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Functional biogeography of herbaceous assemblages along edaphic and climatic gradients in Amazonian forests

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ABSTRACT

Soil, topography, and climate have been identified as strong drivers of functional composition turnover of plant communities, setting the dominant ("optimal") community weighted mean (CWM) trait values. These same environmental factors may also affect disturbance regimes (e.g., the effect of soil fertility increasing tree turnover rates) as they create high-luminosity patches within dense canopy forest, promoting trait diversity, i.e. variance of the mean community trait values within and among communities. We analysed the drivers of functional trait turnover within and among 451 Zingiberales' assemblages across Brazilian Amazonia, based on leaf mass per area (LMA), plant maximum height and seed size of 192 species. We detected functional turnover of the dominant assemblage trait values (given by the CWM) towards lower assemblage mean values of LMA, height and seed size, as soil fertility increased (higher sum of exchangeable bases) and local environments became wetter (bottomlands), in accordance with the expectations of the fast-slow growth trade-off along the whole-plant economic spectrum. Variability in seed size and plant height within assemblages increased towards lower topographic positions and low-nutrient soils, and the variance around dominant height and seed size values among assemblages increased towards bottomlands and regions with more seasonal climate. We conclude that, while soil and topography promote the filtering of a predictable functional composition, climate mostly promoted within and among-assemblage functional variance. Thus, it may be difficult to predict the effects of climate change based solely on the mean functional structure of Amazonian understory communities.

KEYWORDS: ecological gradients, soil fertility, topography, tropical forest, Zingiberales

Biogeografia funcional de comunidades de plantas herbáceas ao longo de gradientes edáficos e climáticos em florestas amazônicas

RESUMO

Solo, topografia e clima tem sido identificados como fortes impulsionadores do turnover da composição funcional de comunidades vegetais, definindo os valores dominantes (média da comunidade, CWM). Esses fatores ambientais também podem afetar os regimes de perturbação (p.ex., a fertilidade do solo aumentando o turnover de árvores), o que cria clareiras com alta luminosidade em florestas com dossel fechado, promovendo a variância dos valores médios de características funcionais dentro e entre comunidades. Neste estudo, avaliamos os determinantes do turnover das características funcionais médias e sua variabilidade dentro e entre 451 assembléias de Zingiberales na Amazônia brasileira, com base na massa foliar por área (LMA), altura máxima da planta e tamanho da semente de 192 espécies. Detectamos um forte turnover dos CWM em direção a valores mais baixos de LMA, altura e tamanho de semente à medida que a fertilidade do solo aumentou e nos baixios, de acordo com as expectativas do trade-off de crescimento rápido vs. lento ao longo do espectro econômico da planta. A variabilidade no tamanho da semente e na altura da planta dentro das assembleias aumentou nos baixios e em solos com poucos nutrientes, e a variância em torno dos valores dominantes de altura e tamanho de semente entre as assembleias aumentou em regiões de clima mais sazonal. Concluímos que, enquanto o solo e a topografia promovem a filtragem da composição funcional, o clima promoveu principalmente a variância funcional. Portanto, pode ser dificil prever os efeitos das mudanças climáticas sobre a estrutura funcional média das comunidades do sub-bosque amazônico.

PALAVRAS-CHAVE: gradientes ecológicos, fertilidade do solo, florestas tropicais, topografia, Zingiberales

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INTRODUCTION

Functional traits represent the phenotypic expression of individuals and relate to population vital rates (growth, recruitment, mortality) and plant life strategies. Direct measurements of life cycle and performance of organisms are not straightforward, especially in highly diverse ecosystems, so ecologists have been using plant functional traits as proxies of plant strategy (Westoby 1998; Reich 2014; Díaz *et al.* 2016). This field has advanced strongly for tropical palms, lianas and especially trees, but less so for tropical herbs, despite their relevant contributions to forest diversity and food-webs (Perea *et al.* 2022).

Plant height, leaf mass per area (LMA) and seed size have been suggested as key indicators of plant strategies (Westoby 1998). In closed-canopy forests, plant height is an indicator of light-related niche position since taller species have more access to light. Seed size indicates reproduction and establishment strategies: species may produce fewer but larger seeds with high supply of reserves, enabling establishment under resources scarcity, or a larger quantity of smaller seeds to enable colonising of micro-sites that are rare in space and time (Dalling *et al.* 1998; Kitajima 2002). LMA summarises the global spectrum of leaf economics, running from fast to slow return of investment in leaf tissues (Wright *et al.* 2004). Theory predicts that when resources are scarce, species grow slowly and invest in highly durable tissues in leaves, stems and/or roots, and the opposite strategy is expected under high resource availability (Reich 2014), i.e., an integrated 'fast–slow' plant economics spectrum aligned with resource availability.

Studies of tree functional turnover patterns in tropical forests have revealed that trait-turnover patterns are governed by climate and edaphic conditions (ter Steege *et al.* 2025; Fyllas *et al.* 2009; Fortunel *et al.* 2014; Muscarella and Uriarte 2016; Joswig *et al.* 2022), and a recent review focused on the Neotropics concluded that resource-limited environments tended towards conservative traits and strategies (Freitas *et al.* 2023). Tree species with slow growth strategies (conservative strategy) tend to successfully establish and live in nutrient-poor soils, whereas fast growth species (acquisitive strategy) are dominant in nutrient-rich soils (ter Steege *et al.* 2025; Fyllas *et al.* 2009; Joswig *et al.* 2022). Climate is expected to modulate leaf traits and plant size at the global scale, but a weak relationship has been often documented for leaf traits (Wright *et al.* 2004, 2017; Maire *et al.* 2015). Indeed, Fyllas *et al.* (2009) found a positive relationship between LMA and annual precipitation in Amazonia, whereas Muscarella and Uriarte (2016) found a negative relationship in Central America.

Because organisms do not access the total amount of water provided by rainfall, water availability depends also on the soil capacity to retain water and the proximity to the water table (Costa *et al.* 2023). Topography influences species variability in hydraulic traits and may be a stronger filter of functional strategies than climate at local (Cosme *et al.* 2017; Oliveira *et al.* 2018) or even regional scales (Garcia *et al.* 2023). Following the theory of an integrated 'fast–slow' plant economics spectrum aligned with resource availability (Reich 2014), we could expect the community means of traits to linearly change along the gradients of soil fertility, climatic and topography. The effects of natural disturbances (e.g., tree falls) are expected to interact with the effects of soil, climate and topography, promoting trait diversity as they create high light patches among a matrix of closed forest, each selecting different plant traits (Sterck *et al* 2011). At the broad regional scale, the expected consequence is the generation of noise in the turnover of the mean plant trait values in communities along those environmental gradients.

Herbaceous plants – and therefore their assemblages – can be expected to follow the same functional trends along environmental gradients as described for other life-forms, even if the absolute trait values are different (Matsuo *et al.* 2023). However, Swenson (2009) described a "reversal of the functional dicot strategy for monocots" - i.e., that species associated to high-luminosity environments had higher LMA, lamina size and culm density (conservative traits) when compared to their congeneric pairs of shaded environments - the opposite of what is found for dicot herbs and trees. If this pattern of response to light is extended to other resources, the turnover of herbs along soil fertility and topography gradients might not follow the patterns described for other life-forms.

