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TITLE: Amazon tree dominance across forest strata

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Abstract

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 small number are common across the region. Indeed, just 227 “hyperdominant” species account for more than 50% of all individuals > 10 cm dbh. 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 unique 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. These results suggest that achieving hyperdominance over large geographic regions has been much more challenging for canopy and emergent tree species than for understorey species. Our results demonstrate that it is essential to consider all forest strata in order 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.

Main text

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 limited[6]. Confronted with such overwhelming diversity, the challenge of monitoring a few hundred hyperdominant species (i.e. those species that together account for 50% of individuals across Amazonia[7]) 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 (e.g. carbon storage and cycling[10]) and may serve as an effective proxy for general biodiversity patterns[11].

Existing studies of Amazonian hyperdominance and regional-scale dominance have been limited by excluding small-stemmed individuals (<10 cm 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-Amazon 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 (e.g. 10-20 cm diameter). The power-law relationship between stem density and diameter means that small-stemmed individuals (e.g. < 20 cm) are at least an order of magnitude more abundant than larger individuals (e.g. > 50 cm)[25]. This skewed understanding of dominance is highlighted by the difference between lists of hyperdominant species assembled using biomass rather than abundance[10]. This disparity suggests that a more nuanced approach that measures dominance separately across forest strata is required.

Based on 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 (e.g. 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 turnover[28]. 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 by juveniles of larger tree species[26].

We know that some taxonomic tree clades contain many hyperdominant species[7], and that genus-level abundance has a significant phylogenetic signal[29], 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 Amazonia[30], and those genera able to occupy canopy and emergent strata are concentrated in specific lineages (e.g. families or orders) that are primarily located within a few deep clades (e.g. 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 location[31]. 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 timescales[34]. 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 equivalent species in other locations. Secondly, understory species are often locally abundant and frequently have fast generation times[35]. Over evolutionary timescales these high abundances and fast generation times may be likely to increase diversification among locally-restricted understory species[36]. 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 (e.g. taller denser canopy in Guiana shield vs 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 1240 floristic inventory plots distributed across lowland Amazonia, which include stems as small as 2.5 cm (Figure 1). 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). Using this dataset, we identify those species dominating different strata of Amazonian forests and ask: Q1. Is hyperdominance a constant phenomenon across Amazonian tree strata? and Q2. 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 Q.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 (i.e. together account for 50% of individuals) varies across size classes and regions from 3 – 12 % (Figure 2A). At the basin-wide Amazonian scale, the proportion of species that qualify as hyperdominant in our dataset (~ 4%) 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 (Figure 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 (i.e. a lower proportion of species are required to account for 50% of individuals). In particular, the 10 – 20 cm size class consistently displays the strongest dominance patterns (Figure 2). The two smallest size classes have weaker dominance patterns, perhaps because smaller-stemmed species are more dispersal limited than larger individuals[32], 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 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 region[16].

The proportion of species that qualified as hyperdominant at the regional scale was generally higher than in basin-scale analyses, i.e. dominance patterns are weaker at the regional scale (Figure 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 (e.g. 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 (Figure 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 type[7]. 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 generally[44].

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 (Figure 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 greater than 10 cm in diameter as equivalent completely overlooks the nuanced vertical stratification of tropical forests. Moreover, even though 10 cm diameter cutoff protocols are well-suited to monitor carbon fluxes[3], 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 (Figure 4 panel A). 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 emphasising 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, i.e. hyperdominant species clearly form distinct regional groups across the first 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 understory[26]. Instead, we find that across all regions, tree species that dominate forest understory tree communities are compositionally distinct from those that dominate the canopy, i.e. in all regions hyperdominant species form a distinct compositional gradient across strata, as reflected by the second NMDS axis (Figure 4). Indeed, there is no difference in potential maximum size among understory dominant species from different regions (Figure S.2).

