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Research article

Local hydrological conditions influence tree diversity and composition across the Amazon basin

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Tree diversity and composition in Amazonia are known to be strongly determined by the water supplied by precipitation. Nevertheless, within the same climatic regime, water availability is modulated by local topography and soil characteristics (hereafter referred to as local hydrological conditions), varying from saturated and poorly drained to well-drained and potentially dry areas. While these conditions may be expected to influence species distribution, the impacts of local hydrological conditions on tree diversity and composition remain poorly understood at the whole Amazon basin scale. Using a dataset of 443 1-ha non-flooded forest plots distributed across the basin, we investigate how local hydrological conditions influence 1) tree alpha diversity, 2) the community-weighted wood density mean (CWM-wd) – a proxy for hydraulic resistance and 3) tree species composition. We find that the effect of local hydrological conditions on tree diversity depends on climate, being more evident in wetter forests, where diversity increases towards locations with well-drained soils. CWM-wd increased towards better drained soils in Southern and Western Amazonia. Tree species composition changed along local soil hydrological gradients in Central-Eastern, Western and Southern Amazonia, and those changes were correlated with changes in the mean wood density of plots. Our results suggest that local hydrological gradients filter species, influencing the diversity and composition of Amazonian forests. Overall, this study shows that the effect of local hydrological conditions is pervasive, extending over wide Amazonian regions, and reinforces the importance of accounting for local topography and hydrology to better understand the likely response and resilience of forests to increased frequency of extreme climate events and rising temperatures.

Keywords: Amazon basin, HAND, species composition, tree diversity, wood density

Introduction

Large-scale patterns of floristic diversity and composition across tropical forests have been well explained by annual precipitation and seasonality (Clinebell et al. 1995, ter Steege et al. 2003, Stropp et al. 2009, Esquivel-Muelbert et al. 2017), besides soil fertility (ter Steege et al. 2006) and neutral processes (Condit et al. 2002, Tuomisto et al. 2003, Coronado et al. 2009, Emilio et al. 2010). Nevertheless, within any given climate, at local scale, water availability for plants is modulated by local topographic and edaphic conditions, giving rise to the local hydrological conditions (Daws et al. 2002, Moeslund et al. 2013, Costa et al. 2022), which in turn affect variations in plant species diversity and composition (Svenning 2001, ter Steege et al. 2003, Jirka et al. 2007, Schietti et al. 2013, Moulatlet et al. 2014, Zuleta et al. 2020). In Amazonia, where the world's largest tropical forest is located, we now understand how local hydrological conditions can modulate the effects of droughts (Sousa et al. 2020, Esteban et al. 2021, Costa et al. 2022), with locally wetter areas constituting potential refuges for diversity (McLaughlin et al. 2017). Global warming is leading to an increase in the frequency and intensity of droughts (Marengo et al. 2018). As a consequence, Amazonian forests are experiencing a reduction in water availability for plants (Pascolini-Campbell et al. 2021), and higher tree mortality and biomass loss (Phillips et al. 2009, Brienen et al. 2015, Berenguer et al. 2021). Therefore, it is crucial to assess the influence of local hydrological conditions on forest diversity, and on taxonomic and functional composition.

The local hydrological conditions of non-flooded forests are mainly determined by elevation (relief), terrain aspect and slope (Moeslund et al. 2013). These characteristics control the land's drainage capacity, the local redistribution of precipitation runoff and the vertical distance to groundwater (Rennó et al. 2008, Nobre et al. 2011, Moeslund et al. 2013). Along a topographic profile, lower areas are moist and often water-saturated, and have soils with low drainage capacity due to the proximity to the water table (Rennó et al. 2008, Nobre et al. 2011, Moeslund et al. 2013). In contrast, the upper areas such as hilltops are typically drier and have well-drained soils due to increasing distance to the water table (Rennó et al. 2008, Nobre et al. 2011, Moeslund et al. 2013, Fan et al. 2017). Besides topography, soil characteristics – especially soil texture – also affect the water availability for plants by regulating water infiltration and the capillary rise (Hacke et al. 2000, Fan et al. 2017). Thus, soil characteristics and topography together determine the local hydrological conditions, and consequently the water availability for plants at the local scale. However, the effect of local hydrological conditions on plants across large regions should also depend on climate, as the variation in precipitation determines how much water enters the system. Therefore, we can expect an interaction between local hydrological conditions and precipitation affecting the plant community properties (Blanchard et al. 2019, Muscarella et al. 2019).

The local hydrological conditions can be expected to affect species richness through physiological or forest dynamics processes. Considering that water deficit imposes a physiological limitation to many plant species (Nepstad et al. 2007, Meir et al. 2015, Giardina et al. 2018), drier local conditions given by the combination of dry climate and deep water tables at high topographic positions should limit the number of species able to colonize and survive. Conversely, even within dry climates, low topographic positions with shallow water tables should provide higher soil moisture, alleviating seasonal water deficits and promoting higher richness (Segura et al. 2003). This scenario should shift under wet climates, where shallow water tables lead to seasonal or permanent waterlogging and anoxia, stressful conditions that can reduce the number of species (Féret and Asner 2014). Shallow water tables also limit root development (Fan et al. 2017), and shallow rooting systems are more prone to uprooting, increasing tree mortality rates (Gale and Hall 2001, Ferry et al. 2010, Toledo et al. 2011). Higher mortality rates could lead to increased richness if the disturbance is moderate or decreased richness if it is intense (Connell

1978, Bongers et al. 2009). This expectation could be reversed under dry climates, where waterlogging is less common, and tree mortality tends to be higher in the upper topographic positions exposed to wind (Segura et al. 2003).

A functional ecology approach provides insights into environmental filtering along environmental gradients through the evaluation of morpho-physio-phenological traits that affect an individual's growth, reproduction and survival (Violle et al. 2007). Earlier studies of non-flooded Amazonian forests at local scales indicate that local hydrological conditions filter functional traits such as wood density (Ferry et al. 2010, Cosme et al. 2017); hydraulic resistance (Oliveira et al. 2019, Fontes et al. 2020, Garcia et al. 2022); leaf traits – e.g. specific leaf area (SLA), leaf nitrogen concentration, leaf size, leaf mass per area, leaf dry matter content, leaf thickness and chlorophyll content (Kraft et al. 2008, Cosme et al. 2017, Schmitt et al. 2020); seed mass (Kraft et al. 2008); and canopy chemical traits (Asner et al. 2015). However, no study has so far determined if hydrological filtering of traits is a widespread phenomenon over the Amazon basin and how it interacts with other environmental factors. A key trait to understand plant hydraulics is wood density, given that higher wood density is associated to higher xylem resistance to embolism (Hacke et al. 2001, Santiago et al. 2004, Hoeber et al. 2014), a trait that is selected in drier climates (Chave et al. 2006, Ibanez et al. 2017, Blanchard et al. 2019) and drier local hydrological conditions (Oliveira et al. 2019). Although other functional traits besides wood density can be relevant to the environmental filtering of species distributions by hydrology, we focused on the trait that tends to have lower intraspecific variation (compared to leaf traits) and broader data coverage.

Filtering of functional traits by the local hydrological conditions can lead to species sorting across hydrological environments, with consequences for species composition and alpha diversity (Valencia et al. 2004, Baldeck et al. 2013, Schietti et al. 2013, Féret and Asner 2014, Moulatlet et al. 2014, Zuleta et al. 2020). This can be evaluated through the correlation between the community average of any trait (e.g. wood density) and the multivariate axes representing species composition (ter Steege et al. 2006). Given that species pools differ among Amazonian regions (ter Steege et al. 2006, 2013) owing to biogeographical and evolutionary causes, it can be expected that the effects of local hydrological conditions on species composition would be detected within regions (as defined by geography and substrate origin in Feldpausch et al. 2011). This is because which species groups are associated with locally wetter or drier conditions along hydrological gradients within each region should depend on which species are present in the region. Furthermore, larger changes in species composition along the gradient of local hydrological conditions may be expected in terrains with ancient well-dissected relief, since these produce stronger hydrological contrast along topography.

The aim of this study was to understand the effects of local hydrological conditions on the properties of tree communities at the Amazon basin scale. We addressed the following specific questions: 1) How do local hydrological conditions influence tree alpha diversity? 2) How do local hydrological conditions influence wood density? 3) How do local hydrological conditions affect tree species compositional change along environmental gradients? The general hypothesis is that local hydrological conditions will influence the environmental filtering of species distributions, thus generating spatial patterns of alpha diversity, mean wood density and species composition. Specifically, we predict that:

1) Tree alpha diversity will decrease in low topographic positions (due to soil–water excess) in climatically wetter forests, but increase in those positions (due to higher local moisture) in climatically drier forests.
2) Forests growing on soils with greater drainage capacity and lower water availability will have higher wood density as it provides higher hydraulic resistance against droughts.
3) Species composition will be sorted along gradients of local hydrological conditions within regions, following changes in community-weighted means of wood density (CWM-wd).

