Canopy functional trait variation across Earth's tropical forests

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Tropical forest canopies represent the biosphere's most significant and concentrated atmospheric interface for carbon, water and energy[1, 2]. Yet, in most Earth Systems Models the diverse and heterogeneous tropical forest biome is represented as a largely uniform ecosystem with either singular or a small number of fixed canopy ecophysiological properties[3]. This situation arises in part out of a lack of understanding of how and why the functional properties of tropical forest canopies vary geographically[4]. Here, we combine field-collected data from more than 1800 vegetation plots and tree traits and merge these with satellite remote sensing, terrain, climate and soil data to predict variation across 13 tree morphological, structural and chemical functional traits, using these to compute and map the functional diversity of tropical forests. This reveals that the tropical Americas, Africa and Asia tend to occupy different portions of the total functional trait space available across tropical forests. Tropical American forests are predicted to have 40% greater functional richness than tropical African and Asian forests. Meanwhile, African forests were the most functionally divergent, 32% and 7% higher than that of tropical American and Asian forests. An uncertainty analysis highlights priority regions for further data collection, which would refine and improve these maps. Our predictions represent a ground-based and remotely enabled global analysis of how and why the functional traits of tropical forest canopies vary across space.

Main

Tropical forests are the most biodiverse terrestrial ecosystems on Earth, accounting for most global diversity, including up to two-thirds of the ~73,000 tree species found on Earth [1]. They are responsible for key ecological functions, such as carbon exchange, nutrient cycling, and the provision of water and energy [2], as well as contributing to over a billion people's livelihoods around the world [5]. Despite the key importance of canopy functional traits (morphological, physiological or phenological attributes that determine function) for forest response to environmental change, our knowledge of the distribution of functional traits and of functional diversity at large spatial scales is limited, and this knowledge gap is particularly acute for tropical forests [6-8]. Although abiotic factors such as water availability, temperature and soil conditions are expected to drive variation in plant functional traits across spatial scales [9-11], we do not fully understand how these factors modulate canopy trait distributions and function [4]. Most global vegetation modelling efforts represent tropical forests as functionally-uniform green slabs of canopy, incorporating little geographical variation in canopy functional properties [3]. This is partially due to the lack of spatially distributed functional trait data from across these regions [12]. In reality, the combination of climate, geology, evolutionary history and biogeography leads to complex but poorly understood trait variation [13]. There is, therefore, a fundamental need to describe and map how plant functional traits vary across tropical forests, as this variation has direct implications for ecosystem functioning and resilience to environmental change [14-16].

Prediction of plant trait distributions across large spatial extents has generally focused on a few traits for which more observational data may be available, such as leaf nitrogen, leaf phosphorus, and specific leaf area, and in fewer cases other leaf traits, such as leaf dry mass and leaf potassium [17-19]. Some advances in mapping trait distributions have been made by integrating plant functional type information with statistical modelling [17, 19] and more recently satellite remote sensing [4, 8]. However, most recent predictive models still makes use of predefined plant functional types to estimate the distribution of single plant trait values, and still use coarse resolution satellite data (e.g. MODIS at 500 m) to map coarse indicators of community level trait values, often with few ground observations available for tropical forests. This suggests the need to generate tools and methods that facilitate the tracking of functional traits across large spatial extents with both high spatial and temporal resolution. Moreover, there is a need to develop methods to compare predictions of plant functional trait values created by different approaches [20]. While plant trait databases [21, 22] may help to model the distribution of functional traits as a function of biotic and abiotic conditions, we are far from having a full representation of the trait values for most tree species across the tropics or even for single regions, such as Amazonia with ca 15,000 tree species [23]. Understanding functional trait variability across continents is crucial for predicting ecosystem responses to environmental changes, including climate change and land use alterations [9]. Recent work from Diaz et al. [24] revealed substantial variation in functional traits across different ecosystems, both within and between plant communities. This variation highlights the relationship of plant traits strategies and different environmental conditions, allowing species to occupy distinct ecological niches.

Tree traits across the tropics

Here, we present the distribution of plant traits across the entirety of the planet's tropical forests by expanding on a new methodology [6] that uses an approach to predict functional traits using the European Space Agency's Sentinel-2 satellite data. We used data for 13 tree functional traits (here onwards referred to as plant traits) spanning leaf morphological (leaf area, specific leaf area, thickness, fresh and dry mass, also including leaf water content) and chemical traits (mass-based calcium, carbon, magnesium, nitrogen, potassium and phosphorus concentrations), and also including predictions for wood density [24, 25]. These plant traits were gathered from across tropical forests from the Americas, Africa and Asia, here including northeast Australia in our broad definition of Asian tropical forests (Fig. 1A). We focus on upper canopy leaf traits that are the primary interface for forest-atmosphere exchange, being part of important processes such as transpiration and photosynthesis [26] and which are directly detectable by spectral remote sensing. The plant traits are hence related to fundamental aspects of leaf morphology, chemistry and tree structure (Extended Data Table 1).

Overall, we expect that acquisitive traits, which enhance the efficient capture and use of resources (e.g., high specific leaf area and leaf nutrient content), will be more prominent in locations with pronounced seasonal variation and nutrient-rich soils. In contrast, conservative traits (e.g., thicker, nutrient-poor leaves, high wood density) are likely to dominate in areas with less seasonal variability and poorer soils. In forests dominated by deciduous species, such as drier tropical forests, we expect species with acquisitive traits to become more prevalent, thereby making these traits more common in the ecosystem. African forests, which have experienced a long-term drying trend [27], generally exhibit lower species diversity [28] and distinct soil conditions [29] compared to American and Asian tropical forests. We expect these differences to result in a narrower distribution of plant trait values when compared to the wetter tropical forests of the Americas and Asia. Additionally, Asian tropical forests contain the widespread distribution of the *Dipterocarpaceae* family [30], which we anticipate will largely define the particular set of dominant traits in those areas, such as those associated with large, tough leaves, which are characteristic of this tree family.

