Norwegian University of Life Sciences
Faculty of Environmental Sciences
and Natural Resource Management

Philosophiae Doctor (PhD)
Thesis 2021:50

Flooding matters: Structure, above-ground biomass, and carbon stocks of an Amazonian forestscape

Flom: betydning for struktur, biomasse og karbonlager i et skogslandskap i Amazonas

Yennie Katarina Bredin

Flooding matters: Structure, above-ground biomass, and carbon stocks of an Amazonian forestscape

Flom: betydning for struktur, biomasse og karbonlager i et skogslandskap i Amazonas

Philosophiae Doctor (PhD) Thesis

Yennie Katarina Bredin

Norwegian University of Life Sciences
Faculty of Environmental Sciences and Natural Resource Management

Ås (2021)

Thesis number 2021:50
ISSN 1894-6402
ISBN 978-82-575-1821-9

Supervisors

Professor Torbjørn Haugaasen (Main Supervisor)
Faculty of Environmental Sciences and Natural Resource Management (MINA)
Norwegian University of Life Sciences (NMBU)
P. O. Box 5003, NMBU, 1432 Ås, Norway.

Professor Carlos Augusto Peres (Co-supervisor)
School of Environmental Sciences
University of East Anglia (UEA)
Norwich NR4 7TJ, UK.

Evaluation Committee

Dr. John Ethan Householder (First Opponent)
Research and Teaching Assistant
Institute of Geography and Geoecology
Karlsruhe Institute of Technology (KIT)
Rastatt, Germany

Dr. Thaise Emilio Lopes de Sousa (Second Opponent)
Visiting Professor in Ecology
Department of Plant Biology, Institute of Biology
University of Campinas (UNICAMP)
Campinas, Brazil

Dr. Ole Martin Bollandsås (Committee coordinator)
Faculty of Environmental Sciences and Natural Resource Management (MINA)
Norwegian University of Life Sciences (NMBU)
P. O. Box 5003, NMBU, 1432 Ås, Norway.

“[…If] we rely on our minds in decision-making processes, we will be correct most of the time. However, if we add the dimension of the human heart to our decisions, we can substantially increase the probability of being right. This does not discount professional objectivity but rather expands the data bases from which we operate. It underscores the reality that we are humans and should act like humans; and that we must remember that there are other humans who are depending on us, the scientists, the resource managers, the decision-makers, to be right.” [1, p.35]

Happy working!

Abstract

Amazonia accounts for approximately half of the world's tropical forests and one quarter of all terrestrial species. The forests retain and circulate large amounts of water and store carbon. Amazonia is thus extremely important both for biodiversity and the global climate. Yet, we know relatively little about the distribution and amount of above-ground biomass stored in these forests.

Unflooded Amazonian terra firme forests grow above the maximum flood level of rivers, streams, and lakes. On their floodplains grow seasonally inundated forests. Every year the floodplain forests experience an enormous flood. Here, woody plants at all stages of their life must endure prolonged inundation. In response to the seasonal flooding, they have developed special tissues and strategies, possibly affecting forest above-ground biomass, and carbon stocks. Exploring these aspects, I describe structure and composition of an Amazonian forestscape in the central Juruá River Basin, Brazil.

Comparing flooded and unflooded forests I found that forest structure differed. Most woody plant species were forest-specific, but some were shared. Flooding affected the below-ground biota. Bacterial community composition varied with woody plant diversity and flooding, but eukaryotes appeared unaffected. Flooding influenced the wood density of the shared tree species. Trees that grew in the seasonally flooded forest had softer wood than terra firme conspecifics. Considering the differences in forest structure, species composition and intraspecific wood density, I investigated how conventional biomass estimation methods performed across the two forests. Regional height allometry and global wood density measurements were relatively well calibrated to terra firme forest. They performed much worse in the floodplain forest. Calibrating the allometric equations with local height data significantly improved biomass estimates in floodplain forest. Combined with forest-specific genus mean wood density, local allometric height produced reliable terra firme and floodplain above-ground woody biomass estimates.

In conclusion, the natural, seasonal floods influence species composition, forest structure and above-ground biomass estimates in the Amazonian forestscape. The results in this dissertation thus implies that flooding must be accounted for when mapping Amazonian carbon stocks.

Keywords: forest ecology, carbon stocks, biomass, Amazonia, floodplain forest

Sammendrag

Amazonas er verdens største gjenværende regnskogområde og svært viktig både for artsmangfoldet og jordens klima. Skogen sirkulerer store mengder vann og lagrer karbon. Tross dette vet vi forholdsvis lite om hvor mye og hvordan biomasse og karbon er disponert i Amazonas' skoger.

Skog som ikke oversvømmes kalles i Amazonas for terra firme. Disse ligger bortenfor den maksimale flomhøyden på elver og innsjøer. På elvebreddene vokser flomsletteskog som oversvømmes årlig. Her må planter i alle livsstadier tåle lange oversvømmelsesperioder. Derfor har de utviklet spesielle organer og strategier. Potensielt påvirker disse skogens biomasse og karbonlager. Gjennom å beskrive strukturen og artssammensetningen i et skoglandskap i de sentrale delene av Juruávassdraget i Amazonas, Brasil, utforsker jeg disse aspektene.

Flomsletteskogen og terra firme-skogen hadde forskjellig skogstruktur. De fleste trevekstene var habitatspesifikke, men skogene hadde også noen felles arter. Flommen påvirket biota i jordsmonnet. Bakteriesamfunnet endret seg med artsrikdom i plantesamfunnet og flomnivå, men eukaryoter var tilsynelatende upåvirket. Flommen påvirket vedtettheten i de felles tresortene. Trær som vokste i flomslettskogen, hadde mykere trevirke enn de som vokste i terra firme. Forskjellene i skogstruktur, artssammensetning og intraspesifikk vedtetthet ble brukt for å undersøke hvordan konvensjonelle metoder for estimering av biomasse presterte i de to skogtypene. Regional høydeallometri og globale målinger av vedtetthet var relativt godt kalibrert til terra firme-skog. De presterte mye dårligere i flomsletteskogen. Kalibrering av de allometriske ligningene med lokale høydedata forbedret biomassestimatene betydelig i flomsletteskogen. Kombinert med skogsspesifikke mål for vedtetthet på slektsnivå, resulterte den lokale høydeallometrien pålitelige biomassestimater både i flomslettskogen og terra firme-skogen.

Jeg konkluderer med at naturlige, årlige flommer i Amazonas påvirker artssammensetning, skogstruktur og biomassestimater. Resultatene i denne avhandlingen viser at flommens innflytelse må tas i betraktning når man kartlegger karbonlager i Amazonas.

Nøkkelord: skogøkologi, karbonlagre, biomasse, Amazonas, flomsletteskog

List of Papers

This thesis is based on the following studies, referred to in the text by their Roman numerals.

I. **Bredin, Y.K.**, Hawes, J., Peres, C. A., Haugaasen T. Structure and composition of terra firme and seasonally flooded várzea forests in the western Brazilian Amazon. *Forests* 2020.

II. **Bredin, Y.K.**, Hess, L.L., Scabin, A.B., Dunthorn, M., Haugaasen T., Peres, C. A., Nilsson, H.R., Antonelli, A., Duarte Ritter, C. Above- and below-ground biodiversity responses to the prolonged flood pulse in central-western Amazonia, Brazil. *In review. Soil Biology and Biochemistry*

III. **Bredin, Y.K.**, Peres, C. A., Haugaasen T. Forest type affects the capacity of Amazonian tree species to store carbon as woody biomass. *Forest Ecology and Management* 2020.

IV. **Bredin, Y.K.**, Socolar, J.B., Schietti, J., Hawes, J.E., Leandro de Assis, R., Peres, C. A., Haugaasen T. Accurate biomass estimation for data-poor forest types. *To be submitted to Forest Ecology and Management*

Contents

1 Introduction

1.1 Amazonia and the global climate

Amazonia represents approximately half of the world's tropical forests and one quarter of all terrestrial species [2]. The forests retain and circulate large amounts of water and store carbon [3–5]. Almost one fifth of all fossil fuel emissions globally are offset by tropical forests [6,7]. Amazonia is thus extremely important for biodiversity and the global climate. However, climate change, deforestation and selective logging severely and adversely affect forests structure, composition, capacity to store carbon, retain water and regulate climate [8–12]. Degradation and destruction of tropical forests is the second most important contributor to global biodiversity loss and climate change [3,6,7].

Recently, accelerated climate change has raised concerns about the future extent and functioning of the Amazonian forestscape [13,14]. Increased extreme weather events, intensified forest fires and increased tree mortality rates threaten to push the Amazon away from a carbon neutral state to become a net source of CO_2, further aggravating the impacts of climate change [15,16]. Projected future of the Amazon and its regional and global climate impacts are highly uncertain [2,13,17–19]. However, the data upon which such projections are based is limited. More ground-based information is therefore needed to improve credibility in climate projections.

Regional and global carbon fluxes, which feed into climate models, are mapped by combining ground-based forest biomass estimates and remotely sensed data [20]. Because of limited information about species compositions and uncertainties in ground-based above-ground biomass estimates, such maps suffer from huge discrepancies [7,21]. Moreover, floristic inventories have largely been conducted close to urban centres and predominantly in a single forest type [21,22]. This results in severe biases in our knowledge of the tree species richness and distribution. Considering the irregular distribution and local rarity of many tropical tree species [23–27], bias and patchiness of floristic data presents one of the biggest challenges for conservationists and climate modellers alike. Hence, on-the-ground efforts are urgently needed to improve our forest inventory coverage and ground-based above-ground biomass estimates.

1.2 The Amazonian forestscape

The Amazon forestscape covers approximately 5 million km^2 and many different forest types. “Unflooded”, upland forests lie above the maximum flood level of rivers, lakes, and perennial streams. Generically, these are referred to as terra firme. Based on soil properties and vegetation cover, terra firme forests can be classed into several different forest types [28–30]. Some examples include campinarana forests on nutrient poor white sand soils, liana forests on mineral-rich soils, and interfluvial upland forests dominated by palms and other tree species [28,31,32]. The most typical, closed-canopy terra firme forests lie on well-drained terrains that tend to be heavily leached and nutrient-poor [32,33]. These are the most extensive and well-studied of all Amazonian forest types [34]

Floodplain forests along rivers and lakes, represent some of the less well studied Amazonian forest types. They cover approximately 516,000 km^2 and include the most species rich wetland forests in the world [35–37]. Based on the properties of the floodwaters, the frequency and duration of floods, soil properties, and the plant communities, these forests may be classed into several different types [38]. The two main categories, include oligotrophic floodplain forests inundated by black- or clear-water rivers, which are nutrient poor but rich in organic solutes and eutrophic várzea forests inundated by white-water rivers (*e.g.* the Amazonas/Solimões, Madeira, Purús, and Juruá). Of these, the várzea forests are the most extensive [36]. Because the white-water rivers drain Andean landscapes that are geologically young and easily erode [39], they bring large amounts of suspended nutrient-rich sediments onto the floodplains [40–42]. These sediments give the rivers their muddy appearance and leave the várzea forests eutrophic, species rich and exceptionally productive [35].

Although species distributional patterns are complex, forest dynamics, seasonality, topography, and the underlying geology seem to be main drivers of structural, compositional, and functional diversification in Amazonia [29,43–46]. For example, dry season length, clay content, soil phosphorus (P) and calcium (Ca), magnesium (Mg) and potassium (K) cation exchange capacity (CEC) appear to be important for the woody plant community composition and above-ground biomass in várzea and terra firme [32,47]. Moreover, flood duration (i.e. hydro-period) seems indicative of forest structural complexity and species composition in várzea forests [38,48–52].

1.3 The flooding gradient

Lowland topography and a high seasonality in rainfall cause Amazonian rivers and lakes to flood adjacent forests on a seasonal basis [53,54]. This flood pulse gives rise to an aquatic and terrestrial phase on the floodplains that lasts for several months. Flood duration and inundation depth vary with the slope of the terrain and distance from the rivers and lakes that flood the landscape [55,56]. Hence, a flooding gradient is created from low-lying várzea that floods to greater depths for longer periods of time to high várzea that floods for shorter periods.

Because of the flood pulse, várzea woody plants, at all stages of their life, must endure periodic waterlogging. So, floodplain plant species have developed specialised strategies to resist flooding [57–59] and are fundamentally different from unflooded species communities. Along the flooding gradient there is also a clear zonation of where different plant species can establish and only highly specialised wetland tree species survive where the flooding is most prolonged [e.g. 35].

Adaptations that woody plants have developed to persist in this highly seasonal environment include dormancy followed by quick growth when times are favourable [60,61]. Specialised tissues include buttress and adventitious roots, and air-filled spaces (lenticels) in the wood [60–62]. These features help woody plants aerate their roots to resist a lack of oxygen at the root level (hypoxia) during the aquatic phase [60–63]. Another important quality in floodplain woody plants is to regrow roots after others have died in the flood [58,64]. Stem nodulation, which involves nitrogen (N) fixating bacteria, also seems more common in flooded areas than in unflooded sites [37]. Since both nitrogen fixation and resource allocation are important to plant development, these adaptations influence plant growth and structure in várzea forests [60,65,66].

Floodplain seasonality hence favour different growth forms along the flooding gradient [35,67–70]. Seasonal dynamics with rising and receding waters cause erosion and sedimentation along the meandering course of white-water rivers [71–73]. This creates new land for colonizing plants [64,69]. Therefore, várzea forests often feature lower vegetation than terra firme [74,75] with more successional and fast growing tree species that have lighter wood [65,66,74]. Wood density moreover fluctuate within tree species, depending on growth conditions [65,66,76–78]. Through inter- and intraspecific variations in wood density, species composition, and forest structure, flooding may thus drive variation in várzea above-ground biomass and carbon stocks.

1.4 Above ground woody biomass and carbon stocks

Above-ground woody biomass and carbon stocks are a function of forest structure variables and wood density. These variables are often measured at the level of individual trees within forest plots. Stand biomass is determined through allometric models by summing the individual biomass of trees at the plot level. Carbon stocks are generally assumed to equal ~half the above-ground biomass. Plot size is typically determined by the purpose of the study and local forest conditions. Where small-scale topographic variability is high, for example, small and narrow floristic plots that follow topographic contours may be preferred since these will present less within-plot variation [79].

1.4.1 Forest structure variables

Structural field measurements for biomass estimation include stem diameter at breast height (DBH) and total height for trees above a certain threshold, commonly a stem diameter above 10 cm. Tree architecture, such as the level of branching and tapering, is also important for tree biomass, but normally these features are considered through allometric equations [80]. Stem diameter is measured to the nearest millimetre with a calliper, DBH tape or converted from circumference measurements made with measuring tape at 1.30 m above the ground [81]. For buttressed trees, stem diameter is measured above buttresses [81].Where direct measurements are not possible, e.g. for sulcate trunks or stranglers, stem diameter may be visually estimated. Whereas stem diameter measurements are rather straight forward, they are not without error [82]. Diameter measurements must therefore be done with care [83].

Direct, ground-based height measurements are typically obtained by felling trees and measuring their stems with a measuring tape [84] but to fell all trees within a plot would be undesirable. Therefore, common practice is to develop or calibrate diameter-height allometries from a subset of destructively sampled trees by which the height of the remaining trees can be inferred [84]. Still, for various reasons, it may not be possible to destructively measure a subset of trees, for example, within protected areas or permanent forest plots. In these cases, two alternative, common and non-destructive field methods are to measure stem height by the tangent (horizonal distance to the trunk and angle to tree top) or sine (distance and angle to tree top) method using a hypsometer [84,85].

These methods mostly provide reliable height measurements [86,87] but measures in taller, well-stratified, closed canopy forests become increasingly difficult as the top of trees are obscured [85,88]. Under like conditions, the sine method systematically underestimate height with -7% [85,88]. Also, *in situ*, visual height estimates may be used. In a study from Espírito Santo, Brazil, da Silva et al., [86] found that visual estimates gave equally reliable height measurements as the hypsometer measurements.

Where no site-specific height measurements are available, regional diameter-height allometries may be applied. Ideally, these should be species specific [89], which for most tropical species is practically unattainable given their sparse distributions and our limited knowledge [25,26]. Thus, another promising, non-destructive method for deriving tree height and volume, is laser scanning of trees by LiDAR (light detection and ranging). However, even LiDAR requires local, field measured diameters for calibration [90]. Therefore, reliable height (or diameter) predictions depend on the calibration of allometric models with information about local diameter-height relationships [91].

1.4.2 Inter- and intraspecific wood density

Wood density is the fraction of structural matter in wood, e.g. the part that is not water or air [92,93]. Accordingly, wood density relates to biomass and amount of carbon captured from the atmosphere and stored in woody vegetation [77,94,95]. Measurements of wood density are made on tree discs from logs or wood cores. Where destructive sampling of trees is not possible, wood cores are preferred. Wood cores should cover the entire radius of the stem to reflect radial change in wood density from pith to bark [93,96,97]. This radial change in wood density, is a result of adaptive growth and resource allocation within trees over the course of their lives [98]. For example, a tree that establish at the upper end of the flooding gradient in a várzea forest may opt to grow tall quickly to escape submersion by the floodwaters [61,99]. Later, once the tree is established, it may invest more in structural strength. Such strategy would imply that the wood density of our tree increases from the pith (wood produced early in life) to the bark.

Because pith and the heartwood are overrepresented in wood core samples, wood cores should be divided into segments [93,96,97]. The wood density of each segment must then be weighted by the cross-sectional area of the disc that it represents [96,97]. However, wood density measurements from wood cores are often not weighted and the radial change in wood density is therefore not accounted for [93]. Failure to account for the radial change in wood density could significantly influence the wood density measurement [65,66,78,100–102]. In the case of our example tree, which invested more in quick growth early in life, this would result in an underestimation of the tree biomass. The opposite would be true in species with decreasing wood density from pith to bark.

It thus becomes obvious that wood density is intrinsically linked to growth strategy and species identity [65,103]. Plot mean wood density accordingly depends on the species composition. Where local wood density is unavailable, information about wood density is commonly retrieved from global databases based on species identity [e.g. 104,105]. Species identifications however, are often difficult in tropical rainforests [23–26]. Therefore, many inventories rely on identifications at higher taxonomic levels (i.e. genus or family level). In addition, information about wood density for many tropical species is often missing. This could be problematic since wood density varies greatly among and within species depending on local growing conditions [65,66,76–78]. Using taxonomic or regional mean wood density measurements that are not calibrated to local conditions could grossly under-, or overestimate forest biomass [82,106].

To reduce bias in the spatial representation of Amazonian above-ground biomass and carbon stocks we therefore need more detailed information on tree species composition and wood density in poorly sampled areas. We also need information about intraspecific responses to altered environmental conditions and how these vary across the forestscape.

1.4.3 Uncertainty in biomass estimates

Failure to consider forest-specific differences in species composition, functional traits, tree architecture, and diameter-height relationships could result in considerable biomass estimation error [91,107,108]. Because conventionally used pantropical climate-based diameter-height allometries and global mean wood density values are based on data primarily derived from well-sampled upland forests [e.g. cf. ,88,104,105] they may underperform in undersampled forests [100,106]. If potential bias from such methods could be quantified, systematic errors and uncertainties could also be accounted for in above-ground biomass and carbon estimates [109,110]. Information on how well structural and compositional drivers of above-ground biomass in data-poor forests are captured, or not, by conventional estimation methods will therefore improve credibility in above-ground biomass and carbon stock estimates.

1.4.4 Targeting várzea floodplain forests

Várzea forests represent some of the most extensive [36], yet data poor forests in Amazonia [21]. Similarly, the Juruá basin with extensive stretches of adjacent várzea and terra firme forests, represents an important but undersampled floristic region [22]. Hence, in this thesis I target várzea forest along the Juruá River to explore how flooding – through structural and functional variables – and commonly used biomass estimation methods affect forest above-ground biomass and carbon stock estimates in an Amazonian forestscape.

2 Aim

i. Describe patterns in forest structure, woody plant species diversity and community composition across várzea and terra firme forest in the central Juruá (Manuscript 1),

ii. Describe patterns in forest below-ground diversity and community composition relative to the flooding gradient and variation in woody plant species diversity (Manuscript 2)

iii. Investigate how flooding affects wood density in trees by studying conspecifics in várzea and terra firme forest (Manuscript 3), and

iv. Understand how quality in wood density and tree height measurements (e.g. lower taxonomic resolution or geographic precision) affect biomass estimates in a data poor forest relative to more well sampled forest (Manuscript 4).

3 Results and discussion

Here I highlight the main findings from Paper I – IV to extend the discussion on these finding beyond the scope of the individual papers. I analyse how these findings relate to literature on forest structure, species diversity and above-ground woody biomass and deliberate over the influence of flooding on Amazonian carbon stocks.

3.1 Paper I:

3.1.1 Forest specialists drive the woody plant diversity

First, we confirmed that várzea and terra firme woody plant communities differed in structure and species compositions [35,50,74,111–113]. These differences between floodplain and upland forests were caused by exclusivity in habitat preferences among plants. Consequently, most woody plant species were found in either várzea or terra firme. In fact, várzea forests have the greatest number of endemic (habitat specific) floodplain species in the world [37]. Only ~20% of várzea tree species are expected to occur in both low and high habitat [35], but very little is known about the number of species that are shared among várzea and upland forest [37]. In the Juruá, approximately one quarter of the species (24%) was shared. Most of these shared species occurred predominantly in one forest type and ~13% were very rare in both forests. These differences in species composition underpin the supplementary value of seasonally flooded forests and the adjacent "unflooded" forests for Amazonian woody plant diversity.

3.1.2 Adaptations to forest dynamics determine forest structure

Várzea forests grow along rivers and lakes and have more edge habitat than terra firme forests. This makes várzea forests more exposed to wind but also erosion by the seasonal floodwaters that unseat large landmasses at the outer bends of meandering rivers and deposit sediments across the floodplains and at the inner bends [73]. Such instability favours woody lianas and pioneer species that thrive in disturbed areas [64,69,114–116]. High seasonality and deposition of nutrient rich sediments favour palms, which prefer dynamic habitat with weakly structured, nutrient rich soils [117–119]. These dynamics could also cause seasonal growth spurts in várzea trees [65] and promote greater stem diameters with potentially lighter wood density [96]. Larger stem diameters with increased air spaces in várzea trees would help aerate their roots during the flooded phase [37,61]. Larger stem diameters could furthermore increase stability against wind and flood exposure in várzea woody plants [120]. In the less fertile, less seasonal and less wind exposed terra firme, trees may in contrast grow more evenly and slowly. Slower lateral growth in woody plants tend to increase structural matter per unit volume wood. This would support higher stems [56] and in the Juruá, we confirm that upland trees were taller than várzea trees [74].

3.1.3 Complimentary forest structure variables could regulate carbon stocks

At the level of stands, structural and functional differences, such as different species composition, the proportions of trees and other life forms, stem density, and tree size interact to determine the amount of standing, living woody biomass [121]. Accordingly, forest biomass vary across the landscape [122]. In the Juruá, higher stem diameters and subsequent basal area in várzea stands is potentially counterbalanced by taller terra firme stems. Várzea and terra firme forest biomass and carbon stocks are likely to be driven by different, but potentially complimentary, species and forest structure variables.

3.2 Paper II:

Change in community composition and woody plant species diversity seem to be driven by seasonal floods and soil fertility (paper I). So, we tested how edaphic physicochemical properties and substrate biota - important determinants of nutrient availability, plant health and forest productivity [123] - were affected by hydroperiod and flood depth.

3.2.1 Flooding but not hydroperiod, boosts nutrient content and influence soil structure

Through physicochemical soil analyses we could confirm that várzea and terra firme soils were distinct, but várzea soil properties did not vary with hydroperiod or flood depth. Both forests were poor in phosphorus (P), but the clayey várzea soils were rich in magnesium (Mg), potassium (K), and calcium (Ca) and had a high cation exchange capacity (CEC). These properties are important for plant productivity as soils with balanced exchangeable magnesium, potassium, and calcium cations can improve plant growth [124]. Moreover, potassium could be important in plant resistance to waterlogging by reducing oxidative damage to plant membranes and the photosynthetic potential caused by hypoxia [125]. In contrast, high sand content, aluminium (Al), and very low pH (≤4.0) characterised the terra firme soils.

High acidity and aluminium are characteristic of highly leached, nutrient poor terra firme soils [32,33]. Because the sampled terra firme forests in the Juruá were situated on paleo-várzea sediments we expected them to be richer in nutrients [126,127]. To the contrary the Juruá terra firme soils were very similar to other terra firme soils further to the west and east in the Brazilian Amazon [128]. This suggests that nutrients soon leach from várzea sediments once they no longer flood and thus no longer receive the annual deposit of nutrient rich sediments. Another potentially interesting observation is that very acidic conditions could make aluminium unstable and toxic for certain plants when present in high concentration [129]. Perhaps this could contribute to the segregation of várzea and terra firme woody plant communities by rendering terra firme soil less suitable for várzea woody plants.

3.2.2 Bacteria, but not eukaryote communities, vary with hydroperiod

Targeting prokaryote (bacteria) and eukaryote biota in soil and litter using a metabarcoding approach, we found bacterial community composition to vary weakly with flooding and woody plant diversity. This result could indicate that below-ground bacteria present different tolerances to hydrological stressors and or interdependencies with certain plant species along the flooding gradient. This would be congruent with more nodulation in seasonally flooded plant communities compared to unflooded sites [37]. Eukaryote community composition was in contrast apparently unaffected by flooding, edaphic properties, and floristic diversity in both várzea and terra firme. Both várzea and terra firme had high proportions of fungi, mostly saprotrophs, highlighting their role in forest nutrient cycling [123]. The high prevalence of fungi in the eukaryote communities could relate to a low abundance of fungivores [130], since we failed to detect nematodes (except for one observation in terra firme).

3.2.3 Below-ground diversity does not reflect above-ground diversity

There was no relationship between above- and below-ground diversity across the várzea or terra firme forests. This result was in part expected since the várzea flood-waters could have carried organisms across the entire flooding gradient, but that is not the case in terra firme. Indeed, in terra firme there was a slight indication that bacterial diversity might correlate with woody plant diversity, although this was not significant. Hence, our results echo those of Cameron[131] and Ritter [132] who found no clear relationship between below- and above-ground biota diversity globally or in Amazonia.

3.3. Paper III:

Diversity within as well as among species is important for forest resilience and functioning. Returning to the shared tree species (paper I) we investigated how within species diversity affect wood density and carbon stocks across flooded and unflooded forests.

3.3.1 Flooded trees store less carbon per unit volume wood

Tree species occurring in both várzea and terra firme forests tended to adapt to their local environments by developing lower wood density in floodplain habitat. With decreased taxonomic accuracy (genus and family level instead of species), the difference in wood density between várzea and terra firme trees became larger. At the family level, switched wood densities (e.g. terra firme values in várzea and vice versa) overestimated várzea above-ground biomass with +17% and underestimated terra firme above-ground biomass with -14%. Furthermore, our results show that for large trees the bias in wood density might be even greater than for small trees. Ignoring intraspecific differences among habitats could therefore result in very erroneous estimates of forest biomass that systematically bias regional carbon stock estimates and impair the accuracy of climate models. Considering that most studies fail to account for forest type in their above-ground biomass estimates [82,84] and that large trees tend to have disproportionate influence on forest above-ground biomass [133,134], this is not trivial. We support the call for more habitat-specific wood density data [122]. Where site-specific measurements are absent, we recommend adjustments of regional wood density values to the local forest type.

3.3.2 Shared species show plasticity in interspecific responses to flooding

Responses among species, genera and families to flooding were not consistent. Some species, genera and families had lighter, others greater, or similar wood density across várzea and terra firme. For example, the Clusiaceae and Sapotaceae families had highest or similar wood density in várzea. All other families had highest wood density in terra firme. From the results in this paper (paper III), we cannot discern whether the variations are due to different responses among conspecifics to hydrological stressors or soil nutrient availability. However, as we saw in paper II, várzea soils are richer in nutrients than terra firme soils. This may promote rapid growth in várzea plants during the low-water season, particularly in younger individuals [73,99]. Additionally, várzea plants commonly produce air-filled lenticels in their wood to avoid a lack of oxygen at the root level during the high-water season [60–62] and they have developed strategies [e.g. 64] to cope with the high levels of erosion and alluvial sedimentation present on the floodplains [73]. Thus, we speculate that shared tree species in flooded and unflooded forests can respond to altered environmental condition by adapting their growth strategies. We suggest that high soil nutrient availability, seasonal growth spurts and specialised tissues are likely to cause lower wood densities in várzea trees compared to terra firme conspecifics.

3.4 Paper IV:

Functional traits (paper III), forest structure and diameter-height relationships (paper I) vary between várzea and terra firme. Failure to consider these forest-specific differences could result in erroneous biomass estimates [91,107,108]. To quantify the expected error and uncertainty associated with commonly used estimation methods, we test how flooding – through structural and functional variables – affect above-ground biomass and carbon stock estimates in the Juruá forests.

3.4.1 Conventional methods – data in data out

Regional allometric height performed well in the terra firme forest and produced similar results in the Juruá (overestimation of -3–10%) as previously shown for an upland forest in Malaysia [135]. Global mean wood density overestimated terra firme biomass, although on average with less than the 10% error rate assumed in Chave et al. [82]. This suggests that existing methods for large-scale above-ground biomass mapping are reasonably well-calibrated for upland forests.

Regional allometric height consistently overestimated floodplain biomass (by up to 10–19%). Similarly, work from Madagascar showed that regional allometric height performed poorly in forests with high endemism [108]. Hence, pantropical climate-based height allometries seem to induce substantial errors in poorly sampled forests. Combinations with commonly used global mean wood density produced large overestimates in várzea biomass estimates. This is consistent with paper III and with work from central Africa that showed estimated biomass errors of up to 40% with global mean wood density [100]. These results are likely applicable to other poorly sampled forest types across the tropics. Regional height allometries and global wood density data should therefore be sparingly in data-poor forest types.

Contrary to da Silva et al.[86], we found that for both várzea and terra firme our visual height estimates consistently underestimated above-ground biomass. This is of course a result that depends on the skill and training of the person performing the estimates. However, just as this argument could favour the conclusions in da Silva et al. [86], the discrepancy between our studies shows how erratic the method performance can be.

3.4.2 Local allometric height with unweighted, forest-specific wood density produce reliable biomass estimates

Local height calibration data significantly improve above-ground biomass estimates based on general-purpose allometric equations in data-poor floodplain forest. Locally calibrated diameter-height relationships following Sullivan et al. [91] showed no systematic estimation biases in floodplain or upland biomass estimates (95% CI: VZ = -1–5%, TF = -2–8%). Local allometric height also performed well with local, forest-specific, wood density values, weighted or unweighted, at different taxonomic levels (várzea = -3–6%; terra firme = -8–12%).

Forest specific wood density of lower taxonomic accuracy and/or omission of radial change in wood density induced small differences on várzea and terra firme biomass estimates. This result is in agreement with paper III and with Baker et al. [43] as both studies report low variation among taxa within taxonomic levels. Our results may, however, seem contrary to studies that advocate the use of radially weighted wood densities in biomass estimates [93,96,97]. Such studies have found large effects on individuals or species with large radial variations along the core. In this study, we see very small and systematic under- or overestimates for some unweighted wood densities when combined with measured tree heights (paper IV, Fig. 2e-f). The regression results further indicate that stem diameter and radial trends in wood density could affect the biomass estimates. However, when unweighted wood densities were combined with local allometric height our biomass estimates improved. Local height allometry and unweighted wood densities did not produce systematic bias. Uncertainties around mean estimates were within the same ranges as for radially weighted wood densities but better centred around zero. There were no indications that radial trends in wood density or tree diameter size would affect the estimates.

In conclusion, our results align with previous studies, but show that forest-specific unweighted wood density, combined with local allometric height, reduce the errors of the separate measurements to produce better above-ground biomass estimates. In the absence of direct, individual measurements, local allometric height and forest-specific unweighted genus mean wood density produce the most accurate várzea and terra firme biomass estimates. We believe that these results are transferable to other, undersampled tropical forests. In data poor forests, short of destructively sampled trees, forest-specific height allometries and/or wood density measurements, we recommend local height calibration data, field-measured diameters, and local, forest-specific wood density to calibrate global mean wood density measurements.

4 Conclusions

Chapters I through IV reveal the importance of flooding in determining forest structure, above- and below-ground species composition, wood density and forest biomass across the Amazonian forestscape. They showcase the complimentary value of seasonally flooded and "unflooded" forests for the Amazonian woody plant diversity and provide a handy guide to reduce bias in ground-based above-ground biomass estimates. Take home messages from this thesis are:

- Forest specialists determine várzea and terra firme woody plant composition.
- Different proportions of trees and other lifeforms, species composition, stem density, and tree size drive forest structure in várzea and terra firme. Hence, biomass and carbon stocks are likely to be driven by different, but potentially complimentary, forest structure variables in the two forests.
- Studying below-ground communities along complex environmental gradients can further our understanding of the patterns in below-ground biodiversity, their roles in the dynamics of seasonally flooded forests, and their potential responses to anthropogenic pressure and climate change.
- The many questions left open highlight the need for further investigations of Amazonian soil biodiversity and its ecology.
- High soil nutrient availability, rapid seasonal growth, and specialised tissues are likely to cause lower wood densities in várzea trees compared to conspecific terra firme trees.
- Tree species occurring in both flooded and unflooded forests seem to adapt to their local environment. This indicates an intraspecific phenotypic plasticity in responses to different environmental stressors.
- Existing methods for large-scale above-ground biomass mapping are well-calibrated for terra firme forest.
- Uncertainty in above-ground biomass estimates from data-poor tropical forests could be greatly reduced by local height calibration data, field-measured stem diameters, and local, forest-specific wood density to calibrate global wood density to the forest type of interest.

5 Future research

5.1 The missing soil fauna

We did not pick up on nematodes and arthropods in our soil samples (paper II). This was surprising since previous studies with the same methods and primers always registered these groups. Both nematodes and arthropods are common in soils. It is therefore questionable if these groups were truly absent from the Juruá soils. Yet, our positive and negative controls worked well, and we got a good number of reads in our samples. Hence, the result is not an obvious artefact of the method used. We hypothesise that the absence of nematodes and arthropods in the várzea soils could be due to a high clay content and seasonal floods that would render várzea soil and litter unfit for nematode occupation. This would, however, not explain the absence of soil animals in our terra firme samples since these were not flooded and relatively clay-free. To test our hypothesis, we need further studies in soils with a gradual difference in clay proportion and specific primers targeting nematodes [136] alongside morphological examination of the diversity in the samples.

5.2 Above-ground – below-ground diversity relationships

There was no relationship between above- and below-ground diversity across the different forest types included in this thesis. This result was partly expected since the seasonal flood waters could carry DNA across all várzea flood levels and mask any pattern, but not for terra firme. Indeed, bacterial diversity in terra firme appeared to correlate with woody plant diversity (paper II, Fig. 3A). A more exhaustive study, in area and samples, could serve to refute or confirm this potential correlation. It would furthermore be interesting to test for specific interactions between specific taxa. For example, more nodulation has been observed in flooded areas than in unflooded areas [37]. In the várzea forest, the bacterial community composition co-correlated with woody plant diversity along the flooding gradient. Hence, it would be interesting to study interactions between nitrogen fixating bacteria and woody plant species (e.g. in the Fabaceae family) in more detail to better understand the correlations between bacteria and woody plants.

5.3 Epigenetics and phenotypic responses

Intraspecific variations in wood density reported on in this thesis (paper III) and by Parolin [cf. 65] suggest that tree species have intraspecific phenotypic plasticity in responding to different environmental stressors. For example, in Norway spruce (*Picea* *abies*), a high latitude species to which temperature is a limiting factor, studies show that trees adapt their bud set and bud burst dependent on the temperature sum that they are exposed to during zygotic development [137]. This means that Norway spruce has an epigenetic mechanism that allows them to adapt their bud phenology in response to the environmental conditions that they experienced during early development. If the same mechanism exists in the tree species that are shared between várzea and terra firme this could imply that they adjust their growth and wood phenology dependent of the amount of flooding exposure they experience as zygotic embryos. To test this, an experimental design based on tree species that occur in both flooded and unflooded forests could be set up with genetically identical (i.e. cloned) trees exposed to different flooding times. This type of experiment could inform us about how rapidly várzea and terra firme trees would be able to respond to changed climatic conditions. More data on intraspecific responses in trees to altered environmental conditions across the tropics could therefore reveal potential future tree species composition and carbon stocks under hydrological and climate change [138].

5.4 Present and future distributions of species and carbon stocks in the Juruá

Using information and insights from papers I, III and IV and a newly developed and detailed topographic map over the middle reaches of the Juruá River Basin, we could model woody plant species distributions and above-ground biomass to examine how carbon stocks are distributed along the flooding gradient of the Juruá forestscape. Expanding on this species distribution model we could add information about projected future alterations in precipitation and flooding regimes. This would allow us to examine how possible climate change scenarios could impact species composition, forest structure, and the carbon holding capacity of the Juruá forests.

6 Acknowledgements

I wish to extend my gratitude to:

My supervisor Torbjørn Haugaasen for this fantastic adventure. For the opportunity to explore some of the most amazing forests in this world. You gave me freedom to make this project mine and directions when I was lost. You encouraged, inspired, and supported me. The work in this thesis is not mine. It is ours. You are a team player and I am glad to have you on my team.

Carlos A Peres, my co-supervisor. You helped me plan for this work and gave me the logistical support and the contacts that I needed in the field. Thank you.

Joseph E. Hawes for all the times that you called me over the phone in the Juruá, for the letters sent upstream and the radiocommunication. You taught me how to find, mark and inventory my plots and you helped me find my bearings in the Juruá. Thank you for always checking on me and for helping me on every step along the way of this PhD.

Ana Cristina Mendes de Oliveira for helping me get through the bureaucracy of working in Brazil. All the wonderful people in the Juruá for giving me a place to stay in Carauarí, for helping me in the field and for generously sharing your homes and your time with me. Mark Abrahams for the most wonderful list of helpful advice. João Vitor Campos-Silva, Whaldener Endo and the rest of the Instituto Juruá team for logistical support. Andressa B. Scabin for helping me with the research licenses. Paulo Apóstolo Costa Lima Assunção (in memoriam), "my botanist", for help in the field and at the herbarium in Manaus. You are greatly missed my friend! Michael J.G. Hopkins and Juliana Schietti with colleagues at National Institute for Amazonia Research (INPA) for logistical assistance and a place to work in Manaus. Lorena M. Rincón for help with the plant specimens. Rita Homem Pelicano for dedicated soil sampling and meticulous lab work. All lab assistants that contributed to the analyses of the wood cores and especially Laura N. Martins for taking upon yourself to sort all the samples and measure the wood densities in the lab. Laura L. Hess for being the most wonderful host at UCSB and for introducing me to the wonderous world as seen through satellite imagery.

Colleagues and friends at NMBU for the open and friendly working environment. Roar Økseter, Ole Martin Bollandsås and Anders Qvale Nyrud for helping me with field equipment and understanding wood density. Kari Margrete Thue, Jan Vermaat, Ole Wiggo

Rørstarand and the administrative team at MINA for helping me get this work done! Douglas Shiel, Meley Mekonen Rannestad, Elildo Carvalho Jr. and Jacob Socolar for all the nice discussions. My partners in crime in the welfare committee, The Tropical and Loud corner on the third floor of Sørhellinga and my fellow PhD students for all the laughs and positive energy.

My Pingu-housemates and the Comidas e Cenas trio for making Ås a nice place to be. Ricardo, Ana and Cecila for being family. Marcos Viejo Somoano for saving me from endless frustration over figure formatting. Solrun, Miguel, Thomas, and Denis for being my PhD companions. Camila Duarte Ritter for all the fun work. Rafael Leandro de Assis for helping me from warmup to the finishing line of this PhD. Felipe for challenging and believing in me. Yogesh for all the joy. Clara for your kindness. Nils for the Wednesday AWs. Nivi for all the love. Micah for your kind heart. Gaki for all happy talks. Sama for inspiring me, widening my horizons, and bringing glitter and Martians into my life. Margie for all the enthusiasm and for making me see things in a new light. Sarah for being a pink superpower. Maja for giving me courage. Elin and Yulia for being my friends, always. Monica for facing your great fear of flying to go to Amazonia with me. Dirce for all the Bloody Maries. The Art Factory group for being amazing. My cousins Ricardo, Zilmara, Clarisse, Saulo, Tássia, Rodrigo, Renato, Maíra, Thaís and Thiago for adopting me into your family. Having you all in my life means the world to me.

My sister Sara, for all your love. Farbror Olle for inspiring me to explore the world. My fantastic family for being amazing!

Mamma och pappa for being my superheroes. For being the most generous, most loving parents. For being my friends. For being a source of strength and inspiration. For always letting me go my own way but never alone.

Christoffer for spinning me around. For hugging me when I need it the most.

Yen, April 2021

7 References

1. Jackson, D.C.; Marmulla, G. The influence of dams on river fisheries. In *Dams, Fish and Fisheries: Opportunities, Challenges, and Conflict Resolution.*; Marmulla, G.G., Ed.; Food & Agriculture Organization, Fisheries Technical Paper 419: Rome, 2001 ISBN 9251046948.
2. Malhi, Y.; Roberts, J.T.; Betts, R.A.; Killeen, T.J.; Li, W.; Nobre, C.A. Climate Change, Deforestation, and the Fate of the Amazon. *Science (80-.).* **2008**, *319*, 169–172, doi:10.1126/science.1146961.
3. Mitchard, E.T.A. The tropical forest carbon cycle and climate change. *Nature* 2018.
4. Bonan, G. *Ecological Climatology: Concepts and Applications.*; 3d ed.; Cambridge University Press: Cambridge, 2015; ISBN 9781107619050.
5. Lima, L.S.; Coe, M.T.; Soares Filho, B.S.; Cuadra, S. V.; Dias, L.C.P.; Costa, M.H.; Lima, L.S.; Rodrigues, H.O. Feedbacks between deforestation, climate, and hydrology in the Southwestern Amazon: Implications for the provision of ecosystem services. *Landsc. Ecol.* **2014**, *29*, doi:10.1007/s10980-013-9962-1.
6. Quéré, C. Le; Andrew, R.M.; Friedlingstein, P.; Sitch, S.; Hauck, J.; Pongratz, J.; Pickers, P.A.; Korsbakken, J.I.; Peters, G.P.; Canadell, J.G. Global Carbon Budget 2018. **2018**, 2141–2194.
7. Friedlingstein, P.; Sullivan, M.O.; Jones, M.W.; Andrew, R.M.; Hauck, J. Global Carbon Budget 2020. **2020**, *2020*, 3269–3340.
8. Esquivel-Muelbert, A.; Baker, T.R.; Dexter, K.G.; Lewis, S.L.; Brienen, R.J.W.W.; Feldpausch, T.R.; Lloyd, J.; Monteagudo-Mendoza, A.; Arroyo, L.; Álvarez-Dávila, E.; et al. Compositional response of Amazon forests to climate change. *Glob. Chang. Biol.* **2018**, *25*, 39–56, doi:10.1111/gcb.14413.
9. Costa, M.H.; Coe, M.T.; Loup Guyot, J. Effects of Climatic Variability and Deforestation on Surface Water Regimes. In *Amazonia and Global Change*; 2013 ISBN 9781118670347.
10. Hilker, T.; Lyapustin, A.I.; Tucker, C.J.; Hall, F.G.; Myneni, R.B.; Wang, Y.; Bi, J.; Mendes de Moura, Y.; Sellers, P.J. Vegetation dynamics and rainfall sensitivity of the Amazon. *Proc. Natl. Acad. Sci.* **2014**, *111*, 16041–16046, doi:10.1073/pnas.1404870111.
11. Aragão, L.E.O.C.; Poulter, B.; Barlow, J.B.; Anderson, L.O.; Malhi, Y.; Saatchi, S.; Phillips, O.L.; Gloor, E. Environmental change and the carbon balance of Amazonian

forests. *Biol. Rev.* **2014**, *89*, 913–931, doi:10.1111/brv.12088.

12. Souza, C.M.; Kirchhoff, F.T.; Oliveira, B.C.; Ribeiro, J.G.; Sales, M.H. Long-term annual surface water change in the Brazilian Amazon Biome: Potential links with deforestation, infrastructure development and climate change. *Water (Switzerland)* **2019**, *11*, 566, doi:10.3390/w11030566.
13. Malhi, Y.; Aragao, L.E.O.C.; Galbraith, D.; Huntingford, C.; Fisher, R.; Zelazowski, P.; Sitch, S.; McSweeney, C.; Meir, P. Exploring the likelihood and mechanism of a climate-change-induced dieback of the Amazon rainforest. *Proc. Natl. Acad. Sci.* **2009**, *106*, 20610–20615, doi:10.1073/pnas.0804619106.
14. Poorter, L.; van der Sande, M.T.; Arets, E.J.M.M.; Ascarrunz, N.; Enquist, B.; Finegan, B.; Licona, J.C.; Martínez-Ramos, M.; Mazzei, L.; Meave, J.A.; et al. Biodiversity and climate determine the functioning of Neotropical forests. *Glob. Ecol. Biogeogr.* **2017**, *26*, 1423–1434, doi:10.1111/geb.12668.
15. Mitchard, T.A. The tropical forest carbon cycle and climate change The carbon balance of tropical forests. *Nature* **2018**, *559*, 527–534, doi:10.1038/s41586-018-0300-2.
16. Gaubert, B.; Stephens, B.B.; Basu, S.; Chevallier, F.; Deng, F.; Kort, E.A.; Patra, P.K.; Peters, W.; Rödenbeck, C.; Saeki, T.; et al. Global atmospheric CO2 inverse models converging on neutral tropical land exchange but diverging on fossil fuel and atmospheric growth rate. *Biogeosciences Discuss.* **2018**, 1–25, doi:10.5194/bg-2018-384.
17. Lovejoy, T.E.; Nobre, C. Amazon Tipping Point. *Sci. Adv.* **2018**, doi:10.1126/sciadv.aat2340.
18. Sheil, D. Forests, atmospheric water and an uncertain future: the new biology of the global water cycle. *For. Ecosyst.* **2018**, *5*, doi:10.1186/s40663-018-0138-y.
19. Gedney, N.; Valdes, P.J. The effect of Amazonian deforestation on the northern hemisphere circulation and climate. *Geophys. Res. Lett.* **2000**, *27*, 3053–3056, doi:10.1029/2000GL011794.
20. Chave, J.; Davies, S.J.; Phillips, O.L.; Lewis, S.L.; Sist, P.; Schepaschenko, D.; Armston, J.; Baker, T.R.; Coomes, D.; Disney, M.; et al. Ground Data are Essential for Biomass Remote Sensing Missions. *Surv. Geophys.* **2019**, *40*, 863–880, doi:10.1007/s10712-019-09528-w.
21. Luize, B.G.; Magalhães, J.L.L.; Queiroz, H.; Lopes, M.A.; Venticinque, E.M.; de Moraes

Novo, E.M.L.; Silva, T.S.F. The tree species pool of Amazonian wetland forests: Which species can assemble in periodically waterlogged habitats? *PLoS One* **2018**, *13*, e0198130, doi:10.1371/journal.pone.0198130.

22. Feeley, K. Are we filling the data void? An assessment of the amount and extent of plant collection records and census data available for tropical South America. *PLoS One* **2015**, *10*, e0125629, doi:10.1371/journal.pone.0125629.
23. Prance, G.T. A comparison of the efficacy of higher taxa and species numbers in the assessment of biodiversity in the neotropics. *Philos. Trans. R. Soc. London Ser. B-Biological Sci.* **1994**, *345*, 89–99, doi:https://doi.org/10.1098/rstb.1994.0090.
24. Gentry, A.H. Changes in plant community diversity and floristic composition on environmental and geographical gradients. *Ann. Missouri Bot. Gard.* **1988**, *75*, 1–34, doi:10.2307/2399464.
25. ter Steege, H.; Mota de Oliveira, S.; Pitman, N.C.A.; Sabatier, D.; Antonelli, A.; Guevara Andino, J.E.; Aymard, G.A.; Salomão, R.P. Towards a dynamic list of Amazonian tree species. *Sci. Rep.* **2019**, *9*, 3501, doi:10.1038/s41598-019-40101-y.
26. Cardoso, D.; Särkinen, T.; Alexander, S.; Amorim, A.M.; Bittrich, V.; Celis, M.; Daly, D.C.; Fiaschi, P.; Funk, V.A.; Giacomin, L.L.; et al. Amazon plant diversity revealed by a taxonomically verified species list. *Proc. Natl. Acad. Sci.* **2017**, *114*, 10695–10700, doi:10.1073/pnas.1706756114.
27. Wallace, A.R. A narrative of travels on the Amazon and Rio Negro 1853, 541.
28. Pires, J.M.; Prance, G.T. The vegetation types of the Brazilian Amazon. In *Key Environments: AMAZONIA*; Prance, G.T., Lovejoy, T.E., Eds.; Pergamon Press, 1985; pp. 109–145.
29. Salovaara, K.J.; Gárdenas, G.G.; Tuomisto, H. Forest classification in an Amazonian rainforest landscape using pteridophytes as indicator species. *Ecography (Cop.).* **2004**, *27*, 689–700.
30. Shepard Jr., G.H.; Yu, D.W.; Lizarralde, M.; Italiano, M. Rain forest habitat classification among the matsigenka of the peruvian Amazon. *J. Ethnobiol.* **2001**, *21*, 1–38.
31. Murça Pires, J. The Amazonian forest. In *The Amazon. Limnology and landscape ecology of a mighty tropical river and its basin.*; Sioli, H., Ed.; Dr W. Junk Publishers, 1984; pp. 581–602 ISBN 978-94-009-6544-7.
32. Sombroek, W. Amazon landforms and soils in relation to biological diversity. *Acta*

Amaz. **2000**, *30*, 81, doi:https://dx.doi.org/10.1590/1809-43922000301100.

33. Sombroek, W. Amazon Soils, Wageningen, 1965.
34. Hess, L.L.; Melack, J.M.; Novo, E.M.L.M.; Barbosa, C.C.F.; Gastil, M. Dual-season mapping of wetland inundation and vegetation for the central Amazon basin. *Remote Sens. Environ.* **2003**, *87*, 404–428, doi:10.1016/j.rse.2003.04.001.
35. Wittmann, F.; Schöngart, J.; Montero, J.C.; Motzer, T.; Junk, W.J.; Piedade, M.T.F.; Queiroz, H.L.; Worbes, M. Tree species composition and diversity gradients in white-water forests across the Amazon Basin. *J. Biogeogr.* **2006**, *33*, 1334–1347, doi:10.1111/j.1365-2699.2006.01495.x.
36. Hess, L.L.; Melack, J.M.; Affonso, A.G.; Barbosa, C.; Gastil-Buhl, M.; Novo, E.M.L.M. Wetlands of the lowland Amazon Basin: extent, vegetative cover, and dual-season inundated area as mapped with JERS-1 synthetic aperture radar. *Wetlands* **2015**, *35*, 745–756, doi:10.1007/s13157-015-0666-y.
37. Parolin, P.; Wittmann, F. Struggle in the flood: tree responses to flooding stress in four tropical floodplain systems. *AoB Plants* **2010**, *2010*, 1–19, doi:10.1093/aobpla/plq003.
38. Junk, W.J.; Piedade, M.T.F.; Schöngart, J.; Cohn-Haft, M.; Adeney, M.J.; Wittmann, F. A classification of major natural habitats of Amazonian white-water river floodplains (várzeas). *Wetl. Ecol. Manag.* **2011**, *31*, 623–640, doi:10.1007/s11273-012-9268-0.
39. Räsänen, M.E.; Salo, J.S.; Kalliola, R.J. Fluvial perturbance in the Western Amazon basin: Regulation by long-term Sub-Andean tectonics. *Science (80-.).* **1987**, *238*, 1398–1401, doi:10.1126/science.238.4832.1398.
40. Irion, G. Soil infertility in the Amazonian rain forest. *Naturwissenschaften* **1978**, *65*, 515–519, doi:10.1007/BF00439791.
41. Furch, K.; Klinge, H. Chemical relationship between vegetation, soil and water in contrasting inundation areas of Amazonia. In *Mineral nutrients in tropical forest and savanna ecosystems.*; Proctor, J., Ed.; Blackwell Scientific Publications: Oxford, 1989; pp. 189–204 ISBN 0-632-02559-X.
42. Furch, K.; Junk, W.J. Physiochemical conditions in the floodplains. In *The central Amazon floodplain: ecology of a pulsing system*; Junk, W.J., Ed.; Springer-Verlag: Berlin (Germany), 1997; pp. 69–108 ISBN 978-3-642-08214-6.
43. Baker, T.R.; Phillips, O.L.; Malhi, Y.; Almeidas, S.; Arroyo, L.; Di Fiore, A.; Erwin, T.;

Killeen, T.J.; Laurance, S.G.; Laurance, W.F.; et al. Variation in wood density determines spatial patterns in Amazonian forest biomass. *Glob. Chang. Biol.* **2004**, *10*, 545–562, doi:10.1111/j.1529-8817.2003.00751.x.

