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RESEARCH ARTICLE

Species functional traits affect regional and local dominance across western Amazonian forests

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Abstract

1. Several studies have documented dominance by few species in Amazonian forests. Dominant species tend to be either locally abundant (local dominants) or regionally frequent (widespread dominants) but rarely both (oligarchs). Here, we explore relationships between dominance and functional traits. We ask whether: (i) dominance is associated with specific functional profiles and (ii) dominance patterns (local vs. widespread dominants) are associated with different functional traits.
2. We combined census data from 503 forest inventory plots across four lowland forest habitats in western Amazonia with trait information for ~2600 tree species, encompassing data collected in the focal plots and data from published sources. We considered traits that relate to leaf, wood, seed and whole-plant strategies: specific leaf area (SLA), leaf area (LA), N content per unit leaf mass (LN), wood density (WD), seed mass (SM) and maximum diameter at breast height (DBH_{max}).
3. Our results reveal that dominant species display different trait combinations depending on the habitat type. Taller dominant species exhibit higher regional

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frequency, associated with higher dispersal ability and lower local abundance, likely due to negative density dependence. Greater SM contributes to higher regional frequency of dominant species via greater dispersal by birds and mammals and seedling survival. Finally, traits related to resource conservation strategies, such as lower SLA, LA, LN and greater WD, favour higher local densities across most habitats, while the opposite pattern was linked to higher regional frequency.

4. *Synthesis*. Our findings reveal that (i) dominance is associated with different functional traits depending on the habitat type, and (ii) different functional trait values define distinct dominance patterns. Our study exemplifies the potential of trait-based approaches to illuminate the ecological mechanisms that may underlie dominance in tropical forests. Finally, accounting for both local abundance and regional frequency when studying dominance is likely to improve our understanding and forecasting of how different species will respond to global change drivers in western Amazonia.

KEYWORDS

abundance–occupancy relationship, Amazonian forests, dominant species, functional strategies, species abundance, tropical tree species

1 | INTRODUCTION

Species abundance rankings in ecological communities usually reveal few abundant species and many relatively rare species (Preston, 1948; Whittaker, 1965). In highly diverse ecosystems such as Amazonian forests (Gentry, 1988), a modest number of tree species dominate across regions, habitats and different forest strata (Draper et al., 2021; Macía & Svenning, 2005; Pitman et al., 2001, 2013; ter Steege et al., 2013). Dominant species are commonly defined as those species that together account for 50% of the total abundance in tropical forests (Draper et al., 2019; Matas-Granados et al., 2024; ter Steege et al., 2013) (Figure 1a). According to the biomass ratio hypothesis (Garnier et al., 2004; Grime, 1998), these dominant tree species play a crucial role in key ecosystem processes, such as carbon storage, net primary productivity and fruit biomass production (Fauset et al., 2015; Staggemeier et al., 2017). Further, they have been shown to be key drivers of large-scale species spatial turnover (Draper et al., 2019). Therefore, clarifying the underlying mechanisms that confer dominance at local and regional scales is essential to better understand how Amazonian forests will respond to global change drivers.

Amazonia encompasses four common lowland forest habitats: (1) *terra firme* forests with well-drained and never flooded soils of variable fertility, from relatively poorer soils in central Amazonia and the Guiana Shield to relatively more fertile soils mostly in western Amazonia (Quesada et al., 2011; Quesada & Lloyd, 2016; ter Steege, 2009); (2) seasonally inundated floodplains that also encompass a wide range of soil fertility, influenced by black-, clear- or white-water rivers depending on the watershed and sedimentary source and load (Junk et al., 2015; Quesada et al., 2011), experiencing large seasonal changes in hydrology and oxygen availability (Baraloto et al., 2011; de Assis et al., 2017; Parolin et al., 2004); (3) swamps that are permanently waterlogged, causing anoxic saturated edaphic conditions, encompassing forests typically dominated by one or a few palm species or specialized dicotyledonous trees, with a wide variation in nutrient status (Kahn, 1991; Lähteenoja & Page, 2011); and (4) white sands that occur on acidic, nutrient-poor sandy soils (Fine & Kembel, 2011; Hoorn, 1993, 1994). Focusing on dominant species in these four contrasting habitat types in lowland western Amazonia, Matas-Granados et al. (2024) revealed different dominance patterns related to species local abundance and regional frequency. Dominant species tend to be locally abundant (local dominants) or regionally frequent (widespread dominants), but rarely both (oligarchs), describing a negative abundance–occupancy relationship exclusively for dominant species in western Amazonian forests (Figure 1b). Therefore, local dominants are those dominant species with high local abundance and low regional frequency; widespread dominants are those dominant species with low local abundance and high regional frequency; and oligarchs are those dominant species with high local abundance and high regional frequency. Moreover, most dominant species tend to dominate in a single habitat type (Draper et al., 2019; ter Steege et al., 2013), likely because contrasting habitats reflect different environmental conditions (e.g. light, water and soil nutrient levels) that select for distinct functional strategies at the community level (Fortunel et al., 2014; ter Steege et al., 2025; Vleminckx et al., 2021). These studies suggest that species may become dominant in different ways, in particular

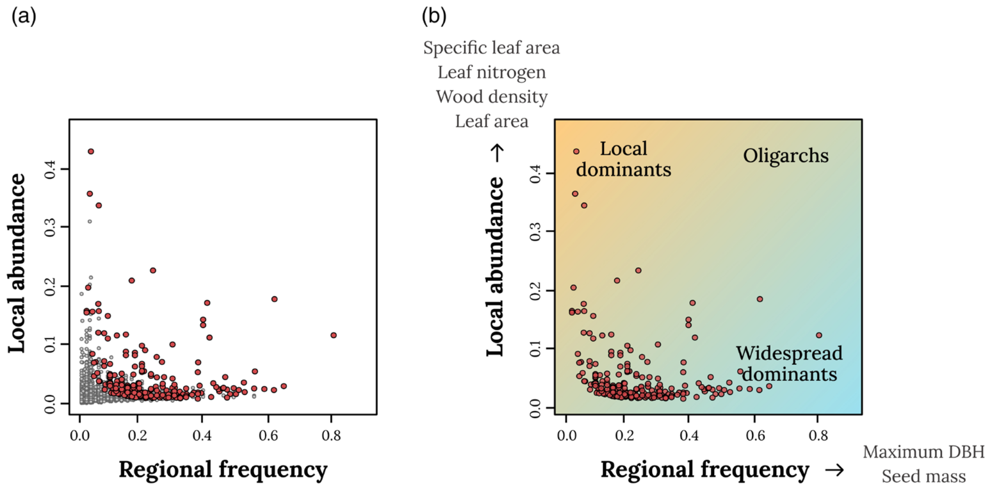

FIGURE 1 (a) Comparison of dominant species (red points) and non-dominant species (grey points) in terms of their local abundance and regional frequency. Inside each habitat type, dominant species were identified as those species that together account for the 50% of the total relative abundance, local abundance was calculated as the average across the plots where each species occurred, and regional frequency as the number of plots where a species occurred divided by total plots in the habitat type. (b) Different dominance patterns found in western Amazonia and functional traits potentially related to local abundance and regional frequency of dominant species. Local dominants are those dominant species with high local abundance and low regional frequency; Widespread dominants are those dominant species with low local abundance and high regional frequency; oligarchs are those dominant species with high local abundance and high regional frequency. Modified from Matas-Granados et al. (2024).

via distinct mechanisms: greater stature associated with the potential for large distance dispersal and establishment abilities may lead to frequent occurrence across large scales (Schurr et al., 2007; Thomson et al., 2011; Westoby et al., 2002), whereas low resource acquisition and high investment in defence could confer higher abundances at local scales (Coley, 1987; Cornwell & Ackerly, 2010; Lamarre et al., 2012; Zang et al., 2021). Considering different dominance patterns is therefore crucial to improve our mechanistic understanding of species dominance.