At the family level, there is a clear positive relationship between the number of hyperdominant species and total species richness per family (Figure S3). 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 based on 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 overrepresented in terms of hyperdominant species in only smaller (e.g. Violaceae and Siparunaceae) or larger size classes (e.g. Moraceae). Alternatively, commonly occurring tree families including Rubiaceae and Lauraceae have consistently fewer hyperdominant species than we would expect based on 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 overrepresented, and account for more than 30% of hyperdominant species.

Phylogenetic structure of hyperdominance across Amazonian tree strata

Our phylogenetic analyses demonstrate that while many lineages contain hyperdominant species (Figure 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 (Figure 6).

We find overall support for our prediction that hyperdominant in larger size classes tend to be concentrated in a few closely related lineages, for example 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 (Figures 6 and S4), 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 (Figure 4 panel B). 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 lineages[34].

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 (e.g. hydraulic traits)[53], appear to be particularly affected by drought[54], and play a crucial role in Amazonian forest carbon storage and cycling[10]. 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 (Figure 6). This dispersed phylogenetic pattern is largely due to understory hyperdominants occurring across the major angiosperm clades (Figure S.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 recognised by previous studies of large stem (>10 cm) dominance[7,12,13].

Our phylogenetic compositional analysis also supports our hypothesis that within understory strata, hyperdominant species from different regions are distantly related (Figure 4 panel B).

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 others[55]. 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 capitalise 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 in order to extract products such as fruits, nuts or building materials[56,57]. Here, we show that many of these “domesticated” hyperdominants (e.g. *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 (e.g. *Bertholletia excelsa*) were also managed during pre-Columbian times[58]. 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, paleoecological 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.

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Author Contribution

FCD and CB conceived the study. FCD, GPA and CB designed the study with input from FC, GA, OLP, and HtS. FCD and JBS performed the analysis with input from CB, GPA, GA, OLP, AD, FCdS and KD. FCD wrote the manuscript with input from CB, FC, GA, OLP, AD, MJM, GPA and HtS. Initials refer to the first 14 authors and the last author. All other coauthors contributed data and had the opportunity to comment on the manuscript.

Data availability

The datasets generated and/or analysed within this study are available from the corresponding author on reasonable request and with permission of relevant data owners.

Code availability

All custom written analytical code used in this study are available online (https://github.com/FreddieDraper/RedGentry)

