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BLANCA MARISOL ALFARO CRUZ

MODELOS ALOMÉTRICOS PARA ESTIMATIVA DA  
BIOMASSA ARBÓREA EM UMA SAVANA AMAZÔNICA

MACAPÁ, AP  
2021

**BLANCA MARISOL ALFARO CRUZ**

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ARBÓREA EM UMA SAVANA AMAZÔNICA**

Dissertação apresentada ao Programa de Pós-Graduação em Biodiversidade Tropical (PPGBIO) da Universidade Federal do Amapá, como requisito parcial à obtenção do título de Mestre em Biodiversidade Tropical.

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UMA SAVANA AMAZÔNICA**



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que me deu sabedoria e forças para vencer todas as dificuldades.

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momentos bons e maus de minha vida e não medir esforços  
para me apoiar em todo momento.

A natureza é o único livro que  
oferece um conteúdo valioso em  
todas as suas folhas.  
**Johann Goethe**

Sonhos determinam o que você quer.  
Ação determina o que você conquista.  
**Aldo Novak**

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## **RESUMO**

Alfarocruz, B. Marisol. Modelos alométricos para estimativa de biomassa arbórea em uma savana amazônica. Dissertação (Mestre em Biodiversidade Tropical) – Programa de Pós-graduação em Biodiversidade Tropical – Pró-Reitoria de Pesquisa e Pós-Graduação - Universidade Federal do Amapá.

As estimativas de biomassa aérea em savanas são essenciais para entender o papel que esses ecossistemas desempenham no ciclo global do carbono, permitindo criar estratégias voltadas à mitigação das mudanças climáticas. No entanto, existem incertezas em relação aos estoques de carbono nas savanas devido à falta de equações locais. Neste estudo desenvolvemos 26 modelos alométricos a partir 150 árvores abatidas em uma área de ~5973 km<sup>2</sup> na savana do Amapá. Os modelos alométricos foram construídos usando diâmetro do tronco, altura total, densidade específica da madeira e diâmetro da copa. A precisão ( $R^2$ ) dos modelos variou de 0,69 a 0,93. O preditor mais importante desses modelos foi o diâmetro da copa, que explicou até 91% da biomassa individual acima do solo. Os modelos alométricos desenvolvidos podem ser usados de forma confiável para prever a biomassa aérea em savanas amazônicas, o que possibilita a diminuição das incertezas nas estimativas no nível local e regional, permitindo definir a contribuição destas áreas no ciclo global do Carbono.

Palavras-chave: alometria; Amapá; árvores; ciclo do carbono; copa; mudança climática.

## **ABSTRACT**

AlfaroCruz, B. Marisol. Allometric models to estimate tree above-ground biomass in savannas of Northeastern Amazonia. Master´s Thesis (Master in Tropical Biodivesity) – Post-Graduate Program in Tropical Biodiversity – Dean of Research and Post-Graduation – Federal University of Amapá.

Estimates of aerial biomass in savannas are essential to understand the role played by these ecosystems in the global carbon cycle, allowing the development of strategies to mitigate climate change. However, there are uncertainties regarding carbon stocks in savannas due to the lack of local equations. In this study, we developed 26 allometric models from 150 trees felled in an area of ~5973 km<sup>2</sup> in the savanna of Amapá, Northeastern Amazonia. Allometric models were fitted using trunk diameter, total height, wood density, and crown diameter. The precision ( $R^2$ ) of the models ranged from 0.69 to 0.93. The most important predictor in our models was crown diameter, which explained up to 91% of individual above-ground biomass. Our allometric models can be used to predict aerial biomass in the Amazonian savannas, contributing to reduce uncertainties in the estimates of carbon stocks at the local and regional levels, allowing to define the contribution of these ecosystems to the global carbon cycle.

Keywords: allometry; Amapá; Amazonian savannas; carbon cycle; crown; climate change.

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## INTRODUÇÃO GERAL

Dentre os ecossistemas tropicais, as savanas ocupam em entorno de  $23 \times 10^6 \text{ km}^2$  e hospedam aproximadamente 20% da população mundial (CIAT 2001). Esses ecossistemas estão presentes na maioria dos continentes, ocupando grandes áreas na América do Sul, África, sudeste Asiático e Austrália, estando presentes também em menores áreas na América Central (Humboldt 1997, Lopez-Hernandez et al. 2005, Goedert et al. 2008, Mora-Fernández et al. 2015). As savanas são formadas principalmente por associações de estrato herbáceo e elementos lenhosos (árvores e arbustos) isolados ou em grupos. Padrões climáticos característicos das savanas são a sazonalidade marcante (verões úmidos e invernos secos), vinculada ao estresse hídrico, e os solos com fortes restrições de fertilidade (Etter 1997, Lopez-Hernandez et al. 2005, Mora-Fernández et al. 2015).

Na América do Sul, as savanas são encontradas ao norte e ao sul da linha do Equador (Humboldt 1997). Ao norte se encontram os Llanos Colombianos e Venezolanos, e na parte Sul a extensão maior de savana é encontrada no Brasil, conhecido como Cerrado (Etter 1997). As savanas da América do Sul??, ocupam uma área de 269 milhões de hectares, dos quais 23 milhões são ocupados pelos Llanos orientais colombianos, 25 milhões nos Llanos na Venezuela, 4 milhões nas savanas da Guiana, 13 milhões nas savanas da Bolívia e 204 milhões são ocupados pelos Cerrados do Brasil (Humboldt 1997, Rippstein et al. 2001, Silva and Bates 2002, Lopez-Hernandez et al. 2005, Mora-Fernández et al. 2015, Mustin et al. 2017).

As savanas da Guiana, Guiana Francesa, Suriname, sul de Venezuela, parte oriental da Colômbia e norte de Brasil, (Etter 1997) são chamadas de savanas amazônicas, apresentando-se com tamanhos diferentes de áreas cujas menores aparecem como enclaves no bioma que é dominado por florestas (Braga 1979, Prance 1996, Humboldt 1997, de Carvalho and Mustin 2017). No Brasil estão distribuídas em toda a bacia Amazônica principalmente na parte oriental, ocupando 7% do total a Amazônia brasileira (Braga 1979, Magnusson et al. 2008). Consistem em uma formação de estratos herbáceos e vegetação lenhosa, apresentando em sua maioria árvores com raízes profundas, folhas e cascas muito grossas e troncos retorcidos, adaptadas para resistir a incêndios (Walter et al. 2008).

Na Amazônia Brasileira, as savanas amazônicas estão presentes nos estados de Rondônia, Roraima, Amazonas, Pará e Amapá (Bridgewater et al. 2004). Na Amazônia oriental, está localizada a segunda maior área de savana da região, com 140.012 km<sup>2</sup>, correspondendo a 7,2% do estado do Amapá com uma distribuição desde o sul até o norte (Macapá a Oiapoque) deste Estado (ZEE. 2008, Mustin et al. 2017). Essa formação savânica é caracterizada por áreas com vegetação arborizada aberta, áreas com uma camada de arbustos mais densos, áreas abertas de gramíneas com poucos arbustos e áreas sazonalmente alagadas (Mochiutti e de Lima 1994). Os principais tipos de vegetação são divididos em savana arbustiva, savana arborizada, e savanas parque, sendo notáveis as variações de composição e de número de espécies (Mustin et al. 2017).

As savanas amazônicas estão sofrendo fortes pressões, causadas por diversas atividades antrópicas que provocam uma degradação acelerada, como resultado dos incêndios acidentais ou provocados para a limpeza das áreas para cultivo, desmatamento para expansão agrícola e silvicultural (plantio de soja e eucalipto), assim como para a atividade pecuária e crescimento urbano (Mustin et al. 2017). Estas áreas estão sendo rapidamente degradadas pelos incêndios frequentes e pelo desmatamento, ameaçando a biodiversidade e os serviços ecossistêmicos providos pelas savanas (Myers et al. 2000, Dias 2008). A fragmentação e os incêndios frequentes nas florestas e savanas causam mudanças nos estoques e na dinâmica global do Carbono e de outros gases de efeito estufa que contribuem para o aquecimento global, sendo uma das grandes preocupações ambientais a nível mundial (Barbosa and Fearnside 2005, Barbosa et al. 2007, do Amaral et al. 2019).

Informações sobre os estoques de Carbono (C), ciclagem e produtividade nas savanas são objeto de questões quanto à sua precisão. Estudos demonstram que as savanas drenam aproximadamente de 1 a 12 Mg C ha<sup>-1</sup> ano<sup>-1</sup>, sendo que a média global é de 7,2 Mg C ha<sup>-1</sup> ano<sup>-1</sup> (Grace et al. 2006, Robinson 2007). Para as savanas da África, estima-se que a biomassa lenhosa é responsável por estocar 11,7 Mg C ha<sup>-1</sup> (Avitabile et al. 2016, Ifo et al. 2018). As savanas brasileiras, em sua biomassa acima do solo estocam 5,91 Mg C ha<sup>-1</sup> (de Oliveira et al. 2019). Um estudo realizado na parte Norte de Minas Gerais onde as áreas de savanas predominam, principalmente as fitofisionomias de savana arborizada e savana arbustiva, os estoques de C variaram em torno de 20 Mg ha<sup>-1</sup> (Scolforo et al. 2015, Scolforo et al. 2016). Resultados de um estudo realizado por Barbosa e Fearnside (2005) encontraram 11,73 Mg ha<sup>-1</sup> nas savanas de Roraima. Mesmo que as savanas

estoquem menor quantidade de C comparadas com a florestas continuas tropicais ( $83,5 \text{ Mg ha}^{-1}$ ) (Abreu et al. 2017), estudos mostram que durante o período de 2002 e 2010, as savanas foram as responsáveis pelo segundo maior aporte de carbono para a atmosfera no Brasil (1.845 Tg) (Brazil 2016).

O crescente interesse em estimar com precisão a biomassa nestas áreas é devido ao papel chave e complexo que desempenham nas mudanças climáticas globais e nas regulações nos ciclos do C e nutrientes (Grace et al. 2006). Estima-se que 50% da biomassa (expressa em massa do material vegetal disponível por unidade de área) seja composta por C (Araújo et al. 1999, Chave et al. 2005). A biomassa de um ecossistema, geralmente é separada em compartimentos: viva ou morta e acima ou abaixo do solo. Acima do solo ela está presente na vegetação viva e nas partes mortas, como troncos, galhos e folhas. Abaixo do solo é composta, principalmente, pelas raízes vivas e mortas. A biomassa arbórea é a soma de cada um dos componentes das plantas (Araújo et al. 1996). A proporção em que é distribuída varia entre os indivíduos, mesmo que sejam da mesma espécie devido à influência de vários fatores como características genéticas, idade e condições ambientais (Castro e Kauffman 1998, Delitti et al. 2001).

A biomassa está relacionada com a estrutura da vegetação, apresentando mudanças em tempo e espaço, sendo que, estas mudanças estão vinculadas a três processos principais: (1) mudanças no uso da terra, (2) eventos naturais e de recuperação e (3) fisiologia ou alterações metabólicas (Brown 1997b, Houghton et al. 2009). Dessa forma, a biomassa é fundamental para realizar análises e monitoramento nos ecossistemas. A acurácia nas estimativas de biomassa é considerada um dos aspectos mais importantes em estudo de biomassa florestal, devendo ser calculada de uma forma que se aproxime aos dados reais, porém, evitando o corte de árvores por meio da utilização de variáveis de mais fácil obtenção (por exemplo: diâmetro do tronco, diâmetro da copa, altura total e densidade da madeira) que possuem relações alométricas com a biomassa da árvore (Chave et al. 2005, Feldpausch et al. 2011, Chave et al. 2014).

Na atualidade, estimativas de biomassa são constantemente requeridas devido a sua importância nos estudos relacionados às mudanças climáticas, já que é um parâmetro indispensável para a determinação dos estoques de C nos ecossistemas (Cairns et al. 1997). No entanto, estas estimativas dependem da acurácia e precisão durante a obtenção dos dados em cada ecossistema. A quantificação da biomassa pode ser por meio de dois métodos: método direto (destrutivo) e método indireto. O primeiro consiste em selecionar

e cortar todo o material acima do solo em uma área previamente definida e, posteriormente, fazer a separação dos componentes e pesar o material para a obtenção do peso fresco ou verde. Após, deve-se retirar amostras de cada um dos componentes, para determinar em laboratório, a relação entre peso seco e peso úmido por meio de secagem em estufa, para enfim, poder estimar o peso seco de toda biomassa fresca em campo (Chave et al. 2001, De Britez 2007). Este método é acurado, mas demanda muito tempo, trabalho e não pode ser aplicado em grandes áreas ou Áreas Protegidas devido aos marcos legais que regulam as atividades de pesquisa nestas áreas (Miranda et al. 2011). O método indireto requer dados de inventários florísticos, uso de sensoriamento remoto e de equações alométricas, mas os métodos indiretos requerem dados obtidos através do método direto para poderem produzir estimativas (Brown 1997b, Soares et al. 2005, Somogyi et al. 2006, Vieira et al. 2008, Qureshi et al. 2012).

A relação estatística existente entre a forma e o tamanho é definida como alometria (Mitteroecker et al. 2013). Os modelos alométricos são definidos como equações matemáticas que facilitam a estimativa do volume, biomassa ou teor de C em árvores, baseado em variáveis mais facilmente mensuráveis que podem assumir diferentes valores e por coeficientes previamente estimados (Alder 1980, Parresol 1999, Guedes-Brunis. et al. 2008). Para desenvolver um modelo alométrico é necessário definir a área de interesse, determinar o tamanho amostral, selecionar os indivíduos para a amostragem, realizar medições das variáveis dendrométricas, corte das árvores, estimar a biomassa e o C. Em seguida é necessário estabelecer a correlação entre as variáveis para proceder com a seleção do melhor modelo considerando diferentes critérios: alto coeficiente de determinação ajustado ( $R^2$  adj), menores valores de Erro Padrão Residual (RSE), e valores mais baixos para o Critério de Informação de Akaike (AIC) (Segura e Andrade-Castañeda 2008).

O desenvolvimento de equações alométricas para estimar os estoques de C e a quantidade de biomassa na atualidade tem se tornado uma necessidade, pois, as informações obtidas são de muita utilidade para projetos de recuperação ou reflorestamento e projetos que visam estimar os impactos da emissão de gases nas mudanças climáticas (Soares et al. 2005). O desenvolvimento de equações alométricas variam em função do tipo de vegetação de acordo com a disponibilidade de dados sobre as medidas dendrométricas (Brown 1997b, Tito et al. 2009). As variáveis alométricas também são influenciadas pelas variáveis bioclimáticas (precipitação e sazonalidade da

precipitação) (Lewis et al. 2004, IPCC, 2006). Assim, o mais adequado seria contar com modelos alométricos para cada tipo de floresta e para cada local, tendo em consideração as mudanças climáticas e as variações existentes entre sítios (Koehler et al. 2005). Entretanto, devido as limitações de recurso, tempo e acesso às áreas, isso não é possível, o que gera muitas incertezas sobre as estimativas de estoque de biomassa e C para as áreas onde não se têm equações alométricas disponíveis.

As equações alométricas podem ser ajustadas com variáveis de mais fácil medição como diâmetro à altura do peito, altura total e densidade da madeira por árvore ou através de variáveis compostas que possuem uma relação proporcional com a biomassa (Brown et al. 1989, Baccini et al. 2004, Chave et al. 2005, Somogyi et al. 2006, Vieira et al. 2008, Ribeiro et al. 2010, De Paula et al. 2011). Tradicionalmente, a biomassa é estimada usando dados obtidos de inventários florestais resultantes de parcelas permanentes ou temporárias, utilizando medidas de diâmetro das árvores ou com a combinação do diâmetro, altura e densidade da madeira (Chambers et al. 2001, Nascimento and Laurance 2002, Malhi et al. 2004, Malhi et al. 2006).

