



Amazon tree dominance across forest strata

The forests of Amazonia are among the most biodiverse plant communities on Earth. Given the immediate threats posed by climate and land-use change, an improved understanding of how this extraordinary biodiversity is spatially organized is urgently required to develop effective conservation strategies. Most Amazonian tree species are extremely rare but a few are common across the region. Indeed, just 227 'hyperdominant' species account for >50% of all individuals >10 cm diameter at 1.3 m in height. Yet, the degree to which the phenomenon of hyperdominance is sensitive to tree size, the extent to which the composition of dominant species changes with size class and how evolutionary history constrains tree hyperdominance, all remain unknown. Here, we use a large floristic dataset to show that, while hyperdominance is a universal phenomenon across forest strata, different species dominate the forest understory, midstory and canopy. We further find that, although species belonging to a range of phylogenetically dispersed lineages have become hyperdominant in small size classes, hyperdominants in large size classes are restricted to a few lineages. Our results demonstrate that it is essential to consider all forest strata to understand regional patterns of dominance and composition in Amazonia. More generally, through the lens of 654 hyperdominant species, we outline a tractable pathway for understanding the functioning of half of Amazonian forests across vertical strata and geographical locations.

The immense diversity of Amazonian forests is one of Earth's great natural wonders and underpins the functioning and resilience of ecosystems^{1,2} that play a crucial role in the global carbon and water cycles^{3–5}. Despite three centuries of investigation, however, our collective understanding of how this diversity is organized at regional scales remains limited⁶. Confronted with such overwhelming diversity, the challenge of monitoring a few hundred hyperdominant species (those species that together account for 50% of individuals across Amazonia⁷) becomes more tractable than monitoring the many thousands of rare species, particularly given the pace of action required for contemporary management decisions^{8,9}. Understanding the ecology and distribution of hyperdominant species is essential because these species dominate key ecosystem processes (for example, carbon storage and cycling¹⁰) and may serve as an effective proxy for general biodiversity patterns¹¹.

Existing studies of Amazonian hyperdominance and regional-scale dominance have been limited by excluding small-stemmed individuals (<10 cm in diameter) and by considering all individuals as equivalent regardless of diameter size class^{7,11–15}. Excluding small-stemmed species represents an important oversight because several thousand Amazonian tree species rarely, or never, reach 10 cm in diameter^{16–20}. While local-scale and taxa-specific dominance has been documented in small size classes^{21–24}, basin-wide hyperdominance in small size classes has not been confirmed. Consequently, species dominating the understory of Amazonian forests at a whole-Ama-zonia scale are not yet identified. Treating all stems >10 cm in diameter as equivalent is also likely to over-emphasize the dominance of mid-statured tree species (10–20 cm diameter). The power-law relationship between stem density and diameter means that small-stemmed individuals (<20 cm) are at least an order of magnitude more abundant than larger individuals (>50 cm)²⁵. This skewed understanding of dominance is highlighted by the difference between lists of hyperdominant species assembled using biomass rather than abundance¹⁰. This disparity suggests that a more nuanced approach that measures dominance separately across forest strata is required.

On the basis of existing local-scale studies and field observations, we expect the composition of hyperdominant species to vary substantially across forest strata due to different environmental

filters (for example, variable light profiles) and different species pools. Existing studies also suggest that compositional similarity between understory and canopy hyperdominant species may vary regionally^{26,27}, perhaps due to regional variation in forest structure and rates of turnover²⁸. For example, western Amazonia is known to have a floristically distinct understory, whereas understory communities in central and eastern Amazonia are thought to be comprised primarily of juveniles of larger tree species²⁶.

We know that some taxonomic tree clades contain many hyperdominant species⁷ and that genus-level abundance has a significant phylogenetic signal²⁹, yet no formal analysis of the phylogenetic structure of hyperdominance has been undertaken. Moreover, we may expect that hyperdominant species in different strata will display different phylogenetic patterns. Specifically, we hypothesize that hyperdominant species in large size classes from across Amazonia will be phylogenetically clustered for several reasons. First, maximum potential tree size has a significant phylogenetic signal in Amazonia³⁰ and those genera able to occupy canopy and emergent strata are concentrated in specific lineages (families or orders) that are primarily located within a few deep clades (such as Fabids and Ericales)³⁰. Second, while there is climatic variation across Amazonia, the above-canopy environment consists of high solar radiation, high temperatures, low humidity and high diurnal variability, irrespective of location³¹. These harsh but spatially consistent environmental conditions provide limited niche space and are likely to filter for a distinct suite of functional characteristics that may only have arisen in species belonging to a few specific lineages. Third, tall trees tend to disperse better than smaller trees and shrubs^{32,33} and at least some common large tree lineages have been well-dispersed throughout Amazonia across evolutionary timescales³⁴. This greater dispersal ability may mean that the strongest competitors for the canopy strata have been able to disperse consistently throughout Amazonia for millennia, thereby becoming hyperdominant across regions.

On the other hand, we may expect hyperdominant species in small understory strata may be more phylogenetically dispersed. First, because small trees and shrubs typically are more likely to be dispersal limited^{32,33}, the strongest understory competitors may be less likely to disperse across regions and outcompete functionally

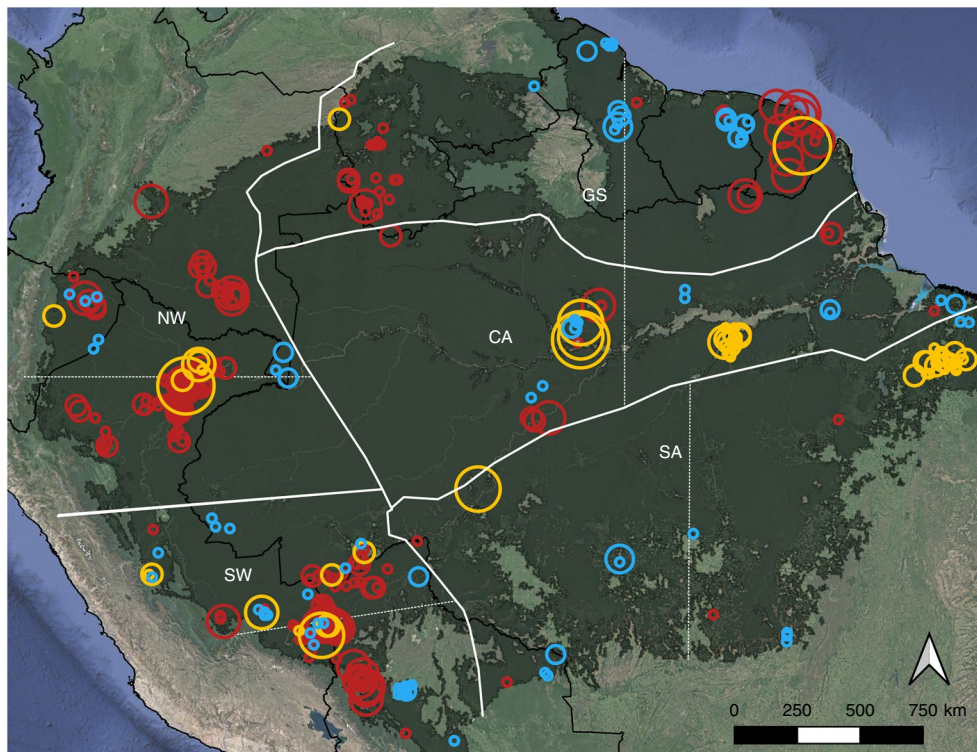


Fig. 1 | Map of study area and 1,240 floristic inventory plots, represented by coloured points. Point size corresponds to number of plots at a given location (range 1–40 plots). Point colour refers to the plot size and diameter cutoff: (1) red points, small plots <1 ha and stems ≥ 2.5 cm; (2) blue points, large plots >1 ha and stems ≥ 10 cm; (3) gold points, large plots >1 ha and stems ≥ 10 cm with nested subplot for small stems ≥ 2.5 cm. Solid white lines indicate the border of the five sampling regions defined for analyses; dashed white lines show the further subdivision of sampling regions into ten sampling zones. Sampling regions have been labelled as follows: northwest Amazonia (NW); southwest Amazonia (SW); southern Amazonia (SA); central Amazonia (CA); and Guiana Shield (GS). The shaded area shows the area defined as Amazonia on the basis of: (1) annual precipitation >1,300 mm; (2) elevation <1,000 m (above sea level); and (3) forest cover >70%. Base map created using TerraMetrics. The arrow symbol indicates north.

equivalent species in other locations. Secondly, understory species are often locally abundant and frequently have fast generation times³⁵. Over evolutionary timescales these high abundances and fast generation times may be likely to increase diversification among locally restricted understory species³⁶. Third, the below-canopy environment is more spatially heterogeneous, due to variation in forest structure and the frequency and size of forest gaps, potentially leading to increased niche partitioning in smaller size classes. Moreover, because forest structure varies across Amazonia (for example, taller denser canopy in Guiana Shield versus shorter more dynamic canopy in western Amazonia)²⁸, smaller-statured species may be exposed to different abiotic and biotic filters across large spatial scales and develop greater local specialization associated with distinct functional characteristics. Therefore, we further predict that understory hyperdominants from different regions should be more distantly related than hyperdominants in larger size classes.