Traits were collected from the Global Ecosystems Monitoring (GEM) network [31], ForestPlots.net [32], BIEN (bien.nceas.ucsb.edu), TRY (www.try-db.org) and Diaz et al. [33]. We incorporated vegetation census data from the GEM and Monitoreo Nacional Forestal (MONAFOR) networks and contributing networks to ForestPlots.net, with geo-located tree individuals from 1814 permanent vegetation plots (Fig. 1A), spanning a wide set of environmental conditions across tropical forests (Fig. 1B) and covering a total of 799.5 ha (Extended Data Table 2). We used the plant traits and vegetation censuses to create pixel-level (from the Sentinel-2 satellites) community weighted mean (CWM) trait values using the method from Aguirre-Gutierrez et al. [6]. The total number of CWM pixels used in our analysis were 79,955, which were distributed across 18 countries in the four tropical continents (Extended Data Table 2). Our vegetation plots are more abundant in the tropical forests of the Americas and it could be thought they mostly represent the environmental conditions in this region than in Africa and Asia. Our principal component analysis (Fig. 1B and 1C) shows that although our sampling sites do not cover all environmental space available across the tropics, especially those climates that are less common in the tropics (dark purple zone in Fig. 1B and 1C), we fundamentally cover the most prominent environmental conditions found across tropical forests.

For each pixel for which we calculated trait CWM, we also extracted surface reflectance data from the Sentinel-2 satellite bands covering the years 2019 to 2022. Based on these spectral bands we also generated the Modified Chlorophyll Absorption Reflectance Index (MCARI), Modified Soil Adjusted Vegetation Index 2 (MSAVI2) and Normalised Difference Red Edge Index (NDRE). Using the grey level co-occurrence matrix for these indices we calculated their Entropy and Correlation as canopy texture variables. We extracted soil texture and chemistry (clay %, sand %, pH, cation exchange capacity) across the sampling plots from the SoilGrids.org and joined these with terrain (slope) and climate (Maximum Climatic Water Deficit (MCWD) and maximum temperature (Tmax)) from the TerraClimate dataset [34]. We used the above-mentioned covariates in Random Forest models that have produced accurate plant trait mapping results [4, 6] to predict CWM plant functional traits at a pantropical scale. Our analysis hence provides insights into the variation in plant trait composition across climatic and soil gradients across tropical forests. We tested for the prediction accuracy and uncertainty in trait predictions while accounting for potential spatial autocorrelation using a plot level spatial block leave-one-out cross-validation [35] (Supplementary Table 1). We present the spatial predictions from the statistical models described above for canopy level morphological traits, wood density (Fig. 2; Supplementary Figures 1 to 7) and chemistry (Fig. 3; Supplementary Figures 8 to 13). Using our 13 plant trait model predictions (maps) we tested fundamental knowledge gaps on the functional composition across tropical American, African and Asian forests.

Models for leaf chemistry and wood density displayed higher accuracy (mean R^2 = 0.66 and 0.48, respectively) than those for leaf morphology traits (mean R^2 = 0.25; Supplementary Table 1). Among these, leaf nitrogen (mean R^2 = 0.53/*Root Mean Squared Error* = 0.29), phosphorus (0.50/0.02) and calcium (0.64/0.22) concentrations had the highest prediction accuracy followed by leaf carbon (0.40/1.42) and potassium (0.46/0.17). Models for SLA (0.32/19.95), leaf dry (0.32/0.58) and fresh mass (0.31/2.24) demonstrated moderate accuracy scores. In contrast, leaf magnesium concentration (0.27/0.06), leaf area (0.22/66.15), leaf water content (0.18/3.92), and leaf thickness 0.17/ 0.79) had lower accuracy. As expected, lower explanatory values were found when testing the models with the plots from Africa or Asia separately as less data were available (Supplementary Table 1). The individual surface reflectance of the Sentinel-2 bands, the derived vegetation indices and the climate/terrain variables obtained on average the highest importance scores across traits, with texture and soil metrics obtaining on average lower importance values (Extended Data Fig. 1). We report variable importance scores per variable and plant trait in Supplementary Figures 1F to 13F.

We make available our trait mapped predictions across the tropics as an online resource where more detail can be obtained across the tropical region (https://pantropicalanalysis.users.earthengine.app/view/pantropical-traits-aguirre-gutierrez-2025). Using the modelled trait maps (Fig. 2A; Fig. 3A; Supplementary Figures 1 to 13) we compared the community weighted mean trait values among continents which provided insights into the variations in plant traits across continents (Supplementary Table 2; Fig. 2B and Fig. 3B; Supplementary Figures 1 to 13). Following our predictions, for most traits, Asian forests show some of the highest average canopy-level trait values, specifically average leaf area (119.3 cm^2), leaf calcium (0.88 %), potassium (0.79 %), magnesium (0.28 %) concentrations, leaf water content (54.8 %), leaf fresh (3.9 g) and dry mass (1.06 g), which is supported by local plot level data [6]. However, similar values were found for leaf phosphorus for Asia and Africa (0.11 %) and slightly lower for the Americas (0.10 %), and also for leaf carbon (~47 %) and leaf nitrogen concentrations (~2.15 %). African forests are predicted to have on average the smallest leaves (average of 100 cm^2), highest leaf thickness (0.85 mm) and specific leaf area (133.9 $cm^2\ g^{-1}$). Wood density is predicted to be, on average, higher in tropical American and African forests (~0.60 g cm^3) as also suggested by Sullivan et al. [36]. These results emphasise Asia's unique trait spectra and how the African flora is adapted to a wide range of current and past environmental conditions [37].