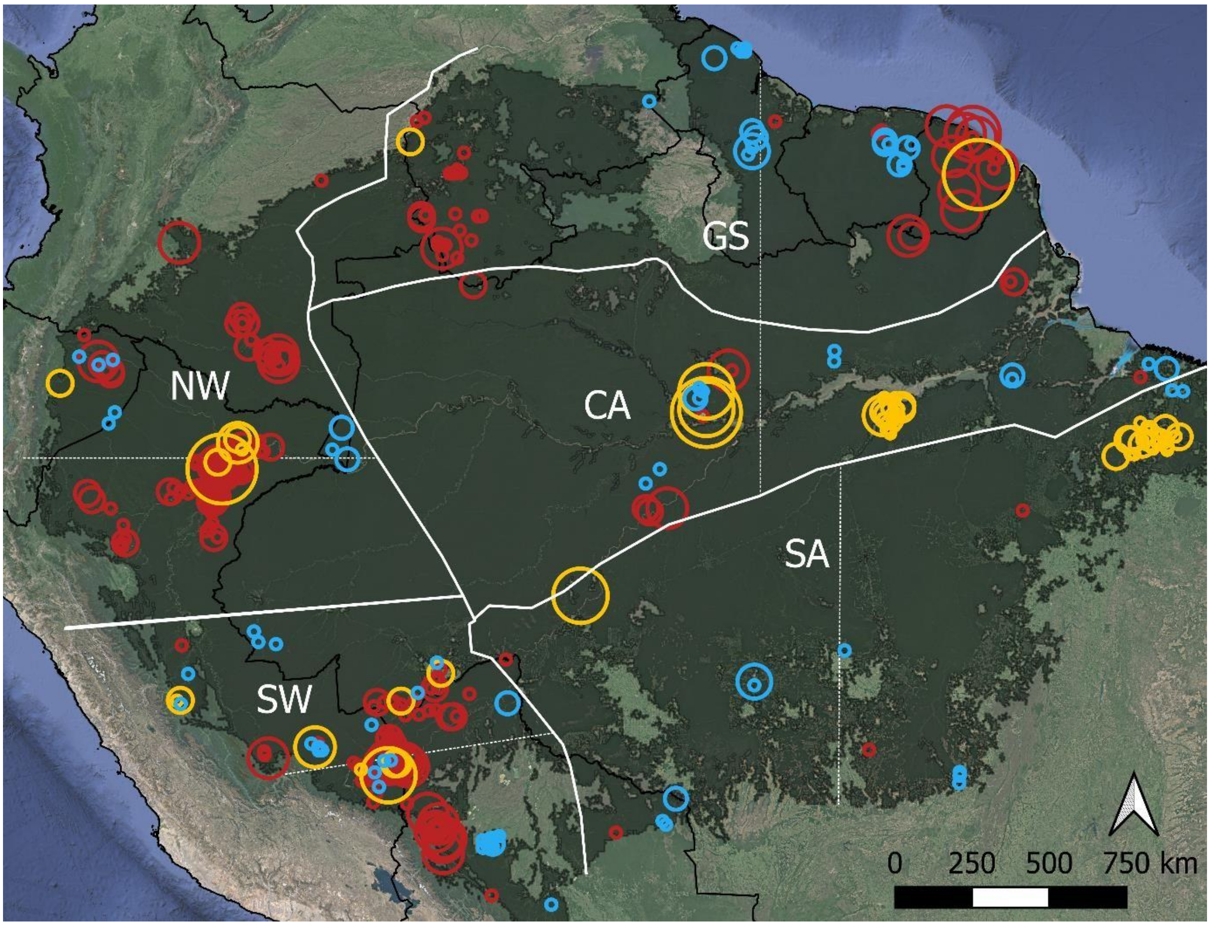

Figure 1. Map of study area and 1240 floristic inventory plots, represented by coloured points. Point size corresponds to number of plots at a given location (range 1 - 40 plots). Point colour refers to the plot size and diameter cut-off: 1. Red points: small plots < 1 ha and stems ≥ 2.5 cm; 2. Blue points: large plots > 1ha 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 10 sampling zones. Sampling regions have been labelled as follows: Northwest Amazonia (NW); Southwest Amazonia (SW); Southern Amazonia (SA); Central Amazonia (CA); Guiana Shield (GS). The shaded area shows the

area defined as Amazonia based on: 1. Annual precipitation > 1300 mm, 2. Elevation < 1000 m (above sea level), and 3. Forest cover > 70%.

