UNIVERSIDAD NACIONAL DE COLOMBIA

Influence of the environmental heterogeneity on the tree species richness – above ground biomass relationship in the Colombian Amazon

Influencia de la heterogeneidad ambiental en la relación riqueza de especies arbóreas - biomasa aérea en la Amazonia colombiana

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To my parents and my director. I am grateful to them for their patience in difficult times.

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Abstract

In this study, we aimed to identify the shape and environmental drivers of the species richness (SR) –rarefied above ground biomass (RAGB) relationship across and within tree communities in the Colombian Amazon. We used a series of 130 0.1 ha plots to answer the next questions: 1) what is the shape of the SR - RAGB relationship both across and within tree communities in the Colombian Amazon? 2) At what extent does environmental heterogeneity drives the shape of the SR - RAGB relationship both across and within tree communities? Our results support the idea that in plant studies that cross community boundaries, the hump-shape will be the dominant form of the SR–RAGB relationship. Within communities, on the contrary, the monotonic shape of the SR–RAGB relationship dominated over the expected no shape or the hump-shaped model.Across communities, total bases and P contents were significantly correlated with the SR–RAGB variation. /Across tree communities in the Colombian Amazon, P contents (R_{MANTEL}=0.45) seem to determine a big portion of the coupled variation in SR and RAGB./ Within communities, in contrast, no soil variable played any significant role on structuring the SR–RAGB relationship, and the environmental stress along with the rate of disturbance associated to flooding and bad drainage of soils must play an important role on defining the shape of the SR–RAGB relationship. Overall, the hump-shape of the SR–RAGB relationship found across spatially distributed communities in the Colombian Amazon, showed to come from adding up the within landscape models. Hence, across communities, there is not any single mechanism structuring this pattern, and the combined action of the rate of disturbance along with soil fertility seem to largely determine the up and down slope of the first and third phases of the curve. However, in the second phase of the curve, species neutrality, which means a lack of influence from species competition, seems to be the main mechanism that controls the plateau of the curve where SR becomes the highest.

Key words: landscape unit, rarefaction analysis, species density, soils fertility, quadratic model.

Resumen

Los objetivos en este estudio fueron identificar la forma y los determinantes ambientales de la relación riqueza de especies (SR) - biomasa aérea con rarefacción (RAGB) entre y dentro de las comunidades arbóreas en la Amazonia colombiana. Usamos una serie de 130 parcelas, cada una de 0.1 hectárea, para responder a las siguientes preguntas: 1) ¿cuál es la forma de la relación SR - RAGB entre y dentro de las comunidades arbóreas en la Amazonia colombiana? 2) ¿hasta qué punto controla la heterogeneidad ambiental la forma de la relación SR - RAGB entre y dentro de las comunidades arbóreas? Nuestros resultados apoyan la idea de que en estudios con plantas que cruzan las fronteras de las comunidades, la forma de joroba es la dominante para la relación SR-RAGB. Dentro de las comunidades, por el contrario, la forma monótona creciente de la relación SR-RAGB predomina respecto a las esperadas en forma de joroba o sin forma. Entre las comunidades, las bases totales y P tuvieron una correlación significativa con la variación de la relación SR-RAGB. Entre comunidades arbóreas de la Amazonía colombiana, el contenido de P (RMANTEL = 0,45) parece determinar una gran parte de la variación conjunta en SR y RAGB. Dentro de las comunidades, en cambio, ninguna variable del suelo jugó un papel importante en la estructuración de la relación SR-RAGB, y el estrés ambiental junto con la tasa de perturbación asociada a las inundaciones y al mal drenaje de los suelos tiene que desempeñar un papel importante en la definición de la forma de la relación SR-RAGB. En general, la forma de joroba de la relación SR-RAGB encontrada entre comunidades espacialmente distribuidas en la Amazonia colombiana mostró provenir de la suma de los modelos dentro de los paisajes. Por lo tanto, entre comunidades, no hay un único mecanismo que estructure este patrón, y la acción combinada de la tasa de perturbación junto con la fertilidad de los suelos parecen determinar en gran medida las pendientes ascendente (primera fase) y descendente (tercera fase) de la curva, respectivamente. Sin embargo, en la segunda fase de la curva, de neutralidad de las especies, que significa la falta de influencia de la competencia entre las especies, parece ser el principal mecanismo en la determinación de la meseta de la curva, donde tanto SR como AGB alcanzan sus máximos.

Palabras clave: unidad de paisaje, análisis de rarefacción, densidad de especies, fertilidad de los suelos, modelo cuadrático.

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INTRODUCTION

Unraveling the main drivers of the relationship between the number of species (NS) and the live aboveground biomass (AGB) have profound implications on developing new tools and strategies for forest management and conservation (Strassburg et al. 2010, Adler et al. 2011, Siikamäki and Newbold 2012, Thomas et al. 2012). On the one hand, the number of species has been considered one of the most useful currencies to define areas of conservation (Myers et al. 2000). On the other hand, the carbon stocks in the AGB represent an ecosystem function that currently appears as the corner stone of one of the most prominent schemes for mitigating climate change, which is known as Reducing Emissions from Deforestation and Degradation (REDD+, UN-REDD 2012). Since the importance of biodiversity on ecosystem resilience has also been recognized even for ecosystems with low AGB (Chapin et al. 1998), improving our understanding about the determinants of the NS - AGB relationship in tropical forests will help maximize the co-benefits of hoarding carbon up while preserving the maximum possible number of species (Venter et al. 2009, Thomas et al. 2012).

Although many studies conducted in different ecosystems and kinds of organisms have referred many kinds of shapes for the NS – AGB relationship (U, monotonic positive, monotonic negative, unimodal and no shape), the unimodal has been found to be the dominant for plants at both local and regional scales (Mittelbach et al. 2001). However, changes in the form of the NS – AGB relationship due to sampling effects, grain, focal scale, and extent of the geographical scale of study have been suggested after abundant theoretical and empirical studies (Chase and Leibold 2002, Guo and Berry 1998, Rosenzweig 1995, Whittaker 2010).

The use of species density (SD: the number of species by area unit), which has been confounded with the use of species richness (SR: the number of species associated with a particular number of individuals), introduces sampling effects due to the sensitivity of the SD to sample size (Gotelli and Colwell 2001). Due to the sampling effect that comes from the use of

SD could distort the shape of the NS - AGB relationship (Oksanen 1996, McGlinn and Palmer 2010), it is recommended to use the rarefied unbiased metric of the ‘true’ SR (Gotelli and Colwell 2001, 2011).

The shape of the SR – AGB relationship also depends on the extent of the geographical scale within which the entire data is bounded. Therefore, to be able to quantify the extent at which environmental filtering shapes the SR - AGB relationship in mature forests distributed along steep environmental gradients, we need to analyze the level of diversity at which the study is performed. In other words, we need to identify whether our study is carried out within communities (alpha diversity) or across communities (gamma diversity) to determine its influence on determining the shape of the SR – AGB relationship (Whittaker 2010).

In this study, we aimed to identify the shape and environmental drivers of the SR - AGB relationship across and within tree communities in the Colombian Amazon. This area encompasses different forest types associated to the main landscape units (Duivenvoorden 1995, Duque et al. 2005). The length of the environmental gradient across the main landscape units is hierarchically defined in terms of flooding, soil drainage, and soil fertility (Duivenvoorden and Lips 1995). Keeping constant the ecosystem type (tropical rain forest), organism (trees), climate and stage of development, but acknowledging that the SR – AGB relationship is a multifactor problem that should not be studied as a simple cause - effect phenomena (Grace 1999), we used rarefaction analysis on a series of 130 0.1 ha plots to answer the next questions: 1) What is the shape of the SR - AGB relationship both across and within tree communities in the Colombian Amazon? 2) At what extent does environmental heterogeneity drives the shape of the SR - AGB relationship both across and within tree communities? This information will help identifying strategies for the conservation and management of both carbon stocks and species diversity in the Colombian Amazon. Based on the current knowledge on the SR - AGB relationship, within each environmentally homogeneous landscape unit (tree community), we predicted: 1. Across communities, we expect the shape of the SR – AGB relationship to be unimodal and significantly determined by the soil fertility variation. 2. That the SR – AGB within mature and undisturbed tree communities in western Amazonia may have not a dominant shape and would not be related to the relative constant fertility of soils.