Material and methods

Vegetation data

We used the Amazon Tree Diversity Network (ATDN) dataset, with plots distributed throughout the Amazon basin (as delimited by Mayorga et al. 2012) (Fig. 1). Our analyses were restricted to 1-ha lowland terra-firme forest plots below 500 a.s.l. (excluding plots on white sand and inundated forests) and to individuals with a diameter $\geq$ 10 cm, excluding all lianas. Plots varied in dimensions and shapes, with most being square or rectangular 1 ha, while 11.7% were 250 $\times$ 40 m and following altitudinal contours (design described in Magnusson et al. 2005). In addition, we considered only plots with at least 80% of individuals identified to species level. As species identification was done by different taxonomists, we excluded 18 634 individuals (8.45% of the total number of individuals; mean = 42, min = 0, max = 173 individuals per plot) that were not identified to the species level to avoid confusion with morphospecies synonymy. This introduced no bias in the analyses, as there was no association between the proportion of morphospecies per plot with the main variables of interest (i.e. local hydrological conditions; Supporting information). By including only those individuals identified at the species level, more robust patterns of alpha diversity and composition are expected (Pos et al. 2014). We also excluded plots with georeferencing problems, such as those with coordinates displaced from terra-firme towards rivers or lakes. Finally, we excluded 18 plots from areas without height above nearest drainage (HAND) data. Thus, we carried out the analyses using 443 plots, which total 210 801 individuals of 3527 species, distributed in 619 genera and 104 families.

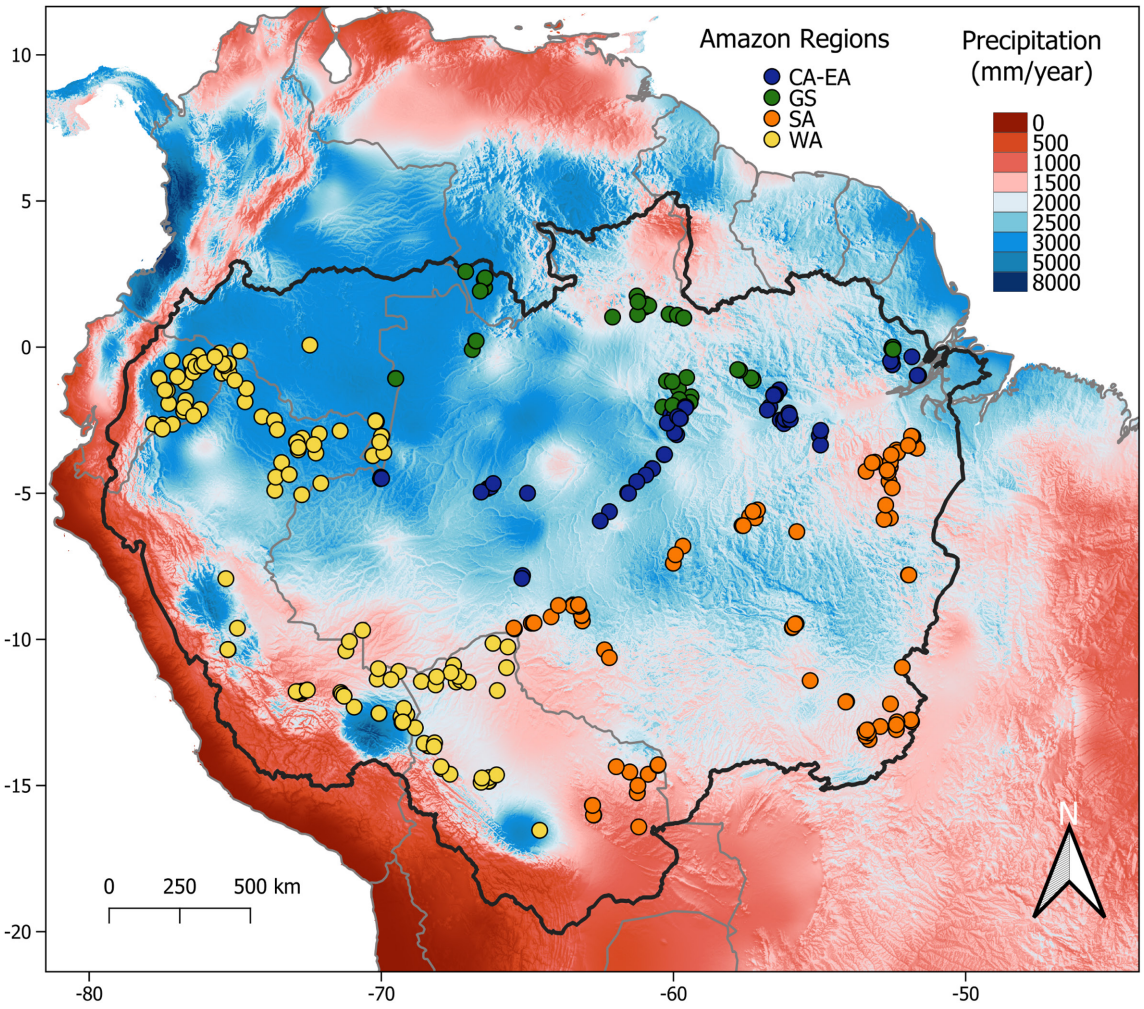

Figure 1. Location of 443 1-ha plots used in this study. The map shows the distribution of plots (coloured dots) across the Amazon basin. The limits of the Amazon basin (black outline) were defined according to Mayorga et al. (2012). Background information shows the annual precipitation layer obtained from CHELSA ver. 1.2 (1979–2013, 30 arcsec of resolution, <http://chelsa-climate.org/> [Karger et al. 2018]). Dot colours indicate the four geomorphological regions (from Feldpausch et al. 2011): Central–East (blue, CA–EA = 122 plots), Guiana Shield (green, GS = 52 plots), South (red, SA = 102 plots) and West (yellow, WA = 167 plots).

Vegetation metrics

Alpha diversity

We quantified species, genus and family diversities for each plot using Fisher's alpha (logarithmic series model), which is based on the number of individuals and species in each plot and is relatively insensitive to the difference in the number of individuals among plots (Fisher et al. 1943).

Wood density

The wood density of each plot was represented by the CWM of the species present in that plot. We obtained wood density data from the global wood density database (Chave et al. 2009, Zanne et al. 2009). When the wood density of a species was not available, we used the mean wood density at the genus, family or plot level (Baker et al. 2004, Rozendaal et al. 2020). We used genus level wood density data for 1381 species out of the 2417 species, and family and plot level data for 170 and 10 species, respectively. Then, we calculated the CWM-wd, which is the estimated mean wood density of the individuals in each plot (Garnier et al. 2004).

Species composition

We excluded species occurring in fewer than two plots to reduce the potential noise generated by the inclusion of rare species in the analysis (Cao et al. 2001, McCune and Grace 2002). The final number of species and individuals in the full dataset for species composition analyses was 241 and 206 459, respectively. This database was the same used in the analyses of wood density.

We first tested if the expectation of species composition differences among regions hold true for the specific dataset used here. This was implemented with a PERMANOVA (Anderson 2001), where the response variable was the matrix of Bray–Curtis dissimilarities in species abundances among plots, and the Amazon regions the independent variables.

This method tests whether plots from the same region are floristically more similar to each other than would be expected by chance. The differences among regions were confirmed (PERMANOVA: $p = 001$, $R^2 = 0.10$).

Given the confirmed differences among regions, we ran one non-metric multidimensional scaling (NMDS) ordination within each of the four Amazonian regions, and the resulting axes were the response variables representing species composition in the generalised least square (GLS) regression analyses (see Data analyses section). Ordinations were run in two dimensions to keep stress close to 0.2 (McCune and Grace 2002), and were based on Bray–Curtis distance matrices calculated over quantitative data – species abundances – standardized by plot (i.e. the abundance of each species divided by the total abundance in each plot). Ordinations based on quantitative data mostly capture the patterns of more abundant species, which tend to have larger contributions to the difference or similarity between plots (McCune and Grace 2002). The variation of the original data captured by the NMDS axes was obtained by regression of the matrix of original floristic distances among samples calculated with the same dissimilarity index used in the ordination method, and the matrix of distances among samples obtained from the final NMDS solution (McCune and Grace 2002).

Environmental variables

The environmental variables considered in the present study were proxies for the hydrological conditions at the local and at the regional scales, and for the soil fertility.

Local hydrological conditions were represented by the HAND, which captures the influence of topography on soil hydrology (Rennó et al. 2008, Nobre et al. 2011), and by one variable capturing the water retention capacity of the soil–soil texture (Hacke et al. 2000). HAND is calculated using information from digital elevation models (DEM) and drainage networks by normalizing the topography (elevation) as a function of the relative height over the nearest drainage. This variable is directly related to the gravitational potential of soil water and, therefore, its values are correlated with the water table depth, providing a representation of the local hydrological conditions. High HAND values mean high drainage potential; low HAND values indicate proximity to the water table, where water accumulates and may create waterlogged conditions (Nobre et al. 2011). We extracted HAND data from layers elaborated by Banon and Novo (2018) with ~30 × 30 m spatial resolution (available at: <www.dsr.inpe.br/amazondrainage/home.php?content=hand>). To capture hydrological variability within each 1 ha plot, we reprojected the layers to ~100 × 100 m resolution using bilinear interpolation, which assigns the output cell value by taking the weighted average of the neighbouring cells. This method is recommended to assign raster values to points in continuous datasets without distinct boundaries. The HAND layer was based on Strahler's sixth order drainages, as it provides more stable information about the drainage capacity and the water condition of the environment across varying geomorphologies (Banon and Novo 2018). Finally, for all analysis, HAND values were log-transformed (base 2) to meet normality assumptions. The soil texture was represented by the percentages of sand or clay. We extracted soil texture data for a depth of 15 cm for each plot from the SoilGrids platform (Hengl et al. 2017) with ~250 × 250 m spatial resolution.