Species functional traits may help identify dominance processes since they reflect key trade-offs that determine species performance and consequently, their abundances and distributions from local to regional scales (Violle et al., 2007). Few studies have addressed associations between species dominance and functional traits in tropical forests. Fauset et al. (2015) found no consistent relationship between species abundance and wood density, and ter Steege et al. (2013) found no clear relationship between dominance and wood density and seed mass. Hence, it remains unclear whether dominant species are functionally distinct from less abundant species, and whether dominant species are functionally distinct between forest habitat types.

In this study, our main objective was to explore the functional traits of dominant tree species in the four main forest habitat types found in western Amazonia (*terra firme* forests, floodplains, swamps and white sands) to help identify underlying mechanisms leading to local and regional dominance in tropical tree species. We focus on key traits that describe major functional dimensions in tropical tree species related to life-history strategies (Díaz et al., 2016; Fortunel, 2023; Kambach et al., 2022; Rüger et al., 2018; Salguero-Gómez et al., 2016; ter Steege et al., 2025). First, specific leaf area (SLA), and leaf nitrogen content (LN) describe the 'leaf economics spectrum', opposing resource conservation with resource acquisition strategies (Grime, 1974, 1977; Wright et al., 2004). Second, seed mass (SM) and maximum plant size relate to dispersal and competitive strategies, influencing the ability to exert competition (e.g. shading) and/or to tolerate competition (e.g. large seed size withstands shade in the establishment phase) (Coomes & Grubb, 2003; Díaz et al., 2016; Moles, 2018; Thomson et al., 2011), with some discrepancies between studies (Aiba et al., 2020; Murray et al., 2005). Third, while wood traits such as wood density (WD), are linked to both leaf economics and plant size dimensions in global datasets (Díaz et al., 2016), they are more independent from these traits in Amazonian tree species (Baraloto et al., 2010; Fortunel et al., 2012; Vleminckx et al., 2021). Finally, leaf area (LA) has been documented to be related to light-capturing surface (Givnish, 1987), water balance (Wright et al., 2006) and growth rates (Mori et al., 2019). Considering these species traits in western Amazonian forests, we specifically ask:

1. Is dominance associated with specific trait values and trait combinations across contrasting western Amazonian forests? Given that environmental conditions filter species traits across Amazonian forests (e.g. Fortunel et al., 2014), we hypothesize that species with trait values better suited to their environment will dominate. Specifically, in stressful habitats where environmental filtering is expected to be stronger, such as permanent waterlogging conditions (e.g. swamps) or nutrient-poor and drought-prone environments (e.g. white sands), we

expect dominance to be associated with trait values related to ecological strategies allowing resource conservation and stress tolerance (i.e. lower SLA, lower LN and higher WD) (Fine et al., 2006; Fortunel et al., 2014; ter Steege et al., 2025). Conversely, in less stressful habitats (e.g. floodplain and *terra firme* forests), without extreme droughts and with greater water availability, we expect that dominant species will display trait values linked to resource acquisition strategies (i.e. higher SLA, higher LN and lower WD) which provide a competitive advantage for light capture in these forests (Fortunel et al., 2014). Finally, we expect dominance to be associated with larger LA, $\mathrm{DBH}_{\mathrm{max}}$ and SM, independently of the habitat where species dominate (Table 1).

2. Are species dominance patterns (locally abundant vs. regionally frequent) defined by different functional traits across different forest types?
   Considering two dominance patterns (local dominants and widespread dominants) and their two components (local abundance and regional frequency) (Figure 1b), we expect different traits to relate to dominance patterns and their components. In particular, we hypothesize that traits related to resource acquisition and defence (e.g. SLA, LA, LN and WD) are linked to the local abundance of dominant species, while traits describing dispersal, establishment and stature (e.g. SM and $\mathrm{DBH}_{\mathrm{max}}$) relate to the regional frequency of dominant species (Figure 1b; Table 1).

2 | METHODS

2.1 | Study area, species data and metrics to characterize dominance patterns

We used an extensive dataset consisting of 503 forest inventory plots (data stored in Matas-Granados et al., 2023), many of them curated at ForestPlots.net (ForestPlots.net et al., 2021; Lopez-Gonzalez et al., 2011), ranging from 0.025 to 0.213 ha, across different mature western Amazonian forests, from Colombia to Bolivia (Figure 2A) (for further details about the study area, species list and data processing see Matas-Granados et al., 2024). Plots covered the four main habitat types found in western Amazonia proportionally to their area in the region (Draper et al., 2014; Kahn, 1991; Pitman et al., 2014; Stropp et al., 2011; ter Steege et al., 2000), with 76% in *terra firme* forests, 11% in floodplains, 7% in swamps and 6% in white sands (Table S1). All trees ≥2.5 cm DBH were recorded and identified to species, representing a total of 93,719 individuals, and 2609 species. Stem density was highest in white sands, intermediate in *terra firme* forests and floodplains, and lowest in swamps (Figure 2B). Basal area was greater in floodplains than in *terra firme* forests, swamps and white sands (Figure 2C).

We defined dominant species as those species that together account for 50% of the total relative abundance of each habitat type, following ter Steege et al. (2013) and Matas-Granados et al. (2024). Total abundance of each species refers to the total

TABLE 1 Hypotheses concerning the direction of the relationships between dominance (= total abundance), local abundance and regional frequency of dominant species with species functional traits across the four main habitat types in western Amazonia forests.

			Habitat types			
			Terra firme	Floodplain	Swamp	White sand
Dominance and functional traits	Total abundance	SLA	+	+	−	−
		LA	+	+	+	+
		LN	+	+	−	−
		$\mathrm{DBH}_{\mathrm{max}}$	+	+	+	+
		WD	−	−	+	+
		SM	+	+	+	+
Dominance patterns and functional traits	Local abundance	SLA	−	−	−	−
		LA	−	−	−	−
		LN	−	−	−	−
		$\mathrm{DBH}_{\mathrm{max}}$	0	0	0	0
		WD	+	+	+	+
		SM	0	0	0	0
	Regional frequency	SLA	0	0	0	0
		LA	0	0	0	0
		LN	0	0	0	0
		$\mathrm{DBH}_{\mathrm{max}}$	+	+	+	+
		WD	0	0	0	0
		SM	+	+	+	+

Note: + and blue: positive relationship, − and red: negative relationship, 0 and grey: no relationship.

