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Synthesis

Economically important species dominate aboveground carbon storage in forests of southwestern Amazonia

N. Galia Selaya [1], Pieter A. Zuidema [2], Christopher Baraloto [3,4], Vincent A. Vos [5,6], Roel J. W. Brienen [7], Nigel Pitman [8], Foster Brown [9,10], Amy E. Duchelle [11], Alejandro Araujo-Murakami [12], Luis A. Oliveira Carillo [13], Guido H. Vasquez Colomo [14], Severo Meo Chupinagua [15], Hugo Fuentes Nay [16] and Stephen Perz [1]

ABSTRACT. Tree species in tropical forests provide economically important goods and ecosystem services. In submontane forests of southwestern Amazonia, we investigated the degree to which tree species important for subsistence and trade contribute to aboveground carbon storage (AGC). We used 41 1-hectare plots to determine the species abundance, basal area, and AGC of stems > 10 cm diameter at breast height (dbh). Economically important taxa were classified using ethnobotanical studies and according to their stem density. These taxa (n = 263) accounted for 45% of total stems, 53% of total basal area, and 56% of total AGC, significantly more than taxa with minor or unknown uses (Welch test at $p < 0.05$). Taxa with 1-2 stems per hectare, or with fewer than 1 stem per hectare (common and rare) accounted for 35% of total AGC, more than the 22% accounted for by dominant taxa. High basal area had a greater impact on AGC than abundance in economic taxa because their populations are skewed to adult trees. Size in these taxa had a median dbh > 40 cm and few stems in regeneration classes of dbh < 10 to 20 cm (e.g., *Bertholletia excelsa*, *Cariniana* spp., *Cedrelinga* spp., *Ceiba* spp., *Dipteryx* spp.), whereas dominant *Tetragastris* spp., and *Pseudolmedia* spp. had most stems in low diameter classes and a median diameter of < 30 cm. *Bertholletia excelsa*, with 1.5 stems per hectare, showed the highest basal area of any species and accounted for 9% of AGC (11 Mg/ha), twice that of the second-ranking species. Our study shows that economic importance and carbon stocks in trees are closely linked in southwestern Amazonia. Unplanned harvests can disrupt synergistic dual roles altering carbon stocks temporally or permanently. Precautionary measures based on species ecology, demography, and regeneration traits should be at the forefront of REDD+ to reconcile maximum harvesting limits, biodiversity conservation, and sustainable forest management.

Key Words: *basal area; Bertholletia excelsa*; carbon storage; economic importance, REDD+; southwestern Amazonia; taxa abundance

INTRODUCTION

Tree species in tropical forests are important sources of both goods and ecosystem services. Thus, there may be trade-offs between direct economic gain from forest use and long-term provision of ecosystem services, such as carbon storage, in these forests. For instance, logging and hunting may (temporarily) change carbon stocks in tropical forests (Putz et al. 2012, Osuri et al. 2016). Therefore, understanding how species harvests influence forest carbon stocks is crucial to balance the short-term economic gains from harvesting with the long-term provision of ecosystem services through carbon storage and biodiversity conservation in tropical forests.

The long-term provision of ecosystem services in tropical forests requires avoiding forest conversion to agriculture as well as establishing the sustainable use of the remaining forests. The global approach to realize this centers on the creation of regulatory and financial incentives to reduce carbon losses from land-use change and forest management. The reduction of emissions from deforestation and degradation (REDD+) mechanism has been adopted in the international agreement to curb climate change and was recognized during the UNFCCC COP21 meeting in Paris in December 2015 (United Nations 2015). In recent years, several tropical countries have developed several projects within the REDD+ framework (Sills et al. 2014). The principle of REDD+ is to put a price on carbon retained in forest lands in developing countries in which unplanned deforestation is imminent; therefore the quantification of current forest carbon stocks and potential loss is critical.

We focused on southwestern Amazonia. This is a region that harbors many tree and palm species with high economic and ecological importance, but that has also experienced extensive human immigration, road building, and intensive logging. These developments may put the natural wealth and provision of ecosystem services at risk (Pfaff et al. 2007, Southworth et al. 2011, Perz et al. 2013). Over the last decade, anthropogenic loss of forest in the region has been exacerbated by severe droughts that have caused extensive fires and concomitant CO_2 emissions (Foley et al. 2007, Marengo et al. 2008, Aragão and Shimabukuro 2010, Lewis et al. 2010). In southwestern Amazonian forests, aboveground biomass stocks have been estimated to range between 100 and 300 Mg ha^{-1} (Asner 2009, Salimon et al. 2011, Saatchi et al. 2011), of which living trees can represent around

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82% of the total (Cummings 2002). These estimates have been derived from forest inventories, allometric equations, and remote-sensing techniques. However, the relative contributions of individual species to the total carbon stocks have only recently begun to receive attention. Fauset et al. (2015) provided the first estimates of species contributions in the entire Amazon, and at the regional level, and showed the important economic species *Bertholletia excelsa*, the Brazil nut tree, ranking third in aboveground woody biomass and accounting for 1.3% of total biomass. This is an especially important finding because *B. excelsa* populations are strongly manipulated by humans: positively due to silvicultural management (Kainer et al. 2014) and negatively because of potentially unsustainable seed harvesting (Peres et al. 2003), and in all likelihood because of illegal logging and fire. As a result, *B. excelsa* represents a unique case in which the policy and economics of nontimber forest harvests may strongly affect regional carbon stocks (Guariguata et al. 2017).

We took a closer look at the many tree and palm species that are economically important for regional livelihoods and explored their contribution to forest carbon stocks. This is important for southwestern Amazonian forests because *B. excelsa* and *Hevea brasiliensis* have long been a cornerstone to support the local economy and alleviate poverty (Zuidema and Boot 2002, Duchelle et al. 2014*a*). It is also important because timber extraction in southwestern Amazonia has been intensified, especially in Brazil nut concessions, and therefore conflicts between harvesting nontimber forest products, logging for timber, and carbon storage and biodiversity conservation are arising (Giudice et al. 2012, Rockwell et al. 2015). Information on the dual contribution of species, both direct economic value and environmental services, is crucial for understanding the influence exerted by forest users on species population structures and carbon stocks and for designing sustainable forest management and climate change mitigation efforts.

We used data from 41 permanent plots distributed in 19 sites in the trinational border region of Bolivia, Brazil, and Peru, representative of the submontane, terra firme, and former floodplain old growth forests in which *B. excelsa* is widely distributed. We studied the contribution of taxa to forest structure and carbon storage. Specifically, we asked the following questions:

1. What is the relative contribution of economically important taxa (both nontimber and timber) to the abundance, basal area, and aboveground carbon stocks of old growth submontane forests in southwestern Amazonia?
2. What is the relationship between the density of economically important taxa and forest aboveground carbon stocks?

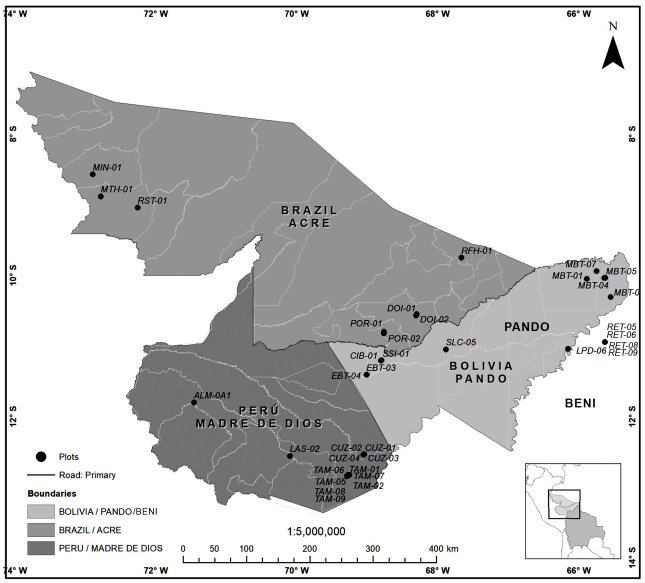
We expect that our study will serve as a baseline for foresters, policy makers, and conservationists to discuss precautionary measures for forest management and performance-based initiatives and payments for environmental services such as REDD+.

