Effects of human disturbance on above-ground carbon stocks in north-west Amazonian *Mauritia flexuosa* peat swamp forests

Yakov Quinteros-Gómez[1,2], Martha Zarco-González[3], Doris Gómez Ticerán[4],
Ángel Endara-Agramont[3], Octavio Monroy-Vilchis[5]

[1] Facultad de Ciencias Biológicas, Universidad Nacional Mayor de San Marcos, Lima, Perú
[2] Escuela de Posgrado, Universidad Privada Norbert Wiener, Lima, Perú
[3] Instituto de Ciencias Agropecuarias y Rurales (UAEMex), Toluca, México
[4] Facultad de Ciencias Matemáticas, Universidad Nacional Mayor de San Marcos, Lima, Perú
[5] Universidad Autónoma del Estado de México (UAEMex), Toluca, México

---

SUMMARY

Mauritia flexuosa palm peat swamp forests concentrate important carbon reserves in the Amazon Basin, but are strongly affected by changes in land use. There is little information about their distribution pattern and carbon stocks in the Andean-Amazonian piedmonts. We studied four palm peat swamp forests of different types in two localities with different management, in the piedmont of the Alto Mayo Valley in San Martín Region, Peru. *M. flexuosa* showed an aggregated distribution (standardised Morisita index) and statistically significant differences in abundance and density between the four forests. The average above-ground carbon stocks of these palm forests were estimated at 61.5 Mg ha^{-1} (41.4–85.0 Mg ha^{-1}), with *M. flexuosa* contributing 45.4 %. In the locality that was managed for conservation (Tingana), the above-ground carbon stocks were 77.9–85.0 Mg ha^{-1}, and thus approximately double those in the locality (Posic) with strong anthropic pressure (41.3–42.3 Mg ha^{-1}).

KEY WORDS: Alto Mayo, Andes, climate change, flooding ecosystems, palm forest, piedmont, tropical

---

INTRODUCTION

Tropical forests host a large portion of the planet's biodiversity (Crowther *et al.* 2015), participate in biogeochemical cycles, and provide environmental services such as soil formation and primary productivity (Meister *et al.* 2012, Quinteros-Gómez *et al.* 2021a). In some tropical locations, seasonal precipitation and floods, as well as intraspecific and interspecific relationships, have favoured the development and survival of resilient plant species adapted to flooded conditions (Casanova & Brock 2000) where primary productivity exceeds the decomposition rate of the accumulated organic matter (Page *et al.* 2011) resulting in the accumulation of a peat layer up to 7.5 m thick (Lähteenoja *et al.* 2011). Tropical peatlands are major terrestrial carbon sinks, storing more than twice as much carbon as all the world's forests combined (Barthelmes *et al.* 2015). In addition, they are important in the flow of greenhouse gases (Finn *et al.* 2020).

Peru is the fourth-richest South American country in peatlands, which occur across the full altitude range from the Amazon Basin through montane (> 2,800 m a.s.l.) forests to the wetlands of the high Andean region (Román-Cuesta *et al.* 2011, Hergoualc'h *et al.* 2017). Peat swamp forests in the Peruvian Amazon are considered to be particularly fragile and vulnerable ecosystems (Fagundes & Ferreira 2016) because they are not protected by law (Lilleskov *et al.* 2019). These ecosystems have a hydromorphic, swampy character (Page *et al.* 2011) and low species richness compared to other Amazonian forest communities (Nebel *et al.* 2001, Honorio *et al.* 2015). The origin of the water and the associated nutrients have favoured the formation of various peatland types (Hergoualc'h *et al.* 2017), of which *Aguajales* (dominated by the palm *Mauritia flexuosa*) are the most dense, extensive (more than 6 million hectares in Peru; Draper *et al.* 2014, Pitman *et al.* 2014) and important economically, environmentally and socioculturally. The fruits of *M. flexuosa* can be eaten fresh or can be used in drinks, ice cream, desserts and even as fishing bait (important value in the regional economy; Horn *et al.* 2012, Gilmore *et al.* 2013, Virapongse *et al.* 2017). Aguajales play an important role in the carbon cycle (IPCC 2008), harbour endemic and endangered species, and provide biological corridors for native fauna (Fagundes & Ferreira 2016, Hergoualc'h *et al.* 2017). They can be termed strategic ecosystems

(Trujillo-González *et al.* 2011) because they provide ecosystem services that directly benefit both native fauna (habitat, food, migration routes) and human communities (Gilmore *et al.* 2013).

