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RESEARCH ARTICLE

Floristic diversity, composition and dominance across Amazonian forest types respond differently to latitude

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Abstract

Aim: The latitudinal biodiversity gradient is considered a first-order biogeographical pattern for most taxonomic groups. Latitudinal variation in plant diversity is not always consistent, and this could be related to the particular characteristics of different forest types. In this study, we compare latitudinal changes in floristic diversity (alpha diversity), composition (beta diversity) and dominance across different tropical forest types: floodplain, *terra firme* and submontane forests.

Location: Western Amazonia (Ecuador, Peru and Bolivia).

Taxon: Woody plants.

Methods: We inventoried 1978 species and 31,203 individuals of vascular plants with a diameter at breast height ≥ 2.5 cm in 118 0.1-ha plots over an 1800 km latitudinal gradient in three different forest types. The relationships between alpha diversity, latitude and forest type were analysed using generalised linear mixed models. Semi-parametric permutational multivariate analysis of variance was used to investigate the effects of latitude and forest type on beta diversity. Dominant species abundances were correlated with non-metric multidimensional scaling ordination axes to reflect their contributions in shaping changes in beta diversity.

Results: Alpha diversity increased towards equatorial latitudes in *terra firme* and submontane forests but remained relatively constant in floodplains. Beta diversity of all forest types changed with latitude, although less clearly in floodplains. Also, in floodplain forests, there were fewer dominant species contributing to beta diversity and more species homogeneous along the gradient.

Main Conclusions: Latitudinal diversity patterns are manifested in alpha and beta diversity since latitude summarizes climatic and edaphic changes. However, we found different responses of each forest type. In floodplain forests, inundation regime is a stronger predictor than latitude, limiting floristic diversity and composition. Changes in dominant species abundance over gradients explained species composition, but floodplain forests harboured more homogeneous dominant species than well drained forests. It is key to study environmental trends and habitat characteristics of each forest type to understand their species diversity and dominance patterns.

KEYWORDS
climatic seasonality, environmental limitations, latitudinal diversity gradient, seasonal flooding, soil heterogeneity, species abundance, tropical forests, turnover, woody plants distribution

1 | INTRODUCTION

Understanding the causes of spatial variations in floristic diversity (alpha diversity) and composition (beta diversity) is a central issue in plant biogeography. Diversity and distribution mechanisms have been studied by biogeographers and ecologists for several decades, thereby yielding many insights into the measurement and quantification of their components, including alpha and beta diversity (Chave, 2008). Alpha diversity is related to local/within-habitat diversity (Melo et al., 2009), whereas beta diversity was originally defined as the degree of community differentiation along environmental gradients (Whittaker, 1960). Beta diversity has recently been used in a wider context to describe species compositional changes at any scale, including communities, habitats or gradients (Jost et al., 2011), regardless of the mechanisms involved (McKnight et al., 2007). Variations in species influence diversity over large scales (Condit et al., 2002) since both alpha and beta diversity are crucial for understanding biogeographical patterns.

The latitudinal gradient is considered a first-order biogeographical pattern and it is a good example of how spatial variation influences floristic patterns (Rull, 2020). The latitudinal gradient itself is not a mechanistic factor (ter Steege, 2010), but it generally summarises changes in environmental conditions, thereby providing a good unimodal predictor of changes in plant diversity (Stropp et al., 2009; ter Steege & Hammond, 2001). Globally, the latitudinal diversity gradient exhibits an increasing trend towards the Equator (Chave, 2008; Willig & Presley, 2013), with a peak at ~2.5°S (Stropp et al., 2009; ter Steege, 2010). This increase in species richness is determined by a combined environmental and geographical gradient (Baselga, 2008) related with the increase in temperature, the reduction in precipitation seasonality (Brown, 2014) and the increase in soil complexity (Higgins et al., 2011), resulting in higher productivity around the equatorial belt. In particular, the stable wet and warm climate of western Amazonia (ter Steege, 2010), characterised by lower extinction and higher species immigration rates (Vasconcelos et al., 2022), have contributed to species diversification, with peaks in areas with less seasonal precipitation (Hoorn et al., 2010) and high topographical relief (Antonelli et al., 2018). In parallel, some studies have also pointed out an increase in beta diversity towards the Equator globally (Nishizawa et al., 2022), and both in the southern (Koleff et al., 2003; Toledo et al., 2011) and northern hemispheres (Dyer et al., 2007; Qian & Ricklefs, 2007). However, this relationship is inconsistent, since beta diversity is driven by the effects of climate, edaphic properties, the species ecological tolerance (Legendre, 2014), and the geographical constraints affecting dispersal limitation (Baselga, 2008). In fact, some studies found that factors other than latitude might shape beta diversity, such as elevation and flooding regimes (McKnight et al., 2007), spatial study extent (Soininen et al., 2007), different forest types (Emilio et al., 2010) or differential responses of organisms (Melo et al., 2009).

Many Amazonian forests are ruled by the 'few common, many rare' law, where a small number of dominant species account for most vascular plants at large scales (Macía & Svenning, 2005; Pitman et al., 2001; ter Steege et al., 2013). It is known that rare species represented by only a few individuals (Whittaker, 1965) contribute more to alpha diversity than common species. However, contradictory results have been obtained regarding the importance of dominant species in determining beta diversity. Some studies indicate that rare species shape floristic composition, and dominant species are a poor proxy for changes in the entire community composition due to their broad niche breadths (Arellano et al., 2014) and wide geographical distribution (Pitman et al., 2001). In addition, dominance by a few species over high floristic heterogeneity is also possible when these few shared species represent most

of the individuals (Arellano, Jørgensen, et al., 2016). By contrast, some authors have suggested that turnover of dominant species is representative of changes in the entire floristic community (Draper et al., 2019), and thus changes in dominance can shape patterns of beta diversity. However, the extent to which these dominant species contribute to beta diversity across forest types is still poorly understood.