Here, we assemble a unique dataset of 1,240 floristic inventory plots distributed across lowland Amazonia, which include stems as small as 2.5 cm (Fig. 1). On the basis of individual diameter measurements and species-level identifications, we implement a spatially stratified resampling approach to estimate basin-wide relative abundances for all tree species across six diameter size classes from the understory (2.5–5 cm) to the forest canopy (>50 cm). Using this dataset, we identify those species dominating different strata of Amazonian forests and ask: (1) Is hyperdominance a constant phenomenon across Amazonian tree strata? and (2) Does the identity of hyperdominant species differ across Amazonian tree strata and how does this vary regionally? We also used a recently developed genus-level molecular phylogeny^{37,38} to ask: (3) Do patterns of

phylogenetic clustering in hyperdominant species vary across forest strata? And does this correspond with our expectations of increased clustering in large-stemmed canopy strata and increased phylogenetic dispersal in small-stemmed understory strata?

Results and discussion

Consistent hyperdominance across strata. We find that hyperdominance occurs throughout the Amazonian flora across forest strata but the proportion of species that qualify as hyperdominant (together account for 50% of individuals) varies across size classes and regions from 3 to 12% (Fig. 2a). At the basin-wide Amazonian scale, the proportion of species that qualify as hyperdominant in our dataset (~4%; Extended Data Fig. 1) is broadly consistent with empirically derived species counts from previous studies^{7,10}. This consistency of hyperdominance across size classes suggests that regional dominance of tree communities is a feature shared across Amazonian forest strata.

A larger species pool will necessarily result in stronger patterns of dominance because it contains more rare species, which will decrease the proportion of species that qualify as hyperdominant, even if the abundance of the most dominant species remains constant. However, the relationship between species richness and the level of dominance we observed in a given size class or region is weak and primarily driven by the basin-wide data (Fig. 2b). Therefore, our results suggest that variation in dominance among size classes and regions is not an artefact reflecting the variable sampling intensity among regions and size classes.

Some size classes are consistently more ‘dominated’ than others (a lower proportion of species are required to account for

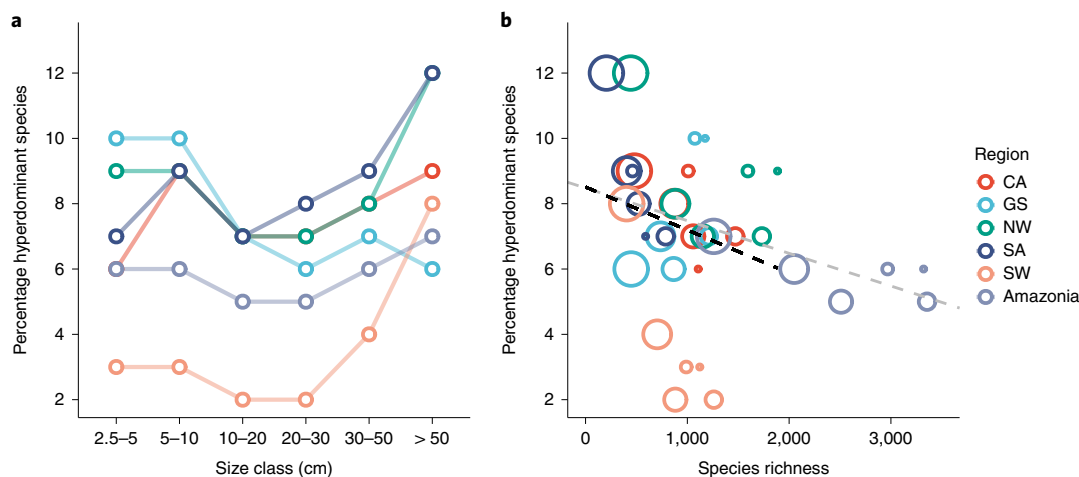


Fig. 2 | Hyperdominance and species richness across size classes. **a**, The proportion of species that are hyperdominant (together account for 50% of individuals) within six size classes across the five Amazonian regions and the basin-wide ‘Amazonia’ dataset. **b**, The relationship between the proportion of species that are hyperdominant and total species richness across six size classes (indicated by symbol size) across the five Amazonian regions and the basin-wide ‘Amazonia’ dataset. Dashed lines show linear regressions on the basis of the five regional datasets (black line; $R^2=0.01$, $P=0.26$) and the five regional datasets plus the basin-wide ‘Amazonia’ dataset (grey line; $R^2=0.08$, $P=0.05$). In **a** and **b**, a lower proportion of hyperdominant species indicates stronger patterns of dominance. Sampling regions as indicated in Fig. 1 are: northwest Amazonia (NW); southwest Amazonia (SW); southern Amazonia (SA); central Amazonia (CA); and Guiana Shield (GS).

50% of individuals). In particular, the 10–20 cm size class consistently displays the strongest dominance patterns (Fig. 2). The two smallest size classes have weaker dominance patterns, perhaps because smaller-stemmed species are more dispersal limited than larger individuals³² and therefore less likely to be dominant over large areas and more likely to locally diversify. A clear exception to this occurs in forests on the Guiana Shield, where patterns of dominance are stronger in larger size classes than in smaller ones. This may be partially explained by the relatively low diversity in the understory of these forests, due perhaps to greater resource limitation imposed by extreme shade from the more structured canopy in addition to low fertility associated with oligotrophic soils in this region¹⁶.

The proportion of species that qualified as hyperdominant at the regional scale was generally higher than in basin-scale analyses (that is, dominance patterns are weaker at the regional scale) (Fig. 2). This pattern is primarily driven by those exceptionally common and widespread species that achieve hyperdominance in two or more regions. However, several of these widespread hyperdominant species may be species complexes, as recently shown for *Protium heptaphyllum* and *Astrocaryum murumuru*^{39,40}. Solving these issues will require more integrative taxonomic studies (for example, incorporating DNA analyses alongside spectroscopy^{39,41}) of other widespread hyperdominant species, which would help to further assess the validity of hyperdominant species identifications.

Southwest Amazonia exhibits stronger patterns of dominance than all other Amazonian regions in all but the largest size class (Fig. 2). It is not immediately clear why this region has such strong patterns of dominance. However, it may be due in part to less environmental heterogeneity in this region, which contains relatively few areas of white-sand forest, swamp forests or seasonally inundated forests^{42,43}. Although we do not explicitly consider habitat type in this study, many hyperdominant species are known to be dominant only in a single habitat type⁷. Therefore, less environmental heterogeneity should lead to fewer hyperdominant species. The strong dominance patterns in southwestern Amazonia matter because several landmark studies have focussed on patterns of dominance in this region^{12,13,21} and these patterns may not be representative of Amazonia more generally⁴⁴.

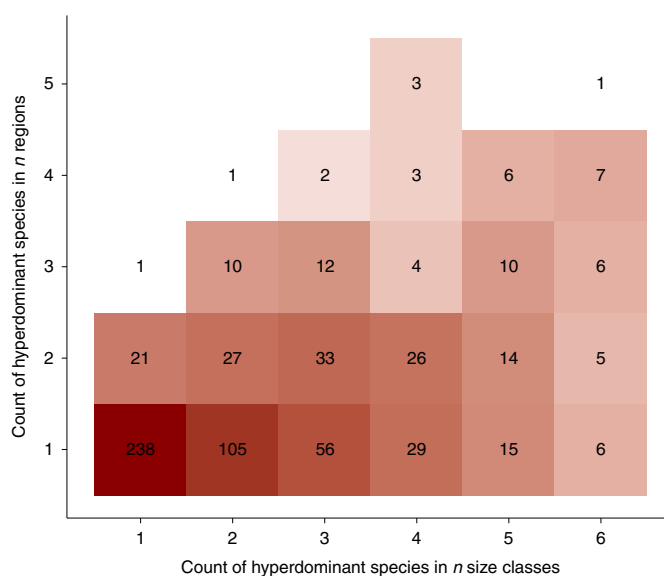


Fig. 3 | A summary of hyperdominance across regions and size classes. Two-dimensional histogram showing the number of species that are hyperdominant in one to six size classes and across one to five regions. Regions and size classes follow the same definitions as in Fig. 2.