Here we investigated the variation of functional traits of 451 herb-assemblages across the Amazon. We focused on assemblages of Zingiberales (hereafter gingers), a very diverse order of monocotyledonous species (Kress *et al.* 2001), accounting for more than 50% of the herb cover in many plots in Amazonia (Costa 2004, 2006). Gingers are rhizomatous herbs, varying in habit from small rosulate (10 cm height) to tall palm-like or scandent plants (5 m tall). Our objective was to determine how resource gradients affect the dominant assemblage functional strategy (given by the trait's community weighted mean, CWM in the inventory plots), the across-assemblage variance of the dominant strategy (variance of CWM across plots), and the within-assemblage variation of traits among individuals (given by the community weighted deviation, CWD, within plots). The traits evaluated were LMA, plant height and seed size, which provide a general description of functional strategies (Westoby 1998). We hypothesised that the dominant functional strategy will change along the resource gradients, with acquisitive strategies (lower CWM of LMA, plant height and seed size) increasing towards high resource levels (fertile soils, wet climate and bottomlands). At the same time, we expected the variance of the dominant functional strategy among and within-assemblages to increase towards nutrient-rich soils, wet climate and bottomlands.

MATERIAL AND METHODS

Biotic and abiotic data were obtained in 451 plots of 500 m^2 distributed along non-inundated (terra-firme) lowland forests in Brazilian Amazonia (Figure 1). Data came from two plot designs: (1) 409 plots of 250 x 2 m following the RAPELD protocol (Costa and Magnusson 2010); and (2) 42 plots of 100 x 5 m sub-sampled from 500 x 5 m plots (UTU plots) (Tuomisto *et al.* 2016). RAPELD plots are placed at 1-km intervals across grids or modules that are distributed across the Amazon lowland basin. RAPELD plots are installed following elevation contour lines to minimize within-plot environmental variation associated with topography (e.g., soils, vertical distance to the water table). UTU plots are not distributed in grids but placed in specifically designated sites using remote sensing imagery (Tuomisto *et al.* 2016). They follow a predetermined compass bearing, thus crossing the local topographical variation to maximize environmental variation within plots. A minimum distance of 1 km is kept between UTU plots. Both RAPELD and UTU plots were sampled in areas that vary from tall mature forest to white sand forests with a simpler canopy structure (regionally known in Brazil as *campinaranas*). We selected the continuous 5-m sub-units with the lowest internal topographical variation from the UTU plots to make the two sampling designs comparable, as previously done in other studies (Moulatlet *et al.* 2017; Tuomisto *et al.* 2019; Zuquim *et al.* 2019).

We counted every ginger clump with a height > 5 cm rooted inside each plot. Clumps were defined as groups of stems or leaves arising from the soil less than 20 cm from each other or based on our field experience of each species. Representative samples were collected to be further identified. All specimens were identified by the first author (FOGF) based on specialised literature and the fertile material was sent to the specialists Helen Kennedy and Paul Maas for confirmation. Vouchers were deposited in herbaria in Brazil (INPA), Canada (UBC), and the Netherlands (U).

We measured or obtained from the literature three functional traits (LMA, plant height and seed size) for the species found in the plots (Maas 1972, 1977; Andersson 1977, 1985; Hagberg 1990; Horvitz and Schemske 1994) plus other scattered information listed in Costa *et al.* (2008). LMA is the ratio between the dry leaf mass and fresh (i.e., completely expanded) leaf area. We adapted the original method to estimate LMA (Pérez-Harguindeguy *et al.* 2013) using small pieces of the lamina of dried material from herbarium specimens. For each individual, a maximum of 4 pieces (on average 3 cm^2) was cut from different parts of the lamina (at middle and close to the base and apex), excluding the main vein. We chose the locations carefully from mature leaves and leaf pieces where the lamina tissue had no or very little shrinkage. LMA was calculated as the average of values obtained from a maximum of six individuals per species or only from one individual, when the species was rare and collected only once. For the few direct field observations, height estimation was based on the 95% quantile. Seed size was obtained using the formula of an ellipse based on the two largest measures of seed dimension obtained from the literature. Out of the 192 species, measures of LMA, plant height and seed size were missing for 23, 23 and 109 species, respectively. In these cases, the trait value was assigned as the mean genus trait value considering only species found in the Amazon region (Borgy *et al.* 2017). Most of the species for which traits could not be measured were rare (< 3 individuals) in the total sampling.

Environmental data was measured in each plot. To represent soil fertility, topographic and climatic gradients we used the sum of exchangeable base cations (Ca^{+2}, Mg^{+2}

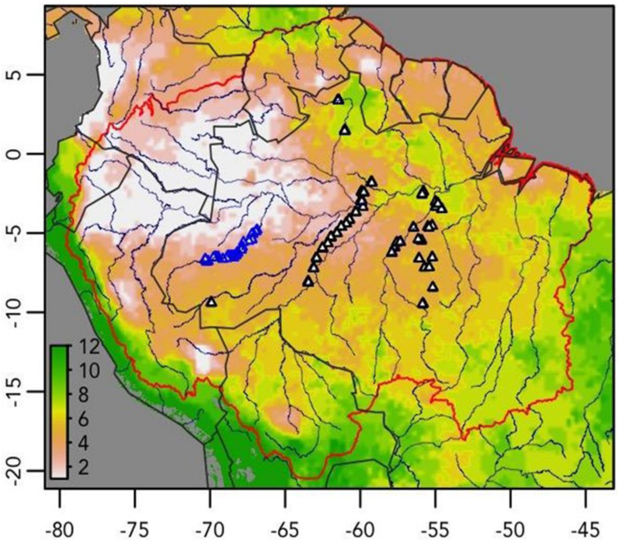

Figure 1. Location of the 451 plots where ginger community and environmental data were obtained in the Brazilian Amazon. The background map represents the dry season length. The legend denotes the maximum number of consecutive months with less than 100 mm of precipitation along the 1998 - 2004 period. Black triangles represent the clusters of RAPELD plots and blue triangles represent UTU plots located along the Juruá River. Clusters may have 5 to 57 plots spaced by at least 1 km.

and K^+ measured in cmol(+) kg^{-1}), the vertical distance from drainage (VDD, in metres) and the dry season length (DSL, in months), respectively. The sum of exchangeable bases is a widely used proxy of soil fertility in Amazonia (Quesada *et al.* 2011) and strongly related to floristic patterns across the basin (Figueiredo *et al.* 2014; Tuomisto *et al.* 2019). The protocols for soil sampling and laboratory analyses are described in previous studies (Figueiredo *et al.* 2014; Tuomisto *et al.* 2016).

The vertical distance from drainage (VDD) was extracted from a SRTM digital elevation model. VDD have been successfully used to explain floristic patterns in Amazonia (Moulatlet *et al.* 2014, 2022). Sites with low VDD are located near drainages or areas where the water table is closer to the soil surface. These areas are in bottomlands, where usually the water availability is higher in comparison with hilltops. VDD values were obtained from published articles. For 198 plots located in the interfluve Purus-Madeira, we obtained VDD values from Moulatlet *et al.* (2014). For 193 plots located north of the Amazon River in central Amazonia and in Pará state, VDD was obtained from Figueiredo *et al.* (2014). For the remaining plots, VDD was calculated using the Vertical Distance to Channel Network algorithm (Bock and Köthe 2008), implemented in the QGis software through the SAGA-toolbox (new data extracted for this study).

Dry season length (DSL) was estimated from data of the TRMM satellite (Kummerow *et al.* 1998), available at http://disc.sci.gsfc.nasa.gov. We converted monthly data from 1998 to 2004 of the TRMM product 3B43 V6 at a 0.25° resolution (about 28 km at the equator) into the dry season length variable, defined as the maximum number of consecutive months with less than 100 mm of precipitation along that period. For each plot, the DSL value was extracted after rescaling the data to a 0.05° (~ 5 km) spatial resolution. We used the *raster* package in R to manipulate and process the TRMM variable (R Core Team 2022, Hijmans 2017).