In this study, we analysed changes in floristic diversity, species composition and dominance across different Amazonian forest types (floodplain, *terra firme* and submontane forests) over an 1800 km latitudinal gradient in western Amazonia. This region is a mosaic of nutrient-poor soils from Miocene sedimentary basins and relatively more recent nutrient-rich soil formed by sediments from the Andean uplift (Higgins et al., 2011; Hoorn et al., 2010; Quesada et al., 2011; Toledo et al., 2011; Tuomisto et al., 2019; Val et al., 2022). It is characterised by high forest productivity, environmental heterogeneity, and fast dynamics and turnover, thereby leading to high speciation in evolutionary time (Hoorn et al., 2010; ter Steege, 2010). Western Amazonia is also noted for its heterogeneous habitat types, which harbour different amounts of floristic variation (Emilio et al., 2010). Each habitat is characterised by its own ecological and evolutionary processes (Guayasamin et al., 2022; Val et al., 2022), physiognomy, seasonal flooding, geomorphological complexity, elevation (Emilio et al., 2010) and seed dispersal limitations (Dambros et al., 2020). These attributes are responsible for changes in floristic composition and diversity (Emilio et al., 2010; ter Steege, 2010; Toledo et al., 2011) along the latitudinal gradient. Many previous studies differentiated Amazonian forest types in their analyses (Draper et al., 2019; Emilio et al., 2010; Oliveira-Filho et al., 2021; Stropp et al., 2009; ter Steege et al., 2019), and others considered *terra firme* and floodplain forests (Assis et al., 2017; Bredin et al., 2020; Myster, 2017), or submontane and *terra firme* forests (Macía, 2008; Macía et al., 2007; Macía & Svenning, 2005). Some studies showed that despite the importance of forest types explaining alpha diversity, latitude usually had a stronger effect than forest types in Amazonia (Stropp et al., 2009). In fact, floristic patterns are the result of the interactions between heterogeneous environmental conditions resulting from both large-scale latitudinal climatic and edaphic trends, biogeographical history and local habitat physiognomy and species dynamics (Bicudo et al., 2019; Brown, 2014; Vasconcelos et al., 2022). Since different forest types are present at similar latitudes, considering forest type in the analyses can add further information on the drivers of floristic variation and biogeographical patterns might be more easily recognised (Vasconcelos et al., 2022).

To the best of our knowledge, this study is the first to focus on the relative contributions of latitude to species diversity, composition and dominance across large scales in three different Amazonian forest types: floodplain, *terra firme* and submontane forests. Our specific objectives were (1) to investigate species diversity (alpha diversity) patterns across forest types along a latitudinal gradient in western Amazonia. We hypothesised that species diversity would increase towards the Equator at similar rates for all forest types; (2) to analyse the effect of latitude on differences in species composition (beta diversity) and whether these changes vary across forest types. We hypothesised that latitude would influence beta diversity similarly for all forest types and (3) to analyse the roles of dominant species in determining changes in beta diversity across latitudinal gradients for each forest type. We hypothesised that changes in dominant species will be representative of changes in the entire floristic community. We considered that this pattern would be similar for each forest type, and dominant species of each forest type would lead patterns in species turnover. The results of this study are expected to improve our understanding of the latitudinal diversity patterns in tropical rainforests, analysed from the habitat scale, with a particular focus on dominant species. By considering forest type in our analysis, we expect to discern the relative importance of large latitudinal climatic and edaphic trends from the effects of the unique attributes characterising the different Amazonian forest types in driving species diversity, composition and dominance patterns.

2 | MATERIALS AND METHODS

2.1 | Study area

We selected 13 western Amazonian forest regions ranging from Ecuador to Bolivia (Figure 1b). The forest regions encompassed one or two different forest types comprising floodplains, *terra firme* and submontane forests. This forest type classification is based on the combination of flooding patterns and elevation, which has been shown to influence floristic variation (Dambros et al., 2020; Emilio et al., 2010; ter Steege, 2010). Amazonian floodplain forests are the most diverse flooded forests in the world (Myster, 2017). Floodplain soils of Western Amazonia are very recent (ca. 5000 years) and the most fertile from the Amazonian basin. They are fed by white-water rivers and runoff water with material from the Andes slopes (Quesada et al., 2011). They are typically found at elevations below 500 m (Bayley et al., 1992; Macía, 2011) with marked flooding seasonality and flat slopes, comprising flooded areas along stream and river systems (Wittmann et al., 2011). Flooding leads to oxygen deficiency and low water conductance (Myster, 2017), affecting community composition, species richness, growth rates, wood density, phenological strategies and fruit/seed morphology (Hawes & Peres, 2016). *Terra firme* forests are found at similar elevations with precipitation regimes and slope inclinations equivalent to those of floodplains; nevertheless, they are well drained and never flooded (Condit et al., 2002). They are characterised by fertile and variable soils, with high diversity (more than 300 species ≥ 10 cm diameter at breast height (DBH) per hectare (Gentry, 1988)), due to the presence over large areas of both rare and dominant species (Pitman et al., 2001). Submontane forests are located at higher elevations between 500 and 1100 m, but they are still well drained and never flooded (Berni, 2017). These areas are known to have high species richness, as montane and lowland species coexist (La Torre-Cuadros