1. METHODS

1.1 Study site

The study area covers about 6000 km^2 and is situated along the stretches of the middle Caquetá and Mesay Rivers in Colombian Amazonia, roughly between 72^o 37.2’ and 70^o 48’ W longitude, and 0^o 4.8’ S and 1^o 31.8’ S latitude (Figure 1). The altitudinal position of each plot was calculated using the Digital Elevation Model at a scale of 30 m (DEM30, Asner et al. 2009). The principal landscape units found here are tierra firme (which are never flooded by river water and include low and high fluvial terraces and a Tertiary sedimentary plain, TF), well-drained floodplains (FP), swampy areas (including permanently inundated backswamps and basins in floodplains or fluvial terraces, SW), and areas covered with white-sand soils (found on high terraces of the Caquetá River and in less dissected parts of the Tertiary sedimentary plain, WS) (Duivenvoorden and Lips 1995, Lips and Duivenvoorden 1996). Soils and landscapes are called well-drained when soil drainage (according to FAO 1977) is imperfectly to well-drained (FAO drainage class ≥ 2), and poorly drained when soils are poorly to very poorly drained (FAO drainage class < 2). The area receives a mean annual precipitation of about 3060 mm (1979-1990) and monthly rainfall is never below 100 mm (Duivenvoorden and Lips 1995). Mean annual temperature is 25.7°C (1980-1989) (Duivenvoorden and Lips 1995).

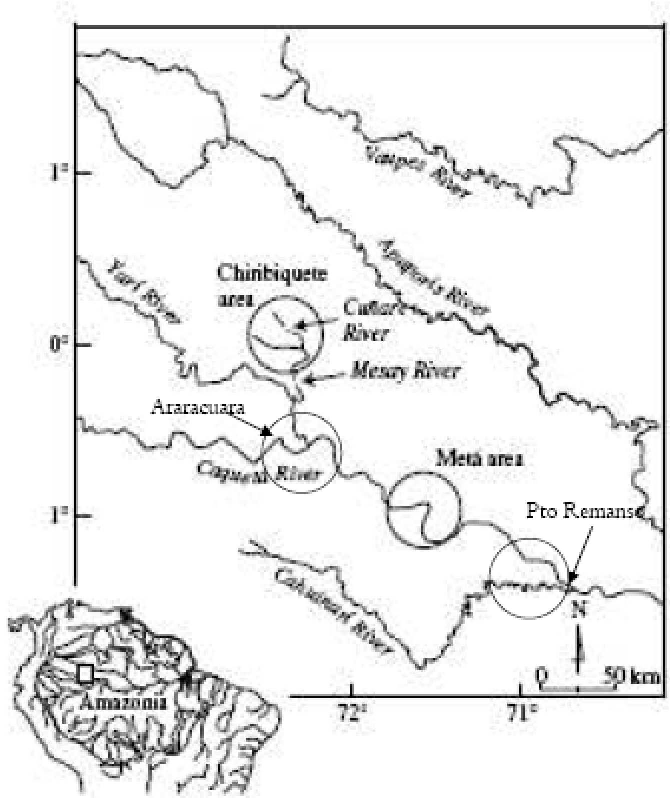


Figure 1. Location of the study area in the middle Caqueta region in Colombian NW Amazonia. Adapted from Duque et al. 2005.

1.2 Field sampling

We conducted a survey of 130 0.1-ha plots that were located in the four landscape units mentioned above (see Duivenvoorden 1996, Duque et al. 2005). We followed a stratified sampling design proportional to the size of the main landscape units. Thus, 60 plots were located on TF, 30 on well-drained FP, 25 on SW, and 15 on WS. To establish the plots, starting locations along the Caquetá, Cahuinarí, Mesay, and Cuñare rivers and the direction of the tracks along which the forests were entered were planned on the basis of the interpretation of aerial photographs and satellite images (Duivenvoorden and Lips 1993, Duivenvoorden et al. 2001). The topography was rapidly described and the forest was visually examined in order to identify more or less homogeneous terrain units. In these units, rectangular plots (20 m width x

50 m long) were located, and were delimited by compass, tape and stakes. All plots were mapped by GPS and were established in mature forests that did not show signs of recent human intervention, at a minimum distance from each other of 500 m. In each plot all trees and palm trees DBH ≥ 10 cm were recorded and collected. How was altitude gotten?

The identification of the botanical collections took place at the COAH, COL, MO, and AAU herbaria. Within families or groups of closely allied families, specimens that could not be identified as species because of a lack of sufficient diagnostic characteristics were clustered into morphospecies on the basis of simultaneous morphological comparisons with all other specimens. Hereafter the term species refers to both morphospecies and botanical species.

1.3 Soil data

Roughly in the central part of 93 (55 in TF, 18 in FP, 10 in WS, and 10 IN SW) of the 130 plots, a soil core was taken at 1.20 m depth to describe the mineral soil horizons (in terms of colour, mottling, horizon boundaries, presence of concretions and texture) and to define soil drainage (in classes of FAO 1977). At each augering position a soil sample was taken at a depth of 65–75 cm (Lips and Duivenvoorden 1996). For analyses, soil samples were dried at temperatures below 40 °C, crumbled and passed through a 2-mm sieve. At the soil laboratory of the Institute for Biodiversity and Ecosystem Dynamics (IBED) at the Universiteit van Amsterdam, total Ca, Mg, K, Na and P contents were determined by means of atomic emission spectrometry from a subsample of 100–200 mg from the sieved fraction, that had been digested in a solution of 48% HF and 2M H2SO4 (after Lim and Jackson 1982). Total content of C and N was determined for the sieved fraction by means of a Carlo Erba 1106 elemental analyser.

1.4 Data analysis

Because species density (SD), which is defined as the number of species per area unit, has shown to be so sensitive to sample size and so to individual density (Condit et al. 1996, Gotelli and Colwell 2001), we used the rarefied species richness (SR), which is defined as the number of species represented by some particular number of individuals, to assess its relationship with the AGB. SR was calculated as the rarefied number of species represented by the average of 1000 random draws without replacement of 40 individuals in each plot (Gotelli and Colwell 2011). Likewise, we defined the rarefied AGB (RAGB) as the average of 1000 random draws without replacement of 40 individuals taken from each 0.1 ha plot. Hereafter we will make the difference between SD and SR, and AGB, which will define the stand above-ground living biomass of each 0.1 ha plot, and the RAGB, which will define the average AGB of 40 individuals randomly taken from the same plot.

To estimate the AGB of each individual, we used the allometric model for Tropical moist forest (Tm) developed by Alvarez et al. (2012), defined by: $\ln(AGB) = 2.406 - 1.289*\ln(DBH) + 1.169*\ln(DBH)^2 - 0.122*\ln(DBH)^3 + 0.445*\ln WD$, where: AGB is expressed in Mg, *DBH* in centimeters, and *WD* is the wood specific gravity (wood density) expressed in g cm^{-3} (Álvarez et al. 2012). We assigned WD values to all individuals according to the taxonomic level of identification following available databases (Chave et al. 2006, Zane et al. 2009). To all those unidentified individuals we assigned the average value of the estimated *WD,* not weighted by AGB, of all the individuals in the plot.

We used a one way analysis of variance (ANOVA) to evaluate differences between landscape units of SD, SR, AGB, RAGB, number of individuals per plot, and contents of Ca, Mg, K, Na, P, C, N, and altitude. Cation contents were log-transformed prior to analysis. When the means were significantly different, we applied the Tukey´s Honest Significant Differences (HSD) test. We used the 130 sampled plots for assessing the structural properties of the forest stands and 93 plots for assessing differences in the soil variables.

We used the 130 sampled plots to evaluate the shape of the log-transformed SR-RAGB relationship across communities, according to four theoretical models: the simple monotonic linear model, the quadratic model, the Michaelis-Menten model, and the two parameter asymptotic exponential model. Both non linear regression models and the quadratic regression model were used to fit data with bumps, unimodally distributed, or with asymptotes (Crawley 2007). To select the best model, we used the Akaike Information Criterion (AIC), which penalizes by the number of data and parameters included in the model (Burnham and Anderson 2004). Within communities, we only tested the monotonic and quadratic models, and used the AIC to select the model that best fitted the SR-RAGB relationship. In those cases in which the quadratic term was no significant, the linear model was chosen. All analyses were done with the R package, version 2.15.1 (R Development Core Team 2012).

