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Functional divergence between Várzea and Igapó forests: a study of the functional trait diversity of the Orinoquía flooded forests

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Functional divergence between Várzea and Igapó forests: a study of the functional trait diversity of the Orinoquia flooded forests

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Abstract. In the Amazon, as well as the Orinoco basin, flooded forests have been classified according to the rivers that flood into Várzea (white water) and Igapó (black water). Furthermore, these river differences have been shown to influence the forest soil composition, so that Várzea is characterized by having nutrient-rich soils while Igapó has nutrient-poor soils. To determine if these differences have driven ecological sorting processes, we evaluated the plant functional diversity of Várzea and Igapó and the influence of external and internal filters on the plant community assembly of each forest. We sampled six functional traits in two, 1 ha plots located in Casanare, Colombia, one in Várzea and the other in Igapó. We found that there is a partial functional differentiation between Várzea and Igapó, and a high functional divergence within each forest. We also observed a greater influence of internal filters on the community assembly of both forest types, compared to external filters. These results contribute to the understanding of community assembly and the expression of functional traits in rich and poor soils, as well as showing the importance of recognizing the functional diversity between and within Várzea and Igapó, despite their low taxonomic diversity.

Key words: Community assembly, environmental filtering, functional diversity, internal filtering, soil nutrient availability, tropical forests.

Introduction

Floodplain forests grow in areas periodically flooded by river overflow and/or by direct precipitation and are characterized by a low taxonomic diversity (Furch 1997; Parolin 2012). In the Amazon basin, these forests were classified in Várzea and Igapó forests by Prance (1979), according to the hydro-chemical properties of the rivers that flood them; in addition, these rivers determine the physical (moisture retention, hydraulic conductivity), chemical (availability of nutrients, sediments, organic matter) and biological soil properties (Parolin *et al.* 2004). In this way, Várzea forests are associated with white water rivers, which contain nutrient-rich sediments derived from the Andes or pre-Andean regions and, therefore, tend to have high productivity (Prance 1979; Furch 1997), while Igapó forests are flooded by black water rivers, which are considered nutrient-poor and with low production potential (Prance 1979; Irion *et al.* 2010). This classification also applies to other important basins in the region, such as the Orinoco basin (Godoy *et al.*

1999), however, in the latter, other types of flooded forests have also been identified: mixed water and clear water forests (Lasso *et al.* 2010). Floodplain forests are strategic environments for different animals and plants, since they offer a temporal-spatial heterogeneity that translates into an important habitat source different from the *terra firme* forests (Furch 1997). This implies that their conservation and proper management require a more comprehensive knowledge.

Although there have been several studies on the flooded forests plant composition in South America (e.g., Ferreira and Prance 1998; Wittmann *et al.* 2006), few have focused on studying their functional diversity (e.g., Mori *et al.* 2019) and in particular, there are no studies of functional traits in the Colombian flooded forests. This is a problem because functional diversity helps to better understand organisms' responses to the constraints and opportunities they face in different habitats (Southwood 1977; Pérez-Harguindeguy 2013). For instance, differences in soil composition may drive species ecological sorting processes (Reich *et al.* 2003) which could result in different diversity patterns as the ones described for the *Várzea* and *Igapó* forests of the Colombian Orinoquia (i.e., Casanare; Cárdenas 2012; Gómez 2017). One way to corroborate this hypothesis is by studying functional traits and their diversity. Functional traits are well-defined and measurable, hereditary, morphological, physiological, or phenological organism characteristics that strongly influence the performance of individuals in a community (Garnier *et al.* 2016). Additionally, it has been suggested that the variation they exhibit represents, to a great extent, the adaptations to the wide range of existing environmental conditions and, therefore, they reflect plant adaptations to environmental conditions such as topography, soil nutrients and water availability (Svenning 1999; Oliveira *et al.* 2019).

In this sense, it would be expected to find functional divergence between plants that inhabit contrasting environments. However, it is important to note that combinations of functional trait values are constrained by biophysical and natural selection forces that involve trade-offs between plant structure and function (Reich 1993). Therefore, these combinations are frequently repeated among distant taxa in a wide geographic range and depend on the correlations that exist between traits (Reich *et al.* 2003). For example, it has been shown that specific leaf area (SLA) is a function of the leaf dry matter content (LDMC) and/or the leaf thickness (Lth) and is usually negatively related to these two components (Garnier *et al.* 2016). Additionally, these trait combinations often form plant life strategies. For example, species with high growth rates are characterized by having lower wood density (WD) and a higher SLA, which in turn is often related with lower LDMC and/or Lth (Garnier *et al.* 2016); these values are advantageous in resource-rich environments. In contrast, species with lower growth rates tend to have higher WD, lower SLA, and higher Lth and LDMC, reflecting investment in strong and persistent tissues, increased nutrient conservation, water use efficiency, and is typical of plant survival in low-resource environments and/or in the presence of stress (Parolin and Worbes 2000; Reich 2014).

In addition, the traditional community assembly theory predicts that filters (abiotic and biotic) operate on the mean trait values of species (Lortie *et al.* 2004). Nevertheless, in order to build a more general theory based on functional traits and overcome the complexity of traditional ecological filters, Violle *et al.* (2012) proposed an assembly theory that involves two filters operating at the individual instead of the species level: external and internal filters. External filters refer to all assembly processes that operate on a larger scale than the community (e.g., climate, environmental filtering, dispersal factors), while internal filters include all assembly processes that occur within the community (e.g., competition and microhabitat heterogeneity). Under this framework, which considers distribution of trait values of individuals at different organization levels, the influence of external filters is expected to be greater in environments with significant limitations (e.g., low nutrient soil content, drought, limited seed dispersal) and lead to convergent distributions of trait values; internal filters are predominant in environments with fewer abiotic restrictions and with increasing competition.

In Colombia, even though flooded forests are found in regions such as the Amazon, Orinoquia, and the Magdalena basins, these forests have been poorly studied, particularly in the Orinoco region (Godoy *et al.* 1999). However, they play a key role in the functioning of ecosystems and promoting biodiversity, since they are an important food source for fish during the flooding and are key to conserving freshwater biodiversity (Goulding 1980; Caicedo-Herrera *et al.* 2018). Therefore, this study aims to evaluate i) the functional diversity of plants from the Várzea and Igapó forests in the Colombian Orinoquia and ii) the effect of external and internal filters on the plant community assembly of each of these forests. If differences in abiotic factors, such as soil composition, have led to the ecological sorting of species, it is expected that there will be functional divergence between the Várzea and Igapó forests. Várzea, with higher nutrient soils, would be characterized with functional trait values associated with a competitive life strategy, reflected in higher growth rates; while Igapó, which has low nutrient soil availability, would present trait values consistent with a conservative life strategy such as lower growth rates and survival under stress conditions. Therefore, external filters are expected to be of greater influence in Igapó and lead to convergent trait distribution, while in Várzea, internal filters would be of greater importance.