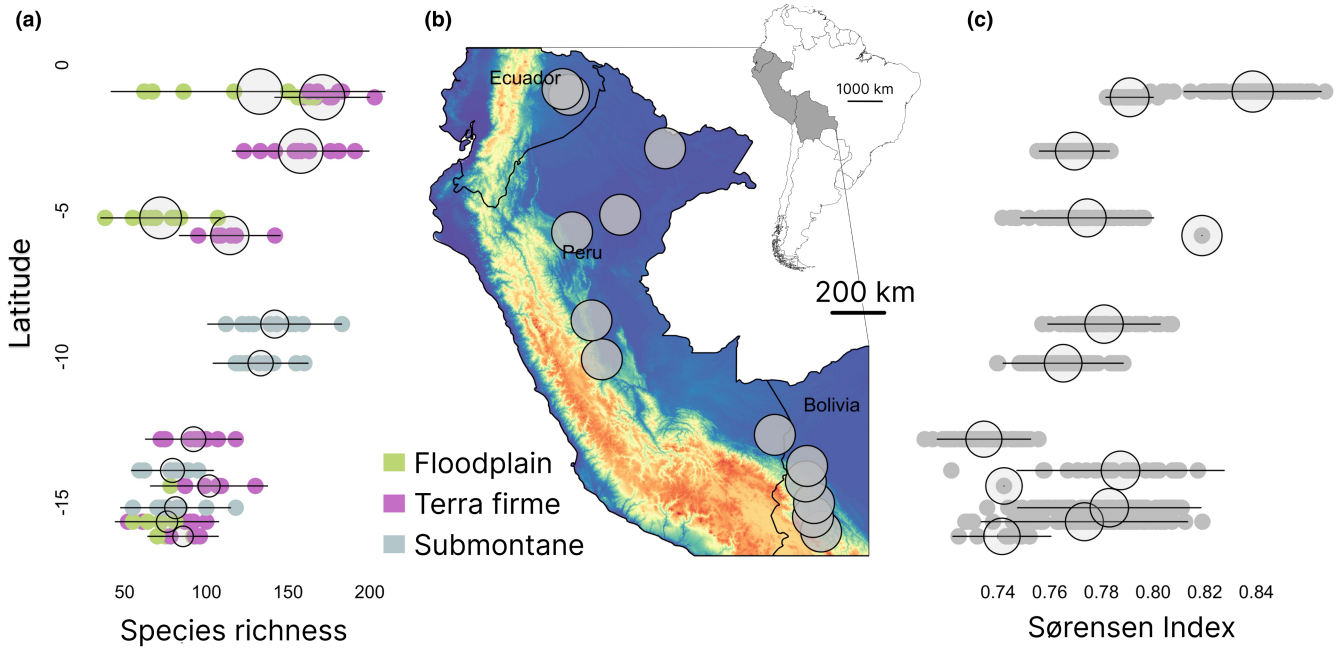

FIGURE 1 (a) Number of vascular woody plant species per plot coloured per forest type: Floodplains in green, *terra firme* in pink and submontane in grey. Means per region are shown in light grey circles and their standard deviation represented by a black line. (b) Locations of the 13 study regions in western Amazonia (Peru, Bolivia and Ecuador) (see Table S1) plotted on a digital elevation model (shuttle radar topography Mission (SRTM)) in WGS84 datum, latitude–longitude coordinate reference system. (c) Sørensen index at each region resampled at a common standard sample size of six plots (samples = 100) in grey calculated with the *beta. Sample* function in the 'betapart' R package version 1.5.4 (Baselga & Orme, 2012). Means and standard deviations are shown in light grey circles.

et al., 2007). Submontane forests are characterised by irregular topography and geologically younger soils with rich sediments (Toledo et al., 2011). They usually have greater diversity than floodplain forests (ter Steege, 2010), but species composition is similar to that of *terra firme* forests (Macía, 2008) with the same limited set of dominant species (Macía & Svenning, 2005), but weaker oligarchies as elevation acts as limiting factor (Arellano, Jørgensen, et al., 2016).

2.2 | Field sampling and floristic identification

Regions were located throughout an 1800 km latitudinal gradient. In each region, six to 14 0.1-ha plots were established between 1997 and 2019 according to a standard sampling protocol (Arellano, Cala, et al., 2016). Plots (50×20 m) were located at least 300 m apart, avoiding areas affected by human activities and natural disturbances that could create large gaps in the canopy. Overall, we sampled 118 plots in floodplain (n = 27), *terra firme* (n = 51) and submontane (n = 40) forests (Table S1). In each plot, we measured and inventoried all individual woody plants (trees, palms, tree ferns and lianas) with DBH ≥ 2.5 cm rooted within the plot limits. In total, 90% of the individuals were identified to species level, whereas 10% remained as morphospecies, which were excluded from the floristic composition analyses. Taxonomic standardisation of species names was based on the Plant List using the R package 'Taxonstand' version 2.4 (Cayuela et al., 2012). Voucher specimens were classified and stored at different herbaria in Ecuador (QCA, QCNE), Bolivia (LPB) and Peru (USM, MOL).

2.3 | Data analysis

2.3.1 | Latitudinal variation in species richness across forest types

Since both climatic and edaphic variables can affect floristic patterns (Bañares-de-Dios et al., 2022), we first retrieved regional values of all BIOCLIM V1.1 layers from the global 'CHELSA' model at 1 km^2 resolution (Karger et al., 2017), and soil data (pH, soil organic carbon in fine earth g/kg, clay, sand, silt, volume fraction of coarse fragments (>2 mm)) from the global 'SoilGrids' database at 1 km^2 resolution and 15 cm depth (Hengl et al., 2017). Pearson's correlation coefficients between the variables and latitude were high ($r > \pm 0.7$); therefore, the latitudinal gradient might imply a gradient also in the selected variables. To deeply understand how these variables covary and their relationship with latitude, we performed a principal component analysis (PCA) including the mentioned variables. The first PCA dimension explained 51% of the total variance. We selected those climatic and edaphic variables with high Pearson correlation with latitude (r_L) and the PCA axis 1 (r_P): temperature seasonality (°C) ($r_L = -0.93$, $r_P = -0.68$) and precipitation seasonality (mm) ($r_L = -0.90$, $r_P = -0.63$) as climatic variables, and pH ($r_L = -0.87$, $r_P = -0.53$) and soil organic carbon content (g/kg) ($r_L = 0.71$, $r_P = 0.70$) as

edaphic variables (Figure S1). Since high correlations between latitude and these climatic and edaphic variables were found, we run the analyses using latitude as the only explanatory variable, considering it as a proxy of environmental variation and to facilitate results interpretation.

For alpha diversity, we calculated seven diversity indices comprising species richness, rarefied species richness, Fisher's alpha, Shannon, Simpson, inverse Simpson and evenness. All these indices were highly correlated ($r > 0.8$) and provided similar information, so we used species richness in further analyses as the simplest measure of species diversity. We used generalised linear mixed models (GLMMs) with a negative binomial error distribution and log-link function to investigate the effects of latitude and forest type as fixed factors on species richness. Region ($n = 13$) was used as a random factor to account for potential spatial autocorrelation among plots sampled within the same region (Zuur et al., 2009). Overall, we fitted eight models with different fixed effects. The most complex model included the interaction between the two predictors, where latitude was expressed in quadratic terms to account for non-linear relationships, whereas the simplest model included only latitude as a predictor. All models were compared using Akaike's information criterion corrected for small sample sizes (AICc). Models with a difference in AICc >2 indicated that the worst model had virtually no support and could be omitted. If there was more than one best model, we selected the simplest within 2 AICc units of the model with the lowest AICc. Model residuals were explored using a simulation-based approach to create readily interpretable scaled residuals for the fitted GLMMs (Hartig, 2020). We calculated two components of R^2 for GLMMs: a marginal R^2 (R^2_m) that only considered the variability explained by fixed effects and a conditional R^2 (R^2_c) that accounted for the variability supported by both fixed and random effects (Nakagawa & Schielzeth, 2013). All models were fitted with the *glmer.nb* function in the R 'lme4' package version 1.1–27-1 (Bates et al., 2015).