METHODS

Study sites

The study was carried out in southwestern Amazonia and included the administrative the regions of Madre de Dios (Peru), Acre (Brazil), and Pando and northern Beni (Bolivia), comprising an extension of ~31 million ha (Fig. 1). The region has a warm and seasonal climate, with an average annual temperature of 26-27 °C. Mean annual precipitation declines from west to east, from 3000 mm in Madre de Dios down to 1551 mm in Riberalta, Bolivia. There is also a north-south precipitation gradient, with 1944 mm in Rio Branco, Acre, Brazil and 1498 in Cobija, and 1551 mm in Riberalta, Bolivia (Navarro and Ferreira 2009), but overall the region is considered moist because of the precipitation range (1500 to 3500 mm) and number of dry months per year (4 months; Chave et al. 2005). Most of the region has an elevation of ~100 to 600 meters above the sea level (masl) and is considered submontane (IBGE 2012). Montane forests > 600 masl are present in small proportion in southwestern Madre de Dios and northwest of Acre. The predominant physiographic types are alluvial, i.e., ancient mostly not flooded or seasonally flooded floodplains, (43% Madre de Dios, 6% Acre, and 19% Pando) and terra firme forests (48% Madre de Dios, 80% Acre, and 78% Pando; DHV Consultores 1997, Escobedo 2008, Salimon 2011). Around 19.7 million hectares (65%) of the total trinational area are classified as potential for timber and nontimber extraction and approximately 8 million hectares, 26% of the total, are titled for Brazil nut (*B. excelsa*) extraction (INRA 2008, IUCN 2008, Soliz 2009, Chávez et al. 2012, TEEB 2013). *Bertholletia excelsa* is distributed in terra firme forest at temperatures of 24.3 to 27.2 ° C and 1400 to 2800 mm of precipitation (Mori and Prance 1998). In broad terms, physiognomic characteristics have been used to classify these forests as dense or open, i.e., mixtures of trees with either bamboo or palms or both (Encarnación et al. 2008, Navarro and Ferreira 2009, Salimon et al. 2011). The region has lost approximately nine percent of its forest cover to date (Southworth et al. 2011).

Fig. 1. Map of the transboundary region of Madre de Dios, Acre, and Pando in southwestern Amazonia showing sites sampled in 19 submontane (terra firme and floodplain) forests.



Sampling methods

We studied 19 sites represented by 41 1-ha permanent plots sampled in the submontane forest, at elevations of 100 to 600 masl. The criteria for selecting sites was to be representative of the main forest types, which at the macro level (thousands of hectares), belong to evergreen seasonal terra firme or to former floodplain mosaics of dense and open bamboo and palm forest types, with bamboo notably in high proportions in the central and western parts, whereas palms were more prevalent in the eastern part of the region (Josse et al. 2007, Mostacedo et al. 2009, Salimon et al. 2011). These sites include forests, typical and representative for the region, which are managed for nontimber and timber products. *Bertholletia excelsa* is widely distributed across these transboundary terra firme forest types, with the exception of the extreme northwest of Acre and the west of Madre de Dios. We did not follow stratified or random sampling because of costs and site access restrictions. Our selection of sites depended also on obtaining permission from local stakeholders. Of the plots, 30 out of 41 were located in terra firme sensu stricto and 11 were in former floodplains of alluvial origin (https://www.forestplots.net/). A description of the sampled sites is in Appendix 1.

Plots were established following RAINFOR protocol (Phillips et al. 2009). In each plot, all individual trees, palms, and lianas with a diameter at breast height of 1.30 m (dbh) > 10 cm were counted, and their diameters at breast height were recorded. The basal area (m^2) of individual trees was calculated as 3.1416*radius^2 and then summed at the plot level. Specimens were identified to species in the field by expert botanists. Large lianas (> 10 cm dbh) were not abundant in our plots, but the large herb *Phenakospermum guianensis* was found in some plots and was included when individuals had a dbh > 10 cm. Bamboo (*Guadua* spp.) usually does not reach 10 cm in diameter and was therefore not included in any of the censuses (Londoño and Peterson 1991). For species that could not be identified in the field, morphospecies and voucher specimens were assigned and subsequently identified by comparing them to herbarium collections and the botanical literature at the Noel Kempff Mercado Natural History Museum, Bolivia (Bolivian specimens), the Universidad Nacional San Antonio Abad del Cusco, Peru (Peruvian specimens), and the University of Leeds, UK (Brazilian specimens).

We counted 21,252 stems across the 41 plots. Of these trees, 16,010 (75%) were identified to 972 species, 4368 (21 %) were assigned to 271 genera, 627 (3%) to 43 families, and 247 (1 %) were either morphospecies or were coded as unknown taxa. All samples were used to obtain a total number of stems to calculate the proportion of abundance, basal area, and carbon stocks of taxa of interest. We use the terms abundance and density to refer to the number of stems per hectare.

We used published ethnobotanical studies and lists of species with economic importance from the region to assign taxa to timber and nontimber groups (Mostacedo et al. 2003, Dauber et al. 2005, Cossio-Solano 2009, Baraloto et al. 2014, Moraes R. 2014, ITTO 2016). We included all taxa reported to have commercial monetary value or importance for subsistence at local, regional, and global scales. If taxa are used for both timber and nontimber products, they were included only in the category of major use. We further specified other potential uses, i.e., construction (including thatching), firewood, medicine, handcraft and latex, resins, and food for humans and wildlife.

To facilitate the analysis, we grouped nontimber and timber taxa (genera and species) into one of three density classes. Taxa with a density of > two stems per hectare were considered dominant. Taxa with one or two individuals per hectare were considered common, whereas taxa with less than one individual per hectare were considered rare (for a similar classification see Pitman et al. 2001).

Aboveground carbon stock estimation

Aboveground carbon stocks (AGC) were estimated using aboveground biomass (AGB) of trees and palms with dbh > 10 cm. We estimated biomass as a function of dbh and wood density following the allometric equation of Goodman et al. (2013). We used this equation because it was developed in the region and because we only measured stem diameter. We used the estimated wood density values for Neotropical species compiled by Zanne et al. (2009). We compared aboveground mass estimated with equations published by Chave et al. (2014) and Goodman et al. (2014) and found no significant differences across the 41 sampled plots at $p < 0.05$ ($F\ 3.532\ p = 0.064$). The Goodman et al. (2014) equation is described below:

$$\mathrm{AGB} = \exp\left(-0.9563 + \left(2.4186 * \ln(\mathrm{D})\right) + \left(1.5241 * \ln(\mathrm{WD})\right)\right) \quad (1)$$

Where:

AGB = aboveground biomass (kg), WD = wood density (g cm^{-3}), and D = diameter at breast height (dbh; cm).

Aboveground biomass of palms was estimated as compiled by Goodman et al. (2013).

$$\mathrm{AGB} = \exp\left(-3.3488 + 2.7483 * \ln(\mathrm{D})\right) \quad (2)$$

We used the factor 0.4735 to convert aboveground biomass into aboveground carbon (Martin and Thomas 2011). Aboveground carbon stored in species was transformed to CO_2-eq (greenhouse gas emitted/reduced in land use and conversion accounting) by multiplying carbon by 3.67, i.e., the ratio between the molar mass of CO_2 and C (Watson et al. 2000). We used a reference price of US$5 per 1 Mg of CO_2-eq to calculate the potential revenue of carbon stored in taxa based on 2014 market prices (Peters-Stanley and Gonzalez 2014).

Statistical analysis

We tested for statistically significant differences in relative abundance, basal area, and aboveground carbon between economically important taxa, taxa with minor or unknown uses, and unknown taxa groups across the 41 1-ha plots. We also tested for significant differences in relative abundance, basal area, and AGC of economically important taxa grouped as dominant, common, and rare. We applied Welch and post hoc Games-Howell tests instead of ANOVA if normality (Shapiro-Wilk) and homogeneity of variances (Levene) tests on each variable were significant at $p < 0.05$ (McDonald 2014; http://blog.minitab.com/blog/adventures-in-statistics/did-welchs-anova-make-fishers-classic-one-way-anova-obsolete). We performed a simple regression analysis between taxa density (independent) and AGC (dependent variable) and developed a scatter plot between taxa

density and median diameter to investigate relationships among these variables. We used the statistical software IBM SPSS V23 2016.

RESULTS

Plot mean stem density, basal area, and aboveground carbon

Mean abundance (508 to 545 individuals per plot), basal area (24 to 25 m²), and aboveground carbon (128 to 129 Mg) differed slightly between plots on terra firme and former floodplains (Table 1). However, analysis of variance showed no significant difference at $p < 0.05$ between these two edaphic types.