44. Higgins, M.A.; Asner, G.P.; Anderson, C.B.; Martin, R.E.; Knapp, D.E.; Tupayachi, R.; Perez, E.; Elespuru, N.; Alonso, A. Regional-scale drivers of forest structure and function in northwestern Amazonia. *PLoS One* **2015**, *10*, 1–19, doi:10.1371/journal.pone.0119887.
45. ter Steege, H.; Pitman, N.C.A.; Phillips, O.L.; Chave, J.; Sabatier, D.; Duque, A.; Molino, J.F.; Prévost, M.F.; Spichiger, R.; Castellanos, H.; et al. Continental-scale patterns of canopy tree composition and function across Amazonia. *Nature* **2006**, *443*, 444–447, doi:10.1038/nature05134.
46. Terborgh, J.; Andresen, E. The composition of Amazonian forests: patterns at local and regional scales. *J. Trop. Ecol.* **1998**, *14*, 645–664, doi:10.1017/s0266467498000455.
47. Toledo, J.J.; Castilho, C. V.; Magnusson, W.E.; Nascimento, H.E.M. Soil controls biomass and dynamics of an Amazonian forest through the shifting of species and traits. *Rev. Bras. Bot.* **2017**, *40*, 451–461, doi:10.1007/s40415-016-0351-2.
48. Alemán, L.A.B.; Barbosa, R.I.; Fernández, I.M. Edaphic Factors and Flooding Periodicity Determining Forest Types in a Topographic Gradient in the Northern Brazilian Amazonia. **2019**, *28*, 1–11, doi:10.9734/IJPSS/2019/v28i630127.
49. Arias, M.E.; Wittmann, F.; Parolin, P.; Murray-Hudson, M.; Cochrane, T.A. Interactions between flooding and upland disturbance drives species diversity in large river floodplains. *Hydrobiologia* **2016**, 1–13, doi:10.1007/s10750-016-2664-3.
50. Assis, R.L.; Wittmann, F.; Haugaasen, T. Effects of hydroperiod and substrate properties on tree alpha diversity and composition in Amazonian floodplain forests. *J. Veg. Sci.* **2015**, *26*, 312–322.
51. Targhetta, N.; Kesselmeier, J.; Wittmann, F. Effects of the hydroedaphic gradient on tree species composition and aboveground wood biomass of oligotrophic forest ecosystems in the central Amazon basin. *Folia Geobot.* **2015**, *50*, 185–205, doi:10.1007/s12224-015-9225-9.
52. Wittmann, F.; Junk, W.J. Sapling communities in Amazonian white-water forests. *J. Biogeogr.* **2003**, *30*, 1533–1544, doi:10.1046/j.1365-2699.2003.00966.x.

53. Kubitzki, K. Themes of diversification in neotropical forest. *Quim. Nova* **1990**, *13*, 4.
54. Junk, W.J. Flood tolerance and tree distribution in Central Amazonian floodplains. In *Tropical forests: Botanical dynamics, speciation and diversity. Academic Press London.*; Nielsen, L.B., Nielsen, I.C., Balslev, H., Eds.; 1989; pp. 47–64.
55. Wittmann, F.; Schöngart, J.; Junk, W.J. Phytogeography, Species Diversity, Community Structure and Dynamics of Central Amazonian Floodplain Forests. In *Amazonian Floodplain Forests. Ecological Studies (Analysis and Synthesis)*; Junk W., Piedade M., Wittmann F., Schöngart J., P.P., Ed.; Springer: Dordrecht, 2010 ISBN 978-90-481-8724-9.
56. Assis, R.L.; Haugaasen, T.; Schöngart, J.; Montero, J.C.; Piedade, M.T.F.; Wittmann, F. Patterns of tree diversity and composition in Amazonian floodplain paleo-várzea forest. *J. Veg. Sci.* **2015**, *26*, 312–322.
57. Parolin, P. Morphological and physiological adjustments to waterlogging and drought in seedlings of Amazonian floodplain trees. *Oecologia* **2001**, *128*, 326–335, doi:10.1007/s004420100660.
58. Parolin, P. Submerged in darkness: Adaptations to prolonged submergence by woody species of the Amazonian floodplains. *Ann. Bot.* **2009**, *103*, 359–376, doi:10.1093/aob/mcn216.
59. Part II Ecological and ecophysiological aspects of Amazonian floodplain forests. In *Amazonian floodplain forests ecophysiology, biodiversity and sustainable management*; Junk, W.J., Piedade, M.T.F., Schöngart, J., Wittmann, F., Parolin, P., Eds.; Springer, 2010; pp. 105–313 ISBN 978-90-481-8724-9.
60. *Amazonian Floodplain Forests Ecophysiology, Biodiversity and Sustainable Management*; Junk, W.J., Piedade, M.T.F., Wittmann, F., Schöngart, J., Parolin, P., Eds.; Springer Heidelberg: London, 2010; ISBN 978-90-481-8724-9.
61. Parolin, P. Diversity of adaptations to flooding in trees of amazonian floodplains. *Pesqui. Bot.* **2012**, *63*, 7–28.
62. Parolin, P.; De Simone, O.; Haase, K.; Waldhoff, D.; Rottenberger, S.; Kuhn, U.; Kesselmeier, J.; Kleiss, B.; Schmidt, W.; Piedade, M.T.F.; et al. Central Amazonian floodplain forests: tree adaptations in a pulsing system. *Bot. Rev.* **2004**, *70*, 357–380, doi:10.1663/0006-8101(2004)070.
63. Angeles, G.; Evert, R.F.; Kozlowski, T.T. Development of lenticels and adventitious roots in flooded Ulmus americana seedlings. *Can. J. For. Res.* **1986**, *16*, 585–590,

doi:10.1139/x86-101.

64. Parolin, P.; Oliveira, A.C.; Piedade, M.T.F.; Wittmann, F.; Junk, W.J. Pioneer trees in Amazonian floodplains: Three key species form monospecific stands in different habitats. *Folia Geobot.* **2002**, *37*, 225–238, doi:https://doi.org/10.1007/BF02804233.
65. Parolin, P. Radial gradients in wood specific gravity in trees of Central Amazonian floodplains. *IAWA J.* **2002**, *23*, 449–457, doi:10.1163/22941932-90000314.
66. Wittmann, F.; Schöngart, J.; Parolin, P.; Worbes, M.; Piedade, M.T.F.; Junk, W.J. Wood specific gravity of trees in Amazonian white-water forests in relation to flooding. *IAWA J.* **2006**, doi:10.1163/22941932-90000153.
67. Worbes, M.; Klinge, H.; Revilla, J.D.; Martius, C. On the dynamics, floristic subdivision and geographical distribution of várzea forests in Central Amazonia. *J. Veg. Sci.* **1992**, *3*, 553–564, doi:10.2307/3235812.
68. Spies, T.A. Forest structure: A key to the ecosystem. *Northwest Sci.* **1998**, *72*, 34–39.
69. Parolin, P. Life history and environment of Cecropia latiloba in Amazonian floodplains. *Rev. Biol. Trop.* **2002**, *50*, 531–545.
70. Wittmann, F.; Anhuf, D.; Funk, W.J. Tree species distribution and community structure of central Amazonian várzea forests by remote-sensing techniques. *J. Trop. Ecol.* **2002**, *18*, 805–820, doi:10.1017/s0266467402002523.
71. Wittmann, F.; Junk, W.J.; Piedade, M.T.F. The várzea forests in Amazonia: Flooding and the highly dynamic geomorphology interact with natural forest succession. *For. Ecol. Manage.* **2004**, *196*, 199–212, doi:10.1016/j.foreco.2004.02.060.
72. Junk, W.J.; Irion, G.; de Mello, J.A.S.N.; Furch, K.; Weber, G.E.; Kern, J.; Darwich, A.; Wassmann, Reiner Martius, C.; Piedade, M.T.F.; Putz, R.; et al. *The central Amazonian Floodplain. Ecology of a pulsing system*; Junk, W.J., Ed.; Springer-Verlag Berlin Heidelberg, 2001; ISBN 9783642624759.
73. Wittmann, F.; Schöngart, J.; De Brito, J.M.; de Oliveira Wittmann, A.; Fernandez Piedade, M.T.; Parolin, P.; Junk, W.J.W.J.; Guillaumet, J.-L.J.L. *Manual of trees from Central Amazonian várzea floodplains*; Cohn-Haft, M., Kossmann Ferraz, I.D., Eds.; Editora INPA: Manaus, 2010; ISBN 978-85-211-0067-6.
74. Myster, R.W. The physical structure of forests in the Amazon Basin: a review. *Bot. Rev.* **2016**, *82*, 407–427, doi:10.1007/s12229-016-9174-x.
75. Myster, R.W. Várzea forest vs. terra firme forest floristics and physical structure in

the Ecuadorean Amazon. *Ecotropica* **2014**, *20*, 35–44.

76. Nogueira, E.M.; Nelson, B.W.; Fearnside, P.M. Wood density in dense forest in central Amazonia, Brazil. *For. Ecol. Manage.* **2005**, *208*, 261–286, doi:10.1016/j.foreco.2004.12.007.

77. Fearnside, P.M. Wood density for estimating forest biomass in the Amazonia. *For. Ecol. Manage.* **1997**, *90*, 59–87.

78. Nogueira, E.M.; Fearnside, P.M.; Nelson, B.W. Normalization of wood density in biomass estimates of Amazon forests. *For. Ecol. Manage.* **2008**, *256*, 990–996, doi:10.1016/j.foreco.2008.06.001.

79. Magnusson, W.E.; Lima, A.P.; Luizão, R.; Luizão, F.; Costa, F.R.C.; Castilho, C.V.; Kinupp, V.F.; Biota RAPELD: a modification of the Gentry method for biodiversity surveys in long-term ecological research sites. *Biota Neotrop.* **2005**, *5*, 1–6.

80. Picard, N.; Saint-André, L.; Henry, M. Manual for building tree volume and biomass allometric equations: from field measurement to prediction.

81. Phillips, O.; Baker, T. *Field manual for plot establishment and remeasurement (Rainfor)*; 2006;

82. Chave, J.; Condit, R.; Aguilar, S.; Hernandez, A.; Lao, S.; Perez, R. Error propagation and sealing for tropical forest biomass estimates. *Philos. Trans. R. Soc. B Biol. Sci.* **2004**, *359*, 409–420, doi:10.1098/rstb.2003.1425.

83. Sheil, D. A critique of permanent plot methods and analysis with examples from Budongo Forest, Uganda. *For. Ecol. Manage.* **1995**, *77*, 11–34, doi:10.1016/0378-1127(95)03583-V.

84. Burt, A.; Calders, K.; Cuni-Sanchez, A.; Gómez-Dans, J.; Lewis, P.; Lewis, S.L.; Malhi, Y.; Phillips, O.L.; Disney, M. Assessment of Bias in Pan-Tropical Biomass Predictions. *Front. For. Glob. Chang.* **2020**, *3:12*, doi:10.3389/ffgc.2020.00012.

85. Larjavaara, M.; Muller-Landau, H.C. Measuring tree height: A quantitative comparison of two common field methods in a moist tropical forest. *Methods Ecol. Evol.* **2013**, *4*, 793–801, doi:10.1111/2041-210X.12071.

86. da Silva, G.F.; Curto, R. de A.; Soares, C.P.B.; Piassi, L. de C. Avaliação de métodos de medição de altura em florestas naturais. *Rev. Arvore* **2012**, *36*, 341–348, doi:10.1590/S0100-67622012000200015.

87. Farve, R. Evaluation of Laser Rangefinders 2010, 1–59.

88. Réjou-Méchain, M.; Barbier, N.; Couteron, P.; Ploton, P.; Vincent, G.; Herold, M.;

Mermoz, S.; Saatchi, S.; Chave, J.; Boissieu, F. de; et al. *Upscaling forest biomass from field to satellite measurements: sources of errors and ways to reduce them*; Springer Netherlands, 2019; ISBN 0123456789.

89. Martínez-Sánchez, J.L.; Martínez-Garza, C.; Cámara, L.; Castillo, O. Species-specific or generic allometric equations: which option is better when estimating the biomass of Mexican tropical humid forests? *Carbon Manag.* **2020**, *11*, 241–249, doi:10.1080/17583004.2020.1738823.

90. Novotný, J.; Navrátilová, B.; Janoutová, R.; Oulehle, F.; Homolová, L. Influence of site-specific conditions on estimation of forest above ground biomass from airborne laser scanning. *Forests* **2020**, *11*, 1–18, doi:10.3390/f11030268.

91. Sullivan, M.J.P.; Lewis, S.L.; Hubau, W.; Qie, L.; Baker, T.R.; Banin, L.F.; Chave, J.; Cuni-Sanchez, A.; Feldpausch, T.R.; Lopez-Gonzalez, G.; et al. Field methods for sampling tree height for tropical forest biomass estimation. *Methods Ecol. Evol.* **2018**, *9*, 1179–1189, doi:DOI: 10.1111/2041-210X.12962.

92. Trevirkets egenskaper. In *Treteknisk håndbok*; Skogstad, P., Ed.; Norsk treteknisk institutt: Oslo, 2009; pp. 20–43 ISBN 978-82-7120-201-9.

93. Williamson, G.B.; Wiemann, M.C. Measuring wood specific gravity...correctly. *Am. J. Bot.* **2010**, *97*, 519–524, doi:10.3732/ajb.0900243.

94. Chave, J.; Réjou-Méchain, M.; Búrquez, A.; Chidumayo, E.; Colgan, M.S.; Delitti, W.B.C.; Duque, A.; Eid, T.; Fearnside, P.M.; Goodman, R.C.; et al. Improved allometric models to estimate the aboveground biomass of tropical trees. *Glob. Chang. Biol.* **2014**, *20*, 3177–3190, doi:10.1111/gcb.12629.

95. Chave, J.; Andalo, C.; Brown, S.; Cairns, M.A.; Chambers, J.Q.; Eamus, D.; Fölster, H.; Fromard, F.; Higuchi, N.; Kira, T.; et al. Tree allometry and improved estimation of carbon stocks and balance in tropical forests. *Oecologia* **2005**, *145*, 87–99, doi:10.1007/s00442-005-0100-x.

96. Muller-Landau, H.C. Interspecific and inter-site variation in wood specific gravity of tropical trees. *Biotropica* **2004**, *36*, 20–32, doi:10.1111/j.1744-7429.2004.tb00292.x.

97. Plourde, B.T.; Boukili, V.K.; Chazdon, R.L.; Rica, C. Radial changes in wood specific gravity of tropical trees : inter- and intraspecific variation during secondary succession. **2015**, 111–120, doi:10.1111/1365-2435.12305.

98. Van Gelder, H.A.; Poorter, L.; Sterck, F.J. Wood mechanics, allometry, and life-history

variation in a tropical rain forest tree community. *New Phytol.* **2006**, *171*, 367–378, doi:10.1111/j.1469-8137.2006.01757.x.

99. Parolin, P. Submergence tolerance vs. escape from submergence: Two strategies of seedling establishment in Amazonian floodplains. *Environ. Exp. Bot.* **2002**, *48*, 177–186, doi:10.1016/S0098-8472(02)00036-9.

100. Bastin, J.; Fayolle, A.; Tarelkin, Y.; Bulcke, J. Van Den Wood Specific Gravity Variations and Biomass of Central African Tree Species : The Simple Choice of the Outer Wood. *PLoS One* **2015**, *10*, 1–16, doi:10.1371/journal.pone.0142146.

101. Baraloto, C.; Rabaud, S.; Molto, Q.; Blanc, L.; Fortunel, C.; Hérault, B.; Dávila, N.; Mesones, I.; Rios, M.; Valderrama, E.; et al. Disentangling stand and environmental correlates of aboveground biomass in Amazonian forests. *Glob. Chang. Biol.* **2011**, *17*, 2677–2688, doi:10.1111/j.1365-2486.2011.02432.x.

102. Muller-Landau, H.C. Interspecific and inter-site variation in wood specific gravity of tropical trees. *Biotropica* **2004**, *36*, 20, doi:10.1646/02119.

103. Souza, F.C. De; Dexter, K.G.; Phillips, O.L.; Pennington, R.T.; Neves, D.; Sullivan, M.J.P.; Alvarez-davila, E.; Alves, Á.; Amaral, I.; Andrade, A.; et al. Evolutionary diversity is associated with wood productivity in Amazonian forests. *Nat. Ecol. Evol.* **2018**, doi:10.1038/s41559-019-1007-y.

104. Chave, J.; Coomes, D.; Jansen, S.; Lewis, S.L.; Swenson, N.G.; Zanne, A.E. Towards a worldwide wood economics spectrum. *Ecol. Lett.* **2009**, *12*, 351–366, doi:10.1111/j.1461-0248.2009.01285.x.

105. Zanne, A.; Lopez-Gonzalez, G.; DA, C.; Ilic, J.; Jansen, S.; SL, L.; RB, M.; NG, S.; MC, W.; Chave, J. Data from: Towards a worldwide wood economics spectrum. *Ecol. Lett.* 2009.

106. Momo, S.T.; Ploton, P.; Martin-Ducup, O.; Lehnebach, R.; Fortunel, C.; Takougoum Sagang, L.B.; Boyemba, F.; Couteron, P.; Fayolle, A.; Libalah, M.; et al. Leveraging Signatures of Plant Functional Strategies in Wood Density Profiles of African Trees to Correct Mass Estimations From Terrestrial Laser Data. *Sci. Rep.* **2020**, *10*, 1–11, doi:10.1038/s41598-020-58733-w.

107. Hunter, M.O.; Keller, M.; Victoria, D.; Morton, D.C. Tree height and tropical forest biomass estimation. **2013**, 8385–8399, doi:10.5194/bg-10-8385-2013.

108. Vieilledent, G.; Vaudry, R.; Andriamanohisoa, S.F.D.; Rakotonarivo, O.S.; Randrianasolo, H.Z.; Razafindrabe, H.N.; Bidaud Rakotoarivony, C.; Ebeling, J.;

Rasamoelina, M. A universal approach to estimate biomass and carbon stock in tropical forests using generic allometric models. *Ecol. Appl.* **2012**, *22*, 572–583, doi:10.1890/11-0039.1.

109. Piponiot, C.; Chave, J.; Herault, B.; Pere, A. Package ' BIOMASS '. **2019**, doi:10.1111/2041-210X.12753>.License.

110. Réjou-Méchain, M.; Tanguy, A.; Piponiot, C.; Chave, J.; Hérault, B. BIOMASS: an R package for estimating above-ground biomass and its uncertainty in tropical forests. *Methods Ecol. Evol.* 2017, *8*, 1163–1167.

111. Haugaasen, T.; Peres, C.A. Floristic, edaphic and structural characteristics of flooded and unflooded forests in the lower Rio Purús region of central Amazonia, Brazil. *Acta Amaz.* **2006**, *25*, 25–36, doi:10.1590/S0044-59672006000100005.

112. Wittmann, F.; Marques, M.C.M.; Júnior, G.D.; Budke, J.C.; Piedade, M.T.F.; De Wittmann, A.O.; Montero, J.C.; Assis, R.L.; Targhetta, N.; Parolin, P.; et al. The Brazilian freshwater wetscape: Changes in tree community diversity and composition on climatic and geographic gradients. *PLoS One* **2017**, *12*, e0175003, doi:10.1371/journal.pone.0175003.

113. Wittmann, F.; Householder, E.; Piedade, M.T.F.; Assis, R.L.; Schöngart, J.; Parolin, P.; Junk, W.J. Habitat specifity, endemism and the neotropical distribution of Amazon white-water floodplain trees. *Ecography (Cop.).* **2013**, *36*, 690–707.

114. Laurance, W.F.; Pérez-Salicrup, Diego Delamônica, P.; Fearnside, P.M.; D'Angelo, S.; Jerozolinski, A.; Pohl, L.; Lovejoy, T.E. Rain forest fragmentation and the structure of Amazonian liana communities. *Ecology* **2001**, *82*, 105–116, doi:https://doi.org/10.1890/0012-9658(2001)082[0105:RFFATS]2.0.CO;2.

115. Campbell, M.; Magrach, A.; Laurance, W.F. Liana Diversity and the Future of Tropical Forests. In *Biodiversity of Lianas, Sustainable Development and Biodiversity*; Parthasarathy, N., Ed.; Springer International Publishing Switzerland, 2015; pp. 255–274 ISBN 9783319145921.

116. Gaglioti, A.L.; Aguiar, D.P.P. Cecropia in Flora do Brasil 2020 em construção Available online: http://floradobrasil.jbrj.gov.br/reflora/floradobrasil/FB24951 (accessed on Sep 4, 2020).

117. de Castilho, C. V.; Magnusson, W.E.; de Araújo, R.N.O.; Luizão, R.C.C.; Luizão, F.J.; Lima, A.P.; Higuchi, N. Variation in aboveground tree live biomass in a central Amazonian Forest: Effects of soil and topography. *For. Ecol. Manage.* **2006**, *234*, 85–

96, doi:10.1016/j.foreco.2006.06.024.

118. Emilio, T.; Quesada, C.A.; Costa, F.R.C.; Magnusson, W.E.; Schietti, J.; Feldpausch, T.R.; Brienen, R.J.W.; Baker, T.R.; Chave, J.; Álvarez, E.; et al. Soil physical conditions limit palm and tree basal area in Amazonian forests. *Plant Ecol. Divers.* **2014**, *7*, 215–229, doi:10.1080/17550874.2013.772257.

119. Nebel, G.; Kvist, L.P.; Vanclay, J.K.; Christensen, H.; Freitas, L.; Ruíz, J. Structure and floristic composition of flood plain forests in the Peruvian Amazon I. Overstorey. *For. Ecol. Manage.* **2001**, *150*, 27–57, doi:10.1016/S0378-1127(00)00680-0.

120. Pasini, D.; Burgess, S.C. Optimal structural features in trees and their application in engineering. *Des. Nat.* **2002**, *3*, 3–15.

121. Schietti, J.; Martins, D.; Emilio, T.; Souza, P.F.; Levis, C.; Baccaro, F.B.; Pinto, J.L.P. da V.; Moulatlet, G.M.; Stark, S.C.; Sarmento, K.; et al. Forest structure along a 600 km transect of natural disturbances and seasonality gradients in central-southern Amazonia. *J. Ecol.* **2016**, *104*, 1335–1346, doi:10.1111/1365-2745.12596.

122. Phillips, O.L.; Sullivan, M.J.P.; Baker, T.R.; Monteagudo Mendoza, A.; Vargas, P.N.; Vásquez, R. Species matter: wood density influences tropical forest biomass at multiple scales. *Surv. Geophys.* **2019**, doi:10.1007/s10712-019-09540-0.

123. Abdul Khalil, H.P.S.; Hossain, M.S.; Rosamah, E.; Azli, N.A.; Saddon, N.; Davoudpoura, Y.; Islam, M.N.; Dungani, R. The role of soil properties and it's interaction towards quality plant fiber: A review. *Renew. Sustain. Energy Rev.* **2015**, *43*, 1006–1015, doi:10.1016/j.rser.2014.11.099.

124. Wacal, C.; Ogata, N.; Basalirwa, D.; Sasagawa, D.; Masunaga, T.; Yamamoto, S.; Nishihara, E. Growth and K Nutrition of Sesame (Sesamum indicum L.) Seedlings as Affected by Balancing Soil Exchangeable Cations Ca, Mg, and K of Continuously Monocropped Soil from Upland Fields Converted Paddy. *Agronomy* **2019**, *9*, doi:10.3390/agronomy9120819.

125. Wang, M.; Zheng, Q.; Shen, Q.; Guo, S. The critical role of potassium in plant stress response. *Int. J. Mol. Sci.* **2013**, *14*, 7370–7390, doi:10.3390/ijms14047370.

126. Assis, R.L.; Haugaasen, T.; Schöngart, J.; Montero, J.C.; Piedade, M.T.F.; Wittmann, F. Patterns of tree diversity and composition in Amazonian floodplain paleo-várzea forest. *J. Veg. Sci.* **2015**, *26*, 312–322, doi:10.1111/jvs.12229.

127. Normand, S.; Vormisto, J.; Svenning, J.C.; Grández, C.; Balslev, H. Geographical and environmental controls of palm beta diversity in paleo-riverine terrace forests in

Amazonian Peru. *Plant Ecol.* **2006**, *186*, 161–176, doi:10.1007/s11258-006-9120-9.

128. Ritter, C.D.; Zizka, A.; Roger, F.; Tuomisto, H.; Barnes, C.; Nilsson, R.H.; Antonelli, A. High-throughput metabarcoding reveals the effect of physicochemical soil properties on soil and litter biodiversity and community turnover across Amazonia. *PeerJ* **2018**, *2018*, doi:10.7717/peerj.5661.
129. Gobat, J.-M.; Aragno, M.; Matthey, W. *The living soil. Fundamentals of soil science and soil biology.*; Science Publishers: Enfield, NH, US., 2004; ISBN 1-57808-210-2.
130. Neher, D.A. Ecology of plant and free-living nematodes in natural and agricultural soil. *Annu. Rev. Phytopathol.* **2010**, *48*, 371–394, doi:10.1146/annurev-phyto-073009-114439.
131. Cameron, E.K.; Martins, I.S.; Lavelle, P.; Mathieu, J.; Tedersoo, L.; Bahram, M.; Gottschall, F.; Guerra, C.A.; Hines, J.; Patoine, G.; et al. Global mismatches in aboveground and belowground biodiversity. *Conserv. Biol.* **2019**, *33*, 1187–1192, doi:10.1111/cobi.13311.
132. Ritter, C.D.; Faurby, S.; Bennett, D.J.; Naka, L.N.; ter Steege, H.; Zizka, A.; Haenel, Q.; Nilsson, R.H.; Antonelli, A. The pitfalls of biodiversity proxies: Differences in richness patterns of birds, trees and understudied diversity across Amazonia. *Sci. Rep.* **2019**, *9*, 1–14, doi:10.1038/s41598-019-55490-3.
133. Slik, J.W.F.; Paoli, G.; Mcguire, K.; Amaral, I.; Barroso, J.; Bastian, M.; Blanc, L.; Bongers, F.; Boundja, P.; Clark, C.; et al. Large trees drive forest aboveground biomass variation in moist lowland forests across the tropics Stable URL : https://www.jstor.org/stable/42568596 Linked references are available on JSTOR for this article : Large trees drive forest aboveground biomass. *Glob. Ecol. Biogeogr.* **2013**, 1261–1271, doi:10.1111/geb.12092.
134. Ali, A.; Lin, S.L.; He, J..; Kong, F.M.; Yu, J.. Big-sized trees overrule remaining trees' attributes and species richness as determinants of aboveground biomass in tropical forests. *Glob. Chang. Biol.* **2019**, *25*, 2810–2824.
135. Rutishauser, E.; Noor'an, F.; Laumonier, Y.; Halperin, J.; Rufi'ie; Hergoualch, K.; Verchot, L. Generic allometric models including height best estimate forest biomass and carbon stocks in Indonesia. *For. Ecol. Manage.* **2013**, *307*, 219–225, doi:10.1016/j.foreco.2013.07.013.
136. Kawanobe, M.; Toyota, K.; Ritz, K. Development and application of a DNA

metabarcoding method for comprehensive analysis of soil nematode communities. *Appl. Soil Ecol.* **2021**, *166*, doi:10.1016/j.apsoil.2021.103974.

137. Skrøppa, T.; Tollefsrud, M.M.; Sperisen, C.; Johnsen, Ø. Rapid change in adaptive performance from one generation to the next in Picea abies-Central European trees in a Nordic environment. *Tree Genet. Genomes* **2010**, *6*, 93–99, doi:10.1007/s11295-009-0231-z.
138. Yang, J.; Cao, M.; Swenson, N.G. Why functional traits do not predict tree demographic rates. *Trends Ecol. Evol.* **2018**, doi:10.1016/j.tree.2018.03.003.

8 Other publications

1. Machado A.F., Ritter C.D., Miranda C.L., **Bredin Y.K.**, Ramos Pereira M.J., Duarte L. (2021) Potential mammalian species for investigating the past connections between Amazonia and the Atlantic Forest. PLoS ONE 16(4): e0250016. https://doi.org/10.1371/journal.pone.0250016
2. Assis, R.L., Wittmann, F., **Bredin, Y.K.**, Schöngart, J., Nobre Quesada, C.A., Piedade, M.T.F., Haugaasen, T., 2019. Above-ground woody biomass distribution in Amazonian floodplain forests: Effects of hydroperiod and substrate properties. For. Ecol. Manage. https://doi.org/10.1016/j.foreco.2018.09.031
3. Gundersen, V., Selvaag, S., Strand, O., **Bredin, Y.K.**, Sandal, R. J. & Hermansen, P. 2019. Ferdsel i to fokusområder i Setesdal-Ryfylke villreinområde. Brokke-Suleskardvegen og Blåsjøområdet. NINA Rapport 1676. Norsk institutt for naturforskning.
4. **Bredin, Y.K.**, Lescureux, N., Linnell, J.D.C., 2018. Local perceptions of jaguar conservation and environmental justice in Goiás, Matto Grosso and Roraima states (Brazil). Glob. Ecol. Conserv. https://doi.org/10.1016/j.gecco.2017.e00369
5. Primmer, E., Termansen, M., **Bredin, Y.K.**, Blicharska, M., García-Llorente, M., Berry, P., Jääskeläinen, T., Bela, G., Fabok, V., Geamana, N., Harrison, P.A., Haslett, J.R., Cosor, G.L., Andersen, A.H.K., 2017. Caught Between Personal and Collective Values: Biodiversity conservation in European decision-making. Environ. Policy Gov. https://doi.org/10.1002/eet.1763
6. Linnell, J. D. C., Kaltenborn, B., **Bredin, Y.K.** & Gjershaug, J. O. 2016. Biodiversity assessment of the Fagaras Mountains, Romania - NINA Report 1236. 86 pp. Norsk institutt for naturforskning.

Paper I

forests
MDPI

Article

Structure and Composition of Terra Firme and Seasonally Flooded Várzea Forests in the Western Brazilian Amazon

Yennie K. Bredin [1,*], **Joseph E. Hawes** [1,2], **Carlos A. Peres** [3,4] **and Torbjørn Haugaasen** [1]

[1] Faculty of Environmental Sciences and Natural Resource Management, Norwegian University of Life Sciences, 1430 Ås, Norway; joseph.hawes@nmbu.no (J.E.H.); torbjorn.haugaasen@nmbu.no (T.H.)
[2] Applied Ecology Research Group, School of Life Sciences, Anglia Ruskin University, Cambridge CB1 1PT, UK
[3] School of Environmental Sciences, University of East Anglia, Norwich NR4 7TJ, UK; c.peres@uea.ac.uk
[4] Departamento de Sistemática e Ecologia, Universidade Federal da Paraíba, João Pessoa, 58051-900 Paraíba, Brazil
* Correspondence: yennie.bredin@nmbu.no

Received: 20 November 2020; Accepted: 15 December 2020; Published: 18 December 2020

Abstract: *Research Highlights*: Rare, or sparsely distributed, species drive the floristic diversity of upland, terra firme and seasonally flooded forests in the central Juruá—a remote and hitherto floristically poorly known area in the Brazilian Amazon. *Background and Objectives*: Floristic inventories are critical for modelling and understanding the role of Amazonian forests in climate regulation, for sustainable management of forest resources and efficient conservation planning. Yet, detailed information about the often complex spatial distributions of many Amazonian woody plants is limited. Here, we provide information about forest structure and species composition from a remote terra firme forest and an adjacent floodplain forest in the western Brazilian Amazon. More specifically, we ask (1) how floristically different are the terra firme and floodplain forests? and (2) how variable is species composition within the same forest type? *Materials and Methods*: Between September 2016 and October 2017, we inventoried 97 plots (each 0.1 ha; 100 × 10 m) placed at least 800 m apart, with 46 plots in terra firme forest and 51 in seasonally flooded forest. We included all trees, hemi-epiphytes and palms with diameter at breast height (dbh) > 10 cm and woody lianas > 5 cm dbh. We examine forest structure, family- and species-level floristic composition and species diversity within and between forest types using family and species importance values, rarefaction curves and dissimilarity matrices. *Results*: Terra firme forest and seasonally flooded forest woody plant communities differ both in structure and species composition, which was highly variable within forest types. Many species were shared between terra firme and seasonally flooded forests, but most species were forest type-specific. Whereas species richness was greatest in the terra firme forest, floodplain species richness was among the highest regionally. *Conclusions*: Floodplain forests are a crucial complement to terra firme forests in terms of Amazonian woody plant diversity.

Keywords: Amazon; forest structure; floodplain forest; paleo-várzea; plant diversity; species composition; terra firme; várzea; woody plants

1. Introduction

Floristic inventories are critical for modelling and understanding the role of Amazonian forests in climate regulation, for sustainable management of forest resources and efficient conservation planning. Yet, for a number of reasons, floristic inventories in Amazonian forests are notoriously difficult and detailed information about the often complex spatial distributions of many Amazonian trees is limited [1–4]. Additionally, the majority of published floristic inventories have been conducted close to urban centres [5] and focus on terra firme forests [6]. This results in severe biases in our knowledge of tree species richness and distribution, and many remote areas remain neglected and poorly represented in herbaria [7,8].

Considering the irregular distribution and local rarity of many tropical tree species [9], the bias and patchiness of floristic data from the Amazon presents one of the biggest challenges for conservation biologists and climate modellers alike. Although it is the largest remaining tract of tropical forest on Earth, the status of the Amazon is precarious, as threats from deforestation, logging and other disturbances continue to increase [10–13]. Such activities adversely affect forest structure and composition, as well as the forest capacity to store carbon, retain water and regulate climate [14–19]. Thus, we urgently need on-the-ground efforts to improve our forest inventory coverage.

Broadly speaking, Amazonian forests may be divided into upland forests (hereafter, terra firme) that lie above the maximum flood level of rivers and perennial streams, and lowland, forested wetlands that are either seasonally or permanently inundated. In general, closed-canopy terra firme forests lie on well-drained terrains that tend to be heavily leached and nutrient-poor [20,21]. However, some terra firme forests, such as the forests on the elevated terraces alongside the floodplains of the Juruá River, have relatively nutrient-rich soils as they occupy substrates that were once eutrophic floodplains. Such lowland terra firme forests typically fringe the seasonally inundated floodplains but are no longer under the influence of the monomodal flood pulse that dominate the floodplains.

Seasonally flooded forests comprise the second major forest type in the Amazon [22]. Because of the lowland topography of the basin and the high seasonality in rainfall, forests in central Amazonia may endure floods lasting up to 210 days per year and reaching 10–15 m in amplitude [23]. Depending on the hydro-chemical and floristic characteristics, these floodplain forests are divided into seven main types [24]. Of these, the most extensive floodplain forests are those inundated by white-water rivers (e.g., the Amazonas/Solimões, Madeira, Purús and Juruá), and are called várzea. Because the rivers that flood várzea forests drain Andean landscapes that are geologically young and easily erode [25], they bring large amounts of suspended nutrient-rich sediments onto the floodplains [26–28]. These sediments give the rivers their muddy appearance and leave the várzea floodplains eutrophic, species-rich and exceptionally productive [29].

Floodplain forests are severely under-represented in herbaria, with a collection density for wetland forests averaging only 0.05 records per 100 km^2 [6] and many botanical samples lack information about detailed habitat conditions. Várzeas are the best-collected category of floodplain forests in Amazonia, but although a highly important floristic region, inventories have been particularly scarce in the Juruá River region [5]. Moreover, while terra firme forests are comparatively well-represented in Amazonian forest inventories, few studies recognise and focus on the lowland terra firme forests that grow on old eutrophic floodplain sediments (paleo-várzea sediments) adjacent to seasonally inundated várzeas [30]. The Juruá floodplain, with its extensive stretch of adjacent flooded and terra firme forests, is therefore a priority area for botanical inventories to improve our knowledge on Amazonian tree diversity [6].

Here, we present a floristic inventory from lowland terra firme forest and adjacent seasonally inundated várzea forest from the central Juruá River basin. More specifically, we ask (1) how floristically different are terra firme and várzea forests? and (2) how variable is species composition among plots within the same forest type? We use species rarefactions and dissimilarity indices to examine these differences in structure and composition within and between terra firme and várzea forests. We discuss our findings in relation to wider patterns of forest structure and species distributions in the Amazon basin and conclude that várzea forests are an important complement to terra firme forests.

2. Materials and Methods

2.1. Study Area

This study took place in the central Juruá River basin, western Brazilian Amazonia. The region contains both seasonally flooded várzea (VZ) and lowland terra firme forests on paleo-várzea sediments (TF). The study area was located between 05°08′ S, 67°01′ W and 05°87′ S, 67°88′ W and includes the Uacari Sustainable Development Reserve (RDS Uacari, 632,949 ha), but excludes the Médio Juruá Extractive Reserve (ResEx Médio Juruá, 253,227 ha; Figure 1). The climate of the region is wet and tropical. Annual temperatures and rainfall average 27.1 °C and 3679 mm, respectively [31]. The elevation within the inventoried forests ranges from 67 to 153 m above sea level for terra firme and 68–137 m above sea level for várzea. The forests represent structurally intact vegetation.

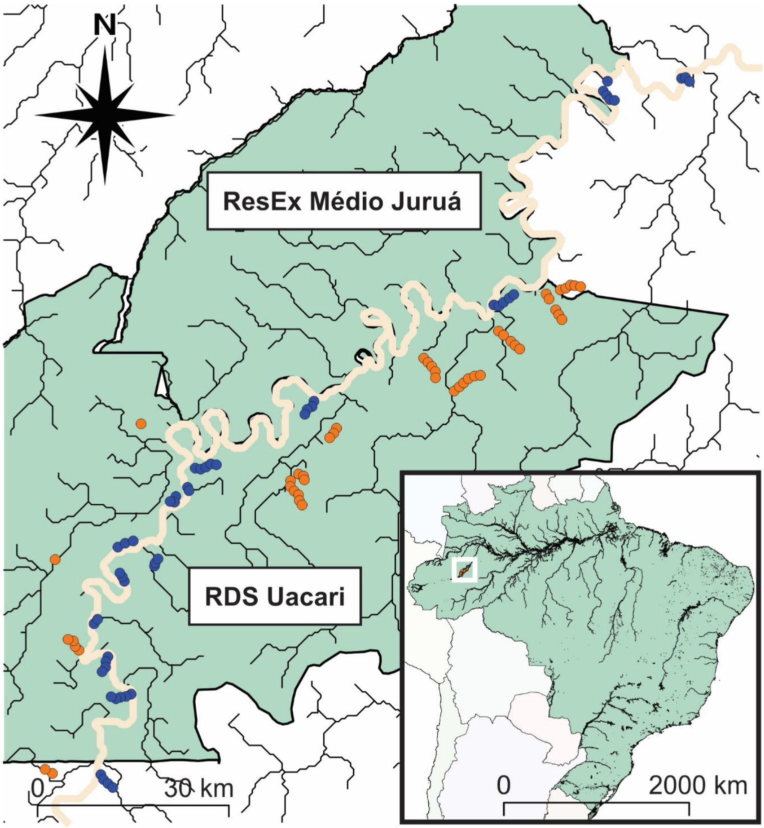

Figure 1. Map showing the study area in western Brazilian Amazonia (indicated by the white square in the inset map) and plot locations of woody plant inventories in terra firme (orange) and várzea forests (dark blue) along 150 km of the Juruá River (in beige). Smaller rivers are shown as black lines. The Médio Juruá Extractive Reserve (ResEx Médio Juruá) and Uacari Sustainable Development Reserve (RDS Uacari) are shown in green with black borders. The map was generated in QGIS v.3.12.2, using background maps from the GADM database of Global Administrative Areas [32]. The shapefiles for the ResEx Médio Juruá and RDS Uacari were provided by Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio) and the Amazonas State Environmental Agency (SEMA-DEMUC), respectively.

2.2. Floristic Inventories and Measurements

Between September 2016 and October 2017, we inventoried 97 plots (each 0.1 ha; 100 × 10 m), with 46 plots in terra firme forest (TF) and 51 in seasonally flooded várzea forest (VZ). The shortest distance between inventory plots was 800 m. To capture várzea forest at different inundation depths and periodicity as well as different soil types, topographic conditions and microhabitats, the plots were placed along transects that extended along the flooding gradient, with increasing elevation at greater distances from the main river channel.

Within each plot, all trees, hemi-epiphytes and palms ≥ 10 cm diameter at breast height (dbh), and all woody lianas ≥ 5 cm dbh, were measured and identified. Peripheral individuals straddling the boundary of the plots were included in the inventory if the mid-point of their trunks fell within the plot. We measured the dbh of buttressed trees immediately above the buttresses. When direct measurement with a dbh-tape was not possible (e.g., sulcate trunks, stranglers or where buttresses were too high), we estimated the diameters. We used a Haglöf Vertex IV and Transponder T3 to measure tree, palm and hemi-epiphyte total heights based on trigonometric calculations using the measuring angle and distance to the trunk [33], and/or estimated total heights where this was not possible. For trees and hemi-epiphytes, we also determined the height of the first branch. For palms, we determined the height of the stem. To remove observer bias, the same person (Y.K.B.) administered all height measurements.

All individuals were aluminium-tagged, numbered and identified in situ and/or in the herbarium at the National Institute of Amazonian Research (INPA), Manaus, Brazil. Skilled INPA herbarium technicians with extensive field and herbarium experience from floristic inventories in the central-western Brazilian Amazon performed all identifications. Vouchers from 1174 individuals were collected and subsequently identified at the INPA herbarium to verify the accuracy of field identifications at the level of genus and species. Individuals that could not be determined to species level were sorted to morpho-species or, where applicable, higher taxonomic levels.

2.3. Data Analyses

To test for differences in woody plant stem density, dbh, basal area (BA), total height, height of first branching, branching depth and proportion of stem with branches in relation to total height, we first ran Shapiro–Wilk's tests of normality and compared the variances of terra firme and várzea using Fisher's F-test. For normally distributed data, we ran Student's two-sample *t*-tests where data conformed to homoscedasticity, or Welch two-sample *t*-tests where they did not. Where the data did not conform to normality, we ran independent two-group Wilcoxon–Mann–Whitney tests.

For each family and species, we calculated the relative density (Rel. Den.), relative dominance (Rel. Dom.), relative diversity (Rel. Div.) and relative frequency (Rel. Freq.). For formulas, see Appendix A. In addition, we calculated the Family Importance Value (FIV = $\sum$ Rel. Den. + Rel. Dom. + Rel. Div.) for each family [34] and the Importance Value Index (IVI = $\sum$ Rel. Dens + Rel. Dom. + Rel. Freq.) for each species [35].

We used the 'BiodiversityR' package version 2.11-1 [36] to calculate indices of species richness and diversity, and to produce species rarefaction curves estimating the expected number of additional species for every additional survey plot, in relation to the mean number of individuals per plot. Species rarefactions were based on 100 permutations.

To investigate the spatial variation in woody plant species composition, we used the 'vegan' package, version 2.5-5 [37]. We tested for spatial autocorrelation among plots using a partial Mantel test with a Bray-Curtis dissimilarity matrix for the woody plant species composition, and a Euclidian distance matrix for the geographic distances [37]. To assess variations in species composition, we used non-metric multidimensional scaling (NMDS) through the *metaMDS* function with the Bray-Curtis dissimilarity index. We used the *envfit* method to fit forest type (i.e., TF or VZ) onto the NMDS ordination as a measure of the correlation of forest type with the NMDS axes. Additionally, we performed a permutational multivariate analysis of variance test (PERMANOVA) with forest type as predictor of the woody plant composition dissimilarity matrices, with the Bray-Curtis index as the response variable.

To analyse for multivariate homogeneity of group dispersions, we used the *betadisper* function in vegan. Analyses for multivariate homogeneity of group dispersions inform us how the variances within groups differ among groups [38]. Defining β-diversity as the variability in species composition among sampling units within groups, tests of multivariate homogeneity of group dispersions may thus inform us about differences in β-diversity between the two forest types [39]. To minimise the influence of the most abundant species on the multivariate dispersion analyses, we first square-root transformed the species abundance matrix [40]. To adjust for potential small sample bias in the analyses, we used the *bias.adjust* option of the *betadisper* function [40,41]. All analyses were run in R, version 3.5.2 [42].

3. Results

3.1. Forest Structure

In total, we recorded 4690 individual trees, 274 palms, 25 hemi-epiphytes and 450 lianas across both terra firme and várzea forests (n = 97 plots; 9.7 ha), yielding 5439 individuals or 5483 stems (Table 1). The dbh size class distributions in the two forest types show inverse J-shaped curves for both the combined tree and hemi-epiphyte assemblages and the lianas (Figure 2). For palms, the size class distribution was a sigmoid shape, showing a slight shift in climax towards larger diameters in várzea palms (20–25 cm dbh) compared to terra firme palms (15–20 cm dbh; Figure 2).

Table 1. Number of plots (Plots) and number of ha. (Ha.) inventoried in terra firme (TF) and várzea (VZ) forests along the Juruá River, western Brazilian Amazon. Number of stems (Stems), including hollow stems, and number of individuals (Inds.), including multi-stemmed individuals, are given as count data with percentiles in parentheses (%). Mean number of stems per plot (Plot mean) is given ± standard deviations (sd). Mean diameter at breast height (dbh) ± sd is in cm, basal area (BA) in m^2 and mean height ± sd in m. All values are given per growth form, forest type and for both forest types combined. Values refer to trees, palms and hemi-epiphytes (hemi-ep.) with dbh ≥ 10 cm and woody lianas ≥ 5 cm dbh. Total height in m is also given as overall minimum (Min), maximum (Max), median and mode values. Differences in stem density, dbh, plot BA and mean total height between várzea and terra firme for normally distributed data were tested with classic Student's two-sample *t*-tests where group variances were homogenous or Welch two-sample *t*-tests where group variances were heterogenous. Where data did not conform to normality, we used independent two-group Wilcoxon–Mann–Whitney tests. Asterisks in the table indicate significant results.

		TF	VZ	Total
	Plots	46	51	97
	Ha.	4.60	5.10	9.70
Stems	Trees (%)	2288 (89.80)	2443 (83.24)	4731 (86.28)
	Hemi-ep. (%)	5 (0.20)	22 (0.75)	27 (0.49)
	Palms (%)	104 (4.08)	170 (5.79)	274 (5.00)
	Lianas (%)	151 (5.93)	300 (10.22)	451 (8.23)
	Total (%)	2548 (100.00)	2935 (100.00)	5483 (100.00)
	Hollow (%)	34 (1.33)	63 (2.15)	97 (1.77)
	Plot mean ± sd	55.39 ± 11.07	57.55 ± 12.29	56.53 ± 11.72
Inds.	Trees (%)	2282 (89.77)	2408 (83.12)	4690 (86.23)
	Hemi-ep. (%)	5 (0.20)	20 (0.69)	25 (0.46)
	Palms (%)	104 (4.09)	170 (5.87)	274 (5.04)
	Lianas (%)	151 (5.94)	299 (10.32)	450 (8.27)
	Total (%)	2542 (100.00)	2897 (100.00)	5439 (100)
	Multi-stemmed (%)	4 (0.16)	30 (1.04)	34 (0.63)
Mean dbh ± sd, cm	Trees	21.85 ± 13.40	22.71 ± 16.09	22.29 ± 14.85
	Hemi-ep.	27.28 ± 9.36	44.05 ± 42.81	40.94 ± 39.22
	Palms ***	16.65 ± 4.60	22.93 ± 6.84	20.54 ± 6.80
	Lianas	8.48 ± 2.79	9.14 ± 4.04	8.92 ± 3.68
	Total	20.85 ± 13.17	21.50 ± 15.93	21.40 ± 14.71

Table 1. *Cont.*

		TF	VZ	Total
BA, m^2	Tree	118.03	148.59	266.62
	Hemi-ep.	0.32	6.38	6.70
	Palm	2.44	7.64	10.08
	Liana	0.94	2.35	3.29
	Total	121.73	164.96	286.69
	Plot mean ± sd *	2.65 ± 0.71	3.23 ± 1.18	2.96 ± 1.03
Mean height ± sd, m	Tree ***	20.16 ± 7.40	16.20 ± 7.71	18.12 ± 7.81
	Hemi-ep.	27.67 ± 8.74	24.30 ± 7.95	24.89 ± 7.92
	Palm	17.88 ± 5.94	16.90 ± 6.12	17.27 ± 6.06
	Overall ***	20.07 ± 7.36	16.29 ± 7.64	18.10 ± 7.74
Overall height, m	Min	3.00	1.70	1.70
	Max	50.00	47.37	50.00
	Median	19.00	15.00	16.43
	Mode	20.00	10.00	15.00

Significant difference between VZ and TF values at * $p < 0.05$ and *** $p < 0.001$.

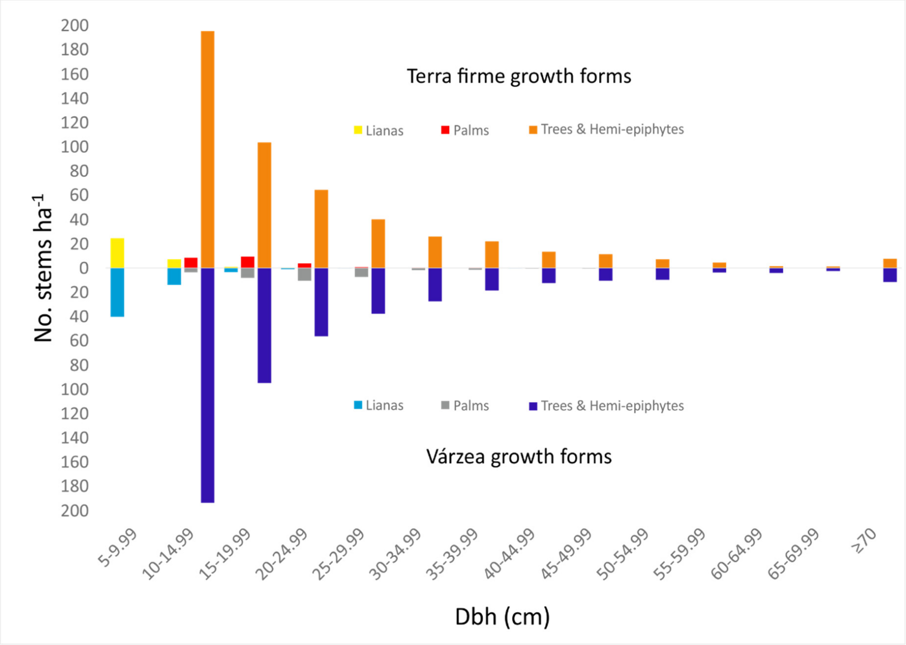

Figure 2. Number of stems per hectare across diameter at breast height (Dbh) size classes with five cm intervals where, e.g., 5–9.99 is from five cm dbh up to, but not including, 10 cm dbh. Values are given per growth form for terra firme (yellow = lianas, red = palms, orange = trees and hemi-epiphytes) and várzea (light blue = lianas, grey = palms, dark blue = trees and hemi-epiphytes) forests along the central reaches of the Juruá River, western Brazilian Amazon.

Smaller trees measuring <30 cm dbh dominated both forest types. These accounted for 72.8% of all inventoried individuals in terra firme (80.9% of all terra firme trees) and 66.4% of all individuals in seasonally inundated forest (79.1% of all várzea trees). Large trees (≥70 cm dbh) represented just 2.0% of all trees (1.5% and 2.4% of the TF and VZ trees, respectively), or 1.7% of all individuals (1.4% and 2.0% of the TF and VZ individuals, respectively). Only 18 (0.4%) trees in the entire sample attained diameters greater than 100 cm dbh, two in terra firme and 16 in várzea. Six of these sixteen emergents were *Hura crepitans* (Euphorbiaceae) in várzea.

Mean total height was greater among terra firme woody plants compared to várzea (Wilcoxon–Mann–Whitney's W = 4,094,644, $p < 0.001$). However, when examining growth forms separately, only trees were significantly taller in terra firme compared to várzea (Wilcoxon–Mann–Whitney's W = 3,676,156, $p < 0.001$). There was no significant height difference between forest types for hemi-epiphytes or palms (Table 1). Palm dbh was significantly lower in terra firme compared to várzea (Wilcoxon–Mann–Whitney's W = 3739.5, $p < 0.001$; Table 1). There was no significant difference in dbh for trees, hemi-epiphytes or lianas. Terra firme had significantly lower basal area (Wilcoxon–Mann–Whitney's W = 818, p-value = 0.01) and fewer palms, hemi-epiphytes, lianas, hollow stems and multi-stemmed individuals compared to várzea (Table 1). The most frequently encountered multi-stemmed várzea species ($n = 5$) was *Theobroma cacao* (Malvaceae). The species most frequently encountered with hollow trunks were *Cecropia* species (VZ: $n = 19$, TF: $n = 16$). Várzea woody plants branched closer to the ground (Wilcoxon–Mann–Whitney's W = 3,520,973, $p < 0.001$), had greater branching depth (Wilcoxon–Mann–Whitney's W = 2,091,770, $p < 0.001$) and had branches along a greater portion of their stems, compared to terra firme trees and hemi-epiphytes (Wilcoxon–Mann–Whitney's W = 1,392,508, $p < 0.001$).