1.5 Environmental determinants of the SR-AGB relationship at different spatial scales

First, we tested whether the SR and the RAGB were independently associated with soil fertility. We used stepwise regression to select the best explanatory variables that better explained both the SR and the RAGB variation across communities. Soil variables were included in their simple and quadratic form, prior the logarithmic transformation of all but N and C. We used a distance matrix approach to identify the main soil factors that determine the observed log-transformed SR-RAGB relationship. For building the distance matrices, in all cases we employed the Euclidean distance. Then, we used a Mantel test (Legendre and Legendre 1998) to evaluate the significance of the correlation between the log-transformed SR-RAGB distance and the distances of the log-transformed soil cation contents. The SR – RAGB matrix was built based on the Euclidean distance of each *X* (RAGB) and *Y* (SR) coordinate that determined the position of each plot within the Cartesian plain. All the same analyses were performed for the entire region (across communities) and within each landscape unit (within communities). The Mantel test analyses were performed with Vegan 17.2 in R (Oksanen 2010).

The variable that best explained the SR – RAGB relationship was graphically described using distance decay under two different approaches. Firstly, we drew the linear trend as represented by the Mantel correlation. Secondly, we used a spline to present the interpolated data according to four segments (five points), which was the one that best fitted the data. The SR – RAGB distance was converted to similarity by subtracting to one (1) the standardized distance divided by the maximum distance observed:

$$SR\_RAGB_{similarity} = 1 - \frac{SR\_RAGBi}{\max(SR\_RAGB)}$$

The analyses and figures were done with the R package, version 2.15.1 (R Development Core Team 2012). Already mentioned for data analysis.

2. RESULTS

2.1 Structural and soil variation between landscape units

All forest structural and soil variables but N were statistically significant. Based on SD, TF had the highest number of species; based on the SR, the number of species in TF did not differ from that in FP. Likewise, the AGB in TF forests was significantly higher only than that found in WS; based on the RAGB, TF and FP differed from both WS and

SW (Figure 2). Total bases (and therefore soil fertility) were significantly higher in FP, but C contents were significantly higher in SW (Table 1).

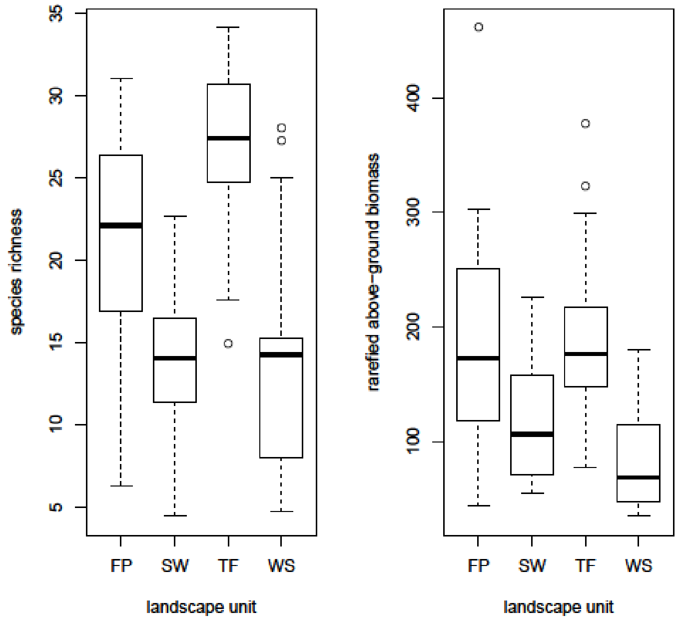


Figure 2. Box – plot that illustrates the trend of the variation of the species richness (SR, left) and the rarefied above ground biomass (RAGB, right). Significant differences are according to Table 1. Landscape units are FP: Flood Plain, SW: Swamps, TF: Tierra Firme, and WS: White Sands. The thick horizontal line represents the median.

2.2 Shape of the SR-AGB relationships

In the entire region, the log-transformed quadratic regression model was the one that best fitted the RSR – RAGB relationship across tree communities in the Colombian Amazon (Table 2; Figure 3). The calculation of the Michaelis – Menten model required 14 iterations to convergence and had an achieved convergence tolerance value of

Table 1. One way anova to identify statistical differences between landscapes units of the plant structural, soils fertility, and altitude (m asl) variables. Different letters in a row represents there statistical differences between landscape units according to the Tukey HSD test (α= 0.05). *P ≤ 0.05, ** P ≤ 0.01, *** P ≤ 0.001, n.s.: non significant. Values for 0.1 he plots. Landscape units are FP: Flood Plain, SW: Swamps, TF: Tierra Firme, and WS: White Sands. SD: species density; NI: number of individuals; AGB: above ground biomass (Mg/0.1 ha). SR: species richness; RAGB: rarefied above ground biomass (Mg/40 ind.). n = sampling size. Altitude: altitudinal position of the plot (m asl)

Variable	**n**	**TF**	**FP**	**WS**	**SW**	**F value**
SD	130	41.9 ± 10.5	27.1 ± 10.7 ^{a,b}	20.7 ± 12.1 ^{b,c}	20.6 ± 8.1 ^{a,c}	36.6***
NI	130	73.1 ± 14.9 ^{a,d}	68.9 ± 22.8 ^{a,b}	88.6 ± 33.8 ^{b,c,d}	108.0 ± 65.4 ^{c}	7.8***
AGB	130	324.3 ± 84.5 ^{b,c}	302.5 ± 146.3 ^{a,b}	189.1 ± 112.8 ^{d}	270.2 ± 112.4 ^{a,c,d}	6.5***
SR	130	27.3 ± 4.0	20.71 ± 7.0	14.38 ± 7.4 ^{a}	13.7 ± 4.7 ^{a}	49.3***
RAGB	130	183.8 ± 58.5 ^{a}	186.4 ± 88.8 ^{a}	86.8 ± 51.5 ^{b}	112.5 ± 45.9 ^{b}	15.5***
Na	93	19.0 ± 19.5 ^{a,c}	198.2 ± 225.6	2.2 ± 2.9 ^{b,c}	22.4 ± 11.7 ^{a,b}	16.0***
K	93	97.4 ± 97.3 ^{a,c}	275.1 ± 155.4	8.0 ± 21.3 ^{b,c}	128.6 ± 74.9 ^{a,b}	17.8***
Ca	93	2.7 ± 3.8 ^{a,c}	98.0 ± 131.2	1.5 ± 0.9 ^{b,c}	10.7 ± 22.9 ^{a,b}	12.9***
Mg	93	49.8 ± 46.3 ^{a,c}	212.1 ± 169.3	4.7 ± 11.5 ^{b,c}	60.0 ± 35.9 ^{a,b}	20.5***
P	93	6.1 ± 2.4	10.4 ± 6.1 ^{a}	0.9 ± 1.1	10.4 ± 8.8 ^{a}	13.5***
C	93	0.4 ± 0.2 ^{a,c}	0.5 ± 0.2 ^{a,b}	0.9 ± 1.2 ^{b,c}	7.6 ± 12.7	9.2***
N	93	0.1 ± 0.3 ^{b,d,f}	0.1 ± 0.0 ^{a,b,c}	0.0 ± 0.0 ^{c,e,f}	0.1 ± 0.0 ^{a,d,e}	0.9 n.s.
Altitude	130	128.2 ± 27.4 ^{b}	111.7 ± 17.1 ^{a}	153.1 ± 441.9	112.2 ± 17.7 ^{a,b}	10.8***

5.905e-07; the calculation of the Asymptotic model required 14 iterations to convergence and had an achieved convergence tolerance value of 2.735e-06.

