



Forest structure and live aboveground biomass variation along an elevational gradient of tropical Atlantic moist forest (Brazil)

Luciana F. Alves^{a,b,*}, Simone A. Vieira^c, Marcos A. Scaranello^c, Plinio B. Camargo^c, Flavio A.M. Santos^d, Carlos A. Joly^d, Luiz A. Martinelli^c

^a INSTAAR, University of Colorado, Campus Box 450, Boulder, CO 80309, USA

^b Instituto de Botânica, São Paulo, SP, Brazil

^c CENA/Esalq, Universidade de São Paulo, CP 96, Piracicaba 13400-970, SP, Brazil

^d Departamento de Biologia Vegetal, Universidade Estadual de Campinas, CP 6109, Campinas 13083-970, SP, Brazil

ARTICLE INFO

Article history:

Received 10 February 2010

Received in revised form 15 May 2010

Accepted 17 May 2010

Keywords:

Aboveground biomass

Carbon pools

Tropical forest

Stem size distribution

Brazil

Topography

ABSTRACT

Live aboveground biomass (AGB) is an important source of uncertainty in the carbon balance from the tropical regions in part due scarcity of reliable estimates of live AGB and its variation across landscapes and forest types. Studies of forest structure and biomass stocks of Neotropical forests are biased toward Amazonian and Central American sites. In particular, standardized estimates of aboveground biomass stocks for the Brazilian Atlantic forest are rarely available. Notwithstanding the role of environmental variables that control the distribution and abundance of biomass in tropical lowland forests has been the subject of considerable research, the effect of short, steep elevational gradients on tropical forest structure and carbon dynamics is not well known. In order to evaluate forest structure and live AGB variation along an elevational gradient (0–1100 m a.s.l.) of coastal Atlantic Forest in SE Brazil, we carried out a standard census of woody stems ≥ 4.8 cm dbh in 13 1-ha permanent plots established on four different sites in 2006–2007. Live AGB ranged from 166.3 Mg ha⁻¹ (bootstrapped 95% CI: 144.4,187.0) to 283.2 Mg ha⁻¹ (bootstrapped 95% CI: 253.0,325.2) and increased with elevation. We found that local-scale topographic variation associated with elevation influences the distribution of trees >50 cm dbh and total live AGB. Across all elevations, we found more stems (64–75%) with limited crown illumination but the largest proportion of the live AGB (68–85%) was stored in stems with highly illuminated or fully exposed crowns. Topography, disturbance and associated changes in light and nutrient supply probably control biomass distribution along this short but representative elevational gradient. Our findings also showed that intact Atlantic forest sites stored substantial amounts of carbon aboveground. The live tree AGB of the stands was found to be lower than Central Amazonian forests, but within the range of Neotropical forests, in particular when compared to Central American forests. Our comparative data suggests that differences in live tree AGB among Neotropical forests are probably related to the heterogeneous distribution of large and medium-sized diameter trees within forests and how the live biomass is partitioned among those size classes, in accordance with general trends found by previous studies. In addition, the elevational variation in live AGB stocks suggests a large spatial variability over coastal Atlantic forests in Brazil, clearly indicating that it is important to consider regional differences in biomass stocks for evaluating the role of this threatened tropical biome in the global carbon cycle.

© 2010 Elsevier B.V. All rights reserved.

1. Introduction

Biomass is a key property of ecosystems (Chapin et al., 2002; Fahey and Knapp, 2007) that results from the mass balance between rates of gain due to productivity and losses due respiration and mortality (Keeling and Phillips, 2007a). In tropical forests, the live

aboveground biomass (AGB) pool plays an important role in the global carbon cycle, accounting for a significant fraction of the total carbon pool and nutrient stocks (Brown and Lugo, 1984; Dixon et al., 1994; Brown et al., 1995; Phillips et al., 1998). AGB estimates are still an important source of uncertainty in the carbon balance from the tropical regions in part because of a scarcity of reliable estimates of live AGB and its variation across landscapes and forest types (Houghton, 2007; Saatchi et al., 2007; Houghton et al., 2009). Therefore, improved local and regional AGB estimates provide essential data that enable the extrapolation of biomass stocks to ecosystems or biome-wide carbon cycle modeling, as well as

* Corresponding author at: INSTAAR, University of Colorado, Campus Box 450, Boulder, CO 80309, USA. Tel.: +1 303 492 7926; fax: +1 303 492 6388.

E-mail addresses: lu.falves@gmail.com, luciana.alves@colorado.edu (L.F. Alves).

to allow reliable emission estimates from land use change scenarios (Urquiza-Haas et al., 2007; Houghton et al., 2009; Loarie et al., 2009).

Tropical South America represents the greatest concentration of tropical rain forest in the world, extending over the Amazonian region (885 million hectares), and extra-Amazonian areas in the Pacific coast of Colombia and Ecuador, and the Atlantic coast and Iguaçú and Paraná River valleys of Brazil (85 million hectares) (FAO, 2000). The Atlantic Forest Domain (Morellato and Haddad, 2000; Oliveira-Filho and Fontes, 2000), considered as one of the global centers of vascular plant diversity and endemism (Mutke and Barthlott, 2005; Guedes-Bruni et al., 2009; Murray-Smith et al., 2009), and one of the most threatened tropical forest regions in the world (Myers et al., 2000; Laurance, 2009), still covers about 14 million hectares (Galindo-Leal and Camara, 2003), or 16.5% of the total extra-Amazonian tropical rain forest in South America. Despite its extent, forest carbon pools and fluxes of the Atlantic Forest have seldom been studied, and standardized estimates of aboveground stocks of live and dead biomass are rarely available. The only comparable studies published to date are those of Tiepolo et al. (2002) and Rolim et al. (2005) that reported aboveground carbon stocks (Tiepolo et al., 2002) and changes (Rolim et al., 2005) for two Atlantic Forest sites.

Live aboveground biomass stocks vary widely among Neotropical forests due to regional differences in stem size distribution, soil fertility and topography, as well as disturbance (Clark and Clark, 2000; DeWalt and Chave, 2004; Vieira et al., 2004; Rolim et al., 2005; Sarmiento et al., 2005; Castilho et al., 2006; Malhi et al., 2006; Muller-Landau et al., 2006; Urquiza-Haas et al., 2007). Differences in live aboveground biomass among Neotropical forests may also be related to local canopy height variation as well as average wood density and forest composition (Baker et al., 2004; Chave et al., 2005; Vieira et al., 2008; Nogueira et al., 2008). Understanding the role of environmental variables that control the distribution and abundance of biomass in tropical lowland forests has been the subject of considerable research (Clark and Clark, 2000; DeWalt and Chave, 2004; Vieira et al., 2004; Baker et al., 2004). Nonetheless, the effect of short (<2000 m elevational range), steep elevational gradients on tropical forest structure and carbon dynamics is not well known (Lieberman et al., 1996; Bruijnzeel and Veneklaas, 1998; Waide et al., 1998; Takyu et al., 2002, 2003; Leuschner et al., 2007; Zach et al., 2010).

Depending on latitude and regional climate, the elevational rate of change in vegetation structure with elevation varies greatly, resulting in short (<2000 m) or long (>2000 m) gradients (Grubb, 1977; Bruijnzeel and Veneklaas, 1998; Bruijnzeel, 2002). In short elevational gradients vegetation zonation can be compressed ("Massenerhebung" effect; Richards, 1996) allowing the appearance of cloud montane forests in lower elevations (Grubb, 1977). Short elevational gradients in tropical regions may display stronger edaphic discontinuities over short distances due to steep topography and microclimate variation than long elevational gradients (Ashton, 2003; Silver et al., 1999; Daws et al., 2002; Takyu et al., 2003). Air temperature, solar radiation and atmospheric pressure variability are primarily a function of elevation (Korner, 2007), but other environmental conditions, including light availability (photosynthetically active radiation), soil moisture and temperature, and nutrients are expected to co-vary along short elevational gradients in the tropics due to steep topography (Proctor et al., 1983; Silver et al., 1999; Daws et al., 2002; Takyu et al., 2003; Aiba et al., 2004); biotic factors such as rates of microbial decomposition are likely to reflect these features (Lieberman et al., 1996; Abril and Bucher, 2008). Therefore, differences in forest structure and biomass stocks may be found among sites over short distances. The general trends for long tropical elevational gradients are a decline in forest stature and live aboveground biomass while stem density

increases with elevation (Grubb, 1977; Raich et al., 1997; Tanner et al., 1998; Waide et al., 1998; Aiba and Kitayama, 1999; Kitayama and Aiba, 2002; Moser et al., 2007). This pattern has been explained as a result of climatic constraints on photosynthesis and transpiration and nutrient uptake with increasing elevation (Bruijnzeel and Veneklaas, 1998; Kitayama and Aiba, 2002; Raich et al., 2006).

Our study is focused on a geologically and topographically complex region located along the *Serra do Mar* mountain range covered by a floristically diverse old-growth, tropical Atlantic moist forest (Oliveira-Filho and Fontes, 2000; Murray-Smith et al., 2009) in SE Brazil. Given the limited information about live aboveground biomass stocks for the Atlantic Forest, our goals are: (1) to quantify how biomass is spatially distributed along the elevational gradient; (2) to evaluate the spatial pattern of biomass distribution within the landscape in relation to environmental gradients including climate, soil moisture and chemical properties; and (3) to compare this estimate obtained for a large-scale network of permanent plots to those observed across Neotropical forests. To the best of our knowledge no prior studies have investigated the effect of elevational gradients on forest structure and live aboveground biomass in the Atlantic Forest. Therefore, quantifying the complex three-dimensional forest structure of this threatened tropical forest is the first step to understand aboveground biomass partitioning and carbon dynamics (Broadbent et al., 2008).

2. Materials and methods

2.1. Study site and sampling design

We assessed forest structure and live aboveground biomass (AGB) variation at four sites along an elevational gradient (0–1000 m asl) of tropical moist forest in São Paulo state, SE Brazil. The elevational gradient includes a network of 13 1-ha permanent plots established in 2005–2006 to study forest diversity and dynamics, and ecosystem functioning of the Brazilian Coastal Atlantic Forest (Joly et al., 2008). The plot network is located within the *Serra do Mar* State Park (PESM) (23°34'S and 45°02'W; 23°17'S and 45°11'W; 0–1200 m asl) that overlaps with other relevant area, the *Serra da Bocaina* National Park. Together, the region comprises more than 100,000 ha, one of the largest protected Atlantic Forest remnants in Brazil (Ribeiro et al., 2009). The predominant vegetation type is tropical moist evergreen forest (Holdridge, 1947) or lowland to lower montane rainforest, following Oliveira-Filho and Fontes (2000), with a tall canopy stratified into lower, canopy and emergent layers, and abundant epiphytes, ferns, bromeliads, and lianas (Morellato and Haddad, 2000).

The geological and topographic complexity of the *Serra do Mar* mountain range (Suguio and Martin, 1978) has resulted in extreme habitat and microclimate heterogeneity along the Atlantic coast of São Paulo and Rio de Janeiro states. The region was shaped by tectonic activity in the Tertiary and by sea-level changes at low elevations associated with glacial cycles in the Quaternary (Suguio and Martin, 1978; Souza et al., 2005; Pierre-Ledru et al., 2009). This complex landscape has likely played important roles in the current distribution of habitat heterogeneity and biota (Carnaval and Moritz, 2008; Fitzpatrick et al., 2009), and even possibly promoting gradients of soil fertility and water availability (nutrients, soils, hydrology, dynamics). Therefore, we selected four sites to sample the range of elevational conditions at local and regional scales within the north coastal Atlantic Forest in São Paulo (Table 1). Each site corresponded to distinct elevations, also representing four different forest types or physiognomies according to the Brazilian National Classification System for Vegetation (IBGE; Veloso et al., 1991): seasonally flooded coastal forest at sea level (also known as *restinga*, a vegetation mosaic growing

Table 1

Stand site and physical–chemical characterization of the surface soil layer (0–5 cm) sampled at four sites along the elevational gradient of tropical moist forest (Atlantic forest, Brazil). Mean values (\pm standard errors; $n = 32$). Adapted from Martins et al. (in review).

