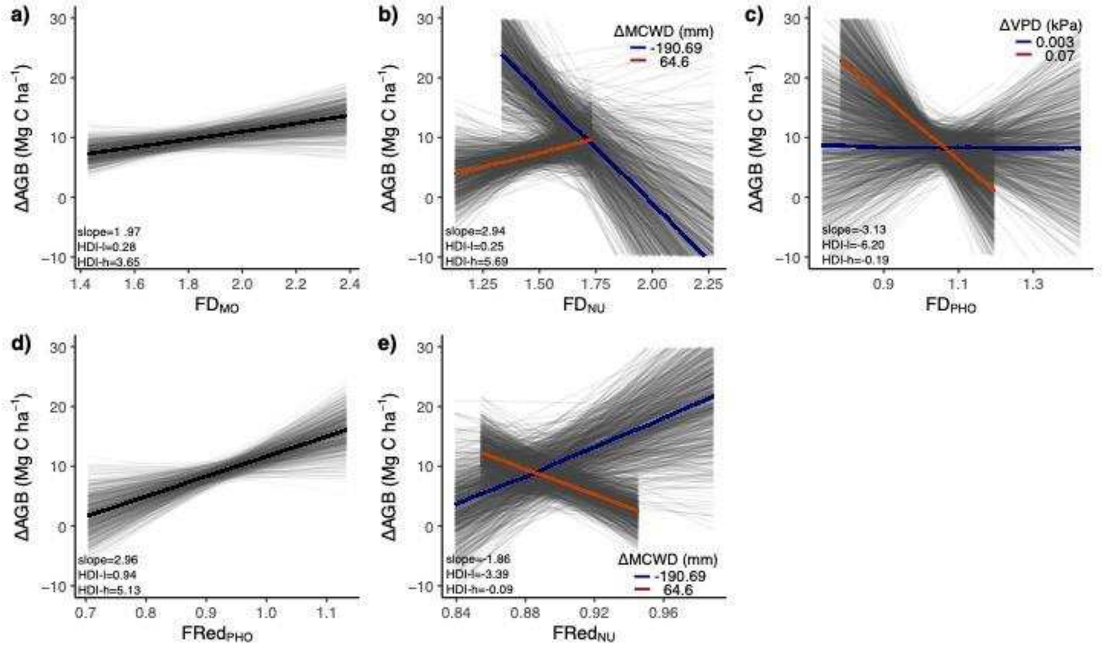


Figure 6. The strength of changes in aboveground biomass (ΔAGB) after extreme events such as the 2015 El Niño (from Bennett et al. [38]) are related to the local functional diversity (FD; a-c) and functional redundancy (FRed; d-e) for sites in Africa. The x axis shows the FD or FRed scores for the morphological/structural (MO), nutrients (NU) and photosynthetic (PHO) traits as extracted from Fig. 3 and Fig. 4 and the Y axis shows the relation with ΔAGB. The ΔAGB shows a clear relation (90% Highest Density Interval, HDI, does not overlap 0) with the diversity indices (Table S7). Thick black lines show the average response and grey shaded lines show 700 random draws from the posterior distribution representing variability of the expected model fit. The blue fitted line in b) shows the effect of FD_{NU} at the largest decrease in ΔMCWD and the red fitted line at the larger increase in ΔMCWD. The blue fitted line in c) shows the effect of FD_{PHO} at the largest decrease in ΔVPD and the red fitted line at the larger increase in ΔVPD. In e) the effect of $FRed_{NU}$ is shown for the largest decrease in ΔMCWD with the blue fitted line, and the red fitted line shows the effect at the largest increase in ΔMCWD. In b, c and e the thick blue and red fitted lines represent the slopes of the interaction between the variable in the X axis and the moderator (i.e. ΔMCWD or ΔVPD). The FD and FRed scores for each trait group (i.e. morphology/structure, nutrients and photosynthetic) are predictions extracted from Fig. 3 and Fig. 4 for the vegetation plots where the ΔAGB was collected. Only model covariates with a clear relationship with the ΔAGB are shown. For full statistical results see Table S7.