Traits in wet and dry tropical forests

A changing climate impacts the distribution and persistence of forests across the tropics. Notably, there is an ongoing debate on the capacity of wet and dry tropical forests to adapt or shift their functional composition given global environmental change [38]. Recent studies have shown that drier tropical forests could be responding faster to a changing climate by shifting their trait composition [39] but also that such drier tropical forests may be becoming more functionally homogeneous, which may negatively affect their capacity to respond to further environmental change [37]. Hence, understanding the distribution of key tree functional traits across tropical forests is key to understanding their potential response to environmental changes including climate.

We determined the extent of tropical broadleaf wet and dry forests using the RESOLVE Ecoregions dataset [40]. Based on this division, wet forests, on average, displayed higher leaf area and leaf carbon concentration in comparison to dry forests (Supplementary Figure 1C; Supplementary Table 3). In contrast, dry forests, which are characterised by the presence of stronger and longer dry seasons, exhibited higher average values for leaf chemistry traits such as leaf magnesium, nitrogen, calcium, potassium, phosphorus, and also for specific leaf area (Supplementary Figures 1D to 13D; Supplementary Table 3). These distinct strategies possibly ensure optimal nutrient utilisation for drought avoidance based on the leaf economics spectrum of 'low' leaf construction costs for fast energy gains amid challenging environmental conditions [41]. Remarkably, both wet and dry tropical forests converge in certain traits, with comparable mean levels of leaf thickness, dry and fresh mass, leaf water content, and wood density underscoring their shared strategies. However, these similar average trait values could also be due to the fact that both strategies, i.e. drought avoidance and drought tolerance, can be present across both wet and dry forests, potentially ensuring resilience across tropical forest types [42]. These findings from our comprehensive trait predictions provide crucial insights into the intricate linkages between environmental factors and plant traits across continents, contributing to our understanding of ecological diversity and adaptation strategies in diverse tropical forest ecosystems. Our findings shed light on the diverse plant trait patterns observed across continents, enhancing our understanding of global ecological variations [24].

Areas across the wet tropics, which are highly species diverse, tended to have slightly more uncertain predictions (i.e., higher standard error, SE) for most traits than drier tropical forests (Supplementary Figures 1 to 13 middle panel). Our results for leaf morphology and tree structural traits such as fresh mass and wood density showed higher uncertainty in predictions (SE = 0.4-1.6 g and 0.02-0.05 g cm^3 respectively) across wetter locations such as central Amazonia, central Africa and Borneo. However, for most other morphological and leaf nutrients traits, their prediction uncertainty was low in the majority of the tropics (Supplementary Figures 1 to 13 middle panel). Overall, the uncertainty in the predictions of some traits may result from searching for simple relationships between individual traits and the environment while tree individuals represent a combination of traits and trait values that may be interpreted as functional strategies or syndromes. It is the syndrome rather than the individual trait that is selected for in nature. Our findings on the uncertainty of trait predictions give an insight into areas across the tropics that may benefit the most from more extensive field trait campaigns (Supplementary Figure 1 to 13 middle panel; Extended Data Fig. 2).

Functional diversity of tropical forests

The resilience of an ecosystem to environmental change can be partially assessed by the diversity of its functional trait values. According to the biodiversity–ecosystem functioning insurance hypothesis [43], ecosystems with greater taxonomic and functional diversity are less affected by changes in the environment. Recent studies support this, showing that tropical forests with higher functional diversity and high functional redundancy tend to be less adversely affected by extreme weather effects such as El Niño than less functionally diverse and redundant forests [44]. Hence, functional diversity indicators such as functional richness and functional divergence can shed light on the capacity of ecosystems to respond to global environmental change. Therefore, determining the functional diversity of tropical forest ecosystems will enhance our understanding of their resilience and the possible impacts of environmental change on ecosystem functioning and its services to people.

To generate a pantropical understanding of the functional diversity of tropical forests across the Americas, Africa and Asia, and how these three compare to each other, we first built a Principal Component Analysis (PCA) that offers insights into the distribution of ecological strategies or syndromes of plant communities [45] across tropical forests. This PCA was based on the pixel values from the spatial predictions (maps) of canopy and wood density traits (Fig. 2. Fig. 3 and Supplementary Figures 1-13). The first two PCA axes (Fig. 4A and Fig. 4B), explain 43.9% (PC1) and 20.6% (PC2) of the pantropical trait variance respectively, and highlight key traits driving the functional space across tropical forests at a pantropical extent. In our analysis leaf nutrients such as Ca, N, P, K and Mg are the main traits loading PC1 (-0.39, -0.25, -0.39, -0.39 respectively; Supplementary Table 4), with carbon (0.35) and wood density (0.27) in opposite directions. PC2 is mainly loaded by leaf structural and morphological characteristics such as dry mass (0.52), fresh mass (0.43), area (0.47) and SLA (-0.32) (Fig. 4A and Fig. 4B).

Following the PCA results, central-west Amazonia, central Africa, and to some extent some areas of SE Asia, show areas with trait syndromes related to higher wood density and leaf carbon (Fig. 4C, PC1, top panel), but also higher leaf area and leaf fresh and dry mass (Fig. 4C, PC2, bottom panel). Wood density is closely related to plant mechanical and hydraulic properties and has been shown to have a negative relationship with mortality given increased physical strength and resistance to drought-induced embolism [46]. The highest leaf carbon concentration (C) values are predicted to be found in wet regions with relatively infertile soils in the Americas, Africa and Asia, such as northwest Amazonia, Central Africa and much of Borneo, and tend to decline towards drier tropical forests (Fig. 3A to panel; Supplementary Figure 8). An alternative strategy for dry forest tree species is deciduousness, which leads to low leaf carbon concentration because of lower investment in leaf defence and longevity. On dry forests with fertile soils, we expect deciduousness as a dominant strategy (thus low C), but on less fertile soils we would expect a transition to an evergreen strategy (higher C) to conserve resources. Higher leaf carbon, and generally also higher leaf fresh and dry mass, reflect an increased investment in leaf structural and physical defences [47], which favour longer leaf life span and thus higher investment in compounds like lignin, tannins and soluble phenolics that contain high carbon levels [48].