Stem density, basal area, and carbon stocks of tree species in economic classes

Of the 1298 taxa (species and genera) present in our plots, 263 were exploited for commercial or subsistence purposes. The list of economically important taxa and their densities are presented in Appendix 2. Taxa exploited for nontimber or timber products accounted for 45% of all stems, 53% of the total basal area, and 56% of total AGC. Taxa with minor or unknown uses accounted for 51% of all stems but accounted for both lower basal area (43%) and AGC (40%). Unknown taxa represented only four percent of total stems (Table 2). Welch tests showed there were significant statistical differences between stems grouped as economically important, minor or unknown use, and unknown taxa when compared for density (stems ha^{-1}), i.e., $F(2, 75.68) = 288.73$, $p < 0.001$, basal area ($m^2\ ha^{-1}$) $F(2, 73.05) = 212.28$, and aboveground carbon ($Mg\ ha^{-1}$) $F(2, 72.89) = 203.28$, $p < 0.001$ (Table 3). Games-Howell post hoc tests showed significant results for all pairwise comparison at $p < 0.05$, except for density between groups of economic importance and minor or unknown use taxa.

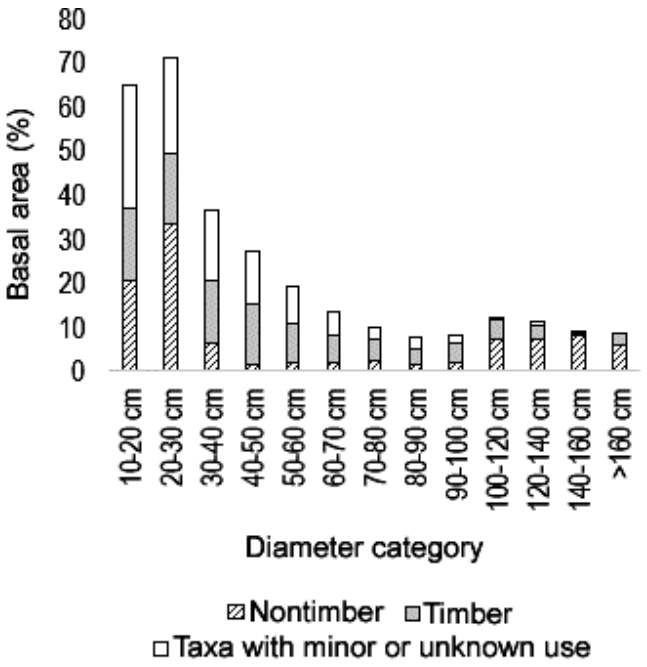
We related the proportion of basal area (%) with stem diameter classes (cm) of taxa grouped in nontimber, timber, and minor or unknown use. The nontimber group showed a bimodal shape with peaks at small diameter classes of 10-20 cm and at above 100 cm in diameter. The timber group showed more than a half of basal area skewed to diameter classes above 40 cm (Fig. 2). Minor or unknown use species had more than half of their basal area in diameter classes below 40 cm.

Relationship between stem density and carbon stock

The dominant group had 32% of total stem abundance compared to 13% for both common and rare economically important taxa. Common and rare taxa had a higher basal area (27% of the total) than that of the dominant group (26%). Dominant taxa stored 22% of the total AGC, whereas common and rare together stored 35% (Table 4). Welch tests showed there were significant differences between dominant, common, and rare groups for abundance $F(2, 69.65) = 128.49$, $p = 0.000$, basal area $F(2,79.23) = 35.93$, $p = 0.000$, and aboveground carbon $F(2,78.31) = 6.58$, $p = 0.002$ (Table 5). The post hoc Games-Howell for AGC was not significant between stems of dominant and rare taxa ($p = 0.98$), but significant between common vs. dominant and common vs. rare ($p = 0.001$).

We ranked taxa in proportion to their contribution to carbon stocks in our 41 plots. The 62 taxa with the highest carbon stocks are shown in Table 6. The emblematic nontimber and common *B. excelsa* had the highest aboveground carbon stock (11.28 Mg ha^{-1}), representing as much as nine percent of the total. The dominant exploited taxa *Tetragastris* spp., *Pseudolmedia* spp., *Brosimum* spp., *Eschweleira* spp., *Iriartea deltoidea*, and *Euterpe precatoria* also show high values of carbon stocks. Rare commercial important timber taxa, such as *Apuleia leiocarpa*, *Cedrelinga cateniformis*, *Couratari macrosperma*, *Dipteryx odorata*, *Cariniana micrantha*, and *Ceiba pentandra* also rank among the taxa with the highest carbon stocks (Table 6).

Fig. 2. Contribution of diameter classes (cm) to the basal area (%) in species and genera used for nontimber products (hatched bars), timber products (gray bars). Taxa with minor or unknown use are shown (white bars). Taxa were sampled in 41 1-ha permanent plots located in terra firme and floodplain forests in southwestern Amazonia.



A scatter plot between density (stems per hectare) and median of diameter (cm) for economically important taxa shows nontimber *B. excelsa* (common) and timber *Ceiba* spp., *Cariniana* spp., and *Dipteryx* spp. (rare) are among the ones skewed to median above 45 cm at density values below 2 stems per hectare, whereas *Tetragastris* spp., *Pseudolmedia* spp., and *Euterpe precatoria*, among other dominant ones, have a median diameter below 30 cm (Fig. 3). These taxa showed an inverse-J abundance distribution curve (figure not shown).

The regression analysis between taxa density and aboveground carbon stocks showed a positive relationship ($r^2 = 0.43$, $F = 289.9$, $p < 0.000$; Fig. 4). There was one prominent outlier in this relation: *B. excelsa* was the species with the highest AGC stock by far but realized this carbon stock at a relatively low density (1.54 trees per hectare). The explanation for this outlier is the very high median dbh (100 cm) of *B. excelsa* trees. In this species, 64% of the stems are > 45 cm in dbh. The strongly skewed population structure of this species also caused it to be the species with the highest basal area values in this study.

Table 1. Mean density (number of stems ha^{-1}), basal area (m^2 ha^{-1}), and carbon (Mg ha^{-1}) of 41 plots of 1 ha each (30 terra firme and 11 floodplain forests) located in southwestern Amazonia. Standard deviation and analysis of variance results (F and significance at $p < 0.05$) are shown. Degrees of freedom were 1 in numerator and 39 in denominator.

	Mean density	SD	F	sig	Mean basal area (m^2)	SD	F	sig	Mean AGC (Mg)	SD	F	sig
Terra firme	508	86	1.523	0.2	24	39	0.33	0.57	128	22	0.029	0.87
Former floodplain	545	83			25	5			129	12		

Table 2. Taxa classified according to their major uses as nontimber (food, fibers, latex, medicine, construction, and thatching) and timber (wood for furniture, construction, and firewood). The genus level was used for calculation if use occurs irrespective of species level. Values of minor or unknown use and unknown taxa are shown. Number of taxa, abundance, basal area, and aboveground carbon in absolute values and percentage are shown. Taxa were sampled in 41 1-ha permanent plots located in 19 terra firme and floodplain forests in southwestern Amazonia.

Taxa use category	Number of taxa	Absolute stems abundance	(%) of total abundance	Absolute basal area (m^2)	(%) of total basal area	Absolute aboveground carbon (Mg)	(%) of total aboveground carbon
Species or genera primarily used for nontimber products	22	3331	16	160	16	806	15
Species or genera primarily used for timber products	241	6246	29	370	37	2162	41
Taxa with minor or unknown use	980	10,801	51	439	43	2088	40
Unknown taxa and use	55	874	4	40	4	212	4
Total	1298	21,252	100	1009	100	5268	100

Table 3. Welch tests statistics (F) for density (stems ha^{-1}), basal area (m^2 ha^{-1}), and aboveground carbon (Mg ha^{-1}) of species and genera used for nontimber and timber products, of species and genera with minor and unknown use and unknown taxa. Sampled plots (N), mean, standard deviation, degrees of freedom (df1 and df2), and significance level at $p < 0.005$ are shown. Taxa were sampled in 41 1-ha permanent plots located in terra firme and floodplain forests in southwestern Amazonia.