Discussion

Changes in forest cover affect the local surface temperature by means of the exchanges of water and energy [39]. At the same time climate change is altering land conditions affecting the regional climate and in the near future global warming is likely to cause the emergence of unprecedented climatic conditions in tropical regions [39]. Therefore, determining the distribution of more and less resilient tropical forests (e.g. regarding the maintenance of their functioning) to a changing climate and understanding the mechanisms causing such changes in resilience is pivotal for the conservation of biodiversity and ecosystem functioning. Here we provide spatially explicit models of forest functional diversity and functional redundancy that may aid on this endeavour. However, such predictions may not directly reflect the actual resilience of forest towards climate change as other biological (e.g. competition, dispersal) and climatic (e.g. ground water depth, microclimate) may also play a pivotal role on the responses of tropical forests to a changing environment.

Theory on niche complementarity predicts that more diverse systems make more efficient use of ecosystem properties given the complementarity of species in the use of resources available [40, 41]. High functional complementarity and functional redundancy may be more easily achieved in areas with high taxonomic richness. Such complementarity may also increase the performance of diverse communities in the face of more stressful environments given facilitative interaction between species [42]. It can be therefore expected that more functionally diverse and more functionally redundant communities would experience lower change in performance (e.g. lower mortality, lower biomass decrease) with changes in environmental conditions (e.g. ΔMCWD, ΔVPD). In our study we observed that the functional diversity levels are not significantly related to the taxonomic diversity found in the study sites across the tropics but that functional redundancy tends to be, especially for redundancy in morphological/structure and foliar nutrients traits. This points to the role of taxonomic diversity on the possible resilience of tropical ecosystems. We show that forest communities located in areas with lower soil and atmospheric water stress are generally more functionally diverse and more functionally redundant in morphological/structural, nutrients and photosynthetic traits than communities in drier areas. Such higher functional diversity and higher functional redundancy may be one reason why such forests have experienced weaker compositional and ecosystem functioning changes (e.g. carbon capture) as a result of a drying climate in comparison to forests in drier areas, as shown for forests across water availability gradients in West Africa [32, 33] and the Amazon [25, 34]. The higher functional diversity in these wetter forests can be the result of their high water availability (low MCWD and VPD, Table S2) [43, 44]. These conditions facilitate the adaptation, by means of a varied species morphology and structure [45], to a diverse set of light and moisture conditions under and at the canopy. Overall, our results support our expectation of lower functional diversity in the sites with lower long-term water availability, and are in agreement with what has been recently found not only for functional diversity but also for taxonomic and phylogenetic diversity in some local forests [32, 46]. Higher diversity and higher redundancy in functional traits may enhance ecosystem functioning, such as the ability of plant communities for carbon capture [47, 48], and thus show smaller reductions in biomass and lower mortality [49] under changes in climatic conditions. Our results are consistent with recent studies carried out in temperate forests [48] and with few tree taxa [26], which suggest a positive functional diversity-productivity relationship.

Tropical forests that experienced the largest decreases in soil water availability across the last half century, which corresponds to intermediate to high long-term average MCWD (e.g. some forests in Panama, Peru and southern Mexico), tend to have high morphology/structure and nutrients FD and FRed and high photosynthetic FD. The high functional diversity and high functional redundancy potentially points to the capabilities of such forests to better withstand the effects of a drying environment than other locations with low FD and FRed levels. Our findings show that atmospheric water availability (VPD) and its changes in the last decades mediate the FD and FRed levels across tropical forest ecosystems. Forests that experienced larger decreases in VPD over the last half century tend to be functionally redundant in morphological and nutrients traits even with increases in soil water availability (here the MCWD). However, such forests are not necessarily redundant in photosynthesis traits. One explanation for this pattern of higher redundancy of forests that experienced larger increases in MCWD and VPD is that such increases in water stress occurred in a variety of forests which are located all across the long-term mean MCWD and VPD spectrum (See Table S2). That means that these forests may well be composed of species with a wide range of functional adaptations to local conditions, adaptations that could have a possible mechanistic link via leaf phenology [50], some adapted to long periods of droughts but also others adapted to high water availability across the year. As tropical forests that increased the most in soil and atmospheric water availability are located across the long-term water availability gradient, these forests might be composed of species that have evolved with different leaf strategies ranging from evergreen to sclerophyllous and deciduous [21]. Leaf adaptations to different environments may thus also explain the pattern of increasing diversity and redundancy of leaf nutrients and photosynthesis traits in these forests that experienced larger decreases in water availability. An important further step in future analyses will be to include as much information as possible not only on the changes in climate but also on the contemporary changes in functional diversity and functional redundancy. This would allow establishing a more direct link between the effects of a changing climate on forest functioning. Moreover, while our study showed clear relations with proxies of water availability at a pantropical scale (MCWD and VPD), other environmental variables at fine scale including local topography and ground water availability may also contribute for determining local FD and FRed levels.