O uso de duas ou mais variáveis em um mesmo modelo pode proporcionar melhorias nas estimativas de biomassa, tal como o uso do diâmetro e altura, onde a altura regula quantidades de biomassa associadas ao comprimento do tronco e profundidade da copa. No entanto, tomar esta medida com precisão em florestas de dossel fechado torna-se difícil, porém, nas áreas de savanas é possível obter medidas do tamanho da copa mais facilmente, pois, a vegetação é mais baixa e dispersa (Brown et al. 1989, Zheng et al. 2004, Hunter et al. 2013, Larjavaara and Muller-Landau 2013). Na ausência da altura total, o uso de diâmetro torna-se mais comum, sendo esta uma medida mais prática de se adquirir em campo (Williams and Schreuder 2000, Chave et al. 2001).

O desenvolvimento de modelos alométricos requer um grande esforço amostral em termos de indivíduos abatidos (mínimo 100 árvores sensu Chave et al. 2001), variação de tamanhos e de espécies, além de medidas rigorosas da densidade da madeira (Woodcock and Shier 2002, Chave et al. 2004). No entanto, a vantagem para os modelos alométricos desenvolvidos com amostras bem espacializadas, é que podem ser aplicados para realizar estimativas de biomassa em grandes áreas com maior precisão já que possuem uma melhor representatividade espacial (Brown and Lugo 1992, Chave et al. 2005).

As equações criadas para estimar as quantidades de biomassa e C armazenado na vegetação em um sítio ou ecossistema específico, podem ser usadas para estimar a biomassa em ambientes similares (Vieira et al. 2008). Equações desenvolvidas para uma região em particular, baseadas em uma amostra razoável de indivíduos, é sempre melhor do que aplicar equações gerais desenvolvidas com amostras coletadas em áreas distantes (Brown et al. 1989). Estimar com precisão as estimativas de biomassa nas savanas no Estado de Amapá requer o desenvolvimento de modelos específicos para esta área mediante a validação de equações utilizando dados obtidos com o método direto. Nesse sentido, este estudo pretende contribuir efetivamente para melhorar essas estimativas por meio da construção de modelos alométricos com boa capacidade de previsão da biomassa arbórea através de medidas da estrutura (áerea) das árvores e arbustos em diferentes fitofisionomias da savana amazônica presente no Amapá.

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## HIPÓTESES

- 2.1 A biomassa aérea de árvores e arbustos das savanas amazônicas do Amapá é relacionada positivamente com diâmetro médio da copa, pois a maior quantidade de biomassa se concentra nos galhos.
- 2.2 A biomassa aérea total de árvores e arbustos das savanas amazônicas é representada principalmente pelos componentes da copa (galhos gravetos).
- 2.3 A biomassa aérea total das savanas amazônicas é representada principalmente pelos indivíduos com um diâmetro maiores a 10 cm, pois quanto maior diâmetro maior a quantidade de biomassa.
- 2.4 A inclusão do volume como variável preditora nos modelos, melhora as estimativas de biomassa aérea de árvores e arbustos das savanas amazônicas do Amapá.
- 2.5 As variáveis de déficit hídrico (déficit climatológico máximo de água-CWD e uma medida de estresse ambiental - E) estão negativamente correlacionados com a biomassa aérea de árvores e arbustos das savanas amazônicas, pois restrições de chuva nos períodos secos influenciam negativamente o tamanho das árvores.

## OBJETIVOS

### GERAL

- Desenvolver modelos alométricos para determinar indiretamente a biomassa aérea das árvores e arbustos nas savanas amazônicas do Amapá

### ESPECÍFICOS

- Ajustar equações para estimar a biomassa aérea nas savanas amazônicas do Amapá;
- Determinar quais dos atributos das árvores (diâmetro à altura do solo, altura total, diâmetro médio da copa e densidade da madeira) e suas combinações explicam a variação da biomassa;
- Determinar se o volume estimado ( $\text{volume} \times \text{altura}$ ) e massa estimada ( $\text{volume} \times \text{altura} \times \text{densidade da madeira}$ ) são melhores preditores de biomassa que as combinações de variáveis de tamanho e densidade;
- Avaliar o efeito das variáveis de déficit hídrico (CWD e E) sobre a biomassa;

ARTIGO CIENTÍFICO

**Allometric models to estimate tree aboveground biomass in savannas of northeastern Amazonia**

*Submetido ao periódico Forest Ecology and Management*

## ALLOMETRIC MODELS TO ESTIMATE TREE ABOVEGROUND BIOMASS IN SAVANNAS OF NORTHEASTERN AMAZONIA

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### ABSTRACT

Estimates of aboveground biomass (AGB) in savannas are essential to understand the role played by these ecosystems in the global carbon cycle, allowing the development of strategies to mitigate climate change. However, there are uncertainties associated to carbon stocks in Amazonian savannas due to the lack of local equations. In this study, we developed 26 allometric models from 150 trees felled in sites covering an area of ~5973 km<sup>2</sup> in the savanna of Amapá, Northeastern Amazonia. Allometric models were fit using stem diameter, total height, wood density, and crown diameter. The precision ( $R^2$ ) of the models ranged from 0.69 to 0.93. The most important predictor of tree biomass as crown

diameter, which explained up to 91% of the individual AGB. Our allometric models can be used to reduce the uncertainties in the estimates of AGB for Amazonian savannas of Amapá, contributing to and allow to define the contribution of this ecosystem to the global carbon cycle.

**Keywords:** allometry, Amazonian savannas, carbon cycle, biomass, climate change.

## INTRODUCTION

Tropical savannas are important for the economy of local populations worldwide, as well as for the provision of several ecosystem services, including carbon storage. These ecosystems occupy one-fifth of the earth's surface (Sankaran et al. 2005, Paiva et al. 2011) and are located in the Neotropics, Africa, Southeast Asia, and Australia (Lopez-Hernandez et al. 2005). In South America, the largest savanna areas are represented by the Brazilian *Cerrado*, the savannas of French Guiana, Paraguay, Bolivia, and *Los Llanos* region in Colombia and Venezuela (Rippstein et al. 2001, Silva and Bates 2002, de Carvalho and Mustin 2017).

Although the largest area of South American savanna is found in the *Cerrado* biome (Midwest of Brazil), there are other sites less studied, highly threatened, and of great ecological and cultural relevance inserted in the Amazonian Biome, known as Amazonian Savannas (Ratter et al. 2003, de Carvalho and Mustin 2017). Such savannas are distributed as patches within a landscape predominantly covered by forests and occupy an area of  $\sim 267,000 \text{ Km}^2$ , with  $\sim 42\%$  of it in Brazil, with the largest areas in the states of Roraima ( $\sim 10\%$ ) and Amapá ( $\sim 5\%$ ). Particularly these savanna ecosystems are undergoing an accelerated process of change in land use and occupation, mainly due to agrobusiness expansion for soybean production and also to increase plantation forests of eucalyptus and acacia (Fernandes et al. 2016, Mustin et al. 2017, Urquiza et al. 2018, Toledo and Nascimento 2019, Carvalho et al. 2020). Stocks of aboveground carbon (AGC) in savanna of Roraima State (Northern Amazonia) are estimated to be  $\sim 6.8 \times 10^6 \text{ Mg}$  (Barbosa and Fearnside 2005b) and  $\sim 3.3 \times 10^6 \text{ Mg}$  (JJT, unpublished data) in Amapá (Northeastern Amazonia), thus the accelerated loss of vegetation of these ecosystems will result in significant fast changes in carbon stocks, consequently contributing to the acceleration of global warming (Barbosa and Fearnside 2005b).

Although carbon stocks of Amazonian savannas are lower (four times on average) when compared with *terra-firme* forests (Watson et al. 2000), between 2002 and 2010

savannas have represented the second-major apport of net carbon emissions (1.845 Tg) in Brazil (Brazil 2016). Therefore, this fact reinforces the importance of savannas on the climate change scenario, as they are environments easily convertible into plantations and because they are very unprotected by legislation, since, according to the Brazilian Forest Code, only 35% of the area of rural properties in Amazonian savannas must be reserved for conservation (Art. 12, Lei N° 12.651/2012).

In the context of climate change, it is essential to understand the dynamics of carbon in the Amazonian savannas. This requires accurate estimates of total biomass that can be readily converted to carbon (~ 40% biomass is carbon) (Barbosa and Fearnside 2005b). The improvements of policies for mitigation of climate change depend on the mapping of terrestrial carbon stocks (Saatchi et al. 2011, Nogueira et al. 2017). However, current estimates are inaccurate due to high intra- and inter-specific variability in tree attributes (i.e. trunk diameter, height, and wood density) and mainly due to the very limited amount of allometric equations available for biomass estimation in both forests and savannas in the tropics (see Barbosa and Fearnside 2005a, Chave et al. 2005, Chave et al. 2014, Roitman et al. 2018).

In order to reduce uncertainties about carbon stocks and emissions, it is necessary to carry out a mapping of terrestrial carbon stocks to accurately determine the impacts of land use change on carbon emissions (Barbosa and Fearnside 2005a, Chave et al. 2005, Nogueira et al. 2008b, Chave et al. 2014, Nogueira et al. 2015, Nogueira et al. 2017, Roitman et al. 2018). Trees are the main component of AGB and accurate estimates of carbon stocks are dependent on liable estimates of tree biomass, which can be converted to carbon (Mugasha et al. 2013, Picard et al. 2015). Biomass estimates can be performed indirectly using allometric models to convert tree attributes (diameter, height, wood density) into dry weight (Brown et al. 1989, Brown et al. 1999, Picard et al. 2012, Goodman et al. 2014). In the past two decades, many models for the quantification of AGB have been published. These models are based on the relationship of predictor variables, such as diameter to breast height (DBH), total height, wood density and canopy diameter (Brown et al. 1989, Brown et al. 1999, Baker et al. 2004, Chave et al. 2004, Chave et al. 2005, Nogueira et al. 2008b, Návar 2009b, Návar 2009a, Chave et al. 2014, Ngomanda et al. 2014, Sileshi 2014, Maulana et al. 2016). Other models using composite terms (i.e. DBH × height × wood density) were also developed (Chave et al. 2005, Nogueira et al. 2008b, Chave et al. 2014, Ngomanda et al. 2014, Ploton et al. 2016, Xiang

et al. 2016). However, a limited number of felled trees was used for the construction and validation of these allometric models considering the high diversity of species and forest types in the tropics.

Particularly, there is a lack of equations for biomass estimates in the tropical savannah of South America (Ribeiro et al. 2011, Roitman et al. 2018, Sanquetta and Venturoli 2019). For Amazonian savannas, there is only one available equation built with trees from savannas of Roraima (Barbosa and Fearnside 2005a), which is used to estimate biomass in other savannah patches in the Amazonia.

Nonetheless, there are differences in species composition and vegetation structure between Amazonian savannas (see Barbosa and Fearnside 2005a, Costa Neto 2014) entailing in the propagation of error when the equation developed for one region (Roraima) is used to estimate biomass in other region (e.g. Amapá). Due to the rapid expansion of agribusiness over the savannas of Amapá, it is crucial to improve the estimates of biomass for this patch, which can be possible through the development of local equations that include all the different vegetation types and the most abundant species. Therefore, we built models with trees from different savannah types fascies (from grasslands to parklands) under different climatic regimes spanning an area of 5973.08 km<sup>2</sup> of savannas in Amapá. We felled 150 trees of 19 representative species of the region, and we fit 26 models with different combinations of size attributes (trunk diameter, total height, crown size) and wood density to model the individual variation in tree biomass. Additionally, we include climatic variables that represent the water deficit and taxonomic identity to improve the models.

## METHODS

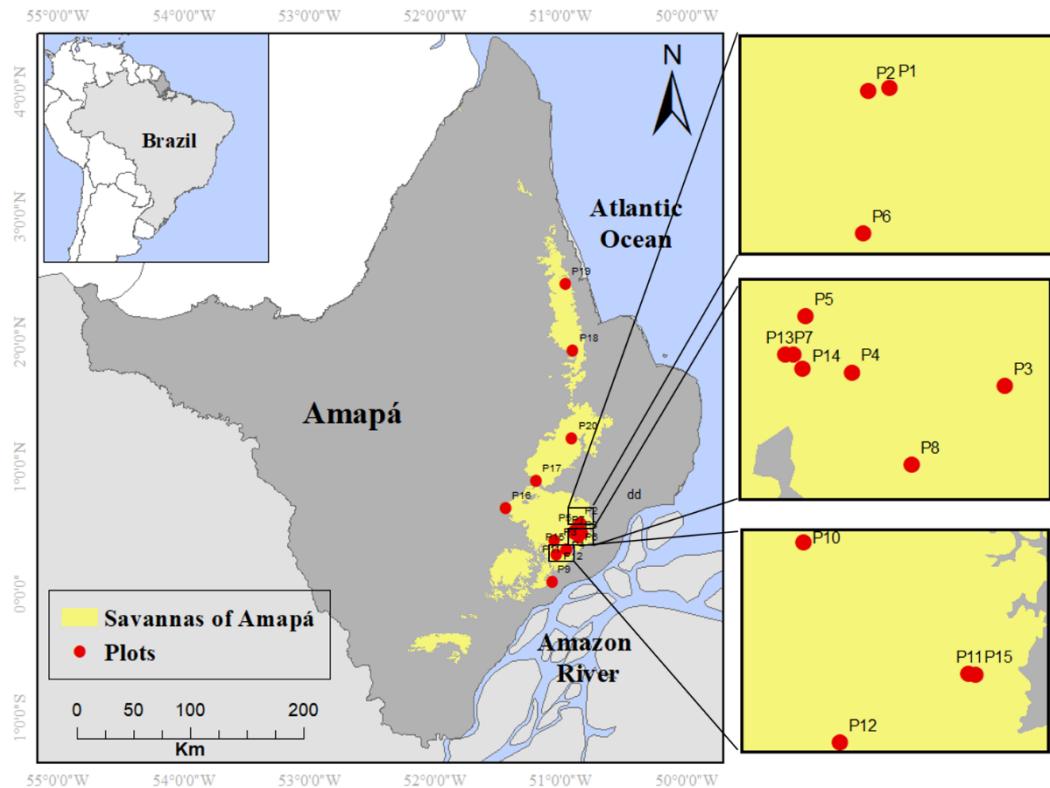
### STUDY AREA

This study was carried out in an Amazonian savanna in the northeast part of the biome, in the state of Amapá, Brazil. The savannas comprise ~ 9% of the state's territory (de Carvalho and Mustin 2017), distributed in the eastern portion of the state, along a stretch from north to south, extending from the Guiana Shield to the Amazon River estuary, between the coordinates 04°30' N to 01°10' N and 50°00' W to 52°00' W, (Fig 1). The climate is tropical monsoon, according to the Köppen's classification, with average temperatures of 26°C to 28°C and precipitation between 2.500 mm to 3.500 mm, with a marked dry season from August to November (ZEE 2008). Interpolated

precipitation data (1977-2007) from the Global Precipitation Climatology Project generated by satellite and calibrated with rain gauges shown an increasing gradient in annual precipitation (2100 mm - 2900 mm) from southwest to northeast (Souza and Cunha 2010). In the three wettest months (March to May) the accumulated precipitation varies from 900 mm to 1200 mm per month and in the driest period (September to November) it rains less than 300 mm. A dry corridor of ~ 150 km wide, cuts the region in the middle from east to west, where it rains < 150 mm per month during dry season. The main types of soil present in the region are Ferralsols (Oxisols in the US soil system) derived from sandy-clay, sandy and clay-silt sediments of low fertility (Rodrigues et al. 2000).