Hydrological conditions at the regional scale were represented by the historical average of the maximum cumulative water deficit (MCWD) for each plot. MCWD is the measure of the annual water deficit that considers both the duration and the intensity of the dry season (Aragão et al. 2007). MCWD represents the most negative value of water deficit (WD), given by the difference between precipitation (P) and evapotranspiration (E) within each year. For each month (n), WD is quantified as:

$$\text{if } WD_{n-1} - E_n + P_n < 0;$$
$$\text{then } WD_n = WD_{n-1} - E_n + P_n;$$
$$\text{else } WD_n = 0.$$

For this calculation, we considered the hydrological year, so the starting point for the calculation was not necessarily the first month of the calendar year, but the wettest month (n − 1) of the first year of the time series, according to Esquivel-Muelbert et al. (2019). The precipitation data were obtained from the TerraClimate platform (Abatzoglou et al. 2018) with ~ 4 × 4 km spatial resolution from 1959 to 2018. We assumed the evapotranspiration to be fixed at 100 mm per month, being an approximation (mean) from soil evapotranspiration obtained in different locations in Amazonia (Aragão et al. 2007).

We estimated soil fertility using soil cation concentration (SCC, i.e. the sum of Mg^{+2}, Ca^{+2} and K^{+1}). SCC is an indicator of soil fertility correlated with the most limiting nutrient in the tropical regions – phosphorus availability (Quesada et al. 2009, Moulatlet et al. 2017, Figueiredo et al. 2018). We obtained SCC values from the layer produced by Zuquim et al. (2019), with ~11 × 11 km spatial resolution, which was reprojected to ~ 5 × 5 km resolution using the bilinear method.

Four Amazonian regions (Central and Eastern Amazonia, Guiana Shield, Southern Amazonia and Western Amazonia), defined by geography and substrate origin in Feldpausch et al. (2011), were used to constrain the analyses of species composition, given their expected effect on the species pool (ter Steege et al. 2013). Central and Eastern Amazonia are characterized by having nutrient-poor soils derived from reworked rocks and late Cretaceous sediments that experienced weathering for more than 20 million years (Irion 1978, Quesada et al. 2010), and the relief is either flat or undulated (Sombroek 2000). The Guiana Shield and Southern Amazonia have weathered, nutrient-poor soils formed on ancient Cretaceous crystalline substrates (Irion 1978, Quesada et al. 2010), and the relief is characterized by hilly dissected lands and rounded hills (Sombroek 2000). Western Amazonia is formed on more recent pre-Andean sediments from the Cretaceous–Tertiary

and Pliocene periods, where large areas dominated by shallow soils that can contribute to the fertility of the underlying soils through the weathering of the source material (Irion 1978, Quesada et al. 2010), the relief is characterized by undulating to rolling land (Sombroek 2000).

Data analyses

We modelled each of the response variables – Fisher's alpha at species, genus and family levels, the CWM-wd of the entire Amazon basin, and the NMDS axes 1 and 2 of the ordinations of species composition for each Amazon region – as a function of the proxies for the hydrological conditions at the local scale (HAND and soil texture) and at the regional scale (MCWD), plus soil fertility (SCC), using GLS models. We also included in the models the interaction between HAND and MCWD, expected to affect the water conditions for plants (Blanchard et al. 2019, Muscarella et al. 2019). Sand or clay were included in alternative GLS models to avoid multicollinearity, and the textural class in the best performing models was retained. We included a term to account for the spatial autocorrelation, specifying the most appropriate autocorrelation structure for each model, selected from the lowest values of the Akaike information criterion (AIC) (Supporting information). We examined the multicollinearity among variables, using the variance inflation factor (VIF) available in the *vif* function of the *car* package (Fox et al. 2021). A VIF greater than 5 is a signal of collinearity (Dormann et al. 2013). In each of our GLS models, all variables had VIF < 4 (Supporting information), indicating that collinearity was unlikely to affect our results. Furthermore, the pairwise correlation among variables was low (rho < 0.31) (Supporting information). We report the partial effects of variables from multiple models, i.e. the effect of a variable when the effects of others are held constant (Allen 1997). To visualize and report the individual or interaction effects of the explanatory variables on the response variables we used partial plots of the significant effects ($p > 0.05$) identified by each GLS model, and the classes were defined based on the standard deviation around the mean of each of these variables. To compare the effect size of the explanatory variables on the response variables, all variables were standardized to have mean of zero and standard deviation of one.

We applied a logarithmic transformation to Fisher's alpha values at the species level to ensure normal distribution of residuals; this transformation was not necessary for genus and family levels. In the models for Fisher's alpha we included an exponential variance structure for MCWD to reduce the effect of heteroscedasticity in the models, i.e. a decrease in residual variance for the response variable (Fisher's alpha) along the explanatory variable (MCWD) (Zuur et al. 2009). The selection of the variance structure was based on the lowest values of AIC (Zuur et al. 2009) (Supporting information).

The models for species composition were run within each Amazonian region, using as response variables the NMDS-1 and NMDS-2 axes of the ordination carried on the plots belonging to each region. We first tested for the correlation between the first two NMDS ordination axes, to determine if both could be used as separate response variables. The independence among axes was confirmed (Supporting information), thus the GLS models including all the factors described above were run for each axis within each region. We conducted another test of the effect of hydrological and soil predictors on species composition by running an ordination based on all plots (following the same standards used before), and modelling the two resulting axes as a function of MCWD, HAND, %Clay and SCC, and including regions in interaction with HAND. This provides an assessment of how general the effects detected in the first approach are. Finally, to determine if species composition and wood density are correlated we performed Spearman's correlation tests between species composition axes (NMDS-1 and NMDS-2) and the CWM-wd of the plots of each region and adjusted probability values with the Bonferroni correction (Armstrong 2014).

All analyses were carried out in R (R ver. 4.0.2). The *nlme* package (Pinheiro et al. 2021) was used for GLS models, the *vegan* package (Oksanen et al. 2020) for NMDS ordinations, the *adonis* function from the *vegan* R package for PERMANOVA and the *corr.test* function from the *psych* package (Revelle 2021) for correlation tests.

Results

Tree alpha diversity

Fisher's alpha at species and genus levels was mainly influenced by maximum climatological water deficit (MCWD) and by the interaction between the HAND and MCWD, whereas at family level it was influenced by MCWD and the soil cation concentration (SCC) (Table 1). MCWD had the largest relative contribution in the models at all taxonomic levels (Table 1, Fig. 2a–c). The Fisher's alpha diversity at all taxonomic levels increased towards wetter forests, with less negative MCWD values (Fig. 3a–c). The partial effect of the interaction between MCWD and HAND (Fig. 3d, e) indicated that in climatically wetter forests (MCWD between -136.7 and −1.60 mm, corresponding approximately to 1–2 dry months in the year, 222 plots) the Fisher's alpha of species and genera were higher in plots with high HAND values, i.e. well-drained areas with deep water tables, such as the plateaus and hilltops (Fig. 3d, e, blue). However, in climatically drier forests (MCWD between −429.6 and −138.0 mm, > 2 dry months, 221 plots), there was a subtle tendency towards greater diversity in sites with low HAND values, i.e. the zones with higher water availability and water table close to the surface, corresponding to bottomlands and riparian forests (Fig. 3d, e, red). Family alpha diversity increased towards forests with higher SCC (Fig. 3f). There was a marginally significant interaction between MCWD and HAND at the family level (Table 1), with a similar trend to that observed at species and genus levels (Supporting information).

Table 1. Standardized coefficients and their respective probabilities, resulting from the generalized least square (GLS) models for tree alpha diversity (i.e. Fisher's alpha (FA) for species: FA-species, FA-genus and FA-family) and the community weighted mean of wood density (CWM-wd) for 443 1-ha plots across the Amazon basin. MCWD – maximum cumulative water deficit, HAND – height above nearest drainage, SCC – soil cation concentration and soil texture (% Clay). ':' = interaction. *, ** and *** indicate significant coefficients with $p < 0.05$, $p < 0.01$ and $p < 0.001$, respectively.

	MCWD	HAND	SCC	%Clay	HAND:MCWD	Region	HAND:Region	R^2
FA-Species	0.495***	0.035	0.097	0.012	0.086*	–	–	0.64
FA-Genus	0.507***	0.06	0.133	0.078	0.107**	–	–	0.63
FA-Family	0.457***	−0.006	0.247**	0.037	0.063	–	–	0.57
CWM-wd	−0.055	0.06	−0.4***	0.034	0.14	−0.369**	4.58*	0.76

Wood density

The CWM-wd differed among the Amazonian regions, and was affected by SCC and the interaction between HAND and the regions (Table 1, Fig. 2d). CWM-wd strongly decreased with SCC (Fig. 3g). CWM-wd was higher in Central, Eastern Amazonia and Guiana Shield forests, and lower in Southern and Western Amazonian forests (Fig. 3h). The effect of HAND can be seen in Southern and Western Amazonian forests, where the CWM-wd increased with HAND, i.e. towards uplands and well-drained areas (Fig. 3i). Furthermore, there was a tendency (marginally significant, Table 1) for an average increase in the CWM-wd towards forests with higher HAND values all over the basin (Supporting information).