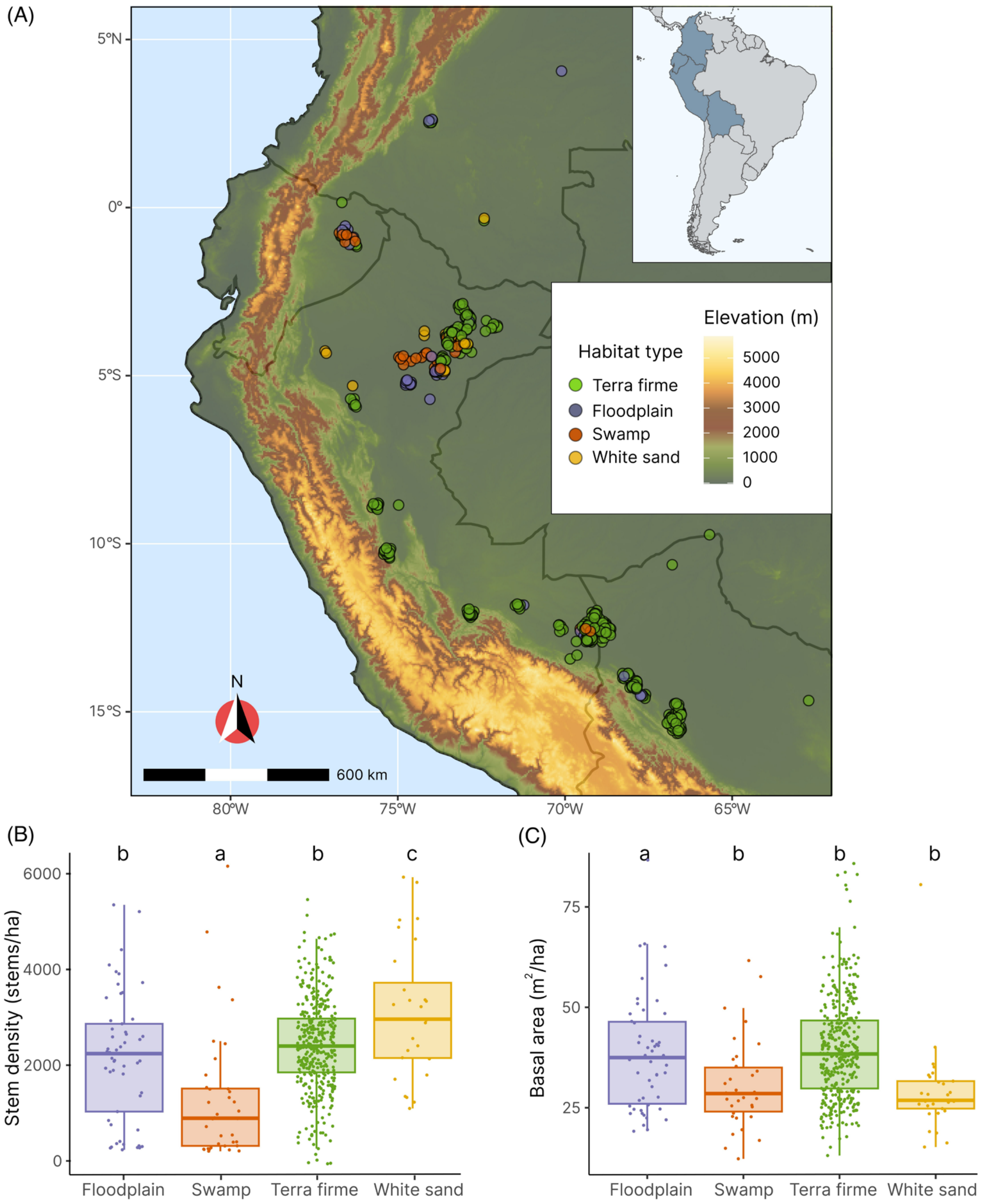

FIGURE 2 (A) Map of the study area showing the location of the forest inventory plots, (B) stem density (≥2.5 cm DBH) and (C) basal area in the four forest habitat types. Different letters show significant differences between habitats (ANOVA; Tukey post hoc multiple comparisons, $p < 0.001$).

number of individuals summed over plots within each habitat (ter Steege et al., 2013), and it does not indicate how these individuals are spatially distributed. We considered this variable as a general measurement of dominance, broadly used in previous studies in tropical forests (Draper et al., 2019, 2021; Matas-Granados et al., 2024; ter Steege et al., 2013). Since plot size varied among datasets, we used the 'total relative abundance', following Matas-Granados et al. (2024). We identified dominant species separately by habitat type. We defined two main aspects of dominance for each dominant species in each habitat type: (1) local abundance of dominant species, calculated as the mean local relative abundance (individuals of the species in a plot divided by total individuals in the plot), averaged across the plots where each dominant species occurred and (2) regional frequency of dominant species, calculated as the number of plots where a species occurred divided by total plots in the habitat type (Table S2).

2.2 | Trait data

We considered six plant functional traits as they related to resource acquisition, dispersal, defence and competitive ability (Chave et al., 2009; Kunstler et al., 2016; Wright et al., 2004) and can capture differences in species' ecological strategies (Díaz et al., 2016; Westoby, 1998): SLA, LA, LN, DBH_{max} as a proxy of maximum plant height (Norberg, 1988), WD and SM (Table S3).

We used the plot inventories to determine the maximum diameter at breast height as the 95th percentile of each species (King et al., 2006). Other trait data were compiled from various sources following standardized protocols (Cornelissen et al., 2003; Pérez-Harguindeguy et al., 2013), including (i) previous work by different research groups (Baraloto et al., 2010; Ben Saadi et al., 2022; Fortunel et al., 2012; Garwood et al., 2024; Hietz et al., 2017; Kraft et al., 2008, 2010; Matas-Granados et al., 2025a, 2025b; Metz et al., 2023; Vleminckx et al., 2021; Wright et al., 2010, 2024); (ii) publicly available trait databases such as TRY (Kattge et al., 2020), funAndes (Báez et al., 2022), the Seed Information Database (Society for Ecological Restoration, International Network for Seed Based Restoration and Royal Botanic Gardens Kew, 2023) and the Global Wood Density Database (Chave et al., 2009; Zanne et al., 2009); and (iii) additional sources for seed mass (Acosta-Rojas et al., 2023; Ordóñez-Parra et al., 2023; Williams & Brodie, 2023). When more than one measure per species was available, we calculated the species mean trait value. The compiled trait dataset represented between 29% (for SM) and 100% (for DBH_{max}) of our 2609 species, with a mean species coverage of 55% per trait, and all species had information for at least one of the six traits (Table S4). Considering the number of individuals per species for which trait data were available, our trait dataset represented between 44% (for SM) and 100% (for DBH_{max}) of the total 93,719 individuals (Table S5). We log transformed all trait values (except WD) to improve normality for subsequent analyses. As protocols can vary between studies, we compiled data for SLA and LA including and excluding petiole, and data for WD taken from the branch or from the sapwood and heartwood. Species coverages were greater when using SLA and LA measured without the petiole and WD measured from the branch, and they were correlated with SLA and LA measured with petiole and WD measured from the trunk, respectively (Figure S1; Table S6). Hereafter, we report findings for SLA and LA excluding the petiole, and WD measured from the branch (details for the other traits are provided in the Supporting Information).