2.3.2 | Latitudinal variation in species compositions across forest types

The definition and partitioning of beta diversity, as well as its independence from alpha diversity, have been thoroughly debated (see Baselga, 2010, 2013; Jost, 2007; Legendre, 2014; Tuomisto, 2010). Here we consider beta diversity as the similarity in composition of species' identities among sampling units along a latitudinal gradient. To investigate the effects of latitude and forest type on beta diversity, we conducted semi-parametric permutational multivariate analysis of variance (PERMANOVA) (Anderson, 2001) with 999 permutations using the Bray–Curtis dissimilarity distances based on abundance data (Bacaro et al., 2012). To visualise the variation in species compositions throughout the latitudinal gradient, we performed non-metric multidimensional scaling (NMDS) with the *metaMDS* function in the R 'vegan' package version 2.5–7 (Oksanen et al., 2020) (k = 2, stress = 0.19, tries = 45). Data were square-root transformed and subjected to Wisconsin double standardisation. To better understand the differences in species compositions per forest type, NMDS ordination was conducted for each forest type (floodplain: k = 2, stress = 0.14, tries = 20; *terra firme*: k = 2, stress = 0.17, tries = 20; submontane: k = 2, stress = 0.11, tries = 20). In addition, we performed a principal coordination analysis (PCoA) to further investigate the patterns of floristic dissimilarity. Then, we used linear mixed models to determine the effects of latitude and forest type on floristic dissimilarity (PCoA axis 1). Region ($n = 13$) was used as a random factor. We fitted four models with different combinations of fixed effects (i.e. latitude and forest type). The most complex model included the interaction between the two predictors, whereas in the simplest model, no explanatory variables were included. All models were compared using Akaike's information criterion corrected for small sample sizes (AICc).

2.3.3 | Dominant species selection and distribution analysis

Dominant species sensu ter Steege et al. (2013) can be defined as those that account for at least 50% of all individual trees in a community. Following this definition, we obtained 129 species from our entire data set (Table S2). However, including such a large number of dominant species would inhibit the interpretation of the distribution pattern of each individual species (Figure S2). Thus, we only analysed the 10 most abundant species per forest type to obtain a clearer understanding of the species abundance distributions with visualisations that were easier to interpret. This selection comprised 25 different species, which accounted for 22.2% of the total individuals studied. To visualise the contributions of dominant species to the overall change in the floristic composition pattern, dominant species were located according to their correlations with the NMDS axes within each forest type. To analyse the dominant species responsible for driving the variation in the plot composition along the latitudinal gradient, we correlated the log-transformed abundance of each species with the NMDS axes using the *envfit* function in the 'vegan' R package (Oksanen et al., 2020). The abundance of dominant species is an important community structure metric (Dornelas et al., 2011) because communities differ in terms of their dominant species abundance distributions (Arellano et al., 2017). To explain their distribution along latitude, we used a stream-graph visualisation approach with the 'ggstream' R package version 0.1.0 (Sjoberg, 2021), which showed changes in abundance with round edges on a central baseline for different categories (dominant species) along a continuous gradient (latitude). Missing latitude data were interpolated with non-linear cubic splines using the *smooth. spline* function in the 'stats' R package version 4.1.1. All analyses were conducted in R v4.0.1 (R Development Core Team, 2010).

3 | RESULTS

3.1 | Latitudinal variation in species richness across forest types

The 118 0.1-ha plots contained 31,203 woody plant individuals with DBH ≥2.5 cm, and 1978 species that belonged to 557 genera and 112 families. Species richness and dissimilarity index increased towards

equatorial latitudes (Figure 1a,c) across all forest types. Species richness was lowest in floodplain forests compared to *terra firme* and submontane forests (Figure 2a). Comparisons of alternative models to investigate the relationships between species richness, latitude and forest type yielded two best-fit models (Table 1). Both models indicated a consistent effect of the two explanatory variables, including a quadratic effect of latitude and its interaction with forest type, but they differed in terms of the interaction between latitude and forest type. Both models predicted similar species richness at southern latitudes, which increased towards equatorial latitudes for all forest types. However, forest type trends had different slopes, where species richness increased most with latitude in submontane forests and least in floodplain forests (Figure 2b; Figure S3).

3.2 | Latitudinal variation in species composition across forest types

Results obtained by PERMANOVA showed that forest type, latitude and their interaction contributed to explain the changes in floristic composition (Table 2). The full model explained 21% of the variation in species composition. However, we were unable to separate the relative contributions of latitude and forest type because of the interaction between these two predictors. Thus, all forest types were intermingled along the latitudinal gradient, and no clear pattern could be identified by NMDS ordination because no floristic clustering was detected between plots of the same forest type or at similar latitudes (Figure 3a). The results from the linear mixed models are consistent with those obtained with the PERMANOVA, with the best-fit model including the interaction between latitude and forest type as fixed effects, and region as random effect (Table S3; Figure S4). The individual NMDS (k = 2) conducted for each forest type indicated a more striking effect of latitude on species composition. In general, species overlap occurred between plots at the same latitude. Three groups were identified for floodplain plots with equivalent distances between them, thereby indicating no effect of latitudinal gradient (Figure 3b). For *terra firme* or submontane forests, latitude divided the plots into northern and southern groups in terms of their floristic composition, and further partitions within each group represented different clusters at the same latitude, particularly in *terra firme* forests.