Syndromes related to higher leaf nutrients (Fig. 4C top panel PC1) and higher specific leaf area (Fig. 4C middle panel PC2) are opposed to the patterns explained above, with higher leaf nutrients and intermediate specific leaf area values found across tropical dry forests and increasing leaf water content predicted across the Andes and high elevations of SE Asia (Fig. 4C bottom panel PC3). Leaf nutrients are generally lowest in wet central west Amazon, Central Africa and wet forests of insular SE Asia (Fig. 3) and tends to increase across dry forests in south and south-eastern Brazil, West Africa, eastern Madagascar, most of the tropical forests in India and northern SE Asian (Fig. 3 and Fig. 4 PC3). This supports an important role for soil physical and chemical properties in shaping leaf phosphorus distributions (Fig. 3A bottom panel; Fig. 4A, and 4C; Supplementary Figure 13) [49]. We predict a consistently high leaf area across much of insular SE Asia (Fig. 4C). This is in agreement with previous plot level analyses [31] that found a larger leaf area for forests in Malaysian Borneo than in those from other tropical regions. Many of the wet Bornean Forest canopies are dominated by a single family (*Dipterocarpaceae*) [30] with a particular set of traits, such as large, tough leaves, and this biogeographical feature may explain some of the leaf morphological differences between Asian and other forests. In the tropical Americas, syndromes related to lower SLA values are found across the Andes, mountains of southern Brazil and also in the extremely wet and nutrient-poor areas of NW Amazonia such as across the sandy soils of upper Rio Negro. Lower SLA can be found across Central Africa and in Asia across the mountains of New Guinea (Fig. 4C bottom panel). Plants with lower SLA tend to have thicker leaves, which are more resistant to herbivory and decomposition and lower SLA values indicate a conservative strategy where resources are invested in long-lasting leaves but often with lower photosynthetic capacity [25].

Building upon our PCA analysis generated above, we calculated the trait functional diversity, here by means of their trait functional richness (FRich) and functional divergence (FDiv), across tropical forests (Fig. 4A) and calculated how these FRich and FDiv differ between the forests of tropical Americas, Africa and Asia (Fig. 4B). FRich represents the size of the functional trait space and FDiv indicates the distribution of CWM trait abundances within the functional trait space [45]. The overall FRich across tropical forests is calculated to be 111.7 with a pantropical FDiv of 0.46 (Fig. 4A). The observed FRich values of 109.2 for the Americas, 66.5 for Africa, and 63.5 for Asia point to large differences in the diversity of functional trait values within these regions (Fig. 4B). The higher FRich of the Americas suggests these forests have a broader array of plant strategies and adaptations, potentially influenced by diverse environmental niches and historical factors [50] and congruent with the most taxonomically diverse tropical forests being in the tropical Americas [1, 23]. In contrast, the lower FRich in Africa and Asia suggests that specific environmental filters or historical biogeographic constraints shape the functional traits of plant communities in these regions [51]. The FDiv values ranged from 0.42 for the Americas to 0.61 for Africa, and 0.57 for Asia, revealing varying degrees of dissimilarity in functional trait space among tropical forests (Fig. 4B). Higher FDiv values imply greater divergence, suggesting stronger niche differentiation or competitive interactions. The comparatively lower FDiv in the Americas might imply a higher degree of functional redundancy across communities. Conversely, the higher FDiv in Africa and Asia suggests a more specialised resource utilisation pattern, potentially due to intense interspecific competition or specific ecological constraints in these regions. Regions with higher functional divergence might exhibit higher ecosystem stability due to niche complementarity, whereas regions with lower divergence may face challenges in adapting to changing environmental conditions. The observed patterns have implications for ecosystem functioning, biodiversity conservation, and ecosystem services provision.

Understanding the tree trait composition and functional diversity across the tropics is of pivotal importance for global biodiversity and ecosystems modelling and conservation efforts [52]. While dynamic global vegetation models (DGVM) and species distribution models (SDMs) help to assess impacts of a changing climate, DGVMs often rely on broad plant functional types and SDMs commonly overlook functional trait composition and diversity (but see [53]). By incorporating trait-based mechanisms and functional trait diversity, models can better capture the variability in plant responses, potentially making more realistic predictions related to carbon cycling [54,] vegetation distribution [55], and ecosystem composition and resilience [44]. DGVMs and SDMs could include plant traits and plant functional diversity estimates to advance our understanding on ecosystem functioning and responses to global environmental change.

Our capacity to use artificial intelligence to map plant functional traits by means of Deep Learning models applied to field trait [56] data or even photographs [57] is quickly developing. These models can process vast amounts of remote sensing data to identify and classify diverse biodiversity metrics [58], and particularly convolutional neural networks, have been integrated with spectral data to map plant traits using field data [59] and recently also citizen science approaches [60]. There have been recent developments of new satellites with hyperspectral and high spatial resolution capabilities and on the availability of large amount of tree censuses and trait data across the tropics. This opens new venues for the coming years for testing the capabilities of large machine learning models, possibly involving deep learning, for using data across time and space from multiple sources. However, to obtain robust and reliable indicators of plant functional diversity and biodiversity levels across ecosystems AI models should complement and not replace traditional ecological methods - especially the direct field sampling and botanical identification of individual trees by experts. There is a need for tools that can generate predictions of biodiversity at high temporal resolution and our approach represents a way forward in this direction. Going forward, there is the potential to track plant functional diversity across time, e.g. on a yearly basis, using satellite remote sensing data such as that from the Sentinel-2 satellites. Such an application would certainly require major efforts on field ecological data collection, availability of new satellite data, modelling algorithms, computing power and storage capabilities. All of this can be achieved by strong and fair collaborations between field researchers, universities and other public and private research organisation.