Site parameter	Forest type			
	<i>Restinga</i> (seasonally flooded forest)	Lowland	Submontane	Montane
Plot code	A	B, C, D, E	G, H, I, J	K, L, M, N
Plots (1 ha)	1	4	4	4
Elevation (m a.s.l.)	0–50	50–100	100–500	500–1200
Topography	Flat (0–10°)	Gentle (10–30°)	Steep (>30°)	Steep (>30°)
Soil type	Quartzipsamment	Inceptisols	Inceptisols	Inceptisols
Soil texture (%)	88.1% sandy 6.1% clay	60.4% sandy 31.5% clay	66.7% sandy 16.4% clay	57.4% sandy 20.3% clay
Soil pH ^a	3.4	3.6	3.6	3.5
CEC (mmol _c kg ⁻¹)	111.6	138.4	193.2	163.0
P (mg kg ⁻¹)	11.5	17.6	12.9	21.2
SB (mmol _c kg ⁻¹)	4.2	12.9	22.5	15.8

^a pH expressed in CaCl.

on poor sandy soil along the Brazilian coast (Joly et al., 1999; Scarano, 2002); lowland (100 m); submontane (400 m); and montane forest (1000 m) (Table 1). Each forest type has been previously distinguished by their underlying forest diversity and composition (Sanchez et al., 1999; Sanchez, 2001; Joly et al., unpublished data). Myrtaceae, Rubiaceae, Fabaceae, and Lauraceae are the richest families (Joly et al., unpublished data). Common canopy tree species with dbh > 30 cm include: *Hieronyma achorneoides*, *Virola bicuhyba*, *Eriotheca pentaphylla*, *Sloanea guianensis*, *Cryptocaria mandiocanna*, *Ecclinusa ramiflora*, *Licania hoehnei*, and *Chrysophyllum viride*. Lianas are particularly abundant in gaps at lowland forest sites (Alves et al., unpublished data).

The seasonally flooded coastal forest at sea level (herein *restinga*) has undergone some hydrologic disturbances due to the construction of a highway in the late 1960s (SMA-Secretaria do Meio and Ambiente, 1998). The steep topography and remote locations of the permanent plots >100 m have partially limited human impacts on the vegetation. However, recent signs of illegal palm heart harvest and hunting of small game have been observed. The lowland plots are located near (~1 km) areas of long-term settlement and slash and burn agriculture, but no signs or reports of land-use within the plot area have been detected, except the presence of a historical trail (SMA-Secretaria do Meio and Ambiente, 1998).

For lowland, submontane, and montane forest sites, we established four 1-ha plots (100 m × 100 m) with the aim to represent the forest heterogeneity (Table 1); the minimum distance among plots within each site was 50 m. One additional 1-ha plot was established at the *restinga* forest (Table 1) due to its limited representativeness within the Park limits. Because the topography is complex over short geographical distances at mid- and high-elevation (hilly and undulating terrain to steeply dissected slopes, including scars of landslides), all plots were demarcated and surveyed with an electronic theodolite (total station) every 10 m. All plots have the same area when projected to the horizontal plane. The most common slope classes ranges from flat (0–10°) to gentle (10–30°) at *restinga* and lowland forests plots, respectively, to steep (>30°) at submontane and montane (Table 1).

The elevational gradient consists of two parent material types. Crystalline basement with predominance of gneiss, migmatite and granite underlay the lowland, submontane and montane sites (IPT-Instituto de Pesquisas Tecnológicas, 2000), and sedimentary rocks lay beneath the *restinga* forest (IPT-Instituto de Pesquisas Tecnológicas, 2000). Soils at 100, 400 and 1000 m are predominantly *Inceptisols*, without significant difference in soil depth with elevation, still poor soils in terms of nutrients, but less sandy and relatively nutrient rich compared to soils in the *restinga* forest

(*Quartzipsamment*) (Martins et al., in review; Table 1). Moisture content, total nitrogen and carbon, and ammonium and nitrate soil concentrations increase with elevation while decomposition rates of organic matter and soil N₂O and CO₂ emissions to the atmosphere decrease with elevation (Sousa Neto, 2008).

Complex topography and the proximity to the ocean control the distribution of rainfall on the coast of São Paulo state (Silva-Dias et al., 1995). The region receives ca. 2500 mm of rainfall annually, and monthly average temperature range from 19.1 to 25.5 °C (Sentelhas et al., 1999). The climate is humid subtropical with hot summers (Cfa type in Köppen), typically with one month per year with <50 mm rainfall, and up to three months per year (June–August) with <100 mm rainfall (Sentelhas et al., 1999). Frequent cloud cover and drizzle brought by ocean winds reaches the submontane and montane sites (Silva-Dias et al., 1995); at higher altitudes, air and soil temperatures are lower, with a high incidence of low level clouds and fog formation that reduce annual irradiance (Sousa Neto, 2008).

2.2. Inventory protocol

In 2006 and 2007; we performed a standard forest census (following Clark, 2002; Phillips and Baker, 2001) for each 1-ha plot of the permanent network. We measured to the nearest 1 mm the diameter at 1.3 m height (dbh) or above any buttresses or stem irregularities of all live stems ≥ 4.8 cm, including trees, palms, and tree ferns. We marked all stems with numbered aluminum tags with plot code, and mapped them to the nearest 10 cm. We checked diameter records on a tree-by-tree basis; treatment of outliers and measurement problems followed standard procedures (Condit, 1998; Chave et al., 2003). We categorized stems by life form (trees, palms and tree ferns), and canopy position or crown illumination index (CII) (Clark and Clark, 1992). This index, when well-calibrated among observers, provides a rapid and simple method to estimate individual canopy light environment integrated over long periods for tropical trees (see Clark and Clark, 1992; Keeling and Phillips, 2007b for details), with strong correlations found between CII and canopy openness and light site factors (Clark and Clark, 1992; Davies et al., 1998; Keeling and Phillips, 2007b). For tree and palm stems, we estimated total height by applying fitted height–diameter allometric equations developed by Scaranello et al. (unpublished data) for each site along the elevational gradient. From the entire survey database, Scaranello et al. (unpublished data) randomly selected 431 trees and 142 palms stratified by dbh class (<10, 10–30, 30–50 and >50 cm) and by site to perform height measurements using a handheld laser range finder (Impulse-200LR, Laser Technology Inc., Englewood, Colorado) or a telescoping rod.

Table 2

Allometric equations used to estimate stem AGB dry biomass (Mg ha^{-1}) at four sites along the elevational gradient of tropical moist forest (Atlantic forest, Brazil). DBH: diameter at breast height, H : total height, ρ : wood density (g cm^{-3}).

Life form	Allometric equation	Source
Trees	$\exp(-2.977 + \ln(\rho \times \text{DBH}^2 \times H))$	Chave et al. (2005)
Palms	$\exp(((57.236 + 0.9285 \ln(\text{DBH}^2)) \times 105.001) / 10^3)$	Nascimento and Laurance (2002)
Tree ferns	$-4266348 / (1 - (2792284 \exp(0.313677 \times H)))$	Tiepolo et al. (2002)

Height was modeled as a function of diameter using a non-linear Weibull model for trees and a linear model for palms (see Appendix B; Appendix A). For tree ferns, total height was estimated visually by a single observer.

2.3. Allometric equations to estimate live aboveground biomass (AGB)

We used the census data (tree, palm, and tree fern stems ≥ 4.8 cm) from the permanent plots (2006–2007) to estimate the live aboveground biomass (AGB). For regional-scale comparisons of AGB estimates, an allometric equation that incorporates environmental, compositional, and forest structural traits that vary significantly at regional scales, is required (Brown, 1997; Baker et al., 2004). As there are no available allometric equations developed destructively for old-growth Atlantic forest sites encompassing a range of tree diameters suitable for this study (Vieira et al., 2008; but see Burger and Delitti, 2008 for a secondary-growth Atlantic forest site), we applied a pantropical allometric model developed by Chave et al. (2005) for tropical moist forests to estimate the AGB for live trees 4.8 cm dbh (Table 2). Chave's et al. (2005) allometric equations can be used to estimate forest biomass and carbon stocks across a wide range of tropical forest types (Gibbs et al., 2007; Asner et al., 2009) including the coastal Atlantic forest (see Vieira et al., 2008). The model in Chave et al. (2005), calibrated based on destructive data for stems 5–156 cm dbh ($n = 2410$), expresses AGB in kg as a function of diameter at breast height (dbh), total tree height, and average wood density. To estimate total tree height from dbh, we applied stand-specific allometric equations developed by Scaranello et al. (unpublished data), as described above. Because a complete list of tree species sampled across the permanent plots is not yet available, we compiled a list of 402 tree species with its respective abundance (stems ha^{-1}) from previous forest inventories carried out in the same region (Tabarelli, 1997; Sanchez, 2001; see Appendices B and C). We used these data to estimate a weighted average wood density (ρ_{weighted}) values for each elevation (*restinga*, lowland, submontane, and montane forests):

$$\rho_{\text{weighted}} = \sum_i \frac{(S_i \times \rho_i)}{N_{\text{Stems}}}$$

where S_i is the number of stems ha^{-1} of species i , ρ_i is the wood density value for the species i , and N_{Stems} is the total number of stems ha^{-1} sampled by site. We updated genera and species names listed in those inventories using the Tropicos database from the Missouri Botanical Garden (<http://www.tropicos.org/>). Additional corrections were made to conform families to the Angiosperm Phylogeny Group (APG II, 2003). Wood density values at genus and species level were obtained in Chave et al. (2006) and complemented with national data sources (Mainieri and Chimelo, 1989; Carvalho, 1994). For species lacking data on wood density, we used average values for genus, because a large proportion (ca. 74%) of species-level wood density variation for Neotropical forests can be explained at this taxonomical level (see Chave et al., 2006). We obtained wood density data at genus and species level for 65% and 26% of 402 *taxa* sampled in those previous inventories, respectively (Appendix B). Weighted average wood density values (ρ_{weighted}) calculated by elevation are shown in Appendix C. For

palms (≥ 4.8 cm dbh), we converted dbh data to AGB using the equation developed by Hughes (1997; *apud* Nascimento and Laurance, 2002) (Table 2). For tree ferns, we estimated the AGB by following the allometric equation provided in Tiepolo et al. (2002) based on destructive sampling (Table 2).

2.4. Statistical analysis

In order to evaluate forest structure and biomass variation along the elevational gradient, we calculated the following variables by plot: total stem density (≥ 4.8 cm and ≥ 10 cm dbh) and stem density by size class (< 10 , 10–30, 30–50, ≥ 50 cm dbh), and estimated total live stem biomass (AGB) and AGB by size class. We pooled stems and AGB into wide size classes to facilitate comparison with similar studies on biomass and forest structure in the Neotropical region (as in Vieira et al., 2004; Pyle et al., 2008). Each 1-ha permanent plot was considered a replicate within each forest type ($n = 4$), except for the *restinga* forest that has very limited representation in the region because of beachfront development. For this forest type, the 1-ha plot was split into four 50 \times 50 m (0.25 ha) sub-plots (the minimal sample size for tropical forest inventories; e.g., Chave et al., 2004, 2008) that although pseudo-replicated (*sensu* Hurlbert, 1984), allowed us to perform consistent analyses across the elevational gradient including this forest type. Previously, we checked that the contiguous 0.25 ha subplot estimate for the *restinga* forest was not biased by spatial autocorrelation (Legendre and Legendre, 1998) at that scale (data not shown). We represented sampling effort uncertainty for our field-based estimates of mean live AGB and stem density with 95% confidence intervals calculated using a non-parametric bootstrap analysis (Efron and Tibshirani, 1993); a similar approach was adopted by Chave et al. (2008), and Pyle et al. (2008). Bootstrap samples of 1-ha plots (and quarter-hectare sub-plots for the *restinga* forest) were drawn 1,000 times to generate estimates of 95% confidence intervals around mean live AGB and stem density using the bootstrap bias-corrected and accelerated (BCa) method (Efron, 1987; Efron and Tibshirani, 1993; all analyses performed in R. 2.10.1). This is an efficient and accurate method to generate bootstrap confidence intervals because it adjusts for both bias and skewness in the bootstrap distribution (Efron, 1987). We inferred whether there were significant differences among forest types by checking for non-overlapping confidence limits. We also performed a non-parametric analysis (Spearman's rank correlation) to assess if individual canopy light environment (CII) and size (dbh) were correlated within forest types across elevational sites. We contrasted differences in canopy height among forest types by plotting estimated height against dbh of all tree and palm stems ≥ 4.8 cm.