Materials and methods

Study area

This study was carried out in Finca La Visión, located in Paz de Ariporo, Casanare, Colombia, in two vegetation plots of one hectare each (100 x 100 m); these plots were established in 2011, one in a Várzea and the other one in an Igapó forest (Cárdenas 2012). This region is characterized by a rainy season between April and August, with a flood phase lasting around seven months (April–October). In the rainy season, the Várzea forest (5° 40.255'N, 70° 06.609'W) is flooded by the Meta River, which is one of the main

Orinoco river tributaries and transports nutrient-rich sediments received from the Andes mountain range (white waters). The Igapó forest (5° 40.040'N, 70° 08.946'W) is flooded by the Caño Pica-Pico, which is an intermittent river located in Casanare and transports small amounts of sediment (black water). Although these plots are only 4.5 km apart (Fig. 1), it has been shown that there are differences in their soil composition. Gómez (2015) found that Várzea soil is associated with a higher content of Ca, Mg and P, while Igapó presents a higher concentration of inorganic C, N and Al.

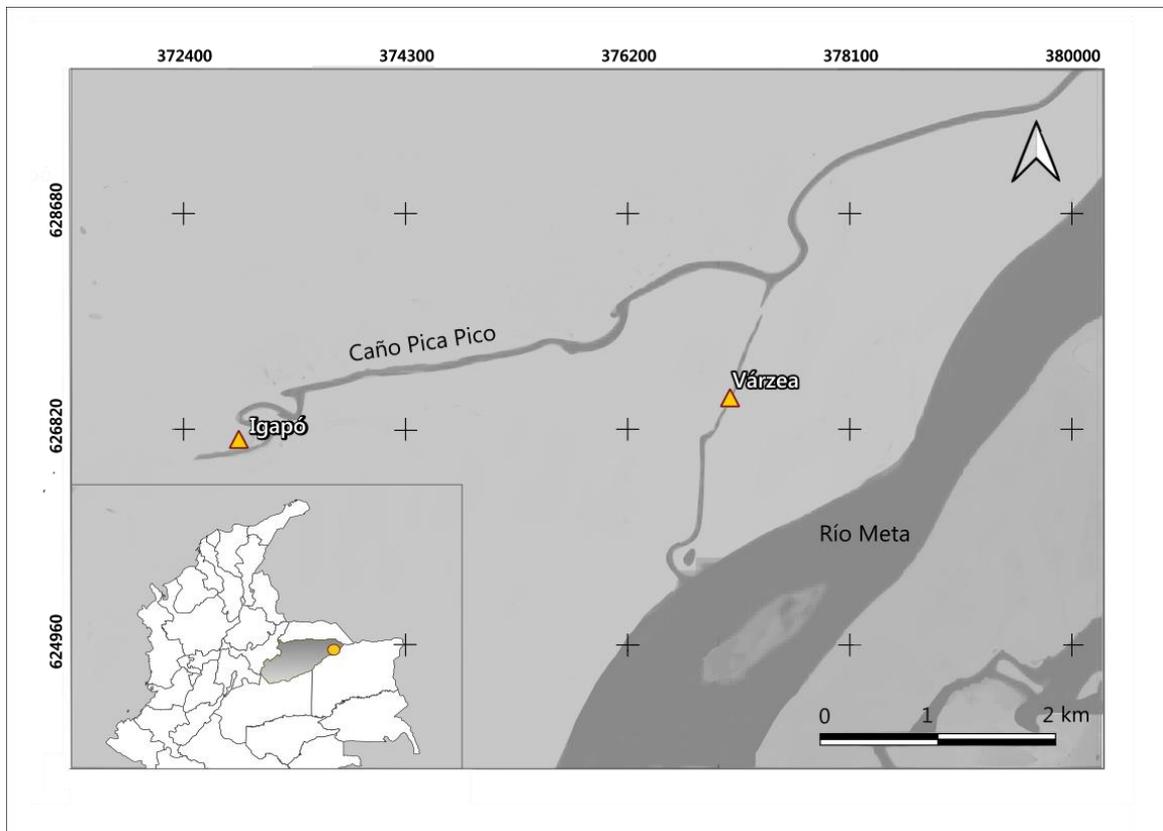


Fig. 1. Distribution of sampled floodplain forest plots (1 ha) in Casanare, Colombia. The yellow triangles represent the location of each plot: Igapó on the left and Várzea on the right. The location of Casanare is indicated in gray in the Colombian thumbnail and the yellow circle denotes the study area.

Sampling and measurement of functional traits

Functional traits were sampled in the dry season of December 2019. We selected the sampled species according to their relative abundance based on previous plant inventories with DBH \geq 10 cm (Cárdenas 2012). We chose species with at least ten individuals per plot, seven in Várzea and eight in Igapó; these species collectively represent more than 80% of the relative abundance for both forests (Table S1). We measured six functional traits associated with plant growth and survival: leaf area (LA [cm^2]), specific leaf area

(SLA [$\text{mm}^2 \text{mg}^{-1}$]), leaf thickness (Lth [mm]), leaf dry matter content (LDMC [mg g^{-1}]), wood density (WD [g cm^3]) and plant height (H [m]) (Table S2).

We measured functional traits following standardized trait protocols (Pérez-Harguindeguy *et al.* 2013). Leaf traits were measured on five leaves exposed to the sun per individual without including petiole or rachis, and we sampled five individuals per species, with the exception of three compound leafed species in which, due to sampling difficulties, only four individuals per species were sampled. To measure leaf area (LA), we scanned the leaves and ImageJ digital image processing program (Schneider *et al.* 2012) was used to calculate the area. Specific leaf area (SLA) was determined based on LA and the leaf dry weight obtained after drying the leaves in an oven at 80°C for 48 h. Leaf dry matter content (LDMC) was calculated from the leaf dry weight and the leaf wet weight measured in the field. Leaf thickness (Lth) was obtained by averaging the values of three measurements per leaf (always consistent in the different individuals and species) with a digital Vernier caliper at the sampling site. Height (H) was measured in five adult individuals per species at the field site using a laser clinometer. Finally, to determine wood density (WD), we took samples at 1.3 m height using a 5.15 mm diameter core borer. The volume was calculated by measuring the length and diameter of each sample, while the wood dry weight was obtained after drying the samples in an oven at 100°C for 48 h (Williamson and Wiemann 2010). Wood density was calculated in five individuals per species, except for two species in the Várzea forest (four individuals per species). This was due to the damage of the two borers used in the field while extracting samples of *Tachigali vaupesiana* and *Mouriri guianensis*, which are species with high wood density.

Statistical analysis

We ran a principal component analysis (PCA) to describe the values of the six traits sampled in two dimensions. Likewise, statistical tests (T-test or Wilcoxon test) were done to compare the average values of each functional trait between Várzea and Igapó. To assess the functional diversity components of each forest, we calculated the following functional diversity indices: FRic (Richness), FEve (Evenness), FDiv (Divergence), FDis (Dispersion), and Community Weighted Mean (CWM) (Cornwell *et al.* 2006; Villéger *et al.* 2008; Laliberté and Legendre 2010). All the indices are independent estimators and are described in detail in Table 1.