2.3 | Data analyses

2.3.1 | Relationship between dominance and functional traits

In previous work (Matas-Granados et al., 2024), a specific threshold to classify species as dominant or non-dominant was established using species total relative abundance. Here, for the first question, we used total relative abundance for every species as a proxy for dominance (specifically, we used its logarithm due to its skewed distribution) to provide continuous information across the entire range of dominance among species. We conducted both multivariate and univariate analyses to evaluate trait differences with respect to species' total relative abundance.

First, we performed principal component analyses (PCAs) with scaled species functional trait values to characterize the main dimensions of functional variation among all species within each habitat type separately and to illustrate trait relationships. We extracted species scores for axes 1 and 2, as these together accounted for more than 55% of functional variation across all habitat types. To test the relationship between total relative abundance and axes 1 and 2, we built two linear models (LMs) for each habitat type separately: one with axis 1 as the dependent variable and the other with axis 2. In both models, species total relative abundance was the explanatory variable. Given that few species had values for all six traits (16% of all species), we repeated the analyses without SM (34% species had values for the remaining five traits) and present these results in the main text. Second, for each trait separately, we conducted LMs to test relationships between functional traits and species total relative abundance. Since trait coverage was systematically lower for non-dominant species compared to dominant species—resulting in an unbalanced sampling design (Table S4)—we applied permutation (999 shuffles within dominant and non-dominant species groups) to derive 95% confidence intervals for the null distribution of the F-statistics for each predictor. This approach ensures robust and reliable statistical inference despite sampling imbalance.

To account for potential bias due to disproportionate sampling of species functional traits clustered in specific lineages (i.e. some lineages could be more represented than others) (Tables S7 and S8), we subsampled one species per genus from the species list of each habitat type 100 times and performed all the multivariate and univariate analyses each time to compare the subsampled results to our observed results.

2.3.2 | Traits' influence on local abundance and regional frequency of dominant species

For the second question, we evaluated the potential drivers of local and regional dominance, and therefore focused exclusively on the dominant species. To explore the role of traits in describing the local abundance and regional frequency of dominant species within each of the four habitat types separately, we built Bayesian models as follows:

$$\text{Local abundance}_{S,H} = \text{trait}_S + \text{habitat type} + \text{trait}_S \times \text{habitat type} + (1|\,\text{Species})$$

$$\text{Regional frequency}_{S,H} = \text{trait}_S + \text{habitat type} + \text{trait}_S \times \text{habitat type} + (1|\,\text{Species})$$

where subscripts S and H refer to species identity and the habitat type, respectively, and species was considered as a random factor since 22% of the dominant species were dominants in more than one habitat type (Table S2). We used a beta error distribution because both dependent variables are proportions (ranging between 0 and 1) that follow the beta distribution (Ferrari & Cribari-Neto, 2004).

We built a unique model for each combination of dependent variable (local abundance and regional frequency) and single traits (Table S3), resulting in 12 models. All traits were rescaled to facilitate model comparisons. We fitted all models with weakly informative priors. Specifically, priors were flat for fixed factors, Student *t* distributions with three degrees of freedom for the random factor and gamma distributions for the *phi* parameter of the beta distribution. Model convergence was tested visually with trace and density plots and numerically estimating if *Rhat* was equal to one (Table S9). Models usually converged after 4000 iterations. Model fit was evaluated using Bayesian R^2 (Table S10). Hereafter, we focused on the interaction between trait and habitat (i.e. the slopes of the relationships), but all parameter estimates can be found in the Supporting Information. All analyses were conducted in R v4.1.3 (R Core Team, 2022), using package '*brms*' (Bürkner, 2017).

3 | RESULTS

3.1 | Relationship between dominance and functional traits

Across the four habitat types, SLA and LN were positively related to the first axis of the PCA, whereas LA and DBH_{max} were positively related to the second axis (Figure 3a–d; Table S11). WD aligned negatively with the first and second axes. When running the PCA with SM for a subset of species, we found that SM was negatively correlated with SLA and LN across all habitat types (Figure S2). Therefore, the first axis of the PCA relates to leaf economics, opposing thicker, low-nitrogen leaves against thinner, high-nitrogen leaves. The second axis relates to the size of trees and their components, via plant stature and leaf size. WD and SM are correlated with both PCA axes.

The results of the LMs considering two main axes of functional variation and species total relative abundance in each habitat type separately showed that: (i) species total relative abundance was positively correlated with axis 2 in *terra firme* forests, indicating that species with higher total abundance had slightly larger leaves and plant size (Figure 3a,e,i; Tables S6 and S12); (ii) species total relative abundance was positively correlated with axis 1 in floodplain forests, indicating that species with higher total abundance had thinner, higher nitrogen leaves and lighter wood (Figure 3b,f,j; Tables S6 and S12); (iii) species total relative abundance was negatively correlated with axis 1 in swamp and white sand forests, indicating that species with higher total abundance had thicker, lower nitrogen leaves and denser wood, and positively correlated with axis 2 in white sand forests, indicating that species with higher total abundance had larger leaves and plant size (Figure 3c,d,g,h,k,l; Tables S6 and S12). For the