Our study reveals and maps for the first time the geographical variation in the functional composition of the tropical moist and dry forests, where at least two thirds of Earth's ~73,000 tree species are found [1]. Our trait predictions may indicate deep physiological constraints of adaptation to long-term climate and provide the basis for forecasting how shifting climates will impact tropical forest functional composition, and help develop a more mechanistic understanding and realistic predictive ecology across spatiotemporal scales. Built from unique, geolocated field records combined with an array of spectral, textural and environmental data, our maps represent data-informed spatial hypotheses that assist in identification of priority areas for further field data collection, especially across tropical forests in Africa and Asia where less data is available. The ultimate accuracy of the plant functional trait predictions depends on the sample coverage, the accuracy of the field measurements, and the quality of the pantropical covariates used to spatially extrapolate our models. Undoubtedly, predictions will improve as new environmental data sets become available and as vegetation census and trait data expand further over space and time. Nevertheless, these maps represent a major advance on previous site-based speculation on the geographical variation on the ecophysiology of the entire tropical forest biome, and thereby inform our understanding of tropical forests functioning in the context of the whole Earth system.

Figure legends

Figure 1. Study area showing the distribution of 1814 vegetation plots across the original biome space for tropical forests (grey background) in the Americas (659.6 ha), Africa (124.6 ha) and Asia (15.4 ha) (A). Principal component analysis (**B**) PC1 and PC2, (**C**) PC3, depicting the environmental space found across the tropics (yellow and green colours show higher map pixel counts representing area covered) based on mean maximum air temperature (T_{max}), soil moisture (SM), solar radiation (SR), slope, maximum climatic water deficit (MCWD), soil cation exchange capacity (CEC), soil pH, sand and clay amount. The grey, violet and orange points show the location of the sampling plots in environmental space found across the tropics. PC1 accounts for 27% of explained variance, PC2 for 24% and PC3 for 14%, with all three accounting for 65% of total explained variance. PC1 is mainly loaded by water deficit index MCWD (-0.47), SR (0.50) and soil pH (0.59), PC2 by the soil sand (0.57), clay (-0.53) and CEC (-0.44), and PC3 by SM (-0.63) and T_{max} (-0.49). Climate data were derived for each pixel from the TerraClimate project [34] and soil data from SoilGrids.org.

Figure 2. Predicted distribution of a selection of community weighted mean morphological and structural plant traits (A) and boxplots (B) showing the CWM trait distribution values for tropical American (AM), African (AF) and Asian (AS) forests extracted from the spatial predictions. In (A), red to orange show areas with low to intermediate trait values, while light to dark blue depict areas with intermediate to high trait values. The remaining morphological traits and the spatial predictions of their uncertainty are shown in Supplementary Figures 1-7. In B) the horizontal black line depicts the median CWM trait value and vertical lines show the whiskers extending to the largest CWM trait value or not further than 1.5 times the interquartile range. For visualisation purposes, we excluded the extreme lowest and highest 1% of values in the maps in A) and outliers in B). $Area_L$: leaf area, SLA: specific leaf area, $Thickness_L$: leaf thickness and WD: wood density. For statistical

model results see Supplementary Table 1. For significance of differences between CWM trait mean values, obtained using a T-test with Bonferroni correction, see Supplementary Table 2.

Figure 3. Predicted distribution of a selection of community weighted mean leaf nutrient plant traits (A) and boxplots (B) showing the CWM trait distribution values for tropical American (AM), African (AF) and Asian (AS) forests extracted from the spatial predictions. In (A), red to orange show areas with low to intermediate trait values while light to dark blue depict areas with intermediate to high trait values. The remaining chemistry traits and the spatial predictions of their uncertainty are shown in Supplementary Figures 8-13. In B) the horizontal black line depicts the median CWM trait value and vertical lines show the whiskers extending to the largest CWM trait value or not further than 1.5 times the interquartile range. For visualisation purposes, we excluded the extreme lowest and highest 1% of values in the maps in A) and outliers in B). C_L: leaf carbon concentration, Ca_L: leaf calcium concentration, N_L: leaf nitrogen concentration and P_L: leaf phosphorus concentration. For statistical model results see Supplementary Table 1. For significance of differences between CWM trait mean values, obtained using a T-test with Bonferroni correction, see Supplementary Table 2.

Figure 4. Functional trait space of plants across tropical forests in the Americas, Africa and Asia (including Australia), A) with principal component PC1 explaining 43.9% and PC2 20.6% of the variance in plant traits distributions. In (B) is the distribution of functional trait space for the tropical American (left), African (middle) and Asian (right; including Australia) forests separately. (C) Shows PC1 (top panel), PC2 (middle panel) and PC3 (bottom panel explaining 13% of the variance) from (A) predicted across tropical forests and depicts co-occurring trait syndromes or strategies with insets zooming in to show greater details of the predicted plant strategies. In (A) arrows indicate the contribution and direction of each trait for the PCA. (A) and (B) show the probabilistic density distribution defined by the two first principal components (PC1 and PC2) space of the 13 plant functional traits used: Area: leaf area, C: leaf carbon concentration, Ca: leaf calcium concentration, K: leaf potassium concentration, Mg: leaf magnesium concentration, N: leaf nitrogen concentration, P: leaf phosphorus concentration, DM: leaf dry mass, FM: leaf fresh mass, SLA: specific leaf area, Thickness: leaf thickness, WC: leaf water content, WD: wood density (see Extended Data Table 1 for a description of the trait used). Within (A) and (B) the inner colour gradient represents the density of pixels in the PC trait space. Thick contour lines depict the 0.5 and 0.99 quantiles. The FRich shows the functional richness and the FDiv the functional divergence for the global trait space across continents (A) and for tropical American (B, left), African (B, middle) and Asian (B, right) forests.