Within communities not a single model fitted the SR – RAGB relationship within forest

2.3 Shape of the species richness-rarefied above ground biomass relationships

In the entire region, the log-transformed quadratic regression model was the one that best fitted the SR – RAGB relationship across tree communities in the Colombian Amazon (Table 2; Figure 3). The calculation of the Michaelis – Menten model required 14 iterations to convergence and achieved a tolerance value of 5.905e-07, the

Table 2. Tested models for the species richness (SR) – rarefied above ground biomass relationship (RAGB) across tree communities in the Colombian Amazon. R^2: coefficient of determination; Adj. R^2: adjusted R^2; RSE: Residual Standard Error; AIC: Akaike Information Criterion; Shapiro-Wilk (normality test for residuals) Significance levels: *P ≤ 0.05, ** P ≤ 0.01, *** P ≤ 0.001, ns: non significant.

Model name	**Model**	**R^2**	**Adj. R^2**	**RSE**	**D.f.**	**AIC**	**F-statistic**	**Shapiro-Wilk**
Log (Linear regression)	log(SR) = 0.13 + 0.58 *log(RAGB)	0.41	0.41	0.36	128	106.27	89.05 ***	0.99^{ns}
Log (Quadratic regression)	log(SR) = - 8.27 + 4.13*log(RAGB) - 0.37*((log(RAGB))^2	0.49	0.48	0.34	127	89.93	60.5 ***	0.97^{ns}
Michaelis-Menten model	log(SR) = 0.67 log(RAGB) /(1 + 0.02*log(RAGB))			0.36	128	105.51		0.98^{ns}
Asymptotic exponential model	log(SR) = 3.44 - 90.54 exp (-1.11*log(RAGB))			0.34	127	91.76		0.97^{ns}

calculation of the exponential asymptotic model required 14 iterations to convergence an achieved a tolerance value of 2.735e-06.

Within communities not a single model fitted the SR – RAGB relationship within forest types, and monotonic (FP and WS), unimodal (SW), and no shape (TF) (Table 3) were all represented in different forest communities (Figure 4).

2.4 Environmental determinants of the SR-AGB relationship

Across communities, both SR and RAGB were significantly associated with soil fertility (Figure 5). After partialling out the influence of the soil variables on determining either the SR or the RAGB variation, the altitudinal position was not significantly associated with either the SR or the RAGB. According to the Mantel test, across communities, the SR – RAGB relationship was significantly associated with K, Mg, and P, being maximum with the last (Table 4). The geographical distance between plots did not show any significant influence on structuring the SR – RAGB relationship. Within communities, there was not significant correlation between the

SR-RAGB relationship and any of the environmental (soil variables) or geographic (coordinates and altitude) variables evaluated (Table 5).

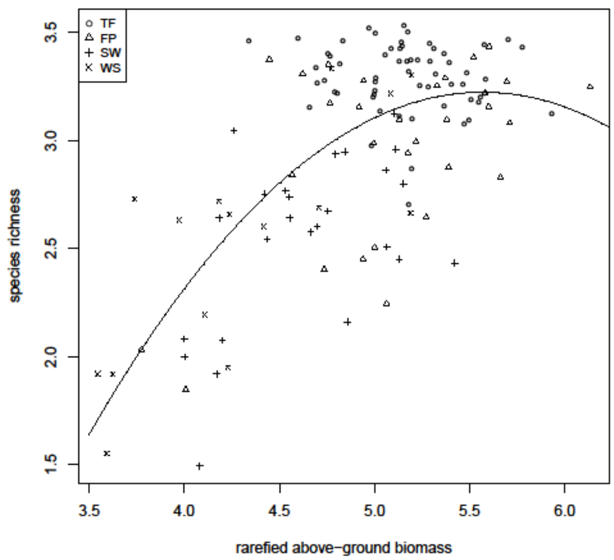


Figure 3. Across communities species richness (SR) – rarefied above ground biomass (RAGB) relationship as represented by the quadratic model. FP: Flood Plain; SW: Swamps; TF: Tierra Firme; and WS: White Sands.

3. DISCUSSION

3.1 Shape of the SR-RAGB relationships

According to our expectations, across tree communities, the hump-shaped unimodal model was the best describing the SR – RAGB relationship for tree communities in the Colombian Amazon. Therefore, our results support the general idea that at the landscape scale in plant studies that cross community boundaries, the hump-shape will be the dominant form of the SR – RAGB relationship (Rosenzweig 1995, Guo and Berry 1998, Grace 1999, Mittelbach et al. 2001). As reported in previous studies at the landscape scale (Mittelbach et al. 2001), the hump-shaped tree SR - RAGB relationship was largely driven by the magnitude of the changes of the environmental gradients among landscape units (see Lips and Duivenvoorden 1996). The first phase of the hump-shaped SR - RAGB curve showed a positive slope rising from WS and SW, crossing the plateau dominated by the TF forests, to end with a trend beginning to decline in the FP forests. Because SW represents the second landscape unit with the most fertile soils (after FP), we can not claim that the three phases that structure the SR - RAGB relationship entirely follow a soil fertility gradient.

The linear model was the best model when we assessed the SD – AGB relationship (Figure A3). However, the overall SD – AGB relationship became weaker than the SR – RAGB (R^2 adjusted decreased from 0.48 to 0.25), and even difficult to differentiate from either the monotonic or the asymptotic models (Table A1). It is not necessay to say that it was difficult to differentiate because the shape changed. This comparative analysis illustrates the sampling effect introduced by increasing stem density or plot size (sampling grain) on the instability of the dominant hump-shape of

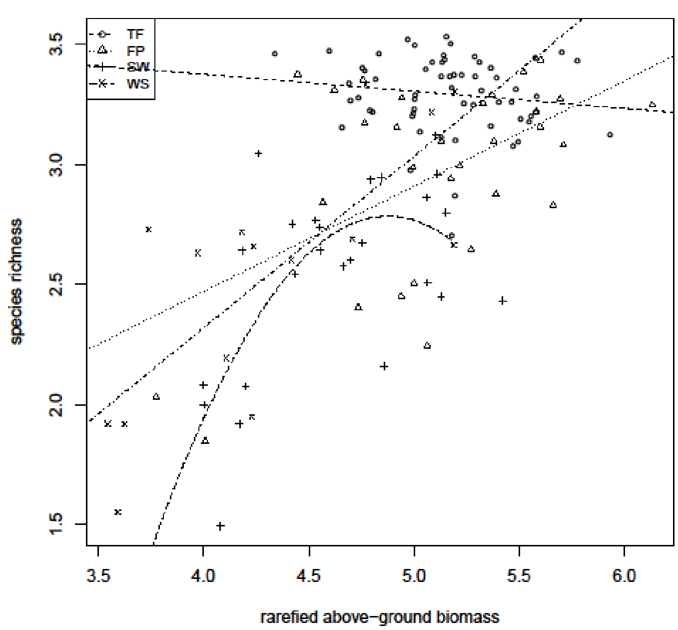


Figure 4. Within communities SR – RAGB relationship. FP: Flood Plain; SW: Swamps; TF: Tierra Firme; and WS: White Sands

Table 3. Within communities significant models that best described the species richness (SR) - rarefied above ground biomass (RAGB) relationship. regression models by landscape unit. R^2: coefficient of determination; Adj. R^2: adjusted R^2; RSE: Residual Standard Error; AIC: Akaike Information Criterion; Shapiro-Wilk (normality test for residuals) Significance levels: *P ≤ 0.05, ** P ≤ 0.01, *** P ≤ 0.001, ns: non significant.

Landscape unit	Best regression model	D.f.	R^2	Adj. R^2	RSE	AIC	F-statistic	Shapiro-Wilk
FP	log(SR) = 0.72 + 0.44*log(RAGB)	28	0.29	0.27	0.36	27.65	11.51 **	0.98^{ns}
WS	log(SR) = -0.54 + 0.71*log(RAGB)	13	0.59	0.55	0.36	15.58	18.41 ***	0.96^{ns}
SW	log(SR) = -23.31 + 10.70*log(RAGB) - 1.10*(log(RAGB))^2	22	0.46	0.41	0.31	16.38	9.49 *	0.97^{ns}

the SD – AGB relationship claimed for plant communities (Whittaker 2010, Adler et al. 2011). Although the length of the gradient and the sample size considered in this study were large enough to expect to have detected the real shape of the SR – RAGB relationship (Mittelbach et al. 2001, Whittaker 2010), the lack of a clear third decreasing phase of the curve for the observed tree SR – RAGB relationship in the Colombian Amazon rises questions about whether an enlargement of the sampling size would corroborate the unimodal hump-shape or would promote a monotonic one (Chisholm et al. in prep).