3.2. Floristic Diversity

In total, 931 species were recorded in the lowland terra firme and várzea forests combined (Table 2). Of these, 625 species occurred in terra firme and 526 in várzea (Table 2). Two hundred and twenty species (23.6%) were shared among terra firme and várzea forests, comprising 44.4% of all individuals. However, most species were unique to either terra firme (43.5%; Table 2) or várzea (32.9%; Table 2) and many species occurred only in a single plot (TF: 45.6%, $n = 285$; VZ: 42.2%, $n = 222$). Most of the shared species were rare and occurred with few observations in one forest type and single observations in the other (69.5%, $n = 153$), or as singletons in both forest types (13.2%, $n = 29$). Only 44 (20.0%) of the 220 shared species had 10 or more individuals recorded in at least one forest type. Three species (1.4%) had 10 or more individuals recorded in both forest types. Although the species rarefaction curves clearly indicate a greater species richness in terra firme compared to várzea, the curves did not reach an asymptote for either forest type (Figure 3).

Table 2. Number of species (Spp.), number of genera (Gen.) and number of families (Fam.) found within the terra firme (TF) and várzea (VZ) forests along the Juruá River, western Brazilian Amazon. Values are given as counts per growth form, forest type and for both forest types combined, with percentiles of individuals not identified to each taxonomic level in parentheses (N/A, %). In addition, the numbers of Spp., Gen. and Fam. that were unique to either forest type (Unique) or occurred as singletons in either or both forest types (Singleton) are given as counts and percentiles in parenthesis (%). All values refer to trees, palms and hemi-epiphytes (hemi-ep.) with dbh ≥ 10 cm and woody lianas ≥ 5 cm dbh.

		TF	**VZ**	**Total**
Spp.	Trees (N/A, %)	576 (4.08)	466 (4.98)	847 (4.54)
	Hemi-ep. (N/A, %)	3 (0.00)	9 (5.00)	11 (4.00)
	Palms (N/A, %)	7 (4.81)	5 (0.00)	9 (1.82)
	Lianas (N/A, %)	41 (29.80)	58 (21.74)	79 (24.44)
	Total (N/A, %)	625 (5.63)	526 (6.42)	931 (6.05)
	Unique (%)	405 (43.50)	306 (32.87)	711 (76.37)
	Singleton (%)	285 (45.60)	222 (42.21)	314 (33.73)
Gen.	Trees (N/A, %)	214 (2.50)	188 (1.00)	273 (1.73)
	Hemi-ep. (N/A, %)	2 (0.00)	2 (0.00)	2 (0.00)
	Palms (N/A, %)	7 (3.85)	4 (0.00)	7 (1.46)

Table 2. *Cont.*

		TF	VZ	Total
	Lianas (N/A, %)	31 (23.18)	45 (14.72)	54 (17.56)
	Total (N/A, %)	247 (3.78)	226 (2.35)	317 (3.02)
	Unique (%)	91 (28.71)	70 (22.08)	161 (50.79)
	Singleton (%)	66 (26.72)	42 (18.58)	56 (17.67)
Fam.	Trees (N/A, %)	63 (1.97)	53 (0.58)	67 (1.26)
	Hemi-ep. (N/A, %)	2 (0.00)	2 (0.00)	2 (0.00)
	Palms (N/A, %)	1 (0.00)	1 (0.00)	1 (0.00)
	Lianas (N/A, %)	17 (17.88)	23 (12.71)	28 (14.44)
	Total (N/A, %)	69 (2.83)	63 (1.79)	77 (2.28)
	Unique (%)	14 (18.18)	8 (10.39)	22 (28.57)
	Singleton (%)	9 (13.04)	4 (6.35)	6 (7.79)

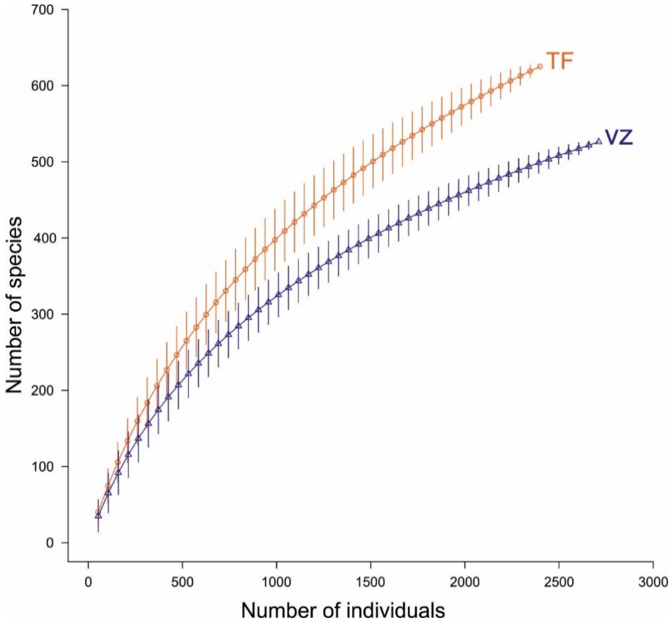

Figure 3. Sample-based rarefaction curves, scaled by the number of pooled individuals per survey plot (sample) for terra firme forest (TF, in orange) and várzea forest (VZ, in blue). The bars indicate ±2 standard deviations.

3.3. Family Importance Value

Leguminosae (Fabaceae) dominated the family importance value (FIV) in both forest types, mainly because of the large number of species in this super-family (TF: FIV = 40.93; 15.7%; VZ: FIV = 38.98; 13.9%; Table 3; Table 4). In both forest types, Lecythidaceae was the second most important family, followed by Sapotaceae. In terra firme, Lecythidaceae represented both the highest number of individuals (n = 383) and the greatest basal area (BA) (Table 3). In várzea, Lecythidaceae was the second most dominant family, Sapotaceae was the second most species-rich family and Annonaceae was the second most abundant family (Table 4). The full FIV list for all families is presented in Supplementary Table S1.

Table 3. The ten most important families in lowland terra firme, listed in descending order of family importance value (FIV). Values are based on all woody plants with species identifications. The number of individuals (No. Inds.) and the number of species within each family (No. Spp.) are given as counts. Basal area (BA) in m^2. Relative density (Rel. Den.), relative dominance (Rel. Dom.) and relative diversity (Rel. Div.) are given as percentages, where 100 equals 100% (Supplementary Table S1).

Family	No. Inds.	BA (m^2)	No. Spp.	Rel. Den.	Rel. Dom.	Rel. Div.	FIV
Leguminosae	286	16.12	98	11.58	13.67	15.68	40.93
Lecythidaceae	383	20.70	30	15.51	17.55	4.80	37.86
Sapotaceae	163	9.54	47	6.60	8.09	7.52	22.21
Chrysobalanaceae	186	9.61	33	7.53	8.15	5.28	20.96
Myristicaceae	203	8.49	21	8.22	7.20	3.36	18.78
Moraceae	134	8.68	31	5.43	7.36	4.96	17.75
Lauraceae	91	6.50	30	3.68	5.51	4.80	14.00
Burseraceae	114	3.03	34	4.62	2.57	5.44	12.62
Urticaceae	73	4.35	17	2.96	3.69	2.72	9.36
Malvaceae	89	2.26	21	3.60	1.92	3.36	8.88
Subtotal	1722	89.26	362	69.72	75.70	57.92	203.34
Remaining	748	28.65	263	30.28	24.30	42.08	96.66
Total	2470	117.91	625	100	100	100	300

Table 4. The ten most important várzea families listed in descending order of family importance value (FIV). Values are based on all woody plants with species identifications. The number of individuals (No. Inds.) and the number of species within each family (No. Spp.) are given as counts. Basal area (BA) in m^2. Relative density (Rel. Den.), relative dominance (Rel. Dom.) and relative diversity (Rel. Div.) are given as percentages, where 100 equals 100% (Supplementary Table S1).

Family	No. Inds.	BA (m^2)	No. Spp.	Rel. Den.	Rel. Dom.	Rel. Div.	FIV
Leguminosae	357	20.46	73	12.55	12.55	13.88	38.98
Lecythidaceae	201	19.05	22	7.07	11.69	4.18	22.94
Sapotaceae	201	13.66	38	7.07	8.38	7.22	22.67
Annonaceae	279	8.70	35	9.81	5.34	6.65	21.80
Euphorbiaceae	138	17.05	22	4.85	10.46	4.18	19.50
Malvaceae	134	9.16	24	4.71	5.62	4.56	14.89
Arecaceae	170	7.64	5	5.98	4.69	0.95	11.61
Urticaceae	65	8.21	15	2.28	5.04	2.85	10.18
Myristicaceae	107	7.66	8	3.76	4.70	1.52	9.98
Moraceae	64	4.15	22	2.25	2.55	4.18	8.98
Subtotal	1716	115.75	264	60.32	71.01	50.19	181.51
Remaining	1129	47.26	262	39.68	28.99	49.81	118.49
Total	2845	163.01	526	100	100	100	300

3.4. Species Importance Value Index

Three *Eschweilera* spp. (Lecythidaceae) top the terra firme Importance Value Index (IVI). Of these, *Eschweilera coriacea* was the most important, largely due to the high basal area derived from its large stems and high abundance (Table 5). In várzea, *Hura crepitans* (Euphorbiaceae) was the most important tree species and dominated the basal area, despite its relatively low abundance (Table 6). Palms (Arecaceae) were abundant in both forest types and both *Euterpe precatoria* (TF) and *Astrocaryum jauari* (VZ) were among the most important species. None of the 10 most important species were shared between terra firme and várzea. The IVI for all species is presented in Supplementary Table S2.

Table 5. The ten most important species in lowland terra firme, listed in descending order of Importance Value Index (IVI). Values are based on all woody plants with species identifications. Growth forms (G.F.) observed for each species are given as t = tree, l = liana and p = palm. The number of individuals within each species (No. Inds.) and the number of plots in which each species occurs (Plot occ.) are given as counts. Relative density (Rel. Den.), relative dominance (Rel. Dom.) and relative frequency (Rel. Freq.) are given as percentages, where 100 equals 100% (Supplementary Table S2).

No.	Species	Family	G.F.	No. Inds.	BA (m^2)	Plot occ.	Rel. Den.	Rel. Dom.	Rel. Freq.	IVI
1	*Eschweilera coriacea* (DC.) S.A.Mori	Lecythidaceae	t, l	87	4.13	33	3.63	3.58	1.79	8.99
2	*Eschweilera wachenheimii* (Benoist) Sandwith	Lecythidaceae	t	103	3.11	36	4.29	2.69	1.95	8.94
3	*Eschweilera truncata* A.C.Sm.	Lecythidaceae	t	59	3.20	18	2.46	2.77	0.98	6.21
4	*Euterpe precatoria* Mart.	Arecaceae	p	55	1.07	17	2.29	0.93	0.92	4.14
5	*Eschweilera grandiflora* (Aubl.) Sandwith	Lecythidaceae	t	37	1.80	18	1.54	1.56	0.98	4.08
6	*Osteophloeum platyspermum* (Spruce ex A.DC.) Warb.	Myristicaceae	t	23	2.34	17	0.96	2.03	0.92	3.91
7	*Pouteria guianensis* Aubl.	Sapotaceae	t	30	1.74	20	1.25	1.50	1.09	3.84
8	*Iryanthera hostmannii* (Benth.) Warb.	Myristicaceae	t	36	1.34	21	1.50	1.16	1.14	3.80
9	*Cariniana micrantha* Ducke	Lecythidaceae	t	10	3.27	9	0.42	2.83	0.49	3.73
10	*Brosimum rubescens* Taub.	Moraceae	t	15	2.26	13	0.63	1.95	0.71	3.29
10	Subtotal	-	-	455	24.26	202	18.97	20.99	10.97	50.92
615	Remaining	-	-	1944	91.30	1640	81.03	79.01	89.03	249.08
625	Grand total	-	-	2399	115.56	1842	100	100	100	300

Table 6. The ten most important várzea species, listed in descending order of Importance Value Index (IVI). Values are based on all woody plants with species identifications. Growth forms (G.F.) observed for each species are given as t = tree and p = palm. The number of individuals within each species (No. Inds.) and the number of plots in which each species occurs (Plot occ.) are given as counts. Relative density (Rel. Den.), relative dominance (Rel. Dom.) and relative frequency (Rel. Freq.) are given as percentages, where 100 equals 100% (Supplementary Table S2).

No.	Species	Family	G.F.	No. Inds.	BA (m^2)	Plot occ.	Rel. Den.	Rel. Dom.	Rel. Freq.	IVI
1	*Hura crepitans* L.	Euphorbiaceae	t	14	11.68	9	0.52	7.47	0.50	8.49
2	*Virola surinamensis* (Rol. ex Rottb.) Warb.	Myristicaceae	t	56	5.98	26	2.07	3.83	1.45	7.34
3	*Eschweilera ovalifolia* (DC.) Nied.	Lecythidaceae	t	50	5.75	22	1.84	3.68	1.23	6.75
4	*Astrocaryum jauari* Mart.	Arecaceae	p	59	2.88	11	2.18	1.85	0.61	4.64
5	*Garcinia madruno* (Kunth) Hammel	Clusiaceae	t	57	1.61	20	2.10	1.03	1.12	4.25
6	*Tapura juruana* (Ule) Rizzini	Dichapetalaceae	t	32	2.66	22	1.18	1.70	1.23	4.11
7	*Leonia glycycarpa* Ruiz & Pav.	Violaceae	t	44	1.60	25	1.62	1.02	1.39	4.04
8	*Eschweilera parviflora* (Aubl.) Miers	Lecythidaceae	t	35	2.65	18	1.29	1.70	1.00	3.99
9	*Pouteria glomerata* (Miq.) Radlk.	Sapotaceae	t	39	2.08	19	1.44	1.33	1.06	3.83
10	*Himatanthus sucuuba* (Spruce ex Müll.Arg.) Woodson	Apocynaceae	t	38	2.12	19	1.40	1.36	1.06	3.82
10	Subtotal	-	-	424	39.02	191	15.64	24.96	10.65	51.26
516	Remaining	-	-	2287	117.29	1602	84.36	75.04	89.35	248.74
526	Grand total	-	-	2711	156.31	1793	100	100	100	300

3.5. Community Composition

Overall dissimilarity in species composition was high among plots. Only four between-plot Bray-Curtis dissimilarities were below 60%, all within várzea. The lowest recorded Bray-Curtis dissimilarity between forest types was 79.6% (Supplementary Table S3). No species occurred in all plots of either forest type and only two species occurred in more than half of the terra firme plots: *Eschweilera wachenheimii* (Lecythidaceae; $n = 36$) and *Eschweilera coriacea* (Lecythidaceae; $n = 33$). Despite a lower total species richness in várzea, only *Virola surinamensis* (Myristicaceae) occurred in at least half of the várzea plots ($n = 26$).

We found greater resemblance in species composition among plots within the same forest type than when comparing plots between forest types (*envfit*: $R^2 = 0.59$, $p < 0.001$; PERMANOVA: $R^2 = 0.11$, $F = 11.27$, $p = 0.001$; Figure 4), although there was spatial autocorrelation between plots (Mantel test: $r = 0.19$, $p = 0.001$). Multivariate dispersion of inventory plots indicates that neither várzea nor terra firme plots are more clustered around their respective multivariate means than the other (*betadisper*: $F = 0.30$, N.Perm = 99, $p = 0.57$). Thus, both forest types show a similar variation in species composition among plots.

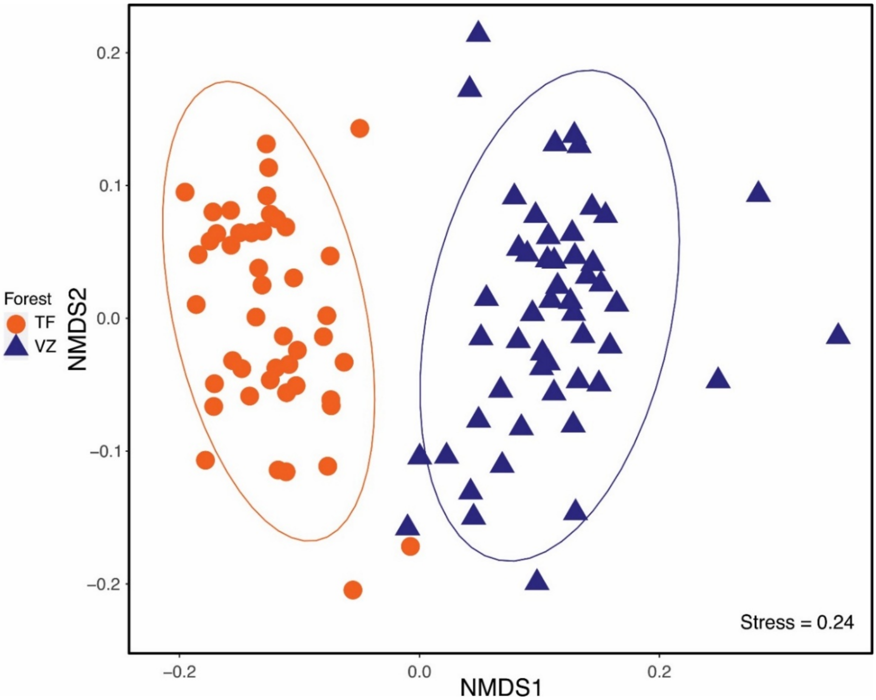

Figure 4. Non-metric multidimensional scaling (NMDS) ordination showing the relative position of inventory plots in terra firme forest (orange circles) and várzea forests (dark blue triangles), along axes NMDS1 and NMDS2. Ellipses represent 95% confidence intervals (CI) around group centroids. Plot positions within ordination space are based on Bray-Curtis dissimilarities. The stress measure indicates similarity of observed distance to ordination distance.

4. Discussion

4.1. Forest Structure

As seen from the high number of late-successional species characteristic of the central Juruá and the different strata that these represent, our inventory is typical of structurally intact and late-successional forests [43–45]. Both the terra firme and várzea forests of the central Juruá had well-stratified canopies featuring emergent trees of up to ca. 50 and 47 m, respectively.

The várzea forest had a greater diversity in growth forms than terra firme, and more multi-stemmed or hollow individuals. This may reflect the differences in disturbance regimes between the two forest types, with higher levels of disturbance in várzea forests driven by the impact of seasonal floods and their proximity to the Juruá River. For example, woody lianas typically occur in disturbed areas, such as secondary forests or forest edges [46,47]. In structurally intact terra firme forests, lianas are likely to become dominant only in treefall gaps [47], whereas with both natural clearings and the river margin, the propensity of edge habitat is considerably larger in structurally intact várzea forests. Similarly, the high number of hollow individuals that we observed in várzea forest was mostly driven by pioneer species typical of disturbed floodplain habitat, such as *Cecropia* spp. [48–50]. Moreover, since palms are associated with highly dynamic forests on weakly structured and nutrient-rich soils [51–53], the higher frequency and size of palms recorded in várzea may further reflect the influence of flooding on substrate properties and forest dynamics.

Both the terra firme and várzea forests had similar stem densities and high proportions of smaller trees (i.e., 10–30 cm dbh). However, trees grew taller in terra firme, whereas BA and degree of branching were significantly higher in várzea. These structural differences between terra firme and várzea woody plants may result from differences in forest dynamics and substrate fertility. High seasonality and substrate fertility in várzea might cause trees to grow quicker or better during favourable times of the year (i.e., dynamic growth in response to the changing environment) [54], thus supporting higher BA but potentially lighter wood density [55]. In contrast, less seasonal variability and lower substrate fertility in terra firme may cause woody plants to grow slower, but more evenly, throughout the year. Slow lateral growth results in more structural matter per unit volume wood, and thus greater stability, supportive of higher stems [56].

Structural and functional differences between forest types interact to determine the amount of standing, living woody biomass across the forest landscape. Therefore, the higher BA and degree of branching in várzea woody plants is potentially counterbalanced by taller terra firme stems, plus previous findings from the same region which show that terra firme trees store more carbon per unit volume than várzea conspecifics [57]. Hence, both várzea and terra firme may produce similar amounts of standing, live woody biomass in the Juruá. This would compare to a case from the southern Amazon where dry season length and storm frequency affected stem density and individual biomass of trees and palms differently across two forest types but resulted in similar forest biomass due to complementary responses in structural variables to these environmental stresses [58].

4.2. Floristic Composition and Diversity

In the Juruá, almost one quarter of all woody plant species (23.6%) occurred in both terra firme and várzea. Our findings thus support previous reports of several shared species among terra firme and seasonally flooded forests [29,59]. However, most of these occurred predominantly in one forest type or as singletons in both forest types. This could indicate that many of the shared species are generally rare within the forest matrix or represent outlier observations of individuals in one of the forest types where they would straddle the extremes of their environmental tolerance limits [60–63]. Thus, we see that differences in environmental stress, e.g., seasonal flooding versus no seasonal flooding, between várzea and terra firme forests limit species distributions and cause the woody plant communities to shift. The great dissimilarity in species composition among várzea forest plots may result from the diversity of microhabitats and successional stages they cover along the hydro-topographic gradient [29,43]. This variability in species composition contributed to a high total species richness. The species rarefactions suggest that the central Juruá várzeas are some of the most species-rich floodplains in the Amazon [24,64].

Amazonian terra firme forests are well-documented to be more species-rich than seasonally flooded forests [17]. This is supported by our study, where terra firme displayed a higher total species richness than the várzea forest. At the Amazon basin-wide scale, the greater diversity in terra firme woody plants is attributed to habitat availability (terra firme comprises ca. 87% of available forest habitat in the Amazon compared to ca. 13% forested floodplain habitat) [3,65], habitat stability [66], a diversity in climatic and edaphic conditions [67–70] and the evolutionary dynamics of land formations, e.g., through processes that undo or induce dispersal barriers and subsequent speciation [71]. At local scales, a higher diversity in terra firme woody plant communities compared to its floodplain counterpart may also be attributed to a greater stability and longer history. Terra firme habitat has been available for colonisation by woody plants for much longer than present várzea habitat. Moreover, even at this local scale, the rate of disturbance in the terra firme is much lower compared to the várzea, where forest habitat is formed and eroded on a dynamic, seasonal basis [43,72]. Given these different drivers of woody plant diversification across seasonally flooded and terra firme forests, it is perhaps not surprising that terra firme and várzea forests in the Juruá showed similar levels of variation in species composition among plots around their respective multivariate means (i.e., similar β-diversities).

4.3. Important Families and Species

In accordance with previous work from central Amazonia, Leguminosae (Fabaceae), Lecythidaceae, Sapotaceae and Myristicaceae were among the most important families in both terra firme and várzea forests [73–75]. For other Amazonian regions, however, these families may be considerably less common. As an example, Lecythidaceae is much less important in terra firme forests of western (e.g., References [76–78]) and eastern Amazonia (e.g., References [79,80]). Our survey further corroborates the importance of Chrysobalanaceae and Moraceae in terra firme forests [73–75] and of Annonaceae and Euphorbiaceae in várzea forests [6,59,79,81]. Additionally, palms constitute an important part of both the Juruá and Amazonian arborescent flora.

A recent study found that six of the ten most common Amazonian arborescent species were palms [82]. In the Juruá, palms contributed 4%–6% of the inventoried individuals and 2%–5% of the total BA in the terra firme and várzea forests, respectively. *Euterpe precatoria*, potentially the most common woody species across the entire Amazon [83], was the most prominent terra firme palm species for the Juruá, where it was twice as common and more widespread than in várzea. *Astrocaryum jauari* was the most important várzea palm species. Overall, however, *Eschweilera* tree species were particularly prominent in the terra firme forest and *Eschweilera coriacea* was the most common tree, both for the Juruá and the Amazon at large [82]. *Hura crepitans* (Euphorbiaceae) was the most important floodplain species. In fact, *Hura crepitans*, as well as *Virola surinamensis* (Myristicaceae), the second most important várzea species in the Juruá, are both scarce in many floodplain areas across the Amazon basin due to logging [84,85]. Their importance in the central Juruá may therefore reflect the protected status of these floodplains [86].

Together, the most conspicuous woody plant species of the Juruá represented the entire terra firme and várzea canopy strata. In terra firme, *Cariniana micrantha* is an emergent tree, *Eschweilera coriacea*, *Eschweilera truncata* and *Euterpe precatoria* are common upper-canopy features, *Brosimum rubescens* occurs mid- to upper-canopy, *Osteophloeum platyspermum* grows mid-canopy and *Eschweilera grandiflora*, *Iryanthera hostmannii* and *Eschweilera wachenheimii* feature in the understorey [87–90]. In várzea, *Hura crepitans* and *Virola surinamensis* are upper-canopy to emergent trees, *Astrocaryum jauari* and *Eschweilera parviflora* grow in the upper canopy, *Tapura juruana*, *Pouteria glomerata*, *Himatanthus sucuuba*, *Pouteria procera* and *Leonia glycycarpa* occur mid-canopy, and *Theobroma cacao* grows in the understorey [91]. Except for *Pouteria glomerata*, a late-secondary forest species, the other characteristic várzea species are late-successional species [91].

5. Conclusions

Rare or sparsely distributed species drive most of the woody plant diversity in both low-lying terra firme forests on paleo-várzea sediments and seasonally flooded várzea forests on the floodplain of the central Juruá River basin. Both terra firme and várzea show high variation in plot-level species composition, demonstrating heterogeneity within forest types, even at small spatial scales. Although species richness was highest in terra firme, the Juruá várzea forest contain more woody species than most inventories have recorded for Amazonian floodplain forests. Given the high species turnover across terra firme and várzea, floodplain forests are clearly an important complement to terra firme woody plant diversity. The high proportion of singleton observations and forest type specialists in the central Juruá highlight the need for further floristic inventories from a wider range of geographically remote areas if we are to discover and properly describe the Amazonian flora. As a step in that direction, this study helps address the patchy botanical records of sparsely distributed Amazonian woody species.

Supplementary Materials: The following are available online at http://www.mdpi.com/1999-4907/11/12/1361/s1, Table S1: Family Importance Value, Table S2: Species Importance Value Index, Table S3: Bray-Curtis Dissimilarity Matrix.

Author Contributions: Conceptualisation and methodology, Y.K.B., J.E.H., C.A.P. and T.H.; investigation, data curation and formal analysis, Y.K.B.; writing—original draft preparation, Y.K.B. and T.H.; writing—review and editing, Y.K.B., J.E.H., C.A.P. and T.H. All authors have read and agreed to the published version of the manuscript.

Funding: Y.K.B. was financed by the Norwegian University of Life Sciences (NMBU) as part of their PhD program in tropical ecology and an internal travel grant from NMBU. J.E.H. was supported by the Research Council of Norway (project no. 288086) and internal funding from Anglia Ruskin University.

Acknowledgments: This publication is part of the Instituto Juruá series (www.institutojurua.org.br). We thank the Secretaria do Estado do Meio Ambiente e Desenvolvimento Sustentável do Amazonas (SEMA—DEMUC) and Instituto Brasileiro do Meio Ambiente e Recursos Naturais Renováveis (IBAMA)/Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio) for authorising the research. We are grateful to the members from the Projeto Médio Juruá team for logistical support and extend special thanks to Andressa Scabin. We thank Michael J.G. Hopkins, Rafael Leandro de Assis and Juliana Schietti with colleagues at the National Institute for Amazonian Research (INPA) for providing logistical assistance and a place to work in Manaus. We thank Paulo Apóstolo Costa Lima Assunção and Alexandro Elias dos Santos, assisted by Lorena M. Rincón, for identifying the species in the field and at INPA. Marcos Viejo Somoano has been of great help with the graphical layout of the figures. Finally, we thank our local field assistants, Associação dos Produtores Rurais de Carauari (ASPROC), Operação Amazônia Nativa (OPAN), and the people of the central Juruá, who, in various ways, assisted us throughout our work.

Conflicts of Interest: The authors declare no conflict of interest. The funders had no role in the design of the study; in the collection, analyses, or interpretation of data; in the writing of the manuscript, or in the decision to publish the results.

Appendix A

Formulas for calculating (a) relative density (Rel. Den.), (b) relative dominance (Rel. Dom.), (c) relative diversity (Rel. Div.) and (d) relative frequency (Rel. Freq.).

$$(\mathrm{a})\ \mathrm{Rel.Den.} = \frac{\text{No. of individuals of a family or species} \times 100}{\text{Total no. of individuals in sample}}$$

$$(\mathrm{b})\ \mathrm{Rel.Dom.} = \frac{\text{Basal area of a family or species} \times 100}{\text{Total basal area in sample}}$$

$$(\mathrm{c})\ \mathrm{Rel.Div.} = \frac{\text{No. of species in a family} \times 100}{\text{Total no. of species}}$$

$$(\mathrm{d})\ \mathrm{Rel.Freq.} = \frac{\text{Sampling units containing a species} \times 100}{\text{Sum of all frequencies}}$$

References

1. Prance, G.T. A comparison of the efficacy of higher taxa and species numbers in the assessment of biodiversity in the neotropics. *Philos. Trans. R. Soc. B Biol. Sci.* **1994**, *345*, 89–99. [CrossRef]
2. Gentry, A.H. Changes in plant community diversity and floristic composition on environmental and geographical gradients. *Ann. Mo. Bot. Gard.* **1988**, *75*, 1–34. [CrossRef]
3. Ter Steege, H.; De Oliveira, S.M.; Pitman, N.; Sabatier, D.; Antonelli, A.; Andino, J.E.G.; Aymard, G.A.; Salomão, R.P. Towards a dynamic list of Amazonian tree species. *Sci. Rep.* **2019**, *9*, 1–5. [CrossRef] [PubMed]
4. Cardoso, D.; Särkinen, T.; Alexander, S.; Amorim, A.M.; Bittrich, V.; Celis, M.; Daly, D.C.; Fiaschi, P.; Funk, V.A.; Giacomin, L.L.; et al. Amazon plant diversity revealed by a taxonomically verified species list. *Proc. Natl. Acad. Sci. USA* **2017**, *114*, 10695–10700. [CrossRef] [PubMed]
5. Feeley, K.J. Are we filling the data void? An assessment of the amount and extent of plant collection records and census data available for tropical South America. *PLoS ONE* **2015**, *10*, e0125629. [CrossRef] [PubMed]
6. Luize, B.G.; Magalhães, J.L.L.; Queiroz, H.; Lopes, M.A.; Venticinque, E.M.; de Moraes Novo, E.M.L.; Silva, T.S.F. The tree species pool of Amazonian wetland forests: Which species can assemble in periodically waterlogged habitats? *PLoS ONE* **2018**, *13*, e0198130. [CrossRef]
7. Hopkins, M.J.G. Are we close to knowing the plant diversity of the Amazon? *An. Acad. Bras. Ciênc.* **2018**, *91*, e20190396. [CrossRef]
8. Hopkins, M.J.G. Modelling the known and unknown plant biodiversity of the Amazon basin. *J. Biogeogr.* **2007**, *34*, 1400–1411. [CrossRef]
9. Wallace, A.R. *A Narrative of Travels on the Amazon and Rio Negro*; Ward, Lock: London, UK, 1853; p. 541.
10. Kalamandeen, M.; Gloor, E.; Mitchard, E.T.A.; Quincey, D.; Ziv, G.; Spracklen, D.; Spracklen, B.; Adami, M.; Aragão, L.; Galbraith, D. Pervasive rise of small-scale deforestation in Amazonia. *Sci. Rep.* **2018**, *8*, 1600. [CrossRef]
11. Aragão, L.E.O.C.; Malhi, Y.; Barbier, N.; Lima, A.; Shimabukuro, Y.; Anderson, L.; Saatchi, S. Interactions between rainfall, deforestation and fires during recent years in the Brazilian Amazonia. *Philos. Trans. R. Soc. B Biol. Sci.* **2008**, *363*, 1779–1785. [CrossRef]
12. Souza, J.C.M.; Kirchhoff, F.T.; Oliveira, B.C.; Ribeiro, J.G.; Sales, M.H. Long-term annual surface water change in the Brazilian Amazon biome: Potential links with deforestation, infrastructure development and climate change. *Water* **2019**, *11*, 566. [CrossRef]
13. de Area Leão Pereira, E.J.; Silveira Ferreira, P.J.; de Santana Ribeiro, L.C.; Sabadini Carvalho, T.; de Barros Pereira, H.B. Policy in Brazil (2016–2019) threaten conservation of the Amazon rainforest. *Environ. Sci. Policy* **2019**, *100*, 8–12. [CrossRef]
14. Esquivel-Muelbert, A.; Baker, T.R.; Dexter, K.G.; Lewis, S.L.; Brienen, R.J.W.; Feldpausch, T.R.; Lloyd, J.; Monteagudo-Mendoza, A.; Arroyo, L.; Álvarez-Dávila, E.; et al. Compositional response of Amazon forests to climate change. *Glob. Chang. Biol.* **2019**, *25*, 39–56. [CrossRef] [PubMed]
15. Costa, M.H.; Coe, M.T.; Guyot, J.L.; Batistella, M.; Artaxo, P.; Nobre, C.; Bustamante, M.; Luizao, F.J. Effects of climatic variability and deforestation on surface water regimes. In *Sea Ice*; American Geophysical Union (AGU): Washington, DC, USA, 2009; pp. 543–553.
16. Hilker, T.; Lyapustin, A.I.; Tucker, C.J.; Hall, F.G.; Myneni, R.B.; Wang, Y.; Bi, J.; De Moura, Y.M.; Sellers, P.J. Vegetation dynamics and rainfall sensitivity of the Amazon. *Proc. Natl. Acad. Sci. USA* **2014**, *111*, 16041–16046. [CrossRef] [PubMed]
17. Wittmann, F.; Marques, M.C.M.; Júnior, G.D.; Budke, J.C.; Piedade, M.T.F.; Wittmann, A.D.O.; Montero, J.C.; De Assis, R.L.; Targhetta, N.; Parolin, P.; et al. The Brazilian freshwater wetscape: Changes in tree community diversity and composition on climatic and geographic gradients. *PLoS ONE* **2017**, *12*, e0175003. [CrossRef]
18. Aleixo, I.; Norris, D.; Hemerik, L.; Barbosa, A.; Prata, E.; Costa, F.; Poorter, L. Amazonian rainforest tree mortality driven by climate and functional traits. *Nat. Clim. Chang.* **2019**, *9*, 384–388. [CrossRef]
19. Aragão, L.E.O.C.; Poulter, B.; Barlow, J.B.; Anderson, L.O.; Malhi, Y.; Saatchi, S.; Phillips, O.L.; Gloor, E. Environmental change and the carbon balance of Amazonian forests. *Biol. Rev.* **2014**, *89*, 913–931. [CrossRef]
20. Sombroek, W. *Amazon Soils, Wageningen*; Netherlands, Centre for Agricultural Publications and Documentation: Wageningen, The Netherlands, 1965.
21. Sombroek, W. Amazon landforms and soils in relation to biological diversity. *Acta Amaz.* **2000**, *30*, 81. [CrossRef]

22. Pires, J.M.; Prance, G.T. The vegetation types of the Brazilian Amazon. In *Key Environments: AMAZONIA*; Prance, G.T., Lovejoy, T.E., Eds.; Pergamon Press: Oxford, UK, 1985; pp. 109–145.
23. Parolin, P.; Ferreira, L.V.; Albernaz, A.L.K.; Almeida, S.S. Tree species distribution in Várzea forests of Brazilian Amazonia. *Folia Geobot. Phytotaxon.* **2004**, *39*, 371–383. [CrossRef]
24. Junk, W.J.; Piedade, M.T.F. An introduction to South American wetland forests: Distribution, definitions and general characterization. In *Forest-Water Interactions*; Springer Science and Business Media LLC: Berlin, Germany, 2010; pp. 3–25.
25. Räsänen, M.E.; Salo, J.S.; Kalliola, R.J. Fluvial perturbance in the western Amazon basin: Regulation by long-term Sub-Andean tectonics. *Science* **1987**, *238*, 1398–1401. [CrossRef]
26. Irion, G. Soil infertility in the Amazonian rain forest. *Naturwissenschaften* **1978**, *65*, 515–519. [CrossRef]
27. Furch, K.; Klinge, H. Chemical relationship between vegetation, soil and water in contrasting inundation areas of Amazonia. In *Mineral Nutrients in Tropical Forest and Savanna Ecosystems*; Proctor, J., Ed.; Blackwell Scientific Publications: Oxford, UK, 1989; pp. 189–204. ISBN 0-632-02559-X.
28. Furch, K.; Junk, W.J. Physiochemical conditions in the floodplains. In *The Central Amazon Floodplain: Ecology of a Pulsing System*; Junk, W.J., Ed.; Springer: Berlin, Germany, 1997; pp. 69–108. ISBN 978-3-642-08214-6.
29. Wittmann, F.; Schongart, J.; Montero, J.C.; Motzer, T.; Junk, W.J.; Piedade, M.T.F.; Queiroz, H.L.; Worbes, M. Tree species composition and diversity gradients in white-water forests across the Amazon basin. *J. Biogeogr.* **2006**, *33*, 1334–1347. [CrossRef]
30. Normand, S.; Vormisto, J.; Svenning, J.; Grández, C.; Balslev, H. Geographical and environmental controls of palm beta diversity in paleo-riverine terrace forests in Amazonian Peru. *Plant Ecol.* **2006**, *186*, 161–176. [CrossRef]
31. Hawes, J.E.; Peres, C.A. Patterns of plant phenology in Amazonian seasonally flooded and unflooded forests. *Biotropica* **2016**, *48*, 465–475. [CrossRef]
32. GADM Database. 2015. Available online: www.gadm.org (accessed on 4 May 2020).
33. *HAGLÖF SWEDEN AB Vertex IV and Transponder T3 Manual January 2007, v.1.0*; Haglöf Sweden AB: Långsele, Sweden, 2007; pp. 1–27.
34. Mori, S.A.; Boom, B.M.; De Carvalino, A.M.; Dos Santos, T.S. Ecological importance of Myrtaceae in an eastern Brazilian wet forest. *Biotropica* **1983**, *15*, 68. [CrossRef]
35. Worbes, M.; Klinge, H.; Revilla, J.D.; Martius, C. On the dynamics, floristic subdivision and geographical distribution of várzea forests in central Amazonia. *J. Veg. Sci.* **1992**, *3*, 553–564. [CrossRef]
36. Kindt, R.; Coe, R. *Tree Diversity Analysis. A Manual and Software for Common Statistical Methods for Ecological and Biodiversity Studies*; World Agroforestry Centre (ICRAF): Nairobi, Kenya, 2005; ISBN 92-9059-179-X.
37. Oksanen, J.; Blanchet, F.G.; Friendly, M.; Kindt, R.; Legendre, P.; McGlinn, D.; Minchin, P.R.; O'Hara, R.B.; Simpson, G.L.; Solymos, P.; et al. *Vegan: Community Ecology Package*; R Package, 2019; Available online: https://CRAN.R-project.org/package=vegan (accessed on 4 May 2020).
38. Anderson, M.J. Distance-based tests for homogeneity of multivariate dispersions. *Biometrics* **2005**, *62*, 245–253. [CrossRef]
39. Anderson, M.J.; Ellingsen, K.E.; McArdle, B.H. Multivariate dispersion as a measure of beta diversity. *Ecol. Lett.* **2006**, *9*, 683–693. [CrossRef]
40. Stier, A.; Geange, S.W.; Hanson, K.M.; Bolker, B.M. Predator density and timing of arrival affect reef fish community assembly. *Ecology* **2013**, *94*, 1057–1068. [CrossRef]
41. O'Neill, M.E.; Mathews, K.L. A weighted least squares approach to Levene's test of homogeneity of variance. *Aust. N. Z. J. Stat.* **2000**, *42*, 81–100. [CrossRef]
42. R Environment R Core Team. *R: A Language and Environment for Statistical Computing*; R Environment R Core Team, 2018; Available online: https://www.r-project.org/ (accessed on 4 May 2020).
43. Wittmann, A.D.O.; Schöngart, J.; Junk, W.J. Phytogeography, species diversity, community structure and dynamics of central Amazonian floodplain forests. In *Forest-Water Interactions*; Springer Science and Business Media LLC: Berlin, Germany, 2010; pp. 61–102.
44. Montgomery, R.A.; Chazdon, R.L. Forest structure, canopy architecture, and light transmittance in tropical wet forests. *Ecology* **2001**, *82*, 2707–2718. [CrossRef]
45. Myster, R.W. The physical structure of forests in the Amazon basin: A review. *Bot. Rev.* **2016**, *82*, 407–427. [CrossRef]

46. Laurance, W.F.; Pérez-Salicrup, D.; Delamônica, P.; Fearnside, P.M.; D'Angelo, S.; Jerozolinski, A.; Pohl, L.; Lovejoy, T.E. Rain forest fragmentation and the structure of Amazonian liana communities. *Ecology* **2001**, *82*, 105–116. [CrossRef]
47. Campbell, M.J.; Magrach, A.; Laurance, S. Liana diversity and the future of tropical forests. In *Sustainable Development and Biodiversity*; Springer Science and Business Media LLC: Berlin, Germany, 2015; Volume 5, pp. 255–274.
48. Gaglioti, A.L.; Aguiar, D.P.P. Cecropia in Flora do Brasil 2020 em construção. Available online: http://floradobrasil.jbrj.gov.br/reflora/floradobrasil/FB24951 (accessed on 4 September 2020).
49. Parolin, P.; Oliveira, A.C.; Piedade, M.T.F.; Wittmann, F.; Junk, W.J. Pioneer trees in Amazonian floodplains: Three key species form monospecific stands in different habitats. *Folia Geobot. Phytotaxon.* **2002**, *37*, 225–238. [CrossRef]
50. Parolin, P. Life history and environment of *Cecropia latiloba* in Amazonian floodplains. *Rev. Biol. Trop.* **2002**, *50*, 531–545.
51. De Castilho, C.V.; Magnusson, W.E.; De Araújo, R.N.O.; Luizão, R.C.; Luizão, F.J.; Lima, A.P.; Higuchi, N. Variation in aboveground tree live biomass in a central Amazonian Forest: Effects of soil and topography. *For. Ecol. Manag.* **2006**, *234*, 85–96. [CrossRef]
52. Emilio, T.; Quesada, C.A.; Costa, F.R.C.; Magnusson, W.E.; Schietti, J.; Feldpausch, T.R.; Brienen, R.J.W.; Baker, T.R.; Chave, J.; Álvarez, E.; et al. Soil physical conditions limit palm and tree basal area in Amazonian forests. *Plant Ecol. Divers.* **2013**, *7*, 215–229. [CrossRef]
53. Nebel, G.; Kvist, L.P.; Vanclay, J.K.; Christensen, H.; Freitas, L.; Ruíz, J. Structure and floristic composition of flood plain forests in the Peruvian Amazon. *For. Ecol. Manag.* **2001**, *150*, 27–57. [CrossRef]
54. Parolin, P. Radial gradients in wood specific gravity in trees of central Amazonian floodplains. *IAWA J.* **2002**, *23*, 449–457. [CrossRef]
55. Muller-Landau, H.C. Interspecific and inter-site variation in wood specific gravity of tropical trees. *Biotropica* **2004**, *36*, 20. [CrossRef]
56. Chave, J.; Coomes, D.; Jansen, S.; Lewis, S.L.; Swenson, N.G.; Zanne, A.E. Towards a worldwide wood economics spectrum. *Ecol. Lett.* **2009**, *12*, 351–366. [CrossRef]
57. Bredin, Y.K.; Peres, C.A.; Haugaasen, T. Forest type affects the capacity of Amazonian tree species to store carbon as woody biomass. *For. Ecol. Manag.* **2020**, *473*, 118297. [CrossRef]
58. Schietti, J.; Martins, D.; Emilio, T.; Souza, P.F.; Levis, C.; Baccaro, F.B.; Pinto, J.L.P.d.V.; Moulatlet, G.M.; Stark, S.C.; Sarmento, K.; et al. Forest structure along a 600 km transect of natural disturbances and seasonality gradients in central-southern Amazonia. *J. Ecol.* **2016**, *104*, 1335–1346. [CrossRef]
59. de Jesus Veiga Carim, M.; Wittmann, F.K.; Piedade, M.T.F.; a Silva Guimarães, J.R.; de Cássia Leôncio Tostes, L. Composition, diversity, and structure of tidal "Várzea" and "Igapó" floodplain forests in eastern Amazonia, Brazil. *Braz. J. Bot.* **2016**, *40*, 115–124. [CrossRef]
60. Parolin, P.; De Simone, O.; Haase, K.; Waldhoff, D.; Rottenberger, S.; Kuhn, U.; Kesselmeier, J.; Kleiss, B.; Schmidt, W.; Pledade, M.T.F.; et al. Central Amazonian floodplain forests: Tree adaptations in a pulsing system. *Bot. Rev.* **2004**, *70*, 357–380. [CrossRef]
61. Junk, W.J.; Piedade, M.T.F.; Schöngart, J.; Wittmann, F.; Parolin, P. (Eds.) Part II Ecological and ecophysiological aspects of Amazonian floodplain forests. In *Amazonian Floodplain Forests Ecophysiology, Biodiversity and Sustainable Management*; Springer: Berlin, Germany, 2010; pp. 105–313. ISBN 978-90-481-8724-9.
62. Parolin, P. Submerged in darkness: Adaptations to prolonged submergence by woody species of the Amazonian floodplains. *Ann. Bot.* **2008**, *103*, 359–376. [CrossRef]
63. Parolin, P. Morphological and physiological adjustments to waterlogging and drought in seedlings of Amazonian floodplain trees. *Oecologia* **2001**, *128*, 326–335. [CrossRef]
64. Wittmann, F.; Anhuf, D.; Funk, W.J. Tree species distribution and community structure of central Amazonian várzea forests by remote-sensing techniques. *J. Trop. Ecol.* **2002**, *18*, 805–820. [CrossRef]
65. Hess, L. Dual-season mapping of wetland inundation and vegetation for the central Amazon basin. *Remote Sens. Environ.* **2003**, *87*, 404–428. [CrossRef]
66. Ter Steege, H. Contribution of current and historical processes to patterns of tree diversity and composition in the Amazon. In *Amazonia: Landscape and Species Evolution. A Look into the Past*; Hoorn, C., Wesselingh, F.P., Eds.; Wiley-Blackwell: Hoboken, NJ, USA, 2010; ISBN 9781444306408.

67. Quesada, C.A.; Lloyd, J.; Schwarz, M.; Patiño, S.; Baker, T.R.; Czimczik, C.; Fyllas, N.M.; Martinelli, L.; Nardoto, G.B.; Schmerler, J.; et al. Variations in chemical and physical properties of Amazon forest soils in relation to their genesis. *Biogeosciences* **2010**, *7*, 1515–1541. [CrossRef]
68. Zuquim, G.; Costa, F.R.C.; Tuomisto, H.; Moulatlet, G.M.; Figueiredo, F.O.G. The importance of soils in predicting the future of plant habitat suitability in a tropical forest. *Plant Soil* **2019**, *450*, 151–170. [CrossRef]
69. Ter Steege, H.; Pitman, N.C.A.; Phillips, O.L.; Chave, J.; Sabatier, D.; Duque, A.; Molino, J.-F.; Prévost, M.-F.; Spichiger, R.; Castellanos, H.; et al. Continental-scale patterns of canopy tree composition and function across Amazonia. *Nat. Cell Biol.* **2006**, *443*, 444–447. [CrossRef]
70. Quesada, C.A.; Phillips, O.L.; Schwarz, M.; Czimczik, C.I.; Baker, T.R.; Patiño, S.; Fyllas, N.M.; Hodnett, M.G.; Herrera, R.; Almeida, S.; et al. Basin-wide variations in Amazon forest structure and function are mediated by both soils and climate. *Biogeosciences* **2012**, *9*, 2203–2246. [CrossRef]
71. Ruokolainen, K.; Moulatlet, G.M.; Zuquim, G.; Hoorn, C.; Tuomisto, H. Geologically recent rearrangements in central Amazonian river network and their importance for the riverine barrier hypothesis. *Front. Biogeogr.* **2019**, *11*, e45046. [CrossRef]
72. Wittmann, F.; Junk, W.J.; Piedade, M.T. The várzea forests in Amazonia: Flooding and the highly dynamic geomorphology interact with natural forest succession. *For. Ecol. Manag.* **2004**, *196*, 199–212. [CrossRef]
73. Haugaasen, T.; Peres, C.A. Floristic, edaphic and structural characteristics of flooded and unflooded forests in the lower Rio Purús region of central Amazonia, Brazil. *Acta Amaz.* **2006**, *36*, 25–35. [CrossRef]
74. Prance, G.T.; Rodrigues, W.A.; Da Silva, M.F. Inventário florestal de um hectare de mata de terra firme km 30 da Estrada Manaus-Itacoatiara. *Acta Amaz.* **1976**, *6*, 9–35. [CrossRef]
75. Lima Filho, D.A.; Matos, F.D.A.; Amaral, L.; Revilla, J.D.; Coelho, L.S.; Ramos, J.F.; Santos, J.L. Inventário florístico de floresta ombrófila densa de terra firme, na região do Rio Urucu-Amazonas, Brasil. *Acta Amaz.* **2001**, *31*, 565. [CrossRef]
76. Balslev, H.; Luteyn, J.L.; Øllgaard, B.; Holm-Nielsen, L.B. Composition and structure of adjacent unflooded and floodplain forest in Amazonian Ecuador. *Opera Bot.* **1987**, *92*, 37–57.
77. Boom, B.M. A forest inventory in Amazonian Bolivia. *Biotropica* **1986**, *18*, 287. [CrossRef]
78. Faber-Langendoen, N.; Gentry, A.H. The structure and diversity of rain forests at Bajo Calima, Choco region, western Colombia. *Biotropica* **1991**, *23*, 2–11. [CrossRef]
79. Campbell, D.G.; Daly, D.C.; Prance, G.T.; Maciel, U.N. Quantitative ecological inventory of terra firme and varzea tropical forest on the Rio Xingu, Brazilian Amazon. *Brittonia* **1986**, *38*, 369–393. [CrossRef]
80. Almeida, S.S.; Lisboa, P.L.B.; Silva, A.S.L. Diversidade florística de uma comunidade arbórea na estação cientifíca 'Ferreira Penna', em Caxiuanã (Pará). *Bol. Mus. Para. Emílio Goeldi Sér. Bot.* **1993**, *9*, 93–128.
81. De Assis, R.; Wittmann, A.D.O.; Bredin, Y.K.; Schöngart, J.; Quesada, C.A.N.; Piedade, M.T.F.; Haugaasen, T. Above-ground woody biomass distribution in Amazonian floodplain forests: Effects of hydroperiod and substrate properties. *For. Ecol. Manag.* **2019**, *432*, 365–375. [CrossRef]
82. ter Steege, H.; Prado, P.I.; Lima, R.A.F.d.; Pos, E.; de Souza Coelho, L.; de Andrade Lima Filho, D.; Salomão, R.P.; Amaral, I.L.; de Almeida Matos, F.D.; Castilho, C.V.; et al. Biased-corrected richness estimates for the Amazonian tree flora. *Sci. Rep.* **2020**, *10*, 1–13. [CrossRef]
83. Peacock, J.; Cerón, C.E.; Aragão, L.E.O.C.; Réjou-Méchain, M.; Levis, C.; van der Hout, P.; van der Meer, P.J.; de Oliveira, E.A.; Huamantupa-Chuquimaco, I.; Laurance, S.G.W.; et al. Hyperdominance in Amazonian forest carbon cycling. *Nat. Commun.* **2015**, *6*, 6857. [CrossRef]
84. Albernaz, A.K.M.; Ayres, J.M. Selective logging along the middle Solimoes River. *Adv. Econ. Bot.* **1999**, *13*, 135–151.
85. Marinho, T.A.D.S.; Piedade, M.T.F.; Wittmann, A.D.O. Distribution and population structure of four central Amazonian high-várzea timber species. *Wetl. Ecol. Manag.* **2010**, *18*, 665–677. [CrossRef]
86. Mesquita de Azevedo, L.A.; da Silva Cruz, F.A.; Dias, A.; Batista, G.; Jeanne, G.d.S.; de Amaral Carvalho, J.; Kasecker, T.; Santiago, H.C.; Lederman, M.R.; Bendezú Estupiñán, G.M.; et al. *Plano de gestão da reserva de desenvolvimento sustentável de Uacari. Management Plan, 222*; Governo do estado; Secretária de estado do meio ambiente e desenvolvimento sustentável; Centro estadual de unidades de conservação: Amazonas, Carauari, Brazil, 2010.
87. Menores, A.; Grande, R.; Reserva, N. Myristicaceae. In *Flora da Reserva Ducke: Guia de identificação das plantas vasculares de uma floresta de terra-firme na Amazônia central*; Ribeiro, J.E.L.d.S., Hopkins, M.J.C., Virentini, A., Suthers, C.A., Costa, M.A.d.S., de Brito, J.M., de Souza, M.A.D., Martins, H.P., Lohmann, L.G., Assuncão, P.A.C.L., et al., Eds.; INPA: Manaus, Brazil, 1999; pp. 136–145.