Species composition

The two-dimensional NMDS solution produced high congruence between species composition distances observed in the original space and those obtained in the reduced space, low stress and > 50% of the variation of the original composition was captured in all the regions (Supporting information). The results of the GLS models (Table 2) showed

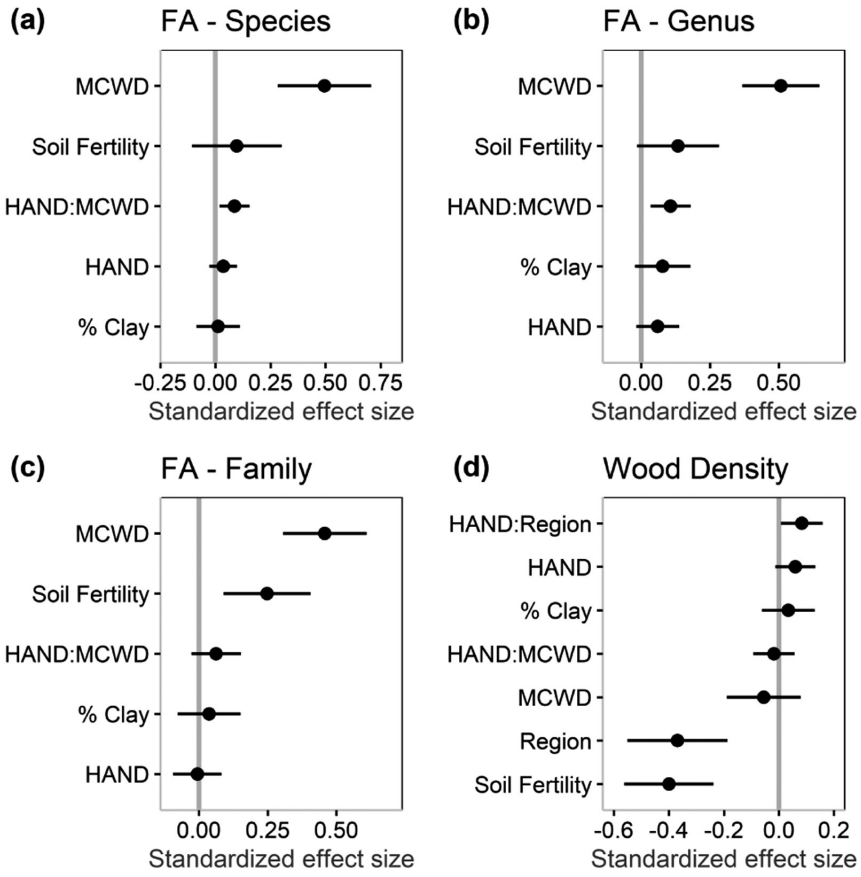

Figure 2. Standardized effect of the variables used in the generalized least square (GLS) models for alpha diversity and community weighted mean of wood density (CWM-wd) in the Amazon basin. Species (a), genus (b) and family (c) alpha diversity were mainly influenced by the maximum cumulative water deficit (MCWD). CWM-wd was mainly influenced by SCC (soil fertility) and the Amazonian regions (d). For each term in the model, the points represent the standardized effect and the lines represent standard deviation 1. ":" = interaction.

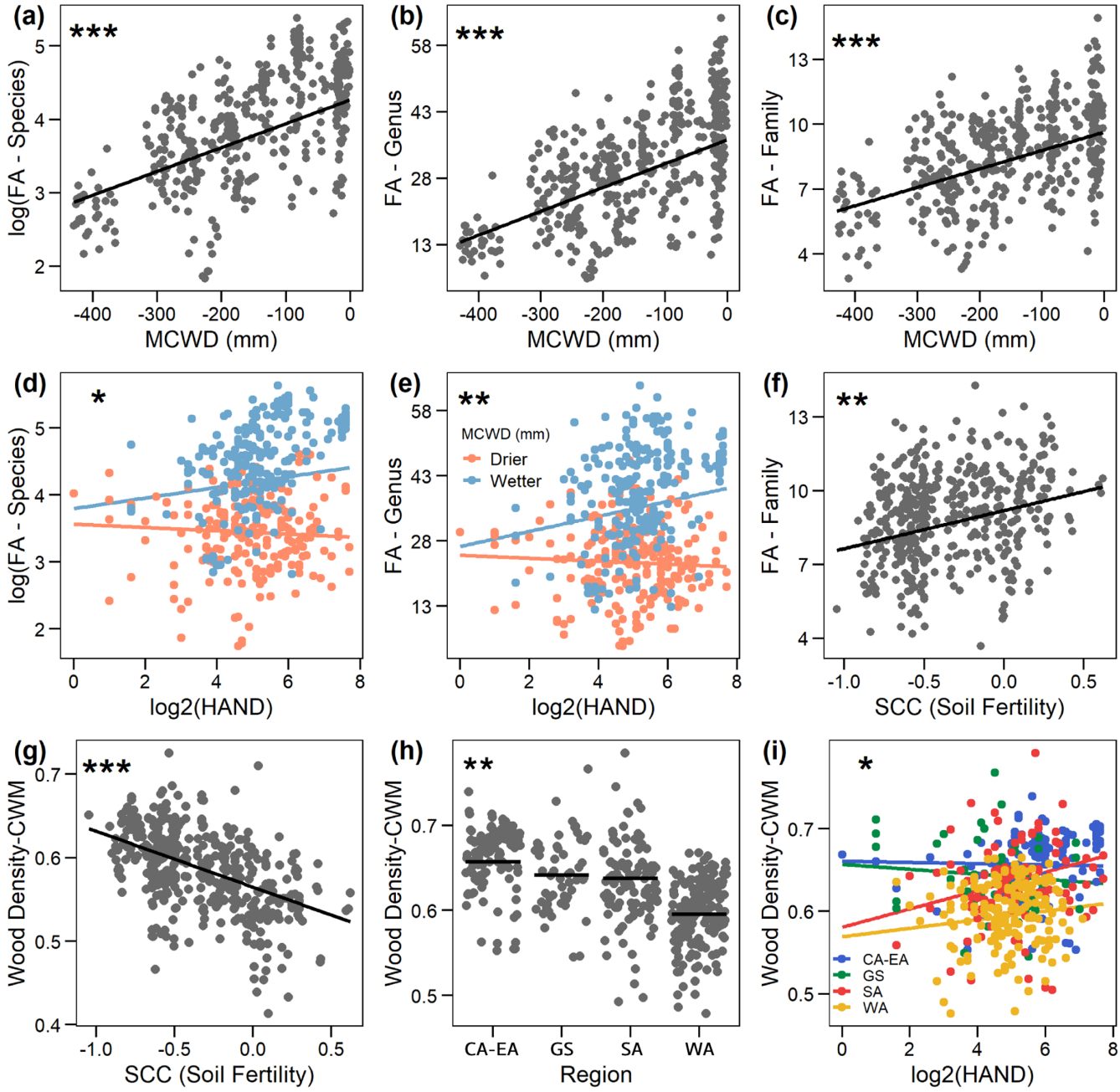

Figure 3. Partial effect of maximum cumulative water deficit (MCWD) on species (a), genus (b) and family (c). Partial effect of the interaction between height above nearest drainage (HAND) and maximum cumulative water deficit (MCWD) on the species (d) and genus (e) Fisher alpha diversity. Panels (d) and (e) show the HAND effect in wetter (blue) and drier (red) forests. In order to visualize the interaction between MCWD and HAND, the number of plots was divided into two groups based on the median. Red is used for plots with MCWD values with higher water deficit (between −429.6 and −138.0, 221 plots); and blue is for plots with MCWD values with less water deficit (between −136.7 and −1.60, 222 plots). Partial effect of soil cation concentration (SCC), a proxy of soil fertility, on family Fisher alpha diversity (f). Partial effect of SCC (g) and Amazon regions (h) on the community weighted mean of wood density (CWM-wd). Partial effect of the interaction between HAND and Amazon regions on CWM-wd (i). Different colours represent the four Amazon regions: Central and Eastern Amazonia (blue, CA–EA = 122 plots), Guiana Shield (green, GS = 52 plots), Southern Amazonia (red, AS = 102 plots) and West Amazonia (yellow, WA = 167 plots). *, ** and *** indicate significant effects with $p < 0.01$ and $p < 0.001$, respectively.

Table 2. Standardized coefficients and their respective significance probabilities, resulting from the generalized least square (GLS) models for tree species composition (i.e. coordinates of non-metric multidimensional scaling (NMDS) axes 1 and 2; NMDS 1 and NMDS 2) within Amazon regions (CA–EA = Central and Eastern Amazonia, 122 plots; GS = Guiana Shield, 52 plots; SA = South Amazonia, 102 plots; WA = Western Amazonia, 167 plots). ':' = interaction. *, ** and *** indicate significant coefficients with $p < 0.05$, $p < 0.01$ and $p < 0.001$, respectively. MCWD, maximum cumulative water deficit; SCC, soil cation concentration; HAND, height above nearest drainage.