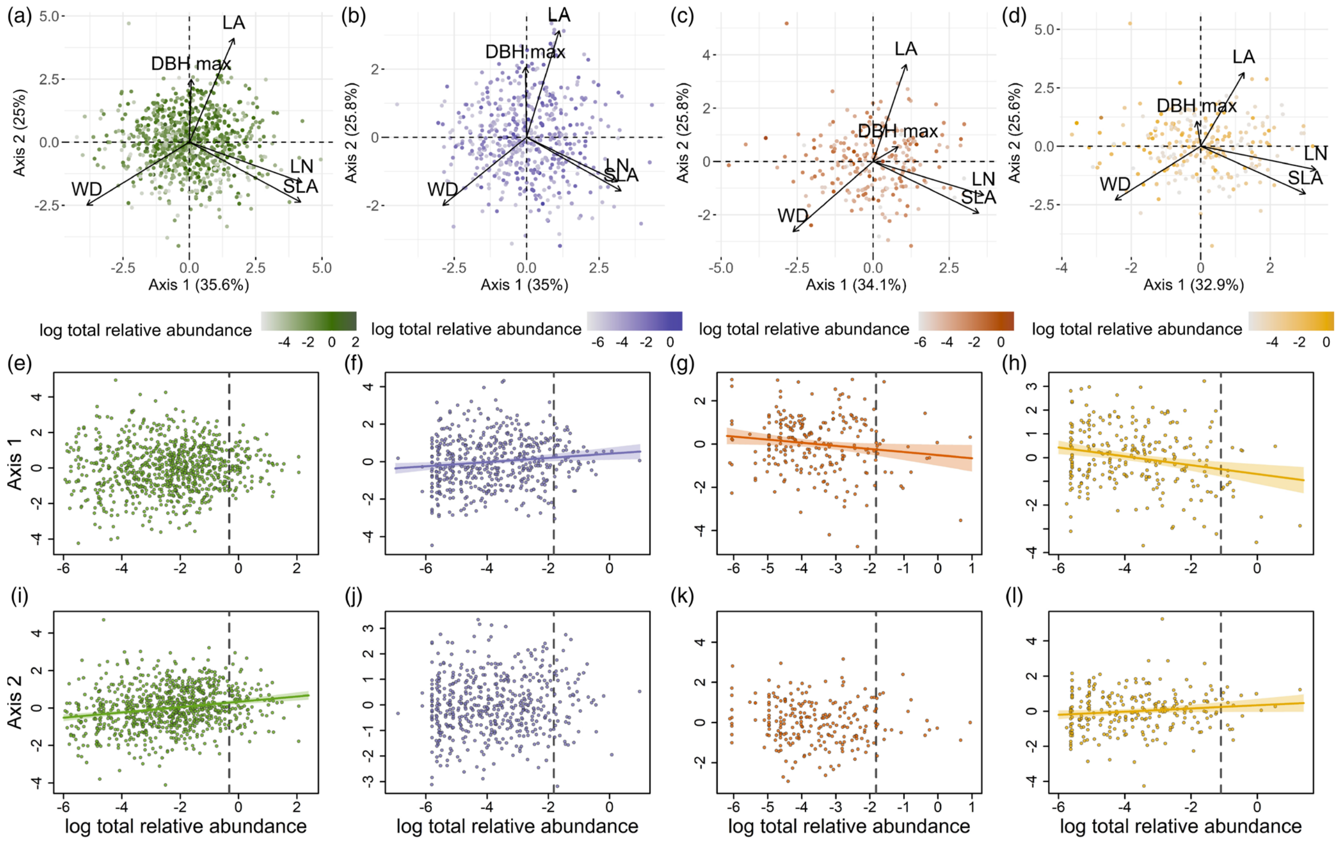

FIGURE 3 Principal component analyses (PCAs) for five functional traits (a–d) and scatter plots relating the first two PCA axes and total relative abundance (e–l) for *terra firme* (green, first column), floodplain (blue, second column), swamp (orange, third column) and white sand (yellow, final column) forests in western Amazonia. For the scatter plots, solid lines represent statically significant linear fits, and shading represents 95% confidence intervals. Grey vertical lines show the threshold between dominant (right) and non-dominant (left) species. Trait abbreviations are provided in Table S3.

subset of 423 species with values for all six traits, no significant relationships were found except for the positive relationship between axis 2 and species total abundance in *terra firme* forests (Figure S2). When accounting for potential imbalanced sampling across phylogeny, similar results were found only for axis 1 in swamp forests, suggesting a consistent, significant negative relationship between axis 1 and species total abundance in 56 out of 100 subsampled models in swamp forests (Figure S3).

The univariate analyses revealed that: (i) species with higher total abundance in *terra firme* forests had significantly lower SLA and higher LA, DBH_{max} and SM (Figure 4a–f; Tables S6 and S13); (ii) species with higher total abundance in floodplain forests had higher LA and DBH_{max} and lower WD (Figure 4g–l; Tables S6 and S13); (iii) species with higher total abundance in swamp forests had lower SLA and LN and higher SM (Figure 4m–r; Tables S6 and S13); (iv) species with higher total abundance in white sand forests had lower SLA

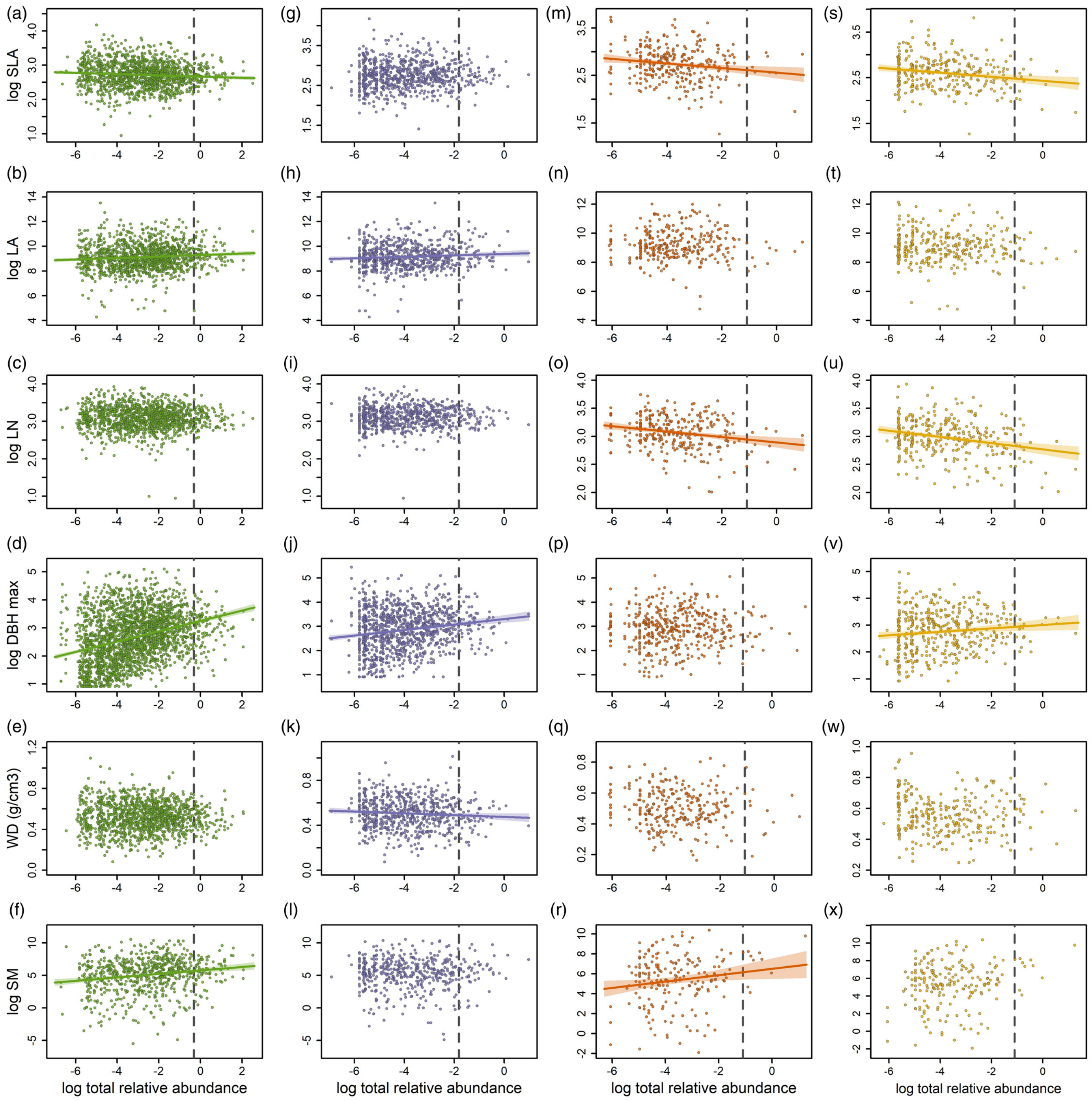

FIGURE 4 Relationships between six functional traits and total relative abundance for species in terra firme (green) (a–f), floodplain (blue) (g–l), swamp (orange) (m–r) and white sand (yellow) (s–x) forests in western Amazonia. Solid lines represent statistically significant linear model fits, and shading represents 95% confidence intervals. Grey vertical lines show the threshold between dominant (right) and non-dominant (left) species. Trait abbreviations are provided in Table S3.