Use	N	Mean	Standard deviation	Welch test asymptotically F distributed.	df1	df2	Significance level
Density (stems ha^{-1})							
Species or genera economically important	41	233.59	63.82	288.73	2.00	75.68	0.000
Species or genera with minor importance or unknown use	41	263.44	61.83				
Unknown taxa	39	22.41	39.86				
Total	121	175.64	120.61				
Basal area (m^2 ha^{-1})							
Species or genera economically important	41	12.95	4.27	212.28	2.00	73.05	0.000
Species or genera with minor importance or unknown use	41	10.70	3.17				
Unknown taxa	39	1.02	2.00				
Total	121	8.34	6.11				
Aboveground carbon (Mg ha^{-1})							
Species or genera economically important	41	72.38	25.50	203.27	2.00	72.89	0.000
Species or genera with minor importance or unknown use	41	50.93	14.65				
Unknown taxa	39	5.43	10.29				
Total	121	43.53	33.12				

Table 4. Economically important nontimber and timber (including construction wood and firewood uses) taxa classified as dominant (taxa with a density of > two stems per hectare), common (taxa with one to two individuals per hectare), or rare (taxa with fewer than one individual per hectare). Number of taxa, abundance (number of stems), basal area (m^2), and aboveground carbon (Mg) in absolute value and percentage are shown. Values of minor or unknown use and unknown taxa are shown. Taxa were sampled in 41 1-ha plots located in terra firme and floodplain forests in southwestern Amazonia.

Taxa density category	Number of taxa	Number of stems	% of total abundance	Absolute basal area (m^2)	% of total basal area	Absolute aboveground carbon (Mg)	% of total aboveground carbon
Dominant							
Species or genera primarily used for nontimber products	8	2991	14	92	9	253	5
Species or genera primarily used for timber products	17	3925	18	169	17	899	17
Common							
Species or genera primarily used for nontimber products	2	111	1	49	5	469	9
Species or genera primarily used for timber products	12	706	3	40	4	216	4
Rare							
Species or genera primarily used for nontimber products	12	229	1	19	2	84	1
Species or genera primarily used for timber products	212	1615	8	161	16	1046	20
Other categories							
Taxa with minor or unknown use	980	10,801	51	439	43	2088	40
Unknown taxa and use	55	874	4	40	4	212	4
Total	1298	21,252	100	1009	100	5268	100

Fig. 3. Relationship between median diameter (cm) and density (stems per hectare) of species and genera primarily used for nontimber and timber products. Species and genera with the highest median diameter are labeled. Taxa were sampled in 41 1-ha permanent plots located in terra firme and floodplain forests in southwestern Amazonia.

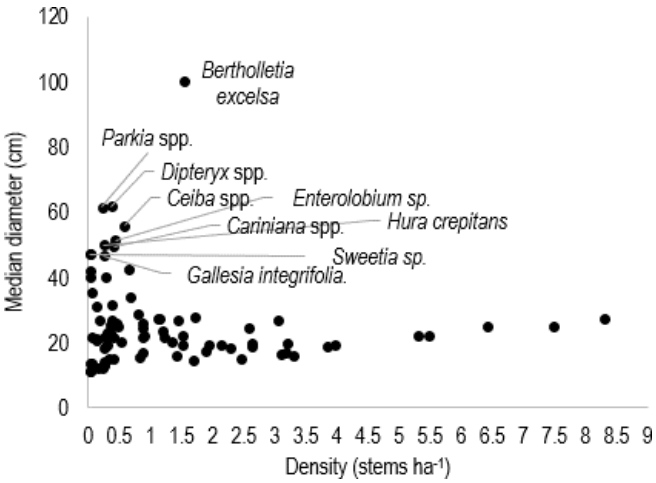
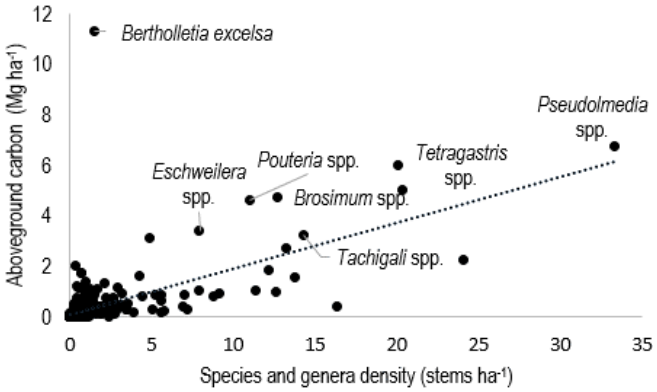


Fig. 4. Relationship between density (stems per hectare) and aboveground carbon (AGC; Mg per hectare) of species and genera sampled in 41 1-ha permanent plots located in terra firme and floodplain forests in southwestern Amazonia. Species and genera with the highest AGC values are labeled. $R^2 = 0.43$.



Estimated value of aboveground carbon in CO_2-eq units

The average aboveground carbon stock per hectare was 128.48 Mg. This is equivalent to 471.51 Mg CO_2-eq ha^{-1}. At a referential price of US$5 per Mg CO_2-eq (Peters-Stanley and Gonzalez 2014), the monetary value of the carbon per hectare in southwestern Amazonia is US$2357 (Table 7). From the total potential value of carbon stored in the plot network, the equivalent to US$1328 is the aboveground CO_2-eq value of economically important taxa utilized for commercial and livelihood purposes. *Bertholletia excelsa* alone has a CO_2-eq value of US$207 ha^{-1}.

DISCUSSION

Economically important tree species (> 10 cm dbh) contribute significantly to forest structure and aboveground carbon storage

Table 5. Welch tests (F) for density (stems ha^{-1}), basal area (m^2 ha^{-1}), and aboveground carbon (Mg ha^{-1}) of economically important nontimber and timber taxa grouped into dominant taxa (> two stems per hectare), common taxa (one to two stems per hectare), and rare taxa (fewer than one stem per hectare). Mean, standard error, degrees of freedom (df1 and df2), and significance at $p < 0.05$ per variable are shown. Values for minor and unknown use and unknown taxa were excluded from the analysis. Taxa were sampled in 41 1-ha permanent plots located in 19 terra firme and floodplain forests in southwestern Amazonia.

Taxa density categories	Mean	Standard error	Welch test asymptotically F distributed.	df1	df2	Sig
Density (stems ha^{-1})						
Dominant	169	9.77	128.49	2	69.65	0.000
Common	20	1.89				
Rare	45	2.70				
Basal area (m^2 ha^{-1})						
Dominant	6	0.39	35.933	2	79.23	0.000
Common	2	0.31				
Rare	4	0.37				
Aboveground carbon (Mg ha^{-1})						
Dominant	28	1.89	6.583	2	78.31	0.002
Common	17	2.69				
Rare	28	2.33				

relative to taxa with minor or unknown economic use as inferred from 19 sites sampled in moist, submontane, terra firme and floodplain forest of southwestern Amazonia. The anthropogenic influence on these forests has received great attention in the last decade: ethnobotanical studies suggest that pre-Columbian peoples domesticated and dispersed at least 138 different crops for subsistence and trade, of which 68% were trees or woody perennials (Giux 2009, Scoles and Gribles 2011, Shepard and Ramirez 2011, Clement et al. 2015, Thomas et al. 2015, Levis et al. 2017). Other ethnobotanical studies in Madre de Dios, Peru reported 94% of woody stems in a 6.1 ha tree inventory to be useful (Phillips et al. 1994). In the same study, people indicated that 20% of species had commercial value and that 80% were used for subsistence. Thus, the potential contribution of ethnobotanical species to the economy and carbon stocks in southwestern Amazonia may be even higher than what we found in our study. Additionally, within economically important trees and palm taxa, there are key species that provide food for wildlife; these provide another reason to improve forest management.

Common and rare economic taxa contribute 35% of total aboveground carbon stocks versus 22% of that of the dominant class (Table 4). This follows mathematically from allometric equation (1) in which diameter has a much greater impact on aboveground carbon stocks estimation than wood density, especially for taxa with few stems at a high basal area. That said, low abundance is compensated by high basal areas in these taxa. The Brazil nut tree (*B. excelsa*) ranked first in terms of carbon storage, illustrating the dominant role of this economically important species for carbon stocks in forests of southwestern Amazonia. Fauset et al. (2015) ranked *B. excelsa* as the third most important species for Amazonian carbon stocks, which is clearly a very prominent role.