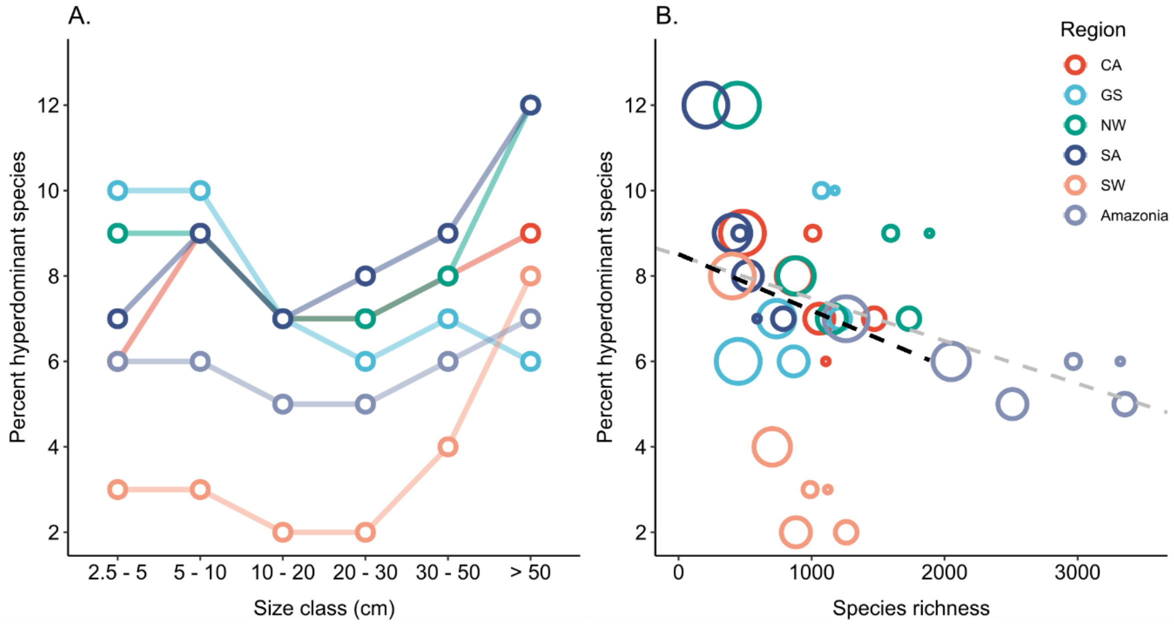

Figure 2. The proportion of species that are hyperdominant (i.e. together account for 50% of individuals) within six size classes across the five Amazonian regions and the basin-wide ‘Amazonia’ dataset (Panel A). The relationship between the proportion of species that are hyperdominant and total species richness across six size classes (indicated by symbol size) across the five Amazonian regions and the basin-wide ‘Amazonia’ dataset (Panel B). Dashed lines show linear regressions based on the five regional data sets (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 both panels, a lower proportion of hyperdominant species indicates stronger patterns of dominance. Sampling regions as indicated in Figure 1 are: Northwest Amazonia (NW); Southwest Amazonia (SW); Southern Amazonia (SA); Central Amazonia (CA); Guiana Shield (GS).

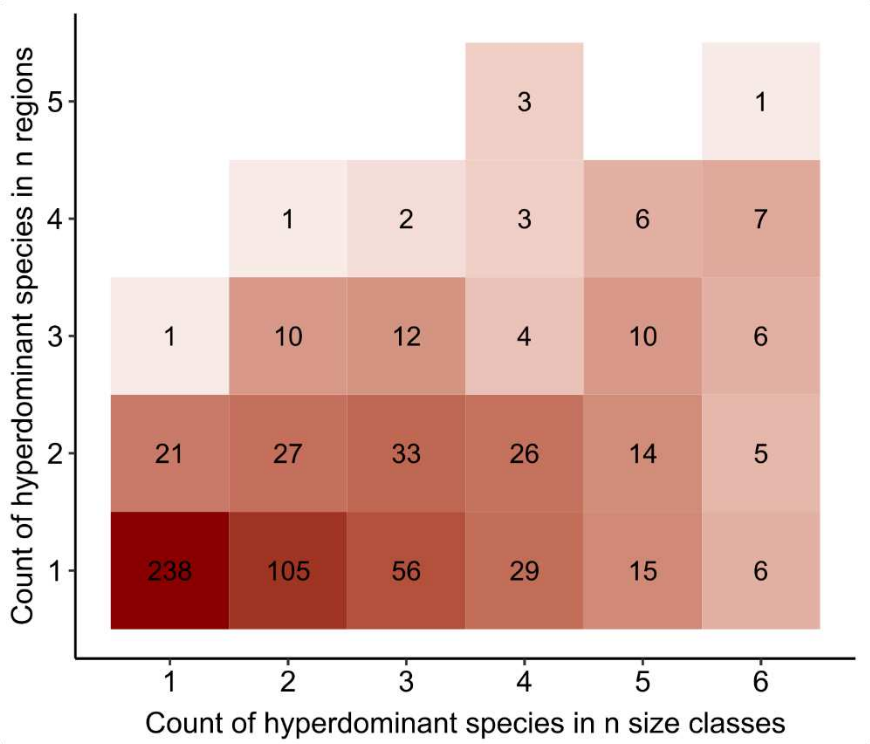

Figure 3. Two-dimensional histogram showing the number of species that are hyperdominant in one to six size classes and across one to five regions. Regions and size classes follow the same definitions as in figure 2.