3.3 | Variation in dominant species with latitude across forest types

Among the 1978 species, we found that the 10 most abundant species per forest type corresponded to 24% of the total individuals in floodplain forests, 14.3% in *terra firme* forests, and 20% in submontane forests. The spatial positions of these species in the NMDS plot showed their relationships with both axes (Figure 3b), where species located in the corners had a significant relationship with the NMDS ordination axes, and thus they were particularly abundant in only a subset of plots, whereas species located in the centre were more evenly distributed across plots (see the correlation values in Table 3). Their relationship with the NMDS axes indicated different patterns across the forest types. In floodplain forests, five species (*Coussarea brevicaulis* K. Krause, *Iriartea deltoidea* Ruiz & Pav., *Otoba parvifolia* A.H. Gentry, *Pentagonia spathicalyx* K. Schum., and *Phytelephas tenuicaulis* A.J. Hend.) had significant correlations with both axes and their abundances peaked mostly at medium latitudes (Figure 3b). Five other species were not correlated with the axes: *Euterpe precatoria* Mart., *Guarea macrophylla* Vahl, *Guarea pterorhachis* Harms, *Rinorea viridifolia* Rusby and *Socratea exorrhiza* (Mart.) H. Wendl. For *terra firme* and submontane forests, all species were significantly correlated with the axes, except for *Siparuna decipiens* (Tul.) A.DC. (p = 0.013) and *Rinorea pubiflora* (Benth.) Sprague & Sandwith (p = 0.132) in *terra firme* forests and *Leonia glycycarpa* Ruiz & Pav. (p = 0.13) in submontane forests (Figure 3b). Similar results were obtained when the analyses were conducted with the most abundant species that accounted for 50% of individuals (sensu ter Steege et al., 2013) instead of the 10 most abundant species, where

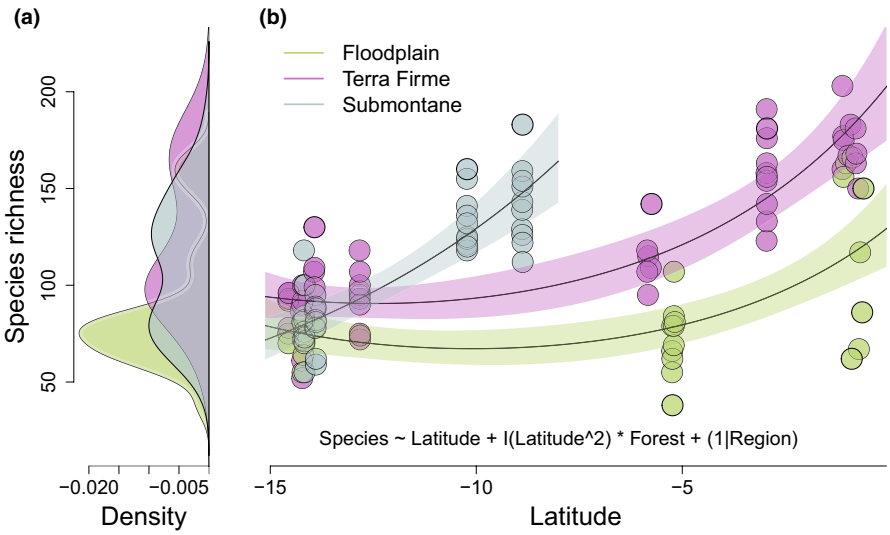

FIGURE 2 Species richness analyses of woody plants in three forest types (floodplain, *terra firme*, and submontane) in western Amazonia (Bolivia, Peru and Ecuador). (a) Density graph showing variations in the species richness per forest type. (b) Best-fit model for the relationship between species richness and latitude for each forest type. Each dot represents a plot, the blacklines are the model predictions, and the coloured polygons are the 95% confidence intervals based on the model predictions.

TABLE 1 Comparison of alternative models for woody plants in western Amazonia. Models include species richness as a function of latitude and forest type. Region is included as a random factor.

Formulation	Df	AICc	R^2m	R^2c
Richness ~ Latitude + (1|Region)	4	1089.20	0.331	0.669
Richness ~ Latitude * Forest + (1|Region)	8	1062.72	0.623	0.713
Richness ~ Latitude + Forest + (1|Region)	6	1068.34	0.509	0.699
Richness ~ Latitude * Forest + I(Latitude^2) + (1|Region)	9	1057.31	0.685	0.721
Richness ~ Latitude + Forest + I(Latitude^2) + (1|Region)	7	1070.26	0.510	0.699
Richness ~ Latitude * Forest + I(Latitude^2) * Forest + (1|Region)	**11**	**1056.82**	**0.715**	**0.733**
Richness ~ Latitude + I(Latitude^2) * Forest + (1|Region)	**9**	**1055.71**	**0.696**	**0.724**

Note: The best-fit models are highlighted in bold.

Abbreviations: AICc, Akaike's information criterion corrected for small sample sizes; Df, degrees of freedom; R^2c, conditional R^2; R^2m, marginal R^2.

TABLE 2 Summary of PERMANOVA test results for the effects of latitude, forest type and their interaction effect on floristic dissimilarities of woody plants in western Amazonia (in terms of pairwise Bray–Curtis indexes).

Parameter	Df	SS	*F*	R^2	*p*
Latitude	1	3.472	9.9682	0.0713	0.001***
Forest type	2	3.502	5.0271	0.0719	0.001***
Latitude:Forest type	2	2.669	3.8317	0.0548	0.001***
Residuals	112	39.010		0.8018	
Total	117	48.653		1.000000	

Abbreviations: Df, degrees of freedom; *F*, *F* statistic; R^2, explained variance; SS, sum of square; *p*, *p*-value (significant values are marked with asteriks ($p < 0.01$ ***)).

58.9% of the dominant species were significantly correlated with the NMDS axes for floodplain forests, 68% for *terra firme* forests and 75% for submontane forests (Table S2; Figure S1).

Overall, abundances of dominant species tended to decrease towards the Equator in all forest types (Figure 3c). In floodplain forests, abundances of dominant species were distributed along the whole gradient, although they decreased towards the Equator, and the same was found for *terra firme* forests, but the decreases in abundances were more noticeable. The same pattern was found in submontane forests but it was less pronounced, although the abundances of two species (*Wettinia augusta* Poepp. & Endl. and *Socratea salazarii* H.E. Moore) increased towards the Equator.