and LN and higher DBH$_{max}$ (Figure 4s–x; Tables S6 and S13). When we considered potential imbalanced sampling across phylogeny, we found that most subsampled LMs showed similar results for (i) LA, DBH$_{max}$ and SM in *terra firme* forests; (ii) DBH$_{max}$ in floodplain forests; (iii) LN and SM in swamp forests; and (iv) SLA and LN in white sand forests (Figure S4; Table S14).

3.2 | Traits influence on local abundance and regional frequency of dominant species

We found that: (i) local abundance of dominant species decreased with DBH$_{max}$ values in *terra firme*, floodplain and swamp forests (Figure 5a; Figures S5a and S6; Table S9), (ii) regional frequency of dominant species increased with DBH$_{max}$ in *terra firme* and swamp forests and increased with SM in *terra firme*, floodplain and swamp forests (Figure 5b; Figures S5b and S6; Table S9).

More specifically by habitat type, we found that: (i) no other associations beyond those reported above existed between local abundance and regional frequency with traits of dominant species in *terra firme* forests (Figure 5; Figures S5 and S6; Table S9); (ii) local abundance of dominant species in floodplains was negatively related to LA and positively related to WD, and regional frequency was positively related to LA and negatively related to WD; (iii) local abundance of dominant species in swamps was negatively related to LN and regional frequency was positively related to LN; and (iv) local abundance of dominant species in white sands was negatively related to SLA and LN and positively related to WD. Table 2 summarizes relationships between functional traits and species total abundance, local abundance and regional frequency for dominant species.

4 | DISCUSSION

Examining key functional traits in tree species from four contrasting forest habitats in western Amazonia, we found that: (i) overall, species dominance, defined as species total relative abundance, is associated with specific trait values; (ii) local abundance and regional frequency of dominant species likely result from different ecological mechanisms; and (iii) these results depend on the specific environmental conditions of each habitat.

4.1 | Functional distinctiveness of dominant species within lowland Amazonian forests

Associations between functional traits and species total relative abundance, as a proxy of dominance, varied among habitats (Table 2). Overall, dominance was related to resource conservation strategies in swamp and white sand forests, and to plant size in *terra firme* and floodplain forests. Therefore, these results support our hypothesis, showing that the functional strategies underlying dominance depend on the abiotic and biotic conditions where species dominate. This suggests that dominant species have functional traits that are optimized to the environmental conditions of each habitat (Cingolani et al., 2007). Since dominance was defined by different functional traits within each forest type, we discuss potential explanations by habitat type hereafter.

Overall, we found that dominance was associated with large DBH$_{max}$ in *terra firme* and floodplain forests (Figures 3i and 4d,j; Figures S3 and S4). This is consistent with previous studies conducted across scales, growth forms and habitats (Aiba et al., 2020; Arellano et al., 2015; Cornwell & Ackerly, 2010; Hordijk et al., 2025;

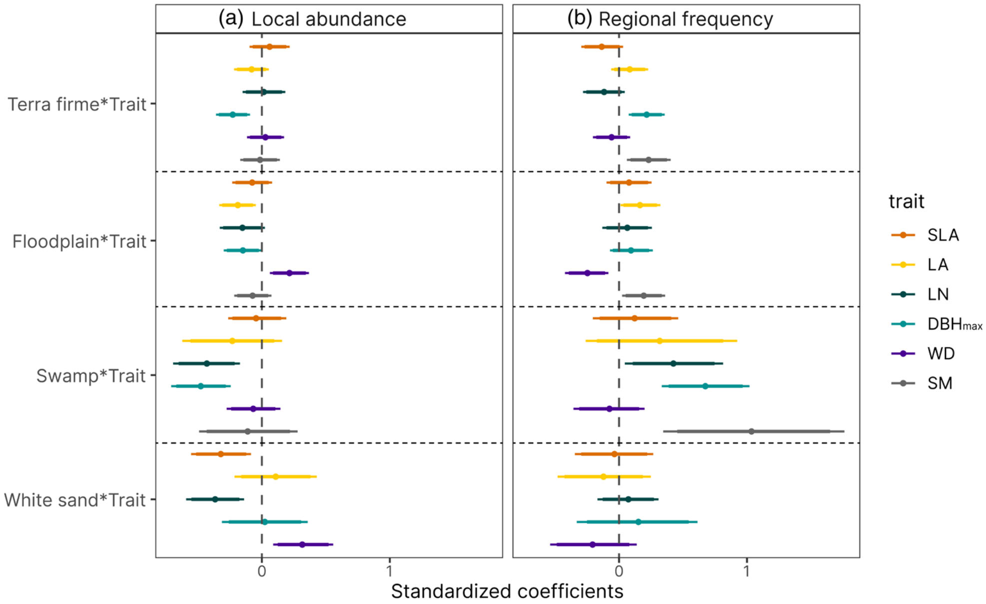

FIGURE 5 Standardized slope coefficients from Bayesian models showing the interaction effect between six functional traits and habitat type on (a) local abundance and (b) regional frequency of dominant species. Points represent the median values, thin lines represent 90% credible intervals and thick lines represent 95% credible intervals of the slope coefficients for each trait. Trait abbreviations are provided in Table S3.

TABLE 2 Results concerning the direction of the relationships between total abundance (considering analyses with and without phylogeny), local abundance and regional frequency of dominant species with species functional traits across the four main habitat types in western Amazonia forests.

			Habitat types			
			Terra firme	Floodplain	Swamp	White sand
Dominance and functional traits	Total abundance	SLA	0	0	0	–
		LA	+	0	0	0
		LN	0	0	–	–
		DBH$_{max}$	+	+	0	0
		WD	0	0	0	0
		SM	+	0	+	0
Dominance patterns and functional traits	Local abundance	SLA	0	0	0	–
		LA	0	–	0	0
		LN	0	0	–	–
		DBH$_{max}$	–	–	–	0
		WD	0	+	0	+
		SM	0	0	0	
	Regional frequency	SLA	0	0	0	0
		LA	0	+	0	0
		LN	0	0	+	0
		DBH$_{max}$	+	0	+	0
		WD	0	–	0	0
		SM	+	+	+	

Note: + and blue: positive relationship, – and red: negative relationship, 0 and grey: no relationship.