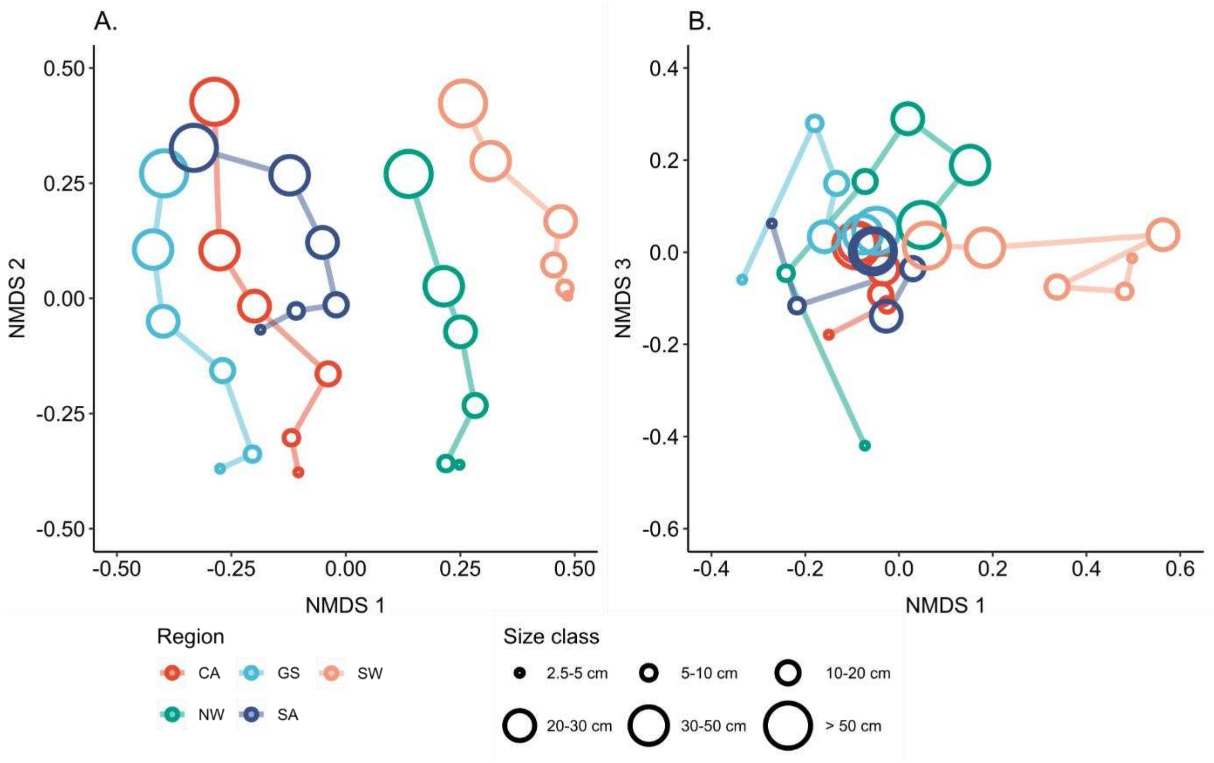

Figure 4. NMDS ordinations showing similarity in composition of hyperdominant species in terms of: A.) Taxonomic species similarity (Jaccard index) and B) deep-node-weighted phylogenetic similarity (community level mean pairwise phylogenetic distance). Sampling regions have been labelled as follows: Northwest Amazonia (NW); Southwest Amazonia (SW); Southern Amazonia (SA); Central Amazonia (CA); Guiana Shield (GS).