The question arises on how representative our sampled plots of southwestern Amazonian forests are, and how does our study reflect the abundance patterns of taxa and aboveground carbon, especially those with very important economic roles such as *B. excelsa* (Guariguata et al 2017). Forest types in the region are diverse because of elevation, geology, and climatic and soil differences, yet most of the region falls in the submontane range of 100-300 masl. Our sites represent evergreen seasonal forest with the presence of *Guadua* spp., which is typical of central and west, and also with a high abundance of *Attalea* spp. and *Phenakospermum guyanense* in the east of the region (Josse et al. 2007, Mostacedo et al. 2009, Navarro and Ferreira 2009, Salimon et al. 2011, Pintaud et al. 2016). Such forest types encompass sites in which *B. excelsa* is widely distributed, managed, and plays an important role in the economy (26% of total region area). Note that 65% of the total transboundary area has been classified as suitable for forest management and potentially includes *B. excelsa* (INRA 2008, IUCN 2008, Soliz 2009, Chávez et al. 2012, TEEB 2013). Unfortunately, high-quality inventories and extended sampling are still scarce in the region. Our results conservatively provide an indication of potential key species contributors to economy and carbon in at least three-quarters of the region, which is a very important regional portion.

How is it possible that *B. excelsa* plays such a prominent role in carbon stocks compared to the rest of economically important taxa and to taxa with minor or unknown use? The most obvious explanation is the population structure of the species, in which a high proportion of trees are in diameter classes above 40 cm (Peres et al. 2003, Zuidema 2003, Licona-Vasquez et al. 2010). This can be explained by the fact that the species is both emergent and long-lived (Camargo et al. 1994, Brienen and Zuidema 2006, Schöngart et al. 2015). It must also be noted that *B. excelsa* has the extra advantage by having a higher stem density than other emergent species, such as *Ceiba* spp. and *Dipteryx* spp. The density of *B. excelsa* (1.5 stems ha^{-1}), in our study, is in the same ranges as found in other similar studies that did not follow a random and stratified sampling (Peres et al. 2003, Zuidema 2003, Nunes et al. 2012, Baraloto et al. 2015; Vaca, *unpublished data*). Note that only 4 of the 41 plots in this study overlap with those reported by Zuidema (2003). Our results also fall in the range of values obtained in a landscape-wide stratified sampling inventory in

Table 6. Species and genera (N = 62) with the highest aboveground carbon (AGC Mgha^{-1}) values at a given density (stems per hectare). Taxa with major economic uses are timber (T), food (F), fruits (A), construction, including thatching (C), medicine (M), handcrafts (H), and as firewood (F), latex (L), between parenthesis if only locally used. Taxa were sampled in 41 permanent plots of 1 hectare each, located in 19 terra firme and floodplain forests in southwestern Amazonia (Killeen et al. 1993, Ledo 1996, TCA 1996, van Andel 2000, Duivenvoorden et al. 2001, Gutiérrez and Silva 2002, Ródriguez et al. 2002, Clavo et al. 2003, Mostacedo et al. 2003, Reynel et al. 2003, INFOBOL 2004, Dauber et al. 2005, Shanley and Medina 2005, Vargas et al. 2005, Thomas and Vandebroek 2006, Vieira et al. 2006, CPM 2008, Khan 2008, Cossio-Solano 2009, Obermüller et al. 2011, Moraes et al. 2014).

Taxa	Density (stems ha^{-1})	AGC (Mg ha^{-1})	Use	Taxa	Density (stems ha^{-1})	AGC (Mg ha^{-1})	Use
Bertholletia excelsa	1.54	11.28	A, T, C, M, U, F	*Endopleura uchi*	0.80	0.75	A
Tetragastris altissima	13.37	4.66	T	*Hymenaea parvifolia*	0.51	0.72	F, T
Pseudolmedia laevis	21.27	4.27	(T), (A)	*Celtis schippii*	4.17	0.72	(A), M
Iriartea deltoidea	23.88	2.24	C, A, M	*Pourouma minor*	5.39	0.70	U
Eschweilera spp.	3.85	1.99	C	*Swartzia* spp.	1.12	0.67	U
Brosimum lactescens	5.51	1.72	T	*Iryanthera juruensis*	7.61	0.65	T, C
Apuleia leiocarpa	0.66	1.72	T	*Castilla ulei*	1.27	0.65	F
Tachigali spp.	5.71	1.62	U	*Inga capitata*	1.93	0.64	(A), F
Pouteria spp.	4.27	1.58	(A)	*Poulsenia armata*	0.90	0.61	U, M, C
Clarisia racemosa	2.98	1.38	T	*Brosimum alicastrum*	0.98	0.60	(A)
Eschweilera coriacea	3.54	1.33	C, M	*Tachigali polyphylla*	5.24	0.60	T, C
Tetragastris panamensis	6.51	1.30	T	*Geissospermum reticulatum*	0.59	0.56	U
Pseudolmedia laevigata	6.49	1.28	(T), (A)	*Parkia* spp.	0.29	0.56	T
Pouteria torta	2.46	1.23	(A)	*Dipteryx alata*	0.05	0.54	T, F, A
Brosimum guianense	3.12	1.22	T, (A)	*Brosimum rubescens*	0.54	0.54	T
Terminalia oblonga	0.29	1.21	T	*Enterolobium schomburgkii*	0.34	0.54	T
Cedrelinga cateniformis	0.49	1.16	T, M	*Aspidosperma macrocarpon*	0.22	0.51	T
Inga spp.	5.78	1.07	A, F	*Gallesia integrifolia*	0.24	0.51	U
Couratari macrosperma	0.56	1.06	T, C, (A)	*Protium* spp.	3.83	0.50	T
Chrysophyllum venezuelanense	1.34	1.05	T, C, M	*Pseudolmedia macrophylla*	2.41	0.50	(A)
Dipteryx odorata	0.12	0.99	T	*Terminalia amazonia*	0.24	0.49	T, C, F
Aspidosperma rigidum	0.63	0.97	T	*Pourouma* spp.	4.15	0.47	U
Peltogyne heterophylla	1.39	0.84	T	*Laetia procera*	0.76	0.47	U
Attalea butyracea	5.66	0.82	C, U	*Pouteria ephedrantha*	0.68	0.46	U
Astronium lecointei	0.85	0.80	T, C	*Brosimum* spp.	2.05	0.44	T
Cariniana micrantha	0.22	0.80	U	*Pseudolmedia* spp.	2.22	0.44	T
Cecropia sciadophylla	4.07	0.79	T, C	*Diplotropis purpurea*	1.17	0.44	U
Siparuna decipiens	10.49	0.78	M	*Heisteria nitida*	0.68	0.44	U
Dialium guianense	1.29	0.77	T	*Hevea brasiliensis*	0.98	0.43	L, T
Ceiba pentandra	0.22	0.77	T	*Euterpe precatoria*	16.29	0.42	A
Leonia glycycarpa	7.90	0.77	U	*Jacaranda copaia*	1.51	0.41	T

Pando (1.1 stems per ha^{-1}) and in Acre (1.9 stems ha^{-1}; DHV 1993, Wadt et al. 2005). The variation in density of *B. excelsa* across Amazonia is high and ranges from 26 stems to less than 1 stem per hectare (Salomão 1991, Zuidema 2003). Groves with more than 5.1 stems ha^{-1} of *B. excelsa* are not as frequent in southwestern Amazonia (Peres and Baider 1997).

For a long time, there have been discussions about the anthropogenic effect on density and conservation of *B. excelsa* trees in the Amazon. Ethnobotanical studies have shown a relationship between *B. excelsa*'s presence close to human settlements that may explain, in part, the density pattern of the species (Giux 2009, Scoles and Gribel 2011, Thomas et al. 2014, Clement et al. 2015). The anthropogenic effect on *B. excelsa* may be also related to local peoples' economic decision of not felling large and productive stems of *B. excelsa*. In fact, the peak production in *B. excelsa* is at the large-diameter classes, i.e., 100 to 150 cm (Kainer et al. 2007; Vaca, *unpublished data*), compared to other commercial species, such as *Copaifera* spp., which can reach peak oil production at 70 cm diameter (Plowden 2004). It is also noteworthy that at a regional level, Brazilian, Bolivian, and Peruvian laws officially prohibit felling of *B. excelsa* trees given their long-term economic importance (Duchelle et al. 2011). The anthropogenic effect on *B. excelsa* is also related to nut harvesting intensities, suspected to cause the low frequency of regeneration cohorts and populations skewed to old senescent trees (Peres et al. 2003, Zuidema 2003, Wadt et al. 2008, Salo et al. 2014). That said, the influence of a single economically important species over carbon stocks in southwestern Amazonia depends on species intrinsic functional traits, but can also be influenced by anthropogenic use.