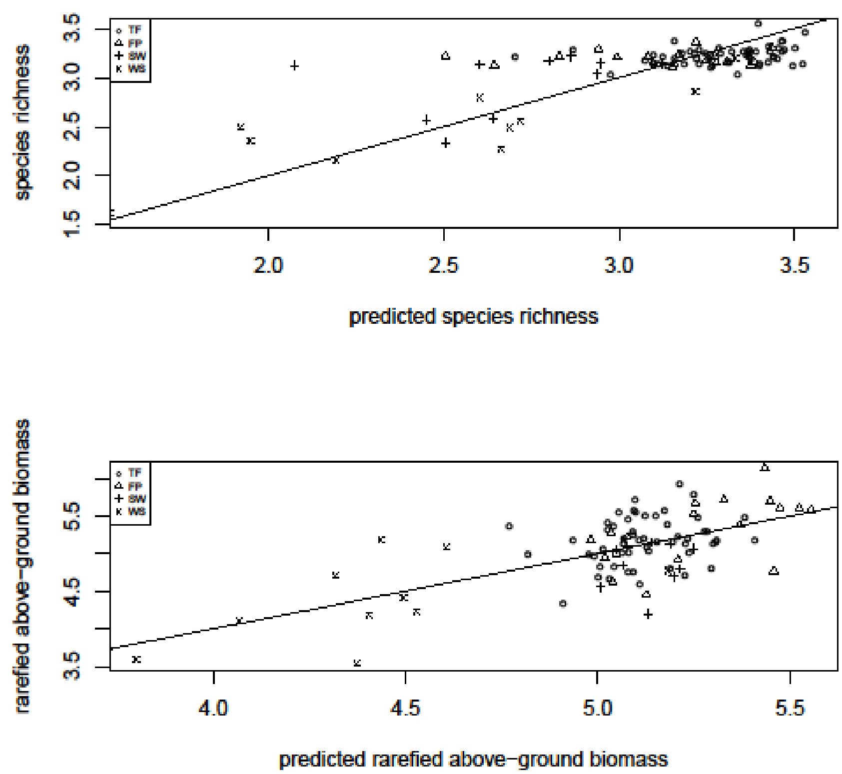


Figure 5.Observed vs predicted values of both the species richness (SR) and the rarefied above ground biomass (RAGB) by the soils fertility. **A.** The best regression model for the SR-soils relationship was: log(SR) = 2.61 + 0.44 log(K) - 0.21 log(Mg) + 0.20 log(P) - 0.10 C + 0.22 N - 0.06 (log(K)^2) + 0.03 (log(Mg)^2) + 0.002 (C^2) **B.** The best regression model for the RAGB – soils relationship was: log(RAGB) = 4.32+ 0.40 log(K) - 0.08 (log(K)^2) + 0.05 (log(Mg)^2). TF: Tierra Firme, FP: Flood Plain, SW: Swamps, and WS: White Sands.

Within communities, on the contrary, the monotonic shape of the SR – RAGB relationship (FP and WS) dominated over the expected no shape (TF) or the hump-shaped model (SW), in contrast to our expectations. Environmental stress associated to flooding and bad drainage of soils seems to play an important role on defining the shape of the SR –RAGB relationship within communities. The no shape found in TF proposes that the lack of a permanent continuous disturbance factor, such as that caused by flooding, rules out species competition and creates a random mosaic of the SR – RAGB variation in this forest type. Since in TF both RAGB and AGB reach the maximum values, our study contradicts the generalized idea that competition increases in habitats with high AGB (Grime 1973, Abrams 1995, Rosenzweig 1995). The fact that in FP the

Table 4. Across communities Mantel correlations between the distance matrix of the log-transformed SR- and the log-transformed RAGB distance matrix (X distance column) and each of the distance matrices of the log-transformed cation contents, the log-transformed geographical distance, and the altitudinal position of the plots (Y distance column). Analyses were based on 999 permutations. Highest Mantel statistic value (r) in **bold**. All significant correlations in *italics* (α= 0.05).

X distance	**Y distance**	**Mantel statistic (r)**	**Significance**
SR - RAGB	Soils	0.19	*0.035*
	Geographical space	-0.11	0.998
	Mg	0.34	*0.001*
	Na	0.18	0.006
	K	0.35	*0.001*
	Ca	0.06	0.21
	P	**0.45**	*0.001*
	C	0.10	0.104
	N	-0.01	0.417
	Altitude	-0.01	0.483

mean SR and RAGB were similar than that found in TF, but the relationship was monotonic, underpin that the rate of disturbance overwhelms the influence of high AGB stocks on shaping the SR – RAGB relationship.

Within the TF tree community, biological spatially structured processes, such as dispersal limitation, have been found to be the main determinants of tree species composition in the Colombian Amazon (Duivenvoorden 1995, Duque et al. 2002, Duivenvoorden and Duque

2010), which reinforces the lack of influence of species competition on determining the random pattern of the SR - RAGB variation in this landscape unit. Likewise, our results within communities do not support the generalized idea that in low-biomass habitats species competition is weak (Reader et al. 1994, Guo and Berry 1998). High dominance of a few number of species that theoretically can inhibit the establishment of co-existing species (Huston 1994), is exactly what we found in WS and SW, which are the landscape units with the lowest RAGB. Therefore, within communities, disturbance rather than competition seems to be the main driver of the SR – RAGB relationship in the Amazon rain forests.

3.2 Environmental determinants of the SR-AGB relationship

3.2.1 Soil fertility and the variation in SR and RAGB

In this study, the SR or point diversity in TF (*sensu* Whittaker 1977) did not differ of that in FP, which contrasts with most of studies that focused on the SD variation across tree communities in the Amazon basin (Gentry 1988, Duivenvoorden 1996). The altitudinal position of the plots was not significant after partialling out the effect of soils on the RAGB. This result contradicts the main claims of a recent study carried out in the same region and that employed remote-sensed tools for assessing the AGB biomass of the region (Asner et al. 2011) where the altitudinal position of the plots was found to be the overriding factor controlling the AGB variation.

Both the SR and the RAGB were independently associated with soil fertility. In both cases, the explanatory variables included quadratic terms that reflect the hump-shaped behavior of the independent variables in relation to the soil fertility variation (Figure 5). Since the independent shape of the SR and RAGB reflects the hump-shape of the above reported SR – RAGB relationship across communities, it directly introduces an expected influence of soil fertility on determining the form of the SR – RAGB relationship.

Table 5. Within communities Mantel correlations between the distance matrix of the log-transformed SR- and the log-transformed RAGB distance matrix (X distance column) and each of the distance matrices of the log-transformed cation contents, the log-transformed geographical distance, and the altitudinal position of the plots (Y distance column). Analyses were based on 999 permutations. There were not any significant correlation at a significance level of 0.05 (α= 0.05).

		Mantel correlation			
X distance	**Y distance**	**TF**	**FP**	**WS**	**SW**
SR - RAGB	Soils	0.06	0.07	0.14	0.03
	Geographical space	-0.05	0.04	-0.08	-0.05
	Mg	0.04	0.06	0.09	0.07
	Na	0.05	0.02	0.27	0.31
	K	0.06	-0.06	0.19	0.16
	Ca	0.06	0.16	0.01	-0.09
	P	-0.05	-0.03	0.11	-0.01
	C	0.06	0.03	0	0.02
	N	0.08	-0.06	-0.1	-0.02
	Altitude	-0.05	-0.12	0.04	-0.04

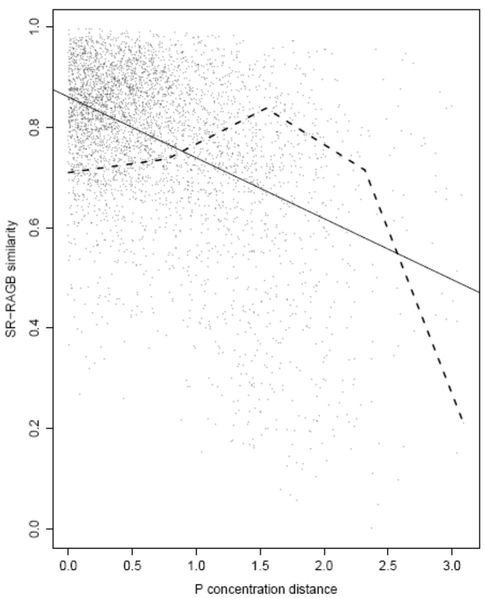


Figure 6. Distance decay of the log-transformed SR – log-transformed RAGB similarity in relation to the distance of the log-transformed P concentration distance between plots. The continuous line illustrates the linear trend depicted by the Mantel correlation (0.45). The dashed line represents the spline trend based on five segments.