Table 1. Functional diversity indices used in this study.

Descriptions and formulas used to calculate the functional diversity indices are modified from Schleuter *et al.* (2010).

Index		Description	Formula
Functional richness (Cornwell <i>et al.</i> 2006; Villéger <i>et al.</i> 2008)	FRic	Convex volume.	Quickhull Algorithm
Functional evenness (Villéger <i>et al.</i> 2008)	FEve	Sum of the length of the MST branches weighted by the relative abundance of the species.	$FEve = \frac{\sum_{i=1}^{S-1} \min \left(PEW_i, \frac{1}{S-1} \right) - \frac{1}{S-1}}{1 - \frac{1}{S-1}}$
Functional divergence (Villéger <i>et al.</i> 2008)	FDiv	Weighted mean distance of traits of individual species to the weighted centroid of all species.	$FDiv = \frac{\Delta d + \overline{dG}}{\Delta d + \overline{dG}}$
Functional dispersion (Laliberté and Legendre 2010)	FDis	Deviation of the average distance from the center of gravity weighted by relative abundance.	$FDis = \frac{\sum a_i z_i}{\sum a_i}$
Community-weighted mean	CWM	Average expected value of a trait in a community.	$CWM = \sum_{i=1}^s W_i X_i$

S : total species richness. PEW : weighted partial evenness. Δd : sum of the variance of the weighted abundance. $\Delta |d|$: variance of absolute weighted abundance from the center of gravity. \overline{dG} : average distance from the center of gravity. a_i : abundance of the species i . z_i : distance of the species i to the weighted centroid. W_i : relative abundance of the i -th species. X_i : value of the trait in the i -th species. FRic is expressed as the proportion of the space occupied (e.g., local community) compared to the maximum volume (e.g., regional pool).

To assess the influence of the external and internal filters on the community assembly of floodplain forests in Casanare, we used the “Trait statistics” (T statistics) of Violle *et al.* (2012), which are based on the comparison of intraspecific and interspecific variation of functional traits at different organizational levels. There are two explicit assumptions under this framework. First, for a specific local community J , external conditions (EJ) select an optimum trait value (TJ). Thus, individuals with trait values close to TJ pass through the external filter to grow and reproduce, while individuals with trait values far from TJ are not established. Second, the internal filters, mostly governed by density-dependent processes, suggest that if most individuals in a community possess trait values close to TJ, then individuals with values far from TJ will have a higher fitness. Taken together, the external and internal filtering processes create a distribution of trait values around TJ where a given local community will have the following properties: (i) the mean trait value in the community is potentially different from the mean trait value in the regional pool; (ii) trait values in the local community will extend around TJ, with a variability that is small with strong external filtering and large with strong internal constraints.

We calculated three T statistics per functional trait for the flooded forest in general (Várzea and Igapó together) and for each forest separately, where we consider as a population all the sampled individuals of the same species; as a community all the individuals or species sampled belonging to a forest type, either Várzea or Igapó; and as a regional pool all the individuals or species sampled in the two forest types: (i) T_IP.IC: the observed ratio between the variance of the populations and the total variance of the communities at the individual level (individuals-populations/communities); this reflects the strength of internal filters on the community assembly and is expected to be predominant in settings with few abiotic constraints and lead to greater variability of the trait values; (ii) T_IC.IR: the observed ratio between the communities variance and the total variance of the regional pool at the individual level (individuals-communities/regional pool) and (iii) T_PC.PR: the observed ratio between the communities variance and the total variance of the regional pool at the population level (populations-communities/regional pool). T_IC.IR and T_PC.PR reflect the strength of external filters since external processes, such as environmental filtering, could significantly restrict the variability of trait values on a larger scale (community and regional level). To assess the importance of the above-mentioned three T statistics, the observed values were compared with the values obtained from simulated communities (n = 1000 randomizations) by calculating the standardized effect size (SES):

$$SES = \frac{(I_{obs} - I_{sim})}{\sigma_{sim}} \quad (\text{Eq. 1})$$

Where I_{sim} and σ_{sim} are respectively the average value and the standard deviation of the randomized values. SES measures how deviated the observed index is from the average index of the simulated communities (Gotelli and McCabe 2002). Therefore, negative or positive SES values reflect lower or higher T-statistic values, respectively, than random expectations. This analysis was carried out using the R package, *cati* (Taudière and Violle 2016), in which the randomizations (null models) are adapted to each T statistic as follows: (i) for T_IP.IC, the trait values are permuted within communities, maintaining species composition, but breaking the link between species and trait values; (ii) for T_IC.IR, trait values are permuted for all individuals within communities of the regional pool, maintaining the number of individuals in each community and (iii) for T_PC.PR, the values of traits at the population level are permuted within the communities of the regional pool, maintaining the number of species in each community. The significance of the SES was evaluated for each T statistic in the six functional traits by means of two unilateral tests (lower and upper limit) with a significance level of 5%. In this way, it was determined if the T statistics were significantly higher or lower than the random expectations. All analyzes were performed using the packages *vegan* 2.5-6 (Oksanen *et al.* 2013), *ade4* 1.7-15 (Dray and Dufour 2007), *FD* 1.0-12 (Laliberté *et al.* 2014) and *cati* version 0.99.3 of the statistical software Rstudio 3.6.3 (R Core Team 2020).

Results

Functional traits of Várzea and Igapó forests

The PCA (Fig. 2) shows a partial separation between the Várzea and Igapó trait values through the two main components, but there is a greater differentiation through PC1, which is mainly associated with LDMC and WD, while PC2 is mainly related to Lth and SLA (H and LA do not seem to be explanatory traits). This analysis shows that the Igapó species have higher LDMC and WD values, whereas the Várzea species have higher Lth and lower WD and LDMC values. However, there is an intersection between the two forest types that corresponds to four particular species (two from Várzea and two from Igapó) (Fig. 3), which exhibit some trait values different from the general pattern of each forest; for instance, *Mouriri guianensis*, which belongs to Várzea, has a high wood density (0.7) while *Hydrochorea marginata*, from Igapó, has a low wood density (0.4). Additionally, Igapó presents a more restricted distribution of trait values throughout PC1 and PC2 compared to the trait distribution in Várzea. The main components PC1 (37.37%) and PC2 (19.64%) explain about 57% of the variation in the functional trait values.