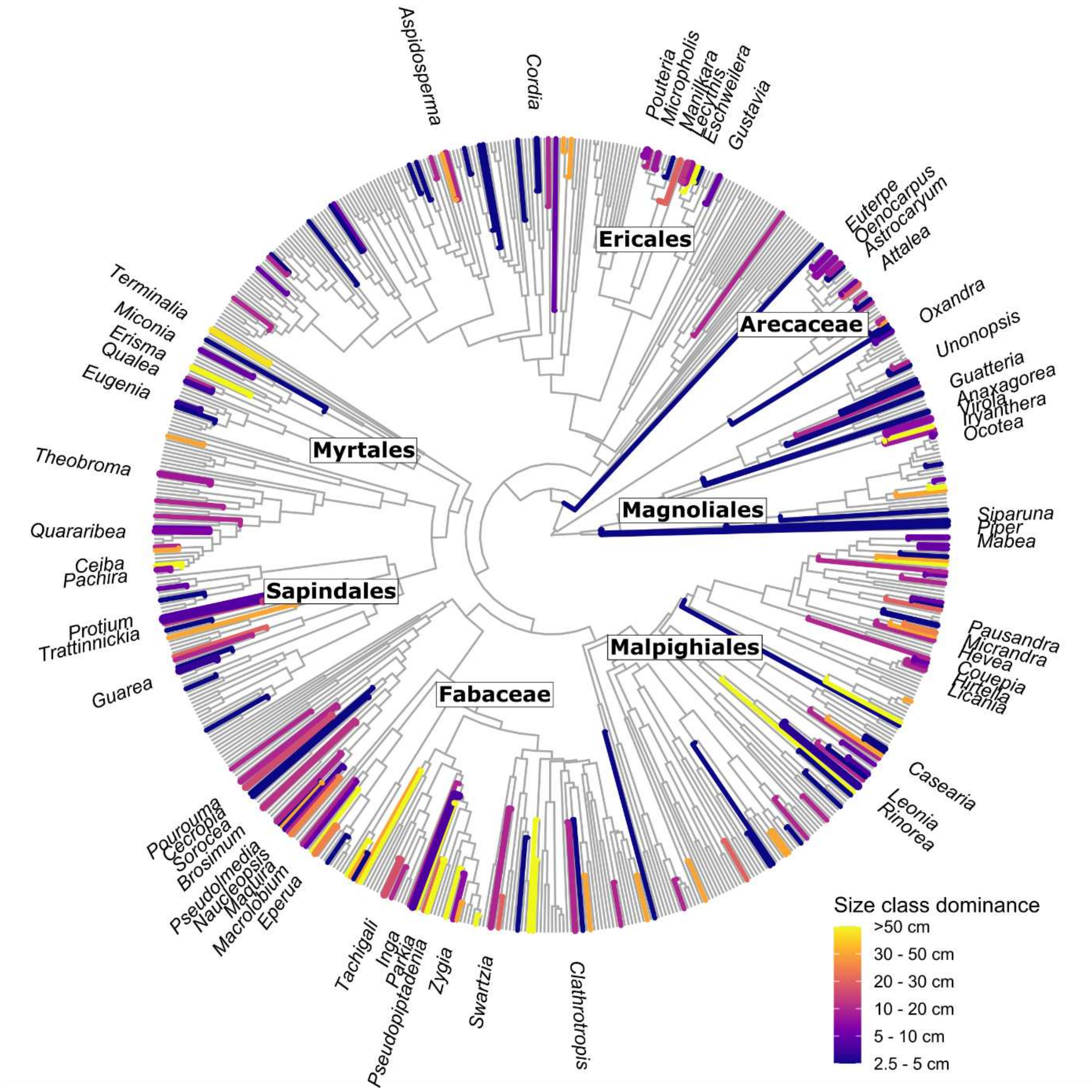

Figure 5. Hyperdominant species mapped onto a genus level Amazonian tree phylogeny. All genera with one or more hyperdominant species have been highlighted. Genera with three or more hyperdominant species have been labelled. Colour corresponds to the size class within which species belonging to that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