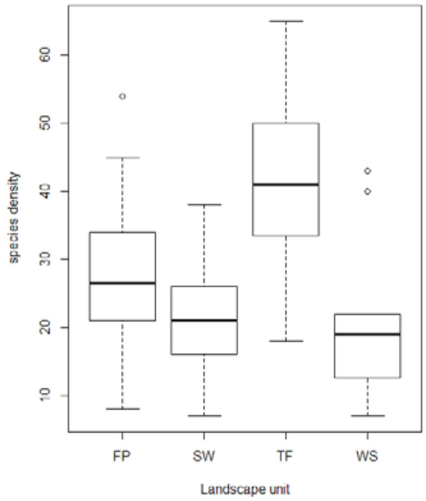
3.2.2 Soil fertility as determinant of the SR-RAGB variation

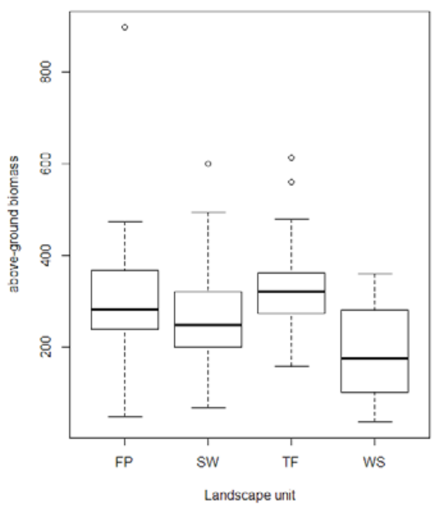
Across communities, total bases and P contents were significantly correlated with the SR – RAGB variation (Table 4). In particular, P concentrations showed the highest correlation (R_{MANTEL} = 0.45) or influence on determining the hump-shape of the SR – RAGB relationship. Positive and significant relationships between soil fertility and both the AGB (Quesada et al. 2009) and the SR (Gentry 1988, Duivenvoorden 1996, Duque et al. 2009) have already been reported in the Amazon forests. Phosphorus is a major nutrient actively involved in the plant photosynthesis that promotes plant growth and therefore plant AGB. However, the influence of the P contents in soils on the SR is more controversial. In Africa, where the P concentration in soils is much higher than that reported in our study (Duivenvoorden 1996), the tree species density declined with the increase of P concentrations in soils (Ashton & Hall 1992).

Across tree communities in the Colombian Amazon forests, P contents enhance forest performance in such a way that it facilitates the likely of determining a big portion of the coupled variation in SR and RAGB (Figure 6). Within communities, in contrast, no soil variable played any significant role on structuring the SR – RAGB relationship. In TF forests, this result is obvious due to the random pattern found in the SR – RAGB relationship. In the other landscape units, however, where the monotonic and quadratic models were fitted, other factors than soils fertility, such as the rate of disturbance, determine the covariation between the SR and the AGB.

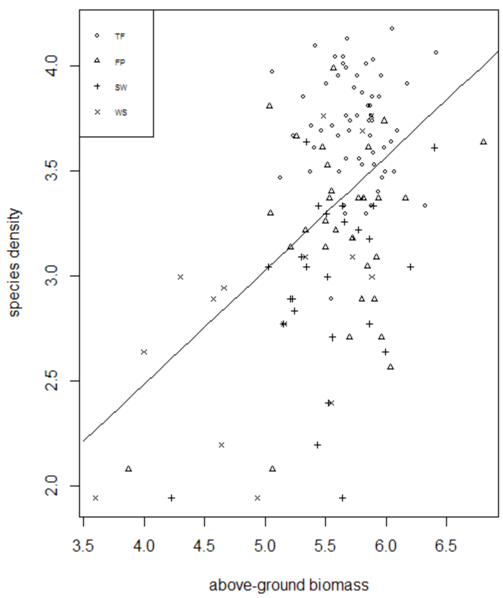
Overall, in temporal studies, an increase in plant competition associated to the increase in the AGB through forest development (Tilman 1982, Huston 1994) has been proposed as the main mechanism determining the phase of species exclusion at an intermediate point of disturbance (Sheil and Burslem, 2003). On the contrary, the hump-shape of the SR – RAGB relationship found across spatially distributed communities in the Colombian Amazon, showed to come from adding up the within landscape models. Hence, across communities, there is not any single mechanism structuring this pattern, and the combined action of the rate of disturbance along with soils fertility seem to largely determine the up and down slope of the first and third phases of the curve. However, in the second phase of the curve, species neutrality (sensu Hubbell 2001), which means a lack of influence from species competition, seems to be the main mechanism that controls the plateau of the curve where both SR and RAGB become the highest.

List of appendices

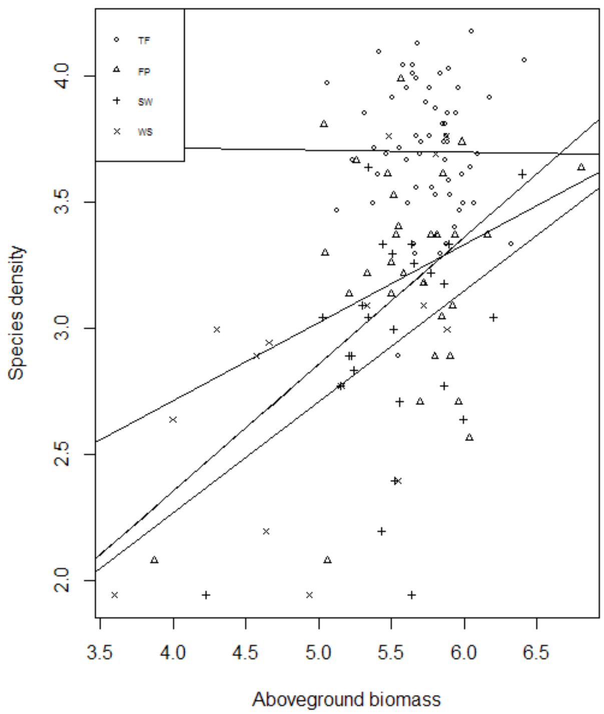




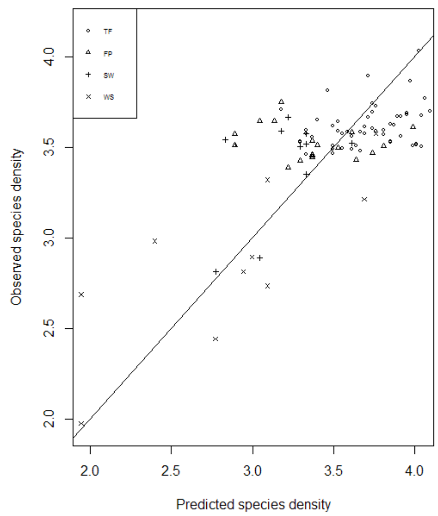
A. **Figure A1.** Box – plot that illustrates the trend of the variation of the species density (SD, left) and the above ground biomass (AGB, right). Significant differences are according to Table 1. Landscape units are FP: Flood Plain, SW: Swamps, TF: Tierra Firme, and WS: White Sands. The thick horizontal line represents the median.