Lisner et al., 2021; Yan et al., 2013). Larger plants, generally associated with greater height (Norberg, 1988), can disperse farther and potentially colonize more locations (Thomson et al., 2011). Additionally, they pre-empt light in stratified canopy layers (Falster & Westoby, 2003) and tend to have deeper, longer roots that allow greater access to soil nutrients and water (Li & Bao, 2015). Together these functional characteristics could give large species an advantage over smaller species colonizing new sites and becoming abundant. In *terra firme* forests, species with higher total abundance were also characterized by greater LA and SM (Figures 3i and 4b,f; Figures S3a and S4). Greater LA is associated with a higher capacity to intercept and compete for light (Denelle et al., 2020). Greater SM is generally associated with higher seedling survival (Lebrija-Trejos et al., 2016) and fleshy fruits (Bolmgren & Eriksson, 2010) (with some exceptions, such as the Lecythidaceae family), which are more attractive to frugivores, the main dispersal vectors in Amazonian forests (Correa et al., 2023). Both traits can confer a competitive advantage in habitats such as *terra firme* forests, which support substantial above-ground biomass that generates strong competition for light and nutrients (Baraloto et al., 2011). In seasonally inundated floodplain, no additional relationships between dominance and the other traits were found, presumably due to sampling imbalance across phylogeny (Figures 3b,f,j and 4g–i; Figures S3b and S4).

In swamps and white sands, dominance was associated with traits related to resource conservation strategies (i.e. lower SLA and/or LN) (Table 2). Lower SLA has been previously reported to be associated with increasing levels of waterlogging in different experimental studies (Poorter et al., 2009). These trait values may enable plants to conserve resources and cope with limited water availability caused by the anoxic conditions around the roots, which hinder water absorption in swamp forests (Junk et al., 2011; Lobo & Joly, 1998; Poorter et al., 2009). The poor sandy soils of white sands, which experience frequent drought stress, increase the cost to repair herbivore-damaged tissue (Fine et al., 2004, 2006). Therefore, traits related to resource conservation strategies and defence are favoured, allowing well-defended, conservative species to become dominant in white sands (Fortunel et al., 2014). Dominant species in swamps also showed higher SM (Figure 4r; Figure S4), consistent with more resources for germinating seedlings (Lebrija-Trejos et al., 2016; Moles, 2018).

In summary, we found that dominance is mainly associated with specific trait values adapted to the environmental conditions that filter species within each habitat type, which confer dominant species a functional advantage to prevail over the rest of the species.

4.2 | Local abundance and regional frequency relate to specific traits in different habitats

Within the set of dominant species, previous research found a strong negative relationship between local abundance and regional frequency, indicating dominant species are either locally abundant (local dominants) or regionally frequent (widespread dominants)

(Figure 1b) (Matas-Granados et al., 2024). We focus hereafter on disentangling the underlying mechanisms driving the two types of dominance. We hypothesized that the two dominance types would be related to different traits (Table 1). We found instances where local abundance and regional frequency of dominant species were associated with (i) different traits or (ii) similar traits, but with opposite signs, and these two results varied among habitats (Table 2; Figure 5). Therefore, these results partly contrast with our initial hypothesis. This finding could in part be due to our focus on traits that may integrate different processes with contrasting effects on dominance patterns at local versus regional scales (Diaz et al., 1998, 2016; Westoby, 1998). Overall, we found that trait values related to resource conservation strategies define local dominants, while traits related to resource acquisition strategies define widespread dominants in floodplain, swamp and white sand forests. These findings suggest that the ecological mechanisms driving the two distinct dominance patterns are likely different. Hereafter, we present first general results across habitat types and later specific results by habitat type.

Large maximum size characterized dominant species with lower local abundance and higher regional frequency (Figure 5). Widespread dominants tended to have larger potential maximum sizes than local dominants (see Figure 1b). Taller species have greater dispersal ability (Thomson et al., 2011) to colonize potentially more places, leading to greater regional frequency, even if they do not achieve high local densities where they establish. Conversely, smaller species suffer less from conspecific negative density dependence, allowing higher densities near parents and thus higher local abundances (Zang et al., 2021). In addition, dominant species with greater SM also exhibit higher regional frequency across all habitat types (Figure 5b). Larger seeds relate to greater dispersal by birds and mammals (Bolmgren & Eriksson, 2010; Muller-Landau & Hardesty, 2005; Thomson et al., 2011), allowing large-seeded species to colonize new locations across forest types.

In *terra firme* forests, local abundance and regional frequency of dominant species showed similar associations with $\mathrm{DBH}_{\mathrm{max}}$ and SM (Figure 5), suggesting that dispersal, survival and competition are key filtering processes in achieving different dominance patterns in these forests as detailed above. Additionally, we note that dominant species in *terra firme* forests have the lowest range of local abundance compared to dominant species in other habitats (0.09 compared to 0.17 in floodplains, 0.38 in swamps and 0.42 in white sands, Table S2), likely due to the higher species diversity in these habitats (Matas-Granados et al., 2024; ter Steege et al., 2000). This narrower range of values could limit our ability to capture the role of traits of dominant species in these forests.

In floodplains, swamps and white sands, local dominants were associated with traits related to resource conservation (Table 2; Figures 1b and 5). Species characterized by resource conservation strategies tend to have slower growth (Díaz et al., 2016; Grime, 1974), but greater defence against natural enemies and more efficient water use in addition to preservation of resources (Candeias & Fraterrigo, 2020; Fine et al., 2006; Moles, 2018). These functional traits might allow resource-conserving species to withstand drought stress associated with an anoxic soil environment during flooding events in floodplains (Poorter et al., 2009), permanent anoxia in swamps (Asner et al., 2015; Mata et al., 2019) and nutrient-poor environments, frequent soil drought and herbivory in white sands (Fine et al., 2004; Fortunel et al., 2014) and therefore, attain higher local abundance. Conversely, widespread dominants in floodplains and swamps exhibited more resource-acquisitive strategies allowing faster growth (Díaz et al., 2016; Mori et al., 2019; Wright et al., 2004), greater recruitment (Rüger et al., 2012, 2020) and greater abilities to colonize new sites (Denelle et al., 2020) and thus, higher regional frequencies. Our results in floodplain and swamp forests partially align with previous studies showing that high WD and low LN values are associated with small range sizes, although the relationship was weak (Chacón-Madrigal et al., 2018). Finally, we found no support for trait effects on regional frequency in white sands.