4 | DISCUSSION

4.1 | Variations in species diversity and composition with latitude across forest types

Our results confirmed the well-known relationship between species diversity and latitudinal gradients in western Amazonian forests as alpha diversity of woody plants increased towards the Equator. This finding is consistent with our predictions and the results obtained in previous studies (e.g., Hoorn et al., 2010; Qian & Ricklefs, 2007; ter Steege et al., 2006; Tuomisto et al., 2019). The variation in latitude implies a variation in climatic variables, including the reduction in temperature and precipitation seasonality that positively influence ecosystem productivity (Rohde, 1992). A higher ecosystem productivity results in higher speciation, and ability to maintain species in the ecosystem (Loreau, 2000), resulting in lower extinction rates (Brown, 2014). Our study showed latitudinal changes in soils properties, with an increase in soil fertility and a decrease in pH towards the Equator (Figure S1; Ben Saadi et al., 2022). These properties affect the species diversity, performance and composition at local scales (Bañares-de-Dios et al., 2022).

In this study, we have shown that alpha diversity was relatively similar for all forest types at southern latitudes, but the increases towards the Equator were different. In floodplain forests, alpha diversity remained similar along the latitudinal gradient, whereas steep increases occurred in *terra firme* and submontane forests. Although we anticipated a greater effect of latitude over forest type on alpha diversity (e.g., Stropp et al., 2009), the different response of each forest type was unexpected. In terms of beta diversity, as expected, we found that latitude strongly influenced the differences in species composition between plots in western Amazonian forests. However, our second hypothesis was rejected because the effect of latitude on the beta diversity pattern was strong but not constant across forest types. Latitude did not have a regular effect on shaping the floristic compositions of the plots in floodplain forests, whereas great floristic changes occurred in both *terra firme* and submontane forests along the latitudinal gradient.

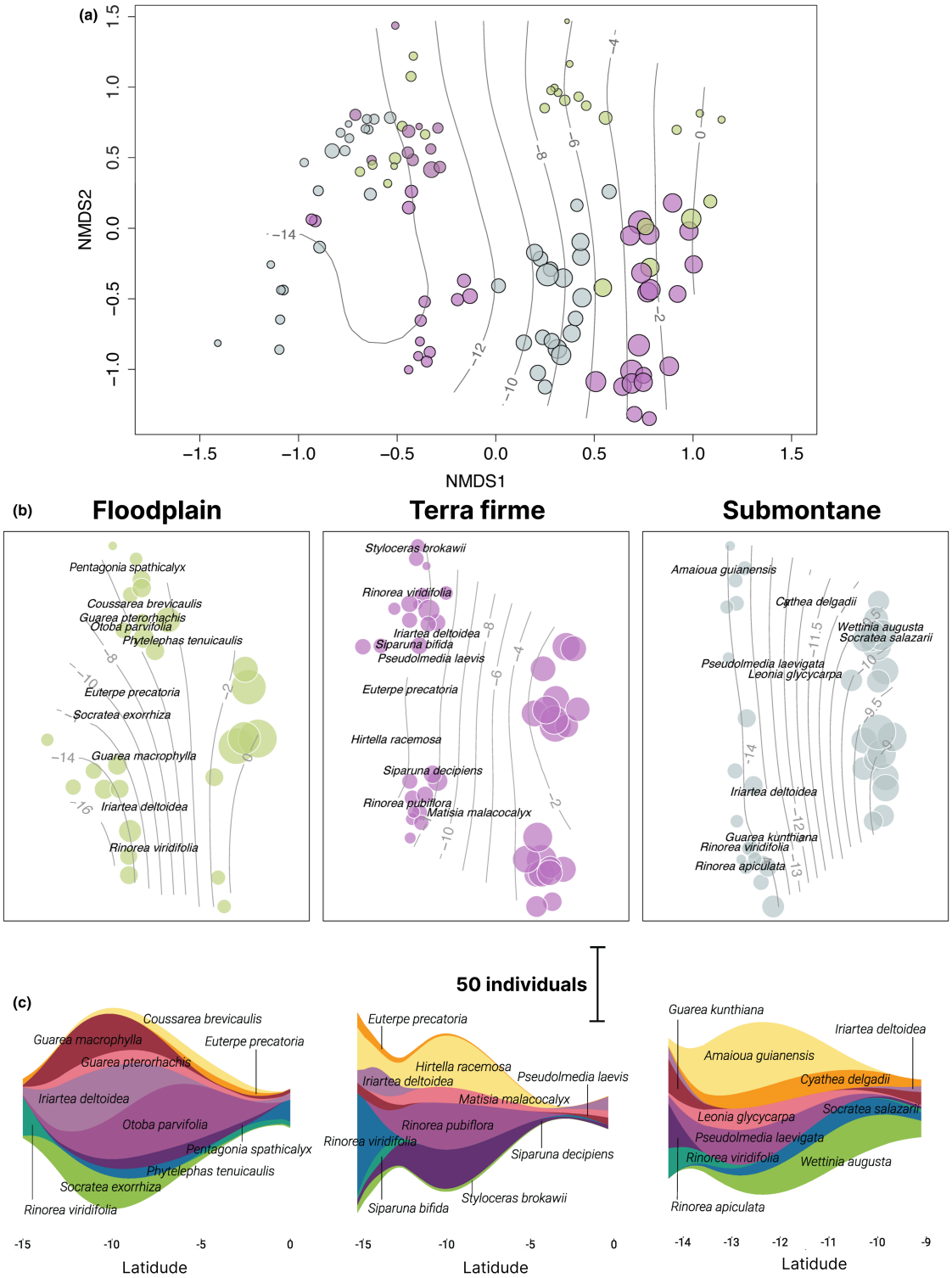

FIGURE 3 Non-metric multidimensional scaling (NMDS) ordinations (a, b) and stream graphs (c) showing floristic composition and dominance results for each forest type across latitude in western Amazonia (Bolivia, Peru and Ecuador). (a) NMDS ordination plot showing the differences in the compositions of vascular woody plant species between the sampled plots in a two-dimensional space (k = 2, stress = 0.19, tries = 45). Floristic distance was calculated using the Bray–Curtis dissimilarity index, where the lines represent the latitude and the colours are the forest types (green for floodplain, purple for *terra firme* and grey for submontane). The size of each dot reflects the total species richness in each plot. (b) Three NMDS (k = 2, tries = 20: Stress = 0.14, stress = 0.17, stress = 0.11) plots for each forest type and their 10 most abundant species placed according to their correlations with the NMDS axes. (c) Three stream graphs showing the abundance of the 10 dominant species across latitude for each forest type. The height of each stream shows the changes in abundance (scale bar represents 50 individuals) and the length of the stream shows the duration of the abundance with increasing latitude. For latitudes with no observations, the abundances were interpolated with nonlinear cubic splines.