Methods

Vegetation plots and plant traits

We gathered vegetation census data from the GEM and Monitoreo Nacional Forestal (MONAFOR) networks and contributing networks to ForestPlots.net, being geo-located tree individuals from 1814 demarcated and identified vegetation plots (Fig. 1A). The vegetation plots covered a wide set of the environmental conditions found across tropical forests (Fig. 1B) and spanned 799.5 ha (Extended Data Table 2). We aimed to match each individual tree to a trait value. All plant functional traits used are part of the Global Ecosystems Monitoring network (GEM; gem.tropicalforests.ox.ac.uk) [31], the MONAFOR network, the ForestPlots (www.ForestPlots.net) [32, 61, 62], BIEN (bien.nceas.ucsb.edu), TRY (www.try-db.org)[22] databases and from local collaborators and Diaz et al. [33], and were collected following a standardised methodology described in Both et al. [63], Martin et al. [64], Enquist et al. [65], Oliveras et al. [66] and Gvozdevaite et al. [67]. For the GEM and ForestPlots.net provided traits, the tree species that contributed the most to plot basal area were sampled with 3–5 replicate individuals per species. Species representing 80% or more of the basal area were sampled for traits in low diversity sites and at least 70% in high diversity sites. For each selected tree a sun and a shade branch were sampled, and in each branch 3–5 leaves were used for trait measurements. Leaf samples were analysed for chemistry (nitrogen: N, phosphorus: P, carbon: C, calcium: Ca, potassium: K and magnesium: Mg concentration) and morphological and structural traits (area: Area, specific leaf area: SLA, thickness: Thickness, fresh mass: FM and water content: WC) (see Extended Data Table 1 for units and definitions). If more than one value per trait per species was available, we used the trait mean at the species level for subsequent analysis. Our approach aimed to cover at least 70% of the canopy area of a pixel within a plot with trait data at species or genus level, often covering more than that (Extended Data Fig. 3). As when species-level trait data were unavailable we used the mean genus-level data, our analysis could be seen as more representative of the genus-level trait responses. When achieving at least 70% coverage was not possible for a given trait in a given pixel, such pixel 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).

Calculating community level trait values

We used the pixel-level community weighted mean (CWM) trait method from Aguirre-Gutierrez et al. [6] in our analysis, where they calculated the CWM of each trait for each 10 × 10 m pixel of the Sentinel-2 imagery based on the canopy area occupied by the single tree crowns of each species encompassed in a given pixel. The total number of CWM pixels used in our analysis were 79,955, from 1814 unique permanent forest plots distributed across 18 countries in the four tropical continents (Extended Data Table 2). A full detailed description of the methods can be found in Aguirre-Gutierrez et al. [6] and we summarise it here. We calculated the CWM trait values for each 10 × 10 m Sentinel-2 pixel falling into a vegetation plot. We first geolocated the vegetation plot and the distribution of each individual tree in the plot. Some of the plots already had their tree crowns mapped. When this was not the case, we calculated the crown area based on regional allometric equations, from which we generated a crown polygon. Then for each pixel we calculated the trait CWM using the individual tree crown horizontal area as the weighting factor. We only used pixels that had at least a 70% basal area coverage with trait value in order to generate the trait CWM.

Sentinel-2 spectral data

The European Space Agency Sentinel-2 satellites (sentinel.esa.int/web/sentinel/missions/sentinel-2) have high multispectral (13 spectral channels covering the visible, near-infrared, and short-wave infrared), spatial (10 m for visible and near-infrared 835 nm, 20 m for other near-infrared and short-wave infrared) and temporal coverage (revisit period of 5 days), in addition to open data availability. This high spatial, radiometric, and temporal resolution, provide the backbone to scale functional traits, such as leaf morphology, water content and covalent chemical bonds without the logistical and field constraints that are common across the tropics [6] and other regions [68]. The Sentinel-2 Level-2A surface reflectance bands, vegetation indices and canopy texture metrics data extraction has been fully described in Aguirre-Gutierrez et al. [6] and here we give a summary of the main steps. We extracted Sentinel-2 Level-2A spectral data at the pixel level for each vegetation plot using the raw band values for bands B2 to B12, excluding bands B9 and B10 as those are used for cirrus, water vapour and cloud detection for the images and dates specified in Supplementary Table 5. Next, we calculated the vegetation indices Modified Chlorophyll Absorption Reflectance Index (MCARI), Modified Soil Adjusted Vegetation Index 2 (MSAVI2), and Normalised Difference Red Edge Index (NDRE).

We also incorporated spatial information by using the spectral indices to derive neighbourhood canopy texture, entropy, and correlation with a 9 x 9 pixel grey level co-occurrence matrix (GLCM) [69].

The GLCM metrics are computed from a matrix that is spatially dependent. The co-occurrence matrix relies on the angular orientation and distance between adjacent pixels, illustrating the frequency of associations between a pixel and its neighbouring pixels. We applied a 9 × 9-pixel kernel window as this window size proved sufficient to capture ample canopy contrast information during the modelling stage without incurring substantial computation time.

We generated spatially explicit predictions across tropical forests in Google Earth Engine (GEE) [70] using surface reflectance Sentinel-2 Level-2A images from June to March of 2019 to 2022 because these months display the lowest cloud cover across most of our study areas. We applied the maskS2clouds and maskEdges to increase the quality of the imagery, especially to detect and mask clouds and cirrus. Based on the images selected we calculated a median spectral reflectance composite value per band and used it for generating the predictive maps. The reader can run the GEE code (Supplementary Table 5) to obtain the number and identity of the imagery used.