Identity of hyperdominant species across strata and region. The identity of hyperdominant species varies substantially across forest strata and region. Over a third (38%) of hyperdominant species are only dominant in a single size class within a single region and nearly two-thirds (62%) are dominant in two or fewer size classes and two or fewer regions (Fig. 3). Only one species, *Eschweilera coriacea*, achieves hyperdominance across all six size classes and all five regions. These results provide clear evidence that hyperdominant tree species composition is vertically stratified throughout Amazonia. Therefore, considering all individuals >10 cm in diameter as equivalent completely overlooks the nuanced vertical stratification of tropical forests. Moreover, even though 10 cm

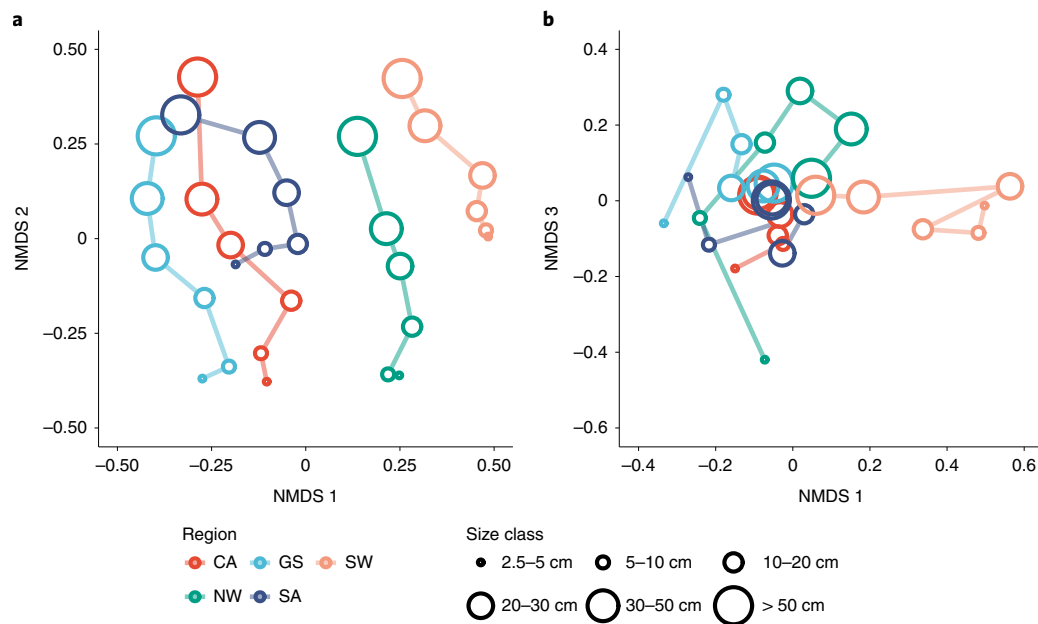


Fig. 4 | Taxonomic and phylogenetic similarity of hyperdominant species assemblages. **a, b**, NMDS ordinations showing similarity in composition of hyperdominant species in terms of: taxonomic species similarity (Jaccard index) (**a**) and deep-node-weighted phylogenetic similarity (community level mean pairwise phylogenetic distance) (**b**). Sampling regions have been labelled as follows: northwest Amazonia (NW); southwest Amazonia (SW); southern Amazonia (SA); central Amazonia (CA); and Guiana Shield (GS).

diameter cutoff protocols are well-suited to monitor carbon fluxes³, alternative plot designs or data treatments may be better suited to monitor spatial variation in floristic diversity and composition^{45–47}.

Our multivariate analysis illustrates two strong axes of compositional variation among hyperdominant tree species (Fig. 4a). The first axis differentiates the five regions, while the second represents a gradient across six tree size classes. This compositional variation across strata is important because our best current methods of observing forests at large scales are through either: (1) remote sensing approaches, which detect only those trees that reach sky-facing canopy positions; or (2) plot networks, which are heavily influenced by species dominant in smaller or intermediate size classes. Our results demonstrate that species dominating the view from above the canopy are different from those that dominate the view from below, thereby emphasizing the mismatch between remotely sensed and plot-based studies. Addressing this mismatch will be essential to successfully integrating field and remote sensing data at large scales in Amazonia.

Despite this compositional mismatch, our data also suggest that, while canopy hyperdominants comprise different species from those that dominate the understory, there is an important association in hyperdominant species composition between size classes within regions. Hyperdominant species clearly form distinct regional groups across the first non-metric multidimensional scaling (NMDS) axis. Therefore, remotely sensed data from forest canopies may serve as an effective proxy for compositional patterns in smaller size classes, as has been found recently in understory tree, fern and lycophyte communities^{48,49}.

Our results contrast with previous observations, which suggest that the understories of eastern Amazonia are primarily composed of juvenile individuals of large-stemmed species whereas western Amazonia has a more specialist and compositionally distinct understory²⁶. Instead, we find that across all regions, tree species that dominate forest understory tree communities are compositionally distinct from those that dominate the canopy. In all regions, hyperdominant species form a distinct compositional gradient across strata, as reflected by the second NMDS axis

(Fig. 4). Indeed, there is no difference in potential maximum size among understory dominant species from different regions (Extended Data Fig. 2).

At the family level, there is a clear positive relationship between the number of hyperdominant species and total species richness per family (Extended Data Fig. 3). However, our statistical null modelling approach shows that at a basin-wide scale several plant families have significantly more or fewer hyperdominant species than would be expected on the basis of their species richness. Moreover, some families have more hyperdominant species than expected across several size classes. For example, *Arecaceae*, *Burseraceae* and *Myristicaceae* have more hyperdominant species than expected across all but the largest size class. Other families are over-represented in terms of hyperdominant species in only smaller (for example, *Violaceae* and *Siparunaceae*) or larger size classes (for example, *Moraceae*). Alternatively, commonly occurring tree families, including *Rubiaceae* and *Lauraceae*, have consistently fewer hyperdominant species than we would expect on the basis of their species richness.

Our results further reinforce the importance of the legume family *Fabaceae* in dominating Amazonian forests. At a basin-wide scale *Fabaceae* is the family with the greatest number of hyperdominant species across all size classes, largely because *Fabaceae* is by far the most species-rich family. While *Fabaceae* species are less common than would be expected by chance given their high species richness in small size classes, in the largest size class *Fabaceae* are significantly over-represented and account for >30% of hyperdominant species.

Phylogenetic structure of hyperdominance across Amazonian tree strata. Our phylogenetic analyses demonstrate that while many lineages contain hyperdominant species (Fig. 5), those species that are hyperdominant in the canopy of Amazonian forests show contrasting phylogenetic patterns to those that are hyperdominant in small understory strata (Fig. 6).

We find overall support for our prediction that hyperdominance in larger size classes tends to be concentrated in a few closely related

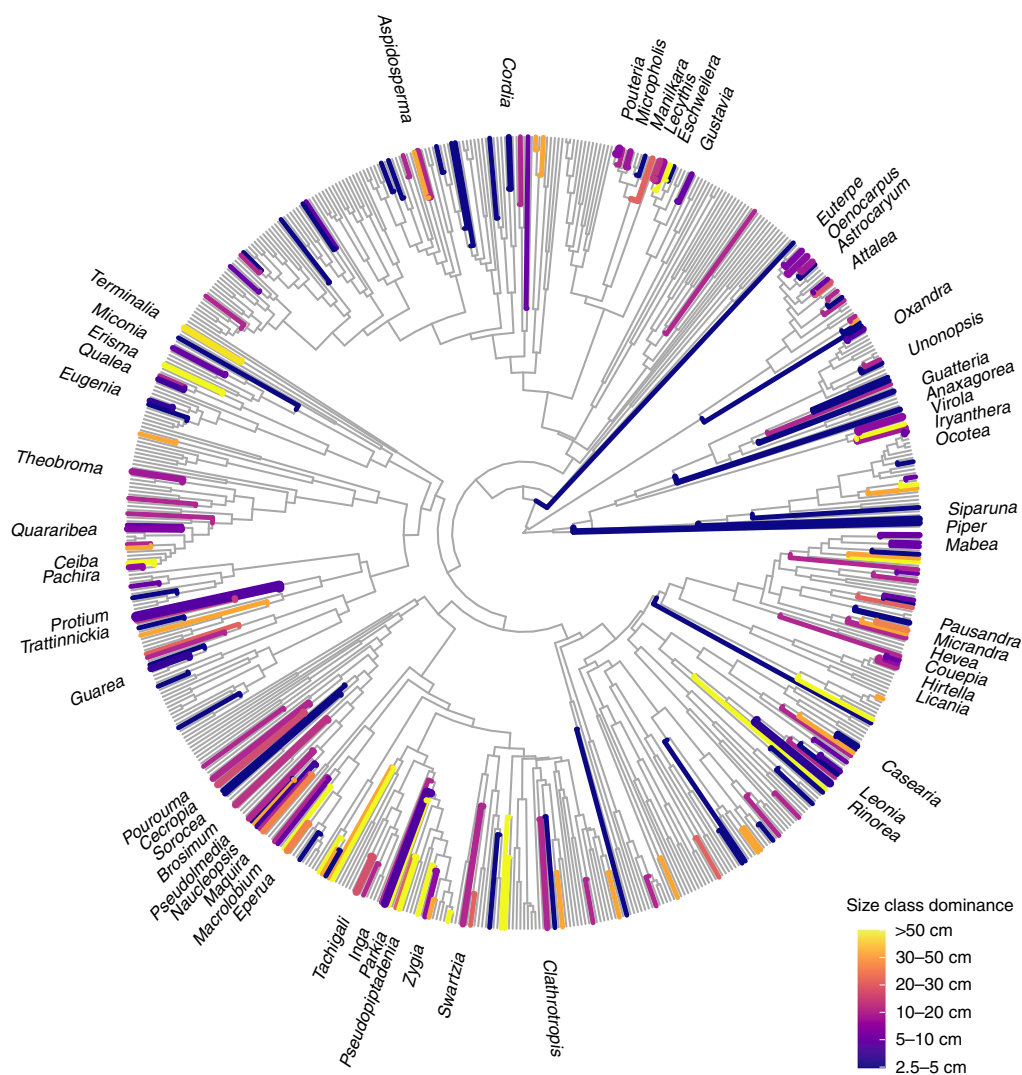


Fig. 5 | Hyperdominant species mapped onto a genus-level Amazonian tree phylogeny. All genera with one or more hyperdominant species have been highlighted. Genera with three or more hyperdominant species have been labelled. Colour corresponds to the size class within which species belonging to that genus are most frequently hyperdominant.

lineages, such as in Fabaceae and Moraceae as well as Lecythidaceae and Sapotaceae. This phylogenetic clustering of canopy hyperdominant species is highlighted by our mean pairwise phylogenetic distance (MPD) null modelling analysis (Fig. 6 and Supplementary Fig. 4), which shows that hyperdominant species in the largest size classes are consistently more closely related than would be expected by chance. Our phylogenetic composition results reveal that canopy strata across the basin are dominated by species belonging to closely related lineages (Fig. 4b). The close phylogenetic relationship among large-stemmed regionally dominant tree species across the basin suggests that these species have been well-dispersed across the basin through evolutionary time, supporting previous studies that found evidence for widespread dispersal in several common Amazonian tree lineages³⁴.