Timber taxa contribute greatly to carbon stocks in our study. This is because forest users harvest trees identified by a vernacular name or a genus-level name that sometimes involve several species. For example, *Ficus* spp., *Inga* spp., *Protium* spp., *Virola* spp., and *Vochysia* spp. each have at least six species in the study area (Cossio-Solano 2009). Rare, commercially important timber taxa

Table 7. CO_2-eq content (Mg ha^{-1} and US$ ha^{-1}) of nontimber and timber species and genera grouped as dominant (taxa with > two stems per hectare), common (taxa with one to two stems per hectare), and rare (taxa with fewer than one stem per hectare). Per-hectare absolute aboveground biomass (AGB), aboveground carbon (AGC), and CO_2-eq values (absolute values divided by the number of sampled plots) are shown. Carbon fraction in biomass was estimated at 0.4735 (Martin and Thomas 2011), CO_2-eq at 3.67 (IPCC 2000), and CO_2-eq value at a reference price of US$5 per Mg. Values for taxa of minor and unknown use and unknown taxa are shown. Taxa were sampled in 41 1-ha permanent plots located in terra firme and floodplain forests in southwestern Amazonia.

Taxa density categories	AGB (Mg ha^{-1})	AGC (Mg ha^{-1})	CO_2-eq (Mg ha^{-1})	CO_2-eq value (US$ ha^{-1})
Dominant				
Species or genera primarily used for nontimber products	13	6	23	113
Species or genera primarily used for timber products	46	22	81	403
Common				
Species or genera primarily used for nontimber products	24	11	42	210
Species or genera primarily used for timber products	11	5	19	97
Rare				
Species or genera primarily used for nontimber products	4	2	7	37
Species or genera primarily used for timber products	54	26	94	468
Taxa with minor or unknown use	108	51	187	935
Unknown taxa and use	11	5	19	95
Total	271	128	472	2 358

contribute more than dominant taxa to aboveground carbon stocks (Table 4). Rareness is a characteristic trait in Amazonian forests (Pitman et al. 2001, Schulze et al. 2008, Hubbell 2013). Our study suggests that rare species may be particularly vulnerable if these are affected by intensifying anthropogenic pressures such as selective logging (Giudice et al. 2012, Dablin 2014, Baraloto et al. 2015) and enhanced mortality due to climate change (Brienen et al. 2015). Brazil prohibits the harvest of trees at abundances lower than 0.03 stems ha^{-1} (Schulze et al. 2008). In Bolivia, restriction applies to 0.25 stems ha^{-1}, yet above these thresholds, a common practice is to treat species equally. That is, the minimum cutting diameter and the retention of 10 to 20% of seed trees are applied irrespective of population structure. Precautionary measures are specifically recommended for *Swietenia macrophylla*, but much less so for other rare species. As a result, errors in estimating maximum harvesting limits because of poor species identification and erroneous timber estimation in forest inventories increase the chances of unsustainable yields and threaten the provision of the dual economic and environmental role of rare taxa.

The harvest intensity (volume extracted per hectare) can affect the recovery rate of aboveground biomass given the positive relationship between volume extraction and biomass recovery time (West et al. 2014). Low biomass recovery rates may occur if harvest intensity and cutting cycles are not harmonized with the demography and ecological requirements for regeneration after logging (seed dispersal and light demand among others) of each taxon. In our study, we found taxa with high commercial value, such as *Ficus* spp., *Ceiba* spp., *Dipteryx* spp., *Cedrelinga cateniformis*, *Cariniana* spp., and *Terminalia oblonga*, having an unbalanced population and distribution of stem sizes. These taxa had stems skewed to high-diameter classes with at least half of the population at sizes above 45 cm diameter and few stems in young categories (10 to 20 cm). Some of these taxa, including nontimber *B. excelsa*, are already in threatened (i.e., vulnerable) categories of IUCN (2015) with data obtained at the landscape level. Studies on natural regeneration and recruitment are still scarce and the ones carried out in the region point out few important species mostly heliophytes being favored by the canopy openness, among them *B. excelsa*, *Cedrela* spp., *Apuleia* spp., and *Couratari* spp. (Myers et al. 2000, Parrota et al. 2002, Mostacedo et al. 2009). Note that our study is limited to trees with dbh > 10 cm as compared to other studies at minimum dbh > 2.5 cm or regeneration sampling of seedlings < 1.3 m height. However, a study in a moist tropical forest of Panama found higher mortality rates in regeneration classes below dbh < 10 cm than in those with dbh > 10 cm, especially in large species (Condit et al. 1995). Research should address regeneration of many more species, their light requirements, and responses to logging gaps to improve silvicultural prescriptions. Inventories may enhance their accuracy by sampling trees < 10 cm dbh coupled with floristic identification to predict species populations and carbon recovery over time.

Guidelines for forest management include a reduced impact logging to facilitate rapid recovery of forest (Putz et al. 2008*a*, *b*). For the southwestern Amazonian forest, where timber and Brazil nut trees are exploited, the logging intensity that modifies the environmental conditions for *B. excelsa* also needs to be addressed, because this species depends on a well-preserved forest to produce. A potential negative effect of increased logging intensity on Brazil nuts' productivity has been shown by Rockwell et al. 2015. A timber harvest limit of 5 m^3 ha^{-1} is prescribed to avoid damage to productive *B. excelsa* trees (Guariguata et al. 2009), but unfortunately, a lack of enforcement of maximum harvesting limits spells an uncertain future for Brazil nut trees and for other important economic species and species key for fauna. Additionally, uncertainty about the sustainability of Brazil nut harvests arises from the potential effect of nut collection on natural regeneration and the negative effect of frequent fires, habitat destruction, and drought on Brazil nut production.

The overall loss of forest economic value is the first step to land-use conversion and concomitant CO_2 emissions. REDD+ has opened up the opportunity to value carbon stocks in tropical

countries to compensate the low opportunity cost of forest-based economies through incentives for conservation and forest management. In Acre (Brazil) and Madre de Dios (Peru), projects are using the carbon market opportunity to generate incentives for conservation and recover economically valuable species and their carbon, including *B. excelsa*, *Dipteryx odorata*, *Cedrelinga cateniformis*, *Euterpe precatoria*, and *Hevea brasiliensis* (TEEB 2013, Bosques Amazónicos 2014, Duchelle et al. 2014*b*). The Bolivian government has rejected the carbon market approach but has created the Conjoint Mechanism for Climate Change Mitigation to support environmentally friendly initiatives (EPB 2012, Rouch 2015). REDD+ incentives are an opportunity for a rigorous revision and application of precautionary measures to adjust maximum harvesting limits and minimum cutting diameters at the species level to guarantee future yields, regeneration, and conservation of key species and their carbon in the southwestern Amazonian forest (van Gardingen et al. 2006, Schulze et al. 2008, Giudice et al. 2012, Rockwell et al. 2015). Permanent plots are a valuable tool to address growth, phenology, and mortality and to inform forest management and climate change mitigation policies.

CONCLUSION

Our study demonstrates that useful tree species in tropical forests have a dual role because they contribute considerably to both carbon storage and subsistence, especially those present in low abundance. In southwestern Amazonia, this dual role is presented most prominently by the Brazil nut tree, *B. excelsa*, which is exploited for nontimber forests products and accounts for around nine percent of the carbon stocks in forests in the region. This is a clear example of a synergy between economic gains and ecological function. Conserving and carefully managing stands of *B. excelsa* is not just important in terms of carbon stocks, but also because fruit production depends on the presence of an intact forest that harbors several other valuable species. Unplanned harvest can disrupt synergistic economic and environmental service roles altering carbon stocks temporarily or permanently. Maximum harvesting limits should address protection for *B. excelsa* populations, as has been the focus of other studies, but also prevent the extinction of other nontimber and timber valuable species by enforcing strict species-based extraction rules. Despite the controversy of market approach fairness to value ecosystem services of tropical forests, carbon stored in trees and palms already has a monetary value that is being channeled to early REDD+ initiatives in southwestern Amazonia. Precautionary measures based on species' ecology, demography, and regeneration traits should be at the forefront of REDD+ to reconcile sustainable yields and conservation of forest values to prevent emissions from land-use change and forest management.