Studies of the extent of swamp forests, flooding, forest structure and richness have focused on alluvial plains (Börner & Zimmermann 2003, Virapongse *et al.* 2017), meaning the location and extent of the highest elevation (piedmont) swamp forests in Peru is unknown (Lähteenoja *et al.* 2009). Historically, the only human activity that was carried out in palm swamp forests was the collection of *M. flexuosa* fruits. However, when the marginal highway of the jungle (now known as IIRSA Norte) was constructed in 1973 under the slogan "The conquest of Peru by the Peruvians", the national government enacted laws to promote human occupation of Amazonian territories by granting subsidies for livestock husbandry and agricultural activities. This resulted in disturbances such as deforestation, changes in land use (Quinteros-Gómez *et al.* 2021b) and intensive destructive harvesting (Romulo *et al.* 2022) in the zone of transition from the Andean region to the Amazon plain which have generated vegetation mosaics, each patch with its own dynamics (Gaya 2014). The outcome is a greater variety of habitats and, consequently, a more complex flora (Fagundes & Ferreira 2016) with enhanced regional beta diversity within which swamp forest remnants are still the main carbon sinks (Draper *et al.* 2014, Draper *et al.* 2018). For *M. flexuosa* the outcome is genetic erosion, a decrease in female individuals (Horn *et al.* 2012) and changes in community structure (Terborgh *et al.* 2008).

The conservation status of Amazonian swamp forests is unknown due to poor monitoring resulting mainly from the difficulty of access to these territories and lack of interest from the government (Morales *et al.* 2018). Furthermore, there is little information on the degradation of Peruvian peatlands and their greenhouse gas emissions. Likewise, the effect of *M. flexuosa* over-exploitation on the structure and function of the swamp forest has not been evaluated. Nowadays it is also a priority to generate information on peatland ecosystem services and their contributions to the storage of water, carbon stocks, and reduction of the greenhouse effect (Freitas Alvarado *et al.* 2006). Based on a previous field survey, carried out between December 2016 and March 2017, we described and compared the floristic composition and structure of plant communities in piedmont swamp forests with different levels of human influence in the Alto Mayo Valley, Peru (Quinteros-Gómez *et al.* 2021b). In the study described here we aimed to build on that work by assessing the aerial biomass and carbon reserves of the same forests.

The earliest methods for quantification of biomass in tropical forests were limited by their low accuracy (Fittkau & Klinge 1973), but the subsequent development of allometric models has added an efficient tool (Somogyi *et al.* 2008). Allometric models are derived using destructive field methods (measuring fresh weights of different parts of the individual; Goodman *et al.* 2013) and even from plant formations (Petersson *et al.* 2012). The availability of specific allometric models for palm species allows better approximations (avoiding over-estimation) to the real biomass values because these models have been designed considering the structural characteristics of palms, for which stem height is the most important predictive variable (Goodman *et al.* 2013). The carbon stock is related to biomass and both of these attributes can be expected to reflect the age of the forest and its level of conservation (Alexandrov 2007). Forests within conservation areas tend to be more diverse (Gonçalves-Souza *et al.* 2021) with higher densities of tree species with considerable basal area, which should increase biomass and carbon stocks.

The objective of the research reported here was to estimate and compare carbon stocks in the above-ground biomass of swamp forests located in a conservation area and in an area with strong anthropic pressure, in the Andean-Amazonian piedmont of the Alto Mayo Valley, Peru.

METHODS

Study sites

The Andean-Amazonian piedmont of the Alto Mayo Valley is a transitional area (20–30 % slope) of late successional forest with slow-growing species producing dense wood, between the *yungas* (mountain forests of the east Peruvian Andes) and the low-lying seasonally flooded zone of Central Huallaga. The climate is humid subtropical with rainfall concentrated in a single wet season lasting from October to April. Annual precipitation and mean temperature are 1,265 mm and 22.8 °C, respectively (PEAM 2004).