Data analysis

To evaluate the effect of environmental gradients on functional trait patterns within and among ginger assemblages, we first estimated the community weighted mean (CWM) [Equation 1] to characterise the dominant trait strategy of each assemblage (i.e., each RAPELD or UTU plot) and the community weighted deviance (CWD) [Equation 2] to characterise the within-assemblage trait variability, according to Díaz *et al.* (2007) and Violle *et al.* (2007).

$$CWM = \sum_{k=1}^{n_j} w_{k,j} \times T_{k,j} \qquad \text{Equation 1}$$

$$CWD = \sqrt{\frac{\sum_{k=1}^{n_j} w_{k,j}(T_{k,i} - CWM)^2}{\sum_{k=1}^{n_j} w_{k,j} - 1}} \qquad \text{Equation 2}$$

where w is the relative abundance of the species j in the assemblage (plot) k, and T is the trait value of the species j in the assemblage k.

The effects of environment on within-assemblage variability were evaluated with multiple GAMLSS (Generalized Additive Models for Location Scale and Shape) regressions (Stasinopoulos and Rigby 2008), which allow the joint estimation of environmental gradients effects on the mean (μ) and variance (σ) of assemblage-trait response. Since the CWD is a descriptor of variance, only its mean response to the environment was evaluated. The turnover of the dominant trait strategy of each assemblage along environmental gradients was evaluated with multiple GAMLSS regressions of each trait CWM against soil fertility, DSL and VDD. As in an ordinary least-squares regression, in GAMLSS the change of a response variable as a function of a predictor variable is evaluated by the mean response. The variance around the mean response of communities to each environmental variable indicates divergence among communities (i.e., variance can increase with the environmental predictor, indicating divergence towards more positive values of the predictor, or the opposite, or even no significant trend), and this was evaluated by the variance parameter of the GAMLSS.

We fitted different models assuming that our response variables (CWM or CWD of each trait) can be represented by general distribution families parameterized by the mean and variance (shape parameters, skewness and kurtosis). Our approach consisted in modelling all parameters as linear and/or non-linear responses to the predictor variables (soil, VDD and DSL) using specific link functions for each parameter. The soil fertility and VDD were logarithmically transformed before the analysis to fit the assumptions of normality required in linear models and because the relative change in these variables is more important than the absolute change (i.e., a unit change in base concentration is more strongly perceived by plants in poor than in rich soils).

Prior to the modelling we tested several distribution families to best fit the distribution of CWD and CWM. For height and seed size, we tested continuous distributions assuming CWM >0 (for either height or seed size), and for CWM-LMA, we also included the distribution families that do not have lower bounds (e.g., normal distribution). The selected family distributions were those with the lowest values of the generalized Akaike information criteria (GAIC) obtained by fitting the available distributions on observed values of CWD or CWM without environmental predictors. Then, we tested the effects of environmental gradients on the CWD or CWM of each trait, modelled with the selected family distribution. If models failed to find an optimal solution after iteractions, the second and third best ranked families were employed.

For plant height and seed size, CWM models were fit using a Box-Cox *t* with four parameters assuming a log link for mean, variance and kurtosis and identity link for the skewness parameter. For LMA, the CWM model was fit using a *t* family distribution with 3 parameters using identity link for mean and log link for variance and skewness parameters. The CWD models were fitted using a zero-adjusted Gamma distribution. When plots had only a single species, CWD was assumed to be zero.

After setting the distribution that best fitted our response variables, we performed a model selection procedure to quantify how well each independent variable explained the variation of each parameter of our response variables. For both CWM and CWD, the model selection procedure started with a forward approach (leave-one-out variable starting with the first one) applied first to the mean model and subsequently to the variance model. The procedure finished running the backward selection (leave-one-out variable starting with the last one) from variance to mean. Only linear relationships between the response and predictor variables were allowed. Since for CWD we only evaluated the mean response, the variance was estimated as the intercept of the variance parameter of a zero-adjusted gamma distribution.

Then, we fitted three types of models: one allowing the environmental variable to affect only the mean (environmental pressure towards a dominant value, i.e. functional turnover); the second allowing the environmental variable to affect variance only (environmental pressure towards among-community divergence); and a third model allowing the environmental variable to affect both mean and variance. The relative effect size of each variable was assessed by the beta coefficients (slopes). Model performance was evaluated using the ΔGAIC and generalised R^2 (Nagelkerke 1991) as implemented for GAMLSS models (Stasinopoulos and Rigby 2008).

GAMLSS were controlled for potential spatial autocorrelation due to plot aggregation within sites by setting site as the random term. Sites were defined as any group of plots within a radius of 10 km. To evaluate the effect of the spatial autocorrelation in distances above 10 km, we computed Moran's I correlograms for the CWM as measured for each of the three functional traits (LMA, seed size and plant height) and for the environmental variables soil fertility, HAND and DSL (Figure S1). Significant autocorrelation in the same distance class for both dependent and independent variables would indicate the potential for spatial factors not related to the tested hypothesis to be affecting the models. The only distance class that showed consistent overlap between dependent and independent variables was the first one, as it is normally expected given the contagious plant dispersal process. This justifies the inclusion of a random factor designed to tackle the expected correlation of samples that are within a 10 km radius.

Finally, we evaluated if the individually modelled trait responses could be related to a general functional strategy. For that, we used Principal Component Analysis (PCA). The traits were scaled prior to the analyses using the function *scale* from the base R package. Then we performed linear multiple regressions with the PC1 as the response variable and the soil fertility, HAND and DSL as explanatory variables.

GAMLSS models were performed using the *gamlss* R-package (Stasinopoulos and Rigby 2008) and model selection was done using the *stepGAICAll.A* function from the same package. Moran's I correlograms were performed using the function *lets.correl* of the R package letsR (Vilela and Villalobos 2015)

RESULTS

We recorded 47,129 ginger individuals from 192 species (Table S1). The minimum, median and maximum abundance per plot were 4, 66 and 897 individuals, respectively. Median species richness per plot was 8, varying from 1 to 23 species. Functional traits were often moderately or weakly intercorrelated at species and community level (Table S1). At the species level, taller species tended to have high LMA (LMA and plant height were positively correlated; Figure 2a). At the community level, the same communities tended to have high variability for both plant height and seed size (the corresponding CWD values were correlated; Figure 2f), and the same communities that had tall species also tended to have large seeds (the corresponding CWM values were correlated; Figure 2i).

We found a weak effect of environmental gradients on the local within-community trait variability, given by the CWD (Table 1). The variation in seed size within communities was slightly higher in communities on nutrient-poor soils ($b = -0.04$) and in bottomlands ($b = -0.06$). The variation in plant height also tended to increase towards nutrient-poor soils, but the best height-environment model had only weak support when compared with a null model (ΔGAIC < 2). Within-community variability in LMA was not significantly related to the environmental variables.

We found significant effects of environmental gradients on the turnover of the mean and variance of the functional trait composition among communities. The best model (lowest ΔGAIC and highest R^2) included significant effects of the environmental variables on both the CWM mean and variance response, except for LMA, for which only the mean response was associated with the environmental gradients (Table 1). Models that included only the mean response of CWM had better performance than models that included only the variance response, except for plant height (Table 1).