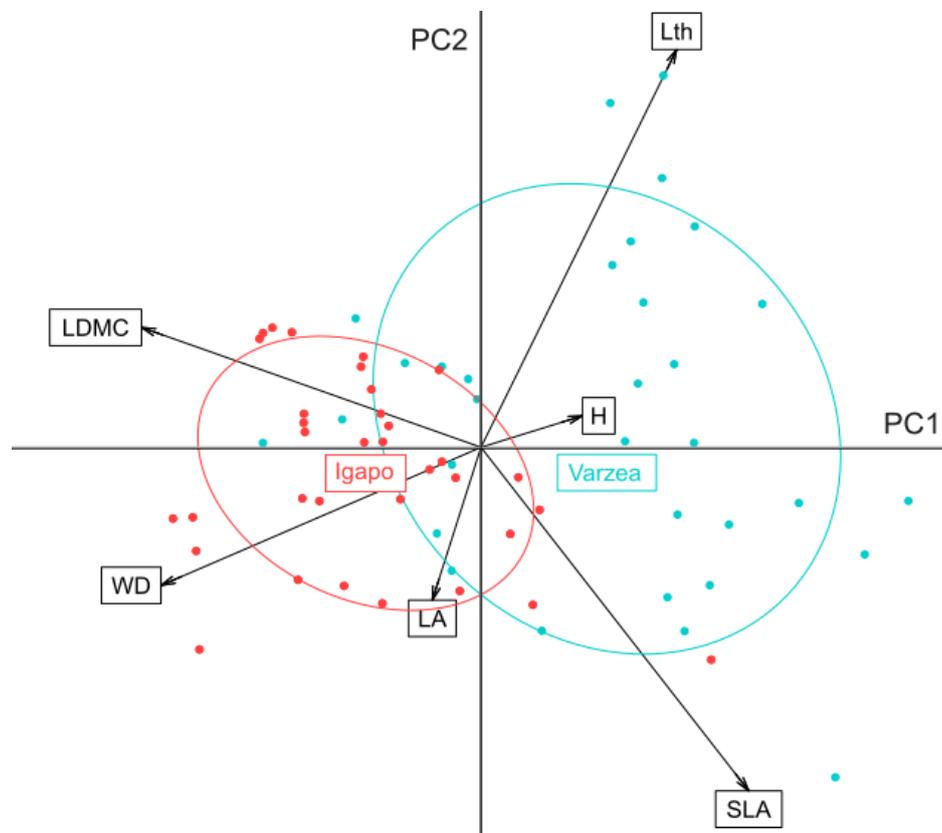


Fig. 2. PCA showing the relationship between the evaluated functional traits and the two types of floodplain forests. Each point represents the individuals sampled and the colors indicate the forest to which they belong to: Várzea (gray) or Igapó (black).

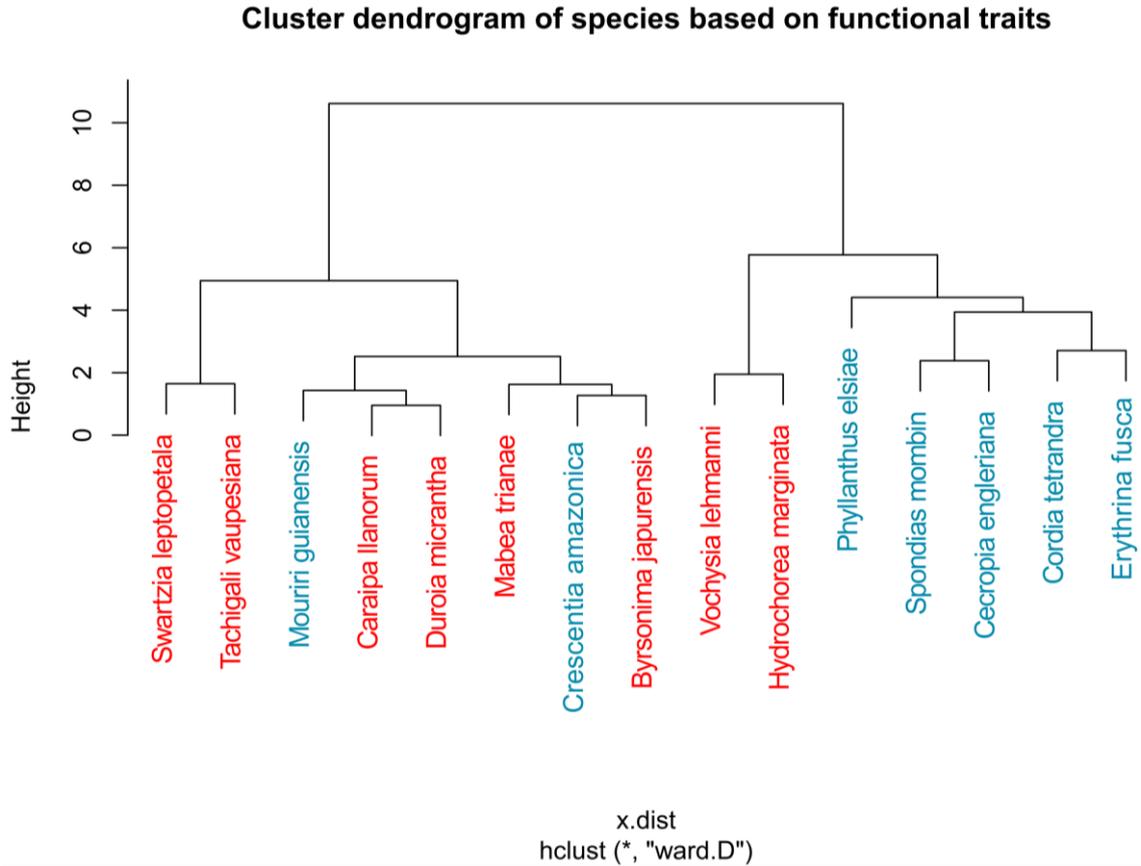


Fig. 3. Cluster dendrogram of the Várzea (gray) and Igapó (black) most abundant species based on the sampled functional traits. Most of the Várzea species are grouped to the right, while most of the Igapó species are found in the group on the left. However, *M. guianensis* and *C. amazónica*, which are Várzea species, are grouped with the Igapó species while *V. lemannii* and *H. marginata*, which are Igapó species, are grouped with the Várzea species.

There are significant differences between the white (Várzea) and black water (Igapó) forests in terms of Lth ($P < 0.05$), WD ($P < 0.05$) and LDMC ($P < 0.01$) (Fig. 4), while LA, SLA and H did not show significant differences ($P > 0.05$). Furthermore, when we observe the CWM values (Table 2), it is evident that the Várzea forest presents SLA and Lth values 1.60 and 1.74 times higher (respectively) than Igapó; Igapó presents LA, LDMC, WD and H values 4.97, 1.85, 1.62 and 1.15 times higher (respectively) than Várzea.