The savannas are quite variable in terms of structure with different phytophysiognomies, with occurrence of open areas dominated by sparse grasses and shrubs up to more dense vegetation dominated by trees and shrubs (Mochiutti and de Lima 1994). The vegetation types found in the savannas of Amapá are clean fields, dirty fields, rupestrian fields, open woodlands (typical *cerrado*) and parklands. Shrubs and small trees show thick barks, twisted branches and trunks, especially for individuals which were exposed to fire.

The clean fields have a herbaceous and shrubby dominant strata, with *Byrsonima verbascifolia* being the species with the greatest abundance. The dirty fields are dominated by grasses with sparse small trees up to 2 m tall. The rupestrian fields have a tree-shrub layer up to 3 m in height and sparse trees, and open woodlands and the parklands show a dense arboreal stratum with high density of individuals (Costa Neto 2014). The most abundant species are *Byrsonima crassifolia*, *B. coccocolobifolia* (both Malpighiaceae), *Ouratea hexasperma* (Ochnaceae), *Salvertia convallariodora*(Vochysiaceae) and *Palicourea rigida* (Rubiaceae) (Costa Neto 2014).



**Fig.1** Study area showing the location of Savannas of Amapá and the 20 plots used in this study.

## SAMPLING DESIGN

Along the savannah, 20 sampling sites were established spanning an area of 5973 km<sup>2</sup> (Fig. 1), comprising dirty fields, open woodlands and parklands. To choose the sites for sampling, we searched for sites with non- or low-disturbed vegetation, trying to include most of savannah types. We have the agreement of all landowners to carry out the work. In 13 sites, 20 plots of 4 × 250 m were installed by following the protocol of the Biodiversity Research Program (PPBio) (Barbosa et al. 2006) during 2019 and 2020. Plots were a minimum distance of 1 km between each other.

## FLORISTIC INVENTORY

We carry out an inventory of all tree or shrub individuals in each plot following the PPBio protocol (Barbosa et al. 2006). The following measures were taken for individual trees and shrubs: stem diameter above the ground (D), stem diameter at 30 cm above the ground (D30), stem height (Hf), total height (H), and the smaller (CS) and larger (CL) crown diameters (C) (measured perpendicularly to each other). The presence of sprouts, fire scars, termites and hollows were also recorded.

Measurements of D and D<sub>30</sub> were taken using a metric tape (0.1 cm precision), and crown diameters were measured using a 10-m tape. The total height of trees up to 3 m tall was taken using a tape, and the height of taller trees was measured with a hypsometer. Trees with D ≥ 10 cm were tagged. The botanical identifications at species level were made by one of us (SVC.-N.) who specialize on savanna flora. Botanical vouchers were collected for unidentified specimens and compared to material deposited in the Hamab Herbarium at *Instituto de Pesquisas Científicas e Tecnológicas do Estado do Amapá*.

#### SELECTION OF TREES FOR DESTRUCTIVE SAMPLING

The development of robust regional allometric models for forests requires a substantial effort with felling of more than 100 trees (Chave et al. 2004, Sileshi 2014). Therefore, we chose a sample size of 150 trees to assure a good fit (Supplementary material: Table S1). As the equation developed by Barbosa and Fearnside (2005a) for savannas in Roraima provided a good fit ( $R^2 = 0.98$ , RSE = 28%) with 130 individuals ranging between 2 and 40 cm in diameter, we consider that our sample would provide a reasonable fit for a similar diameter range (5 to 35 cm).

We used a dataset (4,141 individuals ≥ 5 cm D from 137 plots of 4 × 100 m) collected previously by one of us (SVC-N) to identify how many individuals of which size class and species should be included in the destructive sampling. Within 46 recorded species, 15 contributed with 97.2% of all individuals in the inventory and only three species (*B. crassifolia*, *O. hexasperma* and *S. convallariodora*) accounted for 72.5% of all individuals. We calculated the species relative abundance by different size classes and multiplied it by sample size (150) to obtain the expected number of trees to be felled by each species and size class (Table S1). Then, we used our recent data from the 20 plots to identify which species of which size we should fell in each site. Thus, to avoid damage trees inside the plots, we conducted a tree selection outside the plots for destructive sampling, trying to adjust as close as possible to the previously defined distribution of the number of individuals by species and size class (**Table S1**). We also sought to distribute individuals of the most abundant species on different sampled sites to encompass intraspecific variability in tree attributes related to soil and climate.

## DESTRUCTIVE SAMPLING AND MEASUREMENTS OF TREE ATTRIBUTES

We cut the 150 trees between July 2019 and February 2020. The following attributes were measured for these trees: D, D<sub>30</sub>, H<sub>f</sub>, H, CS and CL to calculate C and wood density ( $\rho$ ). The measurements of D and D<sub>30</sub> were taken using a tape, with a precision of 0.1 mm. To measure H<sub>f</sub>, H, and C we use a 10-meter long Starfer glass fiber tape with a precision of 0.01 m. After measured, the tree was felled. Trees with D  $\geq$  10 cm were cut using a chainsaw (Stihl MS 180) and smaller trees were cut using a machete. We used a plastic tarp (5 × 8m Brasfort polyethylene tarpaulin) disposed on the ground to collect the sawdust, twigs and leaves released during the fall of trees. The trunks and large branches were cut into smaller pieces using the chainsaw. The sawdust produced in one tree was estimated by weighing three times the sawdust released in one cut, calculating the average and multiplying it by the total number of cuts (Lima et al. 2012). After cutting, the tree was divided into four components: leaves, twigs (woody pieces with diameter <5 cm), branches (5  $\leq$  diameter <10 cm), and trunks (diameter  $\geq$  10 cm).

The components were placed separately into plastic bags previously identified and weighed in the field using a commercial digital scale (Lotus Home collection) with a maximum weight of 30 kg and precision of 0.001 kg. The total biomass of each tree was calculated by summing the weight of all components.

## WOOD DENSITY

We estimated wood density (i.e., wood specific gravity) dry mass by green volume (Chave et al. 2006). Samples of ~8 × 2 × 2 cm were extracted using a machete for trees with D between 5 to 10 cm and with a chainsaw for larger trees. Each of the samples was packed in plastic bags properly closed and identified (Muller-Landau 2004). To determine the green volume, the samples were inserted into a container (Becker 1000 mL) with 900 mL of water, placed on a semi-analytical scale BL-3200H Shimadzu (0.01g precision) with a maximum capacity of 3200 g. The sample was submerged in water using a needle to avoid touching the walls and bottom of the container and the value of weight (~ equivalent to the volume in mL) was recorded (Chave et al. 2006).

Subsequently, the samples were placed in the oven (American Lab, model 100/630) to dry at 100 °C. When samples reached constant weight (~2 days), they were

weighed again on a semi-analytical scale (0.01g precision) to obtain the dry weight. Wood was calculated using the following formula:

$$\rho = \frac{P}{V} \quad (1)$$

Where  $\rho$  is the wood density ( $\text{g cm}^{-3}$ ),  $P$  is the dry weight (g) and  $V$  is the green volume ( $\text{cm}^3$ ).

## CONSTRUCTION OF INDIVIDUAL BIOMASS MODELS OF TREES

The individual aboveground biomass AGB (in kg) can be predicted by the trunk diameter  $D$  (cm), total height  $H$  (m) and, wood density  $\rho$  ( $\text{g cm}^{-3}$ ), included in a model proposed by Chave et al. (2005) - based on a general model by Schumacher and Hall (1933) -, which can also include the average crown diameter  $C$  (m), as proposed by Goodman et al. (2014), an hereafter called Model *I.1*:

$$\ln(AGB) = \alpha + \beta_1 \ln(D) + \beta_2 \ln(H) + \beta_3 \ln(\rho) + \beta_4 \ln(C) \quad (2)$$

IF  $B_1 = 2$ ,  $B_2 = 1$ ,  $B_3 = 1$  E  $B_4 = 0$  THE EQUATION ABOVE WILL BE EQUIVALENT TO:

$$AGB = \exp(a) (D^2 H \rho) \quad (3)$$

where it is assumed that the biomass is proportional to the product of trunk basal area, total height and wood density (Chave et al. 2005). This equation can be reorganized with log transformation and addition of the average crown diameter (Model *I.2*):

$$\ln(AGB) = \alpha + \ln(D^2 H \rho) + \beta_4 \ln(C) \quad (4)$$

Assuming  $D^2 H \rho$  as an independent predictor, the equation can be rewritten as (Model *I.3*):

$$\ln(AGB) = \alpha + \beta_2 \ln(D^2 H \rho) + \beta_4 \ln(C) \quad (5)$$

Other models can be derived from the equations above by combining three or two variables, or just using one predictor (Table 1). Models *II.1* and *II.2* use  $D$ ,  $H$  e  $\rho$  from models *I.1* and *I.2* (respectively) if  $C$  does not vary ( $\beta_4 = 0$ ). Models *III.1* and *III.2* include  $D$ ,  $H$ , and  $C$  from models *I.1* and *I.3* (respectively) if  $\rho$  does not vary ( $\beta_3 = 0$ ). Model *IV* includes  $D$ ,  $\rho$  and  $C$  assuming that  $H$  does not vary ( $\beta_2 = 0$ ) and model *V* includes  $H$  and  $C$  assuming that  $D$  is constant ( $\beta_1 = 0$ ), both (*IV* and *V*) being simplifications of model *I.1*

(Table 1). Models *VI.1*, *XII.1*, *XIII.1*, *IX.1* e *X.1* use different combinations of two predictors ( $D + H$ ,  $D + \rho$ ,  $D + C$ ,  $H + \rho$ ,  $H + C$  e  $\rho + C$ , respectively) varying independently and model *VI.2* uses a composite variable  $D^2 H$  as the only predictor. Models *XII.2*, *XIII.2*, *IX.2* and *X.2* use polynomials which quadratic and cubic terms in combination with a second predictor ( $D^x + \rho$ ,  $D^x + C$ ,  $H^x + \rho$ ,  $H^x + C$  e  $C^x + \rho$ ) contribute to reduce an overestimation of AGB often observed for large trees when power functions are used (Chave et al. 2005).

Further, a power function (West et al. 1999) can be used to model the allometric relationships between *AGB* and tree size measures:

$$Y = \alpha X^\beta \quad (6)$$

Where  $Y$  and *AGB*,  $\alpha$  and  $\beta$  are the estimated parameters of the model and  $X$  is a measure of size. Estimates of parameters for the power function with least square can be biased because the method assumes homogeneity of variances, which is often violated in allometric relationships (Chave et al. 2014). For this reason, the variables  $Y$  and  $X$  are usually log transformed, to fulfill this premise:

$$\ln(Y) = \alpha + \beta \ln(X) \quad (7)$$

where  $\ln$  is the natural logarithm.

We tested the linearized version of the power function to adjust AGB as a function of  $D$ ,  $H$ , and  $C$  (models *XII.1*, *XIII.1* and *XIV.1*, respectively: Table 1) and we also used a polynomial (quadratic and cubic terms) to each predictor in separate models (*XII.2*, *XIII.2* and *XIV.2*, respectively) to control for the error associated to large trees.

**Table 1.** Allometric models for the relationships of individual aboveground biomass (AGB in kg) with trunk diameter (D in cm), total height (H in m), wood density ( $\rho$  in g cm<sup>-3</sup>) and average crown diameter (C in m).

Model code	Equation
<i>I.1 DHPC</i>	$\ln(AGB) = \alpha + \beta_1 \ln(D) + \beta_2 \ln(H) + \beta_3 \ln(\rho) + \beta_4 \ln(C)$
<i>I.2 DHPC</i>	$\ln(AGB) = \alpha + \beta_2 \ln(\rho D^2 H) + \beta_4 \ln(C)$
<i>II.1 DHP</i>	$\ln(AGB) = \alpha + \beta_1 \ln(D) + \beta_2 \ln(H) + \beta_3 \ln(\rho)$
<i>II.2 DHP</i>	$\ln(AGB) = \alpha + \beta_2 \ln(D^2 H \rho)$
<i>III.1 DHC</i>	$\ln(AGB) = \alpha + \beta_1 \ln(D) + \beta_2 \ln(H) + \beta_4 \ln(C)$

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<i>III.2 DHC</i>	$\ln(AGB) = \alpha + \beta_2 \ln(D^2 H) + \beta_4 \ln(C)$
<i>IV DPC</i>	$\ln(AGB) = \alpha + \beta_1 \ln(D) + \beta_3 \ln(\rho) + \beta_4 \ln(C)$
<i>V HPC</i>	$\ln(AGB) = \alpha + \beta_2 \ln(H) + \beta_3 \ln(\rho) + \beta_4 \ln(C)$
<i>VI.1 DH</i>	$\ln(AGB) = \alpha + \beta_1 \ln(D) + \beta_2 \ln(H)$
<i>VI.2 DH</i>	$\ln(AGB) = \alpha + \beta_2 \ln(D^2 H)$
<i>VII.1 DP</i>	$\ln(AGB) = \alpha + \beta_1 \ln(D) + \beta_3 \ln(\rho)$
<i>VII.2 DP</i>	$\ln(AGB) = a + b \ln(D) + c \ln(D)^2 + d \ln(D)^3 + \beta_3 \ln(\rho)$
<i>VIII.1 DC</i>	$\ln(AGB) = \alpha + \beta_1 \ln(D) + \beta_4 \ln(C)$
<i>VIII.2 DC</i>	$\ln(AGB) = a + b \ln(D) + c \ln(D)^2 + d \ln(D)^3 + \beta_4 \ln(C)$
<i>IX.1 HP</i>	$\ln(AGB) = \alpha + \beta_2 \ln(H) + \beta_3 \ln(\rho)$
<i>IX.2 HP</i>	$\ln(AGB) = a + b \ln(H) + c \ln(H)^2 + d \ln(H)^3 + \beta_3 \ln(\rho)$
<i>X.1 HC</i>	$\ln(AGB) = \alpha + \beta_2 \ln(H) + \beta_4 \ln(C)$
<i>X.2 HC</i>	$\ln(AGB) = a + b \ln(H) + c \ln(H)^2 + d \ln(H)^3 + \beta_4 \ln(C)$
<i>XI.1 CP</i>	$\ln(AGB) = \alpha + \beta_3 \ln(\rho) + \beta_4 \ln(C)$
<i>XI.2 CP</i>	$\ln(AGB) = a + b \ln(C) + c \ln(C)^2 + d \ln(C)^3 + \beta_3 \ln(\rho)$
<i>XII.1 D</i>	$\ln(AGB) = \alpha + \beta \ln(D)$
<i>XII.2 D</i>	$\ln(AGB) = a + b \ln(D) + c \ln(D)^2 + d \ln(D)^3$
<i>XIII.1 H</i>	$\ln(AGB) = \alpha + \beta \ln(H)$
<i>XIII.2 H</i>	$\ln(AGB) = a + b \ln(H) + c \ln(H)^2 + d \ln(H)^3$
<i>XIV.1 C</i>	$\ln(AGB) = \alpha + \beta \ln(C)$
<i>XIV. 2 C</i>	$\ln(AGB) = a + b \ln(C) + c \ln(C)^2 + d \ln(C)^3$

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## MODEL PREDICTION

When data are log transformed a systematic bias is added to the model which underestimate the value of AGB. In order to minimize this bias, the following correction factor (CF) was used (Baskerville 1972):

$$CF = \exp\left(\frac{RSE^2}{2}\right) \quad (8)$$

where residual standard error (RSE) is obtained from the regression model.