These findings have important implications: if we accept the premise that phylogenetic diversity is an effective proxy for ecological or indeed functional diversity^{50–52}, the high phylogenetic similarity among canopy species suggests there is lower functional diversity within a large proportion of the canopy strata. This low functional diversity may in turn reduce the resilience of these canopy communities to climate change. Previous studies have shown that large canopy trees in Amazonia have distinct trait profiles

(for example, hydraulic traits)⁵³, appear to be particularly affected by drought⁵⁴ and play a crucial role in Amazonian forest carbon storage and cycling¹⁰. We propose that future research should continue to uncover the functional diversity and potential vulnerability both within and among lineages of these canopy hyperdominant species.

We find contrasting phylogenetic patterns in smaller, understory size classes, which are widespread across the phylogeny as we predicted. Indeed, at the basin-wide scale, hyperdominant species in understory size classes are less closely related than expected by chance (Fig. 6). This dispersed phylogenetic pattern is largely due to understory hyperdominants occurring across the major angiosperm clades (Extended Data Fig. 5) but may also be because our list of understory hyperdominant species is composed of both understory specialist taxa as well as larger-statured species that achieve dominance as juveniles. Hence, this mixture of life stages and functional strategies across distinct clades is more likely to lead to a more phylogenetically dispersed assemblage. Nevertheless, our findings highlight that several characteristic understory genera such as *Piper* (Piperaceae), *Rinorea* (Violaceae) and *Miconia* (Melastomataceae) contain numerous hyperdominant species, which have not been recognized by previous studies of large stem (>10 cm) dominance^{7,12,13}.

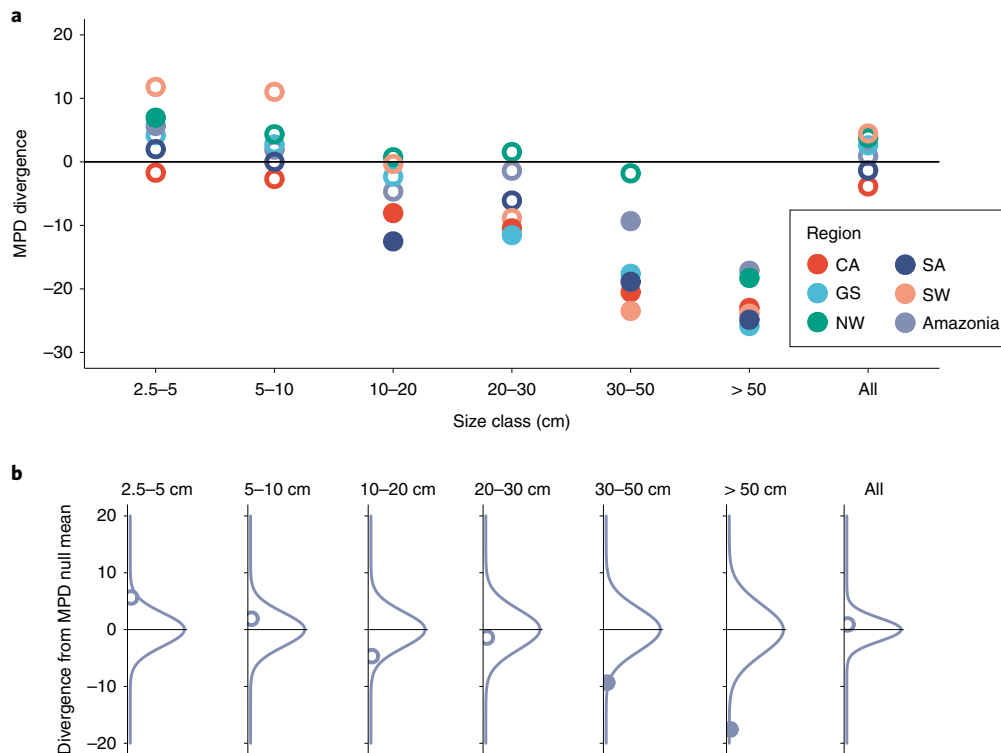


Fig. 6 | Phylogenetic structure of hyperdominant species across size classes. **a**, Divergence of mean pairwise phylogenetic distance (MPD) from null models for each hyperdominant community. Positive numbers indicate greater MPD than expected by chance (that is, species are more distantly related than expected by chance). Negative numbers indicate lower MPD than expected by chance (that is, species are more closely related than expected by chance). Filled symbols indicate hyperdominant communities that were outside the 95% confidence interval of the null distribution. **b**, The null distributions and observed MPD for entire Amazonia hyperdominant communities. Regional null distributions are provided in Extended Data Fig. 4.

Our phylogenetic compositional analysis also supports our hypothesis that within understory strata, hyperdominant species from different regions are distantly related (Fig. 4b). These results are consistent with limited dispersal and diversification of understory hyperdominant species at a basin-wide scale over evolutionary timescales, as has been suggested by others⁵⁵. Furthermore, the ability to become dominant in the understory of Amazonian forests is found across a diverse range of lineages and, therefore, is relatively common. Because many of these lineages are distantly related, this suggests that a range of functional strategies has evolved to achieve hyperdominance in Amazonian understories. Furthermore, the high phylogenetic distance among understory hyperdominant species is consistent with the hypothesis that greater environmental niche space in the forest understory has contributed to higher phylogenetic diversity.

Future directions. The mechanisms that allow certain species to become hyperdominant remain elusive. However, our results provide a basis for testing hypotheses related to specific ecological mechanisms. Future analyses should capitalize on increasingly available functional trait data to tackle these issues. We expect species that dominate the canopy to be functionally distinct from those that dominate the understory. Therefore, a size-class constrained framework may help to illuminate the mechanisms that underpin hyperdominance. In particular, a large-scale assessment of quantitative dispersal traits across a range of species may help to unravel why hyperdominant species in understory size classes display such different phylogenetic patterns to those in the canopy.

Previous studies have presented a compelling case for pre- or post-Columbian peoples increasing the abundance of many

hyperdominant species to extract products such as fruits, nuts or building materials^{56,57}. Here, we show that many of these ‘domesticated’ hyperdominants (for example, *Euterpe precatoria* and *Theobroma cacao*) are in fact only dominant in smaller size classes. One possible explanation is that it is easier to harvest and manage small understory trees and shrubs than large canopy trees; therefore, species that dominate larger size classes may have been less influenced by human activity than species that dominate smaller size classes. It is important to note that this is not the case in all instances and there is substantial evidence that some large-statured species (for example, *Bertholletia excelsa*) were also managed during pre-Columbian times⁵⁸. Further investigation into the role of humans in shaping the composition of Amazon understories may help explain why such distantly related species have become dominant in different Amazonia regions. For example, palaeoecological records may reveal if different groups of indigenous peoples have propagated different tree species in different regions.

Conclusions

There is a pressing demand to quantify and monitor the biodiversity of Amazonia in the coming decades. However, we currently lack the resources necessary to undertake the ‘Linnaean renaissance’ required to fully document the biota of arguably Earth’s most diverse forests. By identifying those species that are hyperdominant across forest strata, we outline a size-class based framework for understanding Amazonian forests, irrespective of strata or location. This framework has revealed that species dominating either the canopy or understories of Amazonian forests not only are taxonomically distinct but also represent different phylogenetic patterns. Species belonging to a range of phylogenetically dispersed

lineages have become hyperdominant in small size classes, whereas species that are hyperdominant in large size classes belong to a few specific lineages.

Methods

Floristic data. Floristic data came from 1,240 forest inventory plots distributed across the Amazon basin (Fig. 1). The plot data fall into two broad categories. Firstly, the RedGentry network consisted of 1,027 small forest plots (typically 0.1 ha but ranging from 0.04 to 0.25 ha) within which all stems with a diameter at 1.3 m in height (dbh) >2.5 cm were measured and identified. Secondly, 520 larger forest plots (typically 1 ha but ranging from 0.5 to 9 ha) from the RAINFOR and ATDN networks were used. Within these larger plots, all stems with a dbh >10 cm were measured and identified. Many of these plots are curated and stored within ForestPlots.net, a cyber-infrastructure initiative that unites plot records and their contributing scientists from the world's tropical forests.

The RedGentry plot data came from a range of sources and therefore included a range of plot sizes and sampling protocols. Most plots were 0.1 ha in size and consisted of ten transects of 2 × 50 m² arranged systematically around a single transect baseline following the 'Gentry protocol'⁴⁶. However, 307 plots were subplots nested within larger 1-ha inventory plots (Fig. 1). Most of these nested 0.1-ha plots were part of the PPBio network.

Taxonomic standardization. It was not possible to standardize morphospecies across datasets as plots were installed by many different botanical teams at different times, often without accompanying herbarium vouchers. Therefore, all individuals that were not identified to species level were excluded from all subsequent analysis. These exclusions lead to a substantial loss of individuals (mean 21% of individuals per plot, Extended Data Fig. 5) and were phylogenetically biased (that is, some families had a higher degree of taxonomic uncertainty than others). Nevertheless, this approach renders our analysis comparable to other landscape analyses conducted on larger stems in this and other regions.