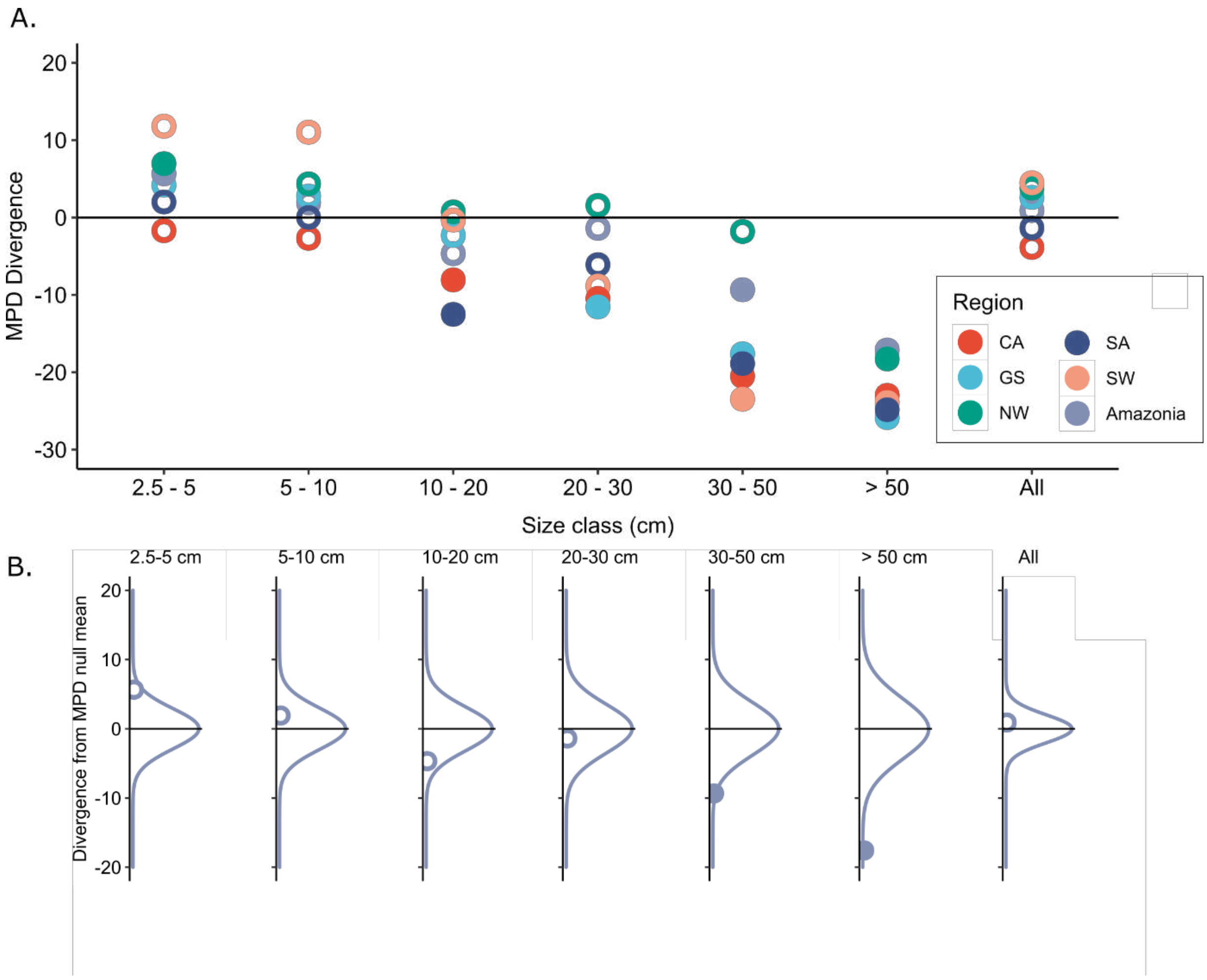

Figure 6. Divergence of mean pairwise phylogenetic distance (MPD) from null models for each hyperdominant community (Panel A). Positive numbers indicate greater MPD than expected by chance (i.e. species are more distantly related than expected by chance.). Negative numbers indicate lower MPD than expected by chance (i.e. 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. Panel B shows the null distributions and observed MPD for entire Amazonia hyperdominant communities. Regional null distributions are provided in Figure S4.

Methods

Floristic data

Floristic data came from 1240 forest inventory plots, distributed across the Amazon basin (Fig. 1). The plot data fall into two broad categories: Firstly, the RedGentry network consisted of 1027 small forest plots (typically 0.1ha but ranging from 0.04- 0.25 ha) within which all stems with a diameter at 1.3 m in height (dbh) greater than 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 greater than 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 10 transects of 2 X 50 m arranged systematically around a single transect baseline following the 'Gentry protocol'[46]. However, 307 plots were subplots nested in within larger 1 ha inventory plots (Fig. 1). The majority of these nested 0.1 ha plots were part of the PPBio network.

Taxonomic standardization

It was not possible to standardise 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, Figure S.7) and were phylogenetically biased, i.e. 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 (TNRS) using the R package taxize[59]. Any species that were not recognised 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[62]. 39 of these were confirmed to be illegitimate Amazonian species because they have ranges either outside of our region (i.e. on another continent). A further 579 species that were described as either 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 likely 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. The majority of these inclusions were small stemmed species that had previously been excluded for being shrubs or treelets. We considered these definitions to be subjective. 37 of these included species 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 layer[63], 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 SRTM digital elevation model[64], lowlands were considered to be land area below 1000m elevation following Cardoso *et al.* (2017)[60]. 3. Precipitation was estimated using the CHIRPS annual mean rainfall data[65], and a minimum mean annual precipitation value of 1300 mm year^{-1} was used to define moist forests following Cardoso et al. (2017)[60]. 4. Tree cover was estimated using the 2010 global forest cover map[66], 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 software[67].