## WATER DEFICIT VARIABLES

In order to determine the effect of water deficit on individual biomass, the maximum climatological water deficit (CWD) and an environmental stress indicator (E) were added to the models (Chave et al. 2014). The CWD is the sum of the difference between monthly precipitation ( $P_i$ ) and monthly evapotranspiration ( $ET_i$ ):

$$CWD = \sum_{i=1}^{12} \text{Min}(P_i - ET_i) . \quad (9)$$

Environmental stress is calculated using CWD, temperature seasonality (TS), and precipitation seasonality (PS):

$$E = (0.178 \times TS - 0.938 \times CWD - 6.61 \times PS) \times 10^{-3} \quad (10)$$

The more negative the CWD and E values, the higher the water deficit. CWD and E values for each site were obtained from a database provided by Chave et al. (2014) through a *raster* image with 2.5 *arcsec* resolution ([http://chave.ups-tlse.fr/pantropical\\_allometry.htm](http://chave.ups-tlse.fr/pantropical_allometry.htm)).

As CWD and E values did not show a normal distribution (Shapiro-Wilk test – W = 0.84802, p = 3.698e-11; W = 0.72016, p = 1.435e-15, respectively) we log transformed the data. As both variables have negative values, the following transformation was applied:  $\ln[X_i + 1 - \min(X)]$ , where each value of the variable  $X_i$  was sum to the result of the subtraction of 1 and the minimum value of X before log transformation.

## MODEL FITTING AND SELECTION

We fit and proceed with model selection within the following set of models: tree traits ( $D$ ,  $H$ ,  $C$  and  $\rho$ ); tree traits + CWD; tree traits + E; tree traits + species identity (S); tree traits + CWD + S; and tree traits + E + S. Models including only tree traits, CWD and E were fit using least-squares method. CWD and E were highly correlated (Pearson's r = -0.79, P < 0.001). To assess whether the addition of species identity improve the fit we used mixed models with species as a random factor and maximum restricted likelihood (RMEL) as estimator.

We used a two steps approach to select the best model within different combinations of predictive variables. First, the following criteria were used to rank the models from best to worst: (i) lower RSE; (ii) higher values of the adjusted  $R^2$ ; and (iii) lower AIC (Akaike Information Criterion). Second, we assessed the performance of the models by calculating the proportional error ( $Error_{prop}$ ) between estimated ( $AGB_{est}$ ) and measured ( $AGB_{meas}$ ) total AGB as follows:

$$Error_{prop} = \frac{(AGB_{est} - AGB_{meas})}{AGB_{meas}} \times 100 \quad (11)$$

Thereafter, we used  $Error_{prop}$  to compare models within the same combination of predictive variables (e.g. D, H and  $\rho$ ). When the best model (selected by goodness of fit criteria) showed an error twice as the subsequent model, we chose the model with smaller  $Error_{prop}$ .

Both the RSE and Error<sub>prop</sub> are measures of accuracy. The former denotes the deviance from expected values along different tree sizes and the latter is a departure from measured total AGB. The R<sup>2</sup><sub>adj</sub> is a measure of precision and indicates the amount of variance explained and depends on the number of predictor variables in the model. The AIC measure the model quality which depends on complexity as a measure of number of parameters (Burnham and Anderson 2002).

We calculated how much variation in individual AGB species identity can explain subtracting the R<sup>2</sup><sub>adj</sub> of a linear model (AGB ~ tree traits) from the R<sup>2</sup><sub>adj</sub> of the mixed model with addition of species (AGB ~ tree traits + species).

The regressions were performed in the R platform (R Core Team 2020), using the “nlme” package (Pinheiro et al. 2018), for linear regression and the “lme4” package (Bates et al. 2015) for mixed linear regression. In mixed models, the “MuMin” (Barton 2020) package was used to calculate the R<sup>2</sup> marginal (R<sup>2</sup>m) and conditional (R<sup>2</sup>c). The marginal R<sup>2</sup> shows the variation explained by fixed factors and conditional R<sup>2</sup> shows the variation explained by both fixed and random factors (Roitman et al. 2018). To calculate RSE, we used the “Metrics” package (Hamner and Frasco 2018). The “ggplot2” package (Wickham et al. 2016) was used for graph building.

## RESULTS

### TREE TRAITS AND ALLOMETRIC RELATIONSHIPS

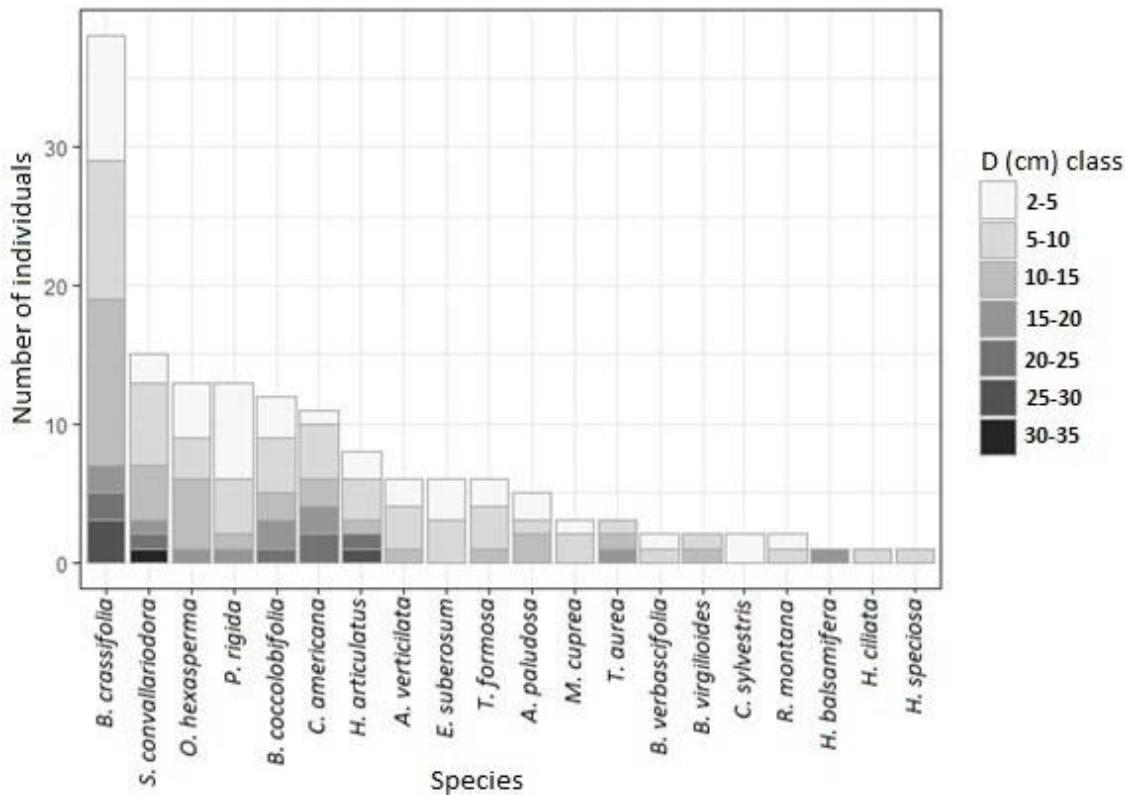
The 150 trees used to estimate biomass were composed by 20 species from 18 genera and 16 families (**Supplementary Material: Table S2**). Almost two thirds of felled trees were small, of which 28% with  $2 \leq D < 5$  cm and 34.67% with  $5 \leq D < 10$  cm (Table 2). Medium-sized trees contributed one third of trees, of which 29.33% with  $10 \leq D < 20$  cm and only 7.33% with  $20 \leq D < 30$  cm, and only one individual (0.67%) was larger than 30 cm. *Byrsonima crassifolia* (25.10%; Malpighiaceae), *Salvertia convallariodora* (10.00%; Vochysiaceae), *Ouratea hexasperma* (8.67%; Ochnaceae), *Palicourea rigida* Kunth (8.67%, Rubiaceae), *Byrsonima cocclobifolia* (8.00%; Malpighiaceae) and *Curatella americana* L. (7.33%; Dilleniaceae) represented more than two-thirds of the sample (Fig. 2). The diameter above the ground varied from 2.22 cm to 32.46 cm ( $9.23 \pm 6.12$  cm; mean  $\pm$  standard deviation) (Fig. 3A). The total height ranged from 0.38 m to 11.2 m ( $2.78 \pm 1.88$  m) (Fig. 3B). The average crown diameter varied between 0.21 to 7.75 m ( $1.95 \pm 1.52$  m) (Fig. 3C), wood density varied between 0.24 g

$\text{cm}^{-3}$  and  $0.77 \text{ g cm}^{-3}$  ( $0.49 \pm 0.10 \text{ g cm}^{-3}$ ) (Fig. 3D) and biomass varied between  $0.03 \text{ kg}$  and  $342.11 \text{ kg}$  ( $17.74 \pm 43.55 \text{ kg}$ ) (Fig. 4). The lowest biomass was found for an individual of *Aegephilla verticillata* and an individual of *S. convallariodora* was the heaviest.

More than two thirds of tree biomass was in the crown (36.84% of twigs, 22.23% of branches and 8.67% of leaves) and the remaining (32.26%) was found in the trunks (Table 2).

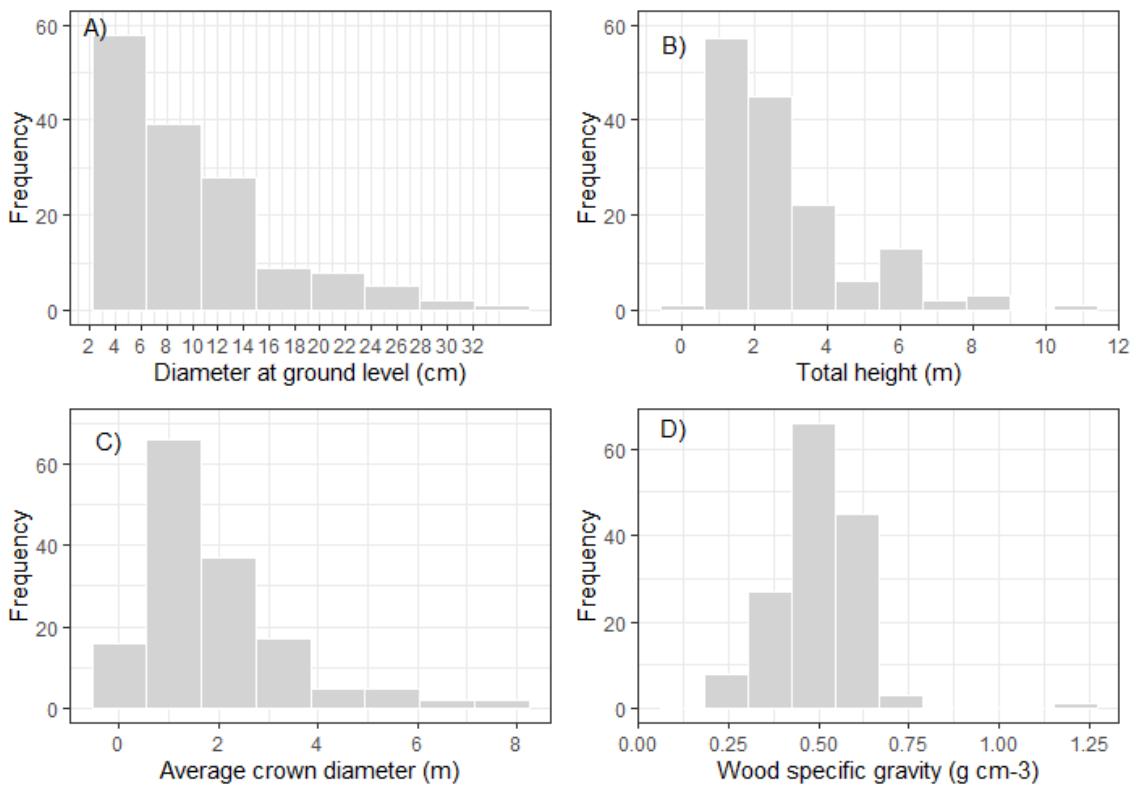
**Table 2.** Distribution of individuals and aboveground biomass (AGB) among tree size classes (diameter above the ground - D) in a sample of 150 trees from the savannas of Amapá, Brazil.

D class (cm)	Number of trees		Total AGB		Leaves	Twig	Branches	Trunk
	(n)	(%)	(kg)	(%)	(%)	(%)	(%)	(%)
2-5	42	28.00	18.44	0.69	0.20	0.49		
5-10	52	34.67	133.30	5.01	0.82	2.79	1.41	
10-15	33	22.00	506.76	19.04	2.30	7.73	5.77	3.24
15-20	11	7.33	415.74	15.62	1.49	6.46	3.30	4.37
20-25	7	4.67	559.52	21.02	1.55	7.71	4.10	7.65
25-30	4	2.66	685.78	25.77	1.82	8.78	6.01	9.16
30-35	1	0.67	342.11	12.85	0.49	2.88	1.64	7.84
Total	150	100	2661.65	100	8.67	36.84	22.23	32.26

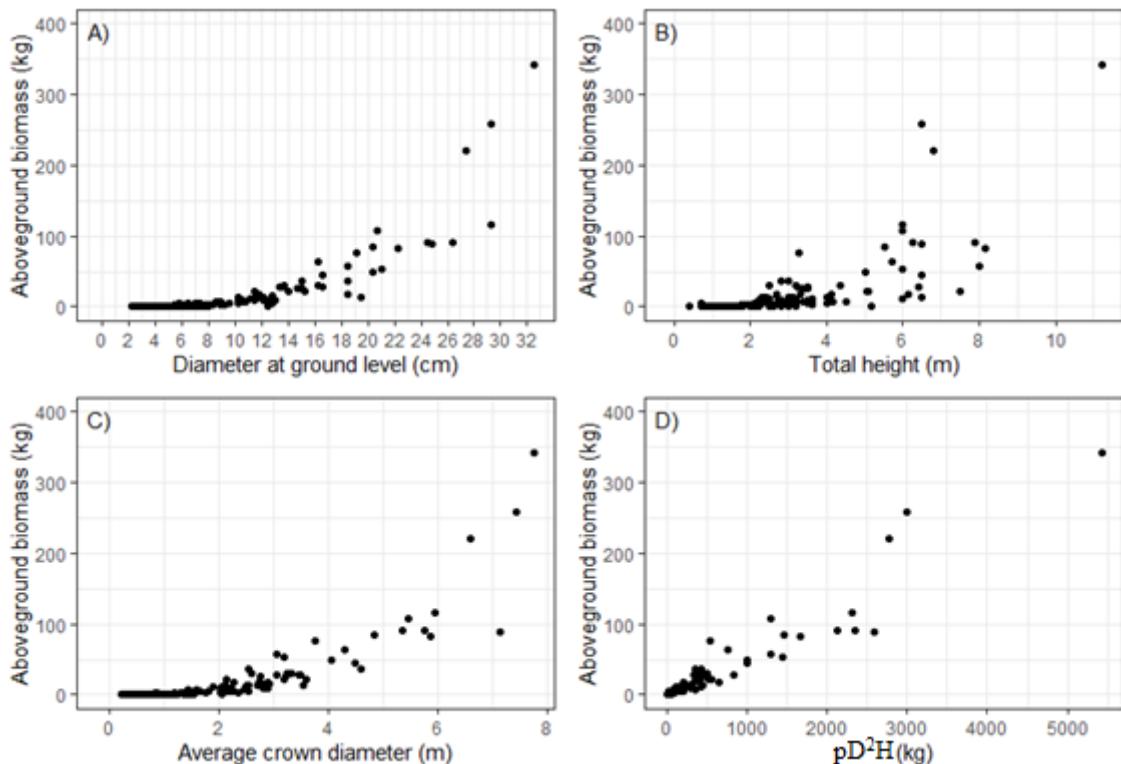


**Fig. 2** Distribution of felled trees according to species and diameter at ground level (D) in the savannas of Amapá, Brazil.