88. Mundo, V. Lecythidaceae. In *Flora da Reserva Ducke: Guia de identificação das plantas vasculares de uma floresta de terra-firme na Amazônia central*; Ribeiro, J.E.L.d.S., Hopkins, M.J.C., Virentini, A., Suthers, C.A., Costa, M.A.d.S., de Brito, J.M., de Souza, M.A.D., Martins, H.P., Lohmann, L.G., Assuncão, P.A.C.L., et al., Eds.; INPA: Manaus, Brazil, 1999; pp. 274–287. ISBN 13 9788521100119.
89. Puig, H.; Fabre, A. Survival and growth of *Iryanthera hostmannii* seedlings and juveniles in the tropical rainforest of French Guyana. *J. Trop. Ecol.* **1997**, *13*, 139–143. [CrossRef]
90. Marimon, B.S.; Felfili, J.M.; Haridasan, M. Studies in monodominant forests in eastern Mato Grosso, Brazil: I. A forest of *Brosimum rubescens* Taub. *Edinb. J. Bot.* **2001**, *58*, 123–137. [CrossRef]
91. Wittmann, F.; Schöngart, J.; De Brito, J.M.; de Oliveira Wittmann, A.; Fernandez Piedade, M.T.; Parolin, P.; Junk, W.J.W.J.; Guillaumet, J.-L.J.L. *Manual of Trees from Central Amazonian Várzea Floodplains*; Cohn-Haft, M., Kossmann Ferraz, I.D., Eds.; Editora INPA: Manaus, Brazil, 2010; ISBN 978-85-211-0067-6.

Paper II

Target journal: Soil Biology and Biochemistry

Above- and below-ground biodiversity responses to the prolonged flood pulse in central-western Amazonia, Brazil.

Yennie K. Bredin[1§*], Laura L. Hess[2], Andressa B. Scabin[3], Micah Dunthorn[4,5,6], Torbjørn Haugaasen[1], Carlos A. Peres[3,7], Henrik R. Nilsson[8], Alexandre Antonelli[8,9,10], Camila D. Ritter[5,11§*]

[1]Faculty of Environmental Sciences and Natural Resource Management, Norwegian University of Life Sciences, Ås, Norway.

[2] Earth Research Institute, University of California Santa Barbara, Santa Barbara, United States of America

[3]Instituto Juruá, Manaus, AM, Brazil

[4]Natural History Museum, University of Oslo, Oslo, Norway.

[5]Eukaryotic Microbiology, University of Duisburg-Essen, Essen, Germany.

[6]Centre for Water and Environmental Research (ZWU), University of Duisburg-Essen, Essen, Germany.

[7] School of Environmental Sciences, University of East Anglia, Norwich NR4 7TJ, Norwich, United Kingdom.

[8]Gothenburg Global Biodiversity Centre, Department of Biological and Environmental Sciences, University of Gothenburg, Gothenburg, Sweden

[9]Department of Plant Sciences, University of Oxford, Oxford, United Kingdom

[10]Royal Botanic Gardens, Kew, Richmond, United Kingdom

[11]Grupo Integrado de Aquicultura e Estudos Ambientais, Departamento de Zootecnia, Universidade Federal do Paraná, Rua dos Funcionários, 1540, Juvevê, 80035-050 Curitiba, PR, Brazil.

*Corresponding authors: Yennie K. Bredin, yennie.bredin@nmbu.no; Camila D. Ritter, kmicaduarte@gmail.com.

[§]Both authors have contributed equally to this work.

Abstract

Amazonia encompasses forests that grow in areas that are periodically inundated by overflowing rivers. The inundation depth and duration vary according to the slope of the terrain, creating a flooding gradient. This gradient directly affects the biota, but the effect on soil organisms remains elusive. Here, we use DNA metabarcoding to estimate prokaryote and eukaryote diversity from soil and litter samples in a seasonally flooded forest and its adjacent unflooded forest in central-western Amazonia using 16S and 18S gene sequences, respectively. We characterize the below-ground diversity and community composition based on Amplicon Sequence Variants (ASVs) along the flooding gradient. We test for the relationship of soil biota with the flooding gradient, soil properties and above-ground woody plant diversity. The flooding gradient did not explain below-ground biodiversity. Nor was the below-ground diversity explained by the above-ground woody plant diversity. However, we found taxonomic groups not previously reported in Amazonian seasonally flooded forests and the flooding gradient and woody plant diversity did, in part, explain the community composition of soil bacteria. Although the effects of the flooding gradient, soil properties and above-ground woody plant diversity is hard to quantify, our results thus indicate that flood stress could influence below-ground bacterial community composition.

Keywords: Amazonia; Below-ground biodiversity; Juruá; Metabarcoding; Seasonally flooded forests; Flooding gradient.

1. Introduction

Amazonia comprises the largest continuous tropical rainforest in the world. Accounting for only 3.6% of the terrestrial global surface, Amazonia harbours 10% of the world's known biodiversity (Maretti, 2014) and potentially hosts the largest Linnaean biodiversity knowledge deficit on Earth (Moura and Jetz, 2021). Amazonia is heterogeneous and encompasses several distinct environments. These include tropical rainforests known as terra firme, non-forested areas, such as the edaphic open areas associated with white sand soils, and seasonally flooded forests (Myster, 2016). Seasonally flooded forests grow in areas that are periodically inundated by overflowing rivers, lakes and perennial streams (Prance, 1996). These forests are characterized by low taxonomic diversity compared to terra firme forests (Haugaasen and Peres, 2006; Myster, 2016; ter Steege and Hammond, 2001). However, they have a characteristic fauna and flora often restricted to these environments (Myster, 2016; Ramalho et al., 2016). At least 9% of the Amazon basin is formed by seasonally or permanently flooded forests (Hess et al., 2015), which are crucial for the maintenance of biodiversity and climatic dynamics in the region (Castello and Macedo, 2016).

Two determinants are decisive for the extent of periodically flooded forests in Amazonia. The first is the uneven annual distribution of rainfall. In most parts of Amazonia, the rainy season is followed by a drier period lasting several months, but this is not synchronous across the basin. The second is the topography of the Amazon basin and its low-lying floodplains. Combined, these factors lead to an annual rise in fluvial discharge which causes an enormous flood pulse (Junk, 1989; Kubitzki, 1990) and gives rise to an aquatic and a terrestrial phase in the flooded areas. The inundation depth and duration of the flood waters vary according to the slope of the terrain and the volume of the rivers that flood the landscape (Assis et al., 2015; Wittmann et al., 2010). This creates a gradient in flood depth and duration from low-lying areas flood to greater depths for longer periods of time to areas higher up in the terrain that flood for shorter periods. This gradient directly affects the biota, generating thresholds for species establishment (Petit and Hampe, 2006). Additionally, the physical and chemical properties of the waters also affect the distribution of biota in inundated areas (Prance, 1979).

In the Amazon basin, seasonally flooded forests can be classified into two major types according to the hydro-chemical characteristics of the rivers that flood them (Assis et al., 2015; Haugaasen and Peres, 2006; Myster, 2016; Prance, 1979). Whereas eutrophic várzea forests are flooded by nutrient-rich white-water rivers originating in the Andes, oligotrophic igapó forests are inundated by nutrient poor, black- or clear-water rivers (Ríos-Villamizar et al., 2020). Thus, fluvial geochemistry determines the physical properties of substrate, such as moisture retention and hydraulic conductivity, accumulation of organic matter, nutrient availability and soil biota (Parolin et al., 2004). It has been demonstrated that changes in above-ground species richness and composition in seasonally flooded forests can occur due to the physicochemical characteristics of the water (Myster, 2016) and/or flood depth (Julião et al., 2018). Few studies have evaluated this difference in soil biota (Ritter et al., 2019b), and to our knowledge no study has yet examined the influence of the flooding gradient on seasonally flooded forest soil biota.

Soil biota represent a large reservoir of terrestrial biodiversity and provide fundamental ecosystem services that are key to the functionality of terrestrial ecosystems (Bardgett and Van Der Putten, 2014; Pereira et al., 2018; Pietramellara et al., 2002). For instance, larger soil invertebrates are responsible for processing large amounts of detritus and make it available to other organisms (García-Palacios et al., 2013; Hättenschwiler and Gasser, 2005). Similarly, micro-organisms are essential for nutrient cycling (Delgado-Baquerizo et al., 2020), and ectomycorrhizal fungi underlie ecosystem processes such as soil carbon cycling (Johnson et al., 2016). Yet, soil biodiversity remains elusive and has been neglected in many global biodiversity assessments and policies (Cameron et al., 2019; Ritter et al., 2017). This omission is undoubtedly related to the scarcity of comprehensive information on soil biodiversity, especially in megadiverse and remote tropical environments, such as Amazonia. Fortunately, molecular approaches, including high throughput sequencing (HTS), such as metabarcoding (Creer et al., 2016), are now able to address many previous obstacles to understanding the diversity and composition of soil communities (Cameron et al., 2019; Ritter et al., 2019b; Tedersoo et al., 2014).

In this study we use a metabarcoding approach to characterize the soil biodiversity along the flooding gradient of an Amazonian várzea landscape. More specifically, we investigate the diversity and composition of soil communities across three flood-levels and explore if, and how, soil biota changes along the flooding gradient. In addition, by comparing the soil communities to the above-ground woody plant community, we examine the degree to which the above- and below-ground biodiversity are congruent. The results are discussed in relation to other studies and interpreted in light of differences experienced by seasonal flooding, soil characteristics and above-ground woody plant diversity. Finally, we draw some general implications to the conservation of Amazonian biota.

2. Materials and Methods

2.1. Study area: We conducted the study in the Uacari Sustainable Development Reserve (RDS Uacari) and nearby forests along the central reaches of the Juruá River, western Brazilian Amazonia (Fig. 1). The climate of the region is hot and humid with a mean annual temperature of ~27°C, average annual rainfall of ~3,679 mm, and a well-defined rainy season from December until May (Hawes and Peres, 2016). We sampled above-ground woody plant communities and below-ground microbial communities at three different flood levels in várzea (VZ) and adjacent upland forest (i.e. terra firme, TF) that does not flood on a seasonal basis. This "unflooded" forest is growing on Pleistocene floodplain sediments (i.e., paleo-várzea sediments; Assis et al., 2015) abandoned by the meandering Juruá River and at higher elevations than the river's maximum flood level. The várzea communities were sampled during the 2016 and 2017 dry seasons and the terra firme communities were sampled in the 2017 wet and dry seasons.

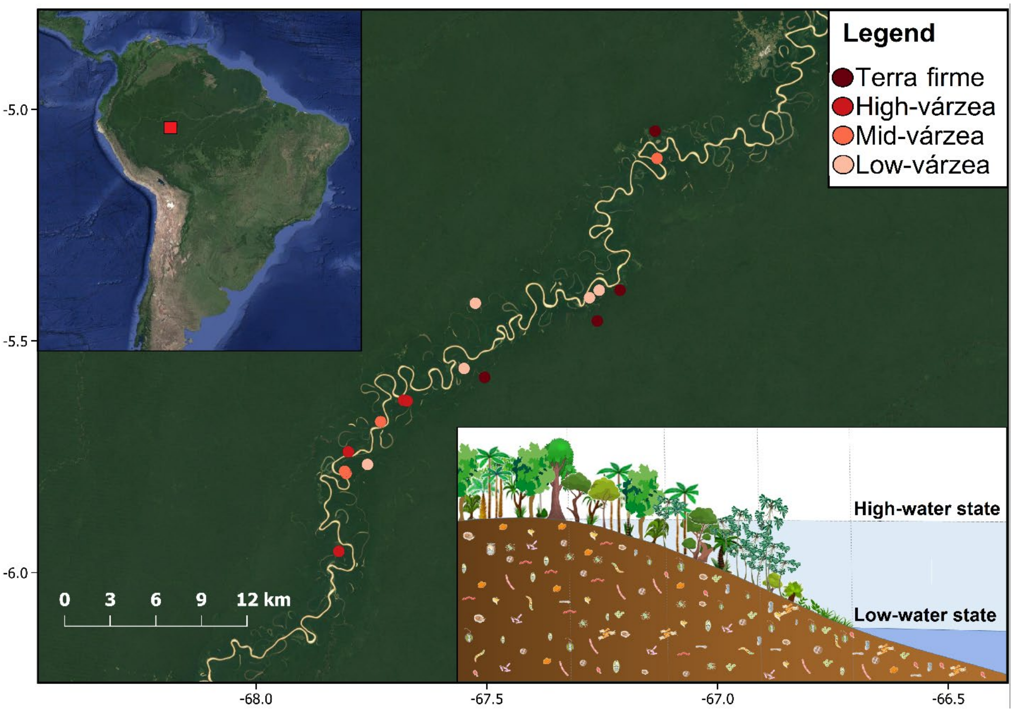

Fig. 1. Sampling localities along the central Juruá River (main map) in the central-western Brazilian Amazon (upper left inset). The lower right inset shows a schematic cross-section of flood levels in the várzea forest, with low- and high-water states separated by the dotted vertical lines. Low-várzea is low-lying and subject to the longest flooding periods (5-12 mo/yr); mid-várzea is subject to intermediate periods of flooding (2-4 mo/yr); and high-várzea is located higher up in the terrain and subject to the shortest flooding periods (0-1 mo/yr). Terra firme forests are beyond the maximum flood levels of rivers and perennial streams.

2.2. Determination of the hydro-topographic gradient: To position the plots along the hydro-topographic gradient, we used inundation period mapped with multi-date ALOS-1 PALSAR satellite imagery (Fine-beam mode, resampled to 30 m) freely available from the Alaska Satellite Facility Distributed Active Archive Center (asf.alaska.edu). Water levels at the Porto Gavião gauge on the Juruá River (66.9W, 4.88S) were retrieved from Brazil's Agência Nacional de Águas (ANA; http://www.snirh.gov.br/hidroweb/serieshistoricas) for each of the 28 PALSAR imaging dates between 2007 and 2011 (9-10 dates for each of 3 PALSAR swaths covering the forest plots). The average number of months inundated per year were calculated over the 47-year Gavião river level record (1972-2018). Due to small-scale variability in flood duration even at the 0.1 ha scale, we defined the flooding gradient by approximating the average number of months each plot was flooded annually. Thus, plots were grouped into the following four flood levels: (1) terra firme = not seasonally flooded (n = 6); (2) high-várzea = 0-1 mo/yr, maximum high-water levels < 1.5 m (n = 6); (3) mid-várzea = 2-4 mo/yr, maximum high-water levels = 1-2 m (n = 6); and (4) low-várzea = 5-12 mo/yr, maximum high-water levels ≥ 2 m (n = 4). Flood depth within each plot was determined by measuring the height of visible watermarks left on tree trunks within each plot after the most recent inundation peak. These measurements were made with a measuring tape to the nearest mm.

2.3. Above-ground woody plant diversity: We used 0.1 ha floristic plots (100 m x 10 m) placed perpendicular to the main river channel to minimize variability in flood depth and duration within plots. We inventoried woody plant diversity as described in Bredin et al. (2020). Briefly, within each floristic plot, all trees, hemiepiphytes, and palms ≥10cm diameter at breast height (dbh) – as well as all high-climbing woody lianas ≥ 5 cm dbh – were measured and identified. Individuals that could not be determined to species level were sorted to morpho-species or, where applicable, higher taxonomic levels. For the following analyses we only retained floristic data from plots where we also obtained information about substrate biota (n = 18).

2.4. Below-ground microbial diversity: To allow for comparisons with other studies of below-ground biodiversity, we used the sampling strategy described in Tedersoo et al. (2014) and Ritter et al. (2019b). Briefly, we superimposed 22 circular plots with a 28 m radius over the floristic plots by matching exactly the midpoints of the circular substrate plot with those of the rectangular floristic plots. Within each circular plot, we randomly selected 20 trees and collected litter and soil samples at the opposite sides of each stem. We first took a litter sample at every sampling point. After removing the leaf litter, we used a soil auger (2.5 cm in diameter) to collect the top 5 cm of the soil. In total, we collected litter and soil at 40 points per plot. The samples were then mixed to provide one composite litter sample and one composite soil sample per plot. For each plot, soil samples were divided into two parts. The first part was sun-dried and transported to the EMBRAPA laboratory in Manaus (Brazil) where physicochemical analyses were performed following standardized procedures (Donagema et al., 2011; Ritter et al., 2018). The second part of the soil samples, as well as the litter samples, were dried with sterilized white silica gel 1–4 mm and transported to the University of Gothenburg, Sweden, for DNA extraction.

2.5. DNA extraction and sequencing: For total DNA extraction, we used the PowerMax® Soil DNA Isolation Kit (MO BIO Laboratories, USA) according to the manufacturer's instructions. We used 10 g (dry weight) from all soil samples and 15 ml of the litter samples (corresponding to 3–10 g of dry weight litter, depending on texture and composition). We checked DNA extraction quality and concentration in a Qubit 30® fluorimeter (Invitrogen, Sweden). The soil and litter samples from which DNA was successfully extracted were sent to Aimethods (Germany) for amplification and sequencing. We targeted prokaryotes with the V3-V4 region (~460 bases) of the 16S rDNA gene using the forward primer (5'-CCTACGGGN GGCWGCAG-3') and the reverse primer (5'-GACTACH VGGGTATCTAATCC-3') from Klindworth et al. (2013). Eukaryotes were targeted with the V7 region of the 18S rDNA gene using the forward and reverse primers (5'-TTTGTCTGSTTAATTSCG-3') and (5'-TCACAGACCTGTTATTGC-3') designed by Guardiola et al. (2015) to yield 100–110 bases long fragments. The 16S rDNA fragment was sequenced with the Illumina MiSeq 2×300 platform, and the 18S rDNA fragment with Illumina Microarray 2×150. We sequenced negative controls in all steps: three for the extraction, two for the amplification, and two for the index ligation.

2.6. Sequence analyses and taxonomic assessment: We used the Cutadapt package (Martin, 2011) in Python v.3.3 (Van Rossum and Drake, 2009) to remove primers. We then used the DADA2 package (Callahan et al., 2016) in R v. 4.0.2 (R Core Team, 2020) to quality filter reads, merge sequences, remove chimeras, and to infer amplicon sequence variants (ASVs). We excluded reads with ambiguous bases (maxN=0). Based on the quality scores of the forward and reverse sequences, each read was required to have <3 or <5 errors, respectively (maxEE=c (3,5), truncQ=2). Therefore, ASVs were inferred for forward and reverse reads for each sample using the run-specific error rates. To assemble paired-end reads, we considered a minimum of 12 base pairs of overlap and excluded reads with mismatches in the overlapping region. Chimeras were removed using the consensus method of "removeBimeraDenovo" implemented in DADA2. We removed ASVs present in negative controls in a proportion larger than 40% of the reads for 18S and all ASVs present in negative control for 16S. We used the SILVAngs 132.1 reference database (Quast et al., 2012) for assessment of the taxonomic composition of the ASVs for both markers. The ASV reads by sample and taxonomic affiliation are provided in the Appendix 1 (for 16S) and Appendix 2 (for 18S). Additionally, we identified the functional guild for the ASVs assigned to the fungal kingdom using the FungalTraits database (Polme et al., 2020).

2.7. *Statistical analysis*: We conducted all analyses in R using RStudio (2015). We used the tidyverse package v. 1.3.0 (Wickham, 2017) for data curation and ggplot2 v. 3.3.2 (Wickham, 2016), ggfortify v. 0.4.11 (Tang et al., 2016), gridExtra v. 2.3 (Auguie and Antonov, 2016), and ggpubr v. 0.4.0 (Kassambara and Kassambara, 2020) for data visualisation (scripts in Appendix 3).

2.7.1. Soil properties – To compare our results with other areas, we included the soil property data from terra firme and várzea in Benjamin Constant (far western Brazilian Amazonia) and Caxiuanã (far eastern Amazonia), available in Ritter et al. (2018), in our data analyses (Appendix 4 Table A1). We first normalized all soil variables to zero mean and unit variance using the "scale'" function of vegan v. 2.4-3 (Oksanen et al., 2010). We then performed a principal component analysis (PCA) to reduce the number of soil property variables for subsequent analyses and visualise soil physicochemical properties in relation to forest type and flood level (i.e. terra firme, high-várzea, mid-várzea, low-várzea, or várzea where information on placement along the flooding gradient was absent).

2.7.2. Alpha diversity – As the richness estimates could be biased by rare ASVs (Haegeman et al., 2013), we calculated ASV Fisher's alpha diversity (i.e., the relationship between the number of ASVs in any given plot and the number of reads of each ASV) using the phyloseq R package v.1.34.0 (McMurdie and Holmes, 2013) separately for the prokaryote (16S) and eukaryote (18S) datasets. For the plant communities we used an abundance species matrix. We calculated the metrics within each plot and compared visually the non-normalized Fisher's alpha diversity indices of the below-ground biota and above-ground plant communities. We analysed soil and litter Fisher's alpha diversity as a function of flood level (modelled as a continuous variable represented by the measured floodwater marks on trees, with terra firme being zero, and categorically according to forest type, i.e. flood level), soil properties (represented by PC1 of the soil PCA), type of sample (litter or soil), and above-ground Fisher's alpha diversity for woody plants. We normalized all the Fisher's alpha diversities to zero mean and unit variance using the "scale'" function in vegan. Thus, we defined a set of models to explain below-ground alpha diversity. The final model set included models with flood level, inundation depth of the last flood, PC1 from the soil properties PCA, type of sample (litter or soil) and woody plant Fisher's alpha diversity as predictor variables, and additional models with interaction terms among the flood levels and sample types with woody plant Fisher's alpha diversity and soil PC1. The final model set also included a constant, intercept-only model, comprising a total of nine models for each dependent variable (Table 1).

Models were selected using an information theory approach based on AIC (Akaike, 1974) and corrected AICs (AICc) for small sample sizes (Burnham and Anderson, 2002). Models with dAIC ≤ 2 were considered equally plausible, and we used the normalized model weight (wi) to contrast the best model to the constant (no-effect) model. We used generalized linear models (Crawley, 2007) with Gaussian error distributions after checking for the distributions of residuals. The GLM analyses were performed using the vegan package, and model selection was carried out using the bbmle package v.1.0.20 (Bolker and Bolker, 2017).

2.7.3. Beta diversity – We constructed two-dimensional non-metric multidimensional scaling (NMDS) ordinations of the abundance (reads) matrices of prokaryotes (16S) and eukaryotes (18S). We first transformed read counts using the 'varianceStabilizingTransformation' function in DESeq2 v.1.30.1 (Love et al., 2014) as suggested by McMurdie & Holmes (2013). This transformation normalizes the count data with respect to sample size (number of reads in each sample) and variances, based on fitted dispersion-mean relationships (Love et al., 2014). We then used the 'metaMDS' function and Bray-Curtis distances in the vegan package to assess community dissimilarity among all samples in the NMDS. We used the 'envfit' method in vegan to fit flood levels and sample types onto the NMDS ordination as a measure of the correlation among these factors with the NMDS axes. Additionally, we constructed two-dimensional non-metric multidimensional scaling (NMDS) ordinations based on the abundance data of the woody plants.

3. Results

We were able to extract, amplify, and sequence DNA for both prokaryotes (16S) and eukaryotes (18S) in 13 soil samples, 17 litter samples for prokaryotes (16S), and 16 litter samples for eukaryotes (18S). We obtained a total of 787,834 reads and 10,213 ASVs for the prokaryotes (16S). After removing the negative controls, we kept 757,827 reads and 9,337 ASVs. For the eukaryotes (18S), we obtained 616,237 reads belonging to 2,267 ASVs and we kept 572,953 reads belonging to 2,004 ASVs after removing the negative controls. See Appendix 4Table A2 for the number of reads and ASV richness for each plot, and Appendix 5 and 6 for krona charts of 16S and 18S taxonomic composition, respectively. The raw sequences are deposited in Genbank under the Bioproject PRJNA723037, BioSample SAMN18800640: Jurua (TaxID: 410658), accession SRA numbers SRR14286278 - SRR14286277.

3.1. *Soil properties:* The principal component analysis showed that edaphic properties varied between terra firme and várzea plots and that flood depth or duration had no apparent effect on várzea soil physicochemical composition (Fig. 2; Appendix 4 Table A3). Hence, várzea soils from Juruá largely overlapped (Fig. 2). Várzea soils were dominated by clay and silt, whereas terra firme soils were sandier (Fig 2). Terra firme soils were less fertile than várzea soils, with lower concentrations of important nutrients, such as potassium (K), calcium (Ca), and magnesium (Mg) (Fig 2). Compared with the terra firme and várzea soils from Benjamin Constant (far western Brazilian Amazonia) and Caxiuanã (far eastern Brazilian Amazonia), the Juruá várzea is characterized by more exchangeable bases and clay, and less phosphorous (P). The Juruá terra firme soils are placed between the Benjamin Constant and Caxiuanã terra firme soils (Fig. 2).

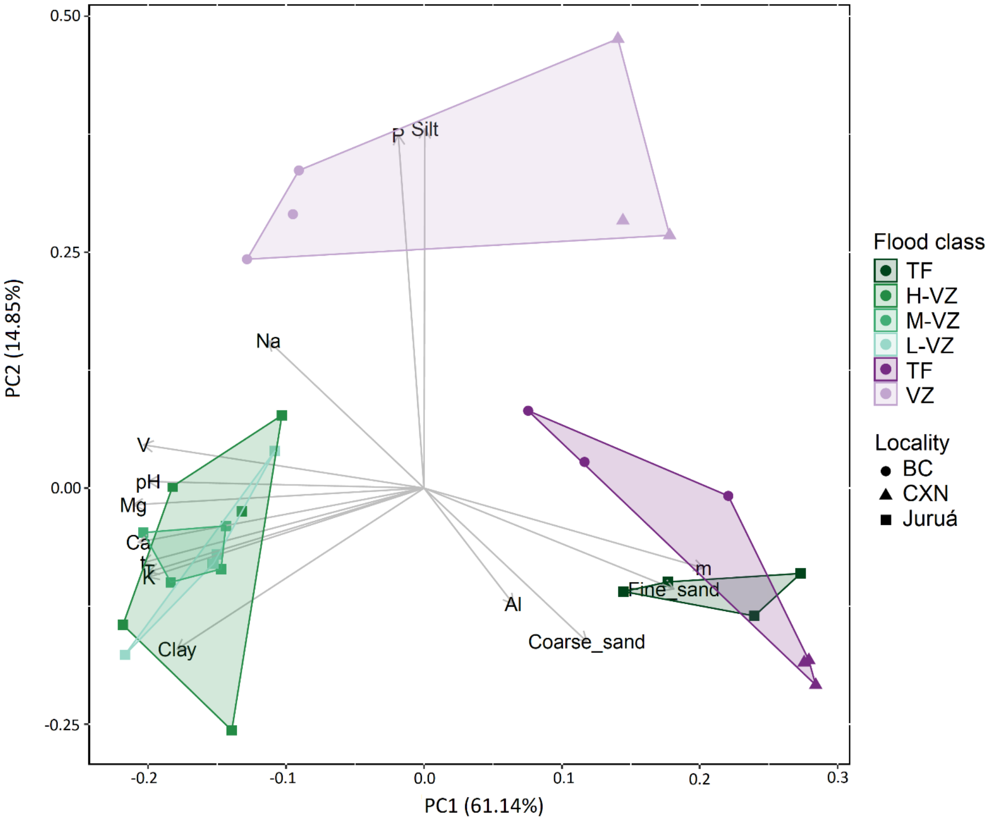

Fig. 2. Principal component analysis (PCA) showing the clustering of inventory plots along the first two PCA axes in relation to the soil physicochemical composition. The colours of the clusters reveal the geographic location (Juruá - this study - in green nuances; Benjamin Constant and Caxiuanã = purple) and the flooding gradient represented by the Juruá flood levels: TF: Terra firme; HV: High-várzea; MV: Mid-várzea; and LV: Low-várzea. The shape of the points indicates plot locality: Juruá = squares, Benjamin Constant = circle; and Caxiuanã = triangles.

3.2. Below-ground taxonomic composition: The taxonomic composition of the prokaryote component shows that the groups with the highest number of ASVs were Alphaproteobacteria (~25% of the taxa identified in our samples, equivalent to ~2000 ASVs per flood level; Fig. 3A; Appendix 4 Fig. A1A), Actinobacteria (~23%, average ~1700 ASVs; Fig. 3A; Appendix 4 Fig. A1A), and Acidobacteria (~18%, average ~1300 ASVs; Fig.

3A; Appendix 4 Fig. A1A). Among eukaryotes, Fungi had the highest number of ASVs (~43%, ~600 ASVs), mainly Ascomycota and Basidiomycota (Fig. 3B; Appendix 4 Fig. A1B) followed by Cercozoa (~18%, ~300 ASVs; Fig. 3B; Appendix 4 Fig S1B) and Ciliophora (~15%, ~250 ASVs; Fig. 3B; Appendix 4 Fig A1B). Most fungi were classified as saprotrophs (Appendix 4 Fig. A2). Other groups present were pathogens, parasites, mycorrhizae fungi and unclassified (Appendix 4 Fig. A2).

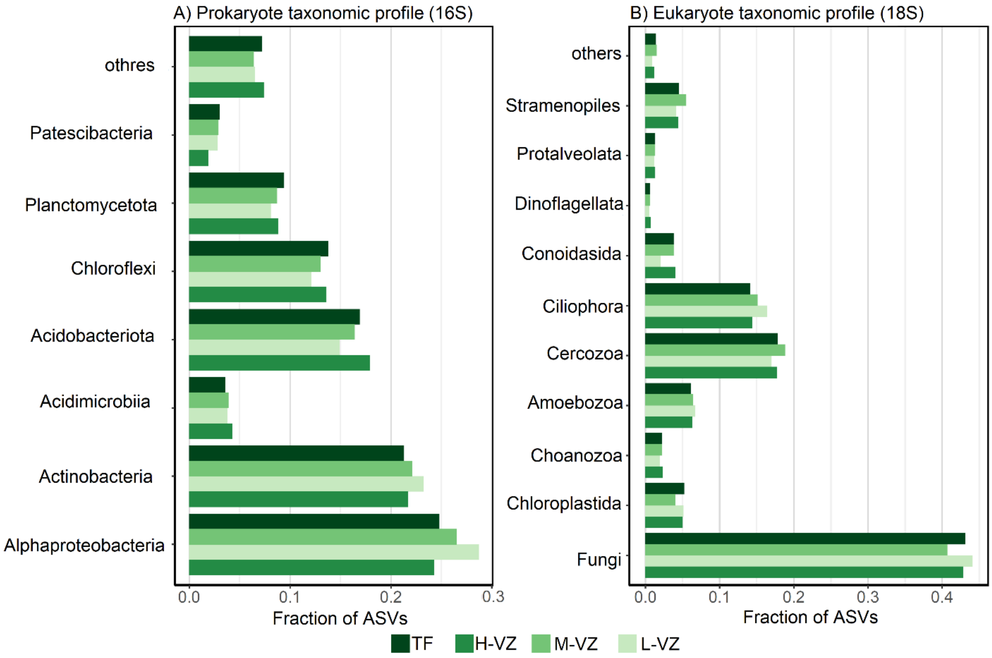

Fig. 3: Fraction of ASVs by taxonomic group and flood level for (A) prokaryotes and (B) eukaryotes. Flood levels are TF: Terra firme; H-VZ: High-várzea; M-VZ: Mid-várzea; and L-VZ: Low-várzea.

3.3. Alpha diversity: We found that the best model to explain bacterial (16S) diversity included woody plant Fisher's alpha diversity and sample type (soil or litter) with an interaction effect between the two (Table 1), but only sample type was significant (Table 2). For eukaryotes (18S), three models had a delta AICc lower than 2 (Table 1). The first model (dAICc = 0) included only sample type, the second (dAICc = 1.1) included only the woody plant Fisher's alpha diversity, and the third model (dAICc = 1.3) included the woody plant Fisher's alpha diversity and sample type with an interaction effect between the two (Table 1). In all models, only sample type was significant (Table 2). Bacterial Fisher's alpha diversity was higher than the Fisher's alpha diversity of either eukaryotes or woody plants. In terra firme, bacterial diversity in soil and litter, but not eukaryotes, appears to correlate with woody plant diversity. For várzea, no pattern was observed (Fig. 4).

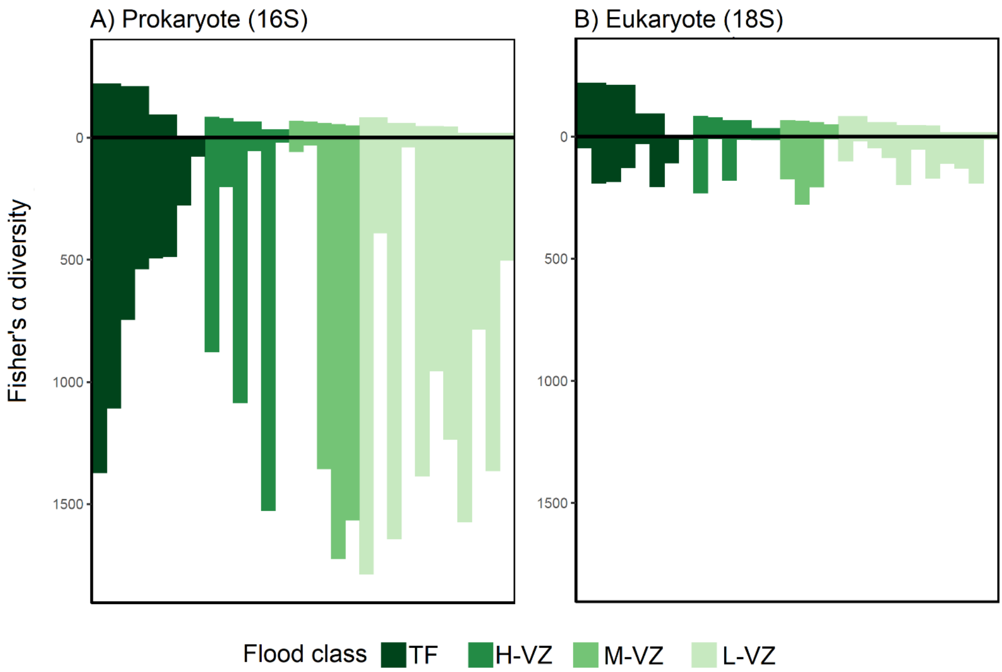

Fig. 4. Above-ground woody plant Fisher's alpha diversity *versus* below-ground Fisher's alpha diversity of A) prokaryotic (16S) and B) eukaryotic (18S) organisms in Juruá litter and soil samples. Prokaryotic and eukaryotic diversity are shown in negative values. Woody plant diversity is shown in positive values. Flood levels are TF: Terra firme; H-VZ: High-várzea; M-VZ: Mid-várzea; and L-VZ: Low-várzea.

3.4. Beta diversity: Community compositions were similar among plots across flood levels and sample types (litter and soil). For bacteria, there is a grouping of terra firme plots with some overlap with várzea plots (Fig. 5A). No clear pattern was observed for soil eukaryotes (Fig. 5B). For woody plant communities, there is a turnover in species compositions across different flood levels (Fig. 5C). The envfit test indicated a significant effect of flood level on both the prokaryote ($R^2 = 0.24$; $p = 0.022$) and woody plant ($R^2 = 0.48$; $p = 0.003$) communities, but not for soil eukaryotes ($R^2 = 0.14$; $p = 0.28$). The envfit test also indicated a significant effect of sample type on the prokaryote ($R^2 = 0.25$; $p = 0.001$) and eukaryote ($R^2 = 0.22$; $p = 0.006$) communities.

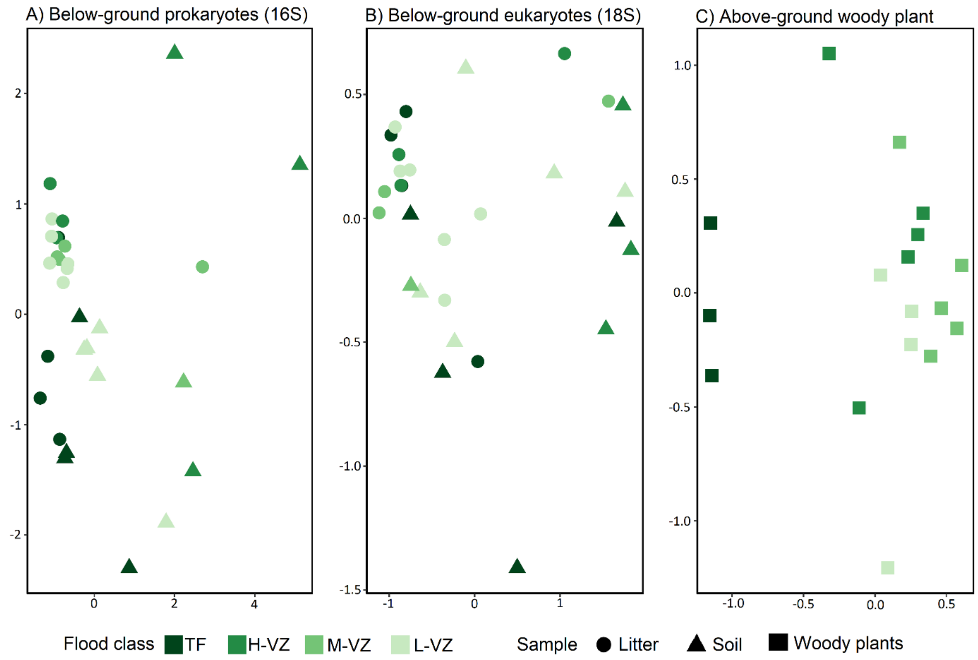

Fig. 5. Community structure in relation to substrate type and flood levels. Visualisation of non-metric multidimensional scaling (NMDS) for (A) prokaryotes (16S), (B) eukaryotes (18S), and (C) woody plants using Bray-Curtis dissimilarity indices. Symbols represent different substrates (i.e. sample types) where filled circles = litter samples and filled triangles = soil samples. Colours represent the different flood levels: TF = Terra firme; H-VZ = High-várzea; M-VZ = Mid-várzea; and L-VZ = Low-várzea.

4. Discussion

Our analyses have documented, for the first time, the degree to which soil and litter biota communities are affected by the flooding gradient in central-western Amazonian forests of varying floristic diversity. We show a weak correlation between soil and litter community composition and inundation period but find that below-ground Fisher's alpha diversity cannot be explained by the flooding gradient. We also show that the edaphic properties differed between terra firme and várzea, but not among várzea forests along the flooding gradient.

4.1. Edaphic properties: Várzea edaphic properties in the Juruá differed from the other two Amazonian várzeas that we included in our analyses (Fig. 2). For instance, the Juruá várzea was poorer in phosphorus (P) and silt, but rich in magnesium (Mg), calcium (Ca), potassium (K), and clay. This high-density clay content in the Juruá várzea may act as a physical barrier to water infiltration. On the other hand, clayey soils also have a high water holding capacity (Hillel, 2013), which prevents it from drying out completely during the non-flooded periods. The high clay content additionally made várzea samples hard to collect and to break once dried. Possibly, this was the main factor that hindered DNA extraction in our study.

Compared to the terra firme soils, the Juruá várzea soils were more fertile, presumably due to the yearly inflow of nutrient-rich alluvial sediments by the Juruá River. Moreover, the Juruá terra firme soils presented similar edaphic properties to those of the terra firme forests in Benjamin Constant and Caxiuanã. This was unexpected since the terra firme forest that we sampled in the Juruá grow on paleo-várzea sediments (Assis et al., 2015), and therefore presumably should have been relatively nutrient rich compared to typically well-drained and heavily leached terra firme soils on older geological formations (Sombroek, 2000). However, these soils presented similar edaphic properties to those of the terra firme forests in Benjamin Constant and Caxiuanã, suggesting that nutrients are soon leached from várzea substrates once they no longer experience flooding and an influx of river sediments.

4.2. Below-ground taxonomic composition: Alphaproteobacteria and Planctomycetes were abundant in our samples, accounting for 40% of our 16S data (Fig. 3A). These groups are known to be very diverse in undisturbed forests (de Carvalho et al., 2016) and they are generally common in Amazonian soils (Ritter et al., 2019b; Zinger et al., 2019). Interestingly, other bacterial groups commonly found in Amazonian soils (Ritter et al., 2019b; Zinger et al., 2019) and elsewhere (Delgado-Baquerizo et al., 2018) – notably Betaproteobacteria and Bacteroidetes - were not present in the Juruá samples. Because these groups are known form a diverse range of habitats, including várzea and terra firme, this surprised us and clearly highlight that we have much to discover about Amazonian soil biodiversity.

Patescibacteria (e.g., the candidate phyla radiation group), not previously reported in other várzea soils, were found in the Juruá samples (Fig. 3A). This group was recently described (Brown et al., 2015) and until now it had only been registered in Amazonian pasture soils (Lemos et al., 2020). An interesting characteristic of Patescibacteria is the small size of their genomes (usually <1.5 Mbp) and their lack of biosynthetic capabilities (Brown et al., 2015). These characteristics indicate that they could be co-metabolic interdependent (He et al., 2015; Lemos et al., 2019). Such interdependencies with other organisms would suggest a restrict occurrence or different functionality dependent on the community in which they occur. Yet, Patescibacteria show similar functional profiles under distinct climate conditions (tropical soils and permafrost; Lemos et al., 2020). Although their apparent plasticity is interesting, very little information is available for this group. The design of new 16S rRNA gene primers that better amplify Patescibacteria is required to elucidate the ecology and distribution of Patescibacteria in Amazonian soils and worldwide. Additionally, analysis of metatranscriptomes could improve our understanding of the metabolism in Patescibacteria and other bacteria under different substrate conditions.

Among the eukaryotes, we found a higher proportion of fungi in the Juruá substrates than previously documented for other areas in Amazonia (Ritter et al., 2019b). Whereas Ritter et al. (2020) found fewer fungi in várzea than in other environments, we found more fungi in várzea than in the adjacent terra firme, most of which were saprotrophs (Appendix 4 Fig. A2). Singer et al. (1983) hypothesized that ectomycorrhizal fungi increase the ability of their host plants to acquire nutrients and water in low-fertility soils, such as in the Amazonian sandy-soil ecosystems. However, we found very few ectomycorrhizal fungi in both várzea (more fertile) and terra firme (less fertile; Appendix 4 Fig. A2). Yet, around 35% of the fungi could be not assigned to any functional guild. This makes comparisons difficult and highlights the need to further investigate Amazonian soil biodiversity and its ecology.

Some eukaryotic groups detected in other Amazonian localities by the same 18S primers as the ones used here (Ritter et al., 2019b; Zinger et al., 2019), were absent in the Juruá samples. Such groups include nematodes and arthropods (Fig. 2B). Although the 18S primers that we used are not optimal for sequencing animals, it was surprising not to find these groups in our samples (except for one nematode sequence in várzea and terra firme). Low nematode diversity in Amazonian várzeas was previously reported by Cares (1984). One reason for the absence of these animals in várzea substrates could be that the high amount of clay in the soil and the seasonal floods, make várzea soil and litter unfit for nematode occupation. However, this does not explain the absence of soil animals in our terra firme samples since these were relatively clay-free and unflooded. To test this hypothesis, we need further studies in soils with a gradual difference in clay proportion and specific primers targeting nematodes (e.g. Kawanobe et al., 2021) alongside morphological examination of the diversity in the samples.

4.3. *Above- versus below-ground diversity:* There was no relationship between above- and below-ground alpha diversity across the different forest types included in this study. This mismatch could be explained by the flood pulse that may have masked any pattern by carrying organisms across all flood levels. A lack of clear relationships between above- and below-ground biodiversity has previously been demonstrated globally (Cameron et al., 2019) and for other Amazonian areas (Ritter et al., 2019a). However, for Amazonia this mismatch was partial. Across habitats, no correspondence was found between below-ground prokaryote or eukaryote alpha diversity and above-ground bird or tree alpha diversity (Ritter et al., 2019a). Nevertheless, there was a gradual decrease in below- and above-ground alpha diversity from the west to the east across the Amazon basin (Ritter et al., 2019a). Indeed, bacterial diversity appears to correlate with woody plant diversity in terra firme forests (Fig. 3A), but due to the sample limitation, just four terra firme plots, we could not find a significance in this relationship.

4.4 *Flooding gradient and community composition:* Most ASVs occur throughout the flooding gradient (Appendix 1 and 2). This result was partly expected since the seasonal flood waters could carry DNA (e.g. of inactive spores, dead or living organisms) across all várzea flood levels. Yet, the bacterial community composition of the Juruá substrate varied with flood level and woody plant diversity. This result indicates that below-ground bacteria may present different tolerances to hydrological stressors and or interdependencies with certain woody plant species. For instance, nodulation caused by nitrogen fixing bacteria are more frequent in Amazonian seasonally flooded forests, indicating that nodulation may be favored in flooded areas (Parolin and Wittmann, 2010).

5. Conclusion

This is the first study to investigate the degree to which soil and litter biota are affected by the flooding gradient in Amazonian forests. In fact, as far as we are aware, substrates from only six other Amazonian várzeas have previously been investigated using a metabarcoding approach, and these studies did not consider the flooding gradient (Ritter et al., 2019b, 2019a; Ritter, 2018). Hence, the DNA barcoding data herein – consisting of a total of 19,550 ASVs, from 14 várzea and four terra firme plots – more than doubles the total database from Amazonian várzeas available to date. Considering the extent of lowland Amazonian floodplain forests, approx. 516,000 km^2 (Hess et al., 2015), the need for more data from different geographical areas is obvious.

Studying below-ground communities along complex environmental gradients, like the one in the present study, offers an excellent opportunity to explore the responses of substrate biota to varying degrees of environmental stressors. Such studies can further our understanding of the patterns in below-ground biodiversity, their roles in the dynamics of seasonally flooded forests, and how these communities might respond to anthropogenic pressure and climate change. Therefore, the characterization of below-ground biodiversity in flooded forests, has theoretical implications for elucidating the patterns of biological diversity distribution. Practical implications include the identification of strategically important areas or areas of greater environmental sensitivity, for the conservation of biological diversity in face of environmental change. This not trivial, as infrastructural development (e.g. hydroelectric dams) and climate change (more frequent extreme floods and droughts) are severely affecting the natural flood pulse and threaten the ecological integrity of seasonally flooded forests across Amazonia (Gloor et al., 2013; Junk et al., 2018; Latrubesse et al., 2020). Increased pressures in these ecosystems highlight the urgency for more studies of this kind to improve our understanding of biodiversity patterns and community structures as these will allow us to better foresee and mitigate climate change impacts on ecosystem functions.

Acknowledgements: This publication is part of the Projeto Médio Juruá series on Resource Management in Amazonian Reserves (www.projetomediojurua.org). We thank the Secretaria do Estado do Meio Ambiente e Desenvolvimento Sustentável do Amazonas (SEMA - DEMUC) and Instituto Brasileiro do Meio Ambiente e Recursos Naturais Renováveis (IBAMA)/Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio) for authorising the research nº60/2016 (RDS Uacari) and nº55077-1 (RESEX Médio Juruá). We are grateful to the members from the Projeto Médio Juruá team for logistical support. We thank Rita Homem Pelicano for dedicated soil sampling in the field! We thank Michael J.G. Hopkins, Rafael Leandro de Assis and Juliana Schietti with colleagues at INPA for providing logistical assistance and a place to work in Manaus. We thank Paulo Apóstolo Costa Lima Assunção (in memoriam) and Alexandro Elias dos Santos, assisted by Lorena M. Rincón, for identifying the woody plant species in the field and at the National Institute for Amazonia Research (INPA). We thank our local field assistants, Associação dos Produtores Rurais de Carauari (ASPROC), Operação Amazônia Nativa (OPAN), and the people of the central Juruá who in various ways assisted us throughout our work. Finally, we thank Heléne Aronson and Katarzyna Wojnicka at the University of Gothenburg for quantifying the sampled DNA.

Funding: Y.K.B. was financed by the Norwegian University of Life Sciences (NMBU) as part of their PhD program in tropical ecology and an internal travel grant from NMBU. CDR was supported by the Alexander von Humboldt Foundation.

References:

Akaike, H., 1974. A new look at the statistical model identification, in: Selected Papers of Hirotugu Akaike. Springer, pp. 215–222.

Assis, R.L., Haugaasen, T., Schöngart, J., Montero, J.C., Piedade, M.T.F., Wittmann, F., 2015. Patterns of tree diversity and composition in Amazonian floodplain paleo-várzea forest. Journal of Vegetation Science 26, 312–322.

Auguie, B., Antonov, A., 2016. gridExtra: Miscellaneous functions for "grid" graphics (Version 2.2. 1)[Computer software].

Bardgett, R.D., Van Der Putten, W.H., 2014. Belowground biodiversity and ecosystem functioning. Nature 515, 505–511.

Barichivich, J., Gloor, E., Peylin, P., Brienen, R.J.W., Schöngart, J., Espinoza, J.C., Pattnayak, K.C., 2018. Recent intensification of Amazon flooding extremes driven by strengthened Walker circulation. Science Advances. doi:10.1126/sciadv.aat8785

Bolker, B., Bolker, M. Ben, 2017. Package 'bbmle.' Tools for General Maximum Likelihood Estimation 641.

Bredin, Y.K., Hawes, J.E., Peres, C.A., Haugaasen, T., 2020. Structure and Composition of Terra Firme and Seasonally Flooded Várzea Forests in the Western Brazilian Amazon. Forests 11, 1361.

Brown, C.T., Hug, L.A., Thomas, B.C., Sharon, I., Castelle, C.J., Singh, A., Wilkins, M.J., Wrighton, K.C., Williams, K.H., Banfield, J.F., 2015. Unusual biology across a group comprising more than 15% of domain Bacteria. Nature 523, 208–211.

Burnham, K.P., Anderson, D.R., 2002. Model selection and.

Callahan, B.J., McMurdie, P.J., Rosen, M.J., Han, A.W., Johnson, A.J.A., Holmes, S.P., 2016. DADA2: high-resolution sample inference from Illumina amplicon data. Nature Methods 13, 581–583.

Cameron, E.K., Martins, I.S., Lavelle, P., Mathieu, J., Tedersoo, L., Bahram, M., Gottschall, F., Guerra, C.A., Hines, J., Patoine, G., Siebert, J., Winter, M., Cesarz, S., Ferlian, O., Kreft, H., Lovejoy, T.E., Montanarella, L., Orgiazzi, A., Pereira, H.M., Phillips, H.R.P., Settele, J., Wall, D.H., Eisenhauer, N., 2019. Global mismatches in aboveground and belowground biodiversity. Conservation Biology 0, 1–6. doi:10.1111/cobi.13311

Cares, J.E., 1984. Fauna fitonematologica de varzea e terra firme nas proximidades de Manaus-AM. UNB.

Castello, L., Macedo, M.N., 2016. Large-scale degradation of Amazonian freshwater ecosystems. Global Change Biology 22, 990–1007.

Crawley, M.J., 2007. Generalized linear models. The R Book 511–526.

Creer, S., Deiner, K., Frey, S., Porazinska, D., Taberlet, P., Thomas, W.K., Potter, C., Bik, H.M., 2016. The ecologist's field guide to sequence-based identification of biodiversity. Methods in Ecology and Evolution 7, 1008–1018. doi:10.1111/2041-210X.12574

de Carvalho, T.S., Jesus, E. da C., Barlow, J., Gardner, T.A., Soares, I.C., Tiedje, J.M., Moreira, F.M. de S., 2016. Land use intensification in the humid tropics increased both alpha and beta diversity of soil bacteria. Ecology 97, 2760–2771.

Delgado-Baquerizo, M., Oliverio, A.M., Brewer, T.E., Benavent-González, A., Eldridge, D.J., Bardgett, R.D., Maestre, F.T., Singh, B.K., Fierer, N., 2018. A global atlas of the dominant bacteria found in soil. Science 359, 320–325. doi:10.1126/science.aap9516

Delgado-Baquerizo, M., Reich, P.B., Trivedi, C., Eldridge, D.J., Abades, S., Alfaro, F.D., Bastida, F., Berhe, A.A., Cutler, N.A., Gallardo, A., 2020. Multiple elements of soil biodiversity drive ecosystem functions across biomes. Nature Ecology & Evolution 4, 210–220.

Donagema, G.K., De Campos, D.B., Calderano, S.B., Teixeira, W.G., Viana, J.M., 2011. Manual de métodos de análise de solo, Embrapa Solos-Documentos (INFOTECA-E). Rio de Janeiro.

García-Palacios, P., Maestre, F.T., Kattge, J., Wall, D.H., 2013. Climate and litter quality differently modulate the effects of soil fauna on litter decomposition across biomes.

Ecology Letters 16, 1045–1053.

Gloor, M., Barichivich, J., Ziv, G., Brienen, R., Schöngart, J., Peylin, P., Ladvocat Cintra, B.B., Feldpausch, T., Phillips, O., Baker, J., 2015. Recent Amazon climate as background for possible ongoing and future changes of Amazon humid forests. Global Biogeochemical Cycles 29. doi:10.1002/2014GB005080

Gloor, M., Brienen, R.J.W., Galbraith, D., Feldpausch, T.R., Schöngart, J., Guyot, J., Espinoza, J.C., Lloyd, J., Phillips, O.L., 2013. Intensification of the Amazon hydrological cycle over the last two decades. Geophysical Research Letters 40, 1729–1733.

Guardiola, M., Uriz, M.J., Taberlet, P., Coissac, E., Wangensteen, O.S., Turon, X., 2015. Deep-sea, deep-sequencing: metabarcoding extracellular DNA from sediments of marine canyons. PLoS One 10, e0139633.

Haegeman, B., Hamelin, J., Moriarty, J., Neal, P., Dushoff, J., Weitz, J.S., 2013. Robust estimation of microbial diversity in theory and in practice. The ISME Journal 7, 1092.

Hättenschwiler, S., Gasser, P., 2005. Soil animals alter plant litter diversity effects on decomposition. Proceedings of the National Academy of Sciences 102, 1519–1524.