Mean and variance turnover of trait values among communities differed strongly between traits and environmental predictors. The mean community LMA was lower in nutrient rich soils and bottomlands, but there was no change in LMA along the dry season length gradient (Figure 3a-c). The standardised rate of change of mean LMA values

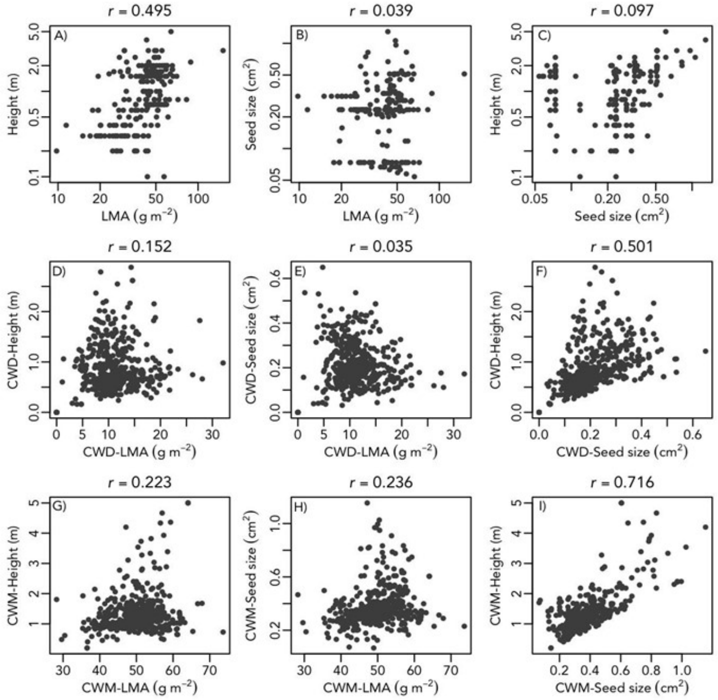

Figure 2. Correlations (Pearson's r) between functional traits of Zingiberales at the species (A – C) and community levels (D – I). Correlations between traits at species level were obtained applying a logarithmic transformation and vertical plot's axis are presented using that scale.

Table 1. Summary results of mixed-effect GAMLSS models for CWD and CWM of 451 herbaceous communities of Zingiberales along environmental gradients in the Amazon. The CWD models were fitted using the zero adjusted gamma distribution family and include only the relationship between the mean (μ) parameter and predictor variables. The CWM models were fit using the three parameters of the *t* family distribution for LMA, the four parameters box-cox *t* for plant height and seed size, and include the relationships between the mean (μ) and/or variance (σ) and the predictor variables. Best models appear in bold and models where predictor variables were not significant (P > 0.05) are not shown. Null models are the first entry for each response variable. Values in brackets denote the scaled β coefficients. SB = sum of exchangeable bases; VDD = vertical distance to the nearest drainage; DSL = dry season length.

Trait	Response variable	Model	ΔGAIC	R^2
LMA	CWD	(μ) ~ 1|random(sites)	0	0.35
	CWM	(μ) ~ 1|random(sites)	63.28	0.38
		(μ) ~ (- 2.52) SB + (1.18) VDD + 1|random(sites)	0	0.469
		(σ) ~ 1		
		(μ) ~ 1	58.59	0.392
		(σ) ~ (0.14) SB		
Plant height	CWD	(μ) ~ 1|random(sites)	1.88	0.381
		(μ) ~ (-0.04) SB + (-0.06) VDD + 1|random(sites)	0	0.386
	CWM	(μ) ~ 1|random(sites)	45.83	0.398
		(μ) ~ (-0.04) SB + (-0.03) VDD + 1|random(sites)	41.73	0.407
		(μ) ~ 1|random(sites)	3.57	0.457
		(σ) ~ (-0.26) VDD + (0.23) DSL		
		(μ) ~ (-0.05) SB + 1|random(sites)	0	0.463
		(σ) ~ (-0.25) VDD + (0.23) DSL		
Seed size	CWD	(μ) ~ 1|random(sites)	11.73	0.469
		(μ) ~ (-0.04) SB + (-0.06) VDD + 1|random(sites)	0	0.487
	CWM	(μ) ~ 1|random(sites)	75.73	0.503
		(μ) ~ (-0.08) SB + (0.05) VDD + 1|random(sites)	37.54	0.548
		(μ) ~ 1|random(sites)	49.44	0.536
		(σ) ~ (-0.36) VDD + (0.23) DSL		
		(μ) ~ (-0.07) SB + (0.08) VDD + 1|random(sites)	0	0.587
		(σ) ~ (-0.58) VDD + (0.29) DSL		

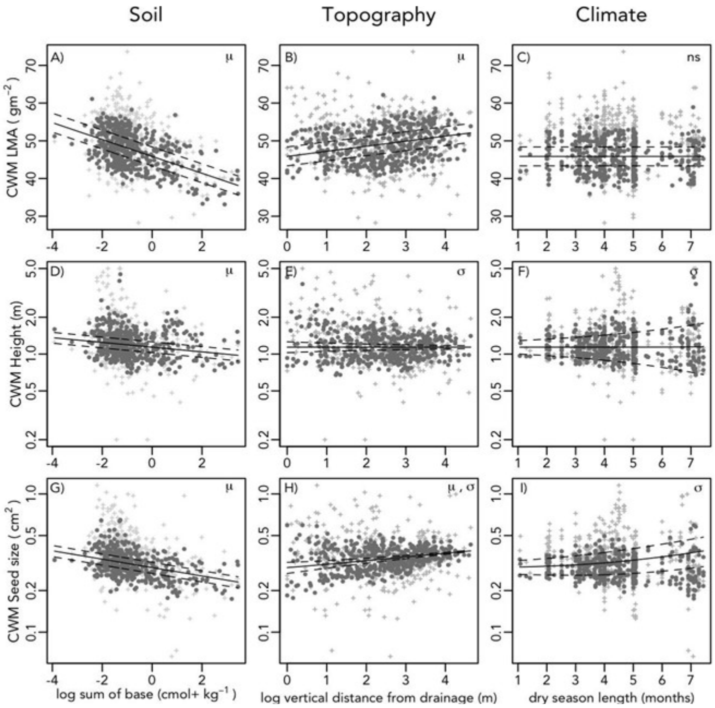

Figure 3. Changes in the community weighted mean (CWM) of 451 herbaceous communities of Zingiberales along environmental gradients in the Amazon. Continuous and dashed lines represent the mean (μ) ± variance (σ) of CWM, respectively. Predicted mean is the 0.5 quantile and predicted variance denotes the interval between the 0.25 and 0.75 quantiles of the *t* family distribution (A - C) and Box-Cox *t* distribution (D - L). For each variable the predicted mean and variance were obtained keeping all other variables constant at their mean values. The μ (mean) and/or σ (variance) symbols displayed in the upper-right corner of panels indicates which of these parameters had a significant association with the predictor variables and 'ns' denotes non-significant association. Vertical axes from E to L are in logarithmic scale. Dots denote the partial residual, and light grey crosses represent the original values.

along the soil exchangeable bases gradient (b = -2.52) was the highest comparing all models and was twice bigger than the rate of change along the VDD gradient (b = 1.18).

The variation of mean height and seed size along environmental gradients was similar (Figure 3d-i), probably due to the high correlation between these two traits at community level (Figure 3f,i). Height and seed size also decreased as soil fertility increased, but with a lower rate of change than for LMA (Table 1; Figure 3a,d,g). Mean seed size slightly decreased in bottomlands, but with a smaller rate of change than the rate at which the variance increased (Table 1; Figure 3h).

We found a significant effect of VDD and DSL on the among-community variance of plant height and seed size, but not of LMA. As expected, the variance on the mean community values of plant height and seed size increased towards bottomlands (Figure 3e,h). We found a wide variation of CWM for plant height and seed size in bottomlands (but not for LMA), while on uplands there was a predominance of communities with intermediate mean stature and medium mean seed size. The variance of the CWM of plant height and seed size increased towards drier conditions, while in wet areas the dominant species were those with medium height and seed size (Figure 3f,i).

The principal component analysis captured 60% of the variation of the LMA, plant height and seed size CWM in the first component and 24.5% in the second component (Figure S2). PC1 was significantly related (adjusted R^2 = 0.16, $p < 0.001$) to the sum of bases (b = 0.5, $p = 0.04$), to the vertical distance from the drainage (b = 0.1, $p < 0.001$) and to the dry season length (b = 0.1, $p = 0.05$), with the same trends found for the individual trait CWM (Figure S3).