Forests with larger functional diversity and larger functional redundancy pools may be more resilient to further climate change. Extreme El Niño events bring about higher temperatures and droughts across tropical forests which can impact the establishment, survival and persistence of tropical forest vegetation, thus also impacting their functioning [38]. The 2015-2016 El Niño event did not seem to strongly reduce carbon gains in African tropical forests. Although we did not measure the functional composition of those tropical forests in Africa before and after the El Niño event, our modelling framework provides a general understanding of the functional diversity and functional redundancy of such forest given long-term climate conditions. Our results show that areas with higher long-term functional diversity and functional redundancy tended to show smaller decreases or larger increases in AGB, thus being more resilient to changes in environmental conditions caused by the 2015-2016 El Niño event. Overall, our results highlight that tropical dry forests, such as those in drier parts of Mexico, Colombia, south-eastern Amazonia and much of West Africa, which have experienced high long-term soil water and atmospheric water stress over the last half century, could be at higher risk than wetter forests of further functional declines given the projected changes in climatic conditions for the coming decades [51]. Further droughts may increase the water stress of drier tropical forests, which may already be at their climatic physiological limits, and could potentially drive them towards alternative stable states [19]. This is in agreement with recent findings for West African [32] and South American drier tropical forests [6, 50], where large and consistent changes in functional diversity [34] and functioning [6] have been observed. It has been hypothesised that low functional diversity and low functional redundancy may pinpoint areas that could be less resilient to further changes in environmental conditions [52]. Recent work in the wet tropics of Australia shows that tree growth has been reduced the most by positive anomalies in atmospheric water deficits in drier forests and for species growing faster in drier conditions than in wetter ones [36]. The net carbon sink of tropical seasonal forests has decreased by 0.13 Mg C ha^{-1} year^{-1} amounting to carbon losses of 3.4% per year, highlighting how the driest and warmest sites are experiencing the largest carbon sink declines and becoming carbon sources [6]. Moreover, the effects of a changing climate on drier tropical forest ecosystems may not only affect tree growth and survival but also strongly decrease their functional trait space available, possibly also affecting their functioning [50]. Both the species-level and forest-level differential demographic sensitivities to a drying climate support this hypothesis of potentially less resilience in already-drier environments.

We also highlight the need for measuring more widely other plant functional traits that have a more direct link to the availability, accessibility and transport of water resources and to adaptations to a drying climate such as plant hydraulic traits (e.g. vessel density, P$_{50}$, hydraulic safety margin, hydraulic conductivity, osmotic potential, root size and depth) which are seldom available for most tropical plant species but that may shed more light into the possible responses of tropical forest to a changing climate [53, 54]. However, recent work has shown there is strong correlation between plant hydraulics and economic traits. For instance wood density may serve as a proxy for hydraulic traits [55] and has been shown to corelated with vessel diameter, branch and tree leaf specific conductivity [56, 57, 58], resistance to embolism [57, 59], sapwood capacitance [60, 61], minimum leaf water potential [62] and leaf water potential at turgor loss [60]. Also, significant relationships between SLA and conduit diameter, seasonal change in pre-dawn leaf water potential and stomatal conductance have been found [62], together with significant correlation between leaf P$_{50}$ and leaf mass per area (LMA) and leaf hydraulic conductivity and LMA [63]. Moreover, the leaf osmotic potential at full turgor and leaf nitrogen content have been shown to be largely correlated [64]. Given that within the hydraulics traits, and thus their leaf and wood economics correlates, and in face of a changing environment, there is a trade-off involving drought avoidance and hydraulic safety. Such trade-off forms an important axis of variation across tropical forests where it is expected that fast-growing species have lower hydraulic safety compared to slow-growing species [54]. Across the tropics species that can quickly transport water resources would tend to be the ones with low wood density, short leaf life span and high rates of resources acquisition [53]. We expect this relationship to scale up from the individual to the ecosystem level and that this is thus reflected in ecosystem characteristics such as above ground biomass.