As stem density and local topography can vary widely among plots even within the same elevation (see Appendices D and E), we applied multiple-regression models with stepwise backward selection of variables to examine the combined effects of site elevation (average elevation in meters asl at 1-ha plot scale), local topography (elevational range in m asl, estimated as the difference between the minimum and maximum elevation values within 1-ha plot), and stand size structure (tree density by size class) on total stand live aboveground biomass variation ($n = 13$; the *restinga* plot not sub-divided for this analysis). To check the significance

Table 3
Stocks of live aboveground biomass (AGB) and stem density of trees, palms and tree ferns sampled along the elevational gradient of tropical moist forest (Atlantic forest, Brazil). Values are means and bootstrapped 95% confidence intervals (in parenthesis); $n = 4$ 1-ha plots replicate for each forest type, except for *restinga* forest ($n = 4$ 0.25-ha plots).

Forest type	Trees		Palms		Tree ferns		Total	
	Stems (ha ⁻¹)	Biomass (Mg ha ⁻¹)	Stems (ha ⁻¹)	Biomass (Mg ha ⁻¹)	Stems (ha ⁻¹)	Biomass (Mg ha ⁻¹)	Stems (ha ⁻¹)	Biomass (Mg ha ⁻¹)
Stems ≥ 4.8 cm								
<i>Restinga</i>	1459 (1254, 1768)	163.5 (142.1, 184.6)	167 (117, 201)	2.8 (1.8, 3.5)	0	0	1626 (1467, 1885)	166.3 (144.4, 187.0)
Lowland	1035 (1008, 1360)	204.8 (187.1, 220.3)	178 (140, 231)	3.9 (2.9, 4.7)	17 (7, 25)	0.2 (0.05, 0.24)	1230 (1170, 1298)	208.9 (192.6, 224.0)
Submontane	1488 (1328, 1644)	247.7 (231.1, 260.6)	227 (186, 284)	6.0 (4.6, 8.4)	11 (9, 15)	0.1 (0.09, 0.50)	1727 (1517, 1926)	253.8 (235.7, 269.6)
Montane	1230 (1108, 1317)	271.3 (241.3, 314.4)	423 (341, 506)	11.1 (9.0, 13.2)	71 (53, 84)	0.8 (0.43, 1.15)	1723 (1454, 1834)	283.2 (253.0, 325.2)
Stems ≥ 10 cm								
<i>Restinga</i>	763 (627, 876)	154.0 (129.8, 176.9)	12 (9, 14)	0.9 (0.3, 1.4)	0	0	775 (650, 890)	154.8 (129.9, 178.3)
Lowland	543 (522, 551)	198.4 (180.7, 211.6)	57 (36, 70)	2.4 (1.7, 3.1)	11 (3, 15)	0.1 (0.03, 0.18)	610 (587, 632)	200.9 (185.5, 216.4)
Submontane	721 (616, 824)	239.3 (223.0, 304.5)	92 (64, 142)	4.3 (3.0, 6.3)	5 (1, 7)	0.05 (0.01, 0.76)	818 (690, 965)	243.6 (226.1, 257.9)
Montane	589 (551, 642)	262.7 (233.6, 304.5)	215 (173, 246)	8.6 (6.3, 9.9)	28 (15, 47)	0.5 (0.12, 0.76)	831 (791, 846)	271.7 (243.0, 311.6)

of multicollinearity in our data (Graham, 2003; Gotelli and Ellison, 2004), we first performed a Pearson's product-moment correlation test with Bonferroni's correction for multiple comparisons (Dunnnett, 1955). This analysis was performed in SYSTAT version 9 (Wilkinson, 1999). We observed only one strong correlation ($r > 0.70$ and $P < 0.001$) between local topography and site elevation ($r_{\text{Pearson}} = 0.85$, $P < 0.001$). Thus, we eliminated site elevation as an exploratory variable in our model as this variable provided no additional explanatory effect beyond those variables already included in the model, and we then run the model with the other five remaining variables. The models were judged by comparison of root mean squared error (RMSE), coefficient of determination (R^2) and slope (b) for model-predicted AGB vs. independent variables. We set $P = 0.10$ for each variable as the probability to enter and to leave the model. We performed this analysis using JMP version 7.0.2 (SAS Institute, 2007).

2.5. Comparison with other neotropical forests

To compare our data on live AGB and tree density (≥ 10 cm dbh) with other studies in Neotropical forests, we synthesized results from selected published studies throughout Central and South America. We extracted data collected from studies conducted at old-growth tropical forests of the Neotropical region without pronounced seasonality (five or less months with average precipitation < 100 mm), spanning from lowland to upper montane moist and wet forests, and that reported data on AGB and stem density for trees with dbh ≥ 10 cm. Those criteria include most of the previously published studies on forest structure and live AGB of this region using standardized methods for permanent plots.

3. Results

3.1. Forest structure and live aboveground biomass (AGB) distribution

On average, we sampled 1576 stems ≥ 4.8 cm dbh per hectare (bootstrapped 95% CI: 1446, 1707; see Appendix C) distributed across different life forms: trees (83%), palms (16%), and tree ferns (1%). For stems ≥ 10 cm dbh, we sampled 759 stems ha⁻¹ (bootstrapped 95% CI: 693, 822). Trees were the dominant life form across all forest types, comprising 72–89% of stems and 96–98% of live AGB ≥ 4.8 cm; and 71–98% of stems and 97–99.5% of live AGB ≥ 10 cm dbh (Table 3). The contribution of palms was highest in the montane forest (24.4% and 25.8% of all stems ≥ 4.8 cm and ≥ 10 cm dbh, respectively), but accounted for less than 5% of the total live AGB (Table 3) because few palms ($n = 13$) had dbh > 30 cm across all plots. Tree ferns showed a minor contribution to the total number of stems as well as to the live AGB along the elevational gradient (Table 3).

We found a progressive increase in stem density and live AGB with elevation (Table 3). The number of stems and live AGB differed significantly among forest types: stem density and estimated AGB were higher in submontane and montane forests than in other forest types. Total stand AGB ranged from 166.3 Mg ha⁻¹ (bootstrapped 95% CI: 144.4, 187.0) in *restinga* forest to 283.2 Mg ha⁻¹ (bootstrapped 95% CI: 253.0, 325.2) in montane forest. Biomass for stems ≥ 10 cm dbh was also greater at higher elevations, exceeding 250 Mg ha⁻¹ at the two highest sites (Table 3).

The distribution of stem density and live AGB by diameter size class showed a contrasting pattern across the elevational gradient (Fig. 1). In general, the smaller size classes held most of the stems and a small fraction of the live AGB. However, the *restinga* forest had more small stems (< 30 cm) and a higher fraction of the total AGB stored in these size classes (61.6%) than any other forest type

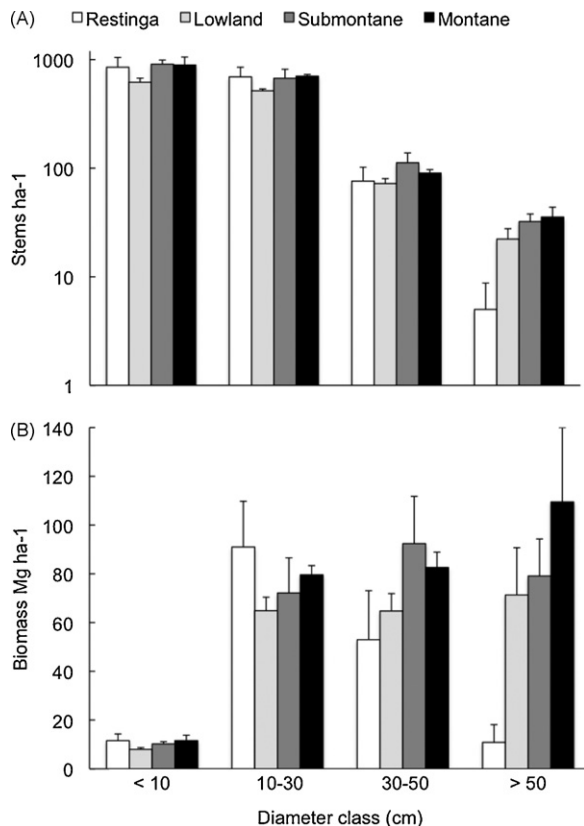


Fig. 1. Distribution of (a) number of stems (ha^{-1}) and (b) biomass (Mg ha^{-1}) by size class (dbh cm) on different forest types along the elevational gradient of tropical moist forest (Atlantic forest, Brazil). Values are means \pm 95% CI; $n = 4$. Note log scale used for the number of stems (ha^{-1}).

(Fig. 1). Large (30–50 cm) and very large (≥ 50 cm) stems were more abundant at submontane and montane forests, accounting for more than 68% of the total live AGB in these sites (Fig. 1).

The height–diameter relationship changed among forest types above 30 cm dbh with the *restinga* forest displaying a smaller canopy stature (17.7 m; 99th quantile) than other forest types (23–25 m; 99th quantile) (Fig. 2). For all forest types, the individual crown illumination index (CII) was positively and significantly correlated with diameter (dbh) ($r_{\text{Spearman}} = 0.51\text{--}0.59$; $P < 0.001$ for all correlations). Across all elevations, we found more stems (64–75%)

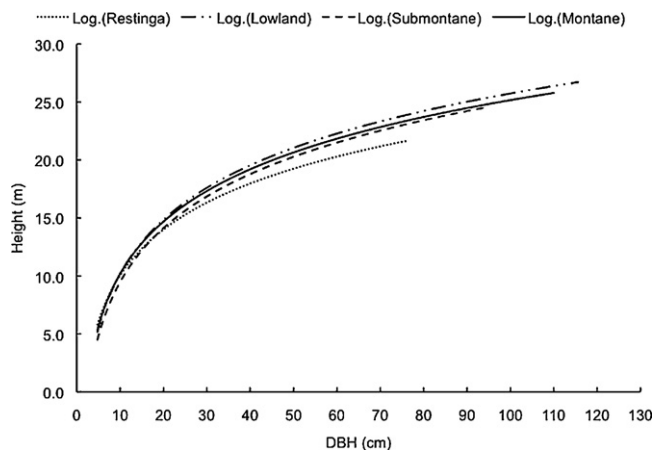


Fig. 2. Log-fitted allometric relationships between diameter and height of stems ≥ 4.8 cm dbh sampled along the elevational gradient of tropical moist forest (Atlantic forest, Brazil).

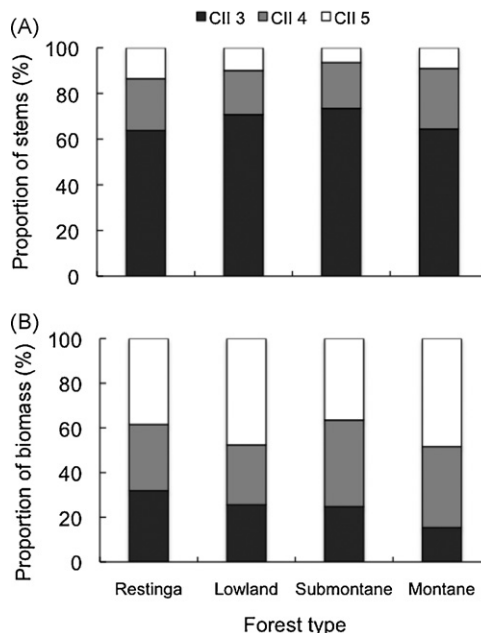


Fig. 3. Proportion of total stems ≥ 4.8 cm dbh and live biomass stored by crown illumination index class (a) and biomass (b) on different forest types along the elevational gradient of tropical moist forest (Atlantic forest, Brazil).

with limited crown illumination (CII class 3; Fig. 3a), but the largest proportion of the live AGB (68–85%) was stored in stems with highly illuminated crowns or crowns fully exposed to light (CII classes 4 and 5; Fig. 3b). The proportion of the biomass stored in stems with CII 4 and 5 increased with elevation, reaching 85% of the live biomass in the montane forest (Fig. 3b) or 239.6 Mg ha^{-1} .