DISCUSSION

Our findings reveal that environmental gradients affected both within and among-assemblage functional patterns of Amazonian gingers. We detected functional turnover of the dominant assemblage trait values (given by the CWM) towards lower assemblage mean values of LMA, plant height and seed size, as soil fertility increased and local environments became wetter (bottomlands), in accordance with the expectations of the fast-slow growth trade-off along the whole-plant economic spectrum (Reich 2014). Functional divergence was detected both within and among assemblages: within-community variability (given by the CWD) in seed size and plant height tended to increase towards bottomlands and nutrient-poor soils, and the variance around dominant plant height and seed size values among communities increased towards bottomlands and more seasonal regions. As the combination of these later environmental conditions lead to more dynamic forests (Quesada *et al.* 2012), our results suggest that higher disturbance levels might drive an increase in the functional divergence among assemblages at regional scales.

We found stronger trends of functional turnover for the assemblage mean trait values (given by the CWM) than for the variance of these values (CWM variance among assemblages), with soil fertility gradients having the strongest filtering effect. Trait values observed along the soil gradient were in strong accordance with the fast-slow growth trade-off, which predicts that acquisitive traits (low LMA, low plant height and small seed size) dominate in highly productive habitats, while conservative traits predominate in low resource conditions (Reich 2014). Indeed, the turnover of assemblage weighted trait means was higher along the soil than along topographic or climatic gradients, reinforcing previous observations that soil fertility is the key driver of regional functional composition across lowland Amazonia (Fyllas *et al.* 2009).

The mean functional trait values also turned over along topographical gradients following the expectation of the acquisitive-conservative strategy trade-off along water-resource gradients (Hoffmann *et al.* 2005; Reich 2014). This relationship depends not only on climate but also on its interaction with topography, as topography is a surrogate for soil moisture (Fan *et al.* 2013), a condition that directly affects plant performance. Hills tend to suffer more from water deficit than bottomlands, favouring the predominance of conservative strategies (high LMA and larger seed size) in the former. A similar trend was observed at a local scale for trees, with species associated with high topographic positions having higher LMA than species associated with bottomlands (Cosme *et al.* 2017; Schmitt *et al.* 2020). Topographic variation has been disregarded in regional scale studies of community functional patterns, which may explain why tight links between changes in functional composition and water deficit have not been found.

We did not find turnover in the mean assemblage trait values along the climate gradient. Previous results on functional changes among tree communities along a rainfall gradient indicate that LMA is higher in wetter regions (Fyllas *et al.* 2009). The lack of a climate effect may be a consequence of at least two factors. First, most trait variation was explained by soil and the topographic gradient, and the local water availability might be more relevant in filtering the traits related to the water-strategy. The absence of a climate effect on LMA could also arise by the mixture of deciduous and non-deciduous species in the seasonally dry regions. Deciduous species are often associated with dry regions and tend to have lower LMA than evergreens (Poorter *et al.* 2009), which could counteract the trend of increasing LMA (a conservative strategy) towards dry regions. Although we have not directly evaluated the phenological habits of species in our dataset, our field observations suggest that some short-statured species of *Goeppertia* and *Chamaecostus* generally associated to drier regions, can exhibit deciduous behaviour. However, as LMA decreased with increasing soil nutrients, we hypothesise that deciduousness should be modulated jointly by drier conditions and high concentrations of nutrients in soils.

The variance of functional composition among assemblages changed along topographic and climatic gradients, but not along the soil nutrient gradient. We found that bottomlands and seasonally dry regions contained assemblages that varied more among each other in plant height and seed size, which are aligned with the expectation that higher disturbance rates should lead to higher functional differences among communities under the same soil and climate conditions. Those differences should arise mostly from the colonization of disturbed patches by the local fast-growth acquisitive functional types.

Higher frequency of disturbances also led to higher within-assemblage trait variance (given by the CWD) of seed size and plant height in bottomlands. Bottomlands tend to be more susceptible to natural disturbance than higher ground, given terrain instability and soil physical constraints, leading to higher rates of tree mortality (de Toledo *et al.* 2011). Higher tree mortality rates lead to higher spatial and temporal light heterogeneity in the understory, which would allow the occupation of these sites by species with more variable seed size and plant height, and their co-occurrence in local communities within bottomlands.

Nutrient-rich soils are associated with higher tree turnover (Quesada *et al.* 2012), which is expected to increase light heterogeneity and lead to higher within-community trait variance. Contrary to this expectation, within-community variance of plant height and seed size slightly increased as soil fertility decreased. A potential explanation is that light may not be a limiting factor in nutrient-poor soils. Although forests with high fertility have potentially more gaps, maybe the gaps close too fast to allow the persistence of a large variety of plant-height/seed strategies. Thus, nutrient-poor soils were found to promote more local variation in plant height through the higher contrast between gaps and closed canopies at the local scale. Alternatively, the strong convergent filtering of species LMA by soil fertility may carry together the filtering of plant height, since these traits are correlated at the species level.

CONCLUSIONS

Our findings revealed that, while soil and topography promote the filtering of a predictable functional composition, climate mostly promoted within and among-assemblage functional variance across Amazon forests. An obvious extension of this study would be the evaluation of the combined effects of these predictors on multiple plant taxa, which would help understanding how environmental gradients affect functional strategies of and how these strategies will influence on the flora survivorship in climate change scenarios.

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DATA AVAILABILITY: The data that support the findings of this study are available in the GitHub repository of the corresponding author (https://github.com/gamamo/Herbs_Functional). New data is attached to the "Supplementary Material" section.

AUTHOR CONTRIBUTIONS:
FIGUEIREDO, F.O.G.: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Project administration, Software, Validation, Visualization, Writing - original draft, Writing - review & editing.
MOULATLET, G.M.; ZUQUIM, G.; EMILIO, T.; SILVEIRA, M.; RODRIGUES, D.: Data curation, Writing - review & editing.
TUOMISTO, H.: Data curation, Funding acquisition, Project administration, Writing - review & editing.
COSTA, F.R.C.: Conceptualization, Data curation, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Validation, Visualization, Writing - original draft, Writing - review & editing.

SUPPLEMENTARY MATERIAL

Figueiredo *et al*. Functional biogeography of herbaceous assemblages along edaphic and climatic gradients in Amazonian forests