Responses to this article can be read online at:
http://www.ecologyandsociety.org/issues/responses.php/9297

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Appendix 1. Description of 19 sites sampled in 41-1 ha forest plots located in Madre de Dios (Peru), Acre (Brazil) and Pando (Bolivia) in southwestern Amazonia

Region	Plot name	X	Y	Altitude	Forest type	Forest composition	Edaphic type	Reference
Madre de Dios	TAM-01	468700	8580079	215	Alluvial	mixed forest	Former floodplain	https://www.forestplots.net/
Madre de Dios	TAM-02	468947	8581150	214	Alluvial	mixed forest	Former floodplain	https://www.forestplots.net/
Madre de Dios	TAM-05	470636	8581609	216	Forest dense	mixed forest	Terra firme	https://www.forestplots.net/
Madre de Dios	TAM-06	467884	8580695	205	Forest dense alluvial	mixed forest	Terra firme	https://www.forestplots.net/
Madre de Dios	TAM-07	471655	8582109	228	Forest dense	mixed forest	Terra firme	https://www.forestplots.net/
Madre de Dios	TAM-08	470766	8582047	225	Forest dense	mixed forest	Terra firme	https://www.forestplots.net/
Madre de Dios	TAM-09	469152	8581543	212	Forest dense alluvial	mixed forest	Former floodplain	https://www.forestplots.net/
Madre de Dios	CUZ-01	493489	8613972	205	Forest dense alluvial	mixed forest	Former floodplain	https://www.forestplots.net/
Madre de Dios	CUZ-02	493718	8613742	209	Forest dense alluvial	mixed forest	Former floodplain	https://www.forestplots.net/
Madre de Dios	CUZ-03	494138	8614363	206	Forest dense alluvial	mixed forest	Former floodplain	https://www.forestplots.net/
Madre de Dios	CUZ-04	494405	8614135	203	Forest dense alluvial	mixed forest	Former floodplain	https://www.forestplots.net/
Madre de Dios	ALM-0A1	231208	8694378	396	Forest dense	mixed forest	Former floodplain	https://www.forestplots.net/
Madre de Dios	ALM-0A2	231208	8694378	396	Forest dense	mixed forest	Former floodplain	https://www.forestplots.net/
Madre de Dios	LAS-02	379762	8611685	200	Forest dense	mixed forest	Former floodplain	https://www.forestplots.net/
Madre de Dios	LAS-0A1	379762	8611685	200	Forest dense	mixed forest	Terra firme	https://www.forestplots.net/
Madre de Dios	LAS-0A2	379762	8611685	200	Forest dense	mixed forest	Terra firme	https://www.forestplots.net/
Acre	POR-01	525027	8803698	276	Forest open palm+dense	mixed forest	Terra firme	https://www.forestplots.net/
Acre	POR-02	525200	8806372	270	Forest open palm+dense	mixed forest	Terra firme	https://www.forestplots.net/
Acre	DOI-01	574810	8831928	198	Forest open palm alluvial	mixed forest	Terra firme	https://www.forestplots.net/

Continuation Appendix 1.

Region	Plot name	X	Y	Altitude	Forest type	Forest composition	Edaphic type	Reference
Acre	DOI-02	575864	8833916	205	Forest open bamboo+palm +dense	bamboo dominated	Terra firme	https://www.forestplots.net/
Acre	RFH-01	645677	8921884	173	Forest open bamboo+palm	mixed forest	Terra firme	https://www.forestplots.net/
Acre	RST-01	140796	8999012	271	Forest open palm+bamboo +dense	mixed forest	Terra firme	https://www.forestplots.net/
Acre	MTH-01	82805	9015922	239	Forest open palm+bamboo	mixed forest	Terra firme	https://www.forestplots.net/
Acre	MIN-01	70250	9050569	230	Forest open palm	mixed forest	Terra firme	https://www.forestplots.net/
Pando	EBT-03	497780	8738956	258	Forest dense	mixed forest	Terra firme	Unpublished
Pando	EBT-04	498267	8739349	281	Forest dense	mixed forest	Terra firme	Unpublished
Pando	SSI-01	520544	8761323	268	Forest dense	mixed forest	Terra firme	Unpublished
Pando	CIB-01	521475	8761560	268	Forest dense	mixed forest	Terra firme	Unpublished
Pando	LPD-06	810785	8778225	145	Forest dense	mixed forest	Terra firme	Unpublished
Pando	SLC-05	621291	8778637	243	Forest dense	mixed forest	Terra firme	Unpublished
Pando	RET-05	859054	8785263	145	Forest dense	mixed forest	Terra firme	https://www.forestplots.net/
Pando	RET-06	859054	8785263	145	Forest dense	mixed forest	Terra firme	https://www.forestplots.net/
Pando	RET-08	859054	8785263	145	Forest dense	mixed forest	Terra firme	https://www.forestplots.net/
Pando	RET-09	859054	8785263	145	Forest dense	mixed forest	Terra firme	https://www.forestplots.net/
Pando	MBT-01	841012	8887308	154	Forest dense	mixed forest	Terra firme	https://www.forestplots.net/
Pando	MBT-02	877414	8858679	145	Forest dense	mixed forest	Terra firme	https://www.forestplots.net/
Pando	MBT-04	869672	8888990	148	Forest open palm	mixed forest	Terra firme	https://www.forestplots.net/
Pando	MBT-05	868261	8888607	147	Forest open palm	mixed forest	Terra firme	https://www.forestplots.net/
Pando	MBT-06	868261	8888607	147	Forest open palm	mixed forest	Terra firme	https://www.forestplots.net/
Pando	MBT-07	856328	8899394	140	Forest dense alluvial+palm+ bamboo	mixed forest	Former floodplain	https://www.forestplots.net/
Pando	MBT-08	856328	8899394	140	Forest dense alluvial+palm+ bamboo	mixed forest	Former floodplain	https://www.forestplots.net/

Appendix 2. Mean density (stems per hectare) of taxa sampled in 41 ha plots in forest of southwestern Amazonia

Non-timber species	stems per hectare	Timber	Stems per hectare	Timber species	Stems per hectare
Iriartea deltoidea	*23.88*	*Clarisia racemosa*	2.98	*Brosimum rubescens*	0.54
Euterpe precatoria	*16.29*	*Virola* spp.	2.78	*Matisia cordata*	0.54
Siparuna decipiens	*10.49*	*Pseudolmedia macrophylla*	2.41	*Virola surinamensis*	0.54
Socratea exorrhiza	*7.00*	*Pseudolmedia* spp.	2.22	*Aniba canelilla*	0.51
Attalea butyracea	*5.66*	*Virola calophylla*	2.10	*Hymenaea parvifolia*	0.51
Oenocarpus bataua	*4.12*	*Brosimum* spp.	2.05	*Inga edulis*	0.51
Theobroma cacao	*3.05*	*Inga capitata*	1.93	*Cedrelinga cateniformis*	0.49
Pouteria torta	*2.46*	*Virola sebifera*	1.83	*Myroxylon balsamum*	0.49
Bertholletia excelsa	*1.54*	*Matisia* spp.	1.76	*Inga marginata*	0.46
Attalea phalerata	*1.17*	*Jacaranda copaia*	1.51	*Tapura juruana*	0.46
Hevea brasiliensis	*0.98*	*Protium amazonicum*	1.51	*Virola elongata*	0.44
Poulsenia armata	*0.90*	*Peltogyne heterophylla*	1.39	*Inga auristellae*	0.41
Oenocarpus mapora	*0.85*	*Ocotea* spp.	1.37	*Ficus* spp.	0.41
Endopleura uchi	*0.80*	*Chrysophyllum venezuelanense*	1.34	*Inga laurina*	0.39
Astrocaryum gratum	*0.59*	*Dialium guianense*	1.29	*Spondias mombin*	0.39
Astrocaryum spp.	*0.51*	*Castilla ulei*	1.27	*Anacardium giganteum*	0.37
Attalea spp.	*0.41*	*Unonopsis matthewsii*	1.02	*Aniba taubertiana*	0.37
Pouteria caimito	*0.29*	*Tachigali paniculata*	1.00	*Calophyllum brasiliense*	0.34
Mauritia flexuosa	*0.12*	*Brosimum alicastrum*	0.98	*Enterolobium schomburgkii*	0.34
Attalea maripa	*0.07*	*Minquartia guianensis*	0.93	*Protium rhynchophyllum*	0.34
Bactris gasipaes	*0.02*	*Aniba* spp.	0.88	*Protium sagotianum*	0.34
Chelyocarpus chuco	*0.02*	*Astronium lecontei*	0.85	*Tabebuia incana*	0.32
Timber		*Aspidosperma vargasii*	0.83	*Cabralea canjerana*	0.29
Pseudolmedia laevis	*21.27*	*Aspidosperma spp.*	0.71	*Cedrela odorata*	0.29
Tetragastris altissima	*13.37*	*Hevea* spp.	0.71	*Cordia alliodora*	0.29
Iryanthera juruensis	*7.61*	*Matisia ochrocalyx*	0.68	*Huberodendron swietenioides*	0.29
Tetragastris panamensis	*6.51*	*Apuleia leiocarpa*	0.66	*Inga alba*	0.29
Pseudolmedia laevigata	*6.49*	*Pseudolmedia murure*	0.66	*Inga chartacea*	0.29
Inga spp.	*5.78*	*Virola flexuosa*	0.66	*Inga punctata*	0.29
Brosimum lactescens	*5.51*	*Iryanthera spp.*	0.66	*Protium aracouchini*	0.29
Celtis schippii	*4.17*	*Ocotea bofo*	0.61	*Terminalia oblonga*	0.29
Protium spp.	*3.83*	*Unonopsis* spp.	0.61	*Protium nodulosum*	0.27
Eschweilera coriacea	*3.54*	*Couratari macrosperma*	0.56	*Couratari* spp.	0.27
Brosimum guianense	*3.12*	*Chrysophyllum* spp.	0.56	*Aniba terminalis*	0.24