Climate, topography and soil data

We used the TerraClimate climate dataset [34] to extract climate data for the study area. These data have an original spatial resolution of ~4.6 km at the Equator and large temporal range (from 1951 to the present). In general, the TerraClimate builds upon the Climatic Research Unit climate data, CRU [55], downscales it and swaps the JRA55 reanalysis product [72] for CRU where there is insufficient station data to inform CRU. From the TerraClimate dataset we calculated the 30-year (encompassing 1988-2017) mean annual maximum temperature (T_{max}) and the maximum climatic water deficit (MCWD) for each vegetation plot. The MCWD is a metric for drought intensity and severity defined as the most negative value of the climatological water deficit (CWD) of a given year and we calculated it following Malhi et al. [73] but using the potential evapotranspiration instead of a fixed evapotranspiration value. We derived topography (slope) from the Shuttle Radar Topography Mission (SRTM) digital elevation model V3 product (SRTM Plus) provided by NASA JPL at an original spatial resolution of ~30 m at the equator [74]. Soil characteristics such as texture and fertility also determine the distribution of plant species [47]. Moreover, drier tropical forests tend to be distributed on more nutrient-rich soils than wetter forests [75], which therefore would also select for species adapted to such conditions. Maps of soil data, i.e., percent sand and clay, pH and cation exchange capacity (CEC), were obtained from the SoilGrids project (https://soilgrids.org) [76] at a spatial resolution of 250 m pixel. All climate, topography and soil datasets were scaled to the Sentinel-2 pixel resolution to take advantage of its spectral reflectance pixel size. All spatial analyses were carried out in the GEE platform.

Mapping plant traits

We modelled each plant functional trait CWM as a function of the spectral, soil, topography and climatic variables using the Random Forests (RF) machine learning algorithm [77] in the R platform [78] with the Ranger function in a High-Performance Computing system. RF stands out as a nonparametric algorithm known for its capabilities against overfitting and for its flexibility with respect to variations in the type and number of variable inputs. This robustness is attributed to the bagging process and the inclusion of random feature selection. Additionally, RF has been widely and successfully applied for modelling and predicting ecological and remote sensing data, both within individual ecosystems and across diverse environments [6, 68, 79, 80, 81]. In order to parametrise the Random Forest models we conducted a comprehensive series of model optimization and regularisation techniques to mitigate overfitting [6]. We determined the number of trees through a cross-validation analysis, exploring a range between 500 and 1500 trees. Similarly, we varied the number of variables randomly sampled as candidates at each split (mtry) within the range of 1 to 10. The final model incorporated the combination of parameters that yielded the lowest Root Mean Square Error (RMSE). We then obtained a map by applying the fitted model to make predictions for the full tropics where tropical wet and tropical dry broadleaf forests are located (as the data used for model fitting belong to these forest types). We determined the extent of the tropical broadleaf wet and dry forest using the RESOLVE Ecoregions dataset [40] (https://ecoregions.appspot.com/) and the tropical countries boundaries dataset (for the GEE app) [82]. We further used the Land-use Cover map from the European Space Agency [83] to delimit the areas classified as forest and the Hansen et al. [84] 30 m forest cover product to further delimit the predictions to areas with a threshold value of a minimum of 25% forest cover in a given pixel. Hence, even though an area may be included in the trait maps, it does not mean it is entirely forested. The accuracy of the predictions was quantified by the explained variance using the R^2. Variable importance was calculated as the decrease in node impurities, from splitting on the focus variable, derived from the Out of Bag (OOB) error. We scaled the variable importance values per covariate to a 0–1 scale for comparison purposes. The GEE code used to carry out the spatial analyses described above is shown in Supplementary Table 5.

In order to assess the uncertainty in model predictions in a spatially explicit manner we used spatial leave-one-out cross-validation [35] for the full dataset. When predicting the Random Forest models, we also obtained their standard error (SE) using the infinitesimal jackknife approach as a measure of prediction uncertainty. From these SE mapped predictions, we also calculated a final map of new field sampling needs by standardising each trait SE mapped prediction from 0 to 1 and obtaining an average value of the sum of those standardised SE maps. From this final field sampling needs map, we calculated the areas belonging to the lowest, middle and highest 33 percentiles and classified these as ‘Low’, ‘Intermediate’ and ‘High’ respectively. This final map could aid in generating field sampling priorities for the traits used in this study.

We tested for differences in the among continent mean community weighted mean trait values using T-test analysis with Bonferroni correction for significance values. As we are working with the pixel predictions per continent we have several millions of pixel-level estimates, which makes it possible to obtain significant P-values ($P<0.05$) just because of the high number of pixels involved. Therefore, we carried out the T-test for the full dataset (comparing continents) and also by first randomly sampling 10% and 1% of the data per continent for the comparisons as to obtain an indication of the possible effect of sample size on the among continents comparison results.

Functional Richness and Divergence

We calculated the functional richness (FRich) and divergence (FDiv) found at pantropical extent and also for the tropical Americas, Africa and Asia. To this end we took the mapped CWM trait predictions and carried out a principal component analysis with them and calculated Trait Probability Functions (TPD) as described in Carmona et al.[45, 85]. Using the mapped predictions, and not only the pixels used to build the trait CWM, allowed us to avoid having a larger representation of the tropical forests in the Americas in comparison to those found in Africa and Asia. To carry out the principal component analysis we used the ‘Princomp’ function in R with the data from the mapped predictions of the thirteen traits. We then used the ‘Funspace’ R function to create the TPDs, with which we would obtain the functional trait space available at a pantropical extent. We also calculated the TDPs for each continent based on the pantropical TDP so these could be compared between each other [45, 85]. Based on these we then calculate the functional richness and functional divergence metrics at a pantropical extent and also for each continent. In our analysis we represent the global TPD (100%) and also highlight the contours containing 50% and 99% of the total probability.

Extended data figures and tables

Extended Data Fig. 1 The importance of spectral, vegetation indices, canopy texture parameters, climate, terrain and soil conditions for model prediction of each plant trait. Area$_L$: leaf area, C$_L$: leaf carbon concentration, Ca$_L$: leaf calcium concentration, DM$_L$: leaf dry mass, FM$_L$: leaf fresh mass, K$_L$: leaf potassium concentration, Mg$_L$: leaf magnesium concentration, N$_L$: leaf nitrogen concentration, P$_L$: leaf phosphorus concentration, SLA: specific leaf area, Thickness$_L$: leaf thickness, WC$_L$: leaf water content, WD: wood density (see Extended Data Table 1 for a description of the trait used). The importance of each variable for each trait can be seen in Supplementary Figures 1 to 13. The importance values were obtained from the RandomForest models.