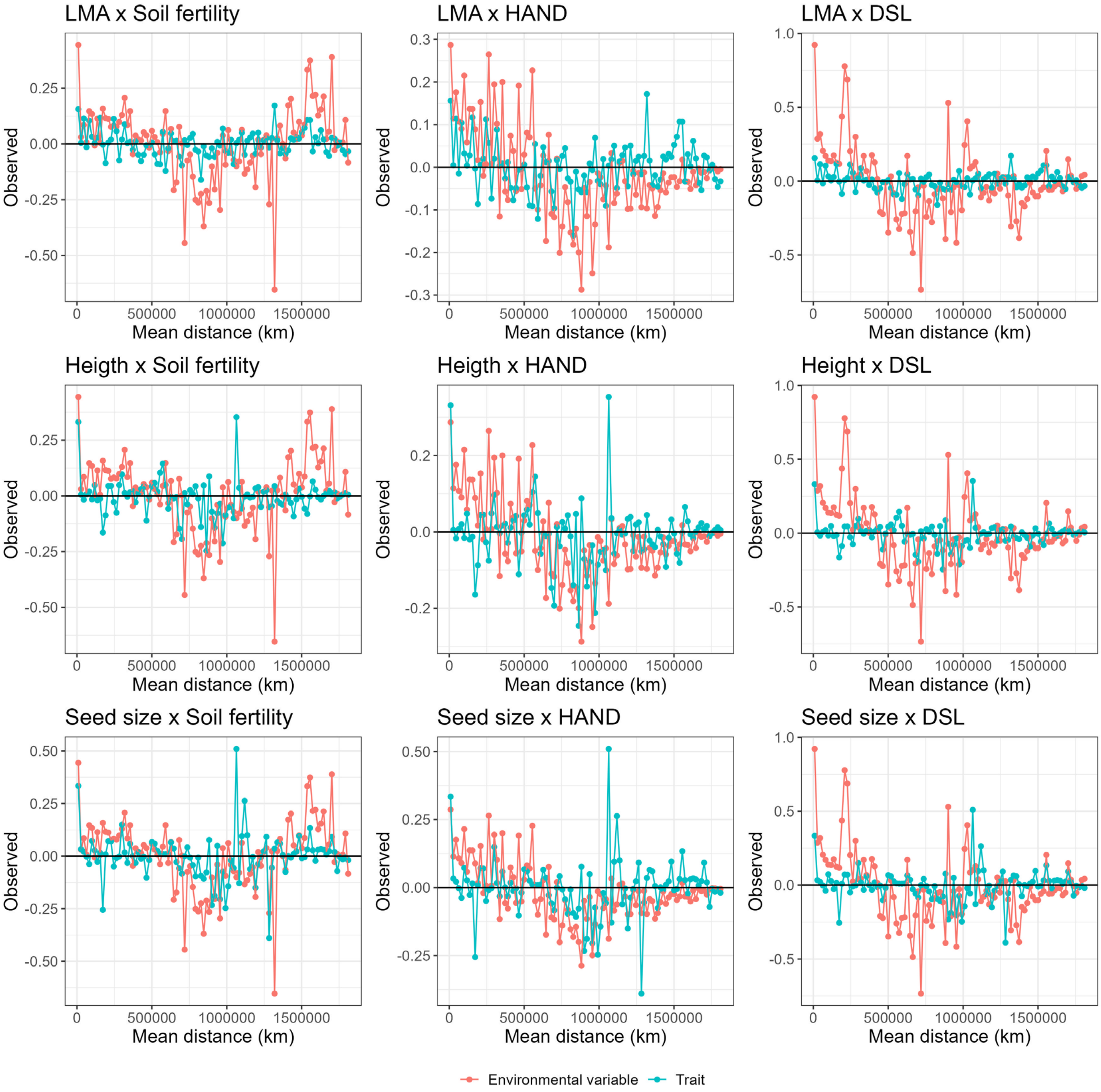

Figure S1. Moran's I correlograms calculated for the community weight means (CWM) of each functional trait (LMA, plant height and seed size) of Zingiberales and also for the environmental variables tested for their effects on the CWM (soil fertility, HAND – the height above the nearest drainage, and climate – measured as the dry season length). Moran's I correlograms were calculated for 100 classes of distance, roughly representing every 10 km in the geographic space with equidistant classes.

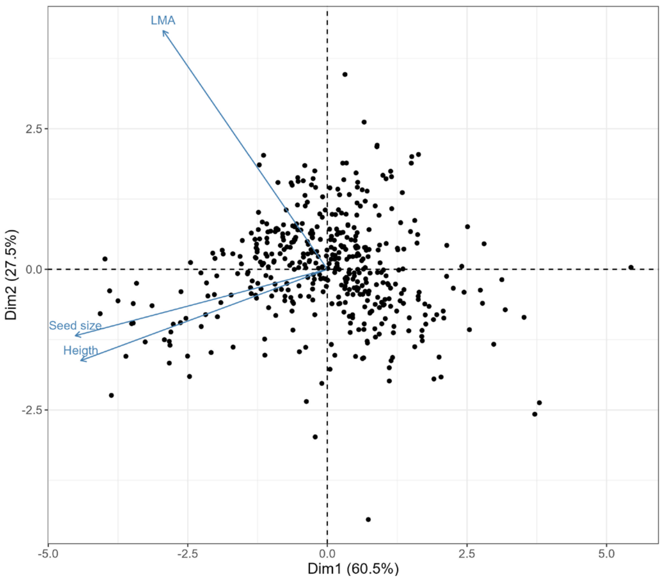

Figure S2. Biplot of the PCA performed with the CWM of three functional traits of Zingiberales in Amazonian sampling plots used in this study (LMA, seed size and plant height). This step is necessary prior to the analysis when variables have different magnitudes. The traits were scaled prior to the analyses using the function scale from the base R package.

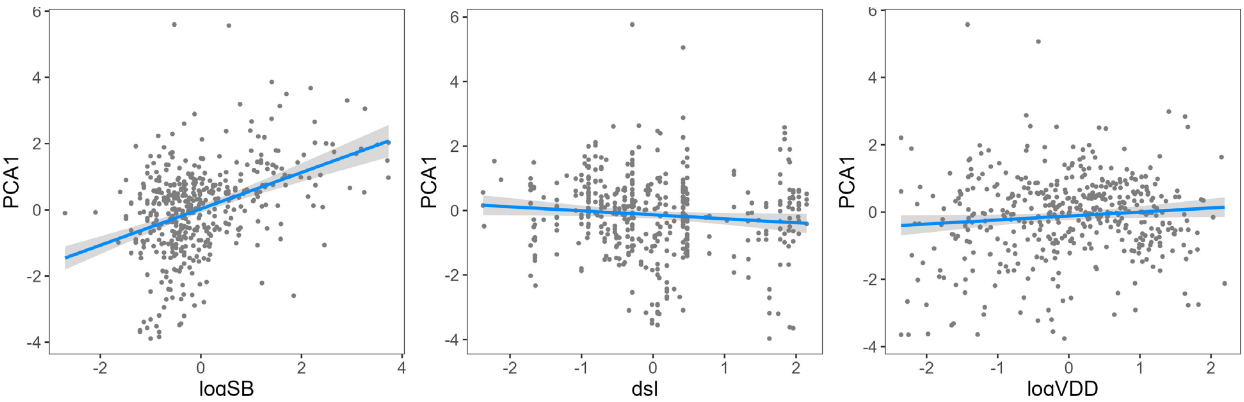

Figure S3. Partial regression from the multiple linear regression model performed with the PC1 (derived from the functional traits; Figure S2) and the explanatory variable sum of bases (logSB), dry season length (dsl) and vertical distance to the drainage (logHAND). The regression was significant at p = 0.001 (Adjusted R2 = 0.16).

Table S1. List of the 192 ginger species and their functional trait values. LMA denotes the leaf mass per area. Species not fully identified have morphotype names as reference for the local voucher collection.

Family	Species	LMA (gm^{-2})	Plant height (m)	Seed size (cm^2)
Costaceae	*Chamaecostus acaulis*	26.59	0.2	0.074
Costaceae	*Chamaecostus congestiflorus*	71.93	0.8	0.074
Costaceae	*Chamaecostus fragilis*	33.46	0.6	0.074
Costaceae	*Chamaecostus fusiformis*	45.89	0.7	0.074
Costaceae	*Chamaecostus* sp1	19.34	0.6	0.074
Costaceae	*Chamaecostus* sp1 pec	17.67	0.6	0.074
Costaceae	*Chamaecostus* sp2	29.26	0.6	0.074
Costaceae	*Chamaecosuts fragilis*	27.18	0.6	0.074
Costaceae	*Costus acreanus*	53.52	1.7	0.074
Costaceae	*Costus amazonicus*	59.98	2.0	0.074
Costaceae	*Costus arabicus*	42.23	1.8	0.074
Costaceae	*Costus fusiformis*	57.44	0.7	0.074
Costaceae	*Costus guanaiensis* var *guanaiensis*	57.09	2.0	0.074
Costaceae	*Costus lasius*	40.67	1.0	0.074
Costaceae	*Costus scaber*	54.11	1.5	0.074
Costaceae	*Costus spiralis*	65.52	2.0	0.074
Costaceae	*Costus sprucei*	40.58	1.5	0.074
Costaceae	*Costus zingiberoides*	28.81	1.5	0.074
Costaceae	*Costus* sp1 acre	43.45	1.5	0.074
Costaceae	*Costus* sp1 cunia	42.29	1.5	0.074