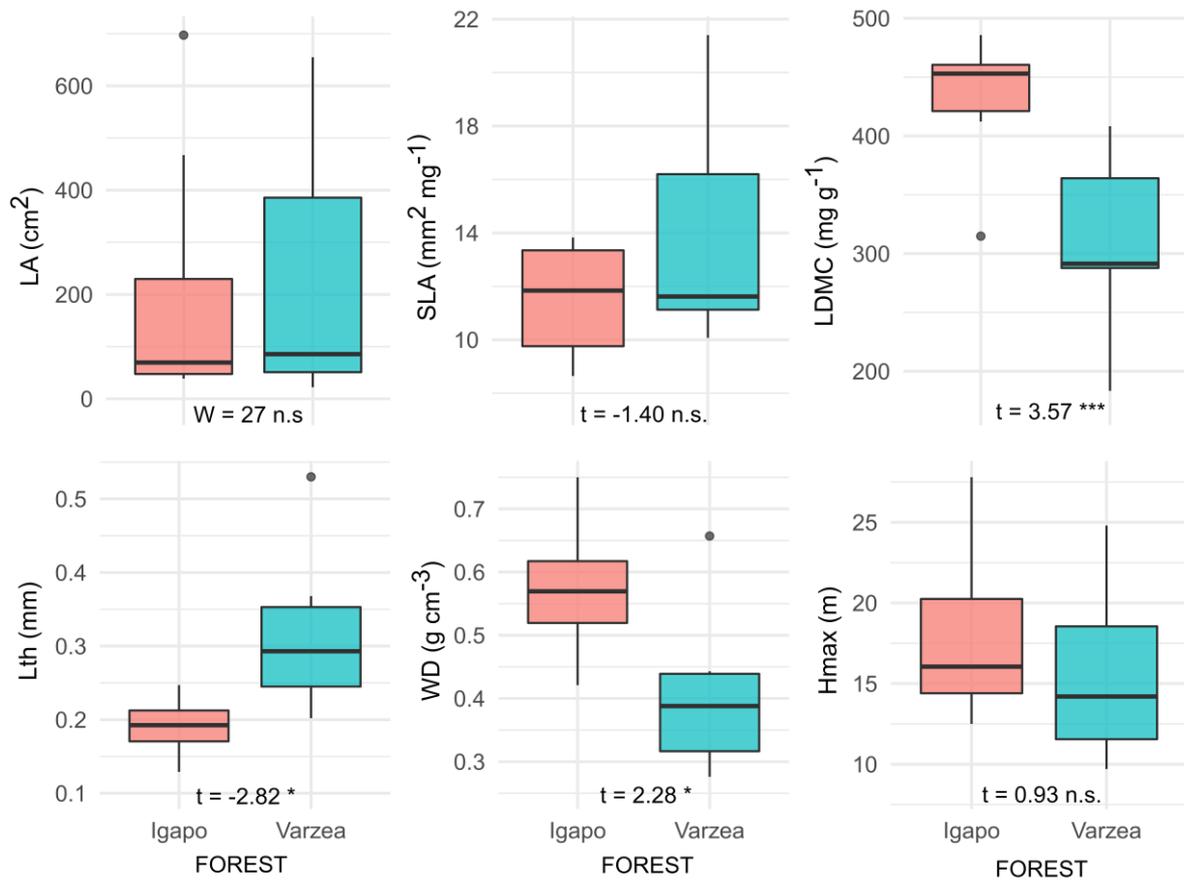


Fig. 4. Variation of functional traits within and between the two types of flooded forest: Várzea (gray) and Igapó (black). At the bottom of each graph is the t or W-value according to the test performed (T-test or Wilcoxon test) to compare forest types. Significant differences are considered to exist when $P < 0.05$; n.s. denotes no significant differences. * symbolizes a $P < 0.05$ and *** symbolizes a $P < 0.005$. LA = leaf area; SLA = specific leaf area; LDMC = leaf dry matter content; Lth = leaf thickness; WD = wood density; H = plant height.

Table 2. Community Weighted Mean (CWM) values

CWM trait values (\pm standard deviation) according to forest type (Várzea and Igapó) for leaf area (LA), specific leaf area (SLA), leaf dry matter content (LDMC), leaf thickness (Lth), wood density (WD) and plant height (H).

	LA (cm ²)	SLA (mm ² mg ⁻¹)	LDMC (mg g ⁻¹)	Lth (mm)	WD (g cm ⁻³)	H (m)
Várzea	97.44 (275.01)	17.55 (4.13)	251.16 (74.58)	0.33 (0.11)	0.42 (0.13)	13.68 (5.38)
Igapó	484.40 (247.73)	10.98 (2.03)	465.30 (53.24)	0.19 (0.04)	0.68 (0.10)	15.80 (5.91)

Functional diversity components of Várzea and Igapó forests

In terms of FRic, both Várzea and Igapó present low values, indicating that the dominant species occupy a reduced functional space. However, the Igapó index is nine times lower than that of Várzea (0.008 and 0.072, respectively). The FEve yielded similar values for both forest types (0.75 for Várzea and 0.68 for Igapó), showing that they have intermediate functional equitability and, therefore, that the distribution of trait values is not entirely uniform within the space niche occupied in any of the forests. Regarding the FDiv, we found high indices for both Várzea and Igapó (0.95 and 0.92, respectively), suggesting that the traits vary widely and that the species abundance and/or traits are clustered at the edges of the occupied niche space. Finally, the FDis indicate that the average distances of the individual species to the centroid of each community are high for both forest types. However, the Várzea index is 1.42 times higher than the Igapó (2.11 and 1.49, respectively).

Importance of internal and external filters on the community assembly of flooded forest

The SES for the functional traits of the floodplain forest, in relation to the null models, is shown in Fig. 5. All the traits show significantly different mean values (negative SES) for the T_IP.IC (individuals-populations/communities), which refers to the influence of the internal filters. In contrast, the external filters show differences in few traits; T_IC.IR (individuals-communities/regional pool) presents significant differences (negative SES) for LDMC and WD while T_PC.PR (populations-communities/regional pool) does not show significant differences for any trait.