3.2. Effects of forest structure, elevation and topography on biomass variation

We found no multifactor model where all factors were significant (Table 4) but a simple two-factor model explained 91% of the variance in total stand-level live AGB along the elevational gradient; the main factors were the abundance of large stems ≥ 50 cm dbh and the elevational range at plot scale. AGB variation of very large stems ≥ 50 cm dbh was also explained by the same factors, plus the negative effect of the abundance of stems 30–50 cm (Table 4). A multi-factor model taking account of site local topography and stem abundance explained 98% of the variance in AGB of stems 30–50 cm dbh. The model explaining 82% of the AGB variation of stems 10–30 cm dbh included only a positive abundance of stems. The abundance of stems < 10 cm dbh and a negative effect of the abundance of large stems (30–50 cm) explained 92% of the variability in AGB of stems < 10 cm along the elevational gradient (Table 4).

3.3. Comparison of Atlantic forest biomass and structure with other neotropical forest sites

Our estimated average of trees ≥ 10 cm dbh per hectare across the elevational gradient of Atlantic forest ($654 \text{ trees ha}^{-1}$; bootstrapped 95% CI: 602, 729) was higher than published studies for neotropical forests (Table 5; $502 \text{ trees ha}^{-1}$; bootstrapped 95% CI: 458, 557), but the estimated AGB obtained along the gradient (213.6 Mg ha^{-1} ; bootstrapped 95% CI: 188.6, 235.8) is within the range of values reported for other Neotropical forests (Table 5; 259.6 Mg ha^{-1} ; bootstrapped 95% CI: 230.3, 283.6). The live tree biomass of submontane and montane Atlantic forest types is comparable to the biomass of more seasonal forests of Central America

Table 4

Summary of multiple-regression models with stepwise backward selection of variables to examine the combined effects of local topography (elevational range), and stand size structure (tree density by size class) on total live aboveground biomass variation, and on live AGB variation of different stem size classes. RMSE: root mean square error.

Biomass component	Predictor variables ^a					F	RMSE	R ²	P
	Local topography		Stand size structure						
			Stems <10	Stems 10–30	Stems 30–50				
Total AGB	1.51	NS	NS	NS	2.29	52.69	14.52	0.91	<0.0001
AGB stems > 50	0.57	NS	NS	–0.53	2.75	50.92	9.09	0.94	<0.0001
AGB stems 30–50	0.42	NS	–0.03	0.68	NS	172.86	2.65	0.98	<0.0001
AGB stems 10–30	NS	NS	0.09	NS	NS	22.46	5.31	0.82	<0.001
AGB stems < 10	NS	0.01	NS	–0.03	NS	54.85	0.63	0.92	<0.0001

^a Values represent the standard coefficient (*b*) associated with each predictor variable that contributed significantly to the model at $P < 0.05$; $n = 13$.

Table 5

Live aboveground biomass (Mg ha^{-1} , trees ≥ 10 cm dbh) of several tropical moist and wet Neotropical forests. Sites arranged by biomass.

Site	MAP (mm y^{-1})	MAT ($^{\circ}\text{C}$)	Elevation (m asl)	Dry months (<100 mm)	Trees (ha^{-1})	Tree AGB (Mg ha^{-1})	Reference
Neotropical forests							
Lowland seasonally dry forest, Mexico	1650	24	6	4	–	109.0	Vargas et al. (2008)
Lowland wet forest, La Selva, Costa Rica	4000	26	30	0	367	148.7	Clark and Clark (2000)
Montane wet forest, Venezuela	3000	11	2820	–	–	157.0	Delaney et al. (1997)
Montane moist forest, Venezuela	2400	15	2400	–	–	173.0	Delaney et al. (1997)
Lowland moist forest, Venezuela	2500	26	270	–	–	179.0	Delaney et al. (1997)
Lowland moist forest, BCI, Panama	2600	27	140	4	377	179.1	DeWalt and Chave (2004)
Lowland wet forest, La Selva, Costa Rica	4000	26	30	0	471	203.2	DeWalt and Chave (2004)
Lowland forests, SW Amazonia (Bolivia, Peru)	–	–	<500	–	–	206.7	Baker et al. (2004)
Lowland forests, NW Amazonia (Peru, Ecuador)	–	–	<500	–	–	220.8	Baker et al. (2004)
Submontane semideciduous forest, La Chonta, Bolivia	1580	25	400–600	4	129	236.6	Broadbent et al. (2008) ^a
Lowland wet forest, Manaus, Brazil	2650	26	50–100	3	654	240.2	DeWalt and Chave (2004)
Lowland moist forest, Rio Branco, Brazil	1940	24	214	4	467	244.1	Vieira et al. (2004)
Lowland moist forest, BCI, Panama	2600	27	140	4	461	260.2	Chave et al. (2003) ^b
Lowland forests, Central & Eastern Amazonia (Brazil)	–	–	<500	–	–	277.5	Baker et al. (2004)
Lowland moist forest, Santarem, Brazil	1909	25	175	5	460	281.2	Vieira et al. (2004)
Lowland semideciduous forest, Roraima, Brazil	2083	25	100	–	364	292.1	Nascimento et al. (2007)
Lowland moist forest, Santarem, Brazil	1920	25	175	5	498	294.8	Rice et al. (2004)
Lowland moist forest, Santarem, Brazil	1909	25	175	5	441	298.0	Pyle et al. (2008)
Lowland moist forest, Rondonia, Brazil	2300	25	61–310	–	450	306.8	Cummings et al., 2002
Lowland wet forest, Manaus, Brazil	2650	26	50–100	3	518	307.6	Castilho et al. (2006) ^b
Lowland wet forest, Nouragues, French Guiana	2757	26	50	2	534	317.0	Chave et al. (2001)
Lowland wet forest, Manaus, Brazil	2650	26	50–100	3	623	325.5	Nascimento and Laurance (2002)
Lowland moist Cocha Cashu, Peru	2165	26	300–400	3	666	332.8	DeWalt and Chave (2004)
Lowland wet forest, Manaus, Brazil	2650	26	50–100	3	621	334.0	Pyle et al. (2008)
Lowland wet forest, Manaus, Brazil	2650	26	50–100	3	626	360.2	Vieira et al. (2004)
Atlantic Forest, Brazil							
Lowland semideciduous forest, Linhares, Brazil	1200	22	28–65	5	–	334.5	Rolim et al. (2005)
Seasonally flooded forest (<i>Restinga</i>), Ubatuba, Brazil	2640	24	10	3	763	154.0	This study
Lowland moist forest, Ubatuba, Brazil	2640	24	100	3	543	198.4	This study
Submontane moist forest, Ubatuba, Brazil	2640	24	400	3	721	239.3	This study
Montane moist forest, Ubatuba, Brazil	2640	24	1000	3	589	262.7	This study

^a Minimum of 20 cm dbh.

^b Include palms.

and Western Amazonia, lowlands of Peru, Ecuador, and Colombia ($250\text{--}300 \text{ Mg ha}^{-1}$; see Malhi et al., 2006; Saatchi et al., 2007), but lower than Central Amazonian and Guyana forests (Table 5). The amount of live biomass stored in trees of *restinga* and lowland forest types at our study sites fall in the low end, similar to transitional and seasonal forests of the southern and northwestern edges of the Amazon basin ($100\text{--}200 \text{ Mg ha}^{-1}$; Saatchi et al., 2007).

4. Discussion

4.1. Forest structure and live aboveground biomass (AGB) distribution

Despite has been shown that the aboveground biomass declines with increasing elevation (Raich et al., 1997; Waide et al., 1998; Aiba and Kitayama, 1999; Kitayama and Aiba, 2002; Moser et al.,

2007; Leuschner et al., 2007) we found an opposite pattern for this short elevational gradient of tropical Atlantic moist forest in Brazil. In the cited studies, soil supply of nutrients became progressively more limiting relative to plant demands at higher, cooler sites thereby limiting forest productivity and biomass accumulation (Raich et al., 1997, 2006; Kitayama and Aiba, 2002). In general decreasing availability of nutrients, especially nitrogen, has been suggested to limit tree height and biomass stocks with increasing elevation (Grubb, 1977; but see Tanner et al., 1998). However, the elevational gradient that we investigated does not follow this classical pattern of nutrient-availability (see Martins et al., in review), providing a notable exception to the pattern of tropical elevational gradients as forest biomass and abundance of large trees increased with elevation.

We identified relations between local topography and forest structure in our study sites explaining a large part of the variation in

biomass distribution along the elevational gradient. We note that the maximum elevation of our short gradient is below or exactly on the lower limit of lower montane forests in the tropics, typically at about 1000–1500 m a.s.l. (Grubb, 1977; Bruijnzeel and Veneklaas, 1998) and a major shift in climate might not be expected (but see Bruijnzeel, 2002). At least three non-mutually exclusive hypotheses for positive increase in aboveground biomass stocks with elevation can be raised here: (1) soil texture and drainage; (2) disturbance regimes; (3) local topographic variation and nutrient supply.

4.2. Soil texture and drainage

At the lower end of the elevational gradient, the poorly drained and extremely poor soils under *restinga* forest are primary factors inhibiting plant growth (Palm et al., 2007), ultimately limiting higher biomass accumulation in this forest type. Canopy variation among *restinga* and other forest types also contributed to explain differences in live AGB (Fig. 3). Frequent summer flooding and lower fertility are stressors that probably limit the total biomass and carbon stocks in *restinga*. Thus, the major differences between the *restinga* and other forest types seem to be driven by differences in soil texture, drainage, and fertility (Table 1; Martins et al., in review).

4.3. Disturbance regimes

Tropical forests are composed by mosaics of stands differing in age and species composition (Whitmore, 1984) and its forest structure is sensitive to canopy disturbance regime and local conditions. Past human disturbance is also an important factor affecting forest structure variation and biomass accumulation among tropical forests (Hughes et al., 1999; Marín-Spiotta et al., 2007; Urquiza-Haas et al., 2007; Clark et al., 1995; Clark, 2007). In the present study, past forest use by local populations in the lowlands may explain part of the heterogeneity in total live AGB among sites. Lowland and *restinga* forests are located closer to the Park's edges, and are more likely to have experienced selective logging, hunting and other land uses. According to Negrelle (2002) the lowlands and coastal plain forests have suffered most from anthropogenic disturbances along the Brazilian coast due to ease of access and the high real-estate value of coastal properties. The lower biomass and higher density of small stems (<30 cm dbh) in the lowland and *restinga* forests suggest that the structure at lower elevations (<100 m) of the Atlantic forest may reflect differences in past human disturbance and recovery processes. At high elevations access has been constrained by the steep topography.

High rates of gap formation (natural or anthropogenic) may accelerate the establishment of many small individuals as a response to improved light and competition conditions (Hubbell et al., 1999; Rüger et al., 2009). Recruitment into small sapling size classes may be favored by more open forest canopy conditions at the *restinga* forest and by the high rates of gap formation in the lowlands. The lowland forest supported more lianas with higher biomass than any other forest type (Alves et al., unpublished data). This observation suggests that lowland plots may be still recovering for past disturbance, as high light availability provided by old gaps is one of the strongest drivers of liana dominance (Schnitzer, 2005).

4.4. Local topographic variation and nutrient supply

Recovery from past disturbance is unlikely to be the only driver for our observations of live AGB variation among Atlantic forest types. Differences in biomass accumulation rates and productivity among lower and higher elevations may also contribute to the observed pattern. Key factors for understanding the elevational

change in live AGB in the Brazilian Atlantic forest are a substantial increase in the contribution of very large stems to the total live AGB, and the importance of local topographic variation (Table 4). In some sense, it seems that local topography (plot slope) controls the abundance of large trees so steeper slopes support more large trees with higher biomass than flat and gentle areas. This fact may be related to the existence of a fine-scale topo-edaphic gradient within high elevation forest sites, as noted by Paoli et al. (2008) in South East Asian forests.

Among the factors controlling the distribution of large size trees in tropical forests, vertical and horizontal gradients in light availability along the canopy mediated by local topography and stand-level disturbance are likely to have a large effect in the Atlantic forest. Along elevational gradients of tropical forests, different sun trajectories across the day and the year create contrasting types of light microhabitats, also exerting influence on several other microclimatic variables, such as soil and air temperature and ground evaporation (Korner, 2007). On steep slopes canopy height are expected to be more variable and the vertical distribution of light more asymmetric than in flat areas; steep topography may also promote the increase of sunlight penetration into lower forest levels. High elevation sites probably are exposed to more sunlight for longer periods of time than low elevation sites. Therefore, the density-topography variation of the larger size classes of stems, notably trees, may be a consequence of favoring conditions promoting growth and fast recruitment into larger size classes on steeper terrains.