Table S1. Continued

Family	Species	LMA (gm^{-2})	Plant height (m)	Seed size (cm^2)
Costaceae	*Costus* sp1 m01	40.58	1.5	0.074
Costaceae	*Costus* sp1 pec	19.36	1.5	0.074
Costaceae	*Costus* sp1 virua_maraca	46.11	1.5	0.074
Costaceae	*Costus* sp2	27.85	1.7	0.074
Costaceae	*Costus* sp2 m01	40.58	1.5	0.074
Costaceae	*Costus* sp3 pec	33.07	1.5	0.074
Costaceae	*Costus* sp4	23.16	1.6	0.074
Costaceae	*Costus* sp5	31.79	1.8	0.074
Costaceae	*Costus* sp6	31.61	1.7	0.074
Costaceae	*Costus* sp7	40.58	1.5	0.074
Costaceae	*Costus* sp7 pec	59.03	1.8	0.074
Costaceae	*Costus* sp8	54.98	1.7	0.074
Costaceae	*Dimerocostus strobilaceus*	49.30	2.5	0.074
Heliconiaceae	*Heliconia acuminata*	43.78	0.9	0.296
Heliconiaceae	*Heliconia aemygdiana*	30.92	2.2	0.821
Heliconiaceae	*Heliconia bihai*	48.09	2.0	0.350
Heliconiaceae	*Heliconia brachyantha*	52.14	1.4	0.236
Heliconiaceae	*Heliconia chartacea*	44.46	2.2	0.334
Heliconiaceae	*Heliconia densiflora* var *angustifolia*	36.10	1.5	0.361
Heliconiaceae	*Heliconia densiflora* var *densiflora*	30.73	1.0	0.361
Heliconiaceae	*Heliconia hirsuta*	25.05	1.7	0.334
Heliconiaceae	*Heliconia juliani*	53.20	2.0	0.304
Heliconiaceae	*Heliconia juruana*	88.56	2.2	0.334
Heliconiaceae	*Heliconia lasiorachis*	42.89	1.7	0.247
Heliconiaceae	*Heliconia lourtegiae*	51.42	0.6	0.334
Heliconiaceae	*Heliconia psittacorum*	40.71	1.3	0.334
Heliconiaceae	*Heliconia rostrata*	49.69	2.5	0.334
Heliconiaceae	*Heliconia schumanniana*	52.14	1.6	0.227
Heliconiaceae	*Heliconia spathocircinata*	42.73	1.8	0.334
Heliconiaceae	*Heliconia stricta*	44.27	1.7	0.371
Heliconiaceae	*Heliconia tenebrosa*	48.72	0.8	0.334
Heliconiaceae	*Heliconia velutina*	46.80	1.8	0.350
Heliconiaceae	*Heliconia* sp1 chandless	43.03	0.8	0.334
Heliconiaceae	*Heliconia* sp1 pec	44.09	1.5	0.334
Heliconiaceae	*Heliconia* sp 46	39.79	2.0	0.334
Marantaceae	*Calathea crotalifera*	45.10	1.7	0.225
Marantaceae	*Calathea lutea*	52.20	2.5	0.250
Marantaceae	*Calathea striata*	44.49	0.9	0.237
Marantaceae	*Ctenanthe eriacae*	37.86	2.0	0.212
Marantaceae	*Ctenanthe* sp1 acre	35.66	0.2	0.212
Marantaceae	*Ctenanthe* sp1 pime	32.03	0.5	0.212
Marantaceae	*Goeppertia altissima*	63.53	1.3	0.454
Marantaceae	*Goeppertia attenuata*	53.23	1.0	0.234
Marantaceae	*Goeppertia cannoides*	70.44	1.5	0.234
Marantaceae	*Goeppertia capitata*	42.48	2.0	0.217
Marantaceae	*Goeppertia comosa*	46.39	2.0	0.217
Marantaceae	*Goeppertia curaraya*	35.19	0.2	0.234
Marantaceae	*Goeppertia elliptica*	50.49	0.7	0.234
Marantaceae	*Goeppertia exscapa*	29.13	0.4	0.234
Marantaceae	*Goeppertia fragilis*	50.65	1.7	0.234
Marantaceae	*Goeppertia fucata*	42.34	0.2	0.106
Marantaceae	*Goeppertia hopkinsii*	25.45	0.7	0.234
Marantaceae	*Goeppertia loeseneri*	37.89	0.8	0.212
Marantaceae	*Goeppertia maassiorum*	50.50	0.5	0.234
Marantaceae	*Goeppertia metallica*	25.97	0.4	0.196
Marantaceae	*Goeppertia micans*	36.56	0.2	0.144
Marantaceae	*Goeppertia microcephala*	43.84	0.2	0.147
Marantaceae	*Goeppertia neblinensis*	42.38	0.8	0.234
Marantaceae	*Goeppertia ovata*	27.44	0.5	0.234
Marantaceae	*Goeppertia panamensis*	19.98	0.3	0.234
Marantaceae	*Goeppertia picturata*	40.80	0.3	0.234
Marantaceae	*Goeppertia polytricha*	29.03	0.3	0.234
Marantaceae	*Goeppertia straminea*	82.77	0.8	0.234
Marantaceae	*Goeppertia taeniosa*	35.12	0.3	0.234
Marantaceae	*Goeppertia variegata*	44.55	1.7	0.454
Marantaceae	*Goeppertia zingiberina*	62.30	0.8	0.279
Marantaceae	*Goeppertia* sp m2	36.17	0.5	0.234
Marantaceae	*Goeppertia* sp m3	36.17	0.5	0.234
Marantaceae	*Goeppertia* sp m4	36.17	0.5	0.234
Marantaceae	*Goeppertia* sp m5	36.17	0.5	0.234
Marantaceae	*Goeppertia* sp m9	36.17	0.5	0.234
Marantaceae	*Goeppertia* sp1 acre	30.34	0.4	0.234
Marantaceae	*Goeppertia* sp brev m10	36.17	0.5	0.234
Marantaceae	*Goeppertia* sp brev uat	35.93	0.7	0.234
Marantaceae	*Goeppertia* sp1 pec	24.65	0.3	0.234
Marantaceae	*Goeppertia* sp11 alt	52.17	1.5	0.454
Marantaceae	*Goeppertia* sp15	20.26	0.3	0.234
Marantaceae	*Goeppertia* sp16	30.22	0.4	0.234
Marantaceae	*Goeppertia* sp17	28.02	0.2	0.234
Marantaceae	*Goeppertia* sp18	19.33	0.3	0.234
Marantaceae	*Goeppertia* sp19	37.08	0.3	0.234
Marantaceae	*Goeppertia* sp2 orna virua	65.39	1.8	0.234
Marantaceae	*Goeppertia* sp20	11.44	0.4	0.234
Marantaceae	*Goeppertia* sp21	35.31	0.3	0.234
Marantaceae	*Goeppertia* sp22	36.17	0.5	0.234
Marantaceae	*Goeppertia* sp24	36.17	0.5	0.234
Marantaceae	*Goeppertia* sp25	25.69	0.3	0.234
Marantaceae	*Goeppertia* sp26	35.59	0.6	0.234
Marantaceae	*Goeppertia* sp28	36.09	0.3	0.234
Marantaceae	*Goeppertia* sp29	61.06	0.5	0.234
Marantaceae	*Goeppertia* sp3	36.17	0.5	0.234
Marantaceae	*Goeppertia* sp3 acre	26.56	0.3	0.234
Marantaceae	*Goeppertia* sp30	37.00	0.6	0.234
Marantaceae	*Goeppertia* sp31	23.40	0.4	0.234
Marantaceae	*Goeppertia* sp32	31.53	0.3	0.234
Marantaceae	*Goeppertia* sp33	43.49	0.1	0.234
Marantaceae	*Goeppertia* sp35	30.01	0.3	0.234
Marantaceae	*Goeppertia* sp36	24.56	0.2	0.234
Marantaceae	*Goeppertia* sp38	36.17	0.5	0.234
Marantaceae	*Goeppertia* sp39	36.17	0.5	0.234
Marantaceae	*Goeppertia* sp4	48.43	0.7	0.234
Marantaceae	*Goeppertia* sp40	28.12	0.3	0.234