TABLE 3 Ten most abundant species of woody plants in each forest type studied in western Amazonia and *p*-values for the correlations with the NMDS axes.

Floodplain		*Terra firme*		Submontane	
Species	***p***	**Species**	***p***	**Species**	***p***
Coussarea brevicaulis	**0.006**	*Hirtella racemosa*	**0.001**	*Amaioua guianensis*	**0.001**
Euterpe precatoria	0.664	*Iriartea deltoidea*	**0.003**	*Cyathea delgadii*	**0.001**
Guarea macrophylla	0.308	*Matisia malacocalyx*	**0.001**	*Guarea kunthiana*	**0.001**
Guarea pterorhachis	0.066	*Otoba parvifolia*	**0.002**	*Iriartea deltoidea*	**0.003**
Iriartea deltoidea	**0.007**	*Pseudolmedia laevis*	**0.001**	*Leonia glycycarpa*	0.133
Otoba parvifolia	**0.001**	*Rinorea pubiflora*	0.132	*Pseudolmedia laevigata*	**0.002**
Pentagonia spathicalyx	**0.001**	*Rinorea viridifolia*	**0.001**	*Rinorea apiculata*	**0.001**
Phytelephas tenuicaulis	**0.004**	*Siparuna bifida*	**0.001**	*Rinorea viridifolia*	**0.001**
Rinorea viridifolia	0.072	*Siparuna decipiens*	0.013	*Socratea salazarii*	**0.008**
Socratea exorrhiza	0.268	*Styloceras brokawii*	**0.001**	*Wettinia augusta*	**0.001**

Note: $p = p$-value (significant values are marked in bold ($p < 0.01$)).

Regional diversity of floodplain forests (mean of 79 species per plot) was the lowest among habitats and it remained relatively constant across the latitudinal gradient, which can be explained by flood pulses acting as strong limiting environmental factors (Oliveira et al., 2018; Wittmann et al., 2011). Prolonged flooding and shallow water tables exposes plants to a lack of oxygen in the rhizosphere (Parolin, 2009), leading to seasonal waterlogging and anoxia, decreasing survival and inhibiting growth (Marca et al., 2022). These conditions reduce the number of species by selecting for species that can tolerate these conditions (Oliveira et al., 2018; Parolin, 2009; Parolin et al., 2004), thereby causing diversity to be zoned along flooding gradients and to remain constant along latitude (Val et al., 2022). Moreover, western Amazonian floodplain soils are fed by similar Andean sediments transported by white-water rivers (Quesada et al., 2011). This, along with the terrain flatness and low elevation, leads to homogeneous soil conditions between sites. Rare species occurrence is susceptible to changing edaphic conditions (Ben Saadi et al., 2022), then the contribution of rare species to alpha diversity decreases in stable soils. Thereby, homogeny in floodplain soils suggests that diversity might be primarily driven by the most limiting factor: flooding regimes and its effect on soil water content and saturation. Despite environmental filtering, regional species richness was still high in floodplain forests, but lower compared with *terra firme* and submontane forests (Parolin et al., 2004; ter Steege, 2010).

Geographical gradients, flooding regimes, edaphic fertility and water table depth are important determinants of beta diversity at large scales across Amazonian floodplains (Assis et al., 2015; Val et al., 2022). In our study, latitude did not have a major influence on the floristic composition of our plots, in contrast to the findings obtained by Emilio et al. (2010). Recent studies have shown that changes in species composition were encompassed with local hydrological gradients in western Amazonia (Marca et al., 2022). We suggest that flooding regimes influence local species compositions through dispersion. Therefore, the high local connectivity between riparian corridors contributes to the creation of a specific species zonal distribution independent of latitude, but dependent on the connections caused by flooding within the same region (Wittmann et al., 2006). This finding demonstrates that seed dispersal through water does not ensure similarity between regions, but it does within them.

By contrast, well-drained forest types exhibited a different pattern. As shown previously, *terra firme* forests were the most diverse habitats (Oliveira et al., 2018; ter Steege, 2010), with a mean diversity of 123 species per plot, whereas in submontane forests was 99 species per plot. Diversity increased steeply towards the Equator in non-flooded forests while beta diversity changed more gradually with latitude compared with floodplain forests. In the absence of other limiting factors, we assume that alpha and beta diversity patterns in non-flooded forests are highly susceptible to latitudinal changes in the precipitation regime and high heterogeneity in soil composition (Quesada et al., 2010). However, the increase in diversity with latitude was steeper in submontane forests and the floristic compositional differences at southern latitudes were higher in submontane forests than in *terra firme* forests, although they were geographically closer. Variation in topography often drive heterogeneity in soil fertility through erosion of the surface and exposition of the underlying material (Quesada et al., 2011). The differences found in nearby southern submontane forests may be attributable to their edaphic complexity (Landeiro et al., 2018). Moreover, the historical changes in landscape connectivity have influenced dispersal, gene flow and diversification (Guayasamin et al., 2022; Val et al., 2022). The presence of hills, steep slopes and higher elevations compared with those further north (Parker & Bailey, 1990) might act as ecological filters to limit species dispersion and distribution (Arellano et al., 2017). However, in this study, we only inventoried submontane forests up to mid-latitudes, and thus the trends in the alpha diversity and beta diversity closer to the Equator remain unknown.

These results showed that changes in both alpha and beta diversity with latitude were similar within each forest type, and thus topographical and environmental limitations might have stronger effects than latitude in shaping the species selection and distribution in certain forest types, particularly in floodplain forests. Understanding which limiting factors characterise each forest type might help to predict future changes in species distributions, dominance and performance. Thus, we recommend conducting further research in heterogeneous environments and across large scales for each forest type independently.