In a model simulation, Robert (2003) showed that on steep slopes, the high incidence of tree falls mainly affected the survival of trees 20–30 cm diameter with asymmetrical crowns, leading to a regulation of the spatial structure of trunks as well as crowns. Trees with more symmetric and stable crowns would display higher growth rates on steep slopes as a consequence of better access of canopy trees to space and light resources (Robert, 2003). Our observations agree with this model. Trees with more exposed crowns (CII 4 and 5) hold most of the live biomass and shade a large number of stems but a small part of the forest biomass in submontane and montane forests, the sites holding the highest biomass stocks and topographic variation.

A positive interaction between soil moisture and nutrient supply could also be driving the biomass accumulation process in high elevation forest sites, as local topography may be an important factor controlling nutrient distribution and soil drainage (Silver et al., 1994; Scatena and Lugo, 1995; Daws et al., 2002; Luizão et al., 2004; Castilho et al., 2006). Soil P and exchangeable bases were positively and significantly related to the abundance of large trees in a lowland forest in SW Borneo (Paoli et al., 2008). While all of the soils along the elevational gradient are strongly dystrophic, with lower pH, higher aluminum concentration and lower base saturation as compared to dystrophic Amazon soils, Martins et al. (in review) also observed greater nutrient availability in submontane and montane sites. Therefore, it is possible that the relatively higher soil fertility of submontane and montane forest sites contributed to live AGB variation along this gradient.

4.5. Comparison of Atlantic forest biomass and structure with other neotropical forests

Palms and tree ferns are structurally important elements of the Brazilian Atlantic forest (Henderson et al., 1995; Negrelle, 2002), and variation among different life forms in abundance and richness is a useful tool to characterize different forest formations and successional stages among Neotropical forests (Gentry, 1988; Negrelle, 2002; Schmitt and Windisch, 2005, 2007). Our study showed that palms and tree ferns tend to attain the maximum density in the montane forest, changing the forest structure in terms of life form

distribution. In particular, *Euterpe edulis* Mart., one of the most abundant species along the coastal Atlantic forest of Brazil (Reis et al., 2000; Scudeller et al., 2001; Martini et al., 2007; Fantini and Guries, 2007) can represent as much as 25% of the stems ≥ 4.8 cm dbh per hectare in our montane Atlantic forest stand. Those results are in agreement with others that have shown the effects of topographic gradients controlling palm species distribution in tropical lowland and montane forests (Kahn and Castro, 1985; Clark et al., 1995; Frangi and Lugo, 1998; Svenning, 1999; Vormisto et al., 2004; Svenning et al., 2009).

Despite their abundance in terms of stem number, palms and tree ferns have a relatively low contribution to live AGB stocks (<5%) in the Atlantic forest, similar to other Neotropical forests (Scatena et al., 1993; Sarmiento et al., 2005; but see Frangi and Lugo, 1985, 1998 for a flood plain palm forest). For instance, in Central Amazonia, palms represent less than 1% of the total biomass (Castilho et al., 2006), and in primary premontane tropical moist forests in Colombia, palms can reach up to 5% of total AGB (Sierra et al., 2007); a similar contribution was found by Clark and Clark (2000) for palms in Costa Rican tropical wet forests (5–7%). Thus, even excluding palms and tree ferns, tree biomass increases with elevation, attaining the maximum value in the montane forest. This pattern is likely the result of the small maximum diameter and the low carbon content of palms and tree ferns. Morphological and physiological constraints on height and diameter increment for those life forms are well known (Niklas, 1993), limiting its maximum size attained and, consequently, their carbon accumulation potential.

The mean total AGB of the stands studied was found to be lower than Central Amazonian forests, but within the range of Neotropical forests, in particular when compared to Central American forests, such as Barro Colorado Island (Panama), and La Selva (Costa Rica) (Table 5). Our data suggest that the Brazilian Atlantic Forest is different from the Brazilian Amazon Forest in terms canopy height (18–25 m), height–diameter relationships, and tree density. In general, the Brazilian Atlantic forest had smaller canopy stature than forests in Central, Eastern and Southern Amazon (Asner et al., 2002; Nogueira et al., 2008). For very large trees (>100 cm dbh), this difference can reach 75% when compared with trees of central Amazon (Scaranello et al., unpublished data). Thus, the application of inappropriate allometric equations can overestimate the live biomass of Atlantic forest stands, as discussed by Vieira et al. (2008). For example, the higher biomass values found by Rolim et al. (2005) for a lowland Atlantic forest in SE Brazil might reflect structural differences between sites, or the application of an allometric equation developed by Chave et al. (2001) for a French Guiana forest with taller and higher wood density trees than the coastal Atlantic forest. Considering trees from the lowland Atlantic forest with 10, 30, 50 cm dbh and applying Chave et al. (2005) and Chave et al. (2001) models, the estimated live AGB was: 31.1, 508.9 and 1783.3 kg for the Chave et al. (2005) pan-tropical equation, and 38.8, 633.0, 2313.6 kg for the allometric equation developed by Chave et al. (2001) for a French Guiana forest. Those values represent an increase of 24–30% in the estimated AGB.

Even taking into account differences in tree height and wood density, variation in forest structure seems to be one of the major drivers affecting the live biomass estimates in tropical forests (Sarmiento et al., 2005). We provided a comparison of tree stem and biomass distribution by major dbh classes among Neotropical sites with available data (Fig. 4). Tree stem density (≥ 10 cm dbh) in the Atlantic forest is higher than *Terra Firme* forests in Amazon and Central America (Table 5), but the proportion of the live biomass stored in stems ≥ 50 cm dbh (32–40%, except for *restinga* forest) is below the threshold (>40%) found for Amazon forests with relatively long dry season (Vieira et al., 2004). Our comparative data suggest that differences in live tree biomass among Neotropical forests are probably related to the heterogeneous distribution of large (≥ 50 cm

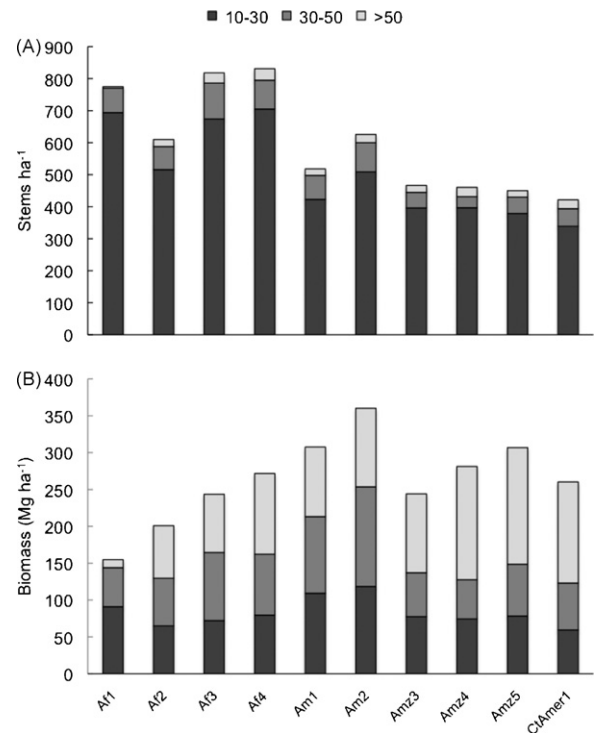


Fig. 4. Distribution of (a) number of stems (ha^{-1}) and (b) biomass (Mg ha^{-1}) by size class (dbh cm) for Atlantic selected Neotropical forests. Atlantic forest (this study): Af1 (*restinga*), Af2 (lowland), Af3 (submontane), Af4 (montane). Amazonia: Am1, Manaus (Castilho et al., 2006); Am2, Manaus (Vieira et al., 2004); Am3, Santarém (Vieira et al., 2004); Am4, Rio Branco (Vieira et al., 2004); Am5, Rondônia (Cummings et al., 2002). Central America: CtAmer1, Panamá (Chave et al., 2003).

and medium-sized (≥ 30 –50 cm) diameter trees within forests and the partitioning of live biomass among those size classes, in accordance with general trends found by previous studies (Brown and Lugo, 1992; Delaney et al., 1997; Clark and Clark, 2000; Vieira et al., 2004; Chambers et al., 2007; Pyle et al., 2008).

4.6. Uncertainties in sampling biomass in the Brazilian Atlantic forest

Wood density and total tree height are important predictive parameters to improve estimates of tropical forest biomass stocks because these traits vary among species, forest types and age, and soil fertility (Muller-Landau, 2004; Chave et al., 2006; ter Steege et al., 2006; Swenson and Enquist, 2007; Nogueira et al., 2008). While development of destructive site-specific allometric equations for the Atlantic forest would reduce uncertainties in regional estimates of biomass stocks, the incorporation of average wood density and tree height estimates in the pantropical allometric equation developed by Chave et al. (2005) for tropical moist forest has been shown to improve AGB estimates for tropical forests in general (Baker et al., 2004; Gibbs et al., 2007; Nogueira et al., 2007, 2008) and particularly for the coastal Atlantic forest (Vieira et al., 2008). Thus, uncertainties caused by regional floristic and canopy height differences among sites were minimized in our study by including average wood density values and an estimate of stem height in the pantropical allometric equation.

While our sample size by forest type was relatively small, our overall estimate of sampling error (95% confidence interval) for live AGB stocks (≥ 4.8 cm dbh) with a sampling effort of four 1-ha plots per forest type is less than 20% (8%, 7%, and 11% for lowland, submontane, and montane forests, respectively), providing a reasonable precision (Keller et al., 2001). The spatial distribution of

live AGB within the Atlantic forest types studied was relatively homogenous, despite the observed topographic heterogeneity. If 10%, sampling uncertainty is desired, we estimate that four plots should be added to the montane Atlantic forest type.

5. Conclusion

We provide the first extensive, landscape-scale estimate available for live AGB in the Brazilian Atlantic forest by evaluating forest structure variation along an elevational gradient. The high capacity of intact Atlantic forest sites for carbon storage aboveground in live biomass stocks for the Atlantic forest is within the range of other Neotropical forests, but is lower than central Amazonian forests. Large and very large trees comprised the most important and most variable live biomass pool, similar to other Neotropical forests; topography and associated changes in light distribution imposed strong controls on biomass distribution along this short but representative elevational gradient of coastal Atlantic forest. In addition, the elevational variation in live AGB stocks suggests a large spatial variability over coastal Atlantic forests in SE Brazil, clearly indicating that it is important to consider regional differences in biomass stocks for evaluating the role of this threatened tropical biome in the global carbon cycle.

Ground-based measurement is one of the most important means to understand and evaluate forest biomass and structure (Clark and Clark, 2000; Gibbs et al., 2007). Forest inventory data are required to enable spatial mapping of estimated forest biomass over a range of scales (Gibbs et al., 2007; Houghton et al., 2009). Our study is the first one to provide relevant information on AGB and forest structure along an elevational gradient of representative Atlantic forest types. The results of our study should improve total AGB estimates for the entire biome when combined with other field and remotely sensed data sets. Future estimates of total AGB for this biome will require more extensive spatial sampling and the addition of important components of forest biomass including coarse wood debris (necromass) and litterfall stocks (Clark et al., 2001; Keller et al., 2004; Rice et al., 2004; Sierra et al., 2007; Palace et al., 2008).

Understanding Atlantic forest structure variation and live aboveground biomass distribution patterns associated with elevational gradients is important if one considers that most of the remnants of this hotspot are located in areas of difficult access, such as steep hills and montane areas (SOS Mata Atlântica and INPE, 2009; Ribeiro et al., 2009). In the coming decades, long-term monitoring of permanent forest plots will be crucial to quantify changes in carbon stocks of the Atlantic forest, to evaluate forest growth response to climate and land use change, and to be a source of quality reference data for international mechanisms to reduce emissions from deforestation and forest degradation (i.e., REDD; Gibbs et al., 2007). Our data also corroborate that habitat protection of a network of state and national parks as well as conservation planning and sustainable management of forest remnants in private lands of the Atlantic Forest should be of high priority because of its importance as carbon stocks in this region.