In summary, this study addresses the need to understand and monitor the responses of tropical forest ecosystems to climate change, such as the negative impacts of a drying climate on the capacity of tropical forests to sequester and store carbon. Current models of ecosystem contribution to climate mitigation lack information on earth systems feedbacks. Our results show how contemporary climate shapes the functional diversity and functional redundancy of tropical forest communities. Across the tropics a diverse set of climatic conditions support a myriad of tropical tree communities with diverse combinations of plant functional traits and different functional diversity and functional redundancy levels. Tropical communities more at risk of shifting towards alternative states could be expected to be currently the ones where lower functional diversity and redundancy is found and that are under already high water stress, such as in the drier tropical forests. From the ecosystems conservation point of view, it is of critical importance to inform decisions by mapping tropical regions in terms of their resilience to future changes in the environment. Conservation efforts need to prioritise and manage ecosystems accordingly, especially including drier tropical forests in the conservation agenda, but also considering that wet tropical forests with higher functional diversity and higher functional redundancy are likely to continue to be long term carbon stores and be more resilient in the face of climate extremes and pathogens.

Methods

Vegetation plots. We collected vegetation census data from 74 permanent vegetation plots that are part of the Global Ecosystems Monitoring network (GEM; www.gem.tropicalforests.ox.ac.uk) [65]. These plots are located in wet tropical forests, seasonally dry tropical forests, and tropical forest-savanna transitional vegetation. The sampled vegetation plots ranged in area from 0.1 to 1 ha, with most (67%) being 1 ha and only one of them being 0.1 ha (Table S2). The plots are located in Australia, Brazil, Colombia, Gabon, Ghana, Malaysian Borneo, Mexico and Peru across the four tropical continents (Table S2). In each plot, all woody plant individuals with a diameter ≥ 10 cm at breast height (DBH) or above buttress roots were measured. In the plots NXV-01 and NXV-10 in Nova Xavantina, here onwards referred to as Brazil-NX, the diameter was measured at 30 cm from the ground level as is standard in drier shorter vegetation monitoring protocols.

Plant functional traits. We directly collected plant functional trait measurements from the most abundant species that would cover at least 70% of plot basal area and that were located in most of the 74 vegetation plots mentioned above (Fig. S1; Table S1). All traits were collected following the GEM network standardised methodology across plots. Forest inventory data were used to stratify tree species by basal area dominance. The tree species that contributed most to basal area abundance were sampled with 3–5 replicate individuals per species. Eighty percent or more of basal area was often achieved in low diversity sites (e.g., montane or dry forests). For each selected tree a sun and a shade branch were sampled and in each branch 3–5 leaves were used for trait measurements. This represented a total sample of 2461 individual trees across the tropics (Fig. S1). We collected plant functional traits related to photosynthetic capacity A_{max} (µmol m^{-2} s^{-1}): light-saturated maximum rates of net photosynthesis at saturated CO_2 (2000 ppm CO_2), A_{sat} (µmol m^{-2} s^{-1}): light-saturated rates of net photosynthesis at ambient CO_2 concentration (400 ppm CO_2), R_{Dark} (µmol m^{-2} s^{-1}): dark respiration. Leaf nutrient concentration traits (%) of Ca: leaf calcium, K: leaf potassium, Mg: leaf magnesium, N: leaf nitrogen and P: leaf phosphorus. Plant morphological and structural traits, A (cm^2): leaf area, DM (g): leaf dry mass, FM (g): leaf fresh mass, LDMC (mg/g): leaf dry matter content, LWC (%): leaf water content, SLA (g/m^2): specific leaf area, T (mm): leaf thickness and WD (g/cm^3): wood density. Further details of measurements for the Peruvian

Andes campaign are given in Martin et al. [66] and Enquist et al. [67], for the Malaysian campaign in Both et al. [68], and for the Ghana and Brazil campaigns in Oliveras et al. [69], Gvozdevaite et al. [70] and for Colombia campaigns in González-M. et al. [50]. For the specific dates of plant functional traits collection see ref. [71]. For the FD and FRed calculations, as both only accept one trait value per species, from the individual level plant functional traits, we averaged the values at species level and when the species had no trait values available, we filled the gaps by averaging the trait values at the genus level. This protocol allowed us to have at least 70% of the plot's basal area covered by traits but often more. Thus, in our analysis the inclusion of plots is trait dependent in the sense that only plots with at least 70% of the BA covered by the focus trait were included in the analysis (see Table S2).