4.2 | Latitudinal patterns of species dominance across forest types

Dominant species were expected to influence patterns of beta diversity. However, we found that not all dominant species were good predictors of beta diversity and that it depended mainly on their local abundance. The uniformity of a species' abundance over the gradient will determine whether it contributes to changes in the beta diversity or not. Some species will have an even distribution over the complete gradient, whereas others will have locally restricted distributions (Toledo et al., 2011), which may differ greatly among areas (Arellano & Macía, 2014; ter Steege et al., 2013). For example, *Iriartea deltoidea* shaped changes in floristic composition because its abundance peaked unevenly at different latitudes, whereas the abundance of *Socratea exorrhiza* remained even along the latitudinal gradient, and thus did not lead to changes in the floristic composition (Figure 3c), although both are widely distributed palms (Toledo et al., 2011). Therefore, in response to the debate whether rare species (Pitman et al., 2001, 2013) or common species (Draper et al., 2019) are the main predictors of changes in beta diversity, our results suggest that local abundances of dominant species should be carefully examined for different forest types.

Dominant species are usually specialised on a single forest type where they perform optimally (Draper et al., 2019; ter Steege et al., 2013, 2019). We found that dominant species were able to dominate in a single forest type (only *Iriartea deltoidea* and *Rinorea viridifolia* were dominant in the three forest types). Indeed, the relationship between dominance and beta diversity was not shared across forest types. The percentage of species that could contribute to changes in beta diversity differed greatly between floodplains (50%) and non-flooded forests (80% in *terra firme* forests and 90% in submontane forests). The same analyses were conducted with dominant species sensu ter Steege et al. (2013) and similar results were obtained (58.9% species in floodplain forests, 68% in *terra firme* forests, and 75% in submontane forests; see Table S2). Although species contributing to changes in beta diversity were found in all forest types, in floodplains their number was especially lower. This locally outstanding dominant species abundance was previously described in floodplains, but acknowledged as rare (Assis et al., 2017). Instead, most of floodplain's dominant species were characterised by even abundances along the latitudinal gradient (e.g., *Euterpe precatoria*, *Guarea macrophylla*). This supports the fact that Amazonian floodplain species have mainly widespread occurrences (Wittmann et al., 2011). These dominant species can withstand frequent flooding events, being characterised by traits that can promote dispersion, colonisation, reproduction and survival under these extreme conditions (Parolin et al., 2004). These species harbour eco-physiological adaptations to endure the limiting conditions of this forest type, such as the development of aerenchyma, adventitious and buttress roots, etc (Junk et al., 2010; Parolin, 2009). For example, *Socratea exorrhiza* and *Euterpe precatoria* Mart. develop aerial roots that facilitate oxygen absorption The lack of these physiological adaptations filters out a subset of species which reduces tree diversity (Marca et al., 2022), while promotes certain species to be able to dominate and be constantly abundant over large scales.

Different relationships were found between dominance and beta diversity for each forest type, but they also shared some similarities. The fluctuations in abundances of dominant species with latitude were similar for all forest types, as they were locally abundant at southern latitudes but unable to reach high abundances close to the Equator (Figure 3c). Species richness increase towards equatorial latitudes might reduce the pool of potentially dominant species from finding available space in local species-rich communities. Competitive exclusion of new species (Olivares & Kessler, 2020) might force dominant species to occur at lower abundances (Arellano et al., 2017), resulting in a dilution of the effect of dominant species in the community as species richness increases (Dornelas et al., 2011).

In summary, each forest type is dominated by a set of different species. Dominant species can be important in leading changes in beta diversity, mainly depending on local fluctuations of their abundances. In *terra firme* and submontane forests, most dominant species were contributing to changes in beta diversity, while in floodplain forests dominant species tended to be homogenously spread along the gradient. Finally, the increase in species richness towards the Equator limits the abundance of dominant species due to competitive exclusion, regardless of the forest type. To understand the distribution and performance of dominant species, we believe it is important to study their contributions to beta diversity.

5 | CONCLUSIONS

Based on our findings, we conclude that there is an increasing latitudinal diversity gradient towards the Equator for both alpha and beta diversity in western Amazonia. Although this pattern is widely known, we found that the effects of latitude are not consistent across forest types. Both the different environmental attributes and the hydrogeomorphic dynamics of each forest type are likely to shape floristic diversity and composition by influencing species dispersion and distribution. Regarding floodplain forests, we found that the flooding regime could be a stronger predictor of floristic composition than latitude, maintaining alpha diversity almost constant along the gradient. On the contrary, *terra firme* and submontane

forests are proven to better respond to latitude, with a greater increase in species richness and a more gradual change in beta diversity towards the Equator. Finally, we found that the three forest types were characterised by different set of dominant species. We showed that dominant species can be indicators of changes in floristic composition, depending mostly on the heterogeneity of their abundances across the latitudinal gradient. In floodplain forests, most dominant species are widespread along the gradient, as they maintain their abundance constant, while in *terra firme* and submontane forests, dominant species tend to be locally abundant. Besides, along the latitudinal gradient, the increase in species richness came along with a reduction in dominant species abundance, probably due to competitive exclusion in the spatial distribution of species. Overall, our study improves the understanding of biogeographical patterns in woody species diversity, composition and dominance along a large latitudinal gradient and across forest types in western Amazonia. By separating the effects of latitude and forest type, we highlighted their complementary importance in determining floristic variation, and we showed that analysing forest types independently could help disentangling the role of macro-climatic trends and habitat characteristics in affecting species distribution and dominance.

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CONFLICT OF INTEREST

The authors have no conflicts of interest to declare.

DATA AVAILABILITY STATEMENT

Data are available from Dryad: https://doi.org/10.5061/dryad.jm63xsjcc

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BIOSKETCH

Julia G. de Aledo is a PhD candidate at the Universidad Autónoma de Madrid, Spain. This paper is part of her PhD thesis, which focuses on biogeographical patterns of floristic, functional and cultural diversity in western Amazonian rainforests. She is mainly interested in understanding the factors that limit species composition, dominance and distributions across latitudinal gradients. Tropical Ecology Lab focuses on plant community ecology, functional and phylogenetic diversity, ethnobotany and conservation.

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SUPPORTING INFORMATION

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