Acknowledgements

This research was supported by the State of São Paulo Research Foundation (FAPESP) as part of the Thematic Project Functional Gradient (FAPESP 03/12595-7 to C. A. Joly and L. A. Martinelli), within the BIOTA/FAPESP Program—The Biodiversity Virtual Institute (<http://www.biota.org.br>). COTEC/IF 41.065/2005 and IBAMA/CGEN 093/2005 permit. F.A.M. Santos was supported by a grant from the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq, Grant No. 304937/2007-0). We gratefully

acknowledge the field assistance of Edmar Manzi, Osvaldo Santos, Salvador Santos, Yvonne Bakker, and several graduate students. We are in debt to the Instituto Florestal de São Paulo (Picinguaba and Santa Virginia research stations) staff for their logistic support during the fieldwork. The authors thank Dr. Michael Keller for his valuable comments on the manuscript and for the English review. We also thank three anonymous reviewers for their helpful comments on a previous version of the manuscript.

Appendices (A–E). Supplementary data

Supplementary data associated with this article can be found, in the online version, at [doi:10.1016/j.foreco.2010.05.023](https://doi.org/10.1016/j.foreco.2010.05.023).

References

- Abril, A.B., Bucher, E.H., 2008. Variation in soil biological characteristics on an elevational gradient in the montane forest of North-west Argentina. *J. Trop. Ecol.* 24, 457–461.
- Aiba, S., Kitayama, K., 1999. Structure, composition and species diversity in an altitude-substrate matrix of rain forest tree communities on Mount Kinabalu, Borneo. *Plant Ecol.* 140, 139–157.
- Aiba, S., Kitayama, K., Takyu, M., 2004. Habitat associations with topography and canopy structure of tree species in a tropical montane forest on Mount Kinabalu, Borneo. *Plant Ecol.* 174, 147–161.
- APG II, 2003. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG II. *Bot. J. Linn. Soc.* 141, 399–436.
- Ashton, P.S., 2003. Floristic zonation of tree communities on wet tropical mountains revisited. *Perspect. Plant Ecol.* 6/1 (2), 87–104.
- Asner, G.P., Hughes, R.F., Varga, T.A., Knapp, D.E., Kennedy-Bowdoin, T., 2009. Environmental and biotic controls over aboveground biomass throughout a tropical rain forest. *Ecosystems* 12, 261–278.
- Asner, G.P., Palace, M., Keller, M., Pereira Jr., R., Silva, J.N.M., Zweede, J.C., 2002. Estimating canopy structure in an Amazon forest from laser range finder and IKONOS satellite observations. *Biotropica* 34, 483–492.
- Baker, T.R., Phillips, O.L., Malhi, Y., Almeida, S., Arroyo, L., Di Fiore, A., Erwin, T., Killeen, T.J., Laurance, S.G., Laurance, W.F., Lewis, S.L., Lloyd, J., Monteagudo, A., Neill, D.A., Patino, S., Pitman, N.C.A., Silva, M., Vasquez-Martinez, R., 2004. Variation in wood density determines spatial patterns in Amazonian forest biomass. *Glob. Change Biol.* 10, 545–562.
- Broadbent, E., Asner, G.P., Pena-Claros, M., Palace, M., Soriano, M., 2008. Spatial partitioning of biomass and diversity in a lowland Bolivian forest: linking field and remote sensing measurements. *Forest Ecol. Manag.* 255, 2602–2616.
- Brown, I.F., Martinelli, L.A., Thomas, W.W., Moreira, M.Z., Ferreira, C.A., Victoria, R.A., 1995. Uncertainty in the biomass of Amazonian forests: an example from Rondonia, Brazil. *Forest Ecol. Manag.* 75, 175–189.
- Brown, S., 1997. Estimating biomass and biomass change of tropical forests: a primer. *FAO Forestry Paper* 134. FAO, Rome.
- Brown, S., Lugo, A.E., 1984. Biomass of tropical forests: a new estimate based on forest volumes. *Science* 223, 1290–1293.
- Brown, S., Lugo, A.E., 1992. Aboveground biomass estimates for tropical moist forests of the Brazilian Amazon. *Interciência* 17, 8–18.
- Brujinzeel, L.A., Veneklaas, E.J., 1998. Climatic conditions and tropical Montane forest productivity: the fog has not lifted yet. *Ecology* 79, 3–9.
- Brujinzeel, L.A., 2002. Hydrology of tropical Montane cloud forests: a reassessment. In: *Proceedings of the Second International Colloquium on Hydrology and Water Management in the Humid Tropics*. Technical Documents in Hydrology No. 52. UNESCO, Paris, pp. 353–383.
- Burger, D.M., Delitti, W.B.C., 2008. Allometric models for estimating the phytomass of a secondary Atlantic Forest area of southeastern Brazil. *Biota Neotropica* 8, <http://www.biotaneotropica.org.br/v8n4/pt/abstract?article=bn03308042008>.
- Burnham, K.P., Anderson, D.R., 2002. *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*. Springer Science, New York, NY.
- Carnaval, A.C., Moritz, C., 2008. Historical climate modelling predicts patterns of current biodiversity in the Brazilian Atlantic forest. *J. Biogeogr.* 35, 1187–1201.
- Carvalho, P.E.R., 1994. *Espécies florestais brasileiras: recomendações silviculturais, potencialidades e uso da madeira*. EMBRAPA, Brasília.
- Castilho, C.V., Magnusson, W.E., Araújo, R.N.O., Luizão, R.C.C., Luizão, F.J., Lima, A.P., Higuchi, N., 2006. Variation in aboveground tree live biomass in a central Amazonian Forest: effect of soil and topography. *Forest Ecol. Manag.* 234, 85–96.
- Chambers, J.Q., Asner, G.P., Morton, D.C., Anderson, L.O., Saatchi, S.S., Espírito-Santo, F.D.B., Palace, M., Souza Jr., C., 2007. Regional ecosystem structure and function: ecological insights from remote sensing of tropical forests. *Trends Ecol. Evol.* 22, 414–423.
- Chapin III, F.S., Matson, P.A., Mooney, H.A., 2002. *Principles of Terrestrial Ecosystem Ecology*. Springer, New York.
- Chave, J., Andalo, C., Brown, S., Cairns, M.A., Chambers, J.C., Eamus, D., Filster, H., Fromard, F., Higuchi, N., Kira, T., Lescur, J.P., Nelson, B.W., Ogawa, H., Puig, H., Riéra, B., Yamakura, T., 2005. Tree allometry and improved estimation of carbon stocks and balance in tropical forests. *Oecologia* 145, 87–99.