Community level functional diversity and functional redundancy

We calculated the functional diversity and functional redundancy of morphological/structural traits, leaf chemistry and photosynthetic traits, which are hypothesised to be of importance for tropical forests to respond to a drying climate (Table S1) [14,21], based on data for species covering at least 70% of the plot basal area (Table S2) and following equations from refs. [35,72,73,74]. The morphological/structural and nutrient related traits used for this analysis are A, FM, DM, LDMC, T, LWC, SLA, WD, Ca, K, Mg, N, P; and A_{sat}, A_{max} and R_{Dark} for photosynthesis. We did not build an index including all functional traits together as this would make their interpretation rather difficult as they point to different axes of the global spectrum of plant form and function [75] and also because of the difference in number of records available for each trait group. Plant functional trait diversity (FD) was calculated at the plot level using the functional dispersion metric, which is closely related to the RaoQ and which represents the mean distance, in trait space, of each single species to the weighted centroid of all species [35]. We used the FD as it can handle any number and type of traits, because it is unaffected by species richness, it weighs the values based on the abundance of species, it is not influenced by outliers and is relatively insensitive to the effects of undersampling [76]. To calculate FD we applied the equation presented by Laliberté and Legendre [35]:

eq. 1 $$FD = \frac{\sum BA_{ip}\, z_{ip}}{\sum BA_{ip}}$$

where BA_{ip} reflects the total plot level basal area of species *i* in plot *p* and z_{ip} is the distance of species *i* in plot *p* to the weighted centroid of the *n* species in trait space. The plant traits were weighted by the relative basal area (in m^2) of each of the species in the plot. Therefore, FD summarises the trait diversity and represents the mean distance in trait space of each species to the centroid of all species in a given community. All numeric traits were standardised during the FD calculation.

We calculated the functional trait redundancy in the community (vegetation plots), FRed, as in Pavoine and Ricotta [73] and Ricotta et al. (*'Rstar'*) [74] and as developed in the 'uniqueness' function of the R 'adiv' package [72]. *'Rstar'* quantifies how redundant a plant community is compared to a scenario where all species would have the most distinct trait values possible. As in the case of FD, *'Rstar'* as calculated in Ricotta et al. [72,73] works with multiple traits and takes into account species abundances. The *'Rstar'* index is complementary to the community-level functional uniqueness index *Ustar* described by Ricotta et al. [73] which is the ratio of the Rao quadratic diversity index *Q* [77, 78], that accounts for species trait dissimilarities and the Simpson index *D*, which considers the species in the community as equally and maximally dissimilar. Thus *Ustar* measures the uniqueness of the community in functional space which is obtained by including interspecies dissimilarities in the calculations of the index. *Rstar*, which is the complement of *Ustar*, represents thus a measure of community-level functional redundancy and is quantified as:

eq. 2 $$Ustar = \frac{1-D}{1-Q}$$

eq. 3 $$Rstar = 1 - Ustar$$

For an in-depth description of the functional redundancy index see refs. [72, 73, 74].

All above-mentioned analyses were carried in the R statistical environment [79] with the 'FD' and 'adiv' packages.