Fieldwork was carried out between January 2018 and July 2019, in two localities (Tingana and Posic) separated by the Mayo River (Rio Mayo; Figure 1). The river is an important influence on floristic diversity because it acts as a geographical barrier that promotes allopatric speciation (Gentry & Ortiz 1993) and heterogeneity among the vegetal community (Bijos *et al.* 2017).
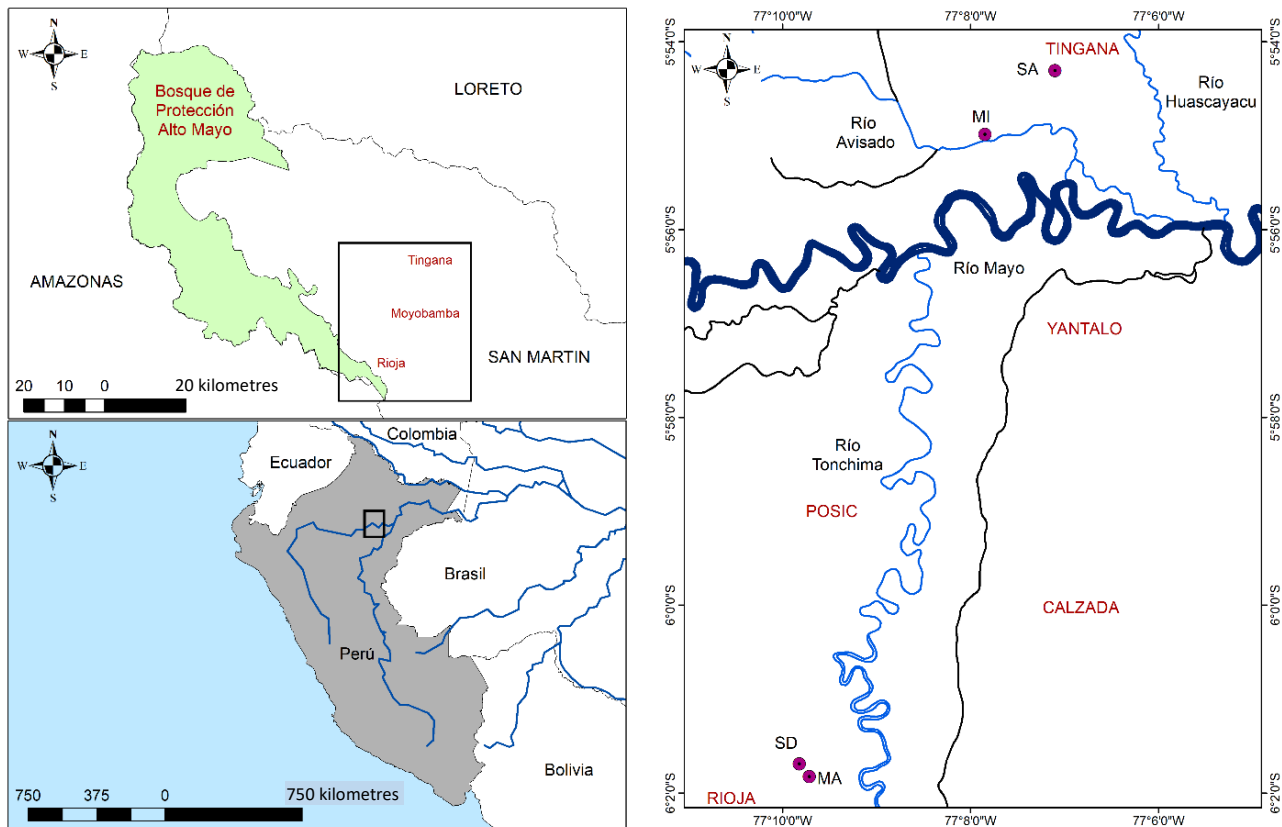
Figure 1. Geographical locations of the four studied palm peat swamp forests in the two localities Tingana (SA, MI) and Posic (SD, MA) of the Alto Mayo Valley, San Martín, Peru.