Spatial standardisation

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 done[7]. 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[68–70].

This approach consisted of the following steps:

1.) Greater Amazonia (as defined above) was divided into 5 regions roughly following previously defined boundaries[7,49]. Each region was then split roughly in half to generate 10 total sampling zones that were broadly similar in area (Area varied from 210,000 to 1081,000 km^2). Each sampling zone contained at least 40 individual plots (at least 20 small plots and at least 10 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 cm, 5 – 10 cm, 10 – 20 cm, 20 – 30 cm, 30 – 50 cm, >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.) 20 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 standardised samples from each plot were then assembled into a single species by plot matrix.

6.) Steps 2 and 3 were repeated 10^6 times, generating 10^6 estimates of abundance for each species across the basin.

7.) The mean and standard deviation of abundance for each species was calculated across the 10^6 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 two-seven 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[71].

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 mean pairwise phylogenetic distance (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 [51.72]. 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 pool[72]. 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[72–74].

MPD is known to be influenced by the extent to which species are divided among the three major angiosperm clades (Magnoliids, Monocots and Eudicots)[75]. 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 (Figure S.5). 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, e.g. 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[76].

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 phylo-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 diversity[50]. The second metric of phylogenetic beta diversity that we used was the generalized version the unifrac method[77], calculated with the R package *GUniFrac*[78]. 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 unifrac 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 communities[50]. The tip-weighted unifrac 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 dimensionally of this multivariate data and visualize the taxonomic and phylogenetic similarities among hyperdominant communities we used Non-metric multidimensional scaling (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[76].

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