Climatic and soil data

In order to investigate the role that long-term climate plays on determining the community trait composition and functional diversity and redundancy across tropical forests we gathered climatic data on the potential evapotranspiration (PET in mm), precipitation accumulation (mm) and VPD (kPa) from the TerraClimate project [80] at a spatial resolution of ~4 × 4 km. The data were obtained for the period from 1958 to 2017. Using the full-term climatic dataset (1958-2017) we calculated the mean annual VPD, PET, precipitation coefficient of variation (CV; as a measure of seasonality in water availability) and the maximum climatological water deficit (MCWD). The MCWD is a metric for drought intensity and severity and is defined as the most negative value of the climatological water deficit (CWD) over each calendar year. The VPD is an indicator of plant transpiration and water loss [14]. CWD is defined as precipitation (P) (mm/month) – PET (mm/month) with a minimum deficit of 0. The MCWD was calculated as in Malhi et al.[13] where MCWD=min(CWD1…CWD12). As a final step we converted the MCWD so that positive values indicate increases in water stress. We also calculated the change in the climatic variables (ΔMCWD, ΔVPD and ΔCV) between a first period corresponding to a climatology of 30 years encompassing 1958-1987 and a second period encompassing the years 1988-2017. The climatology of 30 years to calculate the different time periods climate was selected as recommended by the World Meteorological Organization in order to characterise the average weather conditions for a given area (www.wmo.int/pages/prog/wcp/ccl/faqs.php). There are other possibly relevant predictors of water stress for plants in tropical forests such as the water table depth [17,81]. It has been hypothesised that water table depth drives the distribution of plant species and functional composition, and where it is expected that forest in shallow water table areas show higher mortality during strong drought events (e.g. El Niño) given the presence of species with shallower roots and less adapted traits [17,81]. However, we did not include the water table depth in our analysis given the lack of spatially explicit predictions across the tropics.

We also obtained soil texture (percent clay and sand) and chemistry (soil pH and cation exchange capacity, CEC) gridded data from the SoilGrids project (www.soilgrids.org) and used this as extra covariates in our modelling framework. Although the CEC includes the acid aluminium, which is not a plant nutrient and may be toxic to plants, this is one of the best estimates of the overall potential of the soil to exchange cations (Ca, Mg, and K) that is available at a pantropical extent [82].

We then tested the correlation between all pairs of climatic variables (full-term and their changes) and also between the soil variables. We observed that MCWD and CV had Pearson's correlation coefficients |>0.70| and also CEC and pH and Clay and Sand had correlation coefficients |>0.70| (Fig. S11) and we thus dropped CV and its change, Sand and pH from the analyses as to avoid distorting model coefficients in the modelling stage [83]. We then carried out a principal component analysis (PCA) using the MCWD and VPD climatic variables (average of full-term and their changes) and another with the soil variables to investigate the distribution of the vegetation plots in climate and soil space and to describe how much of this distribution can be explained by each of these. For the PCA analysis we used the 'stats' package in R.

Statistical analysis

Functional Diversity and Functional Redundancy statistical analysis

We investigated the variation in morphological/structural, leaf chemistry and photosynthetic FD and FRed across tropical forests by modelling their relation with mean MCWD, VPD for the period 1958-2017 and their interaction, the ΔMCWD and ΔVPD between the first and second periods and their interaction and soil chemistry (CEC) and texture (Clay%). For the photosynthesis statistical models, given their lower sample size (n=22; Table S2), interaction terms were not included and to avoid overfitting we first tested by means of leave-one-out cross-validation (LOO) [84] if the soil covariates improved or not the models with only climate information. We found soil data did not improve our models (Table S8) and thus left CEC and Clay out of the photosynthesis models. We also calculated the relative change (%) in climatic conditions but this did not improve model predictions (data not shown) and thus we only present results that include the absolute changes in MCWD and VPD. We included the change in MCWD and VPD as we wanted to understand if areas that have experienced stronger changes in climate showed lower or higher functional diversity and functional redundancy than others that have experienced milder climate changes. In the same way we included the interaction between MCWD and VPD (and also between ΔMCWD and ΔVPD) as there may be regions where high values of one of these variables may not be related to the values of the other, e.g. high MCWD may not be related to high VPD. Prior to the statistical modelling we centred and standardised (generated z-scores) all climatic and soil variables.