The two Tingana study sites were located in the Municipal Conservation Area, Water Association, Aguajal Renacal del Alto Mayo (ADECARAM Tingana, ecotourism; 05° 54′ 17.9″ S, 77° 07′ 07.5″ W; Figure 2), which is influenced by the Avisado river (Börner & Zimmermann 2003); and specifically in the Tingana conservation concession (Executive Directorial Resolution of the Regional Government of San Martín), where the only permitted human activities are ecotourism and sustainable harvesting of *M. flexuosa* fruits. The first site was in an area of slightly undulating semi-dense swamp forest (SA), dominated by palm trees in the emergent canopy (*M. flexuosa*, *Euterpe precatoria*) with an average diameter at breast height (DBH) > 23 cm, and characterised by flooding up to 1.5 m. *Virola elongata* was the forest species with the largest basal area. Between the months of May and August we observed many *M. flexuosa* seedlings beneath the parent plants. The second site was in a flood-prone area of mixed swamp forest (MI) close (30 m) to the Avisado River where trees of *Coussapoa trinervia*, *Ficus trigona* and *Virola elongata* (DBH > 30 cm) were prominent. Adaptations of the vegetation such

as stilt roots, aerial roots, trunk fins and pneumatophores associated with the flood level (> 3 m) were apparent, along with large quantities of epiphytic species (orchids, bromeliads and Araceae) on the branches of the largest trees.

The areas sampled in Posic (06° 01′ 43.3″ S, 77° 09′ 43.8″ W; Figure 3) lay within a relict forest surrounded by rice crops 400 m from the Tonchima River. This forest (managed by local families) is subject to strong anthropic pressure due to the selective extraction of forest species, hunting of native fauna and change of land use towards agriculture and livestock husbandry as well as urbanisation. The first Posic study site was in semi-dense to mixed swamp forest (SD) and the second was in mixed swamp forest (MA). Both of these sites were dominated by *M. flexuosa*, *Mauritiella armata* and *Matisia bracteolosa* with few epiphytes, and included deforested spaces with stumps along with some seedlings and juveniles of *Cedrela* sp. There were many gaps in the canopy suggesting the former presence of individuals with DBH > 30 cm and height > 20 m. In the undergrowth there was little regeneration of forest species or palm trees.

Figure 2. The two sampled swamp forests in ADECARAM, Tingana. Above: semi-dense swamp forest (SA); below: flood-prone area of mixed swamp forest (MI).

Figure 3. The two sampled swamp forests in Posic. Above: semi-dense to mixed swamp forest (SD); below: mixed swamp forest (MA).

Field sampling

When specific allometric equations are used to estimate the biomass of various plant families and species, data precision may be influenced by the sampling strategy (Vieira *et al.* 2008, Goodman *et al.* 2013, Romero *et al.* 2020). In our case it was important to avoid: i) sampling units (plots) with less than five individuals, regardless of plot size; ii) wrong coordinates and incompatible methods (linear plots); and iii) joint analysis of tree and non-tree biomass (DBH < 10 cm; Freitas Alvarado *et al.* 2006).

At each study site we established a plot of area 1 hectare (100 × 100 m) that we judged to be representative of the forest in terms of structure and composition whilst also considering accessibility and flooding level (< 1 m). The minimum distance between plots in the same locality was 500 m. Within each plot, all free-standing trees, shrubs and palms with DBH ≥ 10 cm were marked, tagged and tallied, and the height of each individual was recorded using a Suunto clinometer (Lamprecht 1990). In addition, we collected botanical samples for taxonomic identification of species by comparison with herbarium specimens and specialist literature. Botanical nomenclature was based on The Plant List (www.theplantlist.org).

Data analysis

In the current version of PAST software (Hammer *et al.* 2001), the abundance and richness of species were compared between the four plots using the ANOVA test, considering the density of *M. flexuosa* as covariate. Also, the Berger-Parker (BP) dominance index was used to measure species diversity within plots. The BP index describes the relative importance of the most dominant species in an assemblage (Magurran 2004). Then, one-way ANOVA was performed to test the null hypothesis that the BP index did not vary significantly amongst plots (Fisher's test).