Species exclusions. Species names were checked for synonymy and spelling mistakes using the taxonomic names resolution service of the R package `taxize`⁵⁹. Any species that were not recognized in the automated process were checked manually for spelling mistakes. Identifications that could not be easily assigned to a species were considered unidentified morphospecies and were removed from further analysis. Finally, our list of legitimate species names was cross-checked against the most current published checklists^{60,61}. Species that did not occur on this Amazon checklist (887 species) were checked manually against collection records in the Tropicos database (www.tropicos.org). Of these, 39 were confirmed to be illegitimate Amazonian species because they have ranges outside of our region (on another continent). A further 579 species that were described as epiphytes, lianas, herbs or ferns were also excluded from our analysis. These lifeforms were included in some plot datasets and excluded from others. As individual datasets are normally geographically clustered, including them would probably lead to spatially biased species abundance estimates. A further 47 species were excluded because there was no recorded collection since their descriptions (we considered these individuals to be wrongly identified).

Species inclusions. We included 180 species in our analysis that had been excluded from previous analyses or checklists. Most of these inclusions were small-stemmed species that had previously been excluded for being shrubs or treelets. We considered these definitions to be subjective. Of these included species, 37 have previously been considered illegitimate because they occur primarily in savanna or seasonally dry habitats. However, because several of our plots were located close to boundaries between ecosystem types and many species are shared across these boundaries (not necessarily in their optimum habitat), we included these non-core rainforest species in our dataset.

Defining Amazonia. To ensure that our analysis included only plots located in lowland Amazonia and did not incorporate plots in marginal seasonally dry or montane environments, it was necessary to define our study area. We defined lowland Amazonia using four remotely sensed criteria. (1) Watersheds were estimated using the hydrosheds data layer⁶², in addition to the Amazon basin; we also included eastern branches of the Orinoco and all watersheds to the east of that mark in the Guiana Shield. (2) Elevation was measured using the global Shuttle Radar Topography Mission (SRTM) digital elevation model⁶³; lowlands were considered to be land area below 1,000 m elevation following Cardoso et al.⁶⁰. (3) Precipitation was estimated using the CHIRPS annual mean rainfall data⁶⁴ and a minimum mean annual precipitation of 1,300 mm yr⁻¹ was used to define moist forests following Cardoso et al.⁶⁰. (4) Tree cover was estimated using the 2010 global forest cover map⁶⁵ and all pixels with >70% forest cover were included. The four layers were overlaid and the intersecting area was used to define Amazonia. This final layer was then sieved and filtered to reduce speckle, which was primarily driven by the complex patterns of deforestation along the southeastern border. All geospatial analysis was conducted using QGIS software⁶⁶.

Spatial standardization. Many species (27%) occurred fewer than five times across the plot network. Therefore, we did not attempt to generate basin-wide population estimates for most species as other studies have done⁷. Instead, we used only the empirical data from plots to estimate those species likely to be hyperdominant at basin-wide scales, under the assumption that this plot network is reasonably representative of abundances of the most common species.

Plots are not distributed evenly across Amazonia but instead are clustered in space; for example, there are many more plots in western Amazonia than in southern or eastern Amazonia. Furthermore, plots varied in size and, therefore, so did the number of individuals per plot. To account for these biases and to attempt to ensure the Amazonian flora was sampled as evenly as possible, we used a spatially stratified bootstrap resampling approach. All sampling procedures were performed in the statistical language R using the tidyverse packages `dplyr`, `tidyr` and `purrr`^{67–69}.

This approach consisted of the following steps:

- (1) Greater Amazonia (as defined above) was divided into five regions roughly following previously defined boundaries^{7,49}. Each region was then split roughly in half to generate ten total sampling zones that were broadly similar in area (area varied from 210,000 to 1081,000 km²). Each sampling zone contained at least 40 individual plots (at least 20 small plots and at least ten large plots).
- (2) The entire dataset was then divided into six strata-specific datasets. This was done by stratifying the data by dbh into six size classes (2.5–5, 5–10, 10–20, 20–30, 30–50 and >50 cm). Diameter was used as a proxy for tree height because tree height was not measured in most plots and because of the strong allometric relationship between diameter and height.
- (3) Twenty small plots or large plots with nested subplots and five large plots were sampled from each sampling zone at random without replacement. This step ensured spatially even sampling across the basin and the five additional large plots ensured a reasonable number of large individuals were sampled.
- (4) From each of these 25 plots a standard number of individuals (50% of the median individuals per plot per size class) were sampled with replacement, ensuring an even number of individuals was sampled for each plot.
- (5) These standardized samples from each plot were then assembled into a single species by plot matrix.
- (6) Steps (2) and (3) were repeated 10⁶ times, generating 10⁶ estimates of abundance for each species across the basin.
- (7) The mean and standard deviation of abundance for each species was calculated across the 10⁶ estimates of abundance.
- (8) Hyperdominant species were then defined as those species that together account for 50% of the mean total abundance of all individuals within each size class across all iterations.

To identify regionally dominant species, steps (2) to (7) were repeated for each of the five predefined regions individually.

Phylogenetic analyses. To understand where hyperdominant species are situated across the Amazonian phylogeny, we used a published genus-level molecular phylogeny for Amazonian tree species^{37,38}. A genus-level phylogeny was used because a species-level molecular phylogeny for the full Amazonian flora does not yet exist. Genera occurring in our lists of Amazon-wide hyperdominant species were mapped onto the phylogeny, which was then pruned to remove taxa not occurring in our dataset. The final phylogenetic tree contained 646 genus tips. We then plotted the phylogeny for all genera occurring in our dataset using the R package `ggtree`⁷⁰.

The tips of genera that contained hyperdominant species were coloured to highlight their location. Tip colours corresponded to a continuous variable that was the mean size class for hyperdominant species that were in the given genus. Genus labels were given to all genera that contained three or more hyperdominant species.

We used the MPD metric and a null modelling approach to test if hyperdominant species are more closely related to one another than would be expected if hyperdominance were distributed across the phylogeny at random^{51,71}. Because a species-level molecular phylogeny has not been developed across Amazonian plant taxa, we first added species tips with a uniform branch length (0.1) to all tree genera. This approach allowed us to make species-level comparisons using a genus-level phylogeny, while minimizing the assumptions made about within-genus phylogenetic structure. We then calculated MPD among hyperdominant species for each hyperdominant community and compared this observed MPD to a null distribution of expected MPD if we sampled an equivalent number of species at random across a phylogeny with an equivalent species pool⁷¹. Where the observed MPD fell outside two standard deviations of the null distribution, that hyperdominant community was considered to be significantly more clustered (lower MPD) or significantly more dispersed (higher MPD) than we expect by chance. All phylogenetic analysis was conducted in R, using packages `phylomeasures`, `phytools` and `caper`^{71–73}.

MPD is known to be influenced by the extent to which species are divided among the three major angiosperm clades (magnoliids, monocots and eudicots)⁷⁴. Large-stemmed Amazonian tree species are predominantly found within the

eudicots, while small-stemmed species are found across the three clades. These deep-clade distributions are therefore likely to increase phylogenetic clustering within the large-stemmed species and increase phylogenetic overdispersion within small-stemmed species. In part, we account for this in measurement of MPD as we remove genera from the tree that do not occur in the size class/region for which we are measuring MPD. However, to explore the effect of this deep-clade diversity further, we repeated our MPD analysis within eudicots only (Extended Data Fig. 6). This analysis demonstrates that the overall patterns of increased clustering in larger size classes is maintained within eudicots. The analysis also shows that the phylogenetic dispersion found within small-stemmed hyperdominant species is due to these understory hyperdominant species occurring across these deep phylogenetic nodes.

Compositional analyses. To understand how the composition of hyperdominant species varied across size classes and regions we used a multivariate statistical approach. Specifically, we used the Jaccard index as a metric of how similar or different the composition of hyperdominant species was among the 36 communities of a given size classes within a given region (for example, northwest Amazon—2.5–5 cm size class). For clarity, these regional and size class specific groups are hereafter referred to as hyperdominant communities. The Jaccard distances were generated using with the R package *vegan*⁷⁵.

We expanded these compositional analyses not only to consider how taxonomic composition varied among hyperdominant communities but also to quantify how phylogenetically similar hyperdominant communities were among size classes and regions. To do this we again used a multivariate statistical approach; however, this time using two metrics of phylogenetic beta diversity. Both phylogenetic beta diversity metrics were calculated at genus rather than species level as we used the genus-level phylogeny. To account for the fact that some genera contain several hyperdominant species, we used the number of hyperdominant species per genus for each hyperdominant community per size class as our input community matrix.

The first metric that we used was the abundance weighted MPD among hyperdominant communities, which provides a deep/basal node weighted assessment of phylogenetic beta diversity⁵⁰. The second metric of phylogenetic beta diversity that we used was the generalized version the unifracs method⁷⁶, calculated with the R package *GUniFracs*⁷⁷. We used an α value of 0.5, meaning that we moderately weighted genera by the number of hyperdominant species that they contained in that site/size class. The unifracs metric provides a stable tip-weighted assessment of phylogenetic beta diversity.