The relationship of AGB with diameter at ground level, total height, and average crown diameter (Fig. 3A-C) followed a non-linear pattern whereas the relationship with the composite variable that represents trunk mass ( $\rho D^2 H$ ) was linear (Fig. 4D). Overall, the dispersion of biomass values increased with tree size.



**Fig. 3** Distribution of trait values for 150 felled trees sampled in the savannas of Amapá, Brazil.



**Fig. 4** Relationships of aboveground biomass with (A) diameter at ground level, (B) total

height, (C) average crown diameter and (D) trunk mass indicator ( $\rho D^2 H$ ), in the savannas of Amapá, Brazil.

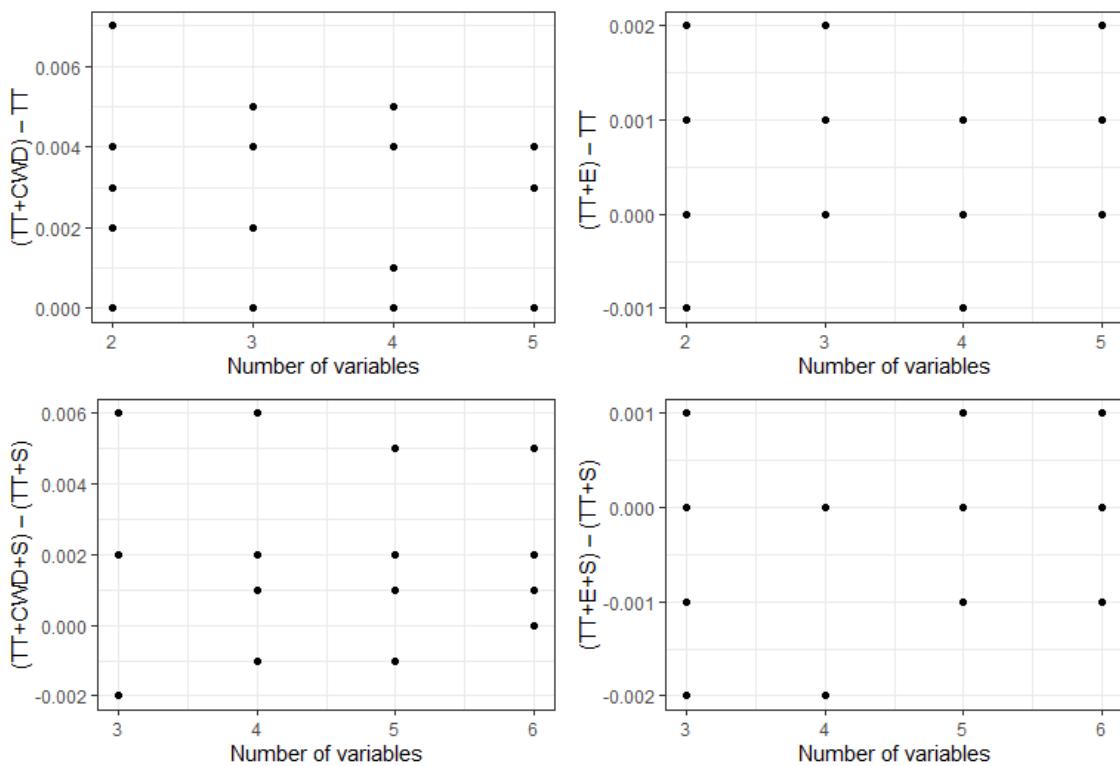
## REGRESSION MODELS OF INDIVIDUAL TREE BIOMASS

Model III.I, which includes the predictor variables of trunk diameter, total height, and crown diameter, provided the best fit ( $RSE = 0.501$ ,  $R^2_{adj} = 0.936$  and  $AIC = 224.3$ ; Table 3). However, models I.1 ( $RSE = 0.502$ ,  $R^2_{adj} = 0.936$  and  $AIC = 225.6$ ), III.2 ( $RSE = 0.504$ ,  $R^2_{adj} = 0.936$  and  $AIC = 225.1$ ) and I.2 ( $RSE = 0.515$ ,  $R^2_{adj} = 0.933$  and  $AIC = 231.7$ ) fit the data as good as the best model. Polynomial models showed the best fit when a single variable was used (Table 3) and among tree traits, average crown diameter showed the highest predictive power in a polynomial model (XIV.2:  $RSE = 0.579$ ,  $R^2_{adj} = 0.915$ ,  $AIC = 267.5$ ; Table 3), followed by total height (XIII.2:  $RSE = 1.002$ ,  $R^2_{adj} = 0.745$ ,  $AIC = 432.2$ ) and diameter at ground level (XII.2:  $RSE = 1.079$ ,  $R^2_{adj} = 0.704$ ,  $AIC = 454.3$ ).

Among the tested models, 77% ( $n = 20$ ) overestimated by 1.67% up to 18.03% the measured AGB while the remainder underestimated by 0.68% to 4.49% the measured AGB (Table 3). The model with average crown diameter and height (X.1) showed the smallest deviation (-0.68%) in relation to the measured AGB followed by the model with average crown diameter, height, and wood density (V), which showed a 1.67% deviation. The model which includes the compound term ( $\rho D^2 H$ ) and average crown diameter (I.2) overestimated by 2% the measured AGB and the polynomial model of crown diameter (VIII.2) underestimated it by around 2%. Another 3 models (IV, VII.1, VIII.1) which include trunk diameter in average crown diameter and wood density, and a fourth model (III.2) with the compound term  $D^2 H$  plus average crown diameter, overestimated measured AGB by less than 5%. Polynomial models of trunk diameter (XII.2) and trunk diameter plus average crown diameter (VII.2) and a linear models of average crown diameter (XIV.1) and crown diameter plus wood density (XI.1) underestimated the measured AGB by less than 5%. The rest of the models overestimated AGB by more than 5%.

The inclusion of species as a random factor did not improve model fit since less than 1% of increase in  $R^2_{adj}$  was achieved with addition of species identity (Fig. 5). The addition of water deficit variables (CWD and E) as well, did not improve model performance also with less than 1% addition to explained variation (Fig. 5). As the

addition of S, CWD and E did not improve model's predictability, we did not calculate the deviance from the measured AGB for these models.



**Fig.5** Differences of  $R^2_{adj}$  of tree trait models (TT) and equivalent models with addition of water deficit variables (CWD and E) and/or species identity (S) related to the number of variables in the models.

**Table 3.** Results of the regression models tested to predict AGB (kg of dry mass) using diameter at ground level (D; cm), total height (H; m), wood density ( $\rho$ ; g/cm<sup>3</sup>), and average crown diameter (C; m) of 150 trees from savannas of Amapá, Brazil. Model fitted parameters are  $\alpha$ ,  $\beta_1$ ,  $\beta_2$ ,  $\beta_3$ ,  $\beta_4$ ,  $b$ ,  $c$  e  $d$ . The degrees of freedom ranged from 144 to 148, and models are ranked according to residual standard error (RSE), adjusted coefficient of determination ( $R^2_{adj}$ ), and value of Akaike Information Criterion (AIC). CF is the correction factor for bias associated to log transformation. The deviance (Error<sub>prop</sub>; %) of estimated total AGB (AGB<sub>est</sub>; kg) from measured total AGB (2661.65 kg) is shown with its rank from lowest to highest.

Model	Equation	$\alpha$	$\beta_1$	$\beta_2$	$\beta_3$	$\beta_4$	$b$	$c$	$d$	RSE	$R^2_{adj}$	AIC	CF	AGB <sub>est</sub>	Error <sub>prop</sub>	Rank
III.1 DHC	$\ln(AGB) = \alpha + \beta_1 \ln(D) + \beta_2 \ln(H) + \beta_4 \ln(C)$	-1.367	0.638	0.590		1.679	...	...	...	0.497	0.937	222.1	1.132	2800.63	5,4	13
I.1 DHPC	$\ln(AGB) = \alpha + \beta_1 \ln(D) + \beta_2 \ln(H) + \beta_3 \ln(\rho) + \beta_4 \ln(C)$	-1.420	0.632	0.596	-0.076	1.689	...	...	...	0.499	0.937	223.9	1.132	2817.51	6,5	15
III.2 DHC	$\ln(AGB) = \alpha + \beta_2 \ln(D^2 H) + \beta_4 \ln(C)$	-1.442	...	0.372		1.761	...	...	...	0.502	0.936	223.9	1.134	2787.42	4,9	12
I.2 DHPC	$\ln(AGB) = \alpha + \beta_2 \ln(\rho D^2 H) + \beta_4 \ln(C)$	-1.092	...	0.357		1.744	...	...	...	0.509	0.934	227.7	1.138	2705.29	2,1	4
VIII.2 DC	$\ln(AGB) = a + b \ln(D) + c \ln(D)^2 + d \ln(D)^3 + \beta_4 \ln(C)$	1.019	...	...		2.022	-2.755	1.694	-0.258	0.533	0.928	243.6	1.152	2605.26	-2,1	3
VIII.1 DC	$\ln(AGB) = \alpha + \beta_1 \ln(D) + \beta_4 \ln(C)$	-1.179	0.714	...		2.040	...	...	...	0.534	0.928	242.6	1.153	2725.63	2,4	6
IV DPC	$\ln(AGB) = \alpha + \beta_1 \ln(D) + \beta_3 \ln(\rho) + \beta_4 \ln(C)$	-1.159	0.716	...	0.031	2.035	...	...	...	0.536	0.927	244.5	1.154	2722.93	2,9	7
V HPC	$\ln(AGB) = \alpha + \beta_2 \ln(H) + \beta_3 \ln(\rho) + \beta_4 \ln(C)$	-0.447	...	0.708	-0.231	2.040	...	...	...	0.552	0.923	253.2	1.164	2690.39	1,7	2
X.1 HC	$\ln(AGB) = \alpha + \beta_2 \ln(H) + \beta_4 \ln(C)$	-0.256	...	0.695		2.018	...	...	...	0.552	0.923	252.4	1.165	2641.08	-0,7	1
X.2 HC	$\ln(AGB) = a + b \ln(H) + c \ln(H)^2 + d \ln(H)^3 + \beta_4 \ln(C)$	-0.226	...	...		2.000	0.485	0.173	-0.022	0.552	0.923	254.5	1.165	2795.74	6,5	14
XIV.2 C	$\ln(AGB) = a + b \ln(C) + c \ln(C)^2 + d \ln(C)^3$	-0.012	...	...	...	2.429	0.333	-0.099	0.579	0.915	267.5	1.182	2919.14	9,7	17	
XI.2 CP	$\ln(AGB) = a + b \ln(C) + c \ln(C)^2 + d \ln(C)^3 + \beta_3 \ln(\rho)$	-0.065	...	...	-0.066	...	2.444	0.334	-0.103	0.579	0.915	268.5	1.182	2917.79	9,6	16
XI.1 CP	$\ln(AGB) = \alpha + \beta_3 \ln(\rho) + \beta_4 \ln(C)$	0.029	...	...	-0.125	2.519	...	...	...	0.600	0.909	277.5	1.197	2565.24	-3,1	8
XIV.1 C	$\ln(AGB) = \alpha + \beta \ln(C)$	0.129	...	...	...	2.502	...	...	...	0.599	0.909	275.8	1.196	2542.56	-4,5	11
II.1 DHP	$\ln(AGB) = \alpha + \beta_1 \ln(D) + \beta_2 \ln(H) + \beta_3 \ln(\rho)$	-2.813	1.429	1.651	0.566	...	...	...	...	0.771	0.849	353.7	1.346	2949.73	13,3	20
VI.1 DH	$\ln(AGB) = \alpha + \beta_1 \ln(D) + \beta_2 \ln(H)$	-3.297	1.424	1.742	...	...	...	...	...	0.778	0.846	355.3	1.353	3118.43	18,0	26

II.2 DHP	$\ln(\text{AGB}) = \alpha + \beta_2 \ln(D^2 H \rho)$	-3.078	...	0.985	...	...	...	...	...	0.818	0.830	369.3	1.397	3061.50	17,2	25
VI.2 DH	$\ln(\text{AGB}) = \alpha + \beta_2 \ln(D^2 H)$	-4.046	...	1.032	...	...	...	...	...	0.840	0.821	377.4	1.423	3020.29	14,2	21
XIII.2 H	$\ln(\text{AGB}) = a + b \ln(H) + c \ln(H)^2 + d \ln(H)^3$	-1.190	...	...	...	...	1.928	1.301	-0.439	0.971	0.7606	422.7	1.602	2993.32	15,8	23
IX.2 HP	$\ln(\text{AGB}) = a + b \ln(H) + c \ln(H)^2 + d \ln(H)^3 + \beta_3 \ln(\rho)$	-0.721	...	0.495	...	1.797	1.230	-0.385	0.969	0.761	423.2	1.599	2995.62	16,3	24	
XIII.1 H	$\ln(\text{AGB}) = \alpha + \beta \ln(H)$	-1.156	...	2.746	...	...	...	...	...	0.995	0.749	428.1	1.640	3028.42	14,6	22
IX.1 HP	$\ln(\text{AGB}) = \alpha + \beta_2 \ln(H) + \beta_3 \ln(\rho)$	-0.719	...	2.669	0.502	...	...	...	...	0.993	0.750	428.4	1.636	2885.37	11,4	18
VII.2 DP	$\ln(\text{AGB}) = a + b \ln(D) + c \ln(D)^2 + d \ln(D)^3 + \beta_3 \ln(\rho)$	1.137	...	1.497	...	-4.225	3.385	-0.531	1.031	0.730	441.7	1.701	2536.92	-4,5	10	
VII.1 DP	$\ln(\text{AGB}) = \alpha + \beta_1 \ln(D) + \beta_3 \ln(\rho)$	-2.917	2.504	...	1.604	...	...	...	...	1.035	0.728	441.0	1.708	2706.80	4,2	9
XII.2 D	$\ln(\text{AGB}) = a + b \ln(D) + c \ln(D)^2 + d \ln(D)^3$	0.351	...	...	...	-5.430	4.203	-0.678	1.079	0.704	454.3	1.790	2600.71	-2,3	5	
XII.1 D	$\ln(\text{AGB}) = \alpha + \beta \ln(D)$	-4.461	2.672	...	...	...	...	...	...	1.092	0.697	456.1	1.815	2984.70	12,2	19

## CHOICE OF THE BEST MODELS

The best models for future estimates and monitoring of biomass stocks in the savannas of Amapá - considering the availability of tree traits and including the correction factor (Eq. 8) - are described below.