4.3 | Caveats

Our study advances our understanding of how functional traits relate to species dominance in Amazonian forests. Nevertheless, some limitations should be acknowledged. First, we found some discrepancies between our main results and those considering potential sampling imbalance across the phylogeny, especially in multivariate approaches (Figures 3 and 4; Figures S3 and S4). We suspect this incongruence is due to the lower number of species considered in multivariate analyses, which likely enhances clustered sampling imbalance in some lineages. Second, our trait dataset is incomplete, with trait coverage skewed towards dominant species. We have tried to reduce this bias by applying permutation to our analyses, but we recognize that our analyses may overlook the functional trait space occupied by rare, infrequent species. Third, although we found clear relationships between traits and dominance, even using species mean trait values, we have not addressed intraspecific trait variation, missing important plasticity that could contribute to a more fine-grained understanding of trait-dominance relationships. Only increased trait sampling in species-rich forests, with attention to local conditions within inventoried plots and continued contribution to public trait repositories will help resolve these issues in future studies.

5 | CONCLUSIONS

Studying how dominant species differ from rarer species functionally provides valuable insights into the mechanisms of species dominance across habitat types in Amazonia. Further, accounting for both local abundance and regional frequency offers a promising way forward in clarifying the ecological processes shaping different species dominance patterns across scales and habitats. Most importantly, we showed that the traits that matter in species dominance patterns vary with environmental variation across Amazonian forest habitats. A trait–environment framework has the potential to forecast changes in species abundances and dominance patterns as anthropogenic atmospheric and climate change alter forest environments across the Amazon.

AUTHOR CONTRIBUTIONS

Laura Matas-Granados, Claire Fortunel and Manuel J. Macía conceived the ideas. Laura Matas-Granados and Claire Fortunel designed the methodology with input from Luis Cayuela. Laura Matas-Granados, Claire Fortunel, Luis Cayuela, Julia G. de Aledo, Celina Ben Saadi, Nathan J. B. Kraft, Christopher Baraloto, S. Joseph Wright, Jason Vleminckx, Nancy C. Garwood, Peter Hietz, Margaret R. Metz and Manuel J. Macía contributed with functional data. Luis Cayuela, Julia G. de Aledo, Celina Ben Saadi, Frederick C. Draper, Timothy R. Baker, Oliver L. Phillips, Eurídice N. Honorio Coronado, Kalle Ruokolainen, Roosevelt García-Villacorta, Katherine H. Roucoux, Maximilien Guèze, Elvis Valderrama Sandoval, Paul V. A. Fine, Carlos A. Amasifuen Guerra, Ricardo Zarate Gomez, Pablo R. Stevenson, Abel Monteagudo-Mendoza, Rodolfo Vasquez Martínez, John Terborgh, Mathias Disney, Roel Brienen, Percy Núñez Vargas, Jhon del Aguila Pasquel, Yadvinder Malhi, Jacob B. Socolar, Gerardo Flores Llampazo, Jim Vega Arenas, Darcy Galiano Cabrera, Javier Silva Espejo, Joey Talbot, Barbara Vinceti, José Reyna Huaymacari, Cecilia Ballón Falcón, Ted R. Feldpausch, Varun Swamy, Julio M. Grandez Rios and Manuel J. Macía contributed with forest inventory data. Laura Matas-Granados conducted the analyses with help from Claire Fortunel. Laura Matas-Granados and Claire Fortunel led the writing of the first draft, with inputs from Luis Cayuela, Julia G. de Aledo and Manuel J. Macía. All authors contributed to the final manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflicts of interest to declare.

PEER REVIEW

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/1365-2745.70214.

DATA AVAILABILITY STATEMENT

Forest inventory plot data are available from the Dryad Digital Repository https://doi.org/10.5061/dryad.pk0p2ngsd (Matas-Granados et al., 2023). Functional data from previously published projects are available from their respective associated publications (Sheet 'Table_compilation' in file 'Traits_species_data' in Dryad Digital Repository https://doi.org/10.5061/dryad.2280gb60q (Matas-Granados et al., 2025b) to see references to each species and trait). Functional data not provided yet (from project 'CGL2016-75414-P' led by Manuel J. Macía and Luis Cayuela) are provided (Sheet 'DISPLAMAZ_data' in file 'Traits_species_data' in https://doi.org/10.5061/dryad.2280gb60q). Maximum diameter at breast height (DBH_{mx}) calculated from forest inventory plot data is also provided (Sheet 'DBH_max' in file 'Traits_species_data' in https://doi.org/10.5061/dryad.2280gb60q). We provide a workflow to generate the compiled trait database (Sheet 'Workflow' in file 'Traits_species_data' in https://doi.org/10.5061/dryad.2280gb60q). The compiled trait database with species mean trait values is also available in https://doi.org/10.5061/dryad.2280gb60q (Sheet 'Traits_values2', for trait data without separating by habitat type, and 'Traits_values_FT' for trait data separating by habitat type in file 'Traits_species_data'). Code to reproduce analyses, figures and tables from the compiled trait database is provided from Zenodo (https://doi.org/10.5281/zenodo.10635771; Matas-Granados et al., 2025a).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1. Summary of forest inventory plot data used in this study and Matas-Granados et al. (2024).

Table S2. List of species found as dominant within each habitat type.

Table S3. Summary of the functional traits used in the study.

Table S4. Proportion coverage of functional trait species data, by species dominance and habitat type.

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Table S7. Phylogenetic signal of functional traits.

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Table S9. Parameters of Bayesian models exploring the effect of nine functional traits, habitat type and their interaction on local abundance and regional frequency of dominant species.

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Table S11. Correlations of SLA, LA, LN, $\mathrm{DBH}_{\mathrm{max}}$ and WD with axes of principal component analysis (PCA) for each habitat type separately.

Table S12. *F* and *p* values from linear models (LMs) exploring the relationship between axes 1 and 2 for PCA and species regional abundance for each habitat type separately.

Table S13. *F* and *p* values from linear models (LMs) exploring the relationship between single functional traits and species regional abundance for each habitat type separately.

Table S14. *F* and *p* mean and standard deviation values from linear models (LMs) exploring the relationship between single functional traits and species regional abundance for subsampling models considering potential bias by phylogeny for each habitat type separately.

Figure S1. Pairwise trait correlations.

Figure S2. Principal component analyses (PCA) on six functional traits, including SM and model predictions of significant linear models (LMs) between two main axes of functional variation and total abundance from species of (a) *terra firme* (green); (b) floodplain (blue); (c) swamp (orange) and (d) white sand (yellow) forests in western Amazonia.

Figure S3. Model predictions of significant linear models (LMs) for subsampling analyses considering potential bias across phylogeny between two main axes of functional variation and total abundance from species of *terra firme* (green); floodplain (blue); swamp (orange) and white sand (yellow) forests in western Amazonia.

Figure S4. Model predictions of significant linear models (LMs) for subsampling analyses considering potential bias across phylogeny of relationships of single functional traits and total abundance from species for *terra firme* (green), floodplain (blue), swamp (orange) and white sand (yellow) forests in western Amazonia.

Figure S5. Standardized coefficients for Bayesian models representing the effect of nine functional traits and their interaction with the habitat type on (a) local abundance and (b) regional frequency of dominant species.

Figure S6. Graphs of predictions for Bayesian models representing the effect of nine functional traits and their interaction with the habitat type on local abundance (lower panels of the diagonal) and regional frequency (upper panels of the diagonal) of dominant species.

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