Because the phylogenetic analysis was conducted using a genus-level phylogeny, we do not account for any within-genus phylogenetic structure that could affect these metrics. However, any within-genus structure will have little effect on patterns of MPD, as this metric is heavily weighted towards deep-node differences among communities⁵⁰. The tip-weighted unifracs method is likely to be more heavily influenced by the missing within-genus structure, therefore these results are only presented in the Supplementary Information.

To reduce the dimensionality of this multivariate data and visualize the taxonomic and phylogenetic similarities among hyperdominant communities we used NMDS. NMDS analyses were run for at least 50 iterations and until a stable solution was reached (stress <0.2). Each NMDS was optimized over three dimensions and displayed in an ordination plots. All NMDS ordinations were performed in the R package *vegan*⁷⁵.

Reporting Summary. Further information on research design is available in the Nature Research Reporting Summary linked to this article.

Data availability

The permanently archived data package of hyperdominant species composition across size classes and regions is available from https://doi.org/10.5521/forestplots.net/2021_2

Code availability

All custom analytical code used in this study are available online in a permanently archived data package at https://doi.org/10.5521/forestplots.net/2021_2

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Author contributions

F.C.D. and C.B. conceived the study. F.C.D., G.P.A. and C.B. designed the study with input from F.R.C.C., G. Arellano, O.L.P. and H.t.S. F.C.D. and J.B.S. performed the analysis with input from C.B., G.P.A., G. Arellano, O.L.P., A. Duque, F.C.d.S. and K.D. F.C.D. wrote the manuscript with input from C.B., F.R.C.C., G. Arellano, O.L.P., A. Duque, M.J.M., G.P.A. and H.t.S. All other coauthors contributed data and had the opportunity to comment on the manuscript.

Competing interests

The authors declare no competing interests.

Additional information

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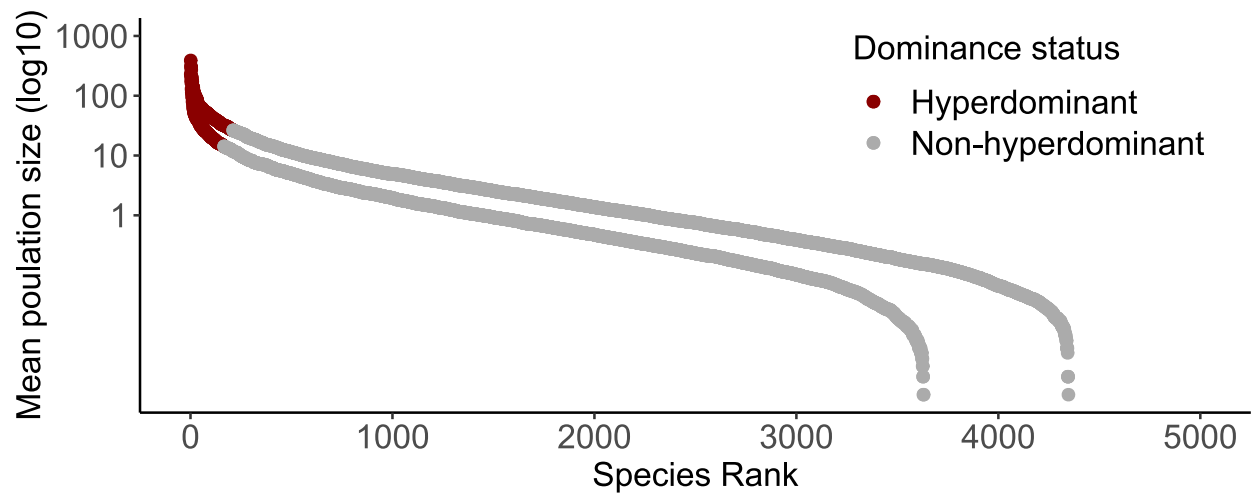
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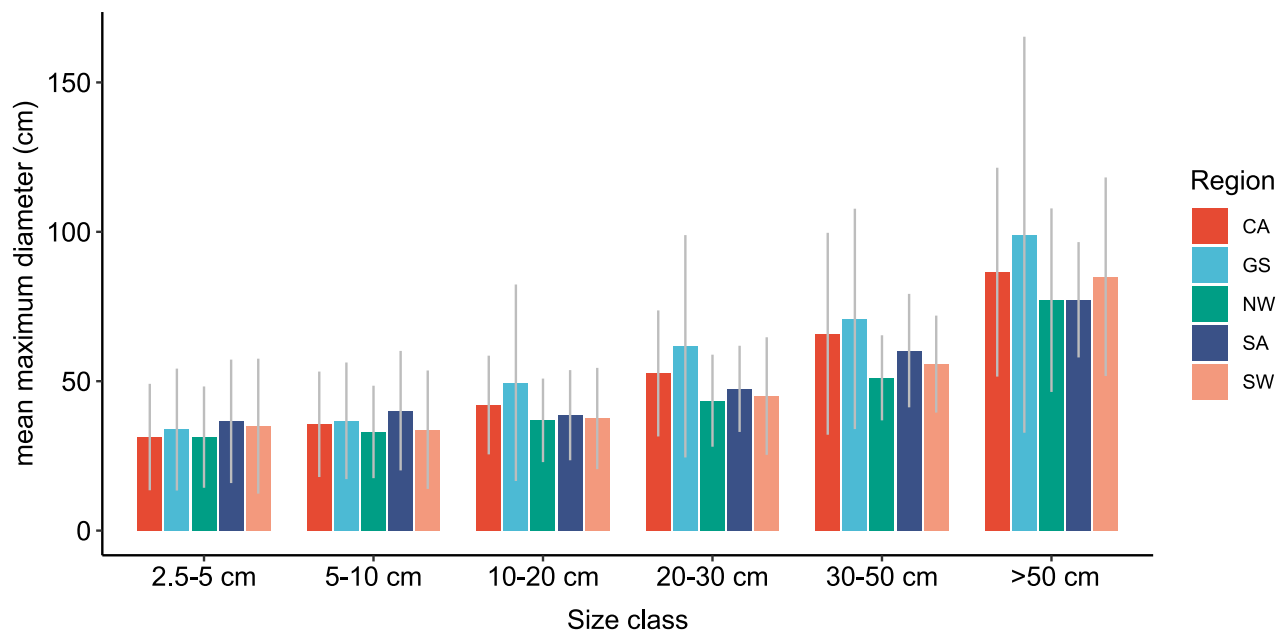
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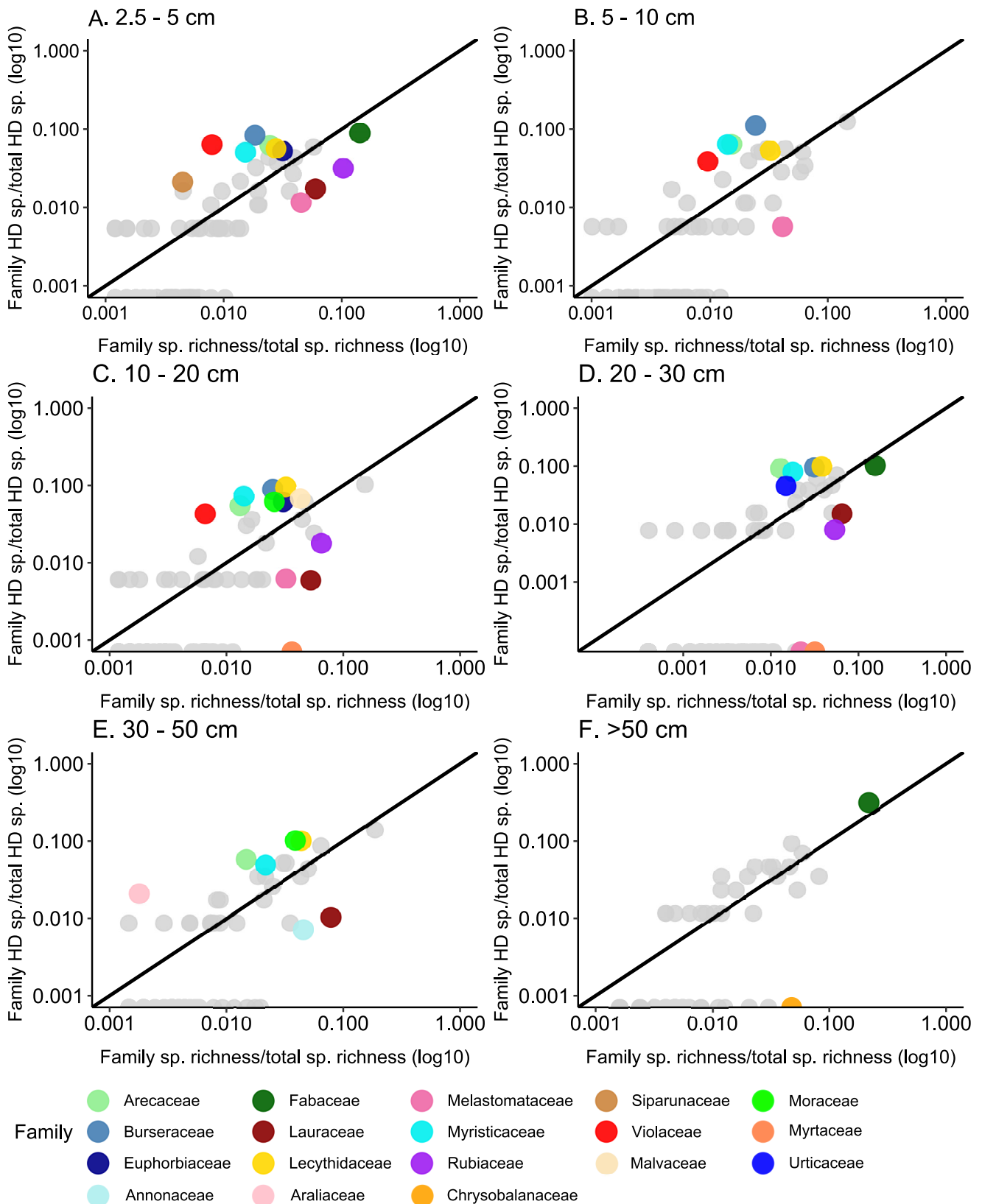
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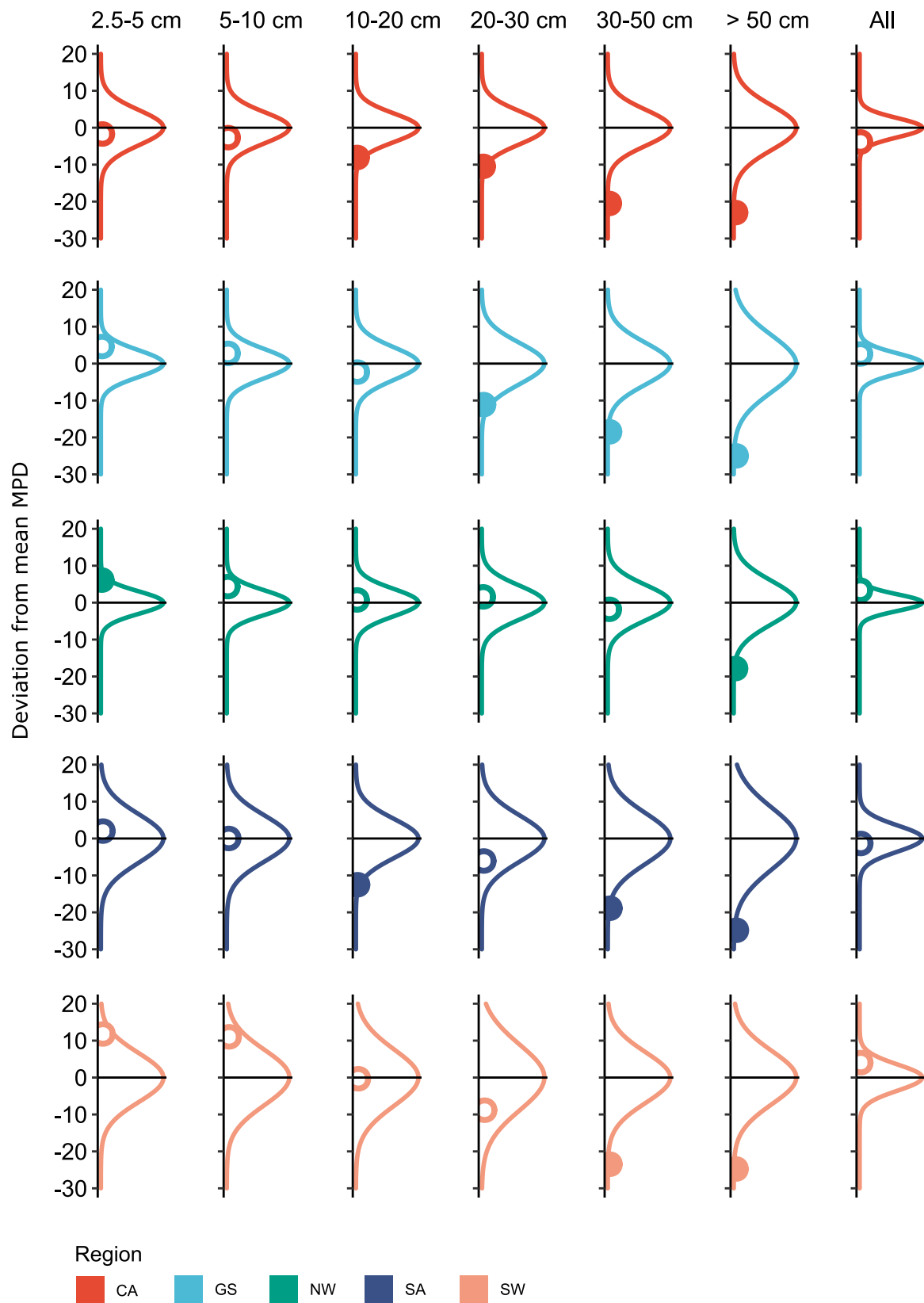
Extended Data Fig. 1 | Amazonian tree rank abundance distribution. Empirical rank abundance distribution for all species in our dataset with a diameter ≥ 2.5 cm (upper line) and ≥ 10 cm (lower line). Values on the Y axis represent mean population estimates for each species recorded in our dataset across the 106 sampling runs at the entire Amazon scale.