Region	Axes	MCWD	HAND	SCC	%Sand	HAND:MCWD	R^2
Species composition							
CA-EA	NMDS-1	0.21	−0.06	−0.55***	−0.11	0.16**	0.78
	NMDS-2	−0,29	−0.14	−0.08	0.05	0.06	−0.12
GS	NMDS-1	−0.02	−0.02	0.42	−0.06	−0.02	0.70
	NMDS-2	−0.01	0.09	−0.08	0.13	0.01	0.37
SA	NMDS-1	0.62***	0.05	−0.30*	0.07	0.02	0.78
	NMDS-2	−0.10	−0.01	−0.39***	0.44***	0.13	0.66
WA	NMDS-1	−0.11	−0.05	0.50***	−0.10*	0.02	0.70
	NMDS-2	−0.75***	0.14**	−0.65***	0.00	−0.02	0.78

that the first NMDS axis of all regions but Guiana, and the second axis of Southern and Western Amazonia regions, were significantly associated with SCC. In Central-Eastern Amazonia there was a significant interaction between MCWD and HAND affecting the first ordination axis (Table 2); in Southern Amazonia, MCWD significantly affected the first ordination axis, and soil texture (% Sand) affected the second axis; and, in Western Amazonia, MCWD and HAND affected the second ordination axis (Table 2, Fig. 4). The patterns detected within regions were congruent with those from an analysis of the whole basin, with species composition changing along HAND in Central-Eastern and Western Amazon regions (Supporting information).

The NMDS axes (CA-EA NMDS-1, SA NMDS-2 and WA NMDS-2) significantly associated with the variables representing the local hydrological conditions – HAND or soil texture – were correlated with the CWM-wd (Supporting information), indicating that wood density increases towards positive values of those ordination axes.

Discussion

In this study, we investigated whether local hydrological conditions influence tree alpha diversity, species composition and wood density across the Amazonian basin. Our results indicated that: 1) tree alpha diversity varies along the gradient of local hydrological conditions as a function of the climatic context, increasing towards well-drained topographic conditions in humid forests, 2) wood density increases towards well-drained topographic conditions in two of the four Amazonian regions, and 3) species composition changes along gradients of local hydrological conditions within three of the four Amazonian regions. We conclude, therefore, that local hydrological conditions are important determinants of the diversity and composition of Amazonian forests.

Tree alpha diversity

Our results show an interaction between HAND and climatic water deficit (as measured by MCWD) on species and genus diversity, expanding the understanding of the Amazonian tree diversity patterns previously described based on climate only (Clinebell et al. 1995, ter Steege et al. 2003, Stropp et al. 2009, Esquivel-Muelbert et al. 2017). We show that within wetter climatic conditions, tree diversity can be either high or low depending on the local hydrological conditions, and thus that fine-scale diversity patterns are also determined by soil water availability, which has important implications to biodiversity conservation under climate change. In forests developing under humid climates, the excess water generated by high precipitation and water convergence to the bottomlands, which have lower drainage capacity due to the shallow water table, generates poorly structured and water-saturated soils (Ferry et al. 2010, Fan et al. 2017, Roebroek et al. 2020). Soil water saturation leads to a reduction in oxygen (Araya et al. 2013, Silvertown et al. 2015, Roebroek et al. 2020) and nitrogen levels (Ferry et al. 2010, Araya et al. 2013) that can decrease survival, and inhibit growth and development, especially of species without adaptations such as adventitious root structure or aerenchyma (Parolin 2001, Parolin et al. 2004). Saturated soils also limit root depth (Fan et al. 2017) and can limit the establishment and survival of trees without efficient attachment structures such as buttress or tabular roots that compensate for the absence of deep roots. Species that attain larger sizes can be especially unstable under these conditions (Wittmann and Parolin 2005). Thus, the physical and physiological limitations for the establishment and performance of many species in waterlogged sites may filter out a small subset of species, reducing tree diversity.

The effects of local hydrological conditions on tree diversity agree with the earlier study of Féret and Asner (2014) in Southwestern Amazonia, although these were much less pronounced than detected here. Lower tree diversity in forests with sandy soils has been found in Central Amazonia (Laurance et al. 2010), where these environments are associated with a shallow water table (Chauvel et al. 1987). Flooded forests also have alpha diversity increasing towards lower levels of flooding (Wittmann et al. 2006, 2010, Assis et al. 2015). Our results indicate that the lower tree diversity associated with water excess, either due to flooding or shallow water table under wet climates, is a pattern that can be generalized to other parts of the Amazonian basin.

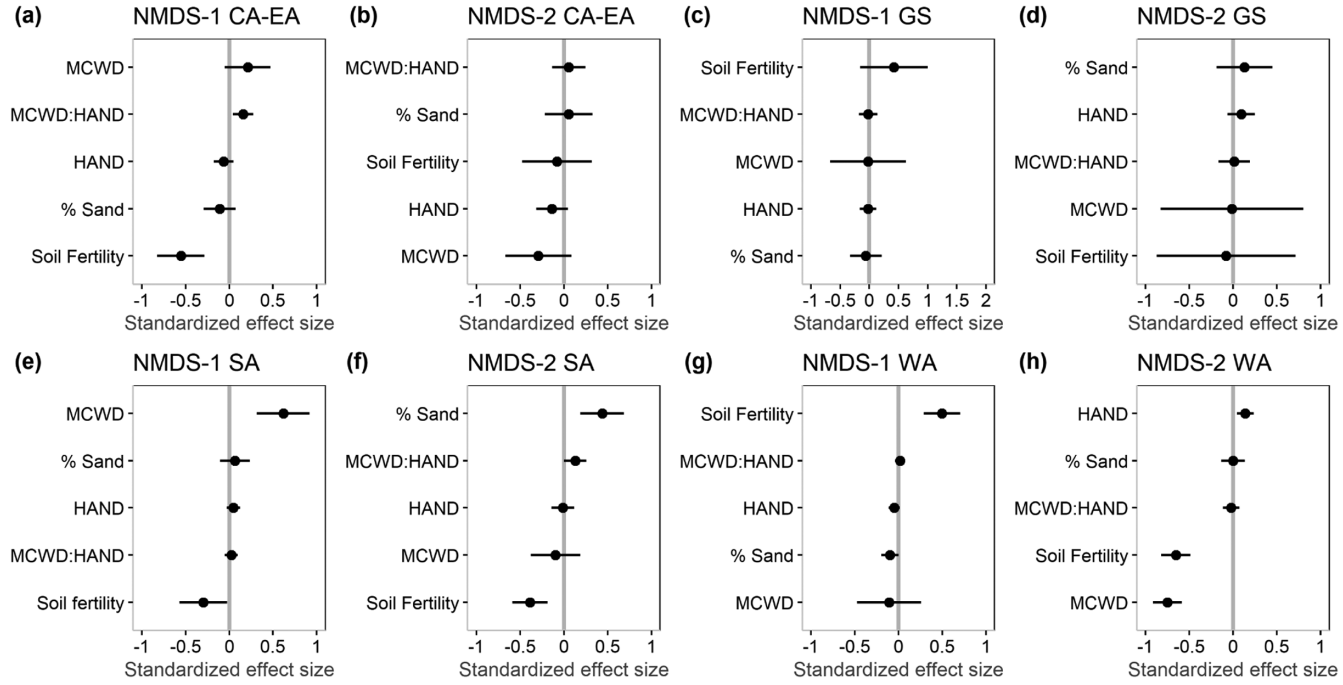

Figure 4. Standardized effect of the variables used in the GLS models for species composition, represented by the first and second NMDS ordination axes (NMDS-1 and NMDS-2, respectively) within each region. Central and Eastern Amazonia (CA-EA; a and b), Guiana Shield (GS; c and d), South Amazonia (SA; e and f) and Western Amazonia (WA; g and h). For each term in the model, the points represent the standardized effect and the lines represent standard deviation 1. ":" = interaction. NDMS, non-metric multidimensional scaling.

In forests with higher climatic water deficit, areas in lower topographic positions harboured a more equal complement of tree diversity to those in higher topographic positions than they do in forests with low climatic water deficit. Under climatic water deficit (i.e. more seasonal climates), the higher soil water availability in low topographic positions (Oliveira-Filho et al. 1998, Segura et al. 2003, Balvanera et al. 2011, Fan et al. 2017) may allow better establishment and an increase in plant diversity compared to hilltops with deep water tables (Segura et al. 2003). However, the faster dynamics (i.e. higher mortality and recruitment rates) in the well-drained upper topographic positions under drier climates (Segura et al. 2003, Brando et al. 2014, Marimon et al. 2014) may also favour an increase in diversity (Connell 1978, Bongers et al. 2009). Although our data do not allow determination of whether these are in fact the mechanisms in action, the hypothesis that disturbances could be regulating the effect of local hydrological conditions on diversity in Amazonian forests with greater climatic water deficit could be tested in future studies.