continue appendix 2

Timber species	Stems per hectare	Timber species	Stems per hectare	Timber species	Stems per hectare
Gallesia integrifolia	0.24	*Mezilaurus itauba*	0.15	*Cariniana estrellensis*	0.07
Guarea guidonia	0.24	*Ocotea rubrinervis*	0.15	*Ceiba speciosa*	0.07
Hura crepitans	0.24	*Virola multinervia*	0.15	*Chorisia insignis*	0.07
Inga coruscans	0.24	*Ceiba* spp.	0.15	*Dipteryx ferrea*	0.07
Inga sarmentosa	0.24	*Clarisia* spp.	0.15	*Dipteryx micrantha*	0.07
Manilkara bidentata	0.24	*Terminalia* spp.	0.15	*Ficus trigona*	0.07
Protium puncticulatum	0.24	*Vochysia* spp.	0.15	*Inga coriacea*	0.07
Schefflera morototoni	0.24	*Amburana cearensis*	0.12	*Inga pavoniana*	0.07
Astronium spp.	0.24	*Andira surinamensis*	0.12	*Inga quaternata*	0.07
Tabebuia spp.	0.24	*Brosimum parinarioides*	0.12	*Inga stipularis*	0.07
Terminalia amazonia	0.24	*Copaifera reticulata*	0.12	*Inga striata*	0.07
Aniba panurensis	0.22	*Couma macrocarpa*	0.12	*Inga suaveolens*	0.07
Aspidosperma macrocarpon	0.22	*Dipteryx odorata*	0.12	*Matisia rhombifolia*	0.07
Cariniana micrantha	0.22	*Ficus gomelleira*	0.12	*Ocotea cernua*	0.07
Ceiba pentandra	0.22	*Inga leiocalycina*	0.12	*Ocotea oblonga*	0.07
Ficus maxima	0.22	*Inga splendens*	0.12	*Ocotea puberula*	0.07
Parkia pendula	0.22	*Virola mollissima*	0.12	*Protium carnosum*	0.07
Protium calendulinum	0.22	*Calycophyllum* spp.	0.12	*Protium neglectum*	0.07
Aniba guianensis	0.20	*Cariniana* spp.	0.12	*Protium paniculatum*	0.07
Inga acreana	0.20	*Chorisia* spp.	0.12	*Protium robustum*	0.07
Protium crassipetalum	0.20	*Mezilaurus* spp.	0.12	*Virola loretensis*	0.07
Chimarrhis spp.	0.20	*Andira inermis*	0.10	*Enterolobium* spp.	0.07
Tetragastris spp.	0.20	*Astronium graveolens*	0.10	*Ceiba insignis*	0.05
Hymenaea oblongifolia	0.17	*Ceiba samauma*	0.10	*Chimarrhis hookeri*	0.05
Inga acrocephala	0.17	*Chimarrhis glabriflora*	0.10	*Chorisia integrifolia*	0.05
Inga bourgonii	0.17	*Inga sertulifera*	0.10	*Chorisia speciosa*	0.05
Inga ruiziana	0.17	*Protium opacum*	0.10	*Couroupita guianensis*	0.05
Matisia bicolor	0.17	*Virola decorticans*	0.10	*Dipteryx alata*	0.05
Pseudolmedia rigida	0.17	*Virola michelii*	0.10	*Ficus citrifolia*	0.05
Aniba muca	0.15	*Virola pavonis*	0.10	*Ficus guianensis*	0.05
Couratari guianensis	0.15	*Virola peruviana*	0.10	*Ficus insipida*	0.05
Hymenaea courbaril	0.15	*Cedrela* spp.	0.10	*Ficus killipii*	0.05
Inga nobilis	0.15	*Hymenaea* spp.	0.10	*Guazuma crinita*	0.05
Inga tenuistipula	0.15	*Aniba puchury-minor*	0.07	*Inga fendleriana*	0.05

continue Appendix 2.

Timber species	Stems per hectare	Timber species	Stems per hectare	Timber species	Stems per hectare
Protium neglectum	0.07	*Cedrela fissilis*	0.02	*Schizolobium amazonicum*	0.02
Protium paniculatum	0.07	*Enterolobium barnebianum*	0.02	*Sweetia fruticosa*	0.02
Protium robustum	0.07	*Ficus caballina*	0.02	*Virola multiflora*	0.02
Virola loretensis	0.07	*Ficus coerulescens*	0.02	*Vitex cymosa*	0.02
Enterolobium spp.	0.07	*Ficus cuatrecasasiana*	0.02	*Vochysia obidensis*	0.02
Ceiba insignis	0.05	*Ficus donnell-smithii*	0.02	*Vochysia stafleui*	0.02
Chimarrhis hookeri	0.05	*Ficus eximia*	0.02	*Pradosia* spp.	0.02
Chorisia integrifolia	0.05	*Ficus krukovii*	0.02	*Protium glabrescens*	0.02
Chorisia speciosa	0.05	*Ficus schultesii*	0.02	*Symphonia* spp.	0.02
Couroupita guianensis	0.05	*Ficus sphenophylla*	0.02		
Dipteryx alata	0.05	*Ficus ypsilophlebia*	0.02		
Ficus citrifolia	0.05	*Hymenaea reticulata*	0.02		
Ficus guianensis	0.05	*Inga acuminata*	0.02		
Ficus insipida	0.05	*Inga aggregata*	0.02		
Ficus killipii	0.05	*Inga bracteosa*	0.02		
Guazuma crinita	0.05	*Inga cinnamomea*	0.02		
Inga fendleriana	0.05	*Inga grandis*	0.02		
Inga heterophylla	0.05	*Inga lateriflora*	0.02		
Inga microcoma	0.05	*Inga macrophylla*	0.02		
Inga spectabilis	0.05	*Inga peltadenia*	0.02		
Inga thibaudiana	0.05	*Inga pezizifera*	0.02		
Inga tomentosa	0.05	*Inga semialata*	0.02		
Mezilaurus subcordata	0.05	*Inga stipulacea*	0.02		
Ocotea camphoromoea	0.05	*Inga velutina*	0.02		
Ocotea tessmannii	0.05	*Inga venusta*	0.02		
Pourouma bicolor	0.05	*Ocotea javitensis*	0.02		
Virola parvifolia	0.05	*Ocotea longifolia*	0.02		
Vochysia inundata	0.05	*Peltogyne confertiflora*	0.02		
Amburana spp.	0.05	*Peltogyne floribunda*	0.02		
Dipteryx spp.	0.05	*Protium insigne*	0.02		
Peltogyne spp.	0.05	*Protium meridionale*	0.02		
Andira multistipula	0.02	*Protium pallidum*	0.02		
Aniba megaphylla	0.02	*Protium spruceanum*	0.02		
Calycophyllum spruceanum	0.02	*Protium tenuifolium*	0.02		