Haugaasen, T., Peres, C.A., 2006. Floristic, edaphic and structural characteristics of flooded and unflooded forests in the lower Rio Purús region of central Amazonia, Brazil. Acta Amazonica 36, 25–35.

Hawes, J.E., Peres, C.A., 2016. Patterns of plant phenology in Amazonian seasonally flooded and unflooded forests. Biotropica 48, 465–475. doi:10.1111/btp.12315

He, X., McLean, J.S., Edlund, A., Yooseph, S., Hall, A.P., Liu, S.-Y., Dorrestein, P.C., Esquenazi, E., Hunter, R.C., Cheng, G., 2015. Cultivation of a human-associated TM7 phylotype reveals a reduced genome and epibiotic parasitic lifestyle. Proceedings of the National Academy of Sciences 112, 244–249.

Hess, L.L., Melack, J.M., Affonso, A.G., Barbosa, C., Gastil-Buhl, M., Novo, E.M.L.M., 2015. Wetlands of the lowland Amazon basin: Extent, vegetative cover, and dual-season inundated area as mapped with JERS-1 synthetic aperture radar. Wetlands 35, 745–756.

Johnson, N.C., Gehring, C., Jansa, J., 2016. Mycorrhizal mediation of soil: fertility, structure, and carbon storage. Elsevier.

Julião, G.R., Venticinque, E.M., Fernandes, G.W., 2018. Influence of Flood Levels on the Richness and Abundance of Galling Insects Associated with Trees from Seasonally Flooded Forests of Central Amazonia, Brazil, in: Igapó (Black-Water Flooded Forests) of the Amazon Basin. Springer, pp. 99–117.

Junk, W., 1989. Flood tolerance and tree distribution in central Amazonian floodplains. Holm-nielsen. Tropical Forests; Botanical Dynamics, Speciation, and Diversity: 47–64.

Junk, W.J., Piedade, M.T.F., da Cunha, C.N., Wittmann, F., Schöngart, J., 2018. Macrohabitat studies in large Brazilian floodplains to support sustainable development in the face of climate change. Ecohydrology & Hydrobiology 18, 334–344.

Kassambara, A., Kassambara, M.A., 2020. Package ‘ggpubr.’

Kawanobe, M., Toyota, K., Ritz, K., 2021. Development and application of a DNA metabarcoding method for comprehensive analysis of soil nematode communities. Applied Soil Ecology 166, 103974.

Klindworth, A., Pruesse, E., Schweer, T., Peplies, J., Quast, C., Horn, M., Glöckner, F.O., 2013. Evaluation of general 16S ribosomal RNA gene PCR primers for classical and next-generation sequencing-based diversity studies. Nucleic Acids Research 41, e1–e1.

Kubitzki, K., 1990. Themes of diversification in neotropical forest. Quimica Nova 13, 4.

Latrubesse, E.M., d’Horta, F.M., Ribas, C.C., Wittmann, F., Zuanon, J., Park, E., Dunne, T., Arima, E.Y., Baker, P.A., 2020. Vulnerability of the biota in riverine and seasonally flooded habitats to damming of Amazonian rivers. Aquatic Conservation: Marine and Freshwater Ecosystems.

Lemos, L.N., Manoharan, L., Mendes, L.W., Venturini, A.M., Pylro, V.S., Tsai, S.M., 2020. Metagenome assembled-genomes reveal similar functional profiles of CPR/Patescibacteria phyla in soils. Environmental Microbiology Reports 12, 651–655.

Lemos, L.N., Medeiros, J.D., Dini-Andreote, F., Fernandes, G.R., Varani, A.M., Oliveira, G., Pylro, V.S., 2019. Genomic signatures and co-occurrence patterns of the ultra-small Saccharimonadia (phylum CPR/Patescibacteria) suggest a symbiotic lifestyle. Molecular Ecology 28, 4259–4271.

Love, M.I., Huber, W., Anders, S., 2014. Moderated estimation of fold change and dispersion for RNA-seq data with DESeq2. Genome Biology 15, 550.

Maretti, C.C., 2014. Amazon: There is Hope! If we all do 'the right thing'…; Deforestation, Protected Areas and Indigenous Territories: Past, evolution and… Which future? Brasilia.

Martin, M., 2011. Cutadapt removes adapter sequences from high-throughput sequencing reads. EMBnet. Journal 17, 10–12.

McMurdie, P.J., Holmes, S., 2013. phyloseq: an R package for reproducible interactive analysis and graphics of microbiome census data. PloS One 8, e61217.

Moura, M.R., Jetz, W., 2021. Shortfalls and opportunities in terrestrial vertebrate species discovery. Nature Ecology & Evolution 1–9.

Myster, R.W., 2016. The physical structure of forests in the Amazon Basin: a review. The Botanical Review 82, 407–427.

Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., O'hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Wagner, H., 2010. Vegan: community ecology package. R package version 1.17-4. Http://Cran. r-Project. Org>. Acesso Em 23, 2010.

Parolin, P. de, De Simone, O., Haase, K., Waldhoff, D., Rottenberger, S., Kuhn, U., Kesselmeier, J., Kleiss, B., Schmidt, W., Pledade, M.T.F., 2004. Central Amazonian floodplain forests: tree adaptations in a pulsing system. The Botanical Review 70, 357–380.

Parolin, P., Wittmann, F., 2010. Struggle in the flood: tree responses to flooding stress in four tropical floodplain systems. AoB Plants 2010.

Pereira, P., Bogunovic, I., Muñoz-Rojas, M., Brevik, E.C., 2018. Soil ecosystem services, sustainability, valuation and management. Current Opinion in Environmental Science & Health 5, 7–13.

Petit, R.J., Hampe, A., 2006. Some evolutionary consequences of being a tree. Annu. Rev. Ecol. Evol. Syst. 37, 187–214.

Pietramellara, G., Ascher, J., Ceccherini, M.T., Renella, G., 2002. Soil as a biological system. Annals of Microbiology 52, 119–132.

Polme, S., Abarenkov, K., Nilsson, R.H., Lindahl, B.D., Clemmensen, K.E., Kauserud, H., Nguyen, N., Kjøller, R., Bates, S.T., Baldrian, P., 2020. FungalTraits: a user-friendly traits database of fungi and fungus-like stramenopiles. Fungal Diversity 105, 1–16.

Prance, G.T., 1996. Islands in Amazonia. Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences 351, 823–833.

Prance, G.T., 1979. Notes on the vegetation of Amazonia III. The terminology of Amazonian forest types subject to inundation. Brittonia 31, 26–38.

Quast, C., Pruesse, E., Yilmaz, P., Gerken, J., Schweer, T., Yarza, P., Peplies, J., Glöckner, F.O., 2012. The SILVA ribosomal RNA gene database project: improved data processing and web-based tools. Nucleic Acids Research 41, D590–D596.

R Core Team, 2020. R: the R project for statistical computing. 2019. URL: Https://Www. r-Project. Org/[Accessed 2020-03-30].

Ramalho, W.P., Andrade, M.S., Matos, L.R.A. de, Vieira, L.J.S., 2016. Amphibians of varzea environments and floating meadows of the oxbow lakes of the Middle Purus River, Amazonas, Brazil. Biota Neotropica 16.

Ríos-Villamizar, E.A., Adeney, J.M., Piedade, M.T.F., Junk, W.J., 2020. New insights on the classification of major Amazonian river water types. Sustainable Water Resources Management 6, 1–16.

Ritter, C.D., Dunthorn, M., Anslan, S., Xavier, V., Tedersoo, L., Henrik, R., Antonelli, A., 2020. Advancing biodiversity assessments with environmental DNA : Long-read technologies help reveal the drivers of Amazonian fungal diversity 00, 1–16. doi:10.1002/ece3.6477

Ritter, C.D. et al., 2018. High-throughput metabarcoding reveals the effect of physicochemical soil properties on soil and litter biodiversity and community turnover across Amazonia. PeerJ 6.

Ritter, C.D., Faurby, S., Bennett, D.J., Naka, L.N., ter Steege, H., Zizka, A., Haenel, Q., Nilsson, R.H., Antonelli, A., 2019a. The pitfalls of biodiversity proxies: Differences in richness patterns of birds, trees and understudied diversity across Amazonia. Scientific Reports 9. doi:10.1038/s41598-019-55490-3

Ritter, C.D., McCrate, G., Nilsson, R.H., Fearnside, P.M., Palme, U., Antonelli, A., 2017. Environmental impact assessment in Brazilian Amazonia: Challenges and prospects to assess biodiversity. Biological Conservation 206, 161–168. doi:10.1016/j.biocon.2016.12.031

Ritter, C.D., Zizka, A., Barnes, C., Nilsson, R.H., Roger, F., Antonelli, A., 2019b. Locality or habitat? Exploring predictors of biodiversity in Amazonia. Ecography 42, 321–333. doi:10.1111/ecog.03833

Ritter, C.D., Zizka, A., Roger, F., Tuomisto, H., Barnes, C., Nilsson, R.H., Antonelli, A., 2018. High-throughput metabarcoding reveals the effect of physicochemical soil properties on soil and litter biodiversity and community turnover across Amazonia. PeerJ 2018, e5661. doi:10.7717/peerj.5661

Singer, R., Araujo, I., Ivory, M.H., 1983. The ectotrophically mycorrhizal fungi of the neotropical lowlands, especially central Amazonia.(Litter decomposition and ectomycorrhiza in Amazonian forests 2.). Beihefte Zur Nova Hedwigia.

Sombroek, W., 2000. Amazon landforms and soils in relation to biological diversity. Acta Amazonica 30, 81.

Sorribas, M.V., Paiva, R.C.D., Melack, J.M., Bravo, J.M., Jones, C., Carvalho, L., Beighley, E., Forsberg, B., Costa, M.H., 2016. Projections of climate change effects on discharge and inundation in the Amazon basin. Climatic Change 136, 555–570. doi:10.1007/s10584-016-1640-2

Tang, Y., Horikoshi, M., Li, W., 2016. ggfortify: unified interface to visualize statistical results of popular R packages. R J. 8, 474.

Team, Rs., 2015. RStudio: integrated development for R. RStudio, Inc., Boston, MA URL Http://Www. Rstudio. Com 42, 84.

Tedersoo, L., Bahram, M., Põlme, S., Kõljalg, U., Yorou, N.S., Wijesundera, R., Ruiz, L.V., Vasco-Palacios, A.M., Thu, P.Q., Suija, A., Smith, M.E., Sharp, C., Saluveer, E., Saitta, A., Rosas, M., Riit, T., Ratkowsky, D., Pritsch, K., Põldmaa, K., Piepenbring, M., Phosri, C., Peterson, M., Parts, K., Pärtel, K., Otsing, E., Nouhra, E., Njouonkou, A.L., Nilsson, R.H., Morgado, L.N., Mayor, J., May, T.W., Majuakim, L., Lodge, D.J., Lee, S.S., Larsson, K.-H., Kohout, P., Hosaka, K., Hiiesalu, I., Henkel, T.W., Harend, H., Guo, L., Greslebin, A., Grelet, G., Geml, J., Gates, G., Dunstan, W., Dunk, C., Drenkhan, R., Dearnaley, J., De Kesel, A., Dang, T., Chen, X., Buegger, F., Brearley, F.Q., Bonito, G., Anslan, S., Abell, S., Abarenkov, K., 2014. Global diversity and geography of soil fungi. Science (New York, N.Y.) 346, 1052–3. doi:10.1126/science.aaa1185

ter Steege, H., Hammond, D.S., 2001. Character convergence, diversity, and disturbance in tropical rain forest in Guyana. Ecology 82, 3197–3212.

Van Rossum, G., Drake, F.L., 2009. Python 3 References Manual. Scotts Valley CA: CreateSpace.

Wickham, H., 2017. tidyverse: Easily Install and Load "Tidyverse" Packages (Version R package version 1.1. 1).

Wickham, H., 2016. ggplot2: elegant graphics for data analysis. Springer.

Wittmann, F., Schöngart, J., Junk, W.J., 2010. Phytogeography, species diversity, community structure and dynamics of central Amazonian floodplain forests, in: Amazonian Floodplain Forests. Springer, pp. 61–102.

Zinger, L., Taberlet, P., Schimann, H., Bonin, A., Boyer, F., De Barba, M., Gaucher, P., Gielly, L., Giguet-Covex, C., Iribar, A., Réjou-Méchain, M., Rayé, G., Rioux, D., Schilling, V., Tymen, B., Viers, J., Zouiten, C., Thuiller, W., Coissac, E., Chave, J., 2019. Body size determines soil community assembly in a tropical forest. Molecular Ecology 28, 528–543. doi:10.1111/mec.14919

Zulkafli, Z., Buytaert, W., Manz, B., Rosas, C.V., Willems, P., Lavado-Casimiro, W., Guyot, J.-L.L., Santini, W., 2016. Projected increases in the annual flood pulse of the Western Amazon. Environmental Research Letters 11, 014013. doi:10.1088/1748-9326/11/1/014013

Tables:

Table 1. Variables used in model selection with their respective delta dAICc and weight values. The best fit model has a dAICc = 0 and is presented in bold as the alternative good models (dAICc =< 2). The response variables are below-ground Fisher's diversity for prokaryotes (16S) and eukaryotes (18S). The independent variables are flood level, sample type, water mark (measured floodwater marks on trees, with terra firme being zero), and the woody plant Fisher's diversity. The model used flood level and sample type as a fixed factor or as interacting variable.

Marker	Model	AICc	dAICc	df	weight
Prokaryote (16S)	~ 1	89	15.9	2	<0.001
	~ Flood level	96.5	23.4	5	<0.001
	~ Sample type	75.5	2.3	3	0.2355
	~ Water mark	89.7	16.5	3	<0.001
	~ PC1	91.9	18.7	3	<0.001
	~ PC1 * Flood level	127.2	54	9	<0.001
	~ Fisher div.	85.6	12.5	3	0.0015
	~ Fisher div. * Flood level	113.3	40.1	9	<0.001
	~ Fisher div. * Sample	73.1	0	5	0.7625
Eukaryote (18S)	~ 1	86.2	3.8	2	0.066
	~ Flood level	94	11.6	5	0.0013
	~ Sample type	**82.4**	**0**	**3**	**0.4357**
	~ Watermark	89.2	6.8	3	0.0148
	~ PC1	91.9	9.4	3	0.0039
	~ PC1 * Flood level	127.2	44.7	9	<0.001
	~ Fisher div.	**83.6**	**1.1**	**3**	**0.2454**
	~ Fisher div. * Flood level	111.7	29.3	9	<0.001
	~ Fisher div. * Sample	**83.7**	**1.3**	**5**	**0.2328**

Table 2. Estimated parameters (values estimated with standardize error, t-value and respective p-value) of the best fit model for 16S and the third best fit model (that included the variables selected) for 18S selected in model selection. The response variables are below-ground Fisher's alpha diversity and (above-ground) woody plant Fisher's alpha diversity with an interaction term between the above-ground alpha diversity and sample type (soil or litter). Significant factors (p , 0.05) are marked in bold.

	Coefficients	Estimate	Std. Error	t value	Pr(>|t|)
Prokaryote (16S)	(Intercept)	0.6427	0.1815	3.54	0.00167
	fisher.alpha	-0.2288	0.1947	-1.175	0.2515
	SampleSoil	**-1.3463**	**0.2774**	**-4.853**	**6.03E-05**
	fisher.alpha:SampleSoil	0.4439	0.2797	1.587	0.12566
Eukaryote (18S)	(Intercept)	0.43232	0.23733	1.822	0.0816
	fisher.alpha	-0.03453	0.25159	-0.137	0.892
	SampleSoil	**-0.89964**	**0.35607**	**-2.527**	**0.0189**
	fisher.alpha:SampleSoil	0.43738	0.36073	1.212	0.2376

Appendix 4

Table A1. Physicochemical soil properties included in our analyses. Locality is the geographic region from where the sample was taken. Juruá indicates samples that we collected for the present study from the central Juruá. BC indicates samples collected in Benjamin Constante, see Ritter et al. (2018)*, CXN indicates samples collected in Caixuanã, see Ritter et al.* (2018)*. Flood level indicates flood level where this information was available otherwise forest type, where TF = terra firme (not seasonally flooded); VZ = várzea (seasonally flooded); HV = high várzea (flooded 0-1 mo/yr); MV = mid várzea (flooded 2-4 mo/yr); and LV = low várzea (flooded 5-12 mo/yr). Coarse, Fine, and Total sand indicate the content of sand with grainsize 2.0-0.2 mm, 0.2-0.05 mm or 2.0-0.05 mm, respectively, in g/kg. Silt and Clay indicate clay and silt content in g/kg. pH is that of sample when dissolved in water. P = phosphorus, K = potassium, and Na = Natrium are given in mg/dm^3. Ca = Calcium, Mg = magnesium, Al = aluminium, H+Al = exchangeable aluminium, SB = sum of exchangeable bases, t = effective cation exchange capacity, T = cation exchange capacity, V = Base Saturation Index, and m = aluminium saturation index are given in cmol$_c$/dm^3.*

Locality	Flood level	Coarse sand	Fine sand	Total sand	Silt	Clay	pH	P	K	Na	Ca	Mg	Al	H+Al	SB	t	T	V	m
Juruá	TF	13.7	418.5	432.2	426.3	141.5	4.0	5.0	46.0	5.0	0.1	0.1	3.6	7.8	0.4	3.9	8.1	4.3	91.1
Juruá	TF	39.4	129.3	168.7	382.8	448.5	4.0	3.0	86.0	45.0	0.4	0.4	8.2	11.7	1.2	9.4	12.9	9.6	86.9
Juruá	LV	5.9	12.9	18.9	512.7	468.5	4.7	10.8	189.0	28.0	9.1	2.8	2.1	8.0	12.6	14.7	20.6	61.0	14.3
Juruá	LV	11.3	15.0	26.3	275.7	698.0	4.7	7.4	146.0	42.0	10.6	3.6	1.9	10.8	14.8	16.6	25.5	57.9	11.1
Juruá	MV	17.4	15.9	33.3	314.2	652.5	4.6	6.3	142.0	34.0	11.8	3.7	1.9	9.8	16.0	17.9	25.7	62.0	10.8
Juruá	MV	4.0	9.3	13.3	441.2	545.5	4.6	8.5	145.0	35.0	13.9	3.1	3.8	9.3	17.5	21.4	26.9	65.2	17.9
Juruá	MV	11.8	15.6	27.3	337.7	635.0	4.6	8.4	147.0	22.0	14.8	3.2	2.0	2.4	18.4	20.4	20.8	88.7	9.7
Juruá	HV	7.1	7.9	15.0	565.0	420.0	4.8	11.3	139.0	23.0	9.7	3.2	1.7	7.7	13.4	15.1	21.1	63.4	11.4
Juruá	HV	11.5	32.4	43.9	6.6	949.5	4.6	11.0	164.0	20.0	11.7	2.9	3.2	9.0	15.1	18.2	24.1	62.6	17.3
Juruá	HV	10.1	10.3	20.4	533.6	446.0	4.6	8.1	156.0	23.0	12.3	4.0	3.5	9.5	16.8	20.3	26.3	63.9	17.3

Locality	Flood level	Coarse sand	Fine sand	Total sand	Silt	Clay	pH	P	K	Na	Ca	Mg	Al	H+Al	SB	t	T	V	m
Juruá	HV	7.1	16.3	23.4	282.1	694.5	5.0	7.0	172.0	23.0	14.8	4.8	0.8	14.2	20.1	20.9	34.3	58.7	4.0
Juruá	MV	16.5	14.3	30.7	295.8	673.5	5.1	4.8	158.0	28.0	12.6	3.8	0.5	7.4	16.9	17.4	24.3	69.7	2.6
Juruá	TF	12.2	13.2	25.4	416.6	558.0	3.8	6.2	69.0	5.0	0.2	0.2	4.2	11.7	0.5	4.8	12.3	4.5	88.5
Juruá	MV	8.0	10.1	18.1	359.4	622.5	4.9	8.1	167.0	34.0	14.7	4.0	0.8	8.6	19.3	20.0	27.9	69.0	3.7
Juruá	LV	6.8	12.1	18.9	321.6	659.5	4.8	7.3	156.0	26.0	12.2	3.2	1.1	8.9	16.0	17.0	24.8	64.3	6.2
Juruá	LV	3.0	13.7	16.7	344.3	639.0	4.4	7.0	161.0	28.0	20.9	4.1	4.1	12.6	25.6	29.6	38.1	67.1	13.7
Juruá	HV	2.1	8.2	10.3	418.2	571.5	4.7	11.1	179.0	36.0	14.6	3.3	1.5	8.6	18.5	19.9	27.1	68.3	7.3
Juruá	TF	54.7	296.8	351.5	395.1	253.5	3.7	8.0	81.0	6.0	0.1	0.3	6.0	13.1	0.6	6.6	13.8	4.6	90.4
BC	TF	10.8	127.4	138.2	524.6	337.2	4.3	10.3	86.0	18.7	3.1	1.2	1.9	6.2	4.7	6.6	10.9	42.3	30.1
BC	TF	9.5	110.9	120.4	527.6	352.0	4.1	10.3	64.0	12.0	2.5	1.4	4.2	7.1	4.0	8.3	11.1	36.1	51.1
BC	TF	9.1	329.2	338.3	414.6	247.2	3.9	9.3	49.7	25.7	0.5	0.3	4.3	7.3	1.0	5.3	8.3	12.2	80.9
BC	VZ	1.4	4.3	5.8	591.1	403.2	4.5	32.0	94.3	36.0	9.8	3.1	1.5	4.2	13.3	14.8	17.5	75.8	10.3
BC	VZ	1.3	2.7	4.0	568.3	427.7	4.7	29.5	96.0	29.7	10.6	2.8	1.3	3.7	13.7	15.0	17.4	78.8	8.5
BC	VZ	5.4	4.7	10.2	521.0	468.8	4.6	23.3	97.0	48.7	11.4	3.5	1.6	5.4	15.3	16.9	20.7	73.9	9.4
CXN	TF	531.5	272.7	804.2	62.3	133.5	3.9	5.1	22.7	14.0	0.2	0.2	1.2	4.6	0.5	1.6	5.1	9.1	72.0
CXN	TF	488.0	269.7	757.7	81.6	160.7	3.7	5.9	27.0	21.3	0.1	0.2	1.5	5.7	0.4	1.9	6.1	7.2	77.2
CXN	TF	557.0	234.2	791.2	59.8	149.0	3.8	8.2	36.0	18.3	0.1	0.2	1.4	5.8	0.5	1.9	6.3	7.8	75.1
CXN	VZ	14.1	91.9	106.0	791.0	103.0	3.8	33.9	54.7	37.7	0.7	0.8	1.7	11.0	1.9	3.5	12.8	14.8	47.1
CXN	VZ	16.2	148.2	164.4	751.1	84.5	4.1	14.0	46.7	25.0	0.4	0.4	1.1	6.3	1.1	2.2	7.3	14.7	52.6
CXN	VZ	11.9	35.6	47.5	831.0	121.5	4.1	12.4	51.3	19.7	0.8	0.7	1.2	6.3	1.8	3.0	8.1	22.2	40.2

Table A2. Number of reads and ASVs per plot. Sample gives information about sample type, either soil, or litter sample. Flood levels are TF = terra firme (not seasonally flooded); HV = high várzea (flooded 0-1 mo/yr); MV = mid várzea (flooded 2-4 mo/yr); and LV = low várzea (flooded 5-12 mo/yr). Lat and Long inform about latitude and longitude. ASV 16S is the number of unique amplicon sequence variants for Prokaryotes within the V3-V4 region (~460 bases) of the 16S rDNA gene. Reads 16S is the number of read amplicon sequence variants for Prokaryotes using the forward primer (5'-CCTACGGGN GGCWGCAG-3') and reverse primer (5'-GACTACH VGGGTATCTAATCC-3') from Klindworth et al. (2013). ASV 18S is the number of unique amplicon sequence variants for Eukaryotes within the V7 region (100–110 bases) of the 18S rDNA gene. Reads 18S is the number of read amplicon sequence variants for Eukaryotes using the forward and reverse primers (5'-TTTGTCTGSTTAATTSCG-3') and (5'-TCACAGACCTGTTATTGC-3') designed by Guardiola et al. (2015).

ID	Sample	Flood level	Lat	Long	ASV 16S	Reads 16S	ASV 18S	Reads 18S
HV1L	Litter	HV	-5.95423	-67.8206	3059	28032	1004	18669
HV5L	Litter	HV	-5.73941	-67.8002	4805	34181	76	15106
HV5S	Soil	HV	-5.73941	-67.8002	30	95	78	16603
HV7S	Soil	HV	-5.62975	-67.6728	70	84	46	11525
HV8L	Litter	HV	-5.62829	-67.6805	3418	24377	875	24647
HV8S	Soil	HV	-5.62829	-67.6805	81	202	60	10593
LV10L	Litter	LV	-5.55946	-67.5495	4477	23487	265	19092
LV10S	Soil	LV	-5.55946	-67.5495	105	680	455	19712

ID	Sample	Flood level	Lat	Long	ASV 16S	Reads 16S	ASV 18S	Reads 18S
LV13L	Litter	LV	-5.41871	-67.525	4238	17393	521	20296
LV13S	Soil	LV	-5.41871	-67.525	1609	24327	112	19043
LV14L	Litter	LV	-5.40669	-67.2777	4496	35647	911	23505
LV14S	Soil	LV	-5.40669	-67.2777	1772	16793	57	4432
LV15L	Litter	LV	-5.40663	-67.2776	5389	47070	579	24503
LV15S	Soil	LV	-5.40663	-67.2776	3161	43808	582	12634
LV16L	Litter	LV	-5.3906	-67.2567	4788	42670	884	18191
LV16S	Soil	LV	-5.3906	-67.2567	3410	33305	276	14095
LV4L	Litter	LV	-5.76675	-67.7586	4292	38921	854	27067
MV11L	Litter	MV	-5.55234	-67.5464	4683	24436	NA	NA
MV18L	Litter	MV	-5.10586	-67.1315	3964	24003	918	18203
MV2S	Soil	MV	-5.78612	-67.8049	110	347	791	16971
MV3L	Litter	MV	-5.78131	-67.8081	5447	49443	52	8799
MV6L	Litter	MV	-5.67433	-67.7302	97	874	1183	20140
TF12L	Litter	TF	-5.45701	-67.2609	4269	29573	258	14856

ID	Sample	Flood level	Lat	Long	ASV 16S	Reads 16S	ASV 18S	Reads 18S
TF12S	Soil	TF	-5.45701	-67.2609	4261	51260	863	18215
TF17L	Litter	TF	-5.39057	-67.2115	2890	35750	872	22443
TF17S	Soil	TF	-5.39057	-67.2115	2238	34608	577	12622
TF19L	Litter	TF	-5.04703	-67.1356	1225	23870	537	17475
TF19S	Soil	TF	-5.04703	-67.1356	219	1364	60	9321
TF9L	Litter	TF	-5.57857	-67.505	2045	32479	894	16777
TF9S	Soil	TF	-5.57857	-67.505	2147	38748	175	17892

Table A3. Proportional contribution of each physicochemical soil variable for the principal components (PC) of our principal components analysis. We also show the proportion of variance explained for each PC in Total and the cumulative of variance explained. Coarse, Fine, and Total sand indicate the content of sand with grainsize 2.0-0.2 mm, 0.2-0.05 mm or 2.0-0.05 mm, respectively, in g/kg. Silt and Clay indicate clay and silt content in g/kg. pH is that of sample when dissolved in water. P = phosphorus, K = potassium, and Na = Natrium are given in mg/dm^3. Ca = Calcium, Mg = magnesium, Al = aluminium, H+Al = exchangeable aluminium, SB = sum of exchangeable bases, t = effective cation exchange capacity, T = cation exchange capacity, V = Base Saturation Index, and m = aluminium saturation index are given in cmol$_c$/dm^3.

Variables	**PC1**	**PC2**	**PC3**	**PC4**	**PC5**	**PC6**	**PC7**	**PC8**	**PC9**	**PC10**	**PC11**	**PC12**	**PC13**	**PC14**	**PC15**
Coarse_sand	0.031355	0.012391	0.019859	0.00558	0.000619	0.000448	0.002505	0.000772	0.000615	0.000161	4.18E-05	2.21E-05	1.13E-06	0	0
Fine_sand	0.048124	0.008143	0.000593	3.84E-07	0.000277	0.005911	0.003119	0.000282	6.95E-05	0.000108	9.05E-05	8E-06	6.57E-07	0	0
Silt	0.000163	0.029029	0.010864	0.005463	0.002373	0.001248	0.001766	0.0002	2.78E-05	2.51E-05	3.01E-05	1.6E-05	6.09E-07	0	0
Clay	0.04755	0.013002	0.004461	0.000992	0.001838	0.004563	0.001675	0.000569	0.000441	3.27E-05	8.15E-06	5.36E-06	1.68E-06	0	0
pH	0.053112	0.000537	0.00377	0.004042	0.00264	0.000107	0.001892	0.000885	0.000487	0.000616	0.000298	9.43E-05	2.81E-07	0	0
P	0.004952	0.028506	0.004503	0.004749	0.006265	0.000226	0.001081	0.000603	0.000626	0.000135	6.56E-05	1.62E-05	2.75E-06	0	0
K	0.052978	0.007188	0.003986	0.001847	0.001054	3.89E-05	5.2E-07	0.000485	0.001879	0.000477	9.47E-07	6.7E-05	3.8E-06	0	0
Na	0.029962	0.011895	0.001466	0.016456	0.004671	0.000212	0.000788	0.000221	0.000168	0.000125	5.51E-06	1.73E-05	1.03E-06	0	0
Ca	0.055003	0.004364	0.001486	0.000537	0.001349	0.00263	0.000844	5.01E-06	0.000634	0.000346	0.000223	3.08E-05	1.26E-05	0	0
Mg	0.055992	0.001348	0.002472	0.00025	2.72E-05	0.001607	0.00032	0.000194	7.35E-05	0.000652	0.000255	0.000179	1.2E-05	0	0
Al	0.017197	0.00936	0.025	0.007041	0.001727	0.000491	0.000549	0.001449	0.000456	0.000272	6.67E-05	6.65E-05	1.26E-06	0	0
t	0.05414	0.006024	0.003904	0.002036	0.001448	0.002609	0.000881	0.000279	0.000406	0.000103	0.000119	2.87E-06	1.32E-05	0	0
T	0.052986	0.006764	0.003902	0.001008	0.000558	0.002139	0.001364	0.001993	2.06E-05	0.000227	1.73E-05	7.35E-05	2.71E-05	0	0
V	0.054043	0.003495	0.00374	0.000535	0.001736	0.000699	0.000673	0.002271	0.00022	0.000262	4.39E-05	9.72E-05	2.46E-05	0	0
m	0.053843	0.006454	0.006913	0.001974	0.000398	2.26E-05	1.14E-05	0.000543	3.56E-05	0.000148	0.000394	0.000204	7.27E-06	0	0
TOTAL	0.6114	0.1485	0.09692	0.05251	0.02698	0.02295	0.01747	0.01075	0.00616	0.00369	0.00166	0.0009	0.00011	0	0
Cumalative Proportion	0.6114	0.7599	0.85681	0.90932	0.9363	0.95925	0.97672	0.98747	0.99364	0.99733	0.99899	0.9999	1	1	1

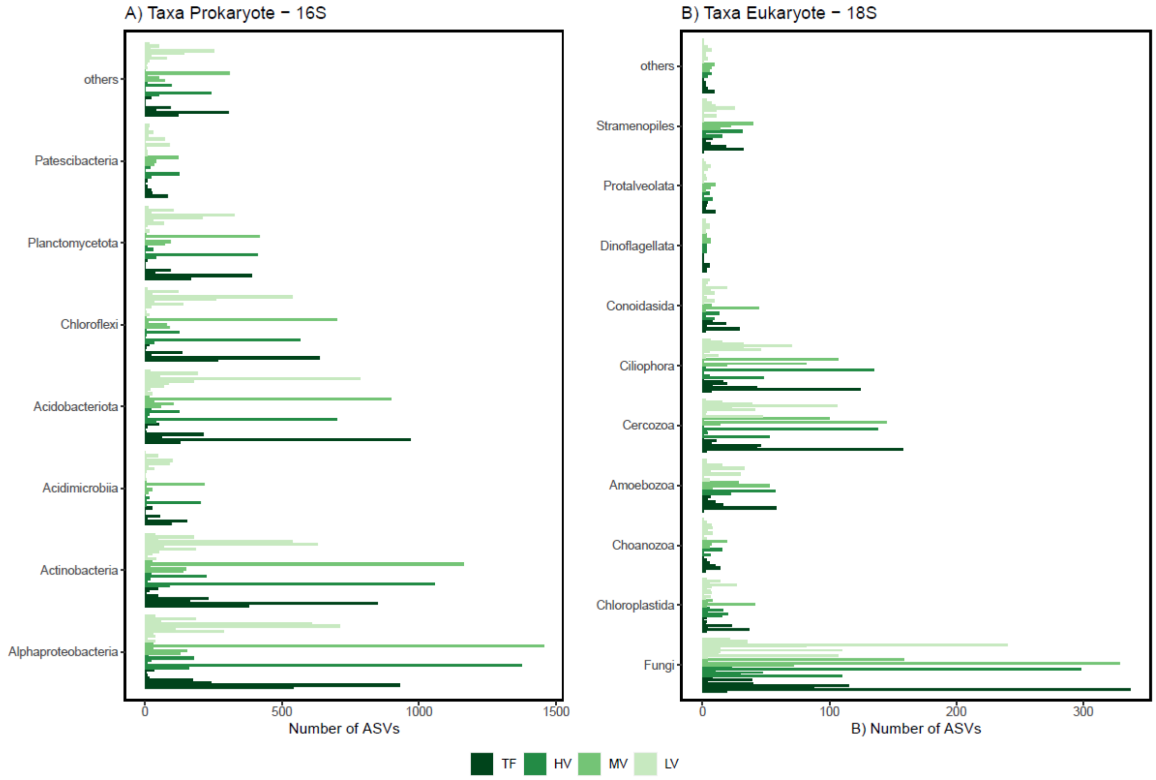

Fig. A1. ***Taxonomic composition of amplicon sequence variants (ASV) communities.*** *Number of ASVs by taxonomic group and flood level for (A) prokaryotes and (B) eukaryotes. Flood levels are TF = terra firme (not seasonally flooded); HV = high várzea (flooded 0-1 mo/yr); MV = mid várzea (flooded 2-4 mo/yr); and LV = low várzea (flooded 5-12 mo/yr).*

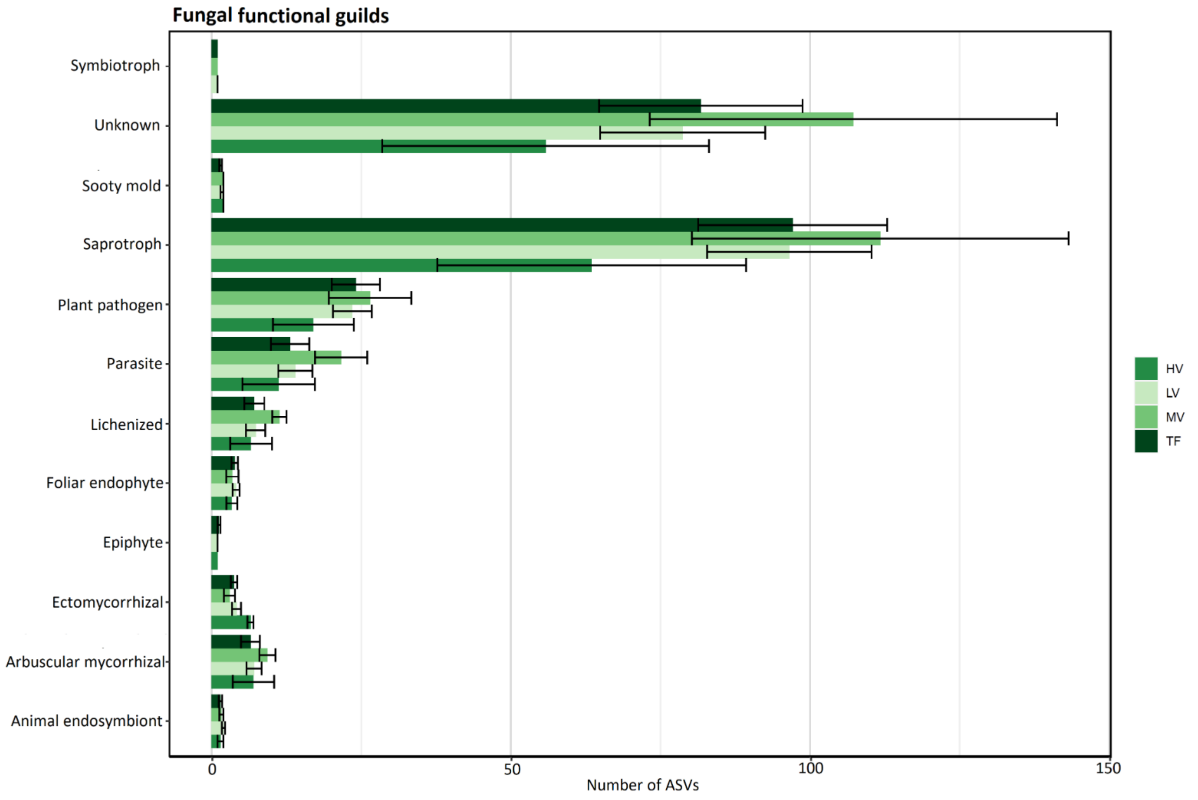

Fig. A2. Guild of fungi observed in the Juruá terra firme (TF; not seasonally flooded), high várzea (HV; flooded 0-1 mo/yr); mid várzea (MV; flooded 2-4 mo/yr); and low várzea (LV; flooded 5-12 mo/yr).

References:

GUARDIOLA, M., URIZ, M.J., TABERLET, P., COISSAC, E., WANGENSTEEN, O.S. & TURON, X. 2015. Deep-sea, deep-sequencing: metabarcoding extracellular DNA from sediments of marine canyons. PLoS One 10(10):e0139633.

KLINDWORTH, A., PRUESSE, E., SCHWEER, T., PEPLIES, J., QUAST, C., HORN, M. & GLÖCKNER, F.O. 2013. Evaluation of general 16S ribosomal RNA gene PCR primers for classical and next-generation sequencing-based diversity studies. Nucleic Acids Res. 41(1):e1–e1.

RITTER, C.D., ZIZKA, A., ROGER, F., TUOMISTO, H., BARNES, C., NILSSON, R.H. & ANTONELLI, A. 2018. High-throughput metabarcoding reveals the effect of physicochemical soil properties on soil and litter biodiversity and community turnover across Amazonia. PeerJ 2018(9):e5661.

Paper III

Forest Ecology and Management 473 (2020) 118297

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Forest type affects the capacity of Amazonian tree species to store carbon as woody biomass

Yennie K. Bredin[a,*], Carlos A. Peres[b,c], Torbjørn Haugaasen[a]

[a] *Faculty of Environmental Sciences and Natural Resource Management, Norwegian University of Life Sciences, Ås, Norway*
[b] *School of Environmental Sciences, University of East Anglia, Norwich NR47TJ, UK*
[c] *Departamento de Sistemática e Ecologia, Universidade Federal da Paraíba, João Pessoa, Paraíba, Brazil*

A R T I C L E I N F O

Keywords:
Biomass
Wood specific gravity
Floodplain forest
Wood density
Terra firme forest
Amazon
Phytomass

A B S T R A C T

For tropical tree species, wood density can vary greatly both within and between species depending on environmental conditions. In Amazonian seasonally flooded forests, yearly flood pulses influence tree growth and floodplain trees have developed specialised strategies to cope with prolonged submersion during flooding. We therefore hypothesised that seasonal floods significantly affect the capacity of trees to store carbon as woody biomass per unit volume and that forest hydrology would be an important factor in determining above-ground woody biomass and carbon stocks across the Amazon Basin. To test these hypotheses, we collected and analysed wood cores from 44 species occurring in both seasonally flooded (*várzea*) forests and adjacent unflooded (*terra firme*) forests along the Juruá River, western Brazilian Amazon. We used wood specific gravity (WSG) as a proxy of woody biomass and carbon. We compared WSG values within species, genera and families and found higher WSG in unflooded forest trees compared to their conspecifics in seasonally flooded várzea. Moreover, the effect of forest type on WSG was strongest at the family level and weakest at the species level. We further assessed the implications of WSG accuracy on above-ground woody tree biomass and found significant differences in AGWB as a function of WSG. Again, the differences became greater with lower taxonomic specificity, but also increased with lower site-specificity and greater tree dimensions. In conclusion, habitat specific WSG is important to quantify and map the spatial distribution of above-ground woody biomass and carbon in Amazonian forests.

1. Introduction

Amazonia represents the largest remaining tract of intact forests and the most species-rich biome on Earth. Forest areas of the Amazon Basin cover approximately 5 million km^2 and contains more than 10,000 tree species (ter Steege et al., 2019). Of these, 8,049 species have been taxonomically verified and are represented by voucher specimens in herbaria (ter Steege et al., 2019). However, this forest domain is not homogenous and contains several different forest types. Upland, or unflooded, forests occur above the flood level of rivers and lakes. Generically, unflooded forests are referred to as terra firme forests, but based on soil properties and vegetation cover, terra firme forests may be classed into several types (Prance and Gardens, 1985; Salovaara et al., 2004; Shepard et al., 2001). Some examples include savanna forests on nutrient poor white sand soils, liana forests on mineral-rich soils, and interfluvial upland forests dominated by palms or different tree species (Murça Pires, 1984; Prance and Gardens, 1985). In addition, dry season length, topography and the underlying geology and forest dynamics seem to be main drivers of terra firme compositional, structural and functional diversification (Baker et al., 2004; Higgins et al., 2015; Salovaara et al., 2004; ter Steege et al., 2006; Terborgh and Andresen, 1998). Such changes may be gradual and give rise to several types of transitional forests. Among these, one less well documented forest type is the unflooded paleo-várzea that occurs on old várzea sediments, which are no longer under direct influence of seasonal floods. Similarly, floodplain forests that occur on floodplains along rivers and lakes may be categorised based on the properties of floodwaters, the frequency and duration of floods, soil properties, and their plant communities (Junk et al., 2011b).

The largest categories of floodplain forests include igapó forests inundated by black-, or clear water, which are nutrient poor and rich in organic solutes. Várzea forests are inundated by white-waters, which carry high amounts of suspended, nutrient-rich sediments. Seasonally inundated paleo-várzeas constitute an intermediate floodplain type that was once flooded by white-waters but are now inundated by black or clear water (Assis et al., 2015a; Junk et al., 2011b, 2011a). Of these, the

---

* Corresponding author.
E-mail address: yennie.bredin@nmbu.no (Y.K. Bredin).

https://doi.org/10.1016/j.foreco.2020.118297
Received 18 January 2020; Received in revised form 8 May 2020; Accepted 1 June 2020

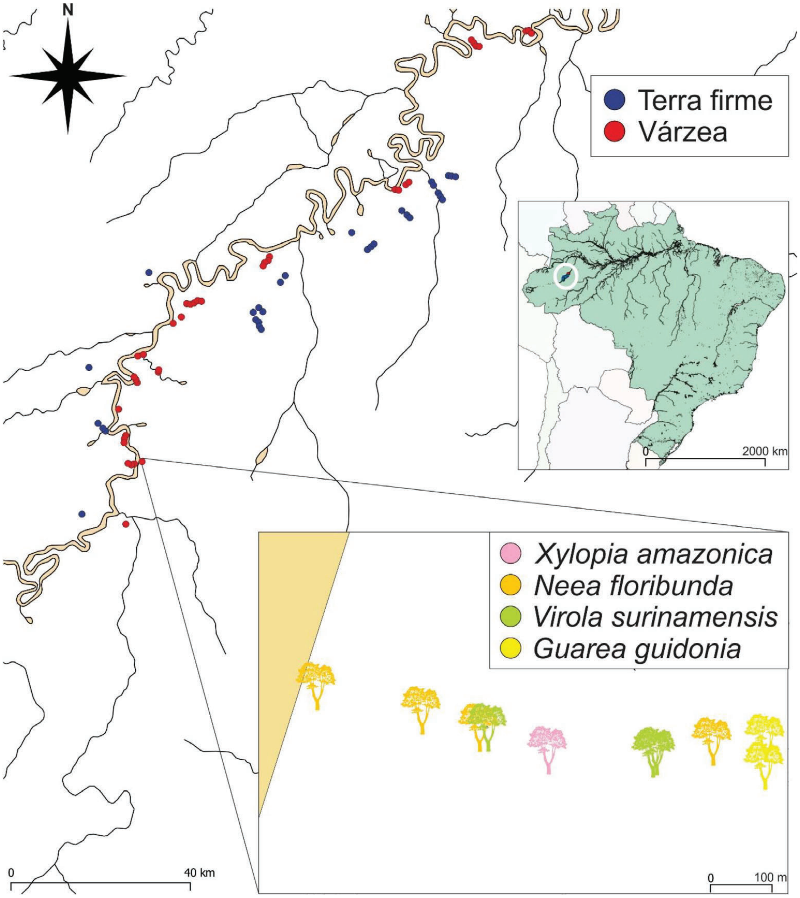

Fig. 1. Map showing the study area in western Brazilian Amazonia (indicated by the white circle in the inset map) and localities of sample trees in terra firme (blue) and várzea (red) along 150 km of the Juruá River (in beige). Smaller rivers and lakes are shown as black lines and in beige, respectively. The bottom-right submap shows the spatial distribution of 10 individual sample trees belonging to four species in one locality. The shortest distance between individual trees at this locality was 7 m. The map was generated in QGIS v.3.12.2 using background maps from the GADM database (Development, 2020; GADM database, 2015). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

várzea floodplains are the most extensive. They cover around 530,000 km^2, at least 270,000 km^2 of which are colonized by forests (Hess et al., 2015, 2003).

Previous studies exploring the ecology, succession and colonization of floodplain forests have found that the annual flood is a major driver of forest composition and structure (Arias et al., 2016; Assis et al., 2015b; Junk et al., 2011a; Targhetta et al., 2015; Wittmann et al., 2013, 2006a). Consequently, there is a clear zonation of tree communities along the hydro-topographic and successional gradients, with highly specialised wetland tree species occurring where flooding is most prolonged (e.g. Wittmann et al., 2006a). Additionally, seasonally inundated várzea forests tend to feature lower statured trees and a larger number of species typically representing light-wooded genera compared to their unflooded forest counterparts (e.g. Myster, 2016; Parolin, 2002; Wittmann et al., 2006b). Hydroperiod may thus drive variation in biomass by influencing tree dimensions, stem density and stand-level WSG in várzea forests, partly because of either succession or changed species composition along the flooding gradient. Due to these apparent differences in forest dynamics, forest structure and tree species composition, above-ground woody biomass (AGWB) is highly variable across the Amazon Basin (Phillips et al., 2019). Moreover, wood properties, such as wood density, fluctuate within species depending on growth conditions both within and among forests (Fearnside, 1997; Nogueira et al., 2008, 2005; Parolin, 2002; Wittmann et al., 2006b). Although such variation has been documented for Amazonian trees, it is rarely incorporated into forest biomass estimates.

Here, we question to what extent WSG values from unflooded forests reflect the relationship between local tree species and AGWB in várzea floodplain forests, given that the seasonal flood pulse affects tree growth and floodplain trees have developed particular strategies to cope with prolonged below-ground anoxic conditions (Junk et al., 2010; Parolin, 2009, 2001). Indeed, we expect generalist species that straddle the boundary of both flooded and unflooded forest to exhibit differences in wood density across forest types. Consequently, we hypothesise that seasonal floods significantly affect the amount of carbon stored as woody biomass per unit volume in tree species occurring across flooded and unflooded forests, and that forest type is an important determinant of AGWB and carbon stocks beyond the level of species composition.

We therefore collected and analysed wood cores from 44 species occurring in both seasonally flooded várzea forests and adjacent terra firme forests in the central Juruá River basin. We use wood specific gravity (WSG) as a proxy of wood density to first answer the question (1) How does forest type influence the ability of trees to store carbon as woody biomass per unit volume across Amazonian flooded and unflooded forests? Next, we apply different WSG values to estimate above-ground tree woody biomass and ask (2) To what extent does accuracy in WSG affect above-ground woody biomass and carbon stock estimates at the level of individual trees across Amazonian flooded and unflooded forests? We conclude by providing some recommendations on applying WSG values across várzea and terra firme forests to quantify and map the spatial distribution of AGWB and carbon stocks across the Amazonian forest macro-mosaic.

2. Methods

2.1. Study area

This study was conducted in the central Juruá River basin, western Brazilian Amazon. This is a region poorly represented by floristic inventories (Feeley, 2015). It includes areas within the Uacari Sustainable Development Reserve (RDS Uacari, 632,949 ha) and neighbouring forests located outside the reserve along 150 km of the Juruá River. The current work was performed in structurally intact seasonally flooded várzea forests (flooded for ca. 1–10 months annualy; Hawes et al., 2012) and unflooded forests on paleo-várzea sediments since long abandoned by the Juruá River (Mesquita de Azevedo et al., 2010), located between 05°08′S, 67°01′W to 05°87′S, 67°88′W (Fig. 1). The terra firme forests of this study should thus be referred to as unflooded paleo-várzea forests. However, since unflooded paleo-várzea is not under the influence of seasonal floodwaters they are fundamentally different from, and must not be confused with, seasonally inundated paleo-várzea forests (cf. Assis et al., 2015a; Junk et al., 2011b, 2011a). For simplicity, the unflooded paleo-várzea forest is herein called terra firme.

The climate of the Juruá region is wet-tropical, with annual temperatures and rainfall averaging 27.1 °C and 3,679 mm, respectively (Hawes and Peres, 2016). The elevation within the study area ranged between 67 and 153 m above sea level (masl) for unflooded forests and 68–137 masl for várzea forests.

2.2. Wood specific gravity

The specific gravity of wood is the numerator of wood specific density and describes the relationship between the dry mass of wood at moisture content 0 and the volume of wood at its saturation point in relation to the density of water (Skogstad, 2009). It is thus a measure of the fraction of structural matter in wood (Williamson and Wiemann, 2010). As such, wood specific gravity (WSG) relates to both estimates of biomass and wood-bound carbon in woody vegetation (Chave et al., 2014, 2005; Fearnside, 1997). Whereas different wood gravity values are widely applied within the timber industry for different purposes, including calculating weights and evaluating wood quality for construction purposes (Skogstad, 2009), WSG is also an important functional trait in forest ecology studies that is central to tree life history, growth strategies and forest ecosystem services (cf. Parolin, 2002; Peres et al., 2016; Souza et al., 2018).

The most widely used wood gravity measure within forest ecological studies is wood basic gravity (WBG). WBG operates with green/fresh volumes of wood in relation to dry weights (Skogstad, 2009). It is therefore widely assumed that WBG better relates to the ecological properties of standing live trees than other wood gravities (Williamson and Wiemann, 2010). However, because WBG operates with green volumes, the moisture content of samples may vary (Simpson, 1993; Skogstad, 2009). A variation in intraspecific WBG across habitats may therefore not only reflect a difference in intrinsic abilities of trees to store carbon as woody biomass, but also the variation in water availability between habitats and among sites. Therefore, we use WSG whereby moisture content among samples is standardised at the water saturation point of the wood (Simpson, 1993; Skogstad, 2009).

2.2.1. Data acquisition

Between September 2016 and November 2017, we collected wood cores from 398 individuals belonging to 44 tree species occurring in both seasonally flooded várzea forest and adjacent terra firme forest along the central reaches of the Juruá River (Table S1). We used a 5.15 mm Haglöf increment borer to sample trees with a diameter at breast height (DBH) of ≥ 10 cm. We extracted wood cores perpendicular to the bark at a height between 1 m and 1.3 m above ground. Where trees had buttressed roots, we extracted wood cores from above the buttress whenever possible. Cores were stored and transported in paper straws. To protect the cores from moisture and fungal attacks, samples were dried and kept with silica gel until they were analysed at the vegetation ecology lab at the National Institute for Amazon Research (INPA), Manaus.

2.2.2. Lab analysis

For this study, we only considered wood cores that covered at least 80% of the bole radius at breast height and included bark. To determine the WSG, wood cores were first saturated by submerging them in water for a minimum of 72 h. Depending on the length of the cores, we divided them into two or more segments. The segments were cut perpendicular to the bark and divided into the following sections; bark, 0–50 mm, 50 mm-pith (or middle based on the length of the radius at breast height), and beyond the middle. Where possible, heartwood and pith were visually determined, and the samples divided into further sub-segments to avoid an overrepresentation of heartwood and pith on the WSG values (Plourde et al., 2015). Saturated wood volume was measured by the water displacement method, using a fine needle to submerge the segments into a beaker of water placed on a scale with precision 0.01 g (Wiemann and Williamson, 2012). We used tap water kept at 24 °C ± 0.6 °C, equivalent to a density of approximately 0.9973 g/cm^3. After recording the saturated wet volumes, we dried the wood cores at 107.5 °C ± 2.5 °C for 72 h. This temperature is slightly higher than what is typically recommended (101–105 °C) (Williamson and Wiemann, 2010). Consequently, WSG measures presented here could be conservative as some volatile compounds may have evaporated (Nogueira et al., 2005). We recorded the dry weights of wood core segments using a scale with a precision of 0.01 g.