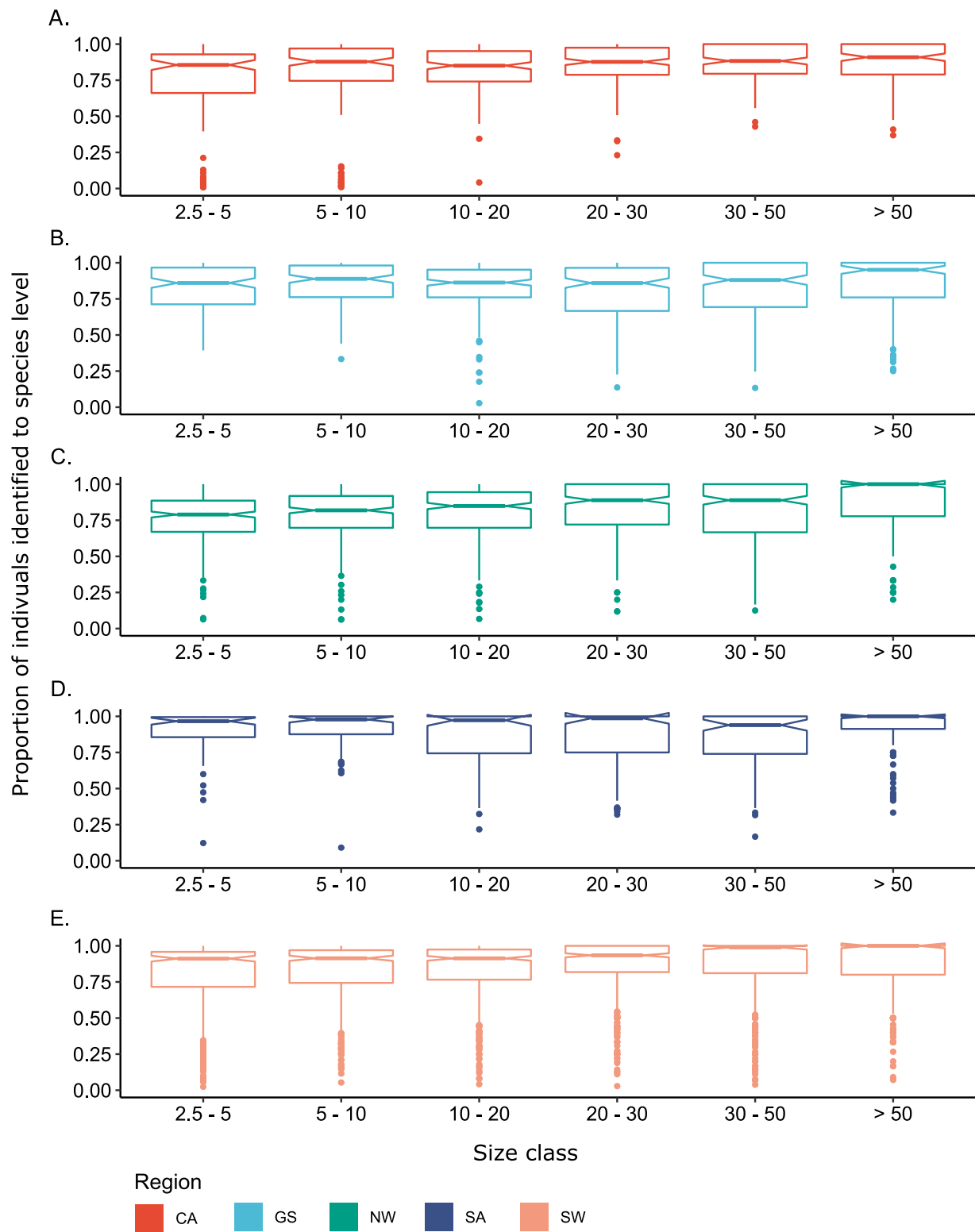
Extended Data Fig. 2 | The mean maximum diameter of hyperdominant tree species across size classes and regions. The mean maximum diameter of hyperdominant tree species across six size classes and five regions. Error bars represent standard deviations surrounding the mean.