When trunk diameter (D), total height (H), wood density ( $\rho$ ), and crown diameter (C) are available, the best model was I.2:

$$(AGB)_{est} = \exp(-0.962 + 0.357 \ln(\rho D^2 H) + 1.744 \ln(C))$$

When D, H, and  $\rho$  are available the best model was II.1:

$$(AGB)_{est} = \exp(-2.516 + 1.429 \ln(D) + 1.651 \ln(H) + 0.566 \ln(\rho))$$

When data on D, H, and C are available, the best model was III.2:

$$(AGB)_{est} = \exp(-1.316 + 0.372 \ln(D^2 H) + 1.761 \ln(C))$$

When D,  $\rho$ , and C are available, the appropriate model was IV:

$$(AGB)_{est} = \exp(-1.015 + 0.716 \ln(D) + 0.031 \ln(\rho) + 2.035 \ln(C))$$

When H,  $\rho$ , and C are available the recommended model was V:

$$(AGB)_{est} = \exp(-0.295 + 0.708 \ln(H) - 0.231 \ln(\rho) + 2.040 \ln(C))$$

When only D and H are available the best model was VI.2:

$$(AGB)_{est} = \exp(-3.693 + 1.032 \ln(D^2 H))$$

When D and  $\rho$  are available the best model was VII.1:

$$(AGB)_{est} = \exp(-2.381 + 0.714 \ln(D) + 2.040 \ln(\rho))$$

When the D and C are available, model VIII.2 was the best choice:

$$(AGB)_{est} = \exp(1.161 - 2.757 \ln(D) + 1.694 \ln(D)^2 - 0.258 \ln(D)^3 + 2.022 \ln(C))$$

When only H and  $\rho$  is available, the best model was IX.1:

$$(AGB)_{est} = \exp(-0.226 + 2.669 \ln(H) + 0.502 \ln(\rho))$$

For H and C, the best choice was model X.1:

$$(AGB)_{est} = \exp(-0.103 + 0.695 \ln(H) + 2.018 \ln(C))$$

When only  $\rho$  and C are available, the best model was XI.1:

$$(AGB)_{est} = \exp(0.209 + -0.125 \ln(\rho) + 2.519 (C))$$

When just one predictive variable is available, the best models were:

For D, model XII.2:

$$(AGB)_{est} = \exp(0.933 + 1.928\ln(D) + 1.301\ln(D)^2 - 0.439\ln(D)^3)$$

For H, model XIII.1:

$$(AGB)_{est} = \exp(-0.661 + 2.746\ln(H))$$

For C, model XIV.1:

$$(AGB)_{est} = \exp(0.308 + 2.502\ln(C))$$

## DISCUSSION

This study is the first to develop allometric equations to estimate the aboveground biomass in savannas of Northeastern Amazonia. We used measures of tree traits (trunk diameter, total height, crown diameter and wood density) to fit models with different combinations of predictive variables, and we tested if the addition of species identity and water deficit variables can increase the predictability of models.

We develop models ( $R^2 = 0.94$ ) for savannas of Amapá using a sample of 150 trees ( $\geq 2$  cm in diameter) of 20 species that represent more than 43% of species and around 97% of individuals in the savannas of the region (Costa Neto 2014). Moreover, the proportion of medium to large trees ( $\geq 20$  cm in diameter) in the sample (~8%) was far higher than frequency (~2%) of these tree sizes in the savannas of Amapá (Costa Neto 2014).

The number of trees and species used to generate allometric equations for savannas vary highly. The allometric equation developed for savannas of Roraima by Barbosa and Fearnside (2005a) used 130 trees and comprised 14 species ( $D \geq 2$  cm and  $R^2 = 0.98$ ), which contributes to > 90% of abundance in the area. For typical *Cerrado* in Central Brazil, Rezende et al. (2006) used 174 trees of 49 species to develop allometric models. The diameter of the trees varied between 5 and 55 cm and the precision of the models was 93%. Roitman et al. (2018) used 114 trees of 8 species, to build models up to 92% in precision. Another study carried out in the *Cerrado* of Central Brazil used 120 trees of 18 species to develop an allometric model with a diameter range of 5.0-27.7 cm, representing 75% of the individuals in the area. The constructed model represents 93% accuracy

(Ribeiro et al. 2011). Studies combining different datasets can increase the predictive power of models for large areas (Chave et al. 2005, Saatchi et al. 2011), however, there is often a loss of precision at the local scale (Feudpausch et al. 2012, Chave et al. 2014). Mugasha et al. (2013) recommended a large number of felled trees ( $> 167$ ) and a wide range in size (1 cm to 110 cm), to build good biomass models for forests (mature tropical forest, rainforest and miombo woodlands). However, to date no analysis was conducted to determine sample size for biomass models in savannas. In the present study, a precision of 94% was obtained with a sample of 150 trees, which is apparently reasonable for local scale biomass estimates.

The present models also encompassed a reasonable part of local flora, which contributes to incorporate most variation in functional traits which are correlated to biomass. A close comparison to the only equation for Amazonian savannas built up to date, in Roraima (Barbosa and Fearnside 2005a), Amapá's sample shared 8 tree species with the Roraima's sample, showing high similarity in composition. However, there are high differences in tree structure, with lower contribution of trunk diameter ( $\beta = 0.646$ ) and higher importance of crown diameter ( $\beta = 1.704$ ) for Amapá's equation vs. higher importance of trunk ( $\beta = 1.589$ ) and lower of crown ( $\beta = 1.025$ ) for in Roraima's equation. These differences associated to tree structure highlight the importance of development of local equations for enclaves of Amazonian savannas.

In this study, we show that the average crown diameter has the highest explanatory power for tree biomass estimates. Previous studies have found similar results, showing that crown is a key variable in biomass estimates mainly in equations with different species (Goodman et al. 2014, Blanchard et al. 2016, Mensah et al. 2016, Ploton et al. 2016). In tropical forests, crown size is also an important variable to estimate biomass, but it has not been included in the models due to the difficulty of measurement in forest inventories. Forests with shorter trees have a larger amount of biomass stored in crown components. Nogueira et al. (2008a) found that the weight of the crown can represent up to 39% of tree biomass in forests in the south of the Amazonia and Goodman et al. (2014) found up to 71% of biomass in tree crowns of a semi-deciduous forest in Peru. Branches, twigs, and leaves represented an average of 90% of tree biomass in this study, explaining why crown diameter has a much greater predictive power than other tree measures. Dimobe et al. (2018a), studying savannas of Sudan, have found that crown explained up to 84% of the variation in biomass. For trees of open forest in the Pantanal of Brazil,

crown size explained up to 90% of variability in biomass (Salis et al. 2006). In the savanna, trees have more space for crown expansion, concentrating more biomass in the leaves and branches, instead of investing in height as forest trees under high stem density (Návar 2009a, Barbeito et al. 2014, Dimobe et al. 2018a). Savannas in general, are open environments with the predominance of a short herbaceous layer, therefore, competition at the canopy level is small, allowing low-height trees to invest more resources in crown components instead of trunk height (Forrester et al. 2017, 2018).

Trunk diameter is related to total height which is correlated with crown size and thus, trunk diameter can be correlated to crown diameter (King 1996, Sterck et al. 2001). Chave et al. (2005) have shown that including height in the allometric models for forest trees, the errors can be decreased from 19.5% to 12.8%. Environmental conditions shape tree growth in height, thus, it can affects the biomass accumulation (Cassol et al. 2018). Trees in savannas face low competition for light and do not need to invest to grow in height as forest trees do. Savanna trees have higher benefit investing in crown expansion than in trunk height, thus the proportion of biomass in crown is higher compared to forest trees (King et al. 2006, Goodman et al. 2014, Blanchard et al. 2016). It may explain why crown diameter was more important than trunk height or diameter to explain variation in aboveground of trees from savannas of Amapá.

The low influence of wood density on predictability of present models may be due to low wood density (average of  $0.49 \text{ g cm}^{-3}$ ) of tree species in our sample. In dense forests of Amazonia, the average wood density is generally higher ( $0.70 \text{ g cm}^{-3}$ ) (Nogueira et al. 2005), and inclusion of wood density in allometric models became frequent (Chave et al. 2005; Goodman et al., 2014). However, the use of wood density in models for savanna trees has low effect on predictability (Roitman et al. 2018) probably because supporting costs are low for small and medium-sized trees like those found in savannas (King et al. 2006, Forrester et al. 2017). Furthermore, wood density is physical property of wood, varying between species and between individuals of the same species, thus representing the physiological strategies associated to tree ontogeny (Nogueira et al. 2021). The lack of an effect of wood density on the accuracy of models is also due to low interspecific variation - responsible for most of the variability in this trait (Chave et al. 2006, Molto et al. 2013) - resulting from the dominance of few tree species in the sample. Intraspecific variation for the five dominant species (61% of the sample) was low (mean

CV 15%). Therefore, wood density seems to be of low importance for tree biomass estimates in savannas of Amapá.

## REGRESSION MODEL OF INDIVIDUAL BIOMASS OF TREES

The best allometric models according to goodness of fit criteria and deviance from measured total AGB were models III.2 and I.2 which explained 94% and 93% of variation in tree AGB. Such models (III.2 and I.2) include composite terms ( $D^2H$  and  $\rho D^2H$ , respectively) and average crown diameter. Models with composite terms (volume  $\times \rho$  or  $D^2H$ ) also showed good performance for trees of typical *Cerrado* in Central Brazil (Resende et al. 2006, Roitman et al. 2018) but did not for *Cerrado* in the southeast region of the biome (Ribeiro et al. 2011). Though RSE and  $R^2_{adj}$  did not rank models with composite terms as best, AIC and the Error<sub>prop</sub> did. AIC applies the principle of parsimony in favor of mathematical simplicity, choosing models with less parameters. Error<sub>prop</sub> is the deviance from measured total AGB, which will weight for differences between estimated and measured AGB of medium and large trees. Indeed, Error<sub>prop</sub> of total AGB of trees  $\geq 20$  cm D was almost three times lower for model with a composite term (I.2) compared to the similar model with all variables separated (I.1). Therefore, our choice for the best models minimized errors associated to medium to large trees, which accounts for most AGB in the ecosystems.

The AGB model developed by Barbosa and Fearnside (2005a) for savannas of Roraima, is the only study which included crown size in AGB models for savannas up to date. However, we found that crown size is more important for trees of savannas of Amapá than Roraima, since the coefficient of crown diameter was ~70% for trees of Amapá. In the present study, the first thirteen models ranked as best included crown diameter as predictor. Further, for forest trees, Goodman et al. (2014) showed that all models which included crown size were better than other models. As crown components comprises most biomass of savanna trees, it is essential to include this variable in AGB models and field inventories.

In our study (66%, n = 8) of models with two variables underestimated the total biomass. The polynomial model of crown diameter explained over 92% in AGB variation. This model can be very useful for estimating tree biomass in savannas given the feasibility of measuring tree crowns in these open vegetations (Ratnam et al. 2011, Toma 2012).

With the addition of species as a random variable in the models, there was no fit improvement. The low diversity of tree species (20) in and high dominance of few species in the sample (68.66% of the individuals belong to 6 species) may reduce interspecific variation and intraspecific variation may not be well represented by species identity in the model. In savannas with a high diversity of species, such as in central Brazil, the inclusion of species as a random variable improve the fit of the models by around 2% (Roitman et al. 2018). The low increase is also associated with the domain of tree oligarchies.

The bioclimatic variables do not improve the fit of the models, which can be explained by the low spatial variation in temperature, precipitation, evapotranspiration and topography in the region. Although these variables are key in spatial AGB variation - , because drought and high temperatures have a negative effect on photosynthetic processes, limiting biomass production (Xu and Zhou 2005) - variation within the studied area does not seem to be enough to generate noticeable differences in models for estimating individual tree AGB.

Studies indicate that the incorporation of the tree height and crown diameter as additional variables to the diameter can improve the prediction of allometric models (Mensah et al. 2016, Xue et al. 2016, Dimobe et al. 2018a, Dimobe et al. 2018b). Total height and diameter are the main predictors used in allometric models for estimating tree biomass (Nogueira et al. 2008b, Feldpausch et al. 2012, Kuyah et al. 2012, Mugasha et al. 2013). However, in our study region, we observed that the best predictor is crown diameter and that the total height and trunk diameter are secondary to explain individual variation of biomass. However, in a West-Africa savannah, the incorporation of the total height improved the adjustments in the models developed for species such as *Combretum glutinosum* and *Terminalia laxiflora* (Dimobe et al. 2018b). Similar observations have been reported for a subtropical forest in China by Xiang et al. (2016), where these variables explained more than 80% of the variability in biomass.

Total height is a very important predictor of biomass in tropical forests (Chave et al. 2005, Feldpausch et al. 2012). In savannas where trees have short height, the allometric relationships between height and crown size is strongly dependent on wood density (Dietze et al. 2008, Návar 2009a, Ducey 2012). In general, open forests have trees with larger crowns and denser forests have taller trees with smaller crowns (Nogueira et al. 2008b), which influences allometric models. Both the total height and the crown diameter

are important to compensate for the variations between height and horizontal growth of the branches, which determines the size of the crown, as the tree allocates more resources to crown when it reaches sufficient height to access the light (King et al. 2006, Poorter et al. 2006, Iida et al. 2012, Blanchard et al. 2016). When the crown is not included in the model along with height, the biomass of the short trees can be underestimated (Goodman et al. 2014). Thus, in savanna areas with short trees, it is essential that both the total height and the crown dimension be included in the models. In addition, individual tree crown measurements can be obtained using high resolution optical images or laser images such as Lidar, which make easier the biomass estimates at the regional and local level (Gougeon 1998, Popescu et al. 2003, Blanchard et al. 2016).

Generic models are capable of providing important information at large scales, but it can generate estimates very far from the true values at local scale (up to 400% error) due to differences in tree architecture, soil, climate, age and, management practices (Kaonga and Bayliss-Smith 2009, Alvarez et al. 2012, Chave et al. 2014, Ngomanda et al. 2014, Aneseyee et al. 2021). Regional biomass estimates require equations that integrate tree traits (wood density, volume, and dendrometric variables) for all aspects of the forest structure that vary at a regional level (Návar 2009b). The performance of destructive sampling (measurement, felling, and weighting of trees) requires a lot of time and resources, in addition of requiring the cutting of trees - changing the sampled habitats -, thus representing challenges for the development of models at regional and local scales, considering the large number of trees required.

The lack of local models is the main source of uncertainties in biomass estimates. For example, Chave et al. (2014) developed a generic model that overestimated the total biomass for an Acacia forest in Ethiopia (Aneseyee et al. 2021), in Vietnam rain forests (Huy et al. 2016), in transition forests in Central Africa (Ngomanda et al. 2014) and in the tropical forests of Colombia (Alvarez et al. 2012). On the other hand, the same model underestimated biomass in Brazil's Atlantic Forest (Fonsêca et al. 2020). The model developed by Chave et al. (2005) underestimated the total biomass for three forest areas in the Colombian Amazonia (Alvarez et al. 2012). Therefore, these inconsistencies found in biomass estimates can lead to erroneous conclusions about the role of forests and savannas in climate change. Due to these uncertainties associated to estimates made by generic models, it is necessary to develop allometric models at a local scale (Jenkins et al. 2003, Lambert et al. 2005, Fayolle et al. 2013, Ngomanda et al. 2014, Aneseyee et al.

2021). Local models are an important tool for greenhouse gases mitigation projects (Brown et al. 1989, Segura and Andrade 2008) within the scope of REDD+ (Reducing Emissions from Deforestation and Forest Degradation), as it allows for better estimates and increase the reliability of the process of carbon credit payment (IPCC 2006, Maulana et al. 2016, Nam et al. 2016, Mahmood et al. 2019). In this way, local carbon estimates are a useful tool for public management to support local land-use policies to mitigate the emission greenhouse gases.

## CONCLUSIONS

The use of allometric models for calculating aboveground biomass in Amazonian savannas is important for the research related to carbon storage and carbon flux. However, most Amazonian savannas still lack local allometric equations, capable to produce robust biomass estimates. Our study showed that the inclusion of crown diameter in allometric models significantly improves biomass estimates in Amazonian savannas. The results presented here make it possible to improve the accuracy of the biomass estimates, allowing us to better understand the role of areas Amazonian savannas in the global carbon cycle.

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## CONCLUSÕES

As equações alométricas geradas neste estudo, podem se utilizar para realizar estimativas de biomassa e monitoramento da dinâmica e sequestro do Carbono, além de permitir estabelecer comparações em pesquisas futuras desenvolvidas a partir de dados de inventário florestal;

Este estudo reforça, que a incorporação do diâmetro do tronco e diâmetro médio da copa, pode melhorar substancialmente as predições de biomassa, assim recomenda-se a incorporação desses atributos em todos os inventários e no desenvolvimento de equações futuras (Hipótese 2.1);

Este estudo demonstrou que pode-se utilizar o diâmetro médio da copa como variável única para estimar a biomassa nas savanas do Amapá, pois, essa variável em um modelo polinomial mostrou um coeficiente de determinação alto ( $R^2= 0.91$ ) (Hipótese 2.1);

Os modelos alométricos foram desenvolvidos especificamente para a biomassa aérea mediante a somatória dos componentes da arvore (folhas, gravetos, galhos e tronco). Os gravetos foram o componente com maior apporte na biomassa total 36.83% (Hipótese 2.2);

O conjunto das árvores usadas em nosso estudo estavam divididos em 7 classes de DAP, 25,75% da biomassa total foi representada por árvores com um diâmetro entre 25-30 cm; (Hipótese 2.3).