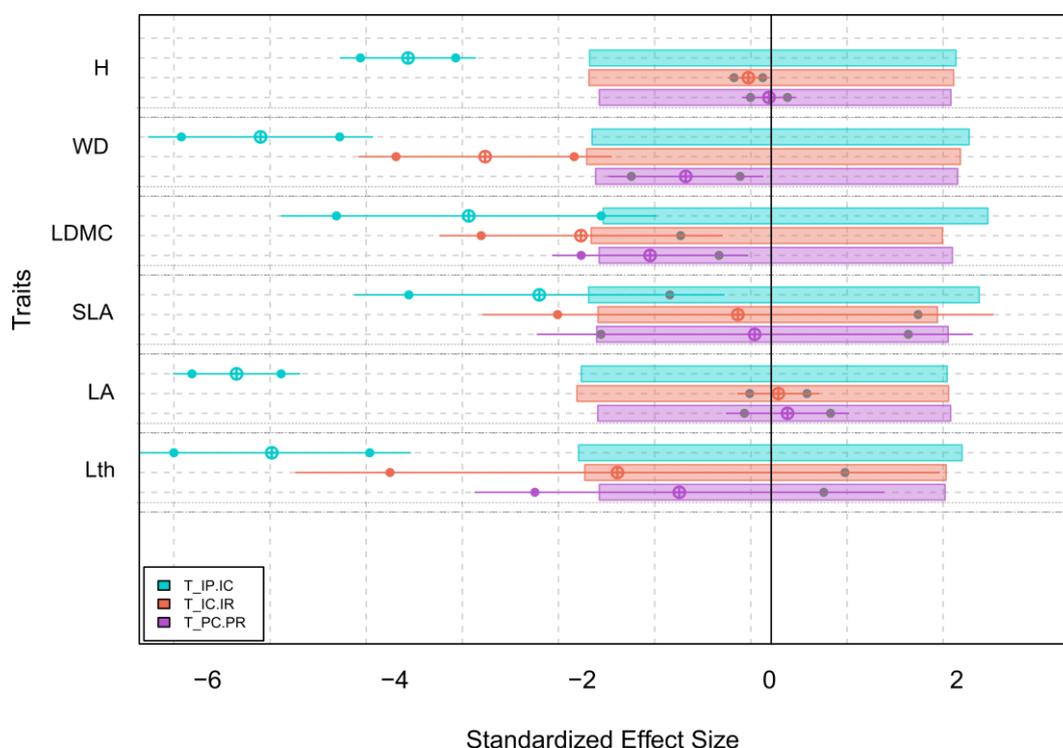


Fig. 5. Standardized effect size (SES) for three T statistics evaluated on six functional traits in the flooded forest (Igapó and Várzea): (1) plant height (H); (2) wood density (WD); (3) leaf dry matter content (LDMC); (4) specific leaf area (SLA); (5) leaf area (LA) and (6) leaf thickness (Lth). The T statistics evaluated are: 1) T_IP.IC (black): ratio observed between the variance of the populations and the total variance of the communities at the individual level, 2) T_IC.IR (dark gray): ratio observed between the variance of each community and the total variance of the regional pool at the individual level and 3) T_PC.PR (light gray): observed ratio between the variance of each community and the total variance of the regional pool at the population level. The filled circles represent the SES values of the two plots sampled according to each statistic and each trait. The crossed circles and the segments respectively represent the mean and standard deviation of the SES values of the two plots for each T statistic. The boxes delimit the confidence interval of each null model by trait: the mean of the SES (crossed circle) is significantly different from the random distribution if it is not within the box ($P < 0.05$).

At the forest level (Fig. 6) we observe that, in the case of Várzea, all traits have significantly lower negative SES values than the null models for the T_IP.IC; T_IC.IR only shows a significant difference (negative SES) for WD while T_PC.PR shows no significant differences. As for the Igapó forest, T_IP.IC presents negative significant differences for all the traits, except for SLA. However, in this case, the T_IC.IR and T_PC.PR show significant differences in more than one trait: T_IC.IR shows significantly lower negative SES values in four of the six traits analyzed (WD, Lth, LDMC, and SLA) while T_PC.PR shows significant differences (negative SES) in three functional traits (Lth, LDMC, and SLA). In both Várzea and Igapó, LA and H traits do not show significant differences for the T_IC.IR and T_PC.PR. P-values of all the tests performed are found in Table S4.

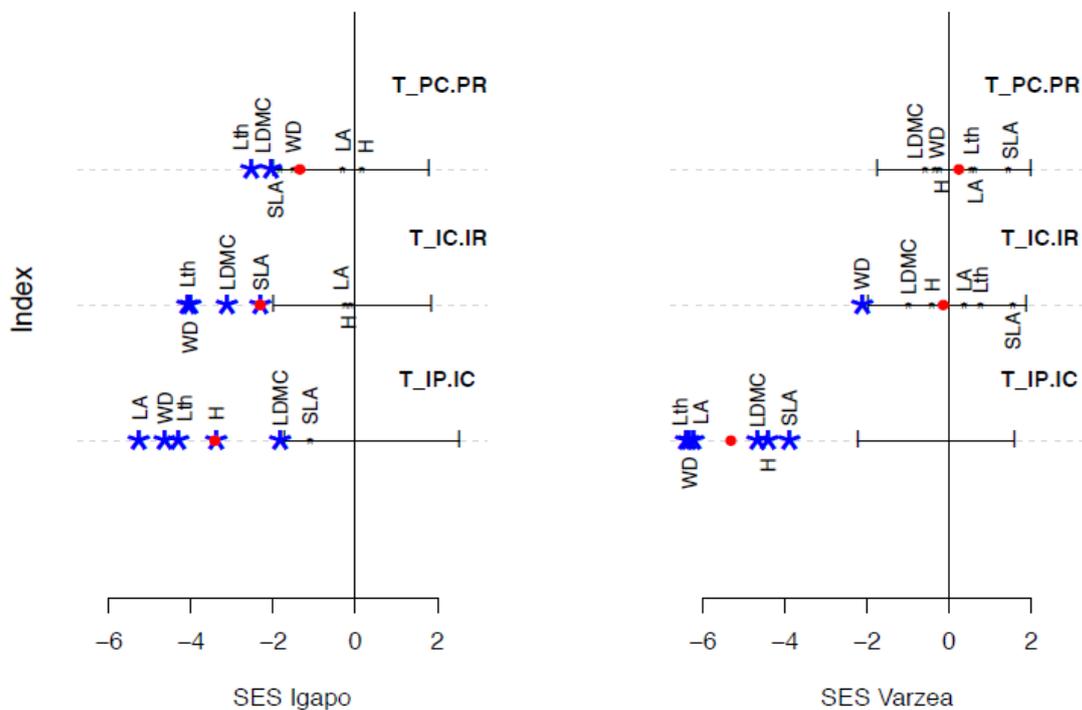


Fig. 6. Standardized effect size (SES) of the six functional traits evaluated for three T statistics according to each forest type: Várzea on the right and Igapó on the left. The T statistics evaluated are: 1) T_IP.IC: observed ratio between the variance of the populations and the total variance of the communities at the individual level, 2) T_IC.IR: observed ratio between the variance of each community and the total variance of the regional pool at the individual level and 3) T_PC.PR: observed ratio between the variance of each community and the total variance of the regional pool at the population level. The segments observed in each figure represent the expected random ranges corresponding to each T statistic. The blue asterisks indicate significantly lower differences compared to the null models ($P < 0.05$). Red dots show the average SES of all traits for each statistic.

Discussion

There is a functional divergence between the Várzea and Igapó forests, although not for all traits. Várzea species are mainly characterized by traits related to high growth rates, while the Igapó species have traits mainly associated with low growth rates, as expected. Regarding the influence of external and internal filters we observed that, as expected, internal filters are more influential than external filters in Várzea. However, in Igapó both filters are important even though we had hypothesized that external would be more influential.