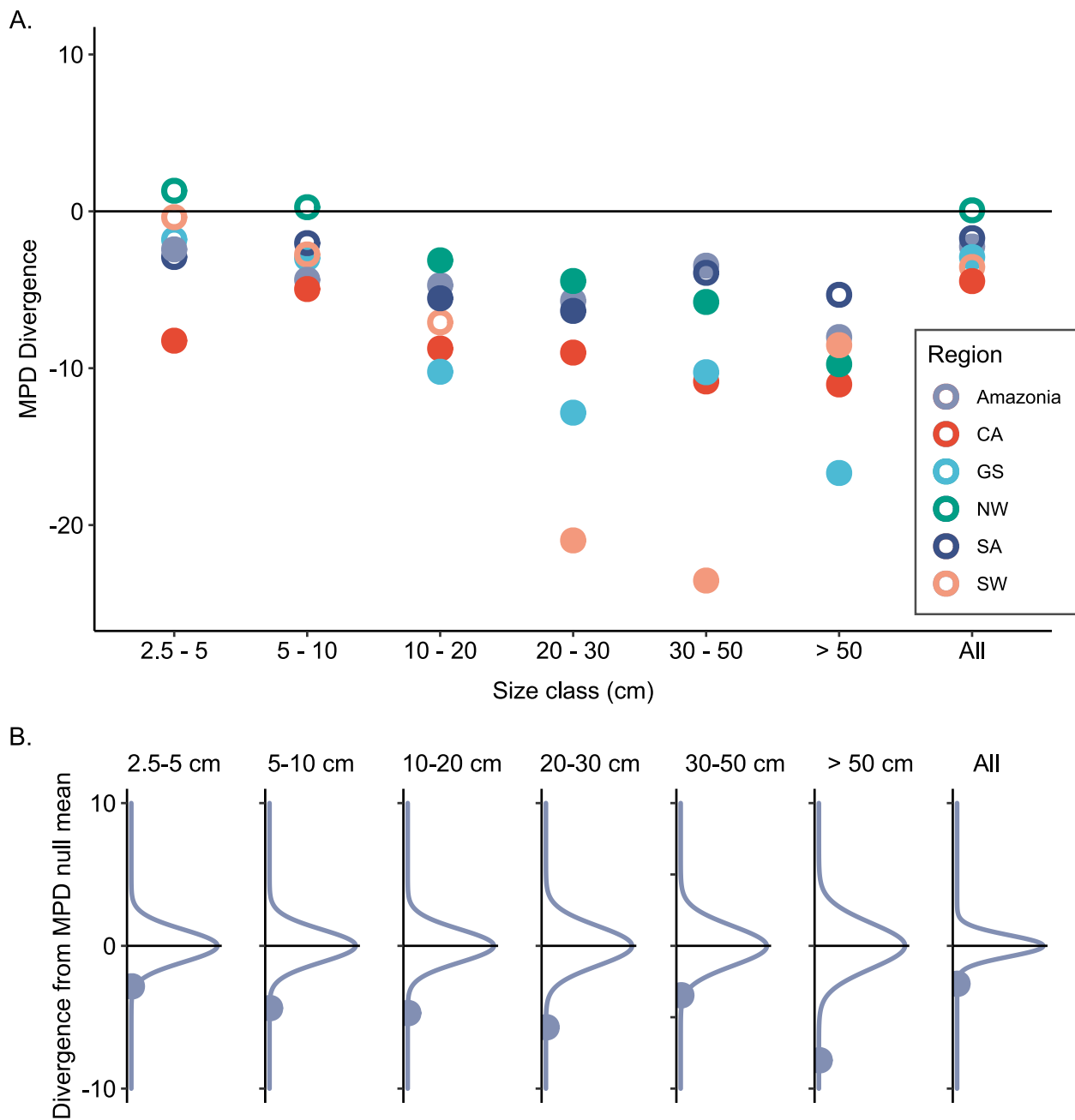
Extended Data Fig. 3 | The relationship between the proportion of observed hyperdominant species per family and the proportion of species richness represented by that family across the six size classes for the basin-wide dataset. The relationship between the proportion of observed hyperdominant species per family and the proportion of species richness represented by that family across the six size classes for the basin-wide dataset. Coloured points represent families that had significantly more or significantly fewer hyperdominant species in a given size than would be expected based on the species richness of the family. All non-significant families have been shaded grey. If the number of hyperdominant species per family was driven purely by the number of species in that family then species would align along the 1:1 line (solid black line).



Extended Data Fig. 4 | The observed mean pairwise phylogenetic distance (MPD) among hyperdominant species and the null distribution of MPD for an equivalent number of species across the six size classes. The observed mean pairwise phylogenetic distance (MPD) among hyperdominant species across the six size classes (points) and the null distribution of MPD for an equivalent number of species (lines). Solid points indicate those hyperdominant communities where the observed MPD was outside two standard deviations from the mean, and therefore considered to be significant. Hollow points indicate hyperdominant communities that had a mean MPD considered to not be statistically significant, that is within 2 standard deviations of the null mean.



Extended Data Fig. 5 | The proportion of morphotypes identified to species level. Box plots describing the proportion of morphotypes identified to species level across the six size classes and five study regions. The middle horizontal line with the boxes shows the median value, the top and bottom hinges of the box denote the 25th and 75th percentiles. Whiskers (vertical lines) denote the interquartile range $\times 1.5$, and notches denote 95% confidence intervals surrounding the median.



Extended Data Fig. 6 | The observed mean pairwise phylogenetic distance (MPD) among hyperdominant species and the null distribution of MPD for an equivalent number of species across the six size classes within Eudicots only. The observed mean pairwise phylogenetic distance (MPD) among hyperdominant species across the six size classes (points) and the null distribution of MPD for an equivalent number of species (lines) within Eudicots only. Solid points indicate those hyperdominant communities where the observed MPD was outside two standard deviations from the mean, and therefore considered to be significant. Hollow points indicate hyperdominant communities that had a mean MPD considered to not be statistically significant, that is within 2 standard deviations of the null mean.

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For all statistical analyses, confirm that the following items are present in the figure legend, table legend, main text, or Methods section.

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Our web collection on [statistics for biologists](#) contains articles on many of the points above.

Software and code

Policy information about [availability of computer code](#)

Data collection no software was used to collect data

Data analysis Data analysis was primarily conducted using the open source programming language R version 4.0.3. The dplyr, tidy, and purrr packages were used for data preparation and the resampling procedures. Packages phylomeasures, phytools, and caper were used to conduct phylogenetic analyses, the vegan package was used to complete the NDMS ordination analysis. Figures were generated using the packages ggplot2, and ggtree. All GIS analyses were conducted using QGIS software version 3.14.1.

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Data

Policy information about [availability of data](#)

All manuscripts must include a [data availability statement](#). This statement should provide the following information, where applicable:

- Accession codes, unique identifiers, or web links for publicly available datasets
- A list of figures that have associated raw data
- A description of any restrictions on data availability

The datasets generated and analysed within this study are owned/managed by many different co-authors. Data are available from the corresponding author on reasonable request and with permission of relevant data owners.

Field-specific reporting

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Life sciences Behavioural & social sciences Ecological, evolutionary & environmental sciences

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Ecological, evolutionary & environmental sciences study design

All studies must disclose on these points even when the disclosure is negative.

Study description	We assembled a dataset of floristic inventory plots. Based on individual diameter measurements and species level identifications, we implement a spatially-stratified resampling approach to estimate basin-wide relative abundances for all tree species across six diameter size classes from the understory (2.5 – 5 cm) to the forest canopy (> 50 cm). We used this dataset to understand patterns of dominance across forest strata (six diameter size classes) and five geographically defined regions.
Research sample	The sample consisted of 1240 floristic inventory plots distributed across lowland Amazonia, each plot contained individual diameter measurements and species level identifications for woody plants >2.5 cm in diameter. The sample was used to represent the entire Amazonian tree flora.
Sampling strategy	We used as many inventory plots as were available across the Amazon basin. Because the plots are not distributed evenly across the basin and because plots varied in size we used a spatially-stratified bootstrap resampling approach to ensure the Amazonian flora was sampled as evenly as possible. This approach is described in detail in the methods text, but briefly consisted of repeatedly sampling a standard number of individuals from a standard number of plots from 10 broadly equivalent subregions across the basin.
Data collection	Data was collected by coauthors. Collections consisted of standardized floristic inventory plots, where all individual trees had their diameter measured and identified to the highest possible taxonomic resolution.
Timing and spatial scale	Data was collected by coauthors over from the late 1980's to present. The spatial scale is the entire Amazon (figure 1)
Data exclusions	All individual that could not be identified to species level were excluded from all analysis. These exclusions are discussed in depth in the methods.
Reproducibility	Data consist of observations and not experiments, therefore it was not relevant to reproduce findings. Re sampling procedures and null model testing ensured robustness of results.
Randomization	Samples groups were defined by geographical regions and sub regions that are explicitly defined. Resampling procedures was done randomly.
Blinding	not relevant to this observational study design.
Did the study involve field work?	<input checked="" type="checkbox"/> Yes <input type="checkbox"/> No

Field work, collection and transport

Field conditions	Fieldwork work was conducted across lowland Amazonian rainforest, climatically defined as <1000 m elevation, >1300 mm annual precipitation and >70% tree cover.
Location	Inventory plots were located across Amazonia (figure 1), coordinates of individual plots are given in the additional supplementary table.
Access & import/export	Where necessary permits were obtained to install vegetation plots and export botanical samples.
Disturbance	Disturbance was kept to an minimum while plot installation took place.

Reporting for specific materials, systems and methods

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Materials & experimental systems

n/a	Included in the study
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<input checked="" type="checkbox"/>	<input type="checkbox"/> Eukaryotic cell lines
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