Extended Data Fig. 2 Predicted distribution of field sampling needs. The map shows the locations where higher standard error of predictions of community weighted mean trait values are found with orange showing high, yellow showing intermediate and green showing low sampling needs. The map was obtained by standardising each community weighted mean standard error (SE) mapped prediction from 0 to 1 and obtaining an average value of the sum of those standardised SE maps. From this final field sampling needs map, we calculated the areas belonging to the lowest, middle and highest 33 percentiles and classified these as ‘Low’, ‘Intermediate’ and ‘High’ respectively. This final map could aid in generating field sampling priorities for the traits used in this study.

Extended Data Fig. 3 Percent area covered by traits at the pixel level. Pixels had a minimum of 70% of the trees basal area covered with trait data in order to enter the analysis. As shown, in several cases we reached higher than 70% basal area coverage at the pixel level. Area$_L$: leaf area, C$_L$: leaf carbon concentration, Ca$_L$: leaf calcium concentration, DM$_L$: leaf dry mass, FM$_L$: leaf fresh mass, K$_L$: leaf potassium concentration, Mg$_L$: leaf magnesium concentration, N$_L$: leaf nitrogen concentration, P$_L$: leaf phosphorus concentration, SLA: specific leaf area, Thickness$_L$: leaf thickness, WC$_L$: leaf water content, WD: wood density.

Extended Data Table 1 Plant functional traits modelled and predicted across the tropics.

Extended Data Table 2 Description of the vegetation plots used across the tropical forests and their abiotic characteristics. N: number of vegetation plots, N Pixels: number of Sentinel-2 satellite pixels used, Area (ha): planimetric pixel area used, MCWD: mean maximum climatic water deficit. Tmax: average maximum temperature, Slope: average terrain slope. The average and coefficient of variation (CV as a percentage) are given for each climatic variable and were calculated using a climatology of the last 30 years (1988 and 2017). The climate data was extracted from the TerraClimate dataset (www.nature.com/articles/sdata2017191) and the slope was derived from the Shuttle Radar Topography Mission (SRTM; www.earthdata.nasa.gov/sensors/srtm).

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Author Contribution

J.A.-G. conceived the study, designed and carried out the analysis, obtained funding for the analyses and wrote the first draft of the paper. S.W.R. and Y.M. contributed to the main ideas of the study. X.D. and H.Z-Z. carried out spatial analyses. Y.M. conceived and implemented the GEM Network, obtained funding for most of the GEM traits field campaigns and commented on earlier versions of the manuscript. H.S, E.T., J.J.C-R., A.F.G., S.M., J.K., S.F., A.F.R., G.W., C.A.J., K.A., S.A-B., C.A.S., E.A.O., D.R. A.A., E.A.-D., G.P.A., T.R.B., M.B., L.P.B., E.B., L.B., D.B., K.B., R.B.L., S.B., J.C.D., D.C., H.C. L., L.C., L.A.C., N.C.C.S.P., A.C.S.Z., R.J.S., R.S.A.S., M.A.I., T.C.D.S.O., B.D., G.D., K.G.D., D.J. R., M.E.-S., L.F.S., T.F.D., J.F., M.F.S., C.A.J.G., B.H., K.J.J., S.K.A., A.K.S., B.K., W.F.L., M.L.D., W.E.M., E.M.C.-F., R.M.S., A.G.M., M.S., B.H.M.-J., R.E.M., D.L.M.V., T.M., W.M., P.M., M. M. M.S., P.S.M., R.M., M.G.N.-M., B.N., J.O.S, I.O.M., P.J.F.P.R., C.P.O., L.P.Z., C.A.P., V.P., C.A. Q., M.R.-M., T.R., G.R.-T., C.R., N.S., R.S.B., B.S.M., A.S., P.S.R., A.E.S.F., Q.S.G., T.S., D.S.-T., M.J.P.S., M.S., W.T.V.S., Y.A.T., P.T.S., M.T.N., E.V., I.C.Z.-B., M.R.D., S.T., M.P, V.B., S.P.C. C., L.J.T.W. E.Z., J.A.Z., D.F.R.P.B., M.S., J.C., B.J.E., J.B., O.L.P. and D.A.C. participated in or coordinated vegetation, trait data and/or soil data collection or processed field data and commented on and approved the manuscript.

Competing interests

The authors declare no competing interests.

Data availability

To comply with the original data owners' requirements, the plant functional traits and vegetation census data that support the findings of this study are available from their sources, GEM [31] at gem.tropicalforests.ox.ac.uk, and ForestPlots [32, 61, 62], www.ForestPlots.net and Diaz et al. [33]. Given data sovereignty from the original data owners raw data on vegetation censuses and trait data are not publicly available but can be requested by contacting all researchers through the ForestPlots [32, 61, 62] data request protocol described in forestplots.net/en/join-forestplots/working-with-data. The processed maps with community level trait predictions from this study are available as an app in Google Earth Engine at https://pantropicalanalysis.users.earthengine.app/view/pantropical-traits-aguirre-gutierrez-2025. Other environmental and plant data are available from their original sources: BIEN (bien.nceas.ucsb.edu), SoilGrids (https://soilgrids.org) and RESOLVE Ecoregions (https://ecoregions.appspot.com), Satellite data from the Senitnel-2 is freely available from the Google EarthEngine platform (https://developers.google.com/earth-engine/datasets/catalog/COPERNICUS_S2_SR_HARMONIZED). R code for graphics and analyses is available on Zenodo DOI 10.5281/zenodo.14509493 (ref. [86]).

Code availability

R code for graphics and analyses is available on Zenodo at https://doi.org/10.5281/zenodo.14509493 (ref. [86]).

Supplementary Information

This file contains the Supplementary Figs. 1–13 and Supplementary Tables 1–7.

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