Earlier studies in the Amazon indicate that soil fertility may have positive (Tuomisto et al. 2002, 2014, Laurance et al. 2010) or negative effects on plant species diversity (Clinebell et al. 1995). In our study, soil fertility (SCC) had a positive influence on tree diversity, but it was only significant at the family level. This result is in agreement with previous large-scale assessments of tropical forests (Phillips et al. 1994) and the Amazon (Baker et al. 2016), where faster dynamics were associated with higher tree diversity. This might be because greater soil fertility leads to the selection of plants with short life cycles, generating higher mortality and recruitment rates, i.e. faster dynamics (Quesada et al. 2012). However, how soil fertility modulates forest disturbances and, consequently, plant diversity is still subject to debate, as other studies have reported that disturbances negatively affect tree diversity (Marra et al. 2014), or simply have no measurable effect (Carreño-Rocabado et al. 2012).

Wood density and species composition

We detected strong effects of soil fertility (here represented by SCC) on tree species composition and community weighted wood density across the Amazon, which are consistent with previous studies (Muller-Landau 2004, ter Steege et al. 2006, Quesada et al. 2012). Wood density decreases with soil fertility, and this was the most important determinant of wood density in the Amazon. However, apart from this regional effect, we detected variation in wood density linked to variation in the local hydrological conditions. Our results show that wood density tends to increase towards higher topographic positions, with better drained soils and deep water table, indicating that the effect of local hydrological conditions is widespread over large extents of the Amazonian forests, mostly on the Southern and Western regions. The effect of local hydrological conditions on wood density is supported by earlier local studies in Amazonia (Kraft et al. 2008, Ferry et al. 2010, Araujo-Murakami et al. 2014, Cosme et al.

2017) and in other biomes (Cornwell and Ackerly 2009, Liu et al. 2014, Jucker et al. 2018, Blanchard et al. 2019). At the same time, we found that climate did not have a significant effect on wood density when other environmental factors are taken into account, in agreement with ter Steege and Hammond (2001), Muller-Landau (2004) and Umaña et al. (2021). This contrasts with the results of Chave et al. (2006), Ibanez et al. (2017) and Blanchard et al. (2019), which reported a higher wood density in drier climates. In the Amazon, forests in drier climates experience greater dynamism, favouring the development of fast-growing species with low wood density (Johnson et al. 2016, Esquivel-Muelbert et al. 2020). We expected to find a climatic context dependence on the effects of local hydrological conditions on wood density such as in Blanchard et al. (2019), but in the present study this pattern was not observed. This suggests that trait selection to respond to local hydrological conditions may involve other traits than wood density in the variety of climatic contexts across the Amazon.

Higher wood density in well-drained soils with a deep water table, and the opposite in wet conditions, is part of a broader selection of functional strategies along hydro-topographic gradients (review in Costa et al. 2022). Several local-scale studies indicate the selection of functional characteristics by local hydrological conditions (Kraft et al. 2008, Ferry et al. 2010, Cosme et al. 2017, Oliveira et al. 2019, Fontes et al. 2020, Schmitt et al. 2020, Garcia et al. 2022). In well-drained areas, with lower water availability and deep water table, species converge towards more conservative traits related to resource use and conservation, with reduced SLA and higher dry matter content (Kraft et al. 2008, Liu et al. 2014, Cosme et al. 2017, Schmitt et al. 2020) and higher seed mass (Kraft et al. 2008, Liu et al. 2014), as well as higher wood density. Furthermore, trees associated with topographically higher and well-drained areas have more drought-resistant hydraulic systems (Oliveira et al. 2019, Fontes et al. 2020, Garcia et al. 2022) and greater root depth (Fan et al. 2017).

Given the selection of functional traits along the gradients of local hydrological conditions, we expected to see a concomitant shift in species composition, as trait selection can be associated with environmental filtering (Keddy 1992, Kraft and Ackerly 2010). We detected changes in species composition along local hydrological gradients in three of the Amazonian regions (HAND in CA–EA and WA, and soil texture in SA) that agree with this expectation. The species composition changes in those regions are correlated with changes in the mean wood density of plots, suggesting that filtering of species traits such as wood density could underlie the species sorting across hydrological environments. In the Central-Eastern region the species composition changes along the hydrological gradient were modulated by the climatic water deficit, suggesting that the trait selection to adjust to the local hydrological conditions may not be uniform across climates and geomorphological regions. This is consistent with patterns observed in other tropical forests (Blanchard et al. 2019, Muscarella et al. 2019), although we did not observe this effect directly on wood density. However, other traits or trait combinations could be responsible for the species sorting along hydrological conditions.

We conclude that the influence of local hydrological conditions on species composition varies among Amazonian regions, in terms of the environmental property affecting soil hydrology that is more relevant for species distribution – either hydro-topography or soil texture – and in terms of the modulation of local hydrology by climate. We acknowledge that the link between changes in species composition and the filtering of traits needs to be better established, by examining other traits and applying formal tests to detect if filtering is stronger than expected by chance.

Limitations of this study

Given the varied nature of the plots included in the ATDN, some issues regarding plot design and geographic coordinates may have affected the results presented here. Although all the plots used in this study were 1-ha, the plot design was not standardized. Some plots were installed following an elevation isoline, which reduces the topographic variation within the plot (Magnusson et al. 2005) and thus improves the representation of the local hydrological conditions. However, most plots were quadrangular or rectangular, and may have incorporated some within-plot hydrological variation, which could make it difficult to adequately represent their hydro-topographic condition. Furthermore, only one geographic coordinate per plot was available, without additional information about the exact place where the coordinates were taken. Our hydrological variable (HAND) was obtained from a 30 m^2 resolution layer but, given the described issues, we had to reproject the HAND layer to a resolution of 100 m^2 to account for the variety of plot designs and possible inaccuracies in geographic location. Thus, the explanatory power of HAND may have been reduced.

Conclusions

At the Amazon basin scale, we have shown that the effect of local hydrological conditions on tree diversity depends on the climatic context: the effect on wood density is general over the basin and the effects on species composition vary among the Amazonian regions. These findings reinforce the importance of local hydrological conditions as determinants of plant communities at large scales. Moreover, our findings highlight the importance of conserving topographically heterogeneous areas for optimum preservation of biodiversity and the functionality of forests. Considering that most Neotropical forests species are restricted to wetter conditions (Esquivel-Muelbert et al. 2017), climatic events such as extreme droughts that have been more frequent in recent decades (Marengo et al. 2018) can be a serious threat to the diversity and functioning of the most diverse forests on the planet. In future scenarios of increases in global temperature and reduction in water availability (IPCC 2021), topographic and hydrological conditions can play an important role in the ecology and distribution of plants.

Low topographic environments with a shallow water table can reduce the impact of extreme heat and drought events (Sousa et al. 2020, Esteban et al. 2021, Costa et al. 2022), being potential refuges for diversity (McLaughlin et al. 2017). Therefore, it is important to consider the local hydrological conditions in modelling studies of species distribution and forecasting the fate of forests under climate change, to allow the promotion of socio-political strategies of conservation and sustainable use of forests.

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Data availability statement

Original data can be obtained by request from Flávia R. C. Costa (flaviacosta001@gmail.com). The anonymised dataset is available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.qnk98sfkg> (Marca-Zevallos et al. 2022).

Supporting information

The Supporting information associated with this article is available with the online version.

References

Abatzoglou, J. T. et al. 2018. TerraClimate, a high-resolution global dataset of monthly climate and climatic water balance from 1958 to 2015. – Sci. Data 5: 1–12.

Allen, M. P. 1997. Model specification in regression analysis. – In: Understanding regression analysis. Springer. doi: <10.1007/978-0-585-25657-3_35>.

Anderson, M. J. 2001. A new method for non-parametric multivariate analysis of variance. – Austral Ecol. 26: 32–46.

Aragão, L. E. O. C. et al. 2007. Spatial patterns and fire response of recent Amazonian droughts. – Geophys. Res. Lett. 34: 1–5.

Araujo-Murakami, A. et al. 2014. The productivity, allocation and cycling of carbon in forests at the dry margin of the Amazon forest in Bolivia. – Plant Ecol. Divers. 7: 55–69.

Araya, Y. N. et al. 2013. Does soil nitrogen availability mediate the response of grassland composition to water regime? – J. Veg. Sci. 24: 506–517.

Armstrong, R. A. 2014. When to use the Bonferroni correction. – Ophthal. Physiol. Opt. 34: 502–508.

Asner, G. P. et al. 2015. Landscape biogeochemistry reflected in shifting distributions of chemical traits in the Amazon forest canopy. – Nat. Geosci. 8: 567–575.

Assis, R. L. et al. 2015. Effects of hydroperiod and substrate properties on tree alpha diversity and composition in Amazonian floodplain forests. – Plant Ecol. 216: 41–54.

Baker, T. R. et al. 2004. Variation in wood density determines spatial patterns in Amazonian forest biomass. – Global Change Biol. 10: 545–562.

Baker, T. R. et al. 2016. Consistent, small effects of treefall disturbances on the composition and diversity of four Amazonian forests. – J. Ecol. 104: 497–506.