To calculate WSG values, we followed the method used by Muller-Landau (2004). In brief, we calculated a single weighted average value per tree based on the values for each segment weighted by the cross-sectional area of the trunk that the segments represented. For trees with replicate wood cores, we averaged the WSG based on the replicas.

2.3. Statistical analysis

To evaluate how WSG vary within tree species, genera and families across terra firme and várzea forests, we adapted the methods used by Mori et al. (2019). We calculated the mean WSG at breast height and associated standard deviation for each species, genus, and family. We paired these values across the two forest types at the level of taxonomic identity to visually inspect differences in WSG between forest types across taxonomic levels using strip plots (R package Lattice v.0.20–38, Sarkar, 2008), and boxplots (R package ggplot2 v.3.3.0, Wickham, 2016). To evaluate the influence of forest type on WSG, we used a linear mixed model for each taxonomic level with forest type as a fixed effect and taxonomic identity as a random effect (Zuur et al., 2013). For the following analyses we used the R packages lmerTest v.3.1–1 (Kuznetsova et al., 2017) and psycho v.0.4.0 (Makowski, 2018). For each taxonomic level, we compared a null model only considering taxonomic identity (R syntax: $\text{model}_0 = \text{WSG} \sim (1|\text{species/genus/family}))$, to a model considering both forest type and taxonomic identity (R syntax: $\text{model}_1 = \text{WSG} \sim \text{Forest type} + (1|\text{species/genus/family})$). To see if models differed with the addition of forest type, we calculated a likelihood ratio by dividing the log-likelihood of the full model (model_1) by the log-likelihood of the null model (model_0). To assess the relative importance of forest type compared to the influence of taxonomic identity, we calculated the marginal and conditional R squares (mR^2 ; cR^2) of the full models (Makowski, 2018; Nakagawa and

Schielzeth, 2013). The mR^2 describes the relative influence of the fixed effect (Forest type) and the cR^2 describes the total explanatory power of both the fixed and random effect for each model (Forest type + taxonomic identity). Similar mR^2 and cR^2 values indicate a negligible influence of taxonomic identity on WSG.

To assess the influence of accuracy in WSG on above-ground woody biomass at the level of individual trees, we used the BIOMASS R package v.2.1.1 (Réjou-Méchain et al., 2017). We calculated the biomass of each tree at each taxonomic level using individual-specific WSG, habitat specific mean WSG, mean WSG from the other forest type (e.g. flooded for unflooded trees and vice versa), and the mean WSG for tropical South America from the Global Wood Density Database (Chave et al., 2009; Zanne et al., 2009). We inspected differences in AGWB estimates at each taxonomic level as a result of the different WSG methods visually through the ggplot function, R package ggplot2 v.3.3.0 (Wickham, 2016, 2009). We plotted the individual AGWB estimates against tree diameter (cm) and tree height (m) and fit linear models to the data through a smoother (Wickham, 2009). To evaluate the influence of accuracy in WSG on AGWB, we fit a linear mixed model with WSG as a fixed effect at each taxonomic level using the R package nlme v.3.1–142 (Pinheiro et al., 2019). Because above-ground woody biomass was estimated for the same individuals several times, we set individual as a random effect and assumed a linear autocorrelation within each individual (R syntax: $\text{model}_1 = \text{AGWB} \sim \text{WSG}$, random = $\sim 1|\text{individual}$, correlation = corLin(form = $\sim \text{WSG}|\text{individual}$). At each taxonomic level, we compared the full model to a null model including a fixed effect of 1 and the random effect (R syntax: $\text{model}_0 = \text{AGWB} \sim 1$, random = $\sim 1|\text{individual}$) through the rcompanion package v.2.3.25 (Mangiafico, 2020). For each full model, we then ran a post-hoc Tukey-adjusted comparison applying the multcompView v.01–8 (Graves et al., 2019), Lsmeans v.2.30–0 (Lenth, 2016), and multcomp v.1.4–13 (Hothorn et al., 2008) packages.

Following the example of Nogueira et al. (2005), we calculated the fractional difference in WSG across the two forest types, e.g. formula 1 (example formula for calculating the fractional difference in WSG using information from unflooded trees to predict the WSG of flooded trees): $\frac{\left(\sum \frac{WSG_{flooded}}{N} - \sum \frac{WSG_{unflooded}}{N}\right)}{\sum \frac{WSG_{flooded}}{N}}$, where N is the total number of observations within each group. In addition, we calculated the mean differences in kg / tree, formula 2b: $\left(\frac{\sum AGWB_{individual} - \sum AGWB_x}{N}\right) \times 1000$, the overall differences in Mg AGWB, formula 2a: $\sum AGWB_{individual} - \sum AGWB_x$, and the differences in percent, formula 2c: $\frac{\sum AGWB_{individual} - \sum AGWB_x}{\sum AGWB_{individual}} \times 100$, for comparisons between AGWB estimates based on the individual WSG values and each of the other WSG methods. In formulas 2a-2c, $AGWB_{individual}$ is AGWB estimated using individual WSG, $AGWB_x$ is AGWB estimated using a different WSG method × , e.g. habitat specific mean WSG, and N is the total number of observations. Hence, we suggest correction levies for WSG values used in AGWB and carbon estimates across seasonally flooded and unflooded forests and show the potential influence that such corrections might have on AGWB estimates. All analyses were performed using the R platform, version 3.5.2 (R Environment R Core Team, 2018).

3. Results

Of the 44 tree species examined here (Table S1), only eight species had three or more individuals sampled in each forest type and are therefore retained in the subsequent analyses. A floristic inventory from the same region (YKB, unpubl. data) showed that the eight focal species represented approximately 3% and 8% of all individuals and 2% and 8% of the total basal area in terra firme and várzea, respectively. At genus level, 12 genera had a minimum sample of five individuals per forest type, and at family level, 14 families had a minimum of five individuals sampled per forest type (Table 1). The 12 genera represented 35% and 24% of all individuals (45% and 27% of the total basal area) and the 14 families represented 72% and 66% of all individuals (76% and 71% of the total basal area) in terra firme and várzea, respectively.

In general, within-species, within-genus and within-family WSG values were higher in terra firme forest compared to várzea. However, the trend was not unidirectional for all species/genera/families and for some the WSG was almost the same across forest types or higher in várzea. Nonetheless, forest type had a significant effect on overall mean WSG across all taxonomic levels (Fig. 2; Table 2). Moreover, the influence of forest type on WSG increased from species to family level. The influence of forest type on WSG was thus strongest at the family level and weakest at the species level (Table 3).

Comparisons of tree AGWB based on different WSG accuracy levels show that there are significant differences in AGWB as a function of WSG and that these differences become greater with lower taxonomic specificity (Table 4, Fig. 3). Differences among AGWB estimates also become greater with increased tree diameter and tree height. Thus, discrepancies among AGWB estimates are greatest for the largest trees (Fig. 3). When terra firme and várzea trees were analysed together, AGWB estimates based on global mean WSG were always significantly different from the AGWB based on individual WSG (Table 4, Fig. 3). Habitat specific WSG always resulted in AGWB estimates that were most similar to the reference values based on individual WSG (Table 4, Fig. 3).

4. Discussion

We found that várzea trees generally had lower WSG compared to their conspecifics in terra firme. At the genus and family levels, this trend became even clearer. Hence, forest type and hydrology clearly affect within-species, within-genera, and within-family WSG of Amazonian trees.

To our knowledge, this is the first study to investigate intraspecific wood gravity across Amazonian forest types with a focus on implications for above-ground woody biomass (AGWB) estimates. Whereas previous studies have demonstrated that shifts in species composition, abundance and tree dimensions across forest types are important determinants of AGWB and carbon stocks in the Amazon, our results imply that the influence of forest type on WSG is an important additional factor to consider in forest biomass estimates. In addition, by comparing AGWB based on different WSG accuracies at the level of individual trees, we found that greater taxonomic accuracy and greater habitat- and geographic specificity always result in better AGWB estimates (assuming that individual WSG best reflects true AGWB). Hence, we show that the difference in intraspecific wood gravity between unflooded and flooded forests result in an overestimation of woody biomass for várzea trees when WSG values from terra firme forests are used. Our results therefore support previous studies that found flooding to be an important determinant of WSG in floodplain trees, and that ignoring habitat-related variability in wood densities leads to large biases in woody biomass estimates (e.g. Phillips et al., 2019; Wittmann et al., 2006b). In fact, using WSG values derived from terra firme forest to predict AGWB in várzea trees or vice versa, even at the species-specific level, would lead to an estimation error of 5–11%. At higher taxonomic levels and for larger trees, the estimation errors become greater. Given the obvious influence that large trees have on the distribution of AGWB across tropical lowland forests (Ali et al., 2019; Slik et al., 2013), we may therefore expect that using habitat non-specific WSG to estimate and predict the distribution of forest biomass may have serious consequences for the mapping of AGWB.

The overlap in species composition between várzea and terra firme forests of the central Juruá may be as high as 44.5% (YKB, unpubl. data). It is likely that a similar overlap can be found elsewhere across Amazonia. Studies that rely on data from the Global Wood Density Database (Chave et al., 2009; Zanne et al., 2009) for biomass estimates in várzea forest, and those that attempt to provide AGWB estimates for

Table 1

Mean WSG at breast height and standard deviation (SD) per forest type and taxonomic level. Number of cores is the total number of individuals that were analysed to obtain WSG and SD values.

Taxonomic level	Scientific name	Unflooded			Flooded		
		No. cores	Mean WSG	SD	No. cores	Mean WSG	SD
Species	*Oxandra xylopioides*, Annonaceae	4	0.86	0.21	4	0.66	0.00
	Symphonia globulifera, Clusiaceae	4	0.59	0.04	3	0.58	0.03
	Theobroma microcarpum, Malvaceae	4	0.51	0.08	5	0.41	0.02
	Carapa guianensis, Meliaceae	5	0.58	0.03	15	0.58	0.07
	Guarea guidonia, Meliaceae	4	0.59	0.06	3	0.50	0.02
	Virola calophylla, Myristicaceae	8	0.43	0.03	19	0.44	0.09
	Virola surinamensis, Myristicaceae	4	0.45	0.04	16	0.42	0.24
	Leonia glycycarpa, Violaceae	5	0.56	0.02	11	0.49	0.12
Genus	*Guatteria*, Annonaceae	9	0.41	0.10	13	0.42	0.08
	Licania, Chrysobalanaceae	16	0.76	0.06	10	0.64	0.07
	Hevea, Euphorbiaceae	6	0.51	0.04	16	0.46	0.05
	Eschweilera, Lecythidaceae	42	0.71	0.08	43	0.63	0.06
	Theobroma, Malvaceae	12	0.55	0.06	16	0.40	0.04
	Carapa, Meliaceae	6	0.58	0.03	15	0.58	0.07
	Guarea, Meliaceae	7	0.62	0.06	7	0.54	0.04
	Brosimum, Moraceae	7	0.68	0.08	5	0.58	0.04
	Virola, Myristicaceae	22	0.46	0.06	43	0.41	0.16
	Neea, Nyctaginaceae	9	0.52	0.08	14	0.41	0.07
	Pouteria, Sapotaceae	5	0.68	0.09	33	0.61	0.08
	Leonia, Violaceae	5	0.56	0.02	14	0.48	0.11
Family	Annonaceae	17	0.54	0.22	90	0.44	0.10
	Chrysobalanaceae	18	0.76	0.06	10	0.64	0.07
	Clusiaceae	7	0.56	0.13	39	0.60	0.10
	Euphorbiaceae	19	0.58	0.08	47	0.43	0.09
	Lauraceae	8	0.63	0.10	20	0.50	0.10
	Lecythidaceae	49	0.70	0.09	64	0.59	0.09
	Leguminosae	17	0.63	0.12	85	0.56	0.14
	Malvaceae	21	0.52	0.12	54	0.37	0.07
	Meliaceae	15	0.62	0.08	23	0.56	0.07
	Moraceae	14	0.65	0.07	17	0.52	0.10
	Myristicaceae	40	0.54	0.11	45	0.41	0.15
	Nyctaginaceae	9	0.52	0.08	15	0.41	0.06
	Sapotaceae	15	0.61	0.08	57	0.60	0.08
	Violaceae	6	0.58	0.04	22	0.51	0.12

the basin as a whole, may thus carry a significant estimation error. This is because local WSG variation across habitat types is not appropriately accounted for. For our focal trees, for example, we found an estimation error of up to 30% when using Tropical South American mean WSG compared to individual WSG. This correspond well to findings from moist tropical Africa where Bastin et al. (2015), found up to 40% difference in tree AGWB while evaluating the effects of local WSG variations and global wood density data on tree AGWB. Conversely, at the species level, we find no difference in AGWB estimates based on global default WSG or species mean WSG for terra firme trees.

Within-species, within-genus, and within-family differences in WSG values were, however, not unidirectional across várzea and terra firme in this study. For some species, genera and families WSG was greater or similar in várzea trees compared to their terra firme conspecifics but WSG values were mostly higher in terra firme trees. Whether these directional differences in WSG are due to variation among species in their responses to soil nutrient availability or hydrological stressors across habitats cannot be determined from the current study. However, flooding arrests tree growth for part of the year, thereby likely stimulating rapid growth during the low-water season (approx. August to January), especially in seedlings and saplings (Wittmann et al., 2010). This growth may be further promoted by the high soil fertility on várzea floodplains. In addition, seasonal changes in water-level introduce elements of mechanical stress in floodplain habitats through the erosion of land and the deposition of alluvial sediments (Wittmann et al., 2010). In response, floodplain trees have developed special tissues and strategies to cope with the variable environmental stressors, which in turn may influence WSG (e.g. Parolin et al., 2002). Hence, we speculate that high soil nutrient availability, rapid seasonal tree growth, and specialised tissues in várzea forest trees are likely to cause lower wood gravities compared to conspecifics in terra firme, particularly in early-successional species.

This would be consistent with Parolin (2002) and Wittmann et al (2006b) who found increasing wood gravities from pith to bark in early successional tree species, but decreasing trends in late successional species. These findings are expected under the assumption that light-wooded trees are associated with fast growth rates (Bastin et al., 2015). In other words, floodplain trees and pioneer species invest in rapid growth during the establishment phase (= light heartwood), and later in structural stability (harder outer wood layer). Conversely, slower growth rates typical of late successional species and assumed investment in greater structural stability during the establishing phase of saplings, result in harder heartwood. However, the 35 floodplain species investigated by Parolin (2002) did not exhibit unidirectional radial changes in wood gravity. These intraspecific variations in both radial trends across different successional stages (cf. Parolin, 2002) and mean intraspecific WSG across habitats (cf. this study) may suggest intraspecific phenotypic plasticity in tree responses to different environmental stressors.

To predict tree survival rates under changing environmental conditions, we need information about how different species respond to abiotic and biotic stressors, and other sources of tree mortality (Yang et al., 2018). Hence, information about intraspecific adaptation in trees to varying environments could be used to predict changes in tree species composition and carbon stocks under, for example, changing climates and forest hydrology (Yang et al., 2018). However, to better

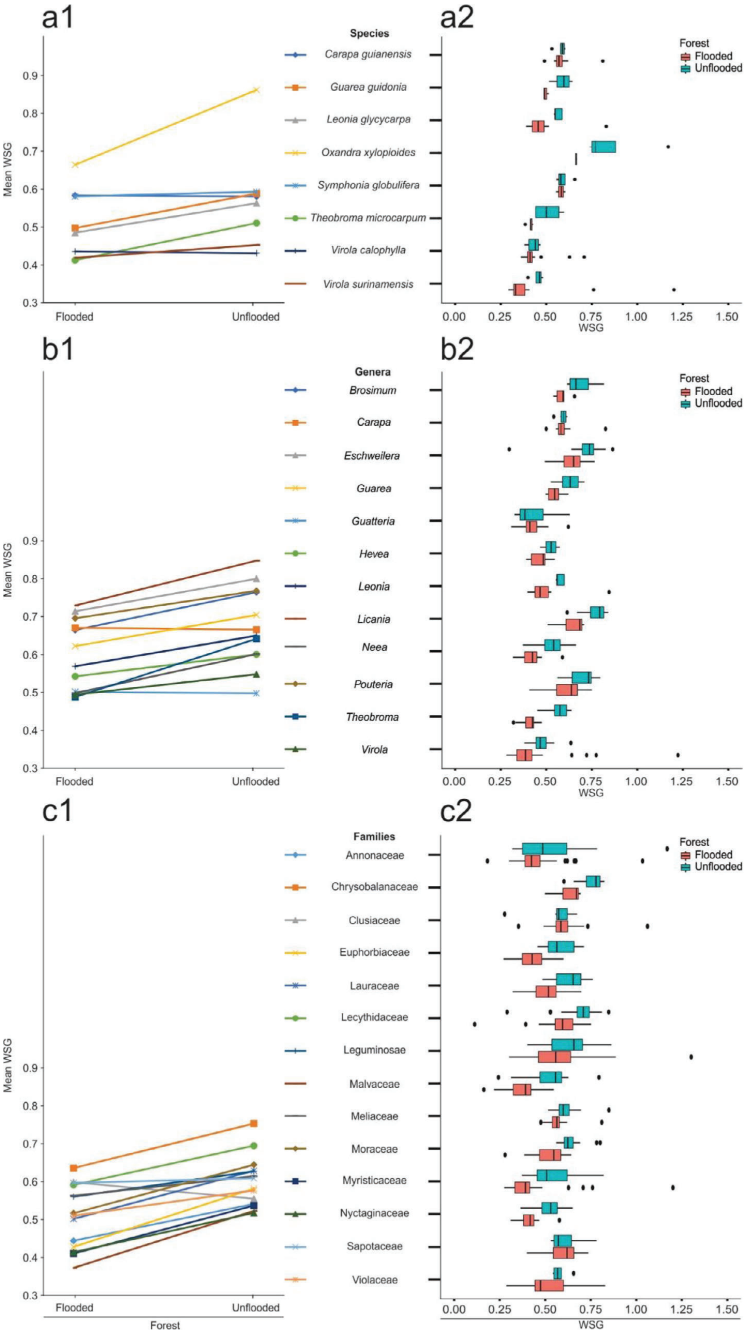

Fig. 2. Wood specific gravity (WSG) at breast height for (a) tree species, (b) genera, and (c) families occurring in both terra firme and várzea forests, with a) n ≥ 3, b) n ≥ 5, and c) n ≥ 5 sampled individuals per forest type. Strip plots (a1-c1) show the intraspecific difference in mean WSG at breast height between flooded (várzea) and unflooded (terra firme) forests. Boxplots (a2-c2) show the intraspecific ranges in WSG within each forest type and taxonomic level. Colour-coded boxes represent the interquartile ranges. Thick black lines indicate median WSG per forest type; whiskers represent one and a half times the interquartile ranges, and solid dots represent outlier observations.

discern potential environmental thresholds in tree survivorship rates and map gradients of WSG change within species and tree communities among forest types on different soil types with varying water availability, we need more information about local WSG from different interfluvial regions and vegetation types across the Amazon and other tropical forest regions.

5. Conclusions:

Reducing biases in AGWB estimates to better account for the spatial

Table 2

Variation in within-species, within-genus, and within-family WSG at breast height across seasonally flooded and unflooded forests. The columns indicate taxonomic level of analyses, β-coefficient, p-value, marginal R^2 (variance explained by the fixed effect, i.e. Forest type; r^2m), conditional R^2 (variance explained by the fixed effect + random effect, i.e. Forest type + Taxonomic identity; r^2c), and likelihood ratio (p-value indicates if models differ; ratio was calculated as model$_1$ / model$_{0,}$ in R-syntax: WSG ~ Forest type + (1| Taxonomic identity) / WSG ~ (1| Taxonomic identity)).

Taxonomic level	WSG ~ Forest type + (1|Taxonomic identity)				likelihood	
	β-coefficient	p-value	r^2m	r^2c	ratio	p-value
Species	−0.050	< 0.05	0.023	0.434	1.031	< 0.05
Genus	−0.077	< 0.001	0.079	0.581	1.090	< 0.001
Family	−0.099	< 0.001	0.150	0.405	1.107	< 0.001

Table 3

Mean WSG at breast height and standard deviation (SD) per forest type (TF = terra firme, VZ = várzea) and taxonomic level for species with minimum three sampled individuals per forest type (Min. idvs.), genera and families with minimum five sampled individuals per forest type. Number of cores is the total number of individuals from which wood cores were analysed per forest type and taxonomic level. WSG adjustments describe the correction levy up (↑) or down (↓) in percent (%) across forest types (From → To) for WSG values from cores sampled at breast height.

Taxonomic level	Forest type	Min. idvs.	No. cores	Mean WSG	SD	From → To	WSG adjustment (%)	Up↑/Down↓
species	TF	3	38	0.56	0.14	uF → F	12.72	↓
species	VZ	3	76	0.49	0.15	F → uF	14.58	↑
genus	TF	5	146	0.61	0.13	uF → F	15.57	↓
genus	VZ	5	229	0.52	0.13	F → uF	18.45	↑
family	TF	5	255	0.61	0.13	uF → F	17.18	↓
family	VZ	5	588	0.51	0.13	F → uF	20.75	↑

Table 4

Differences in AGWB as a function of WSG accuracy. All comparisons use tree AGWB based on individual WSG as a reference value. “Other habitat” denotes WSG from várzea for terra firme trees and vice versa for várzea trees. “Global” WSG refers to Tropical South American mean values retrieved from the Global Wood Density Database (Chave et al., 2009; Zanne et al., 2009). Differences are reported as mean differences in kg per tree, in Mg for all trees combined, and in percent. Negative and positive values indicate overestimations and underestimations in AGWB, respectively.

	Difference in AGWB for terra firme trees			Difference in AGWB for várzea trees			Overall Difference in AGWB		
WSG	Kg/tree	Mg total	%	Kg/tree	Mg total	%	Kg/tree	Mg total	%
Habitat specific species mean	−1.7	−0.064	0	−13.5	−1.016	−4	−9.6	−1.080	−3
Other habitat species mean	17.4	0.643	5	−35.5	−2.665	−11	−18.1	−2.022	−5
Global default mean	−1.7	−0.062	0	−29.9	−2.242	−9	−20.6	−2.304	−6
Habitat specific genus mean	4.9	0.710	2	−1.8	−0.411	−1	0.8	0.300	0
Other habitat genus mean	37.8	5.446	12	−30.7	−6.973	−12	−4.1	−1.527	−1
Global genus mean	−80.6	−11.608	−25	−42.9	−9.747	−16	−57.6	−21.355	−20
Habitat specific family mean	−6.7	−1.691	−2	−0.9	−0.544	0	−2.7	−2.235	−1
Other habitat family mean	38.7	9.782	14	−41.3	−24.103	−17	−17.1	−14.322	−7
Global family mean	−16.8	−4.239	−6	−73.8	−43.110	−30	−56.6	−47.350	−22

distribution of wood bound carbon in Amazonian forests and subsequent monitoring are important goals in climate change science and forest ecology. In this study, we show that applying the same WSG values across forest types would lead to significantly biased AGWB and carbon estimates. Since tree species occurring in both terra firme and várzea forests appear to adapt to their local environments, the topography and seasonal floods may not merely determine where different tree species grow, but also how they express key functional traits, such as WSG. To reduce bias in the spatial representation of forest aboveground woody carbon within the Amazon Basin we require more detailed information on tree species composition and habitat specific WSG values. Where habitat specific WSG values are absent, we recommend adjustments of regional WSGs to the local forest type.

CRediT authorship contribution statement

Yennie K. Bredin: Conceptualization, Methodology, Project administration, Investigation, Data curation, Formal analysis, Resources, Writing - original draft, Writing - review & editing, Visualization. **Carlos A. Peres:** Conceptualization, Funding acquisition, Methodology, Writing - review & editing, Supervision, Validation. **Torbjørn Haugaasen:** Conceptualization, Funding acquisition, Methodology, Writing - review & editing, Supervision, Validation.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

This research was funded by the Norwegian University of Life Sciences. We are grateful to Paulo Apóstolo Costa Lima Assunção and Nancy Lorena Maniguaje Rincón at the National Institute for Amazonian Research (INPA) Herbarium for assisting with species identifications. Special thanks to all the field- and lab assistants who contributed to the present study and in particular Rita Homem Pelicano and Laura N. Martins. We also thank Marcos Viejo Somoano for graphical assistance and two anonymous reviewers for constructive comments on an earlier version of this manuscript.

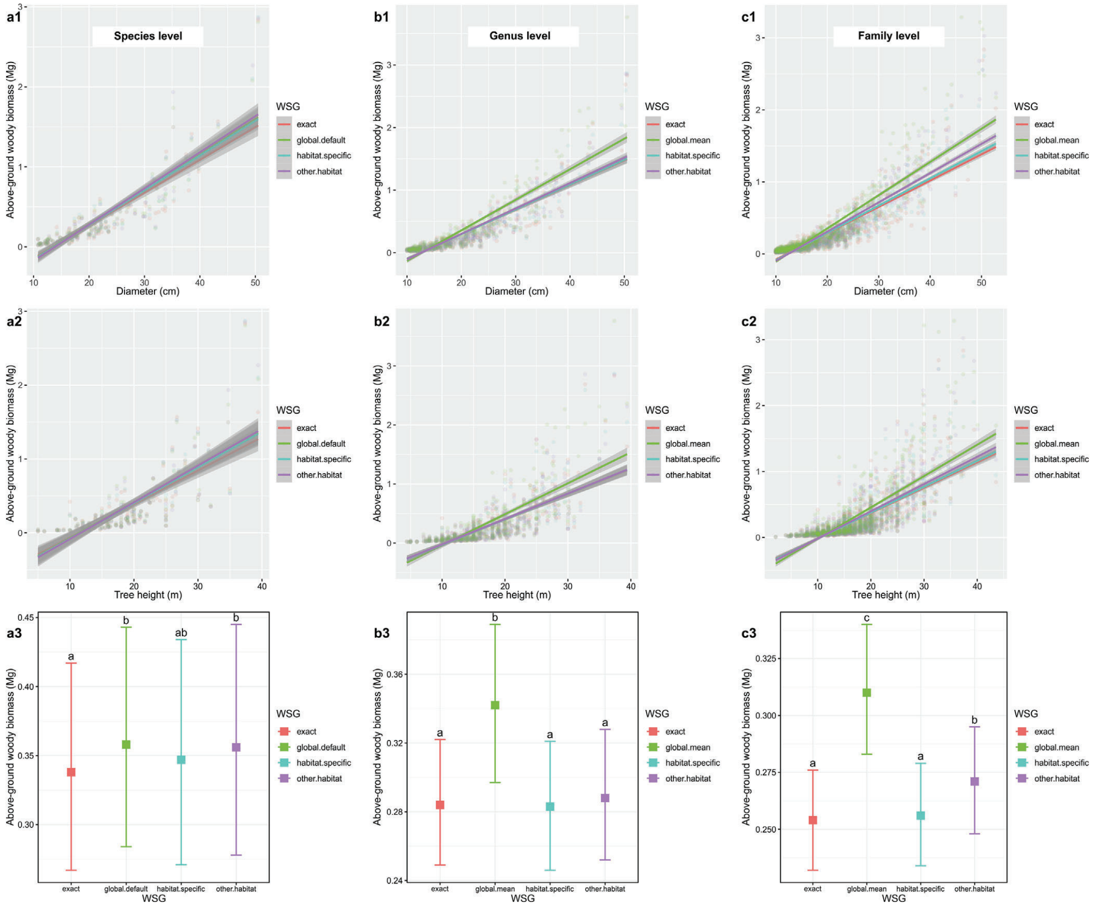

Fig. 3. Above-ground woody biomass (AGWB) calculated at the level of individual trees for a) species, b) genera, and c) families occurring in both terra firme and várzea forests, with a) n ≥ 3, b) n ≥ 5, and c) n ≥ 5 sampled individuals per forest type. Scatter plots (a1-c1) show the trends of variability in tree AGWB in relation to tree diameter in centimetres (cm) as a function of WSG accuracy. Similarly scatter plots (a2-c2) show the trends of variability in tree AGWB in relation to tree height in meters (m) as a function of WSG accuracy. Trends were fit with linear models and show means as solid lines and associated confidence intervals in grey. Boxplots (a3-c3) show mean tree AGWB per accuracy-level as colour-coded boxes where whiskers represent one and a half times the interquartile ranges. Different lower-case letters above the whiskers indicate significant differences in tree AGWB as a function of WSG. Analyses were based on Tukey-adjusted comparisons of means. AGWB estimates were derived using WSG from individual tree cores (“exact”), habitat specific mean WSG (“habitat.specific”), mean WSG from flooded trees for terra firme individuals or vice versa (“other.habitat”) and Tropical South American mean WSG (“global.default” or “global.mean”). WSG set to “global.default” (plots a1-a3), were given as species mean WSG when available, otherwise as genus mean WSG. At the genus-, and family-levels “global.mean” WSG were assigned exclusively at the genus-level (b) or family-level (c).

Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2020.118297.

References

Ali, A., Lin, S.L., He, J., Kong, F.M., Yu, J., 2019. Big-sized trees overrule remaining trees’ attributes and species richness as determinants of aboveground biomass in tropical forests. Glob. Chang. Biol. 25, 2810–2824.

Arias, M.E., Wittmann, F., Parolin, P., Murray-Hudson, M., Cochrane, T.A., 2016. Interactions between flooding and upland disturbance drives species diversity in large river floodplains. Hydrobiologia 1–13. https://doi.org/10.1007/s10750-016-2664-3.

Assis, R.L., Haugaasen, T., Schöngart, J., Montero, J.C., Piedade, M.T.F., Wittmann, F., 2015a. Patterns of tree diversity and composition in Amazonian floodplain paleo-várzea forest. J. Veg. Sci. 26, 312–322. https://doi.org/10.1111/jvs.12229.

Assis, R.L., Wittmann, F., Haugaasen, T., 2015b. Effects of hydroperiod and substrate properties on tree alpha diversity and composition in Amazonian floodplain forests. J. Veg. Sci. 26, 312–322.

Baker, T.R., Phillips, O.L., Malhi, Y., Almeidas, S., Arroyo, L., Di Fiore, A., Erwin, T., Killeen, T.J., Laurance, S.G., Laurance, W.F., Lewis, S.L., Lloyd, J., Monteagudo, A., Neill, D.A., Patiño, S., Pitman, N.C.A., Silva, J.N.M., Martínez, R.V., 2004. Variation in wood density determines spatial patterns in Amazonian forest biomass. Glob. Chang. Biol. 10, 545–562. https://doi.org/10.1111/j.1529-8817.2003.00751.x.

Bastin, J., Fayolle, A., Tarelkin, Y., Bulcke, J., Den, Van, 2015. Wood specific gravity variations and biomass of Central African tree species: The simple choice of the outer wood. PLoS One 10, 1–16. https://doi.org/10.1371/journal.pone.0142146.

Chave, J., Andalo, C., Brown, S., Cairns, M.A., Chambers, J.Q., Eamus, D., Fölster, H., Fromard, F., Higuchi, N., Kira, T., Lescure, J.P., Nelson, B.W., Ogawa, H., Puig, H., Riéra, B., Yamakura, T., 2005. Tree allometry and improved estimation of carbon stocks and balance in tropical forests. Oecologia 145, 87–99. https://doi.org/10.1007/s00442-005-0100-x.

Chave, J., Coomes, D., Jansen, S., Lewis, S.L., Swenson, N.G., Zanne, A.E., 2009. Towards a worldwide wood economics spectrum. Ecol. Lett. 12, 351–366. https://doi.org/10.1111/j.1461-0248.2009.01285.x.

Chave, J., Réjou-Méchain, M., Búrquez, A., Chidumayo, E., Colgan, M.S., Delitti, W.B.C., Duque, A., Eid, T., Fearnside, P.M., Goodman, R.C., Henry, M., Martínez-Yrízar, A., Mugasha, W.A., Muller-Landau, H.C., Mencuccini, M., Nelson, B.W., Ngomanda, A., Nogueira, E.M., Ortiz-Malavassi, E., Pélissier, R., Ploton, P., Ryan, C.M., Saldarriaga, J.G., Vieilledent, G., 2014. Improved allometric models to estimate the aboveground biomass of tropical trees. Glob. Chang. Biol. 20, 3177–3190. https://doi.org/10.1111/gcb.12629.

Development, T.Q., 2020. QGIS Geographic Information System. Open Source. Geospatial Foundation Project.

Fearnside, P.M., 1997. Wood density for estimating forest biomass in the Amazonia. For. Ecol. Manage. 90, 59–87.

Feeley, K., 2015. Are we filling the data void? An assessment of the amount and extent of plant collection records and census data available for tropical South America. PLoS One 10. https://doi.org/10.1371/journal.pone.0125629.

GADM database, 2015.

Graves, S., Piepho, H.-P., Selzer, L., Dorai-Raj, S., 2019. R Package MultcompView: Visualizations of Paired Comparisons. Version 0.1-8. https://cran.r-project.org/package=multcompView.

Hawes, J.E., Peres, C.A., 2016. Patterns of plant phenology in Amazonian seasonally flooded and unflooded forests. Biotropica. https://doi.org/10.1111/btp.12315.

Hawes, J.E., Peres, C.A., Riley, L.B., Hess, L.L., 2012. Landscape-scale variation in structure and biomass of Amazonian seasonally flooded and unflooded forests. For. Ecol. Manage. 281, 163–176. https://doi.org/10.1016/j.foreco.2012.06.023.

Hess, L.L., Melack, J.M., Affonso, A.G., Barbosa, C., Gastil-Buhl, M., Novo, E.M.L.M., 2015. Wetlands of the lowland Amazon Basin: extent, vegetative cover, and dual-season inundated area as mapped with JERS-1 synthetic aperture radar. Wetlands 35, 745–756. https://doi.org/10.1007/s13157-015-0666-y.

Hess, L.L., Melack, J.M., Novo, E.M.L.M., Barbosa, C.C.F., Gastil, M., 2003. Dual-season mapping of wetland inundation and vegetation for the central Amazon basin. Environ. Remote Sens. https://doi.org/10.1016/j.rse.2003.04.001.

Higgins, M.A., Asner, G.P., Anderson, C.B., Martin, R.E., Knapp, D.E., Tupayachi, R., Perez, E., Elespuru, N., Alonso, A., 2015. Regional-scale drivers of forest structure and function in northwestern Amazonia. PLoS One 10, 1–19. https://doi.org/10.1371/journal.pone.0119887.

Hothorn, T., Bretz, F., Westfall, P., 2008. Simultaneous inference in general parametric models. Biometrical J. 50, 346–363.

Junk, W.J., Piedade, M.T.F., Schöngart, J., Cohn-Haft, M., Adeney, J.M., Wittmann, F., 2011a. A classification of major naturally-occurring amazonian lowland wetlands. Wetlands 31, 623–640. https://doi.org/10.1007/s13157-011-0190-7.

Junk, W.J., Piedade, M.T.F., Schöngart, J., Cohn-Haft, M., Adeney, M.J., Wittmann, F., 2011b. A classification of major natural habitats of Amazonian white-water river floodplains (várzeas). Wetl. Ecol. Manag. 31, 623–640. https://doi.org/10.1007/s11273-012-9268-0.

Junk, W.J., Piedade, M.T.F., Schöngart, J., Wittmann, F., Parolin, P., (Eds.), 2010.. Part II Ecological and ecophysiological aspects of Amazonian floodplain forests. In: Amazonian Floodplain Forests Ecophysiology, Biodiversity and Sustainable Management. Springer, pp. 105–313. https://doi.org/10.1007/978-90-481-8725-6.

Kuznetsova, A., Brockhoff, P.B., Christensen, R.H.B., 2017. lmerTest package: tests in linear mixed effects models. J. Stat. Softw. 82, 1–26. https://doi.org/10.18637/jss.v082.i13.

Lenth, R.V., 2016. Least-squares means: the R package lsmeans. J. Stat. Softw. Softw. 69, 1–33. https://doi.org/10.18637/jss.v069.i01.

Makowski, Dominique, 2018. The Psycho package: an efficient and publishing-oriented workflow for psychological science. J. Open Source Softw. 3, 470. https://doi.org/10.21105/joss.00470.

Mangiafico, S., 2020. rcompanion: functions to support extension education program evaluation.

Mesquita de Azevedo, L.A., da Silva Cruz, F.A., Dias, A., Batista, G., Jeanne, G. da S., de Amaral Carvalho, J., Kasecker, T., Santiago, H.C., Lederman, M.R., Bendezú Estupiñán, G.M., Melgaço Ramalho, A.L., Cenegrati Zingra Tinto, A.F., Ravetta, A., Suzy Barros de Lima, A., Carrasco Aguilar, C.V., Marinelli, C.E., de Ville de Goyet, C., Borges Andretti, C., Munari, D., Araújo, E., Moura da SIlva Gomes, E., Waldez, F., Rohe, F., da Cunha Mosqueira, F., da Silva Batista, G., Estupiñam, G.M.B., Alberto Carlos, H.S., Rodrigues Reis, J., Gomes da Silva, J., Quissak, J.H., Villacis Farjado, J. D., Jardim de Queiroz, L., de Jesus de Souza Miranda, M., Cohn-Haft, M., Bianchini, M.C., Sayuri de Queiroz Takahashi, M., da Silva, N.L., Lacerda, N., Pinheiro, P.S., Almeida, P.I.A., Salles Valente, R., Guimarães Frederico, R., Batista, R.F., Barros de Andrade Aima, R., Marques de Souza, S., Vernaschi Vieira da Costa, T., Itaborahy Ferreira, W., de Souza Santiago, A., Xavier Costa Alves, E., Cristina Rayol, K., Otávio Aleixo, F., Kasecker, T., 2010. Plano de gestão da reserva de desenvolvimento sustentável de Uacari. Management plan, 222. Carauari.

Mori, G.B., Schietti, J., Poorter, L., Piedade, M.T.F., 2019. Trait divergence and habitat specialization in tropical floodplain forests trees. PLoS One 14, e0212232. https://doi.org/10.1371/journal.pone.0212232.

Muller-Landau, H.C., 2004. Interspecific and inter-site variation in wood specific gravity of tropical trees. Biotropica 36, 20. https://doi.org/10.1646/02119.

Murça Pires, J., 1984. The Amazonian forest, in: Sioli, H. (Ed.), The Amazon. Limnology and Landscape Ecology of a Mighty Tropical River and Its Basin. Dr W. Junk Publishers, pp. 581–602. https://doi.org/10.1007/978-94-009-6542-3.

Myster, R.W., 2016. The physical structure of forests in the Amazon Basin: a review. Bot. Rev. 82, 407–427. https://doi.org/10.1007/s12229-016-9174-x.

Nakagawa, S., Schielzeth, H., 2013. A general and simple method for obtaining R2 from generalized linear mixed-effects models. Methods Ecol. Evol. 4, 133–142. https://doi.org/10.1111/j.2041-210x.2012.00261.x.

Nogueira, E.M., Fearnside, P.M., Nelson, B.W., 2008. Normalization of wood density in biomass estimates of Amazon forests. For. Ecol. Manage. 256, 990–996. https://doi.org/10.1016/j.foreco.2008.06.001.

Nogueira, E.M., Nelson, B.W., Fearnside, P.M., 2005. Wood density in dense forest in central Amazonia. Brazil. For. Ecol. Manage. 208, 261–286. https://doi.org/10.1016/j.foreco.2004.12.007.

Parolin, P., 2009. Submerged in darkness: Adaptations to prolonged submergence by woody species of the Amazonian floodplains. Ann. Bot. 103, 359–376. https://doi.org/10.1093/aob/mcn216.

Parolin, P., 2002. Radial gradients in wood specific gravity in trees of Central Amazonian floodplains. IAWA J. 23, 449–457. https://doi.org/10.1163/22941932-90000314.

Parolin, P., 2001. Morphological and physiological adjustments to waterlogging and drought in seedlings of Amazonian floodplain trees. Oecologia 128, 326–335. https://doi.org/10.1007/s004420100660.

Parolin, P., Oliveira, A.C., Piedade, M.T.F., Wittmann, F., Junk, W.J., 2002. Pioneer trees in Amazonian floodplains: Three key species form monospecific stands in different habitats. Folia Geobot. 225–238.

Peres, C.A., Emilio, T., Schietti, J., Desmoulière, S., Levi, T., 2016. Dispersal limitation induces long-term biomass collapse in overhunted Amazonian forests. Proc. Natl. Acad. Sci. 113, 892–897.

Phillips, O.L., Sullivan, M.J.P., Baker, T.R., Monteagudo Mendoza, A., Vargas, P.N., Vásquez, R., 2019. Species matter: wood density influences tropical forest biomass at multiple scales. Surv. Geophys. https://doi.org/10.1007/s10712-019-09540-0.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., R Core Team, 2019. Linear and nonlinear mixed effects models.

Plourde, B.T., Boukili, V.K., Chazdon, R.L., Rica, C., 2015. Radial changes in wood speci fi c gravity of tropical trees : inter- and intraspeci fi c variation during secondary succession 111–120. https://doi.org/10.1111/1365-2435.12305.

Prance, G.T., Gardens, R.B., 1985. The vegetation types of the. Brazilian Amazon.

R Environment R Core Team, 2018. R: A language and environment for statistical computing.

Réjou-Méchain, M., Tanguy, A., Piponiot, C., Chave, J., Hérault, B., 2017. BIOMASS: an R package for estimating above-ground biomass and its uncertainty in tropical forests. Methods Ecol. Evol. https://doi.org/10.1111/2041-210X.12753.

Salovaara, K.J., Gárdenas, G.G., Tuomisto, H., 2004. Forest classification in an Amazonian rainforest landscape using pteridophytes as indicator species. Ecography (Cop.) 27, 689–700.

Sarkar, D., 2008. Lattice: multivariate data visualization with R.

Shepard Jr., G.H., Yu, D.W., Lizarralde, M., Italiano, M., 2001. Rain forest habitat classification among the matsigenka of the peruvian Amazon. J. Ethnobiol. 21, 1–38.

Simpson, W.T., 1993. United States Department of Agriculture Forest Service. Forest products laboratory. General technical report FPL-GTR-76. Specific gravity, moisture content, and density relationship for wood.

Skogstad, P. (Ed.), 2009. Trevirkets egenskaper, in: Treteknisk Håndbok. Norsk treteknisk institutt, Oslo, pp. 20–43.

Slik, J.W.F., Paoli, G., Mcguire, K., Amaral, I., Barroso, J., Bastian, M., Blanc, L., Bongers, F., Boundja, P., Clark, C., Dauby, G., Ding, Y., Doucet, J., Eler, E., Ferreira, L., Fredriksson, G., Gillet, J., Harris, D., Leal, M., Malhi, Y., Mansor, A., Martin, E., Miyamoto, K., Araujo-murakami, A., Slik, J.W.F., Paoli, G., Mcguire, K., Amaral, I., Barroso, J., Bastian, M., Blanc, L., Bongers, F., Boundja, P., Clark, C., Collins, M., Dauby, G., Ding, Y., Doucet, J., Eier, E., Rovero, F., Rozak, A., Sheil, D., Silva-espejo, J., Silveira, M., Sunderland, T., Suzuki, E., Tang, J., Theilade, I., Heijden, G., Der, Van, 2013. Large trees drive forest aboveground biomass variation in moist lowland forests across the tropics Stable. Glob. Ecol. Biogeogr. 2013, 1261–1271. https://doi.org/10.1111/geb.12092. URL : https://www.jstor.org/stable/42568596 Linked references are available on JSTOR for this article : Large trees drive forest aboveground biomass.

Souza, F.C De, Dexter, K.G., Phillips, O.L., Pennington, R.T., Neves, D., Sullivan, M.J.P., Alvarez-davila, E., Alves, Á., Amaral, I., Andrade, A., Aragao, L.E.O.C., Araujo-murakami, A., Arets, E.J.M.M., Lola, A., Camargo, P.B De, Fiore, A Di, Feldpausch, T.R., Galbraith, D.R., Gloor, E., Goodman, R.C., Gilpin, M., Herrera, R., 2018. Evolutionary diversity is associated with wood productivity in Amazonian forests. Nat. Ecol. Evol. https://doi.org/10.1038/s41559-019-1007-y.

Targhetta, N., Kesselmeier, J., Wittmann, F., 2015. Effects of the hydroedaphic gradient on tree species composition and aboveground wood biomass of oligotrophic forest ecosystems in the central Amazon basin. Folia Geobot. 50, 185–205. https://doi.org/10.1007/s12224-015-9225-9.

ter Steege, H., Mota de Oliveira, S., Pitman, N.C.A., Sabatier, D., Antonelli, A., Guevara Andino, J.E., Aymard, G.A., Salomão, R.P., 2019. Towards a dynamic list of Amazonian tree species. Sci. Rep. 9, 3501. https://doi.org/10.1038/s41598-019-40101-y.

ter Steege, H., Pitman, N.C.A., Phillips, O.L., Chave, J., Sabatier, D., Duque, A., Molino, J.F., Prévost, M.F., Spichiger, R., Castellanos, H., Von Hildebrand, P., Vásquez, R., 2006. Continental-scale patterns of canopy tree composition and function across Amazonia. Nature. https://doi.org/10.1038/nature05134.

Terborgh, J., Andresen, E., 1998. The composition of Amazonian forests: patterns at local and regional scales. J. Trop. Ecol. 14, 645–664. https://doi.org/10.1017/s0266467498000455.

Wickham, H., 2016. ggplot2: elegant graphics for data analysis.

Wickham, H., 2009. ggplot2: elegant graphics for data analysis. J. Stat. Softw. 35.

Wiemann, M.C., Williamson, G.B., 2012. Density and specific gravity metrics in biomass research. Gen. Tech. Rep. FPL GTR-208.

Williamson, G.B., Wiemann, M.C., 2010. Measuring wood specific gravity...correctly. Am. J. Bot. 97, 519–524. https://doi.org/10.3732/ajb.0900243.

Wittmann, F., Householder, E., Piedade, M.T.F., Assis, R.L., Schöngart, J., Parolin, P., Junk, W.J., 2013. Habitat specifity, endemism and the neotropical distribution of Amazon white-water floodplain trees. Ecography (Cop.) 36, 690–707.

Wittmann, F., Schöngart, J., De Brito, J.M., de Oliveira Wittmann, A., Fernandez Piedade, M.T., Parolin, P., Junk, W.J.W.J., Guillaumet, J.-L.J.L., 2010. Manual of trees from Central Amazonian várzea floodplains. Editora INPA, Manaus.

Wittmann, F., Schöngart, J., Montero, J.C., Motzer, T., Junk, W.J., Piedade, M.T.F., Queiroz, H.L., Worbes, M., 2006a. Tree species composition and diversity gradients in white-water forests across the Amazon Basin. J. Biogeogr. 33, 1334–1347. https://doi.org/10.1111/j.1365-2699.2006.01495.x.

Wittmann, F., Schöngart, J., Parolin, P., Worbes, M., Piedade, M.T.F., Junk, W.J., 2006b. Wood specific gravity of trees in Amazonian white-water forests in relation to flooding. IAWA J. https://doi.org/10.1163/22941932-90000153.

Yang, J., Cao, M., Swenson, N.G., 2018. Why functional traits do not predict tree demographic rates. Trends Ecol. Evol. https://doi.org/10.1016/j.tree.2018.03.003.

Zanne, A., Lopez-Gonzalez, G., DA, C., Ilic, J., Jansen, S., SL, L., RB, M., NG, S., MC, W., Chave, J., 2009. Data from: Towards a worldwide wood economics spectrum. Ecol. Lett. https://doi.org/doi:10.5061/dryad.23.

Zuur, A., Tobergte, D.R., Curtis, S., 2013. Statistics for biology and health. J. Chem. Info Model. https://doi.org/10.1017/CBO9781107415324.004.

Forest Ecology and Management 474 (2020) 118393

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Corrigendum

Corrigendum to “Forest type affects the capacity of Amazonian tree species to store carbon as woody biomass” [For. Ecol. Manage. 473 (2020) 118297]

Yennie K. Bredin[a,*], Carlos A. Peres[b,c], Torbjørn Haugaasen[a]

[a] Faculty of Environmental Sciences and Natural Resource Management, Norwegian University of Life Sciences, Ås, Norway
[b] School of Environmental Sciences, University of East Anglia, Norwich NR47TJ, UK
[c] Departamento de Sistemática e Ecologia, Universidade Federal da Paraíba, João Pessoa, Paraíba, Brazil

The authors regret not to acknowledge the generous help of Juliana Schietti who trained and helped us set up the wood specific gravity analyses at the lab that she coordinated at the National Institute for Amazon Research (INPA), Manaus. Juliana’s guidance and assistance has been essential for the completion of this work and we are most grateful to her for allowing us to run our analyses at the Biodiversity and Functional Ecology Lab (Laboratório de Biodiversidade e Ecologia Funcional). We also thank Juliana for the many methodological and statistical discussions that we have had and from which this work has benefitted greatly.

The authors would like to apologise for any inconvenience caused.

DOI of original article: https://doi.org/10.1016/j.foreco.2020.118297

[*] Corresponding author.

E-mail address: yennie.bredin@nmbu.no (Y.K. Bredin).

https://doi.org/10.1016/j.foreco.2020.118393

Paper IV

To be submitted to: Forest Ecology and Management

Accurate biomass estimation for data-poor forest types.

Yennie K. Bredin[a1*], Jacob B. Socolar[a*], Juliana Schietti[b], Joseph E. Hawes[a], Rafael Leandro de Assis[c], Carlos A. Peres[d,e], Torbjørn Haugaasen[a]

a. Faculty of Environmental Sciences and Natural Resource Management, Norwegian University of Life Sciences, P.O. Box 5003, 1432 Ås, Norway.

b. Departamento de Biologia, Federal University of Amazonas, Manaus, Brazil

c. Natural History Museum, University of Oslo, P.O. Box 1172, Blindern, Oslo 0318 Norway

d. School of Environmental Sciences, University of East Anglia, Norwich NR47TJ, UK.

e. Departamento de Sistemática e Ecologia, Universidade Federal da Paraíba, João Pessoa, Paraíba, Brazil.

1. Correspondence: yennie.bredin@nmbu.no

* These authors contributed equally to this manuscript

Abstract

Accurate and detailed forest biomass and carbon mapping requires reliable ground-based measurements. Uncertainties with these measurements are therefore a major obstacle to modelling global carbon fluxes, particularly in hyper diverse tropical forests. Reducing this uncertainty and understanding the effect of lower-quality measurements on biomass and carbon estimates are therefore important. We used detailed tree inventory data collected in the western Brazilian Amazon to test the degree to which the quality of different variables (taxonomic resolution, geographic precision, tree height, and wood density) affected biomass estimation in two major Amazonian forest types: relatively data-poor seasonally inundated floodplain forest and relatively well sampled upland forest. In general, we found that lower taxonomic accuracy and radial change in local, forest-specific wood density, induced small differences on biomass estimates for both forest types. However, we saw that tree height allometries developed for tropical forests, but based mostly on upland forest trees, and wood density data with lower taxonomic resolution, generally produced larger differences in forest biomass for the data-poor floodplain forest than for the upland forest. Particularly large were overestimates in forest biomass based on combinations of global mean wood density or regional height allometry. The combination of lower-quality measurements that produced the most accurate biomass estimates were local allometric height combined with unweighted genus mean wood density. Our results are likely applicable to other undersampled tropical forest types. We highly recommend the use of local height calibration data, field-measured diameter at breast height, and forest-specific wood-density to calibrate global mean wood density measurements.

1. Introduction

Accurate and detailed forest biomass and carbon mapping requires reliable ground-based measurements. Uncertainties with these measurements are therefore a major obstacle to modelling global carbon fluxes, particularly in tropical forests (Mitchard, 2018; Quéré et al., 2018). Reducing this uncertainty and understanding the effect of lower-quality measurements on biomass and carbon estimates are therefore important (Chave et al., 2019, 2014). Due to limited ground-based measurements, large-scale biomass and carbon mapping are often based on regional height allometries and wood density data. However, hyper-diverse tropical forest regions are not homogeneous and often contain several forest types that differ in both species composition and forest structure. Therefore, regional height allometries or wood density data skewed toward better sampled forest types may not perform equally well across tropical landscapes that include many data-poor forest types. Instead, such treatment may lead to significant errors in regional biomass and carbon estimates.

Amazonia represents the largest remaining tracts of intact tropical rainforests and one of the world's most species rich regions. Covering around 5 million km^2, Amazonia comprise several forest types, including seasonally inundated floodplain forests and upland forests. Upland terra firme forests lie above the maximum flood levels of perennial streams, lakes and rivers and represent the best studied and most extensive forests in Amazonia (Hess et al., 2003). Characteristic terra firme environments include the typical, high statured, closed-canopy forests on sedimentary uplands, but there are also other less well studied upland forests, such as campinarana forests on white sand soils, liana forests on mineral rich soils, and bamboo forests on soils with high base saturation (Anderson, 1981; Cardoso da Silva et al., 1990; Furtado de Mendonça et al., 2014; Murça Pires, 1984; Sombroek, 2000). Similarly, floodplain forests, which cover approximately 800 000 km^2 of the Amazon basin (Melack and Hess, 2010), can be categorized according to soil fertility, inundation periodicity , and the chemical properties of their floodwaters (Junk et al., 2011; Junk and Piedade, 2010). However, in contrast to the typical terra firme forests, floodplain forests are less well studied and therefore represent relatively data-poor forests in Amazonia (Feeley, 2015; Luize et al., 2018). This is true even for the most extensive of the Amazon floodplain forests, the seasonally inundated várzea (Hess et al., 2015). Várzea forests, which occur on highly fertile substrates, are inundated by white-water rivers carrying large amounts of suspended Andean sediment and may endure inundation periods of up to six months per year, as seasonal floodwaters can reach over 10 m in amplitude in central Amazonia (Haugaasen and Peres, 2006). The flora and fauna at all stages of their life cycles are therefore subjected to alternating terrestrial and aquatic phases (flood pulse, sensu Junk et al., 1989).