The spatial aggregation pattern for the most abundant species (more than 20 individuals per plot) was determined using a standardised form of Morisita's index of dispersion (I_p) (Krebs 1999; see Appendix). This is the most consistent index for describing spatial distribution patterns (Pereira *et al.* 2015). The I_p value varies between -1 and +1, where values of $I_p < 0$ indicate a uniform distribution, $I_p = 0$ indicates a random distribution, and values of $I_p > 0$ reveal a grouped distribution pattern (Krebs 1999).

To estimate the above-ground biomass of palms we used the allometric models provided by Goodman *et al.* (2013) for biomass and productivity of woody palms (with different DBH) in *terra firme* and

wetland forests in the Amazon. For other woody species, biomass was determined per stem using allometric equations developed from the diameter of individuals (DBH), height (m) and wood density (Chave *et al.* 2014, Mangwale *et al.* 2017). Wood density values per species were obtained from the Wood Density Database (WDD) (Zanne *et al.* 2009). The allometric models of biomass per tree and total biomass per species were adjusted using the method of ordinary least squares (Fonseca *et al.* 2013), while the predictive capacity of the models was estimated through the prediction error of the model (Chave *et al.* 2005). Carbon content was estimated by multiplying above-ground biomass by the most conservative value of the carbon proportion in wood (0.45; IPCC 2003).

RESULTS

Floristics and spatial aggregation

In total, we assessed 2,065 individuals belonging to 30 families, 60 genera and 79 species (see Table A1 in the Appendix). The best represented families were Leguminosae (8 species, 10 %) and Rubiaceae (7 species, 9 %). Families with greater abundance (≥ 200) were Arecaceae, Malvaceae, Myristicaceae and Leguminosae which together represented 76.6 % of total abundance. The more diverse genera were *Ficus* with five species, and *Inga*, *Myrsine*, *Nectandra* and *Virola* with three species each.

Abundance (F = 3.84; d.f. 3, 99; *p* = 0.01) and density of *M. flexuosa* (F = 5.26; d.f. 19, 99; *p* = 0.01) showed significant differences amongst plots whereas species richness did not (F = 1.36; d.f. 3, 99; *p* = 0.26), even without considering *M. flexuosa* presence (F = 1.47; d.f. 19, 99; *p* = 0.12). In the SA plot, *M. flexuosa*, *Machaerium floribundum* and *Virola elongata* accounted for 62.3 % of total abundance; while in the MI plot, *M. flexuosa* and *V. elongata* accounted for 57.3 %. In the SD plot, *M. flexuosa* and *Matisia bracteolosa* contributed 62.2 % of abundance; whereas in MA the same two species, along with *Ferdinandusa chlorantha* and *Mauritiella armata*, contributed 67.9 %.

The BP dominance index was highest in the most conserved and flooded (MI) area in Tingana and decreased in the order (MI: 0.36 > SD: 0.34 > SA: 0.27 > MA: 0.24). The lowest value was registered for the area closest to the highway. One-way ANOVA detected significant differences in BP index amongst the four plots (F = 21.16; d.f. = 3; P < 0.001). Fisher's test suggested two groups, the first group including MI and SD and the second group consisting of SA and MA.

Only two species were represented by more than 20 individuals in the respective plots. The Standardised Morisita's index indicated clumped distributions of *M. flexuosa* and *V. elongata* in all four plots (Table 1). Additional clumped distributions were identified in just one or two plots, for *E. precatoria* (SA: 0.511) and *M. armata* (SD: 0.498, MA: 0.502).