A inclusão das variáveis de déficit hídrico não apresentou melhoras significativas no ajuste dos modelos alométricos (Hipótese 2.4).

## ANEXOS

### Supplementary Material

**Table S1.** Number of individuals of the main species were distributed in diameter classes for destructive collection based on a previous inventory (Costa Neto 2014) carried out in 137 plots distributed in the Amapá savanna. The observed relative frequency was used to define the number of individuals per species for the allometric equation considering a total of 150 individuals. Individuals were distributed into size classes according to the minimum and maximum values of aboveground diameter (Das) for each species. The relative frequencies for the equation were adjusted to obtain a better distribution of individuals in size classes.

Species	Number individuals inventoried	of Das min. (cm)	Das max. (cm)	Observed relative frequency (%)	Number individuals Equation	Relative Frequency Equation (%)	Diametric classes (cm)/number individuals					
							5-10	10-15	15-20	20-25	25-30	>30
Byrsonima crassifolia (L.) Kunth	1764	4,8	25,8	42,6	32	21,3	8	8	8	8		
Ouratea hexasperma (A.St.-Hil.) Baill.	750	4,8	30,2	18,1	24	16,0	4	4	4	4	4	4
Salvertia convallariodora A.St.-Hil.	489	4,8	27,1	11,8	20	13,3	4	4	4	4	4	4
Palicourea rigida Kunth	289	4,8	25,1	7,0	10	6,7	2	2	2	2	2	2
Curatella americana L.	227	4,8	33,4	5,5	12	8,0	2	2	2	2	2	2
Byrsonima coccobifolia Kunth	226	4,8	22,9	5,5	8	5,3	2	2	2	2		
Himatanthus articulatus (Vahl) Woodson	78	4,8	34,7	1,9	6	4,0	1	1	1	1	1	1

Erythroxylum suberosum A.St.-Hil.	73	4,8	20,7	1,8	6	4,0	2	2	2	
Tocoyena formosa	29	4,8	12,4	0,7	5	3,3	3	2		
(Cham. & Schltdl.) K.Schum.										
Roupala montana Aubl	27	5,1	29,3	0,7	5	3,3	1	1	1	1
Annona paludosa Aubl.	20	4,8	18,5	0,5	5	3,3	2	2	1	
Hirtella ciliata Mart. & Zucc	17	4,8	24,2	0,4	4	2,7	1	1	1	1
Tabebuia aurea (Silva Manso) Benth. & Hook.f. ex 15 S.Moore		6,4	13,7	0,4	4	2,7	2	2		
Bowdichia virgilioides Kunth	12	6,0	28,0	0,3	5	3,3	1	1	1	1
Myrcia amazonica DC.	11	5,1	12,1	0,3	4	2,7	2	2		
30 espécies restantes	114	4,8	52,2	2,8	-	-	-	-	-	-
Total	4141		100		150	100	37	36	29	26
									15	7

**Table S2.** Data of 150 trees collected in 20 places in the savanna of Northeastern Amazonia.

Family	Genus	Diameter at ground height (cm)	Diameter at ground height 30 (cm)	Stem height (m)	Total height (m)	Crown. Max. (m)	Crown. Mim. (m)	Crown diameter (m)	Leaves (kg)	Twig (kg)	Bran ch.kg	Stem (kg)	Total dry biomass (kg)	Wood density (gcm-3)
Vochysiaceae	Salvertia A.St.-Hil.	32,47	30,56	0	11,2	8,5	7	7,75	13,05 6	76,62 8	43,73 3	208,6 93	342,11	0,46
Fabaceae	Bowdichia Kunth	11,78	11,14	0,77	4,12	3	2,75	2,88	5,787	5,605	3,944	2,821	18,157	0,60
Bignoniaceae	Tabebuia	10,50	10,19	1,22	4,15	2,45	2,05	2,25	0,527	2,236	4,273	0	7,036	0,77
Malpighiaceae	Byrsinima Rich. Ex Kunth	6,68	6,37	0,35	1,75	1,58	1,4	1,49	0,705	2,215	0,986	0	3,906	0,59
Malpighiaceae	Byrsinima Rich. Ex Kunth	7,64	6,05	0,72	1,85	1,66	1,23	1,45	0,326	1,675	0,994	0	2,995	0,57
Malpighiaceae	Byrsinima Rich. Ex Kunth	10,19	9,23	0,35	3,4	2,65	2,24	2,45	1,226	3,766	2,52	0	7,512	0,57
Dilleniaceae	Curatella Loefl	16,55	16,23	3,2	6,4	3,8	2,3	3,05	1,185	9,84	6,825	10,15 1	28,001	0,47
Malpighiaceae	Byrsinima Rich. Ex Kunth	19,10	17,83	0,3	3,25	3,8	3,7	3,75	9,714	35,26 7	15,00 8	16,16 6	76,155	0,45
Apocynaceae	Himatanthus Willdenow	12,09	11,46	0,66	3,2	2,1	2	2,05	2,193	3,321	3,682	0,93	10,126	0,31
Malpighiaceae	Byrsinima Rich. Ex Kunth	8,28	7,00	0,71	2,1	1,8	1,7	1,75	0,79	2,433	0,562	0	3,785	0,59
Malpighiaceae	Byrsinima Rich. Ex Kunth	7,96	7,32	0,65	1,9	1,5	1,45	1,48	0,397	1,541	0,944	0	2,881	0,59
Dilleniaceae	Curatella Loefl	8,91	9,55	0,3	2	0,9	0,8	0,85	0,193	0,691	1,086	0	1,97	0,43
Annonaceae	Annona L.	11,78	10,82	2,9	6,5	4,3	2,8	3,55	0,608	4,015	6,502	1,884	13,01	0,50

Proteacea e	Roupala Aubl.	7,00	6,68	0,5	1,4	1,35	0,75	1,05	0,17	0,646	0,416	0	1,232	0,70
Rubiacea e	Palicourea Aubl.	9,55	9,55	0,35	0,7	2	1,6	1,8	0,366	2,88	1,22	0	4,466	0,39
Erythrox ylaceae	Erythroxylum P. Browne	7,32	6,37	0,85	1,3	1,6	1,1	1,35	0,152	0,833	0,527	0	1,512	0,36
Apocyna ceae	Himatanthus Willdenow	5,73	5,09	0,52	1,8	1,14	0,7	0,92	0,24	0	0	0	0,24	0,31
Malpighi aceae	Byrsinima Rich. Ex Kunth	7,32	6,05	0,55	1,9	1,4	1,3	1,35	0,51	1,61	0,445	0	2,564	0,59
Apocyna ceae	Hancornia Gomes	8,91	7,32	1,06	3,5	2,8	2,3	2,55	0,41	2,592	1,155	0	4,157	0,65
Malpighi aceae	Byrsinima Rich. Ex Kunth	7,32	7,00	1,8	2,9	1,6	1,3	1,45	0,557	3,244	1,711	0	5,512	0,57
Ochnacea e	Ouratea Aubl.	11,14	10,19	1,5	3,6	2,1	1,7	1,9	0,696	4,244	6,657	0	11,597	0,60
Malpighi aceae	Byrsinima Rich. Ex Kunth	7,96	7,00	0,85	2,9	0,87	0,78	0,83	0,243	1	0,879	0	2,122	0,57
Malpighi aceae	Byrsinima Rich. Ex Kunth	14,64	12,41	0,91	3,4	3,22	3,2	3,21	3,238	16,03 4	0,669	5,865	25,806	0,57
Malpighi aceae	Byrsinima Rich. Ex Kunth	26,42	22,28	1,1	6,24	5,9	4,8	5,35	1,959	25,30 1	15,74 9	47,51 2	90,522	0,54
Ochnacea e	Ouratea Aubl.	10,19	9,87	1,1	3,1	3	2,5	2,75	1,31	6,468	4,916	0	12,694	0,60
Apocyna ceae	Himatanthus Willdenow	24,51	23,55	1,2	7,9	6,1	5,4	5,75	1,968	29,36 3	19,96 2	40,46 1	91,754	0,45
Annonac eae	Annona L.	2,86	2,22	0,52	1,14	1,29	1,1	1,2	0,133	0,44	0	0	0,573	0,53
Malpighi aceae	Byrsinima Rich. Ex Kunth	13,69	11,46	1	4,35	2,7	2,5	2,6	4,192	12,72 6	5,995	7,044	29,957	0,61
Rubiacea e	Tocoyena Aubl.	5,41	5,09	1,05	2,1	1,6	1,5	1,55	0,44	0,863	0,64	0	1,943	0,59
Rubiacea e	Tocoyena Aubl.	4,77	4,14	0,9	2,5	1,26	1,1	1,18	0,232	1,183	0	0	1,415	0,56

Lamiaceae	Aegiphila Jacq.	6,37	5,73	1,23	2,6	1,2	1	1,1	0,019	0,392	0	0	0,411	0,36
Lamiaceae	Aegiphila Jacq.	4,77	3,82	0,42	0,86	0,31	0,28	0,3	0,022	0,159	0	0	0,181	0,36
Rubiaceae	Palicourea Aubl.	4,46	4,14	0,24	0,97	0,59	0,53	0,56	0,149	0,244	0	0	0,393	0,39
Rubiaceae	Palicourea Aubl.	5,09	4,77	0,38	1,6	1,14	0,7	0,92	0,104	0,104	0	0	0,207	0,49
Dilleniaceae	Curatella Loefl	12,73	10,50	0,45	2,3	1,5	1,3	1,4	0,495	1,494	2,123	1,706	5,817	0,56
Malpighiaceae	Byrsinima Rich. Ex Kunth	7,32	7,00	1,14	2,7	1,7	1,41	1,56	0,548	2,246	2,581	0	5,375	0,57
Erythroxylaceae	Erythroxylum P. Browne	3,18	3,82	0,23	0,75	0,56	0,52	0,54	0,004	0,127	0	0	0,131	0,39
Rubiaceae	Tocoyena Aubl.	4,46	3,82	0,65	1,6	1,42	1,06	1,24	0,036	0,874	0	0	0,91	0,57
Rubiaceae	Palicourea Aubl.	3,50	3,50	0,43	1	0,41	0,35	0,38	0,048	0,165	0	0	0,213	0,25
Lamiaceae	Aegiphila Jacq.	3,82	3,50	0,64	1,12	0,42	0,41	0,42	0,009	0,093	0	0	0,102	0,37
Malpighiaceae	Byrsinima Rich. Ex Kunth	2,54	1,90	0,64	1,17	0,48	0,29	0,39	0,101	0,156	0	0	0,257	0,41
Malpighiaceae	Byrsinima Rich. Ex Kunth	3,18	2,55	0,28	1,52	0,71	0,67	0,69	0,2	0,204	0	0	0,403	0,48
Malpighiaceae	Byrsinima Rich. Ex Kunth	2,22	0,00	0,1	0,38	0,7	0,45	0,58	0,076	0,042	0	0	0,118	0,43
Malpighiaceae	Byrsinima Rich. Ex Kunth	21,01	20,69	1,4	6	3,4	3	3,2	4,483	21,82 <sub>2</sub>	0	26,98 <sub>2</sub>	53,287	0,55
Dilleniaceae	Curatella Loefl	7,64	5,41	0,53	1,98	1,85	1,13	1,49	0,267	0,544	0,448	0	1,259	0,51
Lamiaceae	Aegiphila Jacq.	6,05	5,41	0,92	1,35	0,21	0,2	0,21	0,014	0,016	0	0	0,03	0,39
Malpighiaceae	Byrsinima Rich. Ex Kunth	7,96	7,00	0,58	1,95	1,61	1,19	1,4	0,616	0,248	1,426	0	2,29	0,50

Rubiaceae	Tocoyena Aubl.	6,05	5,41	0,68	2,22	1,13	0,95	1,04	0,249	1,362	0	0	1,612	0,59
Malpighiaceae	Byrsonima Rich. Ex Kunth	12,41	10,19	1,78	3,6	2,19	1,86	2,03	0,641	3,855	3,722	1,003	9,222	0,55
Malpighiaceae	Byrsonima Rich. Ex Kunth	10,19	9,87	0,21	2,2	2,36	2,12	2,24	1,316	3,29	1,047	0,351	6,005	0,53
Malpighiaceae	Byrsonima Rich. Ex Kunth	4,77	3,82	0,3	1,47	0,6	0,55	0,58	0,119	0,46	0	0	0,579	0,47
Malpighiaceae	Byrsonima Rich. Ex Kunth	4,14	2,86	0,42	0,98	0,64	0,63	0,64	0,087	0,272	0	0	0,36	0,62
Erythroxylaceae	Erythroxylum P. Browne	4,77	4,46	0,14	1,08	1,16	0,8	0,98	0,158	0,317	0	0	0,475	0,36
Malpighiaceae	Byrsonima Rich. Ex Kunth	4,14	3,50	0,19	1,23	0,98	0,96	0,97	0,269	0,449	0	0	0,718	0,48
Salicaceae	Casearia Jacq.	3,50	2,86	0,79	1,3	0,96	0,94	0,95	0,175	0,409	0	0	0,584	0,52
Erythroxylaceae	Erythroxylum P. Browne	4,14	3,50	0,79	1,15	0,87	0,7	0,79	0,773	0,183	0	0	0,956	0,36
Ochnaceae	Ouratea Aubl.	3,82	2,86	0,84	1,33	1,39	0,7	1,05	0,072	0,216	0	0	0,287	0,51
Ochnaceae	Ouratea Aubl.	2,28	1,59	0,34	1,2	0,53	0,35	0,44	0,025	0,069	0	0	0,093	0,53
Malpighiaceae	Byrsonima Rich. Ex Kunth	2,86	1,91	0,35	1,48	1,25	0,65	0,95	0,115	0,147	0	0	0,261	0,44
Malpighiaceae	Byrsonima Rich. Ex Kunth	4,13	2,86	0,58	1,45	1,06	0,66	0,86	0,132	0,392	0	0	0,525	0,51
Rubiaceae	Palicourea Aubl.	2,55	2,55	0,14	0,7	0,45	0,38	0,42	0,024	0,07	0	0	0,094	0,28
Rubiaceae	Palicourea Aubl.	5,73	5,41	0,18	1,16	0,51	0,39	0,45	0,069	0,23	0,1	0	0,4	0,33
Rubiaceae	Palicourea Aubl.	4,46	3,50	0,91	1,34	0,68	0,6	0,64	0,044	0,217	0	0	0,26	0,29