Due to these differences in seasonality, várzea and terra firme harbour very different plant communities with different species composition (Assis et al., 2015; Haugaasen and Peres, 2006; Wittmann et al., 2017, 2013), vegetation structure (Bredin et al., 2020a; Myster, 2016; Wittmann et al., 2006a), and wood properties among trees (Bredin et al., 2020b; Parolin, 2002; Wittmann et al., 2006b). We suspect that there may be large errors in above-ground woody biomass (AGWB) estimates if such local forest-specific characteristics are ignored, particularly because tree allometries (based on measurements of diameter at breast height, DBH) and publicly available wood density from global databases are mostly derived from upland forest trees (e.g. cf. Chave et al., 2014; Zanne et al., 2009). However, if we could quantify the potential biases induced by taxonomic or geographic variability in tree parameters, then we could also correct for any potential systematic over- or underestimations across the floodplain and upland forests to improve Amazon AGWB estimates (Réjou-Méchain et al., 2019).

To date, important contributions have been made toward asserting the influence of different field-based methods and approximations on the accuracy of tree height (da Silva et al., 2012; Larjavaara and Muller-Landau, 2013; Réjou-Méchain et al., 2019; Sullivan et al., 2018) and wood density (Bastin et al., 2015; Bredin et al., 2020b; Momo et al., 2020; Nogueira et al., 2008, 2005; Parolin, 2002; Wittmann et al., 2006b). Additionally, open access statistical tools, such as the BIOMASS package (Piponiot et al., 2019; Réjou-Méchain et al., 2017) in R (R Core Team, 2021), allow for known uncertainties in measurements to be accounted for in AGWB estimates. However, to our knowledge, no study has assessed the combined effects of imperfect height and wood density measurements on ground-based AGWB estimates across data-poor tropical forests and taxonomic levels.

Here, we provide an examination of expected deviations and uncertainties in forest AGWB induced by combinations of lower-quality tree height and wood density across terra firme and várzea forests, central-western Amazonia, Brazil. We compare AGWB estimates from *in situ*, individually-measured tree height and stem-specific wood density that accounted for radial variation in the wood (from pith to bark) to AGWB estimates based on lower-quality height and wood density. We used Bayesian statistics to develop a guide to reduce bias in height and wood density measurements and ground-based AGWB estimates by evaluating the following research questions:

(1) How do different methods of determining tree height affect AGWB estimates in Amazonian seasonally flooded várzea and "unflooded" terra firme?

(2) How does taxonomic accuracy and geographic precision affect AGWB estimates across várzea and terra firme forests?

(3) How do radial variations in the wood affect várzea and terra firme AGWB estimates at different taxonomic levels?

(4) How do different combinations of lower-quality tree height and wood density affect AGWB across várzea and terra firme?

Answering these questions, we provide quantitative measurements of expected percent differences in várzea and terra firme AGWB with 95% credible intervals (CI) and estimate differences in megagrams (Mg) per hectare (ha) forest. Hence, we provide a means for quantifying the uncertainties introduced by imperfect taxonomic identifications or lower-quality height and wood density on AGWB estimates across floodplain and upland forests.

2. Methods

2.1 Study area

Tree inventories were performed between September 2016 and October 2017, in the central Juruá River basin, western Brazilian Amazonia (Fig. 1). The region contains forest seasonally flooded by the white-water Juruá River (várzea), and forest situated on paleo-várzea sediments above the Juruá flood level (terra firme). The study area was located between 05°08' S, 67°01' W and 05°87' S, 67°88'W and includes the Uacari Sustainable Development Reserve (RDS Uacari, 632,949 ha) and surrounding forests, but excludes the Médio Juruá Extractive Reserve (ResEx Médio Juruá, 253,227 ha; Fig. 1). The climate of the region is wet and tropical. Annual temperatures and rainfall average 27.1 °C and 3,679 mm, respectively (Hawes and Peres, 2016). The inventoried forests represent structurally intact vegetation with comparable forest structures and species compositions to other terra firme (TF) and várzea (VZ) forests in Amazonia (Bredin et al., 2020a). Elevations ranged from 68-137 m above sea level for várzea and 67-153 m above sea level for terra firme. Field data include 1542 individually sampled trees (VZ = 1137; TF = 405) from 21 várzea plots and seven terra firme plots (each 0.1 ha, 100 m x 10 m, at least 800m apart), and along 26 transects (VZ = 14; TF = 12). For further details about the inventory design and forest structure, see Bredin et al. (2020a).

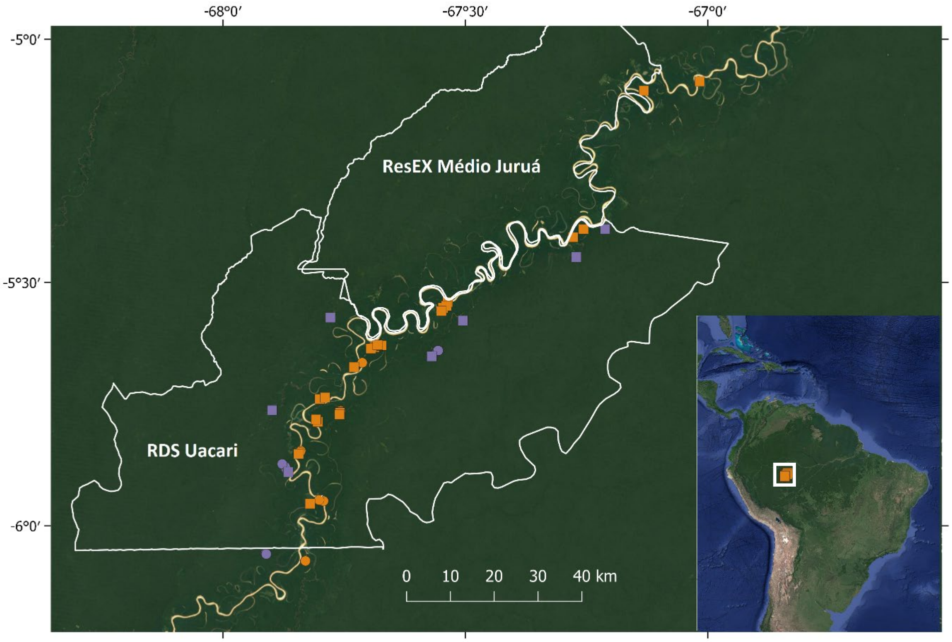

Figure 1. Map showing the study location along 150 km of the Juruá River (main map) in central-western Amazonia (white square in inset map). Filled squares indicate woody plant inventory plots in várzea (purple squares) and terra firme (orange squares). Filled circles indicate individual trees sampled along transects, outside plots in várzea (purple) and terra firme (orange). The delimitations of the Uacari Sustainable Development Reserve (RDS Uacari) and adjacent Médio Juruá Extractive Reserve (ResEX Médio Juruá) are shown in white lines. The map was generated in QGIS v.3.12.2, using background maps from google maps (Google Maps, 2021). *The shapefiles for the ResEx Médio Juruá and RDS Uacari were provided by Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio) and the Amazonas State Environmental Agency (SEMA-DEMUC), respectively.*

2.2 Taxonomic identifications

Trees were identified to species level *in situ* and later verified at the National Institute for Amazon Research (INPA). Skilled INPA herbarium technicians with extensive field and herbarium experience from floristic inventories in the central-western Brazilian Amazon performed all identifications. Individuals that could not be determined to species level were sorted to morpho-species or, where applicable, higher taxonomic levels.

2.3 Diameter at breast height and tree height

We included trees ≥10cm diameter at breast height (DBH). Stem diameter (i.e. DBH) was determined by measuring the circumference of the trunks at 1.30m above the ground using a DBH tape. For buttressed trees, we measured the stem diameter immediately above the buttresses. When direct measurement with a DBH tape was not possible (e.g. sulcate trunks, stranglers or where buttresses were too high), we visually estimated the diameters.

We used a Vertex IV hypsometer and Transponder T3 (HAGLÖF SWEDEN AB, 2007) to measure total tree heights *in situ* on 1085 trees (VZ = 858; TF = 227). Each tree was measured three times. In addition, we visually estimated tree heights. To remove observer bias, the same person (YKB) administered all height (H) measurements.

2.4 Wood (specific) density

Wood density (WD) describes the relationship between the dry mass of wood at moisture content 0 and the volume of wood at a specific moisture content in relation to the density of water (Skogstad, 2009). It is thus a measure of the fraction of structural matter in wood (Williamson and Wiemann, 2010). Wood density therefore relates to both estimates of woody biomass and wood-bound carbon in woody vegetation (Chave et al., 2014, 2005; Fearnside, 1997). Whereas different wood density values are widely applied for different purposes within the timber industry and forest ecological studies, we use wood specific density (WSD) which standardises moisture content among samples at the water saturation point of the wood (Simpson, 1993; Skogstad, 2009). Using wood specific density therefore allows us to better assess the influence of among tree differences in wood density across forest habitats, sample sites and taxonomic entities.

2.4.1 Field samples

We used a 5,15mm Haglöf increment borer to collect wood cores from 1252 trees with stem diameters ≥10cm in várzea forest (n = 921) and adjacent terra firme forest (n = 331). We extracted wood cores perpendicular to the trunk at a height between 1m and 1,3m off the ground. Where trees had buttressed roots, we extracted wood cores from above the buttress. For support and storage, we kept the cores in paper straws. To protect the cores from moisture and fungal attacks, we dried the samples and kept them with silica gel until analysed at the Biodiversity and Functional Ecology Lab (Laboratório de Biodiversidade e Ecologia Funcional), INPA, Manaus.

2.4.2 Lab analyses

To determine wood specific density, wood cores were first saturated with water through submersion for a minimum of 72h. Depending on core length, cores were divided into the following segments; bark, 0-50mm, 50mm-pith (or middle, stem diameter/2, for cores with no visible pith), and beyond pith (for cores with skewed piths). Where possible, heartwood and pith were visually determined and further sub-divided to avoid an overrepresentation of heartwood or pith on the wood specific density values. Saturated wood volume was measured by the water displacement method, using a fine needle to submerge the segments into a beaker of water placed on a scale with precision 0.01g (Vieilledent et al., 2012; Wiemann and Williamson, 2012). We used tap water at 24 ± 0.6°C, equivalent to a density of $\rho H2O \approx 0.9973 g/cm^3$. After recording the saturated wet volumes, we dried the wood cores at 107.5 ± 2.5°C for 72h. This temperature range falls slightly outside the recommended range 101-105°C (Williamson and Wiemann, 2010). In consequence, our wood specific density values are conservative (i.e. leading to slight underestimates of AGWB) as some volatile compounds may have evaporated (Nogueira et al., 2005). We recorded the dry weights of the wood core segments using a precision scale with a 0.01g accuracy.

To determine the radially weighted wood specific density of trees (rWSD), we followed the method used by Muller-Landau (2004). In brief, we calculated a single weighted average wood specific density per tree based on the values for each segment weighted by the cross-sectional area of the trunk that each segment represented (Formula a). To obtain unweighted wood specific density values (uWSD), we simply ignored any radial change along the core following Formula b. For individuals with replicate wood cores, we averaged the radially weighted or unweighted wood specific density values over the number of replicas.

Formula a:

$$\text{rWSD} = \sum_{n=1}^{N} \left(\frac{Mn}{Vn/\rho H2O} \times \frac{An}{AN}\right)$$

Formula b:

$$\text{uWSD} = \frac{MN}{VN/\rho H2O}$$

N = total number of segments per wood core, Mn = dry mass of a segment n at moisture content 0, Vn = saturated wet volume of a segment n, An = cross sectional area of a segment n, AN = total cross sectional area of all N segments, MN = dry mass of all N segments at moisture content 0, and VN = saturated wet volume of all N segments.

Separately within várzea and terra firme, species, genus and family mean wood specific densities were obtained by averaging the radially weighted and unweighted wood specific density values for all stems of a given species, genus or family that was represented by minimum three individuals in our data.

To determine the rate of radial change along wood cores, we omitted the density of the bark and divided the wood specific density of the outer 5cm by the wood specific density of the remaining core segments. Hence, a value >1 indicates an increase in wood specific density from the inner to outer wood. In contrast, a value <1 indicates a decrease in wood specific density from the inner to outer wood. A value = 1 indicates no radial change in wood specific density.

2.5 Analysis

We used R, version 4.0.4 (R Core Team, 2021), to prepare and analyse all data. We used the BIOMASS package version 2.1.4 (Piponiot et al., 2019; Réjou-Méchain et al., 2017) to derive AGWB estimates of each tree in our data based on the field-measured total tree height, the field-measured stem diameter, and stem-specific radially weighted wood specific density (rWSD). The field-measured total height (HM) is taken as the mean of the three field measurements, with normally distributed uncertainty with a standard deviation estimated from data whose magnitude grows linearly with the mean estimate. We compared these "higher-quality" AGWB estimates to AGWB estimated with various alternative lower-quality height and wood density parameters.

To assess bias and uncertainty introduced by height approximations on várzea and terra firme AGWB, respectively, we considered:

h 1) In situ, visual height estimates (HE),

h 2) Local, habitat specific diameter-height (DBH:H) allometric height (HL), and h 3) Regional diameter-height allometric height (HR).

The local, habitat specific diameter-height models were derived separately for várzea and terra firme using the BIOMASS *modelHD* function and field-measured total height from the 10 trees with largest diameter at breast height plus 40 trees stratified by stem diameter in each habitat (Sullivan et al., 2018). For the local diameter-height allometries (VZ and TF) we chose the models with the lowest RSE. Using the BIOMASS *coord* argument, we fit a regional diameter-height model on bioclimatic parameters at the geographic locations of the tree plots (Chave et al., 2014).

To assess bias and uncertainty introduced by wood density approximations (Table S1) on várzea and terra firme AGWB, we considered:

wd 1) radially weighted species mean wood specific density (rWDs),
wd 2) radially weighted genus mean wood specific density (rWDg),
wd 3) radially weighted family mean wood specific density (rWDf),
wd 4) unweighted individual wood specific density (uWSD),
wd 5) unweighted species mean wood specific density (uWDs),
wd 6) unweighted genus mean wood specific density (uWDg),
wd 7) unweighted family mean wood specific density (uWDf), and
wd 8) Global mean wood density (GWD).

Global mean wood density values were derived from the Global Wood Density database (Chave et al., 2009; Zanne et al., 2009) at the lowest possible taxonomic level, *e.g.* species mean wood density where information was available at the species level, through the BIOMASS *getWoodDensity* argument. We used global mean wood density data since Oliver and Coomes (2011) show that global mean wood density gives better results than regional mean wood density values do.

We considered all combinations of lower-quality height and wood density factorially comparing AGWB estimates for each of these lower-quality data alternatives to the AGWB estimated with individually measured tree height and stem-specific radially weighted wood specific density. Hence, we derived 35 deviations from our "ground-based" tree AGWB.

Proper assessment of the AGWB differences between methods required principled handling of the non-independence of the estimates due to shared measurements of some AGWB parameters. For example, when comparing estimates based on radially weighted versus unweighted wood density (both using field-measured total height values), we wished to avoid confounding differences due to the different wood density with variation due to the uncertainty in the parameters for the allometric relationship or variation due to uncertainty in the height measurement. Therefore, we reimplemented the *AGBmonteCarlo* function of the BIOMASS package to generate posterior samples for the difference between two methods, where at each posterior iteration the difference is computed based on the same values (drawn from the appropriate posterior distributions) for all shared parameters (e.g. the height and the allometric parameters). To accomplish this for tree height predicted from the bioclimatic model of Chave et al (2014), we refitted the diameter-height model of Chave et al.'s equation 3 (2014) and predicted AGWB by first predicting height values and then using the allometry of Chave et al.'s equation 3 (2014). This corresponds to the original approach of Chave et al (2014) and differs from the approach of Réjou-Méchain et al. (2017), which estimates AGWB directly based on bioclimatic covariates and stem diameter using a single regression.

We assessed the accuracy of the various methods separately in várzea and terra firme by examining the posterior difference between each two methods for AGWB summed across all stems in each habitat. Subsequently, we explored where the differences in várzea and terra firme forest AGWB arose by regressing the posterior tree-level AGWB ratios (i.e. the ratio of tree-level AGWB estimates derived under different methodologies) on tree diameter at breast height, radial change in wood density, and random intercepts for genus, family, plot and transect using a log link.

Finally, we calculated what the method-specific percent differences would translate into in terms of megagrams (Mg) per hectare (ha) forest. This was done by first estimating plot-level AGWB with measured height and radially weighted wood specific density. To fill in missing data for individual trees without measured height or radially weighted wood specific density measurements, we used those height and wood density methods that produced the smallest percent differences in AGWB across trees for each forest type. Separately for várzea and terra firme, we then multiplied the sum of plot mean AGWB by the expected method-specific deviations in AGWB and divided this value by the total area of all plots.

3. Results

We evaluated 35 different combinations of lower-quality height and wood density measurements in várzea and terra firme, respectively. Of these, 20 várzea combinations and four terra firme combinations under- or overestimated the AGWB across all trees by ≥10% on average. Thirty-four combinations of lower-quality wood density and height measurements (VZ = 15, TF = 19) under- or overestimated AGWB across trees by ≤3%, on average. The remaining 12 combinations of lower-quality wood density and height measurements lead to mean differences in AGWB between >3% and <10%, all in terra firme. Credible interval (CI) widths were generally smaller in várzea, indicating less variation in method performances in várzea than in terra firme (Table S2).

The regressions (VZ = 35, TF = 35; Table S3) showed positive spatial and taxonomic nesting effects within plots, transects, genera, and families. For most regressions, we could not conclude on directions of effects for stem diameter, radial change in wood density or their interactions as the 90%CIs crossed 0 (VZ =25, TF = 30). In four cases, stem diameter had a small positive (VZ = 2) or negative effect (TF = 2) on AGWB. In five cases, radial change in wood density had a negative effect on terra firme AGWB. In 10 várzea cases and four terra firme cases, stem diameter and radial change in wood density had a small positive interaction effect on AGWB.

3.1 Effect of lower-quality tree height on AGWB estimates

The probability density distributions of differences in AGWB by height method showed that local allometric height (HL) produced the best estimates in both várzea (Fig. 2a) and terra firme (Fig. 2b). Visual height estimates (HE) consistently underestimated várzea and terra firme AGWB (Fig. 2a-b; Table 1S). For visual height estimates in várzea, the regression showed a small positive interaction effect between stem diameter and radial change in wood density -thus indicating less sever visual height underestimates of AGWB in várzea trees with both larger stem diameter and increased wood density from pith to bark. Regional allometric height (HR) consistently overestimated várzea AGWB (Fig. 2a; Table S2) but produced no systematic under- or overestimations in terra firme AGWB (Fig. 2b; Table S2).

3.2 Effect of taxonomic accuracy and geographic precision on AGWB

Most forest-specific, radially weighted, mean wood specific densities (rWD) did not systematically under- or overestimate AGWB at the 95%CI level in várzea (Fig. 2c) or terra firme (Fig. 2d). The exceptions were species rWD in várzea and family rWD in terra firme, which produced very small overestimates (Table S2). Decreased taxonomic accuracy shifted the probability densities to the left in várzea (Fig. 2c), and to the right in terra firme (Fig. 2d). The várzea regressions showed a small positive interaction effect for stem diameter and radial change in genus and family rWD (Table S3), but the effect of this interaction on AGWB estimates is not clear. In terra firme, the regression for family rWD showed negative coefficients for stem diameter and radial change in wood density and a positive interaction effect (Table S3). This suggests that overestimates in terra firme trees with family rWD become less severe with increased stem diameter size or increased wood density from pith to bark, but that these moderating effects are reduced in terra firme trees with both larger stem diameter and increased wood density from pith to bark. At the 95%CI level, global wood density overestimated both várzea and terra firme AGWB (Table S2), but global wood density produced particularly large AGWB overestimates in várzea (95%CI = 25–30%; Fig. 2c; Table S2). Additionally, the terra firme regression showed a negative effect for radial change in wood density, suggesting that with increased wood density from pith to bark, biomass underestimates with global wood density become more severe in terra firme trees.

3.3 Effect of radial variations in wood density on AGWB at different taxonomic levels

Ignoring radial change in wood density by using unweighted mean wood specific density (uWD) has relatively little influence on AGWB estimates várzea and terra firme (Fig. 2d-e). In várzea, difference in AGWB were smallest at the family level and in terra firme, they were smallest at the genus level (Table S2). All probability density distributions were tight, indicating small variability in uWD performance (Fig. 2e-f). However, the regressions showed small positive effects of stem diameter for stem-specific uWD and a small positive interaction effect between stem diameter and radial change in wood density for family uWD in both forests. Additionally, in terra firme, the regression for AGWB by family uWD had negative coefficients for stem diameter and radial change in wood density (Table S3). These regression results indicate that underestimates with stem-specific uWD in várzea become less severe with increased tree stem diameter size. Additionally, these results indicate that overestimates with family uWD become less sever in terra firme trees with increased stem diameter or increased wood density from pith to bark, but that these moderating effects would become reduced in terra firme trees with both larger stem diameter and increased wood density from pith to bark. What these regression results would mean for várzea biomass estimates with family uWD or terra firme stem-specific uWD is less clear.

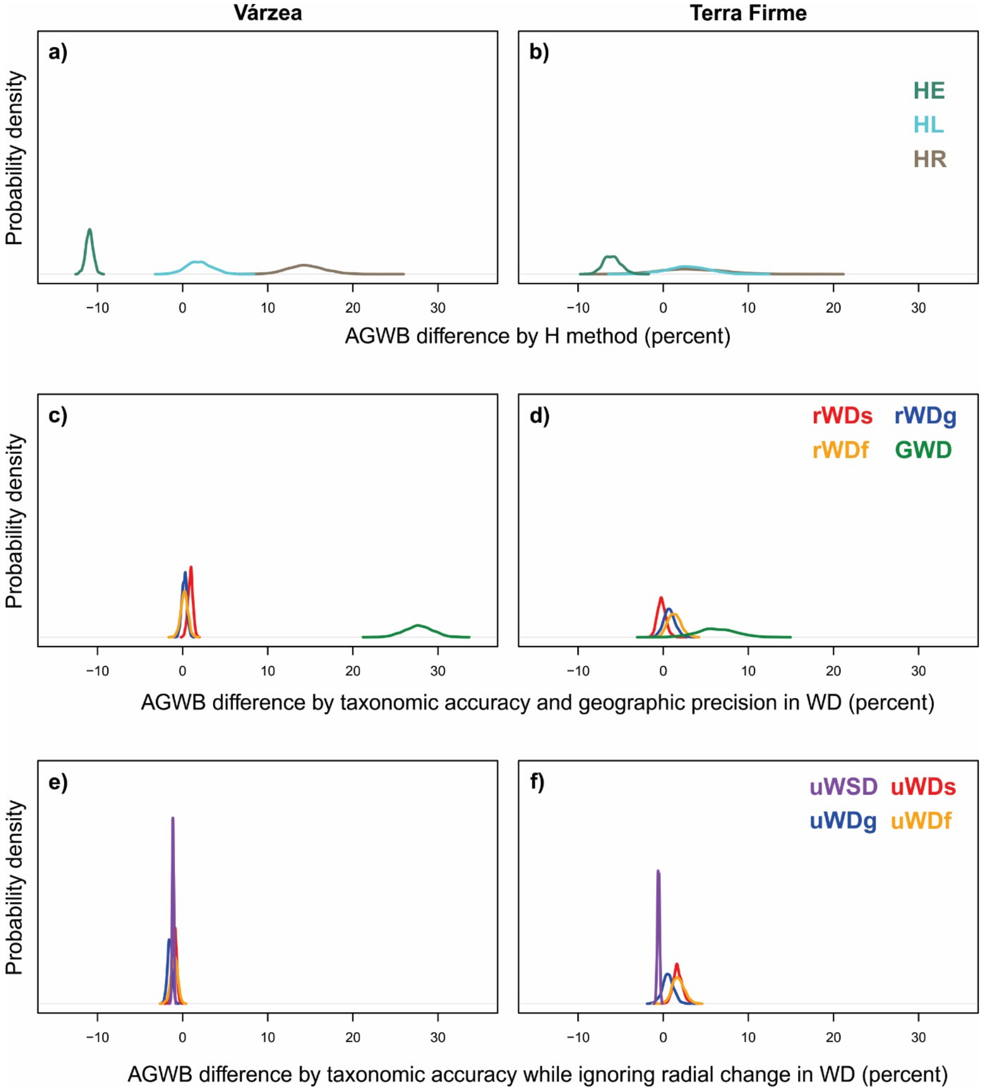

Figure 2. The posterior probability densities show estimated percent difference from várzea and terra firme above-ground woody biomass (AGWB) by height and wood density method. Negative values indicate underestimates in AGWB. Positive values indicate overestimates in AGWB. Where the probability distributions cross 0, methods do not systematically under- or overestimate AGWB. Panels a) and b) show estimated percent

difference in várzea (a) and terra firme (b) AGWB by visual hight estimates (HE), local allometric hight (HL) and regional allometric hight (HR). Panels c) and d) show estimated percent difference in várzea (c) and terra firme (d) AGWB by taxonomic accuracy where rWDs, rWDg, and rWDf are species, genus, and family mean radially weighted wood specific density. GWD is global mean wood density retrieved from the Global Wood Density database (Zanne et al., 2009; Chave et al., 2009) at the lowest possible taxonomic level. Panels e) and f) show estimated percent difference in várzea (e) and terra firme (f) AGWB by unweighted mean wood specific density at the stem-specific (uWSD), species (uWDs), genus (uWDg) and family (uWDf) levels.

3.4 Effect of different combinations of lower-quality tree height and wood density measures on AGWB

3.4.1 Combinations of visually estimated height (HE) with lower-quality wood density

The posterior distributions showed that visual height estimates combined with lower-quality, forest-specific wood density always underestimated várzea AGWB by more than -9% at the 95%CI level (Fig. 3a, Fig. 4a). However, the regressions showed a small positive interaction effect for all visual height estimates combinations with forest-specific wood density in várzea except unweighted wood specific density, suggesting that underestimates become less severe for várzea trees with larger stem diameters and increasing wood density from pith to bark (Table S3). In contrast, visual height estimates combined with global wood density overestimated várzea AGWB with more than 19% (95%CI; Fig. 3a; Table S2). Except for combinations with genus level wood density and global wood density, visual height estimates consistently underestimated terra firme AGWB at the 95%CI level (Fig. 3b, Fig. 4b; Table S2). Most severe were underestimates for visual height estimates combined with species rWD or uWD (95%CI <-16%; Table S2).

3.4.2 Combinations of local allometric height (HL) with lower-quality wood density

Local allometric height combinations with lower-quality forest-specific wood density (radially weighted or not) did not systematically under- or overestimate várzea (Fig. 3c, Fig. 4c) or terra firme AGWB, although in terra firme, 95%CIs were relatively wide and skewed to overestimate AGWB (Fig. 3d, Fig. 4d). In contrast, local allometric height with global wood density overestimated várzea and terra firme AGWB, and in várzea with >20% (Fig. 3c; Table S2).

3.4.3 Combinations of regional allometric height (HR) with lower-quality wood density

The probability density distributions showed systematic overestimations of várzea AGWB for all combinations of regional allometric height with lower-quality wood density (Fig. 3e, Fig. 4e). The largest, overall AGWB difference, among all methods, was observed for combinations of regional allometric height with global wood density in várzea. In contrast, the probability density distributions show that regional allometric height combinations with forest-specific lower-quality wood density do not systematically under- or overestimate terra firme AGWB (Fig. 3f, Fig. 4f). However, there is a tendency for differences in terra firme AGWB to increase with decreased taxonomic accuracy and geographic precision in wood density. Combined with global wood density, regional allometric height overestimated terra firme AGWB with 3–23% at 95%CI (Fig. 3f, Fig. 4f, Table S2). Plus, for regional allometric height with family mean wood density, the regressions showed a negative effect of radial change in wood density and a positive interaction effect between the radial change in wood density and stem diameter. Suggesting that the tendency for combinations of regional allometric height with family mean wood density to overestimate terra firme AGWB would decrease in terra firme trees with increasing wood density from pith to bark, but also that the tendency to overestimate terra firme AGWB would increase for terra firme trees with both larger stem diameter and increasing wood density from pith to bark.

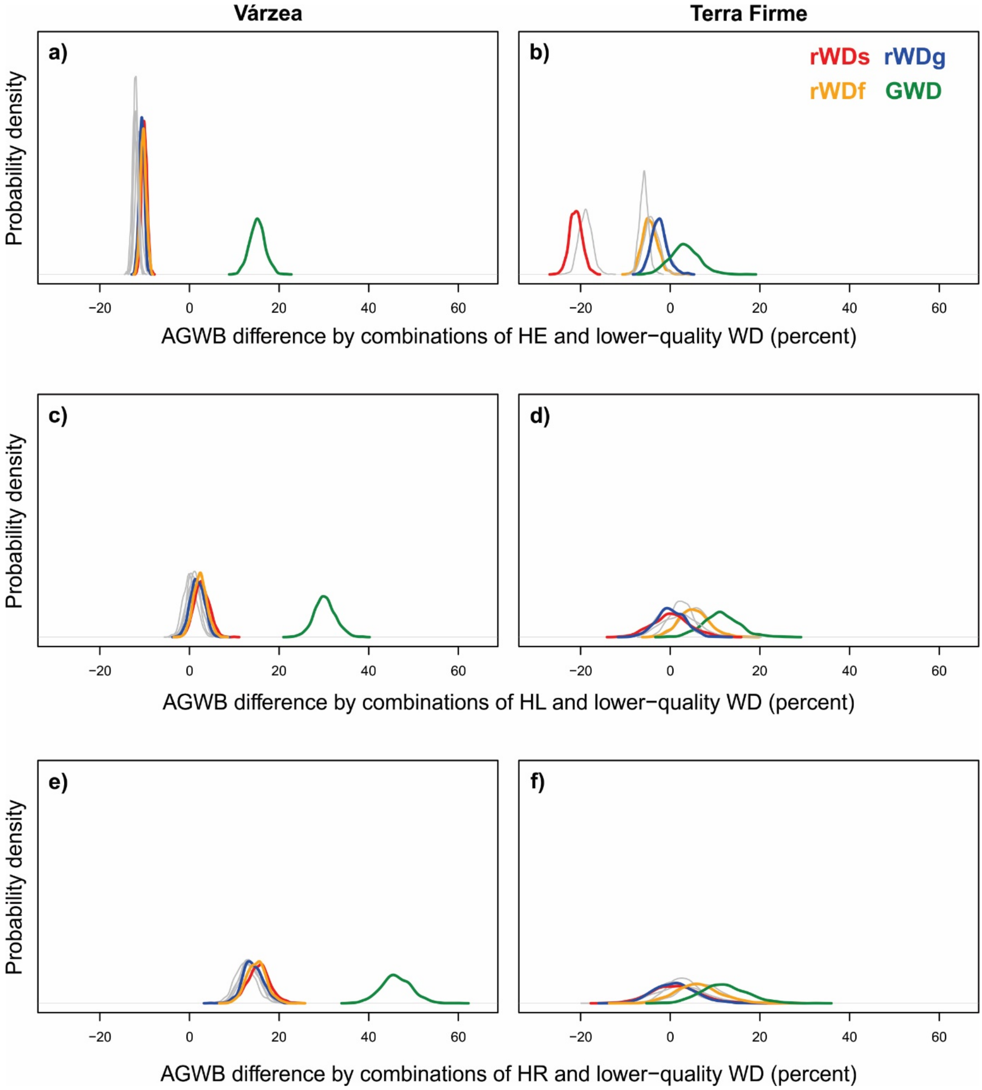

Figure 3. The posterior probability densities show estimated percent difference from várzea and terra firme above-ground woody biomass (AGWB) by combinations of lower-quality height and wood density. Negative values indicate underestimates in AGWB. Positive values indicate overestimates in AGWB. Where the probability distributions cross 0, methods do not systematically under or overestimate AGWB. Panels a) and b) show estimated percent difference in várzea (a) and terra firme (b) AGWB by visually estimated hight (HE) combined with species, genus, or family mean radially weighted wood specific density (rWDs, rWDg, or rWDf) or global mean wood density (GWD) retrieved from the

Global Wood Density database (Zanne et al., 2009; Chave et al., 2009) at the lowest possible taxonomic level. Panels c) and d) show estimated percent difference in várzea (c) and terra firme (d) AGWB by local allometric hight (HL) combined with rWDs, rWDg, rWDf, or GWD. Panels e) and f) show estimated percent difference in várzea (e) and terra firme (f) AGWB by regional allometric hight (HR) combined with rWDs, rWDg, rWDf or GWD.

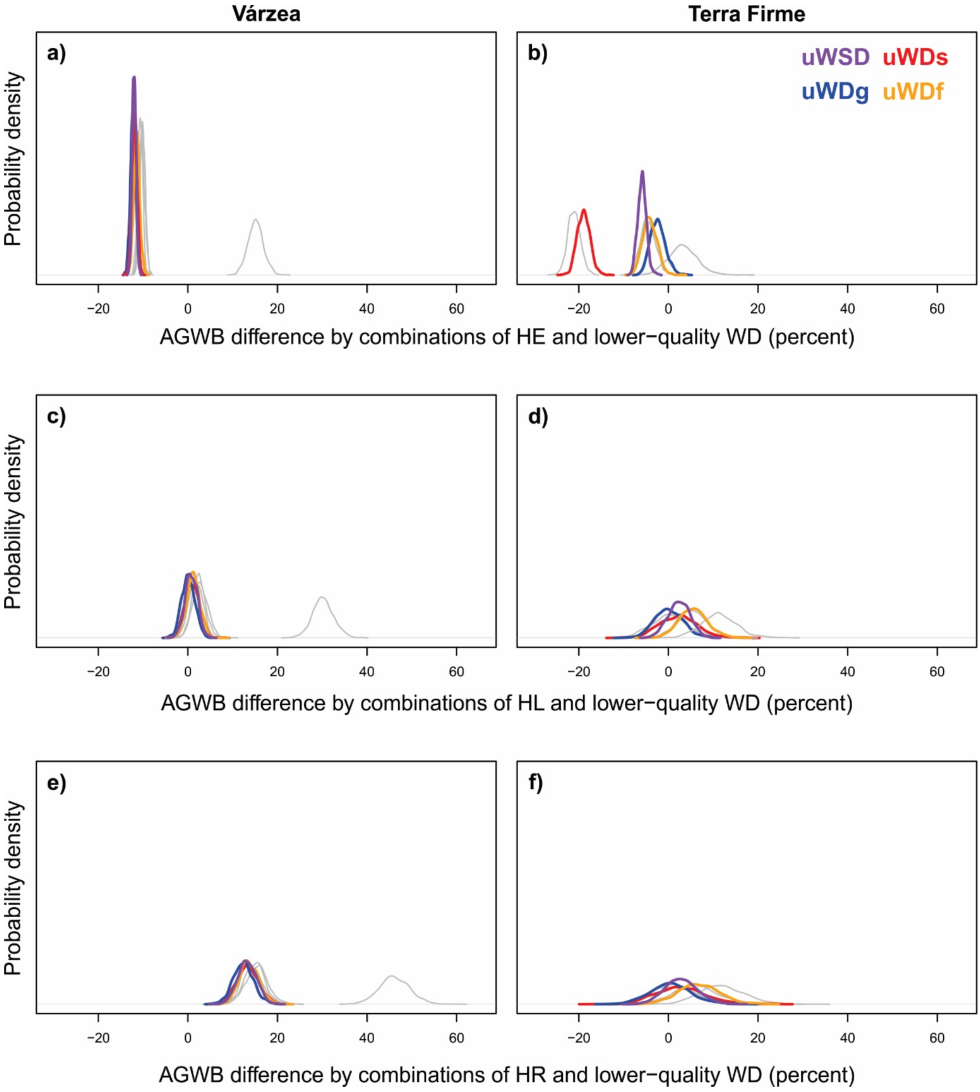

Figure 4. The posterior probability densities show estimated percent difference from várzea and terra firme above-ground woody biomass (AGWB) by combinations of lower-

quality height and unweighted mean wood specific density at the stem-specific (uWSD), species (uWDs), genus (uWDg) and family (uWDf) level. Negative values indicate underestimates in AGWB. Positive values indicate overestimates in AGWB. Where the probability distributions cross 0, methods do not systematically under or overestimate AGWB. Panels a) and b) show estimated percent difference in várzea (a) and terra firme (b) AGWB by visually estimated hight (HE) combined with uWSD, uWDs, uWDg or uWDf. Panels c) and d) show estimated percent difference in várzea (c) and terra firme (d) AGWB by local allometric hight (HL) combined with uWSD, uWDs, uWDg, or uWDf. Panels e) and f) show estimated percent difference in várzea (e) and terra firme (f) AGWB by regional allometric hight (HR) combined with uWSD, uWDs, uWDg, or uWDf.

3.5 AGWB differences in megagrams (Mg) per hectare (ha) forest

Based on the above results, we used local allometric height for individuals without stem-specific measured height and assigned appropriate species, genus, family, or plot mean wood specific density values to individuals without stem-specific radially weighted wood specific density (Table S2). Thus, we estimated várzea and terra firme forests to hold 254 and 224 Mg per ha forest, respectively. Using lower-quality height and wood density data resulted in differences of -31–117 Mg/ha in várzea and -47–27 Mg/ha in terra firme (Table S4). The five smallest and five largest mean differences in várzea ABWG ranged 0–2 Mg/ha and 38–117 Mg/ha, respectively (Fig. 5a). In terra firme, the five smallest AGWB differences ranged -1–1 Mg/ha, whereas the five largest differences under- or overestimated AGWB with -43– -47 or 15–27 Mg/ha, respectively (Fig. 5b).

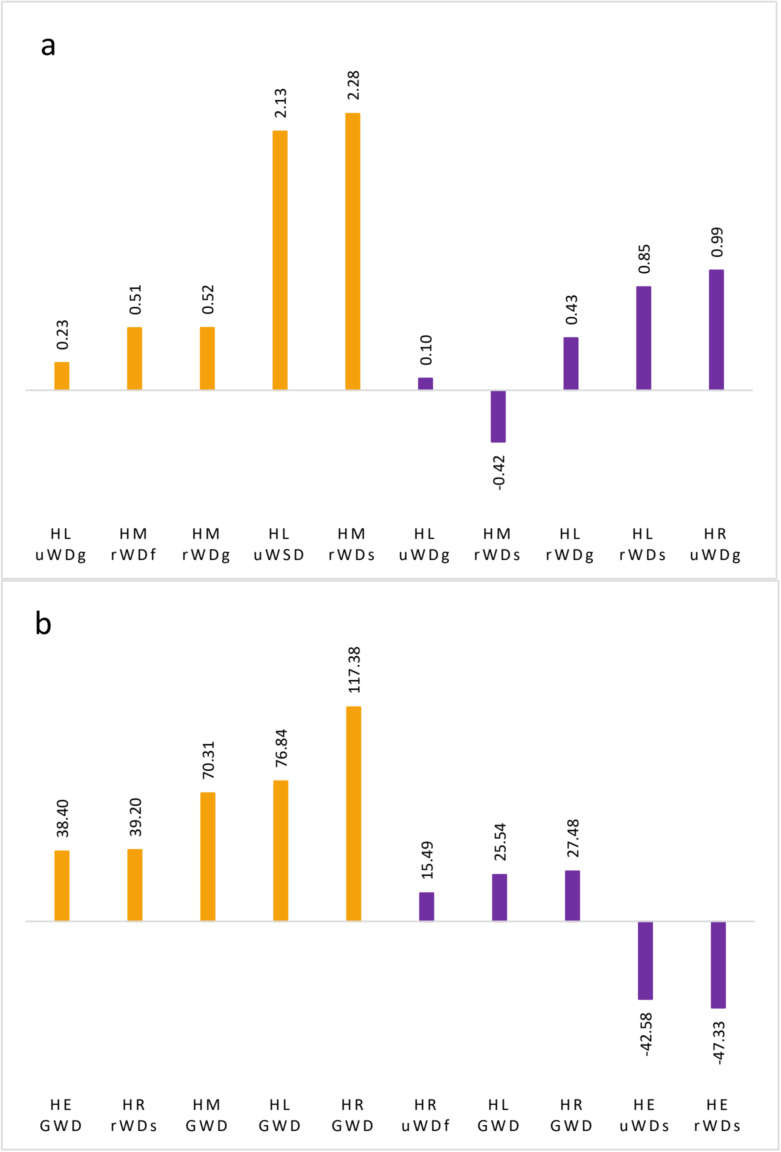

Figure 5. Expected mean difference in above-ground woody biomass (AGWB) in Mg per hectare forest in várzea (orange) and terra firme (purple) by (a) the five "best" combinations with lower-quality data, and (b) the five "worst" combinations with lower-quality data. All comparisons were made with AGWB estimated with individually measured tree height (HM, m) and stem-specific radially weighted wood specific density (g/cm3). Lower-quality height measurements (in m) are: HE = visually estimated height, HL = local allometric height, and HR = regional allometric height. Lower-quality wood

density measurements (in g/cm3) are stem-specific unweighted wood specific density (uWSD),radially weighted or unweighted mean wood specific density (rWD or uWD) at the species (rWDs, uWDs), genus (rWDg, uWDg) or family (rWDf, uWDf) level. Negative values indicate underestimates in AGWB. Positive values indicate overestimates in AGWB.

4. Discussion

Lower-quality measurements regularly overestimated AGWB in várzea forest, particularly when based on global mean wood density or regional height allometry. Thus, regional height allometries and wood density data might not perform well in data-poor forest types.

Because diameter-height relationships vary substantially among sites, Sullivan et al (2018), suggested that local calibrations of allometric diameter-height models might yield superior results to regional or global calibrations. Since diameter-height calibration often is accomplished by felling trees from the area of interest and subsequently measuring their stems with measuring tape (Burt et al., 2020), this is not possible in protected areas or permanent forest plots, such as in our sample site. In these cases, two common, alternative, and non-destructive field methods are to measure tree height by the tangent or sine method using a hypsometer (Burt et al., 2020; Larjavaara and Muller-Landau, 2013). Although such methods largely provide reliable tree heights (da Silva et al., 2012; Farve, 2010), measurements in taller, well-stratified, closed canopy forests become increasingly difficult as the top of trees are obscured (Larjavaara and Muller-Landau, 2013). Therefore, da Silva et al (2012) suggested that *in situ* visual height estimates may be as good as direct heigh measurements by a hypsometer. However, contrary to da Silva et al.(2012), we found that our visual height estimates consistently underestimated várzea and terra firme AGWB.

Locally calibrated diameter-height relationships following Sullivan et al. (2018) showed no systematic estimation biases in floodplain or upland AGWB (95% CI: VZ = -1–5%, TF = -2–8%). Local allometric height also performed well in combinations with local, forest-specific, lower-quality wood density values (i.e. unweighted or mean wood density at different taxonomic levels; 95% CIs ranged within -3–6% in VZ, -8–12% in TF). In contrast, whereas regional allometric height performed well in terra firme (overestimation of -3–10%), it consistently overestimated floodplain AGWB (by up to 10–19%). The upland accuracy is comparable to previous evaluations of upland-forest accuracy in Malaysia (Rutishauser et al., 2013). Likewise, previous work from Madagascar has shown that regional allometric height performs poorly in forests with high endemism (Vieilledent et al., 2012). Hence, pantropical climate-based height allometries seem to be well-calibrated for dominant forest types but induce substantial errors in other forests. We echo the conclusions in Sullivan et al. (2018) and highlight the need for local height calibrations across forest types.

Retrieving wood density data from global databases requires taxonomically resolved inventory data. However, species identifications in tropical rainforests are difficult (Cardoso et al., 2017; Gentry, 1988; Prance, 1994; ter Steege et al., 2019). Therefore, wood density often relies on identifications at higher taxonomic levels (i.e. genus or family level). In addition, species-level wood density is often missing for tropical rainforest species (c.f. Zanne et al., 2009). This is potentially problematic since wood density vary greatly among and within species depending on local growing conditions (Bredin et al., 2020b; Fearnside, 1997; Nogueira et al., 2008, 2005; Parolin, 2002; Wittmann et al., 2006b). Hence, using taxonomic or regional mean wood density measurements across forest types could grossly under- or overestimate forest biomass (Bredin et al., 2020b; Momo et al., 2020).

Here, we used forest-specific wood density when testing for effects of taxonomic accuracy on AGWB estimates in floodplain and upland forests, respectively. Thus, our results show that lower taxonomic accuracy in wood density, which accounts for local growing conditions, had little influence on várzea or terra firme AGWB on their own and in combinations with lower-quality height measurements. This result is in agreement with Baker (2004), who reported low variation among taxa within taxonomic levels. Likewise, Bredin et al. (2020b) found small differences in biomass estimates across taxonomic levels within forest types. For unweighted forest-specific wood densities, our result also indicated very weak or no systematic bias on AGWB estimates and differences among taxonomic levels varied little even when combined with lower-quality height. Overall, unweighted genus mean wood density and local allometric height was the combination that produced the smallest difference in floodplain and upland AGWB. This could be good news, given the laborious work to measure every tree height and to account for radial change in wood cores, especially given the lack of calibration equations for converting unweighted wood densities to radially weighted wood densities (Nogueira et al., 2008). However, as Phillips et al. (2019), Baker et al. (2004) and our large, systematic overestimates for combinations of global mean wood density or regional height allometry show, upscaling biomass estimates to map carbon stocks at regional scales, still requires more collections of wood density and local height calibration data from different, data-poor, forest types.

5. Conclusions

To conclude, existing methods for large-scale AGWB mapping are well-calibrated for terra firme forest, but local height calibration data significantly improve AGWB estimates based on general-purpose allometric equations in data-poor floodplain forest. Nevertheless, a variety of methods that performed well in the terra firme performed much worse in the várzea. These results are likely applicable to other poorly sampled forest types across the tropics. We therefore highly recommend the use of local height calibration data, field-measured stem diameters, and local, forest-specific wood-density to calibrate global wood density to the forest type of interest. By performing these actions, uncertainty in above-ground woody biomass estimates from data-poor tropical forests could be greatly reduced.

6. Author Contributions

Conceptualization and methodology, Y.K.B., and S.J.S.; Investigation and data curation, Y.K.B; Formal analysis, Y.K.B. and S.J.S.; Writing—original draft preparation, Y.K.B.; Writing—review and editing, Y.K.B., .J.B.S., J.S., J.E.H., R.L.A., C.A.P. and T.H. Y.K.B. and S.J.S. contributed equally to this work. All authors have read and agreed to the published version of the manuscript.

7. Funding

Y.K.B. was financed by the Norwegian University of Life Sciences (NMBU) as part of their PhD program in tropical ecology and an internal travel grant from NMBU.

8. Acknowledgments

This publication is part of the Projeto Médio Juruá series on Resource Management in Amazonian Reserves (www.projetomediojurua.org). We thank the Secretaria do Estado do Meio Ambiente e Desenvolvimento Sustentável do Amazonas (SEMA - DEMUC) and Instituto Brasileiro do Meio Ambiente e Recursos Naturais Renováveis

(IBAMA)/Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio) for authorising the research. We are grateful to the members from the Projeto Médio Juruá team for logistical support and extend special thanks to Andressa Scabin. We thank Michael J.G. Hopkins with colleagues at the National Institute for Amazonia Research (INPA) for providing logistical assistance and a place to work in Manaus. We thank Paulo Apóstolo Costa Lima Assunção (in memoriam) and Alexandro Elias dos Santos, assisted by Lorena M. Rincón, for identifying the species in the field and at INPA. Special thanks to all the field and lab assistants who contributed to the present study, particularly Rita Homem Pelicano and Laura N. Martins. We also thank Marcos Viejo Somoano and Camila Duarte Ritter for graphical assistance. Finally, we thank Associação dos Produtores Rurais de Carauari (ASPROC), Operação Amazônia Nativa (OPAN), Associação dos Moradores Agroextrativistas da Reserva de Desenvolvimento Sustentavel Uacari (AMARU), and the people of the central Juruá who in various ways assisted us throughout our work.

9. Conflicts of Interest

The authors declare no conflict of interest. The funders had no role in the design of the study; in the collection, analyses, or interpretation of data; in the writing of the manuscript, or in the decision to publish the results.

10. References

Anderson, A.B., 1981. White-Sand Vegetation of Brazilian Amazonia Author (s): Anthony B . Anderson Published by : The Association for Tropical Biology and Conservation Stable URL : http://www.jstor.org/stable/2388125. Biotropica , 13, 199–210.

Assis, R.L., Wittmann, F., Haugaasen, T., 2015. Effects of hydroperiod and substrate properties on tree alpha diversity and composition in Amazonian floodplain forests. J. Veg. Sci. 26, 312–322.

Baker, T.R., Phillips, O.L., Malhi, Y., Almeidas, S., Arroyo, L., Di Fiore, A., Erwin, T., Killeen, T.J., Laurance, S.G., Laurance, W.F., Lewis, S.L., Lloyd, J., Monteagudo, A., Neill, D.A., Patiño, S., Pitman, N.C.A., Silva, J.N.M., Martínez, R.V., 2004. Variation in wood density determines spatial patterns in Amazonian forest biomass. Glob. Chang. Biol. 10, 545–562. https://doi.org/10.1111/j.1529-8817.2003.00751.x

Bastin, J., Fayolle, A., Tarelkin, Y., Bulcke, J. Van Den, 2015. Wood Specific Gravity Variations and Biomass of Central African Tree Species : The Simple Choice of the Outer Wood. PLoS One 10, 1–16. https://doi.org/10.1371/journal.pone.0142146

Bredin, Y.K., Hawes, J.E., Peres, C.A., Haugaasen, T., 2020a. Structure and composition of terra firme and seasonally flooded várzea forests in the western brazilian amazon. Forests 11, 1–20. https://doi.org/10.3390/f11121361

Bredin, Y.K., Peres, C.A., Haugaasen, T., 2020b. Forest type affects the capacity of Amazonian tree species to store carbon as woody biomass. For. Ecol. Manage. 473, 118297. https://doi.org/10.1016/j.foreco.2020.118297

Burt, A., Calders, K., Cuni-Sanchez, A., Gómez-Dans, J., Lewis, P., Lewis, S.L., Malhi, Y., Phillips, O.L., Disney, M., 2020. Assessment of Bias in Pan-Tropical Biomass Predictions. Front. For. Glob. Chang. 3:12. https://doi.org/10.3389/ffgc.2020.00012

Cardoso, D., Särkinen, T., Alexander, S., Amorim, A.M., Bittrich, V., Celis, M., Daly, D.C., Fiaschi, P., Funk, V.A., Giacomin, L.L., Goldenberg, R., Heiden, G., Iganci, J., Kelloff, C.L., Knapp, S., Cavalcante de Lima, H., Machado, A.F.P., dos Santos, R.M., Mello-Silva, R., Michelangeli, F.A., Mitchell, J., Moonlight, P., de Moraes, P.L.R., Mori, S.A., Nunes, T.S., Pennington, T.D., Pirani, J.R., Prance, G.T., de Queiroz, L.P., Rapini, A., Riina, R., Rincon, C.A.V., Roque, N., Shimizu, G., Sobral, M., Stehmann, J.R., Stevens, W.D., Taylor, C.M., Trovó, M., van den Berg, C., van der Werff, H., Viana, P.L., Zartman, C.E., Forzza, R.C., 2017. Amazon plant diversity revealed by a taxonomically verified species list. Proc. Natl. Acad. Sci. 114, 10695–10700. https://doi.org/10.1073/pnas.1706756114

Cardoso da Silva, T., Pereira de Araújo, A., de Carvalho, A.L., Alves Magnago, A., Miranda, C.A., Rodrigues Hees, D., Cardoso Braz, E.R., Domingues, E., Silva, G.H., Oliveira Rodrigues, I., de Podestá Filho, J.A., Rodrigues Limeira, J.E., dos Santos, J., Hippertt de Cerqueira Leite, L.A., Leita da Silva, L., Cavalcanti da Cunha Bahiana, L., de Oliveira Filho, L.C., Cornejo Ortiz, L.R., Moreira Franco, M. do S., Cardoso de Lima, M.I., Campos Ribeiro, M.Â., Schild Becker, O.M., Pereira, M.F., Jesus de Almeida, V., 1990. Diagnóstico Gcoambiental e Sócio-economico da Área de infuência da BR-364, trecho Porto Velho - Rio Branco. Rio de Janeiro.