- Chave, J., Condit, R., Aguilar, S., Hernandez, A., Lao, S., Perez, R., 2004. Error propagation and scaling for tropical forest biomass estimates. *Philos. Trans. R. Soc. Lond. B, Biol. Sci.* 359, 409–420.
- Chave, J., Condit, R., Lao, S., Caspersen, J.P., Foster, R.B., Hubbell, S.P., 2003. Spatial and temporal variation of biomass in a tropical forest: results from a large census plot in Panama. *J. Ecol.* 91, 240–252.
- Chave, J., Condit, R., Muller-Landau, H.C., et al., 2008. Assessing evidence for pervasive alteration in tropical tree communities. *Plos Biol.* 6, 1–8.
- Chave, J., Muller-Landau, H.C., Baker, T.R., Easdale, T.A., ter Steege, H., Webb, C.O., 2006. Regional and phylogenetic variation of wood density across 2456 Neotropical tree species. *Ecol. Appl.* 16, 2356–2367.
- Chave, J., Riera, B., Dubois, M., 2001. Estimation of biomass in a Neotropical forest of French Guiana: spatial and temporal variability. *J. Trop. Ecol.* 17, 79–96.
- Clark, D.A., 2002. Are tropical forests an important carbon sink? Reanalysis of the long-term plot data. *Ecol. Appl.* 12, 3–7.
- Clark, D.A., 2007. Detecting tropical forests' responses to global climatic and atmospheric change: current challenges and a way forward. *Biotropica* 39, 4–19.
- Clark, D.A., Brown, S., Kicklighter, D.W., Chambers, J.Q., Thomlinson, J.R., Ni, J., Holland, E.A., 2001. Net primary production in tropical forests: an evaluation and synthesis of existing field data. *Ecology* 11, 371–384.
- Clark, D.A., Clark, D.B., 1992. Life history diversity of canopy and emergent trees in a Neotropical rain forest. *Ecol. Monogr.* 62, 315–344.
- Clark, D.A., Clark, D.B., Sandoval, R., Castro, M.V., 1995. Edaphic and human effects on landscape-scale distributions of tropical rain-forest palms. *Ecology* 76, 2581–2594.
- Clark, D.B., Clark, D.A., 2000. Landscape-scale variation in forest structure and biomass in a tropical rain forest. *Forest Ecol. Manag.* 137, 185–198.
- Condit, R., 1998. *Tropical Forest Census Plots: A Comparison With Other Plots*. Springer-Verlag, Berlin.
- Cummings, D.L., Kauffman, J.B., Perry, D.A., Hughes, R.F., 2002. Aboveground biomass and structure of rainforests in the southwestern Brazilian Amazon. *Forest Ecol. Manag.* 163, 293–307.
- Davies, S.J., Palmiotto, P.A., Ashton, P.S., Lee, H.S., Lafrankie, J.V., 1998. Comparative ecology of 11 sympatric species of *Macaranga* in Borneo: tree distribution in relation to horizontal and vertical resource heterogeneity. *J. Ecol.* 86, 662–673.
- Daws, M.I., Mullins, C.E., Burslem, D.F.R.P., Paton, S.R., Dalling, J.W., 2002. Topographic position affects the water regime in a semideciduous tropical forest in Panamá. *Plant Soil* 238, 79–90.
- Delaney, M., Brown, S., Lugo, A.E., Torres-Lezama, A., Bello Quintero, N., 1997. The distribution of organic carbon in major components of forests located in five life zones in Venezuela. *J. Trop. Ecol.* 13, 697–708.
- DeWalt, S.J., Chave, J., 2004. Structure and biomass of four lowland Neotropical forests. *Biotropica* 36, 7–19.
- Dixon, R.K., Brown, S., Houghton, R.A., Solomon, A.M., Trexler, M.C., Wisniewski, J., 1994. Carbon pools and flux of global forest ecosystems. *Science* 263, 185–190.
- Dunnett, C.W., 1955. A multiple comparisons procedure for comparing several treatments with a control. *J. Am. Stat. Assoc.* 50, 1096–1121.
- Efron, B., 1987. Better bootstrap confidence intervals. *J. Am. Stat. Assoc.* 82, 171–185.
- Efron, B., Tibshirani, R., 1993. *An Introduction to the Bootstrap*. Chapman & Hall/CRC, Boca Raton.
- Fahey, T.J., Knapp, A.K., 2007. *Principles and Standards For Measuring Primary Production*. Oxford University Press, New York.
- Fantini, A.C., Guries, R.P., 2007. Forest structure and productivity of palmiteiro (*Euterpe edulis* Martius) in the Brazilian Mata Atlântica. *Forest Ecol. Manag.* 242, 185–194.
- FAO, 2000. *Global Forest Resources Assessment*. United Nations Food and Agriculture Organization, Rome.
- Fitzpatrick, S.W., Brasileiro, C.A., Haddad, D.F.B., Zamudio, K.R., 2009. Geographical variation in genetic structure of an Atlantic Coastal Forest frog reveals regional differences in habitat stability. *Mol. Ecol.* 18, 2877–2896.
- Frangi, J.L., Lugo, A.E., 1985. Ecosystem dynamics of a subtropical floodplain forest. *Ecol. Monogr.* 55, 351–369.
- Frangi, J.L., Lugo, A.E., 1998. A flood plain palm forest in the Luquillo Mountains of Puerto Rico five years after hurricane Hugo. *Biotropica* 30, 339–348.
- Galindo-Leal, C., Camara, I.G., 2003. The Atlantic Forest of South America: biodiversity status, threats, and outlook. In: *Center for Applied Biodiversity Science, Conservation International*. Island Press, Washington.
- Gentry, A.H., 1988. Changes in plant community diversity and floristic composition on environmental and geographical gradients. *Ann. Mol. Bot. Gard.* 75, 1–34.
- Gibbs, H.K., Brown, S., Nilesand, J.O., Foley, J.A., 2007. Monitoring and estimating tropical forest carbon stocks: making REDD a reality. *Environ. Res. Lett.* 2, 1–13.
- Gotelli, N.J., Ellison, A.M., 2004. *A Primer of Ecological Statistics*. Sinauer Associates, Inc., Sunderland, MA.
- Graham, M., 2003. Confronting multicollinearity in ecological multiple regression. *Ecology* 84, 2809–2815.
- Grubb, P.J., 1977. Control of forest growth and distribution on wet tropical mountains: with special reference to mineral nutrition. *Annu. Rev. Ecol. Syst.* 8, 83–107.
- Guedes-Bruni, R.R., Silva, A.G., Mantovani, W., 2009. Rare canopy species in communities within the Atlantic Coastal Forest in Rio de Janeiro State, Brazil. *Biodivers. Conserv.* 18, 387–403.
- Henderson, A., Galeano, G., Bernal, B., 1995. *Field guide to the Palms of the Americas*. Princeton University Press, New Jersey.
- Holdridge, L.R., 1947. Determination of world plant formations from simple climate data. *Science* 105, 367–368.
- Houghton, R.A., 2007. Balancing the global carbon budget. *Annu. Rev. Earth Planet. Sci.* 35, 313–347.
- Houghton, R.A., Hall, F., Goetz, S.J., 2009. Importance of biomass in the global carbon cycle. *J. Geophys. Res.* 114, G00E03.
- Hubbell, S.P., Foster, R.B., O'Brien, S.T., Harms, K.E., Condit, R., Wechsler, B., Wright, S.J., Lao, S.L., 1999. Light-gap disturbances, recruitment limitation, and tree diversity in a Neotropical forest. *Science* 283, 554–557.
- Hughes, R.F., Kauffman, J.B., Jaramillo, V.J., 1999. Biomass, carbon, and nutrient dynamics of secondary forests in a humid tropical region of Mexico. *Ecology* 80, 1892–1907.
- Hurlbert, S.H., 1984. Pseudoreplication and the design of ecological field experiments. *Ecol. Monogr.* 54, 187–211.
- IPT-Instituto de Pesquisas Tecnológicas, 2000. *Diagnóstico da situação atual dos recursos hídricos da Unidade de Gerenciamento dos Recursos Hídricos do Litoral Norte-UGRHI-3: Relatório 46.172*. Governo do Estado de São Paulo, São Paulo.
- Joly, C.A., Aïdar, M.P.M., Klink, C.A., Mcgrath, D.G., Moreira, A.G., Moutinho, P., Nepstad, D.C., Oliveira, A.A., Pott, A., Sampaio, E.V.S.B., 1999. Evolution of the Brazilian phytogeography classification systems: implications for biodiversity conservation. *Ciência e Cultura* 51, 331–348.
- Joly, C.A., Martinelli, L.A., Alves, L.F., Vieira, S.A., Tamashiro, J.Y., Aïdar, M.P.M., Camargo, P.B., Assis, M.A., Bernacci, L.C., 2008. *As Parcelas Permanentes do Projeto Temático Biota Gradiente Funcional: Composição Florística, Estrutura e Funcionamento da Floresta Ombrófila Densa dos Núcleos Picinguaba e Santa Virginia do Parque Estadual da Serra do Mar, Estado de São Paulo, Brasil*. RedeMAP: Rede de Parcelas Permanentes dos Biomas Mata Atlântica e Pampa & Funpar, Curitiba.
- Kahn, F., Castro, A., 1985. The palm community in a forest of Central Amazonia, Brazil. *Biotropica* 17, 210–216.
- Keeling, H.C., Phillips, O.L., 2007a. The global relationship between forest productivity and biomass. *Global Ecol. Biogeogr.* 16, 618–631.
- Keeling, H.C., Phillips, O.L., 2007b. A calibration method for the crown illumination index for assessing forest light environments. *Forest Ecol. Manag.* 242, 431–437.
- Keller, M., Palace, M., Asner, G.P., Pereira, R., Silva, J.N., 2004. Coarse woody debris in undisturbed and logged forests in the eastern Brazilian Amazon. *Glob. Change Biol.* 10, 784–795.
- Keller, M., Pallace, M., Hurr, G., 2001. Biomass estimation in the Tapajós National Forest, Brazil: examination of sampling and allometric uncertainties. *Forest Ecol. Manag.* 154, 371–382.
- Kitayma, K., Aiba, S., 2002. Ecosystem structure and productivity of tropical rain forests along altitudinal gradients with contrasting soil phosphorus pools on Mount Kinabalu, Borneo. *J. Ecol.* 90, 37–51.
- Korner, C., 2007. The use of "altitude" in ecological research. *Trends Ecol. Evol.* 22, 569–574.
- Laurance, W.F., 2009. Conserving the hottest of the hotspots. *Biol. Conserv.* 142, 1137.
- Legendre, P., Legendre, L., 1998. *Numerical Ecology*. Elsevier, Amsterdam.
- Leuschner, C., Moser, G., Bertsch, C., Roderstein, M., Hertel, D., 2007. Large altitudinal increase in tree root/shoot ratio in tropical mountain forests of Ecuador. *Basic Appl. Ecol.* 8, 219–230.
- Lieberman, D., Lieberman, M., Peralta, R., Hartshorn, G.S., 1996. Tropical forest structure and composition on a large-scale altitudinal gradient in Costa Rica. *J. Ecol.* 84, 137–152.
- Loarie, S.R., Asner, G.P., Field, C.B., 2009. Boosted carbon emissions from Amazon deforestation. *Geophys. Res. Lett.* 36, L14810.
- Luizão, R.C., Luizão, F.J., Paiva, R.Q., Monteiro, T.F., Lucinéia, L.S., Kruij, B., 2004. Variation of carbon and nitrogen cycling processes along a topographic gradient in a central Amazonian forest. *Glob. Change Biol.* 10, 592–600.
- Mainieri, C., Chimelo, J.P., 1989. *Fichas de características das madeiras brasileiras*. IPT-Instituto de Pesquisas Tecnológicas, São Paulo.
- Malhi, Y., Wood, D., Baker, T.R., Wright, J., Phillips, O.L., Cochrane, T., Meir, P., Chave, J., Almeida, S., Arroyo, L., Higuchi, N., Killeen, T.J., Laurance, S.G., Laurance, W.F., Lewis, S.L., Monteagudo, A., Neill, D.A., Nunez-Vargas, P., Pitman, N.C.A., Quesada, C.A., Salomão, R., Silva, J.N.M., Lezama, A.T., Terborgh, J., Vásquez-Martinez, R., 2006. The regional variation of aboveground live biomass in old-growth Amazonian forests. *Glob. Change Biol.* 12, 1107–1138.
- Marín-Spiotta, E., Ostertag, R., Silver, W.L., 2007. Long-term patterns in tropical reforestation: plant community composition and aboveground biomass accumulation. *Ecol. Appl.* 17, 828–839.
- Martini, A.M., Fiaschi, P., Amorin, A.M., Paixão, J.L., 2007. A hot-point within a hot-spot: a high diversity site in Brazil's Atlantic Forest. *Biodivers. Conserv.* 16, 3111–3128.
- Martins, S.C., Piccolo, M.C., Camargo, P.B., Vieira, S.A., Alves, L.F., Joly, C.A., Carmo, J.B., Martinelli, L.A., in review. Nutrient, carbon and clay contents of soils throughout an altitudinal gradient in the coastal Atlantic Forest of southeast Brazil (Ubatuba, SP). *Geoderma*.
- Morellato, L.P., Haddad, C.F.B., 2000. Introduction: The Brazilian Atlantic Forest. *Biotropica* 32, 786–792.
- Moser, G., Hertel, D., Leuschner, C., 2007. Altitudinal change in LAI and stand leaf biomass in tropical montane forests: a transect study in Ecuador and a pan-tropical meta-analysis. *Ecosystems* 10, 924–935.
- Muller-Landau, H.C., 2004. Interspecific and inter-site variation in wood specific gravity of tropical trees. *Biotropica* 36, 20–32.
- Muller-Landau, H.C., Condit, R.S., Harms, K.E., Marks, C.O., Thomas, S.C., et al., 2006. Comparing tropical forest tree size distributions with the predictions of metabolic ecology and equilibrium models. *Ecol. Lett.* 9, 589–602.