Salicaceae	<i>Casearia</i> Jacq.	2,86	2,23	0,48	1,55	0,4	0,25	0,33	0,021	0,119	0	0	0,14	0,63
Malpighiaceae	<i>Byrsonima</i> Rich. Ex Kunth	6,68	4,46	0,29	1,8	1,5	1,24	1,37	0,442	1,325	0,129	0	1,896	0,49
Apocynaceae	<i>Himatanthus</i> Willdenow	9,23	7,32	0,4	2	1,2	1,2	1,2	0,776	1,386	0,753	0	2,915	0,45
Malpighiaceae	<i>Byrsonima</i> Rich. Ex Kunth	6,68	6,37	0,59	2,1	2,34	2,34	2,34	0,677	2,347	0,788	0	3,812	0,52
Ochnaceae	<i>Ouratea</i> Aubl.	7,96	6,05	0,34	2	1,2	1,14	1,17	0,205	0,765	0,609	0	1,579	0,43
Vochysiaceae	<i>Salvertia</i> A.St.-Hil.	8,91	7,32	1,17	4,5	1,48	1,35	1,42	0,742	3,298	2,762	0	6,802	0,53
Malpighiaceae	<i>Byrsonima</i> Rich. Ex Kunth	6,37	6,68	0,83	4	2,33	1,9	2,12	0,534	2,647	1,815	0	4,996	0,68
Malpighiaceae	<i>Byrsonima</i> Rich. Ex Kunth	20,37	19,74	1,8	5,5	5,5	4,2	4,85	6,857	27,848	18,446	32,302	85,453	0,64
Malpighiaceae	<i>Byrsonima</i> Rich. Ex Kunth	14,96	14,32	1,31	3,5	2,9	2,6	2,75	1,74	9,576	5,575	10,078	26,969	0,58
Malpighiaceae	<i>Byrsonima</i> Rich. Ex Kunth	11,46	10,82	0,91	3	2,1	2,1	2,1	1,58	5,744	2,262	2,831	12,417	0,54
Lamiaceae	<i>Aegiphila</i> Jacq.	13,05	12,41	1,8	3,5	2,3	2	2,15	0,765	2,03	1,531	4,09	8,416	0,36
Malpighiaceae	<i>Byrsonima</i> Rich. Ex Kunth	10,50	10,50	0,36	2,2	2,15	2,2	2,18	1,279	4,077	2,647	1,248	9,251	0,56
Malpighiaceae	<i>Byrsonima</i> Rich. Ex Kunth	13,69	13,37	1,05	3,2	3,5	3	3,25	2,874	15,934	6,319	5,087	30,215	0,58
Annonaceae	<i>Annona</i> L.	4,46	3,50	0,73	2,8	1,5	0,64	1,07	0,4	0,737	0	0	1,137	0,49
Rubiaceae	<i>Palicourea</i> Aubl.	4,46	3,82	0,44	0,77	0,48	0,35	0,42	0,051	0,193	0	0	0,244	0,47

Malpighiaceae	<i>Byrsinima</i> Rich. Ex Kunth	13,37	10,19	1,11	3,21	3,9	3,1	3,5	3,822	12,79 1	4,245	6,87	27,728	0,59
Malpighiaceae	<i>Byrsinima</i> Rich. Ex Kunth	18,46	9,55	0,5	2,8	2,88	2,2	2,54	2,495	15,21 5	6,327	12,60 4	36,642	0,45
Malpighiaceae	<i>Byrsinima</i> Rich. Ex Kunth	11,46	10,19	0,6	2,3	2,8	2,6	2,7	1,578	7,402	3,1	1,068	13,147	0,62
Ochnaceae	<i>Ouratea</i> Aubl.	11,46	10,50	1,2	2,3	2,8	2,8	2,8	0,757	4,868	3,246	0,907	9,777	0,60
Rubiaceae	<i>Palicourea</i> Aubl.	7,00	6,37	0,45	1,39	1,56	1,3	1,43	0,308	0,681	0,654	0	1,643	0,34
Ochnaceae	<i>Ouratea</i> Aubl.	9,55	7,96	0,69	2,1	2,2	2	2,1	0,548	2,991	1,41	0	4,95	0,62
Ochnaceae	<i>Ouratea</i> Aubl.	16,23	18,14	0,78	2,5	3,45	3,2	3,33	1,186	10,77 7	8,004	10,40 4	30,37	0,67
Apocynaceae	<i>Himatanthus</i> Willdenow	29,28	27,06	1,33	6	6,5	5,4	5,95	9,83	30,66 8	21,09 5	54,79 1	116,385	0,45
Malpighiaceae	<i>Byrsinima</i> Rich. Ex Kunth	13,69	12,73	1,6	3,5	3,9	3	3,45	3,224	10,52 6	6,083	9,215	29,048	0,52
Malpighiaceae	<i>Byrsinima</i> Rich. Ex Kunth	5,09	5,09	0,54	1,5	0,69	0,67	0,68	0,152	1,144	0	0	1,295	0,43
Rubiaceae	<i>Palicourea</i> Aubl.	3,82	2,86	0,97	1,47	0,5	0,41	0,46	0,042	0,222	0	0	0,264	0,27
Fabaceae	<i>Bowdichia</i> Kunth	8,59	7,32	0,83	3	1,8	1,8	1,8	0,402	2,236	2,666	0	5,304	0,63
Malpighiaceae	<i>Byrsinima</i> Rich. Ex Kunth	8,59	8,28	0,42	2,2	2,45	1,8	2,13	1,255	3,835	1,079	0	6,169	0,49
Malpighiaceae	<i>Byrsinima</i> Rich. Ex Kunth	11,78	11,78	0,7	2,7	2,75	2,7	2,73	2,307	9,023	2,263	2,983	16,576	0,55
Malpighiaceae	<i>Byrsinima</i> Rich. Ex Kunth	8,59	7,96	1,17	2,5	2,2	2,2	2,2	1,149	3,599	0	0	4,747	0,48

Malpighiaceae	<i>Byrsonima</i> Rich. Ex Kunth	3,18	2,86	0,48	1,32	0,73	0,62	0,68	0,16	0,265	0	0	0,425	0,45
Rubiaceae	<i>Palicourea</i> Aubl.	4,77	4,46	0,4	1,05	0,96	0,83	0,9	0,115	0,475	0	0	0,59	0,31
Erythroxylaceae	<i>Erythroxylum</i> P. Browne	5,09	4,46	0,46	1,14	0,87	0,74	0,81	0,085	0,633	0	0	0,718	0,45
Dilleniaceae	<i>Curatella</i> Loefl	7,00	6,05	0,61	1,47	1,43	0,76	1,1	0,26	0,386	0,251	0	0,898	0,35
Lamiaceae	<i>Aegiphila</i> Jacq.	5,09	4,46	1,08	1,7	0,78	0,76	0,77	0,055	0,38	0	0	0,436	0,30
Malpighiaceae	<i>Byrsonima</i> Rich. Ex Kunth	16,55	15,28	1,36	6,5	4,6	4,4	4,5	3,003	17,83 <sub>9</sub>	9,603	13,34 <sub>3</sub>	43,787	0,56
Malpighiaceae	<i>Byrsonima</i> Rich. Ex Kunth	12,10	11,46	1,2	4	2,65	2,4	2,53	1,845	4,466	3,499	2,95	12,76	0,56
Dilleniaceae	<i>Curatella</i> Loefl	10,19	8,91	0,7	3,5	1,6	1,6	1,6	1,441	2,853	2,997	0	7,291	0,56
Dilleniaceae	<i>Curatella</i> Loefl	4,14	0,00	0,05	1,2	1,04	0,96	1	0,254	0,328	0	0	0,582	0,43
Annonaceae	<i>Annona</i> L.	12,10	11,14	2,2	6	2,6	2,4	2,5	1,239	2,536	6,486	1,536	11,799	0,49
Dilleniaceae	<i>Curatella</i> Loefl	18,46	15,92	1,98	8	3,1	3	3,05	11,11 <sub>4</sub>	7,767	18,24 <sub>7</sub>	19,74 <sub>4</sub>	56,872	0,47
Malpighiaceae	<i>Byrsonima</i> Rich. Ex Kunth	3,82	2,86	0,48	1,2	0,77	0,48	0,63	0,12	0,247	0	0	0,367	0,44
Humiriaceae	<i>Humiria</i> Aubl.	18,46	14,64	0,57	3,3	2,73	1,8	2,27	1,004	4,578	3,07	8,201	16,853	0,59
Malpighiaceae	<i>Byrsonima</i> Rich. Ex Kunth	2,86	2,23	0,32	1	0,56	0,52	0,54	0,058	0,137	0	0	0,194	0,44
Ochnaceae	<i>Ouratea</i> Aubl.	4,77	4,14	0,38	1,55	0,58	0,47	0,53	0,058	0,711	0	0	0,769	0,48
Ochnaceae	<i>Ouratea</i> Aubl.	6,05	5,41	1,3	2,2	1,4	1,2	1,3	0,316	1,1	1,102	0	2,518	0,54
Apocynaceae	<i>Himatanthus</i> Willdenow	2,55	1,91	0,5	1,05	0,61	0,44	0,53	0,121	0,134	0	0	0,255	0,36

Rubiaceae	<i>Palicourea</i> Aubl.	12,10	11,78	0,34	2,5	2,1	2	2,05	0,72	5,244	3,593	1,526	11,084	0,31
Ochnaceae	<i>Ouratea</i> Aubl.	11,46	10,82	0,9	2,8	3	2,8	2,9	1,132	5,938	2,247	0,893	10,21	0,53
Malpighiaceae	<i>Byrsonima</i> Rich. Ex Kunth	12,73	12,73	0,95	2,7	2,95	2,9	2,93	2,737	7,058	2,412	2,442	14,649	0,49
Rubiaceae	<i>Tocoyena</i> Aubl.	14,96	13,37	1	3	4,9	4,3	4,6	3,215	10,52 6	13,61 4	8,881	36,235	0,53
Malpighiaceae	<i>Byrsonima</i> Rich. Ex Kunth	27,37	26,74	0,95	6,8	7	6,2	6,6	22,84 7	66,01 9	72,44 3	59,55 8	220,866	0,54
Dilleniaceae	<i>Curatella</i> Loefl	20,37	16,87	1,26	5	4,2	3,9	4,05	4,123	9,433	12,47 9	23,71 1	49,747	0,48
Dilleniaceae	<i>Curatella</i> Loefl	5,09	4,46	0,93	1,68	1,35	0,92	1,14	0,111	0,426	0	0	0,537	0,46
Myrtaceae	<i>Myrcia</i> DC.	5,73	5,41	1,2	3,2	1,6	1,5	1,55	0,474	3,14	0,633	0	4,248	0,64
Annonaceae	<i>Annona</i> L.	7,00	6,68	1,26	2,7	2,05	2	2,03	0,636	1,608	1,203	0	3,448	0,51
Ochnaceae	<i>Ouratea</i> Aubl.	10,82	10,19	0,75	2,4	2,9	1,6	2,25	0,418	0,166	4,343	1,945	6,872	0,60
Dilleniaceae	<i>Curatella</i> Loefl	24,83	22,28	0,97	6,5	8,2	6,1	7,15	7,431	29,84 4	21,56 2	30,24 3	89,08	0,65
Chrysobalanaceae	<i>Hirtella</i> L.	6,68	5,73	1,15	3	2,6	2,1	2,35	0,407	1,332	0,479	0	2,218	0,61
Proteaceae	<i>Roupala</i> Aubl.	4,77	3,18	0,41	1,65	0,9	0,7	0,8	0,227	0,413	0	0	0,639	0,57
Myrtaceae	<i>Myrcia</i> DC.	2,86	2,55	1,36	1,8	0,7	0,6	0,65	0,156	0,326	0	0	0,482	0,57
Rubiaceae	<i>Tocoyena</i> Aubl.	6,68	0,00	0,23	2,1	1,9	1,6	1,75	0,313	1,672	0,356	0	2,341	0,51
Malpighiaceae	<i>Byrsonima</i> Rich. Ex Kunth	29,28	27,37	1,46	6,5	7,7	7,2	7,45	13,82 3	111,5 89	50,60 3	82,00 3	258,017	0,54
Bignoniaceae	<i>Tabebuia</i>	7,96	7,64	0,5	2,1	1,5	1,5	1,5	0,99	1,172	1,446	0	3,608	0,54
Vochysiaceae	<i>Salvertia</i> A.St.-Hil.	6,05	5,41	0,97	3	1,15	0,78	0,97	0,369	0,969	0,202	0	1,54	0,43

Vochysiaceae	Salvertia A.St.-Hil.	4,14	4,14	0,55	0,98	0,8	0,57	0,69	0,111	0,326	0	0	0,437	0,31
Myrtaceae	Myrcia DC.	5,41	5,41	1,87	3,2	2,3	1,8	2,05	0,568	0,195	0,851	0	1,614	0,60
Vochysiaceae	Salvertia A.St.-Hil.	14,01	13,37	2,92	7,5	2,38	1,9	2,14	2,961	5,749	9,596	4,523	22,829	0,37
Erythroxylaceae	Erythroxylum P. Browne	6,68	6,37	0,33	0,95	1,04	0,86	0,95	0,137	0,43	0,373	0	0,94	0,36
Vochysiaceae	Salvertia A.St.-Hil.	11,46	11,46	2,12	5,1	4	3,2	3,6	1,118	8,651	9,887	2,759	22,414	0,54
Vochysiaceae	Salvertia A.St.-Hil.	5,09	4,46	0,88	1,44	0,94	0,82	0,88	0,407	0,698	0	0	1,104	0,28
Vochysiaceae	Salvertia A.St.-Hil.	6,37	5,41	1,23	3,6	1,5	1,3	1,4	0,418	2,128	0,282	0	2,829	0,47
Apocynaceae	Himatanthus Willdenow	6,68	6,05	0,3	2,1	0,99	0,93	0,96	0,392	0,854	0,195	0	1,442	0,31
Malpighiaceae	Byrsinima Rich. Ex Kunth	20,69	20,05	0,65	6	6	4,9	5,45	9,168	39,85	28,68 9	29,92 6	107,633	0,51
Apocynaceae	Himatanthus Willdenow	3,82	2,23	0,6	1,5	0,53	0,47	0,5	0,042	0,132	0	0	0,174	0,39
Malpighiaceae	Byrsinima Rich. Ex Kunth	3,82	2,86	0,43	1,4	0,83	0,69	0,76	0,216	0,396	0	0	0,612	0,44
Vochysiaceae	Salvertia A.St.-Hil.	11,78	11,46	2,14	6,12	2,8	2,7	2,75	2,538	5,605	9,228	1,159	18,53	0,49
Ochnaceae	Ouratea Aubl.	4,46	3,50	1,89	2,57	1,19	0,91	1,05	0,094	0,434	0	0	0,528	0,45
Malpighiaceae	Byrsinima Rich. Ex Kunth	2,55	2,55	0,32	1,5	0,6	0,52	0,56	0,117	0,195	0	0	0,311	0,49
Vochysiaceae	Salvertia A.St.-Hil.	7,00	6,37	0,73	2,5	1,7	1,62	1,66	0,855	2,824	1,241	0	4,92	0,47
Vochysiaceae	Salvertia A.St.-Hil.	4,46	3,82	0,31	0,75	0,85	0,53	0,69	0,085	0,312	0	0	0,397	0,30
Vochysiaceae	Salvertia A.St.-Hil.	16,23	16,23	1,4	5,7	4,7	3,9	4,3	5,48	48,83 9	8,548	1,629	64,497	0,51
Rubiaceae	Palicourea Aubl.	19,42	17,19	0,51	2,4	2,75	2,3	2,52	0,889	5,101	2,152	4,606	12,748	0,30

Vochysia ceae	Salvertia A.St.-Hil.	22,28	21,65	2,23	8,17	6,1	5,65	5,88	7,229	47,18 6	8,079	20,07 5	82,569	0,41
Vochysia ceae	Salvertia A.St.-Hil.	5,09	4,14	0,36	1,15	0,97	0,67	0,82	0,336	0,628	0	0	0,964	0,31
Bignonia ceae	Tabebuia	15,28	14,64	2	5,05	3,25	3,1	3,18	1,893	7,175	4,418	9,356	22,842	0,44
Vochysia ceae	Salvertia A.St.-Hil.	12,41	11,14	1,95	5,16	3,3	3,25	3,28	1,533	7,404	7,941	1,69	18,568	0,48