Table S1. Continued

Family	Species	LMA (gm^{-2})	Plant height (m)	Seed size (cm^2)
Marantaceae	*Goeppertia* sp41	44.18	0.3	0.234
Marantaceae	*Hylaeanthe hexantha*	20.19	0.4	0.157
Marantaceae	*Hylaeanthe unilateralis*	19.41	0.6	0.118
Marantaceae	*Ischnosiphon arouma*	58.24	2.0	0.825
Marantaceae	*Ischnosiphon cannoideus*	43.40	1.3	0.200
Marantaceae	*Ischnosiphon cerotus*	43.01	1.5	0.670
Marantaceae	*Ischnosiphon crassispicus*	150.87	3.0	0.512
Marantaceae	*Ischnosiphon gracilis*	47.50	1.7	0.503
Marantaceae	*Ischnosiphon grandibracteatus*	49.00	3.0	0.962
Marantaceae	*Ischnosiphon hirsutus*	32.14	0.8	0.261
Marantaceae	*Ischnosiphon killipii*	29.82	3.0	0.746
Marantaceae	*Ischnosiphon lasiocoleus*	47.20	1.6	0.393
Marantaceae	*Ischnosiphon leucophaeus*	58.62	0.8	0.234
Marantaceae	*Ischnosiphon longiflorus*	42.92	4.0	1.292
Marantaceae	*Ischnosiphon martianus*	57.32	1.2	0.503
Marantaceae	*Ischnosiphon obliquus*	27.44	2.5	0.605
Marantaceae	*Ischnosiphon paryrizinho*	60.17	2.0	0.512
Marantaceae	*Ischnosiphon petiolatus*	53.69	0.9	0.548
Marantaceae	*Ischnosiphon puberulus* var *puberulus*	35.55	2.5	0.512
Marantaceae	*Ischnosiphon puberulus* var *verruculosus*	48.63	2.5	1.060
Marantaceae	*Ischnosiphon* sp1	29.74	3.0	0.512
Marantaceae	*Ischnosiphon* sp10	48.24	1.9	0.512
Marantaceae	*Ischnosiphon* sp2	55.22	3.0	0.512
Marantaceae	*Ischnosiphon* sp4	50.29	3.0	0.512
Marantaceae	*Ischnosiphon* sp5	59.72	1.5	0.512
Marantaceae	*Ischnosiphon* sp6	48.24	1.9	0.512
Marantaceae	*Ischnosiphon* sp7	65.71	1.8	0.512
Marantaceae	*Ischnosiphon* sp8	50.65	2.0	0.512
Marantaceae	*Ischnosiphon* sp9	44.16	3.0	0.512
Marantaceae	*Ischnosiphon surumuensis*	55.39	2.0	0.512
Marantaceae	*Ischnosiphon ursinus*	47.18	1.3	0.512
Marantaceae	*Maranta ciclophylla*	16.97	0.3	0.314
Marantaceae	*Maranta humilis*	20.07	0.4	0.314
Marantaceae	*Maranta* sp1 acre	23.29	0.3	0.314
Marantaceae	*Maranta* sp1 jurua	21.55	0.3	0.314
Marantaceae	*Maranta* sp1 pec	20.22	0.3	0.314
Marantaceae	*Maranta* sp1 pime	25.78	0.3	0.314
Marantaceae	*Maranta* sp2 acre	9.77	0.2	0.314
Marantaceae	*Maranta* sp2 jurua	24.94	0.4	0.314
Marantaceae	*Maranta* sp2 pime	18.75	0.3	0.314
Marantaceae	*Maranta* sp3 pime	15.04	0.3	0.314
Marantaceae	*Monophyllanthe araracuarensis*	59.57	0.7	0.118
Marantaceae	*Monophyllanthe oligophylla*	57.17	0.1	0.118
Marantaceae	*Monotagma angustissimum*	44.98	1.0	0.396

Family	Species	LMA (gm^{-2})	Plant height (m)	Seed size (cm^2)
Marantaceae	*Monotagma aurantispathum*	29.64	0.8	0.227
Marantaceae	*Monotagma breviscapum*	35.96	0.7	0.385
Marantaceae	*Monotagma contractum*	47.59	0.7	0.205
Marantaceae	*Monotagma contrariosum*	44.15	1.0	0.271
Marantaceae	*Monotagma densiflorum*	55.37	1.3	0.227
Marantaceae	*Monotagma exile*	41.66	0.4	0.248
Marantaceae	*Monotagma flavicomum*	30.30	0.3	0.428
Marantaceae	*Monotagma floribundum*	63.34	1.6	0.286
Marantaceae	*Monotagma humile*	29.77	0.4	0.225
Marantaceae	*Monotagma juruanum*	42.57	0.7	0.440
Marantaceae	*Monotagma laxum*	50.52	1.0	0.302
Marantaceae	*Monotagma lilacinum*	46.24	0.7	0.221
Marantaceae	*Monotagma plurispicatum*	48.76	0.8	0.271
Marantaceae	*Monotagma secundum*	53.25	0.7	0.324
Marantaceae	*Monotagma tomentosum*	51.75	0.6	0.319
Marantaceae	*Monotagma tuberosum*	26.04	0.2	0.226
Marantaceae	*Monotagma ulei*	38.73	0.5	0.211
Marantaceae	*Monotagma vaginatum*	44.93	0.7	0.402
Marantaceae	*Monotagma* sp1	57.18	0.7	0.286
Marantaceae	*Monotagma* sp1 acre	54.93	0.7	0.286
Marantaceae	*Monotagma* sp2 pime	51.91	0.7	0.286
Marantaceae	*Monotagma* sp3 m10	35.78	0.3	0.286
Marantaceae	*Monotagma* sp3 pime	46.19	0.4	0.286
Marantaceae	*Monotagma* sp4 pime	42.75	0.6	0.286
Marantaceae	*Monotagma* sp5 cunia	43.50	0.6	0.286
Marantaceae	*Monotagma* sp5 jurua	42.99	0.7	0.286
Strelitziaceae	*Phenakospermum guyannense*	64.07	5.0	0.605
Zingiberaceae	*Renealmia acreana*	50.38	1.5	0.059
Zingiberaceae	*Renealmia alpinia*	44.14	2.0	0.063
Zingiberaceae	*Renealmia aromatica*	48.93	1.7	0.067
Zingiberaceae	*Renealmia breviscapa*	52.62	0.8	0.063
Zingiberaceae	*Renealmia cernua*	58.16	1.5	0.057
Zingiberaceae	*Renealmia floribunda*	66.37	1.5	0.054
Zingiberaceae	*Renealmia monosperma*	40.56	0.3	0.076
Zingiberaceae	*Renealmia thyrsoidea*	39.24	1.5	0.108
Zingiberaceae	*Renealmia* sp1	38.09	1.5	0.067
Zingiberaceae	*Renealmia* sp1 br319	45.85	1.0	0.067
Zingiberaceae	*Renealmia* sp1 pec	45.85	1.0	0.067
Zingiberaceae	*Renealmia* sp1 pime	45.85	1.0	0.067
Zingiberaceae	*Renealmia* sp10	49.30	1.5	0.067
Zingiberaceae	*Renealmia* sp4 jurua	32.88	0.4	0.067
Zingiberaceae	*Renealmia* sp5 jurua	51.48	0.4	0.067
Zingiberaceae	*Renealmia* sp7 jurua	39.76	0.6	0.067
Zingiberaceae	*Renealmia* sp8	40.76	1.0	0.067
Zingiberaceae	*Renealmia* sp9 jurua	45.85	1.0	0.067