Baldeck, C. A. et al. 2013. Soil resources and topography shape local tree community structure in tropical forests. – Proc. R. Soc. B 280: 20122532.

Balvanera, P. et al. 2011. Distribution patterns of tropical dry forest trees along a mesoscale water availability gradient. – Biotropica 43: 414–422.

Banon, L. C. and Novo, E. M. L. M. 2018. Extração da rede de drenagem da Bacia Amazônica por um processo de mineração de dados utilizando MDE SRTM e avaliação do resultado em aplicações nas áreas de geomorfologia, geologia, ecohidrologia e distribuição de espécies. – Projeto FAPESP 2016/13462-0, <www.dsr.inpe.br/amazondrainage>.

Berenguer, E. et al. 2021. Tracking the impacts of El Niño drought and fire in human-modified Amazonian forests. – Proc. Natl Acad. Sci. USA 118: e2019377118.

Blanchard, G. et al. 2019. Regional rainfall and local topography jointly drive tree community assembly in lowland tropical forests of New Caledonia. – J. Veg. Sci. 30: 845–856.

Bongers, F. et al. 2009. The intermediate disturbance hypothesis applies to tropical forests, but disturbance contributes little to tree diversity. – Ecol. Lett. 12: 798–805.

Brando, P. M. et al. 2014. Abrupt increases in Amazonian tree mortality due to drought–fire interactions. – Proc. Natl Acad. Sci. USA 111: 6347–6352.

Brienen, R. J. W. et al. 2015. Long-term decline of the Amazon carbon sink. – Nature 519: 344–348.

Cao, Y. et al. 2001. Rare species in multivariate analysis for bioassessment: some considerations. – J. North Am. Benthol. Soc. 20: 144–153.

Carreño-Rocabado, G. et al. 2012. Effects of disturbance intensity on species and functional diversity in a tropical forest. – J. Ecol. 100: 1453–1463.

Chauvel, A. et al. 1987. On the genesis of the soil mantle of the region of Manaus. – Experientia 43: 234–241.

Chave, J. et al. 2006. Regional and phylogenetic variation of wood density across 2456 neotropical tree species. – Ecol. Appl. 16: 2356–2367.
Chave, J. et al. 2009. Towards a worldwide wood economics spectrum. – Ecol. Lett. 12: 351–366.
Clinebell, R. R. et al. 1995. Prediction of neotropical tree and liana species richness from soil and climatic data. – Biodivers. Conserv. 4: 56–90.
Condit, R. et al. 2002. Beta-diversity in tropical forest trees. – Science 295: 666–669.
Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs. – Science 199: 1302–1310.
Cornwell, W. K. and Ackerly, D. D. 2009. Community assembly and shifts in plant trait distributions across an environmental gradient in coastal California. – Ecol. Monogr. 79: 109–126.
Coronado, E. N. H. et al. 2009. Multi-scale comparisons of tree composition in Amazonian terra firme forests. – Biogeosciences 6: 2719–2731.
Cosme, L. H. M. et al. 2017. The importance of hydraulic architecture to the distribution patterns of trees in a central Amazonian forest. – New Phytol. 215: 113–125.
Costa, F. R. C. et al. 2022. The other side of tropical forest drought: do shallow water table regions of Amazonia act as large-scale hydrological refugia from drought. – New Phytol. <https://doi.org/10.1111/nph.17914>.
Daws, M. I. et al. 2002. Topographic position affects the water regime in a semideciduous tropical forest in Panama. – Plant Soil 238: 79–90.
Dormann, C. F. et al. 2013. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. – Ecography 36: 27–46.
Emilio, T. et al. 2010. Assessing the relationship between forest types and canopy tree beta diversity in Amazonia. – Ecography 33: 738–747.
Esquivel-Muelbert, A. et al. 2017. Seasonal drought limits tree species across the Neotropics. – Ecography 40: 618–629.
Esquivel-Muelbert, A. et al. 2019. Compositional response of Amazon forests to climate change. – Global Change Biol. 25: 39–56.
Esquivel-Muelbert, A. et al. 2020. Tree mode of death and mortality risk factors across Amazon forests. – Nat. Commun. 11: 5515.
Esteban, E. J. L. et al. 2021. The other side of droughts: wet extremes and topography as buffers of negative drought effects in an Amazonian forest. – New Phytol. 229: 1995–2006.
Fan, Y. et al. 2017. Hydrologic regulation of plant rooting depth. – Proc. Natl Acad. Sci. USA 114: 10572–10577.
Feldpausch, T. R. et al. 2011. Height-diameter allometry of tropical forest trees. – Biogeosciences 8: 1081–1106.
Féret, J. B. and Asner, G. P. 2014. Microtopographic controls on lowland Amazonian canopy diversity from imaging spectroscopy. – Ecol. Appl. 24: 1297–1310.
Ferry, B. et al. 2010. Higher treefall rates on slopes and waterlogged soils result in lower stand biomass and productivity in a tropical rain forest. – J. Ecol. 98: 106–116.
Figueiredo, F. O. G. et al. 2018. Beyond climate control on species range: the importance of soil data to predict distribution of Amazonian plant species. – J. Biogeogr. 45: 190–200.
Fisher, R. A. et al. 1943. The relation between the number of species and the number of individuals in a random sample of an animal population. – J. Anim. Ecol. 12: 42–58.
Fontes, C. G. et al. 2020. Convergent evolution of tree hydraulic traits in Amazonian habitats: implications for community assemblage and vulnerability to drought. – New Phytol. 228: 106–120.
Fox, J. et al. 2021. Package 'car': companion to applied regression, ver. 3.0-12. – <https://cran.r-project.org/package=car>.
Gale, N. and Hall, P. 2001. Factors determining the modes of tree death in three Bornean rain forests. – J. Veg. Sci. 12: 337–348.
Garcia, M. N. et al. 2022. Local hydrological gradients structure high intraspecific variability in plant hydraulic traits in two dominant central Amazonian tree species. – J. Exp. Bot. 73: 939–952.
Garnier, E. et al. 2004. Plant functional markers capture ecosystem properties during secondary succession. – Ecology 85: 2630–2637.
Giardina, F. et al. 2018. Tall Amazonian forests are less sensitive to precipitation variability. – Nat. Geosci. 11: 405–409.
Hacke, U. G. et al. 2000. Influence of soil porosity on water use in Pinus taeda. – Oecologia 124: 495–505.
Hacke, U. G. et al. 2001. Trends in wood density and structure are linked to prevention of xylem implosion by negative pressure. – Oecologia 126: 457–461.
Hengl, T. et al. 2017. SoilGrids250m: global gridded soil information based on machine learning. – PLoS One 12: 1–40.
Hoeber, S. et al. 2014. The importance of hydraulic conductivity and wood density to growth performance in eight tree species from a tropical semi-dry climate. – For. Ecol. Manage. 330: 126–136.
Ibanez, T. et al. 2017. Community variation in wood density along a bioclimatic gradient on a hyper-diverse tropical island. – J. Veg. Sci. 28: 19–33.
IPCC 2021. Summary for policymakers. – In: Masson-Delmotte, V. P. et al. (eds), Climate change 2021: the physical science basis. Contribution of working group I to the sixth assessment report of the intergovernmental panel on climate change. Cambridge Univ. Press, pp. 3–32.
Irion, G. 1978. Soil infertility in the Amazonian rain forest. – Naturwissenschaften 65: 515–519.
Jirka, A. S. et al. 2007. Relationships between soil hydrology and forest structure and composition in the southern Brazilian Amazon. – J. Veg. Sci. 18: 183–194.
Johnson, M. O. et al. 2016. Variation in stem mortality rates determines patterns of above-ground biomass in Amazonian forests: implications for dynamic global vegetation models. – Global Change Biol. 22: 3996–4013.
Jucker, T. et al. 2018. Topography shapes the structure, composition and function of tropical forest landscapes. – Ecol. Lett. 21: 989–1000.
Karger, D. N. et al. 2018. Data from: Climatologies at high resolution for the earth's land surface areas. – Dryad Digital Repository, <https://doi.org/10.5061/dryad.kd1d4>.
Keddy, P. A. 1992. Assembly and response rules: two goals for predictive community ecology. – J. Veg. Sci. 3: 157–164.
Kraft, N. J. B. and Ackerly, D. D. 2010. Functional trait and phylogenetic tests of community assembly across spatial scales in an Amazonian forest. – Ecol. Monogr. 80: 401–422.
Kraft, N. J. B. et al. 2008. Functional traits and niche-based tree community assembly in an Amazonian forest. – Science 322: 580–582.
Laurance, S. G. W. et al. 2010. Influence of soils and topography on Amazonian tree diversity: a landscape-scale study. – J. Veg. Sci. 21: 96–106.
Liu, J. et al. 2014. Topography related habitat associations of tree species traits, composition and diversity in a Chinese tropical forest. – For. Ecol. Manage. 330: 75–81.