Functional divergence between Várzea and Igapó forests

Despite the low taxonomic diversity of flooded forests, our results suggest that there is a partial differentiation between the Várzea and Igapó functional trait values (Figs 2, 3 and 4). Igapó showed high WD and LDMC values, which are associated with low growth rates and a high investment in strong and long-lasting tissues; this in turn is related to greater resistance to physical damage and survival under stress conditions (Lavorel and Garnier 2002). Therefore, it is possible that these values respond to the low nutrient availability, characteristic of black water forests (Gómez 2015). In contrast, Várzea presented low WD and LDMC values, indicating that in this forest, species invest less energy in the construction of leaf and wood tissues and, therefore, have high growth rates (Lavorel and Garnier 2002). The dominance of functional traits related to higher growth rates could be associated with the availability of nutrients provided by the white waters of the Meta River.

Additionally, we found that the Várzea species have higher Lth than Igapó (Fig. 4). Unlike what was expected (Garnier *et al.* 2016), in these forests Lth was positively correlated with SLA. However, if we consider that the strongest anatomical driver of Lth variation is the number and thickness of the mesophyll layers (Pérez-Harguindeguy *et al.* 2013), it is possible that in Várzea thick leaves contribute to improving the photosynthetic rate, given the lower concentration of N and inorganic C observed in the soil (Gómez 2017). Finally, although we did not observe significant differences between Várzea and Igapó for SLA, the species in Igapó present lower values (Fig. 4 and Table 2) and could

therefore indicate low photosynthetic and carbon gain rates (Reich 2014), while in Várzea there is no clear trend (Fig. 4). It is possible that there are no significant differences between the H and LA values of Várzea and Igapó (Fig. 4) due to similar light intensity (Gómez 2017).

Internal and external filter influence on the community assembly and its effect on the functional diversity of flooded forests

According to our findings, internal filters are more important than external filters on the community assembly of flooded forests (Fig. 5). This means that despite the stress generated by the flooding or the nutrient availability, local processes are more important in both Várzea and Igapó. Particularly, microhabitat specialization could be more influential because the two forest types exhibited high FDiv and FDis, in addition to the high soil heterogeneity of these forests, associated with distances to the river and nutrient gradients (Gómez 2017). Taken together, this suggests that internal filters (e.g., microhabitat heterogeneity) have led to a high degree of niche differentiation between species in these flooded forests. It is worth mentioning that this is particularly true in Várzea since it exhibits greater trait variability (Fig. 2) and higher FDiv and FDis values, although they occur within a reduced space of functional traits (both Várzea and Igapó have low FRic values).

We also found that external filters are relevant for some traits in the Igapó forest (Fig. 6), since negative T_IC.IR values (individuals-communities/regional pool) and T_PC.PR (populations-communities/regional pool) indicate low variability at the individual and species level. This could be related to the low nutrient availability of black water forests, which would impose nutritional limitations on plants. In addition, the importance of the nutrient availability filter would explain why there is a lower FRic in the Igapó forest. However, a low FRic index could also imply a low buffering capacity against environmental fluctuations, because less trait variability implies a lower probability of resistance to disturbances (Tilman 1996; Mason *et al.* 2005).

In the Várzea forest, external filters seem to be important for only one of the six traits evaluated (Fig. 6), suggesting that, thanks to the nutrient availability provided by the Meta River, external filters would not be as influential and would allow for a higher FRic. These values are associated with a more complete use of the available resources and higher productivity, as well as the ability to deal with environmental fluctuations (Mason *et al.* 2005; Tilman 1996). However, the intermediate FEve values indicate that some parts of the niche space, despite being occupied, are underused, which would decrease productivity and increase the probability of invasion (Mason *et al.* 2005). Discrepancies between the significance of the T_IC.IR and T_PC.PR statistics (Figs 5 and 6), reflect the importance of considering intraspecific variation in this type of analyses even in forests with low taxonomic diversity.

Orinoquia flooded forests compared to other ecosystems

Expression of differentiated growth strategies along gradients has been widely documented; for example, Maracahipes *et al.* (2018) showed that in the Brazilian Cerrado conservative traits, related to a slow growth rate, were associated with species recorded in savannas, while acquisitive traits, related to a fast growth rate, were associated with species found in forests. Similarly, these strategies have been observed in dry and wet tropical forests across different successional states (Lohbeck *et al.* 2015; Poorter *et al.* 2019). Furthermore, it is important to mention that ecological strategies of plants could be influenced by biotic interactions such as herbivory (Birhane *et al.* 2015).

In 2019, Mori *et al.* reported differences between the functional traits of the Várzea and Igapó forests in central Amazonia (Brazil), showing that white water forests have traits associated with rapid growth, while black water forests have traits related to low growth rates, as corroborated in this study. However, abiotic constraints such as nutrient availability appear to be less important in the Orinoquia floodplain forests, since the Igapó trait values in this study (Casanare) are more similar to those reported for Várzea in the Amazon (Mori *et al.* 2019). For instance, in our study the Igapó forest has an average LDMC of 433 mg g⁻¹, while in the Amazon, the LDMC average for Várzea and Igapó was 671 and 1829 mg g⁻¹, respectively. In the same way, while we found an average WD of 0.57 g cm³ in Igapó, Mori *et al.* (2019) reported an average of 0.59 and 0.75 g cm³ for Várzea and Igapó, respectively. This comparison was made using the mean values of functional traits of the genera evaluated in the Amazon (7 in Várzea and 8 in Igapó); although more species were included in the Amazon, these studies are comparable in terms of individuals (ca. 70 individuals in both studies).

Functional differences between the floodplain forests of these two basins could be due to the fact that there is higher conductivity (concentration of dissolved ions) in the main rivers of the Orinoco basin. In a review of the Orinoco and Amazon basin characteristics, Godoy *et al.* (1999) reported that two tributaries of the Orinoco river, the Meta (white water) and the Atabapo (black water), have a higher conductivity (72.9 and 14.6 μS cm⁻¹, respectively) compared to the Solimoes (white water) and Negro (black water) rivers, which are large tributaries of the Amazon River (58.0 and 9.0 μS cm⁻¹, respectively). However, it is necessary to take into account that both basins have a wide diversity and complexity of channels along their river networks. To corroborate this higher conductivity hypothesis in the Orinoco, it is necessary to carry out a greater sampling along these basins, given that, so far we know, these two are the only functional traits studies carried out in tropical flooded forests.

When we compare the functional traits of the floodplain forest with values of the tropical dry forests of Colombia (Thomas *et al.* 2017; retrieved from the global database of functional characteristics of plants, TRY [Kattge *et al.* 2011]), we found that they have similar average trait values for SLA (floodable: 12.68 mm² mg⁻¹ and dry: 12.45 mm² mg⁻¹), LDMC (floodable: 376 mg g⁻¹ and dry: 397 mg g⁻¹) and WD (floodable: 0.49 g cm³ and dry: 0.58 g cm³). This suggests that the same trait values respond to different types of

stress: improving nutrient retention in floodplain forests while allowing hydraulic operation and decreasing water potential during the drought in tropical dry forests (Prado *et al.* 2016). However, based on the three trait values obtained through TRY, it is evident that the dry forest presents a greater variability. For example, while this dry forest has WD values ranging from 0.1 to 3 g cm³, in the floodplain forest, it varies from 0.28 to 0.75 g cm³. Although this comparison could be biased by the small number of individuals sampled in the floodplain forest compared to those in the dry forest, this pattern is worth exploring in more detail, since both forests are under high abiotic stress, which can lead to convergent functional responses in plants.