We tested for spatial autocorrelation effects in the FD and FRed model residuals using the Moran's I test and found a significant effect for the photosynthesis and nutrients FD models and for the FRed nutrients model (Table S9). Thus, for those data we calculated the spatial distance at which such spatial effect decreased and found that a distance of 2 km was sufficient. We then generated an ID for each group of plots (group ID) that were at most 2 km away from each other and included such group ID as a random factor in those statistical models. As some plots were smaller than 1 ha (Table S2) we included the z-scores of plot size as a covariate in all statistical models to account for its possible effect. We log transformed the FD and FRed indices to improve the normality of the data and applied linear mixed-effects models with a Gaussian error structure accounting for difference in plot size and spatial autocorrelation as described above under a Bayesian framework. The mixed-effects models were run with normal diffuse priors with mean 0 and 2.5 standard deviation to adjust the scale of coefficients and 10 standard deviations to adjust the scale of the intercept, three chains and 10000 iterations to avoid issues with model convergence. We computed the highest density intervals (HDI) rendering the range containing the 90% most probable effect values and calculated the ROPE values using such HDI as suggested in Makowski et al. [85]. The 95% HDI was not used as this range has been shown to be unstable with $ESS < 10,000$ (effective sample size) [86]. We considered a climatic variable had an important (significant) effect on the response variable if the 90% HDI did not overlap 0. Posterior density distributions for all models and covariates included in the models are shown in Fig. S12 and Fig. S13.

Based on the statistical models described above we created spatial predictions of Functional Diversity (FD) and Functional Redundancy (FRed) at a pantropical scale. We defined the ‘low’, ‘intermediate’ and ‘high’ FD and FRed groups by defining the range in FD and FRed values and dividing that range between three in order to allocate the FD and FRed predicted values to each of these groups and be able to state what is the predicted percent area of tropical and subtropical dry and moist broadleaf forests with low, medium and high FD and FRed. We also tested the robustness of the spatial predictions of FD and FRed by also developing the models by leaving out the data from one continent (South East Asia and Australia together), fitting the model again, and comparing the resulting spatial predictions to the full model prediction maps by means of Spearman correlations. In Fig. S14 we also highlight locations across the tropics with climate and soil conditions outside of our climatic and soil calibration space, thus not covered by the range in our sampling locations, which may represent locations where our models are extrapolating the relationships found.

Relations between Functional Diversity, Functional Redundancy and Aboveground biomass

We obtained the above ground biomass data (AGB) from an independent set of 100 vegetation plots in Africa before (AGB_{pre}) and after (AGB_{post}) the 2015 El Niño event from Bennett et al. [38] . The plots from Bennet et al. include censuses from 2000 onward where the median plot size is 1 ha, the mean initial census was May 2008, with the mean pre-El Niño census in April 2014, and mean post-El Niño census in February 2017. The plots have a mean monitoring length pre-El Niño of 8.3 years, with a mean length of the El Niño interval being 2.7 years. To calculate AGB Bennet et al. [38] used the BiomasaFP R package, including the calculation of the census interval corrections for AGB where Pre-El Niño means of these variables are time weighted using the census interval lengths. For a full description of the AGB data see Bennett et al. [38]. We calculated the ΔAGB as:

eq. 4 $\Delta AGB = (AGB_{post} - AGB_{pre})$

Before modelling we eliminated statistical outliers in the AGB values, this is values more than 1.5 the interquartile range above the third quartile or below the first quartile. We therefore only used 86 plots in our analysis. We modelled the ΔAGB as a function of the predicted (see methods above) FD and FRed maps scores from each functional group (morphology/structure, nutrients and photosynthesis; Fig. 3 and Fig. 4), one model was built per functional group. Each model included the FD and FRed index (e.g. FD and FRed of nutrients) and their interaction with ΔMCWD and ΔVPD as to test the effect of a changing climate on the effects of FD and FRed on above ground biomass change. We accounted for plot size by including as a covariate in the models and used a Gaussian error structure model under a Bayesian framework. The ΔAGB statistical models were run with normal diffuse priors with three chains and 5000 iterations.

We carried out all statistical analysis in the R statistical environment [79] using the, 'rstanarm', 'loo', 'bayestestR', 'egg' and 'BEST' packages.

Data availability

The vegetation census and plant functional traits data that support the findings of this study are available from their sources (www.ForestPlots.net and gem.tropicalforests.ox.ac.uk/). The processed community-level data used in this study will be made available in a public repository.

Code availability

The main R code used in this study will be deposited in a public repository and can be accessed through the principal investigator upon request.

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