Magnusson, W. E. et al. 2005. RAPELD: a modification of the Gentry method for biodiversity surveys in long-term ecological research sites. – Biota Neotrop. 5: 19–24.
Marca-Zevallos, M. J. et al. 2022. Data from: Local hydrological conditions influence tree diversity and composition across the Amazon basin. – Dryad Digital Repository, <https://doi.org/10.5061/dryad.qnk98sfkg>.
Marengo, J. A. et al. 2018. Changes in climate and land use over the Amazon Region: current and future variability and trends. – Front. Earth Sci. 6: 1–21.
Marimon, B. S. et al. 2014. Disequilibrium and hyperdynamic tree turnover at the forest-cerrado transition zone in southern Amazonia. – Plant Ecol. Divers. 7: 281–292.
Marra, D. M. et al. 2014. Large-scale wind disturbances promote tree diversity in a Central Amazon Forest. – PLoS One 9: e103711.
Mayorga, E. M. G. et al. 2012. LBA-ECO CD-06 Amazon River Basin Land and stream drainage direction maps. – ORNL DAAC, <https://doi.org/10.3334/ORNLDAAC/1086>.
McCune, B. and Grace, J. B. 2002. Analysis of ecological communities. – MjMSoftware.
McLaughlin, B. C. et al. 2017. Hydrologic refugia, plants and climate change. – Global Change Biol. 23: 2941–2961.
Meir, P. et al. 2015. Threshold responses to soil moisture deficit by trees and soil in tropical rain forests: insights from field experiments. – Bioscience 65: 882–892.
Moeslund, J. E. et al. 2013. Topography as a driver of local terrestrial vascular plant diversity patterns. – Nord. J. Bot. 31: 129–144.
Moulatlet, G. M. et al. 2014. Local hydrological conditions explain floristic composition in lowland Amazonian forests. – Biotropica 46: 395–403.
Moulatlet, G. M. et al. 2017. Using digital soil maps to infer edaphic affinities of plant species in Amazonia: problems and prospects. – Ecol. Evol. 7: 8463–8477.
Muller-Landau, H. C. 2004. Interspecific and inter-site variation in wood specific gravity of tropical trees. – Biotropica 36: 20–32.
Muscarella, R. et al. 2019. Effects of topography on tropical forest structure depend on climate context. – J. Ecol. 108: 1–15.
Nepstad, D. C. et al. 2007. Mortality of large trees and lianas following experimental drought in an Amazon forest. – Ecology 88: 2259–2269.
Nobre, A. D. et al. 2011. Height above the nearest drainage – a hydrologically relevant new terrain model. – J. Hydrol. 404: 13–29.
Oksanen, A. J. et al. 2020. vegan: community ecology package, ver. 2.5-7. – <https://CRAN.R-project.org/package=vegan>.
Oliveira, R. S. et al. 2019. Embolism resistance drives the distribution of Amazonian rainforest tree species along hydro-topographic gradients. – New Phytol. 221: 1457–1465.
Oliveira-Filho, A. T. et al. 1998. Effects of canopy gaps, topography and soils on the distribution of woody species in a central Brazilian deciduous dry forest. – Biotropica 30: 362–375.
Parolin, P. 2001. Morphological and physiological adjustments to waterlogging and drought in seedlings of Amazonian floodplain trees. – Oecologia 128: 326–335.
Parolin, P. et al. 2004. Central Amazonian floodplain forests: tree adaptations in a pulsing system. – Bot. Rev. 70: 357–380.
Pascolini-Campbell, M. et al. 2021. A 10 per cent increase in global land evapotranspiration from 2003 to 2019. – Nature 593: 543–547.
Phillips, O. L. et al. 1994. Dynamics and species richness of tropical rain forests. – Proc. Natl Acad. Sci. USA 91: 2805–2809.
Phillips, O. L. et al. 2009. Drought sensitivity of the Amazon rainforest. – Science 323: 1344–1347.
Pinheiro, J. et al. 2021. nlme: linear and nonlinear mixed effects models. – R package ver. 3.1-152, <https://CRAN.R-project.org/package=nlme>.
Pos, E. T. et al. 2014. Are all species necessary to reveal ecologically important patterns? – Ecol. Evol. 4: 4626–4636.
Quesada, C. A. et al. 2009. Regional and large-scale patterns in Amazon forest structure and function are mediated by variations in soil physical and chemical properties. – Biogeosciences 6: 3993–4057.
Quesada, C. A. et al. 2010. Variations in chemical and physical properties of Amazon forest soils in relation to their genesis. – Biogeosciences 7: 1515–1541.
Quesada, C. A. et al. 2012. Basin-wide variations in Amazon forest structure and function are mediated by both soils and climate. – Biogeosciences 9: 2203–2246.
Rennó, C. D. et al. 2008. HAND, a new terrain descriptor using SRTM-DEM : Mapping terra-firme rainforest environments in Amazonia. – Remote Sens. Environ. 112: 3469–3481.
Revelle, W. 2021. psych: procedures for personality and psychological research, ver. 3.0-12. – <https://cran.r-project.org/package=psych>.
Roebroek, C. T. J. et al. 2020. Global distribution of hydrologic controls on forest growth. – Hydrol. Earth Syst. Sci. 24: 4625–4639.
Rozendaal, D. M. A. et al. 2020. Competition influences tree growth, but not mortality, across environmental gradients in Amazonia and tropical Africa. – Ecology 101:e03052.
Santiago, L. S. et al. 2004. Leaf photosynthetic traits scale with hydraulic conductivity and wood density in Panamanian forest canopy trees. – Oecologia 140: 543–550.
Schietti, J. et al. 2013. Vertical distance from drainage drives floristic composition changes in an Amazonian rainforest. – Plant Ecol. Divers. 7: 37–41.
Schmitt, S. et al. 2020. Topography consistently drives intra- and inter-specific leaf trait variation within tree species complexes in a Neotropical forest. – Oikos 129: 1521–1530.
Segura, G. et al. 2003. Tree community structure and stem mortality along a water availability gradient in a Mexican tropical dry forest. – Plant Ecol. 169: 259–271.
Silvertown, J. et al. 2015. Hydrological niches in terrestrial plant communities: a review. – J. Ecol. 103: 93–108.
Sombroek, W. 2000. Amazon landforms and soils in relation to biological diversity. – Acta Amaz. 30: 81–100.
Sousa, T. R. et al. 2020. Palms and trees resist extreme drought in Amazon forests with shallow water tables. – J. Ecol. 108: 2070–2082.
Stropp, J. et al. 2009. Disentangling regional and local tree diversity in the Amazon. – Ecography 32: 46–54.
Svenning, J. 2001. On the role of microenvironmental heterogeneity in the ecology and diversification of neotropical rain-forest palms (Arecaceae). – Bot. Rev. 67: 1–53.
ter Steege, H. and Hammond, D. S. 2001. Character convergence, diversity and disturbance in tropical rain forest in Guyana. – Ecology 82: 3197–3212.
ter Steege, H. et al. 2003. A spatial model of tree α-diversity and tree density for the Amazon. – Biodivers. Conserv. 12: 2255–2277.

ter Steege, H. et al. 2006. Continental-scale patterns of canopy tree composition and function across Amazonia. – Nature 443: 444–447.
ter Steege, H. et al. 2013. Hyperdominance in the Amazonian tree flora. – Science 342: 1243092.
Toledo, J. J. et al. 2011. How much variation in tree mortality is predicted by soil and topography in Central Amazonia? – For. Ecol. Manage. 262: 331–338.
Tuomisto, H. et al. 2002. Distribution and diversity of pteridophytes and Melastomataceae along edaphic gradients in Yasuní National Park, Ecuadorian Amazonia. – Biotropica 34: 516–533.
Tuomisto, H. et al. 2003. Dispersal, environment and floristic variation of western Amazonian forests. – Science 299: 241–244.
Tuomisto, H. et al. 2014. Species richness and diversity along edaphic and climatic gradients in Amazonia. – Ecography 37: 1034–1046.
Umaña, M. N. et al. 2021. Shifts in taxonomic and functional composition of trees along rainfall and phosphorus gradients in central Panama. – J. Ecol. 109: 51–61.
Valencia, R. et al. 2004. Tree species distributions and local habitat variation in the Amazon: large forest plot in eastern Ecuador. – J. Ecol. 92: 214–229.
Violle, C. et al. 2007. Let the concept of trait be functional! – Oikos 116: 882–892.
Wittmann, F. and Parolin, P. 2005. Aboveground roots in Amazonian floodplain trees. – Biotropica 37: 609–619.
Wittmann, F. et al. 2006. Tree species composition and diversity gradients in white-water forests across the Amazon Basin. – J. Biogeogr. 33: 1334–1347.
Wittmann, F. et al. 2010. Phytogeography, species diversity, community structure and dynamics of Central Amazonian floodplain forests. – In: Junk, W. J et al. (eds), Amazonian floodplain forests. Ecological Studies 210. Springer, pp. 61–102.
Zanne, A. E. et al. 2009. Data from: Towards a worldwide wood economics spectrum. – Dryad Digital Repository, <https://doi.org/10.5061/dryad.234>.
Zuleta, D. et al. 2020. Importance of topography for tree species habitat distributions in a terra firme forest in the Colombian Amazon. – Plant Soil 450: 133–149.
Zuquim, G. et al. 2019. Making the most of scarce data : Mapping soil gradients in data-poor areas using species occurrence records. – Methods Ecol. Evol. 10: 788–801.
Zuur, A. F. et al. 2009. Mixed effects models and extensions in ecology with R. – Springer.