Chave, J., Coomes, D., Jansen, S., Lewis, S.L., Swenson, N.G., Zanne, A.E., 2009. Towards a worldwide wood economics spectrum. Ecol. Lett. 12, 351–366. https://doi.org/10.1111/j.1461-0248.2009.01285.x

Chave, J., Davies, S.J., Phillips, O.L., Lewis, S.L., Sist, P., Schepaschenko, D., Armston, J., Baker, T.R., Coomes, D., Disney, M., Duncanson, L., Hérault, B., Labrière, N., Meyer, V., Réjou-Méchain, M., Scipal, K., Saatchi, S., 2019. Ground Data are Essential for Biomass Remote Sensing Missions. Surv. Geophys. 40, 863–880. https://doi.org/10.1007/s10712-019-09528-w

Chave, J., Réjou-Méchain, M., Búrquez, A., Chidumayo, E., Colgan, M.S., Delitti, W.B.C., Duque, A., Eid, T., Fearnside, P.M., Goodman, R.C., Henry, M., Martínez-Yrízar, A., Mugasha, W.A., Muller-Landau, H.C., Mencuccini, M., Nelson, B.W., Ngomanda, A., Nogueira, E.M., Ortiz-Malavassi, E., Pélissier, R., Ploton, P., Ryan, C.M., Saldarriaga, J.G., Vieilledent, G., 2014. Improved allometric models to estimate the aboveground biomass of tropical trees. Glob. Chang. Biol. 20, 3177–3190. https://doi.org/10.1111/gcb.12629

da Silva, G.F., Curto, R. de A., Soares, C.P.B., Piassi, L. de C., 2012. Avaliação de métodos de medição de altura em florestas naturais. Rev. Arvore 36, 341–348. https://doi.org/10.1590/S0100-67622012000200015

Farve, R., 2010. Evaluation of Laser Rangefinders.

Fearnside, P.M., 1997. Wood density for estimating forest biomass in the Amazonia. For. Ecol. Manage. 90, 59–87.

Feeley, K., 2015. Are we filling the data void? An assessment of the amount and extent of plant collection records and census data available for tropical South America. PLoS One 10, e0125629. https://doi.org/10.1371/journal.pone.0125629

Flores, O., Coomes, D.A., 2011. Estimating the wood density of species for carbon stock assessments. Methods Ecol. Evol. 2, 214–220. https://doi.org/10.1111/j.2041-210X.2010.00068.x

Furtado de Mendonça, B.A., Simas, F.N.B., Schaefer, C.E.G.R., Fernandes Filho, E.I., Do Vale, J.F., De Mendonça, J.G.F., 2014. Podzolized soils and paleoenvironmental implications of white-sand vegetation (Campinarana) in the Viruá National Park, Brazil. Geoderma Reg. 2–3, 9–20. https://doi.org/10.1016/j.geodrs.2014.09.004

Gentry, A.H., 1988. Changes in plant community diversity and floristic composition on environmental and geographical gradients. Ann. Missouri Bot. Gard. 75, 1–34. https://doi.org/10.2307/2399464

Google Maps, 2021. Background map [WWW Document]. TerraMetrics, Map data. URL www.google.com/maps (accessed 4.18.21).

HAGLÖF SWEDEN AB, 2007. Vertex IV and Transponder T3 manual January 2007, v.1.0.

Haugaasen, T., Peres, C.A., 2006. Floristic, edaphic and structural characteristics of flooded and unflooded forests in the lower Rio Purús region of central Amazonia, Brazil. Acta Amaz. 25, 25–36. https://doi.org/10.1590/S0044-59672006000100005

Hawes, J.E., Peres, C.A., 2016. Patterns of plant phenology in Amazonian seasonally flooded and unflooded forests. Biotropica 48, 465–475. https://doi.org/10.1111/btp.12315

Hess, L.L., Melack, J.M., Affonso, A.G., Barbosa, C., Gastil-Buhl, M., Novo, E.M.L.M., 2015. Wetlands of the lowland Amazon Basin: extent, vegetative cover, and dual-season inundated area as mapped with JERS-1 synthetic aperture radar. Wetlands 35, 745–756. https://doi.org/10.1007/s13157-015-0666-y

Hess, L.L., Melack, J.M., Novo, E.M.L.M., Barbosa, C.C.F., Gastil, M., 2003. Dual-season mapping of wetland inundation and vegetation for the central Amazon basin. Remote Sens. Environ. 87, 404–428. https://doi.org/10.1016/j.rse.2003.04.001

Junk, W.J., Bayley, P.B., Sparks, R.E., 1989. The flood pulse concept in river-floodplain systems. Can. Spec. Publ. Fish. Aquat. Sci. 106, 110–127.

Junk, W.J., Piedade, M.T.F., 2010. An Introduction to South American Wetland Forests: Distribution, Definitions and General Characterization, in: Junk, W.J., Piedade, M.T.F., Wittmann, F., Schöngart, J., Parolin, P. (Eds.), Amazonian Floodplain Forests. Ecophysiology, Biodiversity and Sustainable Management. Springer, pp. 3–25. https://doi.org/10.1007/978-90-481-8725-6

Junk, W.J., Piedade, M.T.F., Schöngart, J., Cohn-Haft, M., Adeney, J.M., Wittmann, F., 2011.

A classification of major naturally-occurring amazonian lowland wetlands. Wetlands 31, 623–640. https://doi.org/10.1007/s13157-011-0190-7

Larjavaara, M., Muller-Landau, H.C., 2013. Measuring tree height: A quantitative comparison of two common field methods in a moist tropical forest. Methods Ecol. Evol. 4, 793–801. https://doi.org/10.1111/2041-210X.12071

Luize, B.G., Magalhães, J.L.L., Queiroz, H., Lopes, M.A., Venticinque, E.M., de Moraes Novo, E.M.L., Silva, T.S.F., 2018. The tree species pool of Amazonian wetland forests: Which species can assemble in periodically waterlogged habitats? PLoS One 13, e0198130. https://doi.org/10.1371/journal.pone.0198130

Melack, J.M., Hess, L.L., 2010. Remote sensing of the distribution and extent of wetlands in the Amazon basin., in: Junk, W., Piedade, M., Wittmann, F., Schöngart, J., Parolin, P. (Eds.), Central Amazonian Floodplain Forests: Ecophysiology, Biodiversity and Sustainable Management. Springer Verlag, Berlin (Germany), pp. 44–59.

Mitchard, T.A., 2018. The tropical forest carbon cycle and climate change The carbon balance of tropical forests. Nature 559, 527–534. https://doi.org/10.1038/s41586-018-0300-2

Momo, S.T., Ploton, P., Martin-Ducup, O., Lehnebach, R., Fortunel, C., Takougoum Sagang, L.B., Boyemba, F., Couteron, P., Fayolle, A., Libalah, M., Loumeto, J., Medjibe, V., Ngomanda, A., Obiang, D., Pélissier, R., Rossi, V., Yongo, O., Bocko, Y., Fonton, N., Kamdem, N., Katembo, J., Kondaoule, H.J., Maïdou, H.M., Mankou, G., Mbasi, M., Mengui, T., Mofack, G.I.I., Moundounga, C., Moundounga, Q., Nguimbous, L., Ncham, N.N., Asue, F.O.M., Senguela, Y.P., Viard, L., Zapfack, L., Sonké, B., Barbier, N., 2020. Leveraging Signatures of Plant Functional Strategies in Wood Density Profiles of African Trees to Correct Mass Estimations From Terrestrial Laser Data. Sci. Rep. 10, 1–11. https://doi.org/10.1038/s41598-020-58733-w

Muller-Landau, H.C., 2004. Interspecific and inter-site variation in wood specific gravity of tropical trees. Biotropica 36, 20. https://doi.org/10.1646/02119

Murça Pires, J., 1984. The Amazonian forest, in: Sioli, H. (Ed.), The Amazon. Limnology and Landscape Ecology of a Mighty Tropical River and Its Basin. Dr W. Junk Publishers, pp. 581–602. https://doi.org/10.1007/978-94-009-6542-3

Myster, R.W., 2016. The physical structure of forests in the Amazon Basin: a review. Bot. Rev. 82, 407–427. https://doi.org/10.1007/s12229-016-9174-x

Nogueira, E.M., Fearnside, P.M., Nelson, B.W., 2008. Normalization of wood density in biomass estimates of Amazon forests. For. Ecol. Manage. 256, 990–996. https://doi.org/10.1016/j.foreco.2008.06.001

Nogueira, E.M., Nelson, B.W., Fearnside, P.M., 2005. Wood density in dense forest in central Amazonia, Brazil. For. Ecol. Manage. 208, 261–286. https://doi.org/10.1016/j.foreco.2004.12.007

Parolin, P., 2002. Radial gradients in wood specific gravity in trees of Central Amazonian floodplains. IAWA J. 23, 449–457. https://doi.org/10.1163/22941932-90000314

Phillips, O.L., Sullivan, M.J.P., Baker, T.R., Monteagudo Mendoza, A., Vargas, P.N., Vásquez, R., 2019. Species matter: wood density influences tropical forest biomass at multiple scales. Surv. Geophys. https://doi.org/10.1007/s10712-019-09540-0

Piponiot, C., Chave, J., Herault, B., Pere, A., 2019. Package ‘ BIOMASS ’. https://doi.org/10.1111/2041-210X.12753>.License

Prance, G.T., 1994. A comparison of the efficacy of higher taxa and species numbers in the assessment of biodiversity in the neotropics. Philos. Trans. R. Soc. London Ser. B-Biological Sci. 345, 89–99. https://doi.org/https://doi.org/10.1098/rstb.1994.0090

Quéré, C. Le, Andrew, R.M., Friedlingstein, P., Sitch, S., Hauck, J., Pongratz, J., Pickers, P.A., Korsbakken, J.I., Peters, G.P., Canadell, J.G., 2018. Global Carbon Budget 2018 2141–2194.

R Core Team, 2021. R: A language and environment for statistical computing.

Réjou-Méchain, M., Barbier, N., Couteron, P., Ploton, P., Vincent, G., Herold, M., Mermoz, S., Saatchi, S., Chave, J., Boissieu, F. de, Férêt, J.-B., Momo Takoudjou, S., Pélissier, R., de Boissieu, F., Féret, J.-B., Takoudjou, S.M., Pélissier, R., 2019. Upscaling forest biomass from field to satellite measurements: sources of errors and ways to reduce them, Surveys in Geophysics. Springer Netherlands. https://doi.org/10.1007/s10712-019-09532-0

Réjou-Méchain, M., Tanguy, A., Piponiot, C., Chave, J., Hérault, B., 2017. BIOMASS: an R package for estimating above-ground biomass and its uncertainty in tropical forests. Methods Ecol. Evol. https://doi.org/10.1111/2041-210X.12753

Rutishauser, E., Noor'an, F., Laumonier, Y., Halperin, J., Rufi'ie, Hergoualch, K., Verchot, L., 2013. Generic allometric models including height best estimate forest biomass and carbon stocks in Indonesia. For. Ecol. Manage. 307, 219–225. https://doi.org/10.1016/j.foreco.2013.07.013

Sombroek, W., 2000. Amazon landforms and soils in relation to biological diversity. Acta Amaz. 30, 81. https://doi.org/https://dx.doi.org/10.1590/1809-43922000301100

Sullivan, M.J.P., Lewis, S.L., Hubau, W., Qie, L., Baker, T.R., Banin, L.F., Chave, J., Cuni-Sanchez, A., Feldpausch, T.R., Lopez-Gonzalez, G., Arets, E., Ashton, P., Bastin, J.-F., Berry, N.J., Bogaert, J., Boot, R., Brearley, F.Q., Brienen, R., Burslem, D.F.R.P., Canniere, C. de, Chudomelová, M., Dančák, M., Ewango, C., Hédl, R., Lloyd, J., Makana, J.-R., Malhi, Y., Marimon, B.S., Marimon Junior, B.H., Metali, F., Moore, S., Nagy, L., Nuñez Vargas, P., Pendry, C.A., Ramírez-Angulo, H., Reitsma, J., Rutishauser, E., Salim, K.A., Sonké, B., Sukri, R.S., Sunderland, T., Svátek, M., Umunay, P.M., Vasquez Martinez, R., Vernimmen, R.R.E., Vilanova Torre, E., Vleminckx, J., Vos, V., Phillips, O.L., 2018. Field methods for sampling tree height for tropical forest biomass estimation. Methods Ecol. Evol. 9, 1179–1189. https://doi.org/DOI: 10.1111/2041-210X.12962

ter Steege, H., Mota de Oliveira, S., Pitman, N.C.A., Sabatier, D., Antonelli, A., Guevara Andino, J.E., Aymard, G.A., Salomão, R.P., 2019. Towards a dynamic list of Amazonian tree species. Sci. Rep. 9, 3501. https://doi.org/10.1038/s41598-019-40101-y

Vieilledent, G., Vaudry, R., Andriamanohisoa, S.F.D., Rakotonarivo, O.S., Randrianasolo, H.Z., Razafindrabe, H.N., Bidaud Rakotoarivony, C., Ebeling, J., Rasamoelina, M., 2012. A universal approach to estimate biomass and carbon stock in tropical forests using generic allometric models. Ecol. Appl. 22, 572–583. https://doi.org/10.1890/11-0039.1

Wiemann, M.C., Williamson, G.B., 2012. Density and specific gravity metrics in biomass research. Gen. Tech. Rep. FPL GTR-208.

Williamson, G.B., Wiemann, M.C., 2010. Measuring wood specific gravity...correctly. Am. J. Bot. 97, 519–524. https://doi.org/10.3732/ajb.0900243

Wittmann, F., Householder, E., Piedade, M.T.F., Assis, R.L., Schöngart, J., Parolin, P., Junk, W.J., 2013. Habitat specifity, endemism and the neotropical distribution of Amazon white-water floodplain trees. Ecography (Cop.). 36, 690–707.

Wittmann, F., Marques, M.C.M., Júnior, G.D., Budke, J.C., Piedade, M.T.F., De Wittmann, A.O., Montero, J.C., Assis, R.L., Targhetta, N., Parolin, P., Junk, W.J., Householder, J.E., 2017. The Brazilian freshwater wetscape: Changes in tree community diversity and composition on climatic and geographic gradients. PLoS One 12, e0175003. https://doi.org/10.1371/journal.pone.0175003

Wittmann, F., Schöngart, J., Montero, J.C., Motzer, T., Junk, W.J., Piedade, M.T.F., Queiroz, H.L., Worbes, M., 2006a. Tree species composition and diversity gradients in white-water forests across the Amazon Basin. J. Biogeogr. 33, 1334–1347. https://doi.org/10.1111/j.1365-2699.2006.01495.x

Wittmann, F., Schöngart, J., Parolin, P., Worbes, M., Piedade, M.T.F., Junk, W.J., 2006b. Wood specific gravity of trees in Amazonian white-water forests in relation to flooding. IAWA J. https://doi.org/10.1163/22941932-90000153

Zanne, A., Lopez-Gonzalez, G., DA, C., Ilic, J., Jansen, S., SL, L., RB, M., NG, S., MC, W., Chave, J., 2009. Data from: Towards a worldwide wood economics spectrum. Ecol. Lett. https://doi.org/doi:10.5061/dryad.234

11. Supplementary Materials

Table S1. Wood Density Values. Summary statistics for the different wood density (WD) values included in our study of várzea and terra firme forest above-ground woody biomass estimates. Minimum (min), median, mean, and maximum (Max) values are given in g/cm3. rWSD = stem-specific radially weighted wood specific density, rWDs = radially weighted species mean wood specific density, rWDg = radially weighted genus mean wood specific density, rWDf = radially weighted family mean wood specific density, uWSD = stem-specific unweighted wood specific density, uWDs = unweighted species mean wood specific density, uWDg = unweighted genus mean wood specific density, uWDf = unweighted family mean wood specific density, and GWD = Global mean Wood Density at the lowest possible taxonomic level, retrieved from the Global Wood Density Database (Chave et al., 2009; Zanne et al., 2009).

	Várzea				**Terra firme**			
WD	**Min**	**Median**	**Mean**	**Max**	**Min**	**Median**	**Mean**	**Max**
rWSD	0.1244	0.5032	0.5055	1.2982	0.2900	0.6046	0.6118	0.8779
rWDs	0.1825	0.5073	0.5064	0.9304	0.3526	0.6204	0.6177	0.8779
rWDg	0.2321	0.5048	0.5063	0.8524	0.3526	0.6118	0.6155	0.8779
rWDf	0.2321	0.5047	0.5046	0.8038	0.4191	0.5959	0.6125	0.8208
uWSD	0.0526	0.4967	0.4993	0.9813	0.2550	0.6194	0.6161	0.8668
uWDs	0.1214	0.4962	0.5014	0.8842	0.3110	0.6266	0.6256	0.8668
uWDg	0.2207	0.5021	0.5003	0.8842	0.3110	0.6348	0.6205	0.8668
uWDf	0.2207	0.5020	0.4991	0.7261	0.3781	0.6043	0.6128	0.8255
GWD	0.2087	0.6679	0.6485	0.9307	0.2934	0.6565	0.6538	0.9234

Table S2. Method Effects. Effect of lower-quality tree height (H) and wood density (WD) on above-ground woody biomass (AGWB) estimates in várzea and terra firme. Methods are presented in descending order of mean percent difference in AGWB, so that better methods (=smaller effect) are listed first. Yellow highlights indicate the best methods to fill in WD when you have individually measured total tree height (HM). Blue indicate the best methods for filling in missing data when you do not have individually measured total tree height or stem-specific, radially weighted wood density (rWSD). N is the number of trees included for each separate analysis. Minimum (Min), lower (2.5%) Credible Interval (CI), median, mean, upper (97.5%) CI and maximum (Max) deviations from AGWB based on stem-specific and radially weighted measurements are shown as percent of the total AGWB across trees. Negative values indicate underestimations. Positive values indicate overestimations. Height parameters, in m, are individually measured total tree height (HM), visually estimated tree height (HE), local allometric tree height (HL), and regional allometric tree height (HR). Wood density parameters, in g/cm^3, are stem-specific, radially weighted wood specific density (rWSD), stem-specific unweighted wood specific density (uWSD), radially weighted (r) and unweighted (u) species- (s), genus- (g), and family (f) mean wood specific density for all species, genera or families with ≥3 radially weighted wood specific density values (rWDs, uWDs, rWDg, uWDg, rWDf, uWDf), and global mean wood densities at the lowest possible taxonomic level (GWD) retrieved from the Global Wood Density database (Zanne et al., 2009; Chave et al., 2009).

Várzea									**Terra firme**								
N	**WD**	**H**	**Min, %**	**CI 2.5%**	**Median, %**	**Mean, %**	**CI 97.5%**	**Max, %**	**N**	**WD**	**H**	**Min, %**	**CI 2.5%**	**Median, %**	**Mean, %**	**CI 97.5%**	**Max, %**
583	uWDg	HL	-4.5	-3.0	0.1	0.1	3.0	5.8	94	uWDg	HL	-8.9	-6.0	0.0	0.0	6.1	11.0
583	rWDg	HM	-1.1	-0.4	0.2	0.2	0.8	1.2	53	rWDs	HM	-1.5	-1.1	-0.2	-0.2	0.9	2.1
621	rWDf	HM	-1.3	-0.6	0.2	0.2	1.1	1.5	94	rWDg	HL	-9.4	-5.6	0.2	0.2	6.6	10.2
642	uWSD	HL	-3.9	-1.9	0.9	0.8	3.6	6.2	53	rWDs	HL	-11.3	-7.5	0.4	0.4	8.6	15.3
480	rWDs	HM	0.1	0.3	0.9	0.9	1.5	1.9	94	uWDg	HR	-12.0	-8.1	0.2	0.4	9.8	18.7

Várzea									Terra firme								
N	WD	H	Min, %	CI 2.5%	Median, %	Mean, %	CI 97.5%	Max, %	N	WD	H	Min, %	CI 2.5%	Median, %	Mean, %	CI 97.5%	Max, %
480	uWDs	HM	-1.9	-1.4	-0.9	-0.9	-0.5	-0.3	153	uWSD	HM	-1.1	-0.8	-0.6	-0.6	-0.3	-0.1
621	uWDf	HM	-2.3	-1.7	-1.0	-1.0	-0.2	0.5	94	uWDg	HM	-1.4	-0.6	0.6	0.6	1.9	2.8
642	uWSD	HM	-1.5	-1.3	-1.1	-1.1	-0.9	-0.8	94	rWDg	HM	-1.0	-0.5	0.7	0.8	2.2	3.4
480	uWDs	HL	-4.8	-2.3	1.1	1.1	4.4	8.8	94	rWDg	HR	-15.2	-7.5	0.7	0.8	9.6	20.2
621	uWDf	HL	-3.8	-1.6	1.3	1.2	4.2	7.8	53	rWDs	HR	-14.8	-8.4	0.7	1.0	12.8	22.8
583	uWDg	HM	-2.6	-2.0	-1.5	-1.5	-1.0	-0.6	122	rWDf	HM	-0.6	0.0	1.3	1.3	2.8	4.2
583	rWDg	HL	-2.6	-1.1	1.6	1.7	4.6	7.6	53	uWDs	HM	0.1	0.7	1.7	1.7	2.8	3.6
642	rWSD	HL	-2.0	-0.7	1.9	1.9	4.8	6.7	122	uWDf	HM	-0.5	0.4	1.7	1.7	3.1	3.8
621	rWDf	HL	-1.8	-0.4	2.4	2.4	5.3	7.6	53	uWDs	HL	-9.3	-5.5	2.1	2.1	10.6	23.1
480	rWDs	HL	-2.9	-0.5	2.8	2.8	6.1	10.4	153	uWSD	HL	-5.3	-2.4	2.2	2.2	7.0	10.4
430	rWDs	HE	-12.2	-11.2	-10.1	-10.1	-8.8	-8.2	48	rWDg	HE	-6.8	-5.7	-2.4	-2.3	1.6	4.2
551	rWDf	HE	-12.7	-11.5	-10.3	-10.3	-9.1	-8.1	48	uWDg	HE	-7.3	-5.5	-2.4	-2.3	1.7	6.3
517	rWDg	HE	-12.4	-11.8	-10.7	-10.7	-9.4	-8.8	153	uWSD	HR	-8.0	-4.2	2.5	2.6	10.1	16.7
568	rWSD	HE	-12.4	-11.8	-10.9	-10.9	-10.1	-9.7	153	rWSD	HL	-4.8	-1.9	3.0	3.0	8.0	10.9
551	uWDf	HE	-13.6	-12.6	-11.4	-11.4	-10.2	-9.0	70	GWB	HE	-6.2	-3.1	3.2	3.2	9.9	12.5
430	uWDs	HE	-14.0	-13.1	-11.9	-11.9	-10.6	-9.9	153	rWSD	HR	-7.7	-3.3	3.0	3.2	10.3	16.0
568	uWSD	HE	-13.3	-12.8	-12.0	-12.0	-11.1	-10.7	53	uWDs	HR	-12.0	-7.1	2.9	3.4	15.9	22.2
517	uWDg	HE	-14.1	-13.3	-12.2	-12.2	-11.1	-10.2	63	uWDf	HE	-8.3	-7.0	-4.0	-4.0	-0.8	2.0
583	uWDg	HR	5.4	8.1	12.4	12.4	16.6	18.5	63	rWDf	HE	-8.9	-7.4	-4.5	-4.4	-1.0	2.8
642	uWSD	HR	6.6	9.2	13.1	13.2	17.6	19.9	122	rWDf	HL	-3.6	-1.1	5.0	5.1	11.8	16.6

Várzea										Terra firme									
N	WD	H	Min, %	CI 2.5%	Median, %	Mean, %	CI 97.5%	Max, %		N	WD	H	Min, %	CI 2.5%	Median, %	Mean, %	CI 97.5%	Max, %	
480	uWDs	HR	6.0	9.0	13.3	13.4	17.5	21.2		122	uWDf	HL	-6.7	-0.7	5.5	5.5	12.1	16.7	
621	uWDf	HR	6.4	9.4	13.6	13.7	18.1	24.0		70	uWSD	HE	-8.7	-7.8	-5.9	-5.9	-3.8	-2.8	
583	rWDg	HR	6.6	10.2	14.1	14.2	18.8	21.8		70	rWSD	HE	-8.7	-7.9	-6.1	-6.0	-4.0	-3.1	
642	rWSD	HR	7.7	10.5	14.4	14.5	18.9	20.9		153	GWB	HM	-0.9	2.0	6.1	6.2	10.6	13.4	
621	rWDf	HR	8.2	10.2	15.0	15.0	19.5	23.4		122	rWDf	HR	-7.6	-2.1	6.3	6.4	15.7	22.0	
568	GWB	HE	9.9	12.0	15.1	15.1	18.7	21.6		122	uWDf	HR	-5.5	-1.7	6.8	6.9	16.7	24.8	
480	rWDs	HR	7.1	10.5	15.3	15.4	20.4	23.6		153	GWB	HL	-2.5	3.8	11.2	11.4	19.9	28.6	
642	GWB	HM	22.1	24.6	27.6	27.7	30.9	33.4		153	GWB	HR	-2.0	2.9	12.0	12.3	23.1	32.9	
642	GWB	HL	22.3	25.6	30.1	30.3	35.2	39.4		25	uWDs	HE	-24.0	-21.6	-19.1	-19.0	-15.9	-13.3	
642	GWB	HR	36.7	40.1	46.0	46.2	53.4	59.2		25	rWDs	HE	-25.6	-23.9	-21.1	-21.1	-18.0	-16.0	

Table S3. Regression Parameter Values. Estimated posterior regression parameter mean, lower (5%) and upper (95%) credible interval (CI) values to predict log(above-ground woody biomass difference by tree height (H) and wood density (WD) measurements) in várzea (vz) and terra firme (tf) forest. The predictor variables were diameter at breast height (DBH, cm), wood density ratio (WD ratio = outer wood density / inner wood density, g/cm3), and the interaction between diameter at breast height and wood density ratio. The data were spatially and taxonomically nested within genera within families and within plots within transects. Estimated parameter values are given for regression intercepts, β DBH coefficients, β WD ratio coefficients, β interaction coefficients, and standard deviations (σ) of the regression residuals and the nesting factors. Positive coefficient values indicate an increase in effect of the predictor variable. A negative coefficient value indicates a decrease in effect of the predictor variable. Some plots were not nested within transects. For these, there are no σ transect estimates. Height measurements in m, are individually measured total tree height (HM), visually estimated tree height (HE), local allometric tree height (HL), and regional allometric tree height (HR). Wood density measurements in g/cm^3, are stem-specific, radially weighted wood specific density (rWSD), stem-specific unweighted wood specific density (uWSD), radially weighted (r) and unweighted (u) species- (s), genus- (g), and family (f) mean wood specific density for all species, genera or families with ≥3 radially weighted wood specific density values (rWDs, uWDs, rWDg, uWDg, rWDf, uWDf), and global mean wood densities at the lowest possible taxonomic level (GWD) retrieved from the Global Wood Density database (Zanne et al., 2009; Chave et al., 2009).

			Intercept			**β DBH**			**β WD ratio**			**β Interaction**			**σ residual**			**σ plot**			**σ transect**			**σ genus**			**σ family**		
Habitat	**WD**	**H**	**mean**	**5%CI**	**95%CI**	**mean**	**5%CI**	**95%CI**	**mean**	**5%CI**	**95%CI**	**mean**	**5%CI**	**95%CI**	**mean**	**5%CI**	**95%CI**	**mean**	**5%CI**	**95%CI**	**mean**	**5%CI**	**95%CI**	**mean**	**5%CI**	**95%CI**	**mean**	**5%CI**	**95%CI**
vz	GWD	HR	0.73	0.20	1.30	-0.01	-0.04	0.02	-0.19	-0.75	0.32	0.01	-0.02	0.03	0.40	0.37	0.43	0.04	0.00	0.10	0.05	0.00	0.12	0.23	0.17	0.30	0.10	0.03	0.20
tf	GWD	HR	0.74	-0.55	2.00	-0.03	-0.11	0.04	-0.87	-2.05	0.35	0.04	-0.03	0.11	0.38	0.31	0.44	0.18	0.01	0.52				0.10	0.01	0.24	0.13	0.01	0.31
vz	uWDf	HR	0.49	0.04	0.97	-0.01	-0.04	0.01	-0.18	-0.63	0.25	0.01	-0.01	0.03	0.38	0.35	0.40	0.05	0.01	0.11	0.07	0.02	0.15	0.16	0.11	0.22	0.06	0.02	0.12
tf	uWDf	HR	1.04	-0.08	2.17	-0.06	-0.13	0.01	-1.17	-2.18	-0.14	0.06	0.00	0.13	0.33	0.28	0.39	0.16	0.01	0.47				0.05	0.00	0.14	0.05	0.00	0.15

			Intercept			β DBH			β WD ratio			β Interaction			σ residual			σ plot			σ transect			σ genus			σ family		
Habitat	WD	H	mean	5%CI	95%CI	mean	5%CI	95%CI	mean	5%CI	95%CI	mean	5%CI	95%CI	mean	5%CI	95%CI	mean	5%CI	95%CI	mean	5%CI	95%CI	mean	5%CI	95%CI	mean	5%CI	95%CI
vz	uWDg	HR	0.43	-0.06	0.91	-0.01	-0.03	0.02	-0.13	-0.59	0.34	0.00	-0.02	0.03	0.38	0.35	0.41	0.04	0.00	0.09	0.06	0.01	0.12	0.10	0.04	0.16	0.07	0.02	0.13
tf	uWDg	HR	-0.02	-1.53	1.45	0.02	-0.08	0.12	-0.09	-1.45	1.29	-0.01	-0.10	0.08	0.33	0.27	0.39	0.19	0.02	0.57				0.05	0.00	0.13	0.05	0.00	0.14
vz	uWDs	HR	0.46	-0.05	0.96	-0.01	-0.04	0.01	-0.17	-0.65	0.31	0.01	-0.02	0.03	0.35	0.32	0.38	0.03	0.00	0.08	0.04	0.00	0.09	0.11	0.04	0.18	0.08	0.02	0.15
tf	uWDs	HR	0.05	-2.10	2.23	0.02	-0.13	0.17	-0.15	-2.05	1.76	-0.02	-0.15	0.12	0.32	0.24	0.42	0.15	0.01	0.45				0.06	0.00	0.18	0.07	0.00	0.20
vz	uWSD	HR	0.40	-0.05	0.87	0.00	-0.02	0.02	-0.10	-0.54	0.32	0.00	-0.03	0.02	0.35	0.32	0.37	0.03	0.00	0.07	0.04	0.00	0.09	0.10	0.04	0.16	0.06	0.02	0.11
tf	uWSD	HR	0.06	-1.02	1.21	0.00	-0.06	0.06	-0.21	-1.29	0.79	0.00	-0.05	0.07	0.31	0.27	0.36	0.11	0.01	0.35				0.05	0.00	0.13	0.06	0.00	0.17
vz	rWSD	HR	0.41	-0.03	0.83	-0.01	-0.03	0.02	-0.08	-0.48	0.34	0.00	-0.02	0.02	0.34	0.31	0.36	0.03	0.00	0.07	0.03	0.00	0.09	0.10	0.04	0.15	0.05	0.01	0.10
tf	rWSD	HR	0.05	-1.12	1.14	-0.01	-0.07	0.06	-0.20	-1.21	0.88	0.01	-0.05	0.07	0.30	0.25	0.35	0.14	0.01	0.42				0.05	0.00	0.13	0.05	0.00	0.15
vz	rWDs	HR	0.43	-0.02	0.87	-0.01	-0.03	0.01	-0.15	-0.56	0.28	0.01	-0.02	0.03	0.35	0.32	0.38	0.03	0.00	0.08	0.04	0.00	0.10	0.11	0.04	0.17	0.07	0.02	0.14
tf	rWDs	HR	-0.18	-2.29	1.97	0.03	-0.12	0.18	-0.01	-1.90	1.85	-0.02	-0.15	0.11	0.32	0.24	0.41	0.14	0.01	0.45				0.07	0.00	0.19	0.07	0.00	0.21
vz	rWDg	HR	0.47	0.00	0.95	-0.01	-0.04	0.01	-0.15	-0.60	0.30	0.00	-0.02	0.03	0.37	0.35	0.40	0.04	0.01	0.09	0.06	0.01	0.12	0.09	0.03	0.14	0.06	0.01	0.11
tf	rWDg	HR	0.04	-1.30	1.45	0.01	-0.08	0.10	-0.18	-1.45	1.07	-0.01	-0.09	0.08	0.32	0.26	0.38	0.19	0.01	0.56				0.04	0.00	0.12	0.05	0.00	0.14
vz	rWDf	HR	0.53	0.03	1.05	-0.01	-0.04	0.01	-0.21	-0.69	0.25	0.01	-0.01	0.03	0.38	0.35	0.40	0.05	0.01	0.11	0.07	0.02	0.15	0.16	0.10	0.22	0.06	0.01	0.11
tf	rWDf	HR	1.05	-0.09	2.25	-0.06	-0.13	0.01	-1.19	-2.30	-0.15	0.07	0.00	0.13	0.33	0.28	0.39	0.16	0.01	0.47				0.06	0.00	0.15	0.06	0.00	0.17
vz	GWD	HL	0.43	-0.33	1.21	-0.01	-0.04	0.03	-0.19	-0.96	0.54	0.01	-0.03	0.04	0.50	0.44	0.58	0.04	0.00	0.11	0.05	0.00	0.13	0.24	0.15	0.32	0.12	0.03	0.22
tf	GWD	HL	0.66	-0.78	2.02	-0.02	-0.10	0.06	-0.83	-2.09	0.50	0.03	-0.04	0.10	0.38	0.30	0.49	0.18	0.01	0.51				0.11	0.01	0.23	0.14	0.01	0.33
vz	uWDf	HL	0.18	-0.56	0.93	-0.01	-0.04	0.02	-0.18	-0.90	0.52	0.01	-0.02	0.04	0.48	0.42	0.56	0.05	0.01	0.12	0.06	0.01	0.15	0.15	0.04	0.25	0.07	0.01	0.14
tf	uWDf	HL	0.79	-0.54	2.07	-0.04	-0.12	0.03	-0.97	-2.16	0.27	0.05	-0.02	0.12	0.35	0.28	0.44	0.15	0.01	0.42				0.06	0.00	0.15	0.06	0.00	0.19
vz	uWDg	HL	0.17	-0.55	0.90	-0.01	-0.04	0.03	-0.16	-0.86	0.54	0.01	-0.02	0.04	0.48	0.41	0.55	0.04	0.00	0.10	0.05	0.00	0.13	0.09	0.01	0.18	0.07	0.01	0.14
tf	uWDg	HL	-0.08	-1.62	1.44	0.02	-0.07	0.12	-0.09	-1.50	1.32	-0.02	-0.11	0.07	0.35	0.27	0.44	0.21	0.02	0.63				0.06	0.00	0.16	0.06	0.00	0.18
vz	uWDs	HL	0.20	-0.54	0.99	-0.01	-0.04	0.03	-0.20	-0.96	0.50	0.01	-0.02	0.04	0.45	0.39	0.53	0.03	0.00	0.09	0.04	0.00	0.11	0.09	0.02	0.20	0.09	0.01	0.16
tf	uWDs	HL	-0.22	-2.38	1.88	0.04	-0.10	0.19	0.00	-1.83	1.90	-0.03	-0.16	0.09	0.34	0.24	0.49	0.17	0.01	0.56				0.09	0.01	0.27	0.10	0.01	0.28
vz	uWSD	HL	0.11	-0.58	0.82	0.00	-0.03	0.04	-0.11	-0.79	0.56	0.00	-0.03	0.03	0.46	0.40	0.53	0.04	0.00	0.09	0.04	0.00	0.11	0.09	0.01	0.17	0.06	0.01	0.13

			Intercept			β DBH			β WD ratio			β Interaction			σ residual			σ plot			σ transect			σ genus			σ family		
Habitat	WD	H	mean	5%CI	95%CI	mean	5%CI	95%CI	mean	5%CI	95%CI	mean	5%CI	95%CI	mean	5%CI	95%CI	mean	5%CI	95%CI	mean	5%CI	95%CI	mean	5%CI	95%CI	mean	5%CI	95%CI
tf	uWSD	HL	-0.05	-1.24	1.08	0.01	-0.05	0.08	-0.14	-1.22	0.96	0.00	-0.06	0.06	0.34	0.27	0.48	0.11	0.01	0.37				0.05	0.00	0.15	0.06	0.00	0.18
vz	rWSD	HL	0.13	-0.57	0.85	0.00	-0.03	0.03	-0.09	-0.79	0.58	0.00	-0.03	0.03	0.45	0.39	0.53	0.03	0.00	0.08	0.04	0.00	0.10	0.08	0.01	0.17	0.06	0.01	0.13
tf	rWSD	HL	-0.08	-1.30	1.07	0.00	-0.06	0.07	-0.11	-1.19	1.02	0.00	-0.06	0.06	0.33	0.26	0.47	0.13	0.01	0.41				0.05	0.00	0.14	0.06	0.00	0.19
vz	rWDs	HL	0.15	-0.57	0.96	-0.01	-0.04	0.03	-0.15	-0.92	0.54	0.01	-0.02	0.04	0.45	0.39	0.53	0.04	0.00	0.10	0.04	0.00	0.11	0.09	0.01	0.20	0.08	0.01	0.15
tf	rWDs	HL	-0.29	-2.38	1.71	0.04	-0.10	0.18	0.03	-1.76	1.87	-0.03	-0.15	0.09	0.34	0.24	0.48	0.17	0.01	0.53				0.09	0.01	0.25	0.09	0.01	0.28
vz	rWDg	HL	0.19	-0.53	0.89	-0.01	-0.04	0.02	-0.16	-0.84	0.51	0.01	-0.02	0.04	0.48	0.41	0.55	0.04	0.00	0.10	0.05	0.00	0.12	0.08	0.01	0.17	0.06	0.01	0.13
tf	rWDg	HL	-0.15	-1.69	1.34	0.03	-0.06	0.12	-0.05	-1.45	1.35	-0.02	-0.11	0.07	0.35	0.27	0.44	0.21	0.02	0.62				0.05	0.00	0.15	0.06	0.00	0.17
vz	rWDf	HL	0.19	-0.56	0.95	-0.01	-0.04	0.02	-0.17	-0.90	0.54	0.01	-0.02	0.04	0.48	0.42	0.56	0.05	0.01	0.11	0.06	0.01	0.15	0.15	0.04	0.24	0.06	0.01	0.13
tf	rWDf	HL	0.78	-0.58	2.05	-0.04	-0.12	0.04	-0.97	-2.14	0.27	0.05	-0.02	0.12	0.35	0.28	0.44	0.15	0.01	0.44				0.06	0.00	0.15	0.06	0.00	0.18
vz	GWD	HE	0.16	-0.23	0.56	-0.01	-0.03	0.01	-0.11	-0.50	0.25	0.01	-0.01	0.04	0.30	0.28	0.32	0.02	0.00	0.05	0.02	0.00	0.06	0.22	0.17	0.28	0.10	0.04	0.17
tf	GWD	HE	0.37	-1.15	1.85	-0.02	-0.09	0.05	-0.67	-1.86	0.51	0.03	-0.04	0.10	0.30	0.24	0.38	0.70	0.02	2.75				0.07	0.00	0.20	0.06	0.00	0.17
vz	uWDf	HE	-0.10	-0.39	0.20	-0.01	-0.03	0.00	-0.07	-0.35	0.21	0.02	0.00	0.03	0.26	0.25	0.28	0.02	0.00	0.05	0.03	0.00	0.06	0.14	0.10	0.19	0.04	0.01	0.08
tf	uWDf	HE	0.52	-0.99	2.04	-0.03	-0.11	0.04	-0.85	-1.99	0.28	0.05	-0.03	0.12	0.26	0.22	0.31	0.77	0.02	2.90				0.04	0.00	0.11	0.04	0.00	0.10
vz	uWDg	HE	-0.11	-0.39	0.17	-0.01	-0.02	0.01	-0.05	-0.32	0.22	0.01	0.00	0.02	0.27	0.25	0.28	0.02	0.00	0.05	0.03	0.00	0.07	0.03	0.00	0.06	0.03	0.00	0.07
tf	uWDg	HE	-0.18	-2.15	1.84	0.02	-0.09	0.14	-0.17	-1.80	1.56	-0.01	-0.13	0.11	0.29	0.23	0.36	0.78	0.02	2.93				0.06	0.00	0.16	0.06	0.00	0.16
vz	uWDs	HE	0.01	-0.28	0.29	-0.01	-0.03	0.00	-0.15	-0.43	0.12	0.01	0.00	0.03	0.25	0.23	0.27	0.01	0.00	0.03	0.01	0.00	0.03	0.02	0.00	0.05	0.03	0.00	0.07
tf	uWDs	HE	-0.43	-3.81	2.89	0.04	-0.19	0.27	0.29	-2.96	3.50	-0.05	-0.28	0.19	0.35	0.24	0.50	0.91	0.03	3.25				0.12	0.01	0.35	0.12	0.01	0.38
vz	uWSD	HE	-0.11	-0.35	0.13	0.00	-0.01	0.01	-0.07	-0.30	0.16	0.00	-0.01	0.02	0.23	0.22	0.24	0.01	0.00	0.04	0.01	0.00	0.04	0.02	0.00	0.05	0.02	0.00	0.04
tf	uWSD	HE	-0.49	-1.52	0.59	0.02	-0.02	0.07	0.18	-0.53	0.89	-0.01	-0.05	0.03	0.20	0.16	0.24	0.59	0.01	2.48				0.05	0.01	0.12	0.05	0.01	0.11
vz	rWSD	HE	-0.09	-0.31	0.13	-0.01	-0.02	0.00	-0.05	-0.27	0.16	0.01	0.00	0.02	0.21	0.20	0.22	0.01	0.00	0.04	0.02	0.00	0.04	0.03	0.00	0.06	0.03	0.00	0.07
tf	rWSD	HE	-0.51	-1.67	0.61	0.01	-0.03	0.05	0.15	-0.51	0.82	0.00	-0.04	0.04	0.19	0.16	0.23	0.67	0.01	3.00				0.05	0.00	0.11	0.05	0.00	0.11
vz	rWDs	HE	-0.04	-0.32	0.24	-0.01	-0.03	0.00	-0.11	-0.37	0.16	0.01	0.00	0.03	0.25	0.23	0.27	0.01	0.00	0.04	0.01	0.00	0.04	0.03	0.00	0.06	0.03	0.00	0.07
tf	rWDs	HE	-0.51	-3.88	2.97	0.04	-0.19	0.27	0.43	-2.94	3.70	-0.05	-0.28	0.19	0.36	0.24	0.52	0.93	0.03	3.42				0.12	0.01	0.35	0.13	0.01	0.39

			Intercept			β DBH			β WD ratio			β Interaction			σ residual			σ plot			σ transect			σ genus			σ family		
Habitat	WD	H	mean	5%CI	95%CI	mean	5%CI	95%CI	mean	5%CI	95%CI	mean	5%CI	95%CI	mean	5%CI	95%CI	mean	5%CI	95%CI	mean	5%CI	95%CI	mean	5%CI	95%CI	mean	5%CI	95%CI
vz	rWDg	HE	-0.09	-0.37	0.20	-0.01	-0.03	0.00	-0.06	-0.34	0.21	0.01	0.00	0.03	0.27	0.25	0.28	0.02	0.00	0.05	0.03	0.00	0.07	0.03	0.00	0.07	0.03	0.00	0.07
tf	rWDg	HE	-0.36	-2.39	1.65	0.03	-0.09	0.15	-0.04	-1.77	1.64	-0.02	-0.13	0.11	0.29	0.23	0.36	0.82	0.02	3.02				0.07	0.00	0.17	0.06	0.00	0.16
vz	rWDf	HE	-0.06	-0.35	0.22	-0.02	-0.03	0.00	-0.08	-0.36	0.19	0.02	0.00	0.03	0.26	0.25	0.28	0.02	0.00	0.05	0.03	0.00	0.07	0.14	0.10	0.18	0.04	0.01	0.08
tf	rWDf	HE	0.42	-1.27	1.97	-0.03	-0.11	0.05	-0.81	-1.95	0.39	0.04	-0.04	0.12	0.26	0.22	0.32	0.83	0.02	3.36				0.04	0.00	0.12	0.04	0.00	0.11
vz	GWD	HM	0.26	-0.05	0.58	0.00	-0.02	0.02	-0.06	-0.37	0.24	0.00	-0.01	0.02	0.21	0.20	0.23	0.02	0.00	0.05	0.02	0.00	0.05	0.20	0.16	0.25	0.10	0.04	0.16
tf	GWD	HM	0.83	0.08	1.59	-0.03	-0.08	0.01	-0.81	-1.50	-0.13	0.03	-0.01	0.07	0.20	0.16	0.25	0.20	0.05	0.55				0.09	0.01	0.18	0.10	0.02	0.21
vz	uWDf	HM	0.05	-0.13	0.23	0.00	-0.01	0.00	-0.06	-0.23	0.11	0.01	0.00	0.01	0.16	0.15	0.17	0.03	0.01	0.05	0.03	0.01	0.07	0.14	0.11	0.16	0.03	0.01	0.06
tf	uWDf	HM	0.78	0.35	1.21	-0.04	-0.06	-0.01	-0.81	-1.19	-0.42	0.04	0.01	0.06	0.14	0.12	0.15	0.11	0.03	0.30				0.03	0.00	0.07	0.02	0.00	0.06
vz	uWDg	HM	0.04	-0.13	0.20	0.00	-0.01	0.01	-0.05	-0.21	0.10	0.00	-0.01	0.01	0.16	0.15	0.16	0.02	0.00	0.04	0.02	0.00	0.04	0.01	0.00	0.03	0.01	0.00	0.02
tf	uWDg	HM	0.30	-0.18	0.79	0.00	-0.03	0.03	-0.32	-0.78	0.12	0.00	-0.03	0.03	0.13	0.11	0.15	0.05	0.00	0.16				0.02	0.00	0.05	0.02	0.00	0.05
vz	uWDs	HM	-0.04	-0.20	0.11	0.00	-0.01	0.01	0.02	-0.13	0.16	0.00	-0.01	0.01	0.13	0.13	0.14	0.01	0.00	0.03	0.01	0.00	0.02	0.01	0.00	0.02	0.01	0.00	0.02
tf	uWDs	HM	0.61	-0.19	1.39	-0.01	-0.07	0.04	-0.55	-1.26	0.17	0.01	-0.04	0.06	0.14	0.12	0.17	0.06	0.00	0.18				0.03	0.00	0.07	0.03	0.00	0.07
vz	uWSD	HM	-0.01	-0.11	0.09	0.01	0.00	0.01	-0.02	-0.12	0.07	-0.01	-0.01	0.00	0.10	0.09	0.10	0.01	0.00	0.01	0.01	0.00	0.02	0.01	0.00	0.02	0.01	0.00	0.02
tf	uWSD	HM	0.01	-0.13	0.15	0.01	0.00	0.02	-0.01	-0.14	0.11	-0.01	-0.01	0.00	0.05	0.04	0.06	0.02	0.00	0.06				0.01	0.00	0.02	0.01	0.00	0.02
vz	rWDs	HM	-0.10	-0.25	0.05	0.00	-0.01	0.01	0.08	-0.06	0.22	0.00	-0.01	0.01	0.13	0.12	0.14	0.01	0.00	0.03	0.01	0.00	0.03	0.00	0.00	0.01	0.00	0.00	0.01
tf	rWDs	HM	0.52	-0.23	1.29	-0.01	-0.06	0.04	-0.51	-1.20	0.17	0.01	-0.04	0.06	0.14	0.11	0.17	0.06	0.00	0.17				0.02	0.00	0.05	0.02	0.00	0.06
vz	rWDg	HM	0.04	-0.12	0.20	0.00	-0.01	0.00	-0.04	-0.19	0.10	0.00	0.00	0.01	0.15	0.15	0.16	0.02	0.00	0.03	0.02	0.00	0.05	0.01	0.00	0.02	0.01	0.00	0.02
tf	rWDg	HM	0.24	-0.21	0.70	0.01	-0.02	0.04	-0.30	-0.71	0.12	0.00	-0.03	0.02	0.13	0.11	0.14	0.06	0.00	0.17				0.01	0.00	0.03	0.01	0.00	0.04
vz	rWDf	HM	0.06	-0.12	0.25	0.00	-0.01	0.00	-0.06	-0.23	0.11	0.01	0.00	0.01	0.16	0.15	0.17	0.03	0.01	0.06	0.03	0.01	0.06	0.13	0.11	0.16	0.03	0.01	0.05
tf	rWDf	HM	0.77	0.33	1.21	-0.04	-0.06	-0.01	-0.80	-1.19	-0.41	0.04	0.01	0.06	0.14	0.12	0.15	0.11	0.03	0.30				0.03	0.00	0.07	0.02	0.00	0.05

Table S4. Biomass Difference. Aboveground woody biomass (AGWB) in megagrams per hectare (Mg/ha) forest in várzea and terra firme. AGWB estimated with individually measured total tree height (HM, m) and stem-specific, radially weighted wood specific density (rWSD, g/cm3) was compared to all other AGWB estimates based on lower-quality tree height (H, m) and wood density (WD, g/cm3) measurements. The differences in megagrams per hectare (Δ Mg/ha), are sorted from smallest to largest within each forest type. Lower-quality height measurements are HE = visual height estimates, HL = local allometric height, and HR = regional allometric height. Lower-quality wood density measurements are unweighted stem-specific wood specific density = uWSD, radially weighted mean wood specific density = rWD, or unweighted mean wood specific density = uWD across species = s, genera = g, or families = f with ≥3 radially weighted wood specific wood density measurements. AGWB estimations were done using the AGBmonteCarlo function of the BIOMASS R package, version 2.1.4 (Piponiot et al., 2019; Réjou-Méchain et al., 2017).

Várzea				**Terra firme**			
H	**WD**	**AGWB, Mg/ha**	**Δ Mg/ha**	**H**	**WD**	**AGWB, Mg/ha**	**Δ Mg/ha**
HM	rWSD	253.980	0.000	HM	rWSD	224.056	0.000
HL	uWDg	254.206	0.226	HL	uWDg	224.153	0.098
HM	rWDf	254.493	0.514	HM	rWDs	223.631	-0.425
HM	rWDg	254.495	0.515	HL	rWDg	224.487	0.431
HL	uWSD	256.113	2.133	HL	rWDs	224.907	0.851
HM	rWDs	256.258	2.279	HR	uWDg	225.044	0.988
HM	uWDs	251.603	-2.377	HM	uWSD	222.819	-1.237
HM	uWDf	251.465	-2.514	HM	uWDg	225.345	1.290
HL	uWDs	256.699	2.719	HM	rWDg	225.743	1.687

Várzea				**Terra firme**			
H	**WD**	**AGWB, Mg/ha**	**Δ Mg/ha**	**H**	**WD**	**AGWB, Mg/ha**	**Δ Mg/ha**
HM	uWSD	251.112	-2.868	HR	rWDg	225.753	1.698
HL	uWDf	257.095	3.115	HR	rWDs	226.393	2.337
HM	uWDg	250.193	-3.787	HM	rWDf	227.042	2.986
HL	rWDg	258.220	4.240	HM	uWDs	227.859	3.803
HL	rWSD	258.912	4.932	HM	uWDf	227.877	3.821
HL	rWDf	260.178	6.198	HL	uWDs	228.843	4.787
HL	rWDs	260.993	7.013	HL	uWSD	229.044	4.988
HE	rWDs	228.406	-25.574	HE	uWDg	218.866	-5.190
HE	rWDf	227.863	-26.117	HE	rWDg	218.849	-5.206
HE	rWDg	226.920	-27.060	HR	uWSD	229.812	5.757
HE	rWSD	226.183	-27.796	HL	rWSD	230.694	6.639
HE	uWDf	225.062	-28.918	HR	rWSD	231.150	7.094
HE	uWDs	223.788	-30.192	HE	GWD	231.322	7.266
HE	uWSD	223.545	-30.435	HR	uWDs	231.619	7.563
HE	uWDg	222.926	-31.054	HE	uWDf	215.085	-8.971
HR	uWDg	285.419	31.440	HE	rWDf	214.265	-9.791
HR	uWSD	287.423	33.443	HL	rWDf	235.404	11.348
HR	uWDs	287.928	33.948	HL	uWDf	236.461	12.406
HR	uWDf	288.754	34.774	HE	uWSD	210.863	-13.193

Várzea				**Terra firme**			
H	**WD**	**AGWB, Mg/ha**	**Δ Mg/ha**	**H**	**WD**	**AGWB, Mg/ha**	**Δ Mg/ha**
HR	rWDg	290.019	36.040	HE	rWSD	210.570	-13.486
HR	rWSD	290.750	36.770	HM	GWD	237.966	13.911
HR	rWDf	292.044	38.064	HR	rWDf	238.365	14.310
HE	GWD	292.381	38.401	HR	uWDf	239.546	15.490
HR	rWDs	293.180	39.200	HL	GWD	249.594	25.538
HM	GWD	324.288	70.308	HR	GWD	251.533	27.478
HL	GWD	330.817	76.838	HE	uWDs	181.475	-42.580
HR	GWD	371.361	117.382	HE	rWDs	176.726	-47.329

ISBN: 978-82-575-1821-9
ISSN: 1894-6402

Norwegian University
of Life Sciences

Postboks 5003
NO-1432 Ås, Norway
+47 67 23 00 00
www.nmbu.no

110416 / ANDVORDGRAFISK.NO