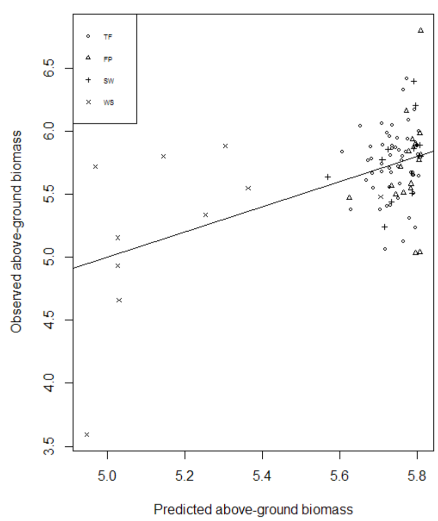


B. **Figure A2.** Across communities species density (SD) –above ground biomass (AGB) relationship as represented by the quadratic model. FP: Flood Plain; SW: Swamps; TF: Tierra Firme; and WS: White Sands.



C. **Figure A3** Within communities species density (SD) –above ground biomass (AGB) relationship. FP: Flood Plain; SW: Swamps; TF: Tierra Firme; and WS: White Sands.





D. **Figure A4** Observed vs predicted values of both the species desnity (SD) and the above ground biomass (AGB) by the soils fertility. A. The best regression model for the SR-soils relationship. B. The best regression model for the RAGB – soils relationship. TF: Tierra Firme, FP: Flood Plain, SW: Swamps, TF: and WS: White Sands.

E. **Table A1** Tested models for the species density (SD) –above ground biomass relationship (AGB) across tree communities in the Colombian Amazon. R^2: coefficient of determination; Adj. R^2: adjusted R^2; RSE: Residual Standard Error; AIC: Akaike Information Criterion; Shapiro-Wilk (normality test for residuals) Significance levels: *P ≤ 0.05, ** P ≤ 0.01, *** P ≤ 0.001, ns: non significant.

Model name	**Model**	**R^2**	**Adj.R^2**	**RSE**	**AIC**	**F-statistic**	**Shapiro Wilk**
Log (Linear regression)	$\log(SR) = 0.32 + 0.54*\log(AGB)$	0.24	0.23	0.46	170.11	40.52 ***	0.98*
Log (Quadratic regression)	$\log(SR) = - 4.47 + 2.40*\log(AGB) - 0.18*(\log(AGB))^2$	0.26	0.25	0.45	168.44	22.49	0.97***
Michaelis-Menten model	$\log(SR) = 0.70 \log(AGB) /(1 + 0.03 \log(AGB))$			0.46	169.62		0.97*
Asymptotic exponential model	$\log(SR) = 4.11 - 17.38 \exp (- 0.57 \log(AGB))$			0.45	168.84		0.97***

LITERATURE CITED

Abrams, P. A. (1995) Monotonic or unimodal diversity-productivity gradient: what does competition theory predict? Ecology 76: 2019-2027.

Adler, P., Seabloom, E., Borer, E., Hillebrand, H., Hautier, Y., Hector, A., Harpole, W. S., O'Halloran, L., Grace, J., Anderson, T. M., Bakker, J. D., Biederman, L. A., Brown, C. S., Buckley, Y. M., Calabrese, L. B., Chu, Ch.-J., Cleland, E. E., Collins, S. L., Cottingham, K. L., Crawley, M. J., Damschen, E. I., Davies, K. F., DeCrappeo, N. M., Fay, P. A., Firn, J., Frater, P., Gasarch, E. I., Gruner, D. S., Hagenah, N., Ris Lambers, J. H., Humphries, H., Jin, V. L., Kay, A.D., Kirkman, K. P., Klein, J. A., Knops, J. M. H., La Pierre, K. J., Lambrinos, J. G., Li, W., MacDougall, A. S., McCulley, R. L., Melbourne, B. A., Mitchell, Ch. E., Moore, J. L., Morgan, J. W., Mortensen, B., Orrock, J. L., Prober, S. M., Pyke, D. A., Risch, A. C., Schuetz, M., Smith, M. D., Stevens, C. J., Sullivan, L. L., Wang, G., Wragg, P. D., Wright, J. P. and Yang, L. H. (2011) Productivity is a poor predictor of plant species richness. Science, 333 (6050): 1750-1753.

Álvarez, E., Duque, Á., Saldarriaga, J., Cabrera, K., de las Salas, G, del Valle, I. , Lema, Á.,Moreno, F., Orrego, S. and Rodríguez, L. (2012) Tree above-ground biomass allometries for carbon stocks estimation in the natural forests of Colombia. Forest Ecology and Management 267: 297–308.

Ashton, P. S. and Hall, P. (1992) Comparisons of structure among mixed dipterocarp

forests of north-western Borneo. Journal of Ecology, 60: 305–324.

Asner, G. P., Knapp, D. E., Balaji, A. and Páez-Acosta, G. (2009) Automated mapping of tropical deforestation and forest degradation: CLASlite, J. Appl. Remote Sens. 3, 033543.

Asner, G. P.,Clark, J. K., Mascaro, J., Galindo García, G. A.;,Chadwick, K. D., Navarrete Encinales, D. A., Paez-Acosta, G., Cabrera Montenegro, E., Kennedy-Bowdoin, T., Duque, A., Balaji, A., von Hildebrand, P., Maatoug, L., Phillips Bernal, J. F., Knapp, D. E., García Dávila, M. C., Jacobson, J. and Ordóñez, M. F. (2012) High-resolution Mapping of Forest Carbon Stocks in the Colombian Amazon. Biogeosciences Discussions9: 2445–2479. www.biogeosciences-Discuss.net/9/2445/2012/.

Burnham, K. P. and Anderson, D. R. (2004) Multimodel Inference: Understanding AIC and BIC in Model Selection. Sociological Methods & Research 33 (2): 261-304.

Chapin, F. S. III, Sala, O.E., Burke, I. C., Grime, J. P., Hooper, D.U., Lauenroth, W.K., Lombard, A., Mooney, H.A., Mosier, A. R., Naeem, S., Pacala, S. W., Roy, J., Steffen, W. L. and Tilman, D. (1998) Ecosystem consequences of changing biodiversity. Bioscience 48 (1): 45-52.

Chase, J. M. and Leibold, M. A. (2002) Spatial scale dictates the productivity-biodiversity relationship. Nature 416: 427-430.

Chave, J., Muller-Landau, H. C., Baker, T. R., Easdale, T. A., ter Steege, H. and Webb Campbell O. (2006) Regional and phylogenetic variation of wood density across 2456 neotropical tree species. Ecological Applications 16: 2356–2367.

Chisholm et al. In preparation.

Condit, R., Hubbell, S. P. , Lafrankie, J. V., Sukumar, R., Manokaran, N., Foster, R. B. and Ashton, P. S. 1996. Species area and species individual relationships for tropical trees: A comparison of a three 50-ha plots. Journal of Ecology 84 (4): 549 – 562.

Crawley, M. J. (2007) The R Book. John Wiley & Sons Ltd., The Atrium, Southern Gate, Chichester, West Sussex PO19 8SQ, England.

Duivenvoorden, J. F. and Lips, J. M. (1993) Ecología del paisaje del Medio Caquetá. Memoria explicativa de los mapas. Tropenbos-Colombia, SantaFé de Bogotá.

Duivenvoorden, J.F. (1995) Tree species composition and rain forest-environment relationships in the middle Caquetá area, Colombia, NW Amazonía. Vegetatio 120:

91-113.

Duivenvoorden, J. F. and Lips, J. M. (1995) A land-ecological study of soils, vegetation and plant diversity in Colombian Amazonia (The Quaternary of Colombia, 20). Wageningen: The Tropenbos Foundation.

Duivenvoorden, J. F. (1996) Patterns of tree species richness in rain forests of the Middle Caqueta Area, Colombia, NW Amazonia. Biotropica 28: 142-158.

Duivenvoorden, J.F., Balsev, H., Cavelier, J., Grandez, C., Tuomisto, H. and Valencia, R. (1999) Non-timber forest plant resource assessment in NW Amazonia. In: NTFP Research in the Tropenbos programme: results and perspectives. Pp. 81-93. The Tropenbos Foundation.

Duivenvoorden, J. F., Balslev, H., Cavalier, J., Grández, C., Tuomisto, H. and Valencia, R. (2001) Evaluación de recursos vegetales no maderables en la Amazonia noroccidental. Institute for Biodiversity and Ecosystem Dynamics, Universiteit van Amsterdam, Amsterdam.

Duivenvoorden J. F. and Duque, A. J. (2010) Composition and diversity of northwestern Amazonian rainforests in a geoecological context. In: Amazonia: Landscape and Species Evolution: A look into the past. Editirs: Hoorn, C. and Wesselingh, F. P. Blackwell Publishing Ltd. DOI: 10.1002/9781444306408.ch22

Duque, A. J., Cavelier, J., Sanchez S., M., Duivenvoorden, J. F. (2002) Different floristic patterns of woody understorey and canopy plants in Colombian Amazonian. Journal of Tropical Ecology 18 (4): 499-525.

Duque, A. J., Duivenvoorden, J. F., Cavelier, J., Sánchez, M., Polanía, C. and León, A. (2005) Ferns and Melastomataceae as Indicators of Vascular Plant Composition in Rain Forests of Colombian Amazonia. Plant Ecology 178 (1): 1-13.

Duque, A. J., Phillips, J. F. von Hildebrand, P., Posada, C. A. Prieto, A., Rudas, A., Suescún, M. and Stevenson, P.. (2009). Distance Decay of Tree Species Similarity in Protected Areas on Terra Firme Forests in Colombian Amazonia. Biotropica 41: 599–607.

FAO (1977) Guidelines for soil profile description. FAO, Rome, Italy.

Gentry, A. H. (1988) Changes in plant community diversity and floristic composition on environmental and geographical gradients. Annals of the Missouri Botanical Garden 75 (1): 1-34.

Gotelli, N. J. and Colwell, R. K. (2001) Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. Ecology Letters 4: 379-391.

Gotelli, N. J. and Colwell R. K. (2011) Estimating species richness. Pages 39-54 *In* A. E. Magurran and B. J. McGill, editors. Frontiers in measuring biodiversity. Oxford University Press, New York.

Grace, J. B. (1999) The factors controlling species density in herbaceous plant communities: an assessment. Perspectives in Plant Ecology, Evolution and Systematics 2: 1–28.

Grime, J. P. (1973) Control of species density in herbaceous vegetation. Journal of Environmental Management 1:151–167.

Guo, Q. and Berry, W. L. (1998) Species richness and biomass: dissection of the hump-shaped relationships. Ecology 79 (7): 2555-2559.

Hubbell, S. P. (2001) The Unified Neutral Theory of Biodiversity and Biogeography. Princeton University Press, Princeton, NJ.

Huston, M. A. (1994) Biological diversity. Cambridge University Press, Cambridge, UK.

Legendre P. and Legendre L. (1998) Numerical Ecology. Elsevier Science, Amsterdam.

Lim, C. H. and Jackson, M. L. (1982) Dissolution for total analysis. Pp. 1–12 in: Methods of Soil Analyses Part 2, 2nd edition. (A.L. Page, editor). Soil Science Society of America, Madison Wisconsin.

Lips, J. M. and Duivenvoorden, J. F. (1996) Regional patterns of well drained upland soil differentiation in the middle Caquetá basin of Colombian Amazonia. Geoderma 72 (3–4): 219–257.

McGlinn, D. J. and Palmer, M. W. (2010) Spatial Structure Alters the Shape of the Unimodal Species Richness-Biomass Relationship in a Neutral Model. Diversity 2: 550-560.

Mittelbach, G. G., Steiner, C. F., Scheiner, S. M., Gross, K. L., Reynolds, H. L., Waide, R. B., Willig, M. R., Dodson, S. I. and Gough, L. (2001) What Is the Observed Relationship between Species Richness and Productivity? Ecology 82 (9): 2381-2396.

Myers, N., Mittermeier. R. A., Mittermeier, C.G., da Fonseca, G. A. B. and Kent, J. 2000. Biodiversity hotspots for conservation priorities. Nature 403: 853–858.

Oksanen, J. (1996) Is the Humped Relationship between species Richness and Biomass an Artefact due to Plot Size? The Journal of Ecology 84 (2): 293-295.

Oksanen, J. (2010) Community Ecology Package project! In: http://vegan.r-forge.r-project.org/.

Quesada, C. A., Lloyd, J., Schwarz, M., Baker, T. R., Phillips, O. L., Patiño, S., Czimczik, C., Hodnett, M. G., Herrera, R., Arneth, A., Lloyd, G., Malhi, Y., Dezzeo, N., Luizão, F. J., Santos, A. J. B., Schmerier, J., Arroyo, L., Silveira, M., Priante Filho, N., Jimenez, E. M., Paiva, R., Vieira, I., Neill, D. A., Silva, N., Peñuela, M. C., Monteagudo, A., Vásquez, R., Prieto, A., Rudas, A., Almeida, S., Higuchi, N., Lezama, A. T., López-González, G., Peacock, J., Fyllas, N. M., Alvarez Dávila, E., Erwin, T., di Fiore, A., Chao, K. J., Honorio, E., Killeen, T., Peña Cruz, A., Pitman, N., Núñez Vargas, P., Salomão, R., Terborgh, J. and Ramírez, H. (2009) *Regional and large-scale patterns in Amazon forest structure and function are mediated by variations in soil physical and chemical properties.* Biogeosciences Discussions 6(2): 3993-4057.

R Development Core Team (2012) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org/.

Reader, R. J., Wilson, S. D., Belcher, J. W., Wisheu, I., Keddy, P. A., Tilman, D., Morris, E. C., Grace, J. B., McGraw, J. B., Olff, H., Turkington, R., Klein, E., Leung, Y., Shipley, B., van Hulst, R., Johansson, M. E., Nilsson, C., Gurevitch, J., Grigulis, K. and Beisner, B. E. (1994) Plant competition in relation to neighbor biomass: an intercontinental study with Poa pratensis. Ecology 75:1753-1760.

Rosenzweig, M. L. (1995) Species diversity in space and time. Cambridge University Press, Cambridge, UK.

Sheil, D. and Burslem, D. F.R.P. (2003) Disturbing hypotheses in tropical forests. Trends in Ecology and Evolution 18 (1): 18-26.

Siikamäki J. and Newbold, S. (2012) Potential Biodiversity Benefits from International Programs to Reduce Carbon Emissions from Deforestation. Ambio 41, Supplement 1: 78-89.

Strassburg, B. B. N., Rodrigues, A. S. L., Gusti, Mykola, A. Balmford, A., Fritz, S., Obersteiner, M., Turner, R. K. and Brooks Th. M. (2012) Impacts of incentives to reduce emissions from deforestation on global species extinctions. Nature Climate Change 2: 350–355.

Thomas, C. D., Anderson, B. J., Moilanen, A., Eigenbrod, F., Heinemeyer, A., Quaife, T., Roy, D. B., Gillings, S., Armsworth, P. R. and Gaston, K. J. (2012) Reconciling biodiversity and carbon conservation. Ecology Letters. doi: 10.1111/ele.12054.

Tilman, D. (1982) Resource competition and community structure. Princeton University Press, Princeton, New Jersey, USA.

UN-REDD (2012). UN-REDD Programme Partner Countries. http://www.un- redd.org/. Last accessed 25 January 2013.

Venter, O., Laurance, W. F., Iwamura, T., Wilson, K. A., Fuller, R. A. and Possingham, H. P. (2009) Harnessing Carbon Payments to Protect Biodiversity. Supporting Online Material for Science **326**: 1368. DOI: 10.1126/science.1180289. www.sciencemag.org/cgi/content/full/326/5958/1368/DC1

Whittaker, R. H. (1977) Evolution of species diversity in land communities. Evolutionary Biology 10: 1–67.

Whittaker, R. J. (2010) Meta-analyses and mega-mistakes: calling time on meta-analysis of the species richness-productivity relationship. Ecology 91 (9): 2522-2533.

Zanne, A. E., Lopez-Gonzalez, G., Coomes, D. A., Ilic, J., Jansen, S., Lewis, S. L., Miller, R. B., Swenson, N. G., Wiemann, M. C. and Chave, J. (2009) Data from: Towards a worldwide wood economics spectrum. Dryad Digital Repository.