Above-ground biomass and carbon stocks
Buchenavia sericocarpa, *Sloanea robusta*, *Aptandra tubicina*, *Oxandra sphaerocarpa*, *Calophyllum longifolium*, *Matayba purgans* and *Tetragastis panamensis* form woods with densities greater than 0.700 g cm^{-3}, while the densities of *Cyathea pilosissima*,

Ficus maxima, *Cedrela montana*, *Picramnia sellowii*, *Aiouea grandifolia*, *Pachira aquatica* and *Hura crepitans* woods are below 0.39 g cm^{-3} (Table A1). Above-ground biomass per plot ranged from 91.95 to 188.98 Mg ha^{-1} (Table 2). The SA plot had the highest biomass and the MI plot had the second highest biomass despite having the lowest abundance (332). Accordingly, the Tingana plots recorded the largest carbon stocks (85.0 and 77.9 Mg ha^{-1}), while the Posic plots registered much lower values (42.3 and 41.3 Mg ha^{-1}). The average carbon stock for the four plots was 61.7 Mg ha^{-1}. *M. flexuosa* and *V. elongata* made up most of the carbon stocks, contributing 45.4 % and 23.7 %, respectively, of the total carbon contained in the aerial biomass of the plots (Table 3).

Table 1. Standardised Morisita index for the two most abundant species in the four sampled *M. flexuosa* palm peat swamp forests in the Alto Mayo Valley (DBH ≥ 10 cm).

	Plot	Standardised Morisita index (I_p)
Mauritia flexuosa	SA	0.508
	MI	0.518
	SD	0.522
	MA	0.530
Virola elongata	SA	0.506
	MI	0.498
	SD	0.514
	MA	0.604

Table 2. Summary of pertinent characteristics of the vegetation ≥ 10 cm DBH per plot, in the four (100 × 100 m) plots established in *M. flexuosa* palm peat swamp forests in the Alto Mayo Valley, Peru.

	SA	MI	SD	MA
Nº. of individuals	683	332	547	503
Richness	37	30	29	30
Nº. of families	20	17	21	20
Mauritia flexuosa density (N ha^{-1})	184	121	156	123
DBH (cm)	23.5 ± 12.8	32 ± 16.2	23.1 ± 15.1	23.1 ± 13.3
Biomass (Mg ha^{-1})	188.9	173.2	94	91.9
Carbon stock (Mg ha^{-1})	85.0	77.9	42.3	41.3

Table 3. Carbon stock (Mg ha^{-1}) in palms and other woody species, per plot.

Locality	Study site	Palms		Other woody species	
		All species	*Mauritia flexuosa*	All species	*Virola elongata*
Tingana	SA	44.31	38.66	40.73	17.86
	MI	28.13	27.04	49.86	36.03
Posic	SD	26.84	25.11	15.47	2.24
	MA	23.47	21.08	17.91	2.35

DISCUSSION

Palm swamps deliver important ecological benefits by reducing global warming through carbon dioxide sequestration, especially when the conditions are suitable for peat formation. Species composition, abundance, DBH and management practices, as well as abiotic characteristics of the study area, influence their carbon stocks and fluxes (Mund & Schulze 2006), and thus the amount of carbon in different pools such as above-ground biomass, dead wood and soil organic matter.

Unfortunately, there is a lack of information on the amount of carbon stored in conservation areas managed by local communities (Bhatta *et al.* 2021), as in Tingana. Our research has shown that, despite their similar climatic conditions and altitude, the forests in Tingana store more above-ground carbon per hectare than those in Posic where the greater anthropic pressure from hunting, selective extraction of medicinal and ornamental plants, livestock husbandry, deforestation and fragmentation generate habitat alteration and biodiversity loss (Riemann *et al.* 2017). The quantification of carbon stocks will support improvements in management of these forests as natural resources.

Species-level calculations increase accuracy in estimating biomass and carbon stocks in tropical forests. In general, they deliver an average of 20 % higher biomass compared to biomass models for template forest species (Goodman *et al.* 2013). In this regard, the WDD is the database of wood density that is most widely used globally for the estimation of biomass and carbon reserves through non-destructive methodologies. However, the allometric equations have some limitations, mainly because the density of wood usually varies between individuals and from place to place, so the development of new forestry research in wood technologies to continuously improve accuracy in the estimation of biomass and carbon stocks is a priority.

In the Amazon Basin, peatland communities are typically dominated by one or more of the palm species *M. flexuosa*, *E. precatoria* and *M. armata* (Pitman *et al.* 1999, Cabrera & Wallace 2007), along with the hyperdominant woody species *S. globulifera*, *V. elongata*, *M. bracteolosa* and genera *Inga*, *Xylopia*, *Ceiba*, with low species richness and high habitat