Paradoxically, Prado *et al.* (2016) found that in tropical dry forests, areas with less nutrient availability had higher biomass productivity, probably due to the functional trait values that they possess. We hypothesized that in floodplain forests, and in particular in black water forests (Igapó), the functional traits filtered by low nutrient availability could be an important driver of biomass productivity; keeping in mind that the high LDMC and WD values that we obtained could be associated with a greater longevity and resistance to physical damage, which in turn would confer a lower mortality rate and a greater accumulation of biomass over time. This would be corroborated by González (2015), who observed a lower mortality rate and greater annual changes in biomass per hectare in the Igapó forests of Vichada (Colombia), compared to *terra firme* forests. Lastly, our trait values (Table S3) are within the ranges reported for tropical forests: LA (2.03—640497 cm²); SLA (6.25—37 mm² mg⁻¹); LDMC (210—640 mg g⁻¹); Lth (0.01—≤0.04 mm); WD (0.23—0.98 g cm³) and H (6.1—40.4 m) (Bongers and Popma 1990; Lebrija *et al.* 2010; Wright *et al.* 2010; Paine *et al.* 2011).

In conclusion, our results indicate that these forests should not be understood as one ("flooded forest"), since the disparities in the soil composition may have led to differences between the magnitudes of the filters that govern community assembly processes. Although internal filters were important in both forest types, the external filters influence in Igapó may have a key effect on the functional trait divergence. However, it is important to note that despite the low taxonomic and functional richness, there is high functional divergence. This has important implications related to the conservation of flooded forests and the ecosystem services they offer, since not all species of a forest type (Várzea or Igapó) have traits associated with a single growth strategy. Finally, our results highlight the need to continue investigating the functional diversity of flooded forests, considering that there are other types of floodplain forests and there could be functional differences based on the hydrographic basins.

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Supplementary material

Table S1. Selected species according to relative abundance (based on Cárdenas 2012). Family and relative abundance for each species are detailed according to the type of forest: Várzea and Igapó.

	Family	Specie	Relative abundance
Várzea	Urticaceae	<i>Cecropia engleriana</i>	0.058
	Boraginaceae	<i>Cordia tetrandra</i>	0.138
	Bignoniaceae	<i>Crescentia amazonica</i>	0.101
	Fabaceae	<i>Erythrina fusca</i>	0.038
	Melastomataceae	<i>Mouriri guianensis</i>	0.029
	Phyllanthaceae	<i>Phyllanthus elsiae</i>	0.554
	Anacardiaceae	<i>Spondias mombin</i>	0.024
Total			0.942
Igapó	Malpighiaceae	<i>Byrsonima japurensis</i>	0.075
	Rubiaceae	<i>Duroia micrantha</i>	0.081
	Fabaceae	<i>Hydrochorea marginata</i>	0.026
	Calophyllaceae	<i>Caraipa llanorum</i>	0.018
	Euphorbiaceae	<i>Mabea trianae</i>	0.033
	Fabaceae	<i>Swartzia leptopetala</i>	0.033
	Fabaceae	<i>Tachigali vaupesiana</i>	0.564
	Vochysiaceae	<i>Vochysia lehmannii</i>	0.051
Total			0.882

Table S2. General description of the functional traits included in this study, which details the acronyms, units of measurement and the associated function.

Functional trait	Associated function	Reference
Leaf area, LA (mm ²)	Light interception area, transpiration, gas exchange.	Lebrija-Trejos <i>et al.</i> 2010.
Specific leaf area, SLA (mm ² mg ⁻¹)	Relative growth rate, leaf life, leaf concentration and photosynthetic capacity.	Lavorel y Garnier 2002; Poorter <i>et al.</i> 2006.
Leaf thickness, Lth (mm)	Physical strength of the leaves, photosynthetic rate and key component of SLA.	Pérez-Harguindeguy <i>et al.</i> 2013.
Leaf dry matter content, LDMC (mg g ⁻¹)	Construction costs, nutrient retention, resistance against herbivory and physical damage.	Poorter <i>et al.</i> 2006.
Wood density, WD (g.cm ⁻³)	Construction costs, growth rate, architecture, resistance to pathogens and mortality rate.	Swenson y Enquist 2008; Chave <i>et al.</i> 2009.
Plant height, H (m)	Growth form, position in the vertical light gradient, competitive vigor, plant fertility and potential shelf life.	Pérez-Harguindeguy <i>et al.</i> 2013.

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Table S3. Mean values (Mean), standard deviation (SD), maximum (Max) and minimum (Min) values of each functional trait according to the forest types: Várzea and Igapó.

	Várzea				Igapó			
	Mean	SD	Max	Min	Mean	SD	Max	Min
LA	233.65	275.01	654.81	22.21	197.75	247.75	697.18	38.61
SLA	13.96	4.13	21.41	10.07	11.56	2.03	13.83	8.64
LDMC	312.41	74.58	408.29	183.40	433.51	53.24	485.78	314.82
Lth	0.32	0.11	0.53	0.20	0.19	0.04	0.25	0.13
WD	0.41	0.13	0.66	0.28	0.57	0.10	0.75	0.42
H	15.56	5.38	24.80	9.7	18.28	5.91	27.80	12.50

Table S4. P-values of the two unilateral statistical tests performed (lower and upper limit) to compare the T statistics with the random expectations, according to each functional trait and forest type. P < 0.05 (bold) indicates significant differences.

		Lth	LA	SLA	LDMC	WD	H
Várzea	T_IP.IC inf	0.001	0.001	0.002	0.001	0.001	0.001
	T_IP.IC sup	1.000	1.000	0.999	1.000	1.000	1.000
	T_IC.IR inf	0.746	0.637	0.939	0.163	0.020	0.332
	T_IC.IR sup	0.255	0.364	0.062	0.838	0.981	0.669
	T_PC.PR inf	0.697	0.707	0.915	0.311	0.410	0.486
	T_PC.PR sup	0.304	0.294	0.859	0.690	0.591	0.515
Igapó	T_IP.IC inf	0.001	0.001	0.090	0.008	0.001	0.002
	T_IP.IC sup	1.000	1.000	0.911	0.993	1.000	1.000
	T_IC.IR inf	0.001	0.374	0.010	0.002	0.002	0.445
	T_IC.IR sup	1.000	0.627	0.991	0.999	0.999	0.556
	T_PC.PR inf	0.004	0.405	0.023	0.027	0.071	0.486
	T_PC.PR sup	0.997	0.596	0.978	0.974	0.930	0.515