- Murray-Smith, C., Brummitt, N.A., Oliveira-Filho, A.T., Bachman, S., Moat, J., Lughadha, E.M.N., Lucas, E.J., 2009. Plant diversity hotspots in the Atlantic Coastal Forests of Brazil. *Conserv. Biol.* 23, 151–163.
- Mutke, J., Barthlott, W., 2005. Patterns of vascular plant diversity at continental to global scales. *Biologische Skrifter* 55, 521–531.
- Myers, N., Mittermeier, R.A., Mittermeier, C.G., Fonseca, G.A.B., Kent, J., 2000. Biodiversity hotspots for conservation priorities. *Nature* 403, 853–858.
- Nascimento, H.E.M., Laurance, W.F., 2002. Total aboveground biomass in central Amazonian rainforests: a landscape-scale study. *Forest Ecol. Manag.* 168, 311–321.
- Nascimento, M.T., Barbosa, R.I., Villela, D.M., Proctor, J., 2007. Above-ground biomass changes over an 11-year period in an Amazon monodominant forest and two other lowland forests. *Plant Ecol.* 192, 181–191.
- Negrelle, R.R.B., 2002. The Atlantic forest in the Volta Velha Reserve: a tropical rain forest site outside the tropics. *Biodivers. Conserv.* 11, 887–917.
- Niklas, K.J., 1993. The scaling of plant height: a comparison among major plant clades and anatomical grades. *Ann. Bot. Lond.* 72, 165–172.
- Nogueira, E.M., Fearnside, P.M., Nelson, B.W., França, M.B., 2007. Wood density in forests of Brazil's 'arc of deforestation': implications for biomass and flux of carbon from land-use change in Amazonia. *Forest Ecol. Manag.* 248, 119–135.
- Nogueira, E.M., Fearnside, P.M., Nelson, B.W., França, M.B., Oliveira, A.C.A., 2008. Tree height in Brazil's 'arc of deforestation': shorter trees in south and southwest Amazonia imply lower biomass. *Forest Ecol. Manag.* 255, 2963–2972.
- Oliveira-Filho, A.T., Fontes, M.A.L., 2000. Patterns of floristic differentiation among Atlantic Forests in southeastern Brazil and the influence of climate. *Biotropica* 32, 793–810.
- Palace, M., Keller, M., Silva, H., 2008. Necromass production: studies in undisturbed and logged Amazon forests. *Ecol. Appl.* 18, 873–884.
- Palm, C., Sanchez, P., Ahamed, S., Awiti, A., 2007. Soils: a contemporary perspective. *Annu. Rev. Environ. Resour.* 32, 99–129.
- Paoli, G., Curran, L., Slik, J., 2008. Soil nutrients affect spatial patterns of above-ground biomass and emergent tree density in southwestern Borneo. *Oecologia* 155, 155–287.
- Phillips, O.L., Baker, T.R., 2001. Field manual for plot establishment and remeasurement. RAINFOR (Amazon Forest Inventory Network). Available at <http://www.geog.leeds.ac.uk/projects/rainfor/>.
- Phillips, O.L., Malhi, Y., Higuchi, N., Laurance, W.F., Núñez, P.V., Vásquez, R.M., Laurance, S.G., Ferreira, L.V., Stern, M., Brown, S., Grace, J., 1998. Changes in the carbon balance of tropical forests: evidence from long-term plots. *Science* 282, 439–442.
- Pierre-Ledru, M., Mourguiart, P., Riccomini, C., 2009. Related changes in biodiversity, insolation and climate in the Atlantic rainforest since the last interglacial. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 271, 140–152.
- Proctor, J., Anderson, J.M., Chai, P., Vallack, H.W., 1983. Ecological studies in four contrasting, lowland rain forests in Gunung Mulu National Park, Sarawak. I. Forest environment, structure and floristics. *J. Ecol.* 71, 239–260.
- Pyle, E.H., Santoni, G.W., Nascimento, H.E.M., Hutya, L.R., Vieira, S., Curran, D.J., van Haren, J., Saleska, S.R., Chow, V.Y., Camargo, P.B., Laurance, W.F., Wofsy, S.C., 2008. Dynamics of carbon, biomass, and structure in two Amazonian forests. *J. Geophys. Res.* 113, G00B08.
- Raich, J.W., Russell, A.E., Kitayama, K., Parton, W.J., Vitousek, P.M., 2006. Temperature influences carbon accumulation in moist tropical forests. *Ecology* 87, 76–87.
- Raich, J.W., Russell, A.E., Vitousek, P.M., 1997. Primary productivity and ecosystem development along an elevational gradient on Mauna Loa, Hawaii. *Ecology* 78, 707–721.
- Reis, M.S., Fantini, A.C., Nodari, R.O., Reis, A., Guerra, M.P., Mantovani, A., 2000. Management and conservation of natural populations in Atlantic rain forest: the case study of palm heart *Euterpe edulis* Martius. *Biotropica* 32, 894–902.
- Ribeiro, M.C., Metzger, J.P., Martensen, A.C., Ponzoni, F.J., Hirota, M.M., 2009. The Brazilian Atlantic Forest: how much is left, and how is the remaining forest distributed? Implications for conservation. *Biol. Conserv.* 142, 1141–1153.
- Rice, A.H., Pyle, E.H., Saleska, S.R., Hutya, L.R., Palace, M., Keller, M., Carmargo, P.B., Portillo, K., Marques, D., Wofsy, S.C., 2004. Carbon balance and vegetation dynamics in an old-growth Amazonian forest. *Ecol. Appl.* 14, S55–S71.
- Richards, P.W., 1996. *The Tropical Rain Forest*, second ed. Cambridge University Press, Cambridge.
- Robert, A., 2003. Simulation of the effect of topography and tree falls on stand dynamics and stand structure of tropical forests. *Ecol. Model.* 167, 287–303.
- Rolim, S.G., Jesus, R.M., Nascimento, H.E.M., Couto, H.T.Z., Chambers, J.C., 2005. Biomass change in an Atlantic tropical moist forest: the ENSO effect in permanent sample plots over a 22-year period. *Oecologia* 142, 238–246.
- Rüger, N., Huth, A., Hubbell, S.P., Condit, R., 2009. Response of recruitment to light availability across a tropical lowland rain forest community. *J. Ecol.* 97, 1360–1368.
- Saatchi, S.S., Houghton, R.A., dos Santos Alvalá, R.C., Soares, J.V., Yu, Y., 2007. Distribution of aboveground live biomass in the Amazon basin. *Glob. Change Biol.* 13, 816–837.
- Sanchez, M., Pedroni, F., Leitao-Filho, H.F., Cesar, O., 1999. Composição florística de um trecho de floresta ripária na Mata Atlântica em Picinguaba, Ubatuba, SP. *Rev. Bras. Bot.* 22, 31–42.
- Sanchez, M., 2001. Composição florística e estrutura da comunidade arbórea num gradiente altitudinal da Mata Atlântica. PhD dissertation. Universidade Estadual de Campinas, Brazil.
- Sarmiento, G., Pinillos, M., Garay, I., 2005. Biomass variability in tropical American lowland rainforests. *Ecotropicos* 18, 1–20.
- SAS Institute, 2007. JMP Version 7.0.2. SAS Institute, Cary, North Carolina, USA.
- Scarano, F.R., 2002. Structure, function, and floristic relationships of plant communities in stressful habitats marginal to the Brazilian Atlantic Rainforest. *Ann. Bot. Lond.* 90, 517–524.
- Scatena, F.N., Lugo, A.E., 1995. Geomorphology, disturbance, and the soil and vegetation of two subtropical wet steepland watersheds of Puerto Rico. *Geomorphology* 13, 199–213.
- Scatena, F.N., Silver, W., Siccama, T., Johnson, A., Sanchez, M.J., 1993. Biomass and nutrient content of the Bisley Experimental Watersheds, Luquillo Experimental Forest, Puerto Rico, before and after Hurricane Hugo, 1989. *Biotropica* 25, 15–27.
- Schmitt, J.L., Windisch, P.G., 2005. Aspectos ecológicos de *Alsophila setosa* Kaulf. (Cyatheaaceae Pteridophyta) no sul do Brasil. *Acta Bot. Bras.* 19, 861–867.
- Schmitt, J.L., Windisch, P.G., 2007. Estrutura populacional e desenvolvimento da fase esporofítica de *Cyathea delgadii* Sternb. (Cyatheaaceae, Monilophyta) no sul do Brasil. *Acta Bot. Bras.* 21, 731–740.
- Schnitzer, S.A., 2005. A mechanistic explanation for global patterns of liana abundance and distribution. *Am. Nat.* 166, 262–276.
- Scudeller, V.V., Martins, F.R., Shepherd, G.J., 2001. Distribution and abundance of arboreal species in the Atlantic ombrophilous dense forest in Southeastern Brazil. *Plant Ecol.* 152, 185–199.
- Sentelhas, P.C., Pereira, A.R., Marin, F.R., Angelocci, L.R., Alfonsi, R.R., Caramori, P.H., Swart, S., 1999. Balanços Hídricos Climatológicos do Brasil-500 balanços hídricos de localidades brasileiras. ESALQ, Piracicaba. Available at: <http://www.bdclima.cnpm.embrapa.br/index.php>.
- Sierra, C.A., del Valle, J.I., Orrego, S.A., Moreno, F.H., Harmon, M.E., Zapata, M., Colomero, G.J., Herrera, M.A., Lara, W., Restrepo, D.E., Berrouet, L.M., Loaiza, L.M., Benjumea, J.F., 2007. Total carbon stocks in a tropical forest landscape of the Porce region, Colombia. *Forest Ecol. Manag.* 243, 299–309.
- Silva-Dias, M.A.E., Vidale, P.E., Blanco, C.M.R., 1995. Case study and numerical simulation of the summer regional circulation in São Paulo, Brazil. *Bound. Layer Meteorol.* 74, 371–388.
- Silver, W.L., Lugo, A.E., Keller, M., 1999. Soil oxygen availability and biogeochemical cycling along elevation and topographic gradients in Puerto Rico. *Biogeochemistry* 44, 301–328.
- Silver, W.L., Scatena, F.N., Johnson, A.H., Siccama, T.G., Sanchez, M.J., 1994. Nutrient availability in a Montane wet tropical forest: spatial patterns and methodological considerations. *Plant Soil* 164, 129–145.
- SMA-Secretaria do Meio Ambiente, 1998. Planos de Manejo das Unidades de Conservação: Parque Estadual da Serra do Mar-Núcleo Picinguaba. Plano de Gestão Ambiental-Fase I, São Paulo.
- SOS Mata Atlântica and INPE, 2009. Atlas dos remanescentes florestais da Mata Atlântica-período 2005–2008. Fundação SOS Mata Atlântica & Instituto Nacional de Pesquisas Espaciais–INPE, São Paulo.
- Sousa Neto, E.R., 2008. Perdas de nitrogênio pela emissão de óxido nítrico (N₂O) e sua relação com a decomposição da serapilheira e biomassa de raízes na floresta de Mata Atlântica. Master thesis. Universidade de São Paulo, Brazil.
- Souza, C.R., Suguio, K., Oliveira, A.M., Oliveira, P.E., 2005. Quaternário do Brasil. Holos Editora, Ribeirão Preto, Brazil.
- Suguio, K., Martin, L., 1978. Quaternary marine formations of the states of São Paulo and southern Rio de Janeiro. In: International Symposium on Coastal Evolution in the Quaternary, University of São Paulo, São Paulo, Brazil, p. 55.
- Svenning, J.C., 1999. Microhabitat specialization in a species-rich palm community in Amazonian Ecuador. *J. Ecol.* 87, 55–65.
- Svenning, J.C., Harvlev, D., Sorensen, M.M., Balslev, H., 2009. Topographic and spatial controls of palm species distributions in a Montane rain forest, southern Ecuador. *Biodivers. Conserv.* 18, 219–228.
- Swenson, N.G., Enquist, B.J., 2007. Ecological and evolutionary determinants of a key plant functional trait: wood density and its community-wide variation across latitude and elevation. *Am. J. Bot.* 94, 451–459.
- Tabarelli, M., 1997. A regeneração da Floresta Atlântica Montana. Ph.D. dissertation. Universidade de São Paulo, Brazil.
- Takyu, M., Aiba, S., Kitayama, K., 2002. Effects of topography on tropical lower montane forests under different geological conditions on Mount Kinabalu, Borneo. *Plant Ecol.* 159, 35–49.
- Takyu, M., Aiba, S., Kitayama, K., 2003. Changes in biomass, productivity and decomposition along topographical gradients under different geological conditions in tropical lower montane forests on Mount Kinabalu, Borneo. *Oecologia* 134, 397–404.
- Tanner, E.V.J., Vitousek, P.M., Cuevas, E., 1998. Experimental investigations of nutrient limitation of forest growth on wet tropical mountains. *Ecology* 79, 10–22.
- ter Steege, H., Pitman, N.C.A., Phillips, O.L., Chave, J., Sabatier, D., Duque, A., Molino, J., Prévost, M., Spichiger, R., Castellanos, H., Hildebrand, P., Vásquez, R., 2006. Continental-scale patterns of canopy tree composition and function across Amazonia. *Nature* 443, 444–447.
- Tiepolo, G., Calmon, M., Ferretti, A.R., 2002. Measuring and monitoring carbon stocks at the Guaraqueçaba Climate Action Project, Paraná, Brazil. In: International Symposium on Forest Carbon Sequestration and Monitoring. Extension Series Taiwan Forestry Research Institute. Available at: http://www.spvs.org.br/download/monitoramento_ingles.pdf, pp. 98–115.
- Urquiza-Haas, T., Dolman, P.M., Peres, C.A., 2007. Regional scale variation in forest structure and biomass in the Yucatan Peninsula, Mexico: effects of forest disturbance. *Forest Ecol. Manag.* 247, 80–90.
- Vargas, E., Allen, M.F., Allen, E.B., 2008. Biomass and carbon accumulation in a fire chronosequence of a seasonally dry tropical forest. *Glob. Change Biol.* 14, 109–124.
- Veloso, H.P., Rangel Filho, A.L.R., Lima, J.C.A., 1991. Classificação da Vegetação Brasileira Adaptada a um Sistema Universal. IBGE, Brasília, Brazil.

- Vieira, S.A., Alves, L.F., Aidar, M.P.M., Araújo, L.S., Baker, T., Batista, J.L.F., Campos, M.C.R., Camargo, P.B., Chave, J., Delitti, W.B., Higuchi, N., Honório, E., Joly, C.A., Keller, M., Martinelli, L.A., Mattos, E.A., Metzker, T., Phillips, O.L., Santos, F.A.M., Shimabukuro, M.T., Silveira, M., Trumbore, S.E., 2008. Estimation of biomass and carbon stocks: the case of the Atlantic Forest. *Biota Neotropica* 8, <http://www.biotaneotropica.org.br/v8n2/pt/fullpaper?bn00108022008+en>. doi: 10.1590/S1676-06032008000200001.
- Vieira, S.A., Camargo, P.B., Selhorst, D., Silva, R., Hutyra, L., Chambers, J.Q., Brown, I.F., Higuchi, N., Santos, J., Wofsy, S.C., Trumbore, S.E., Martinelli, L.A., 2004. Forest structure and carbon dynamics in Amazonian tropical rain forests. *Oecologia* 140, 468–479.
- Vormisto, J., Tuomisto, H., Oksanen, J., 2004. Palm distribution patterns in Amazonian rainforests: what is the role of topographic variation? *J. Veg. Sci.* 15, 485–494.
- Waide, R.B., Zimmerman, J.K., Scatena, F.N., 1998. Controls of primary productivity: lessons from the Luquillo Mountains in Puerto Rico. *Ecology* 79, 31–37.
- Whitmore, T.C., 1984. *Tropical Rain Forests of the Far East*. Clarendon.
- Wilkinson, L., 1999. *SYSTAT, Version 9*. SYSTAT, Evanston, IL.
- Zach, A., Horna, V., Leuschner, C., Zimmermann, R., 2010. Patterns of wood carbon dioxide efflux across a 2000-m elevation transect in an Andean moist forest. *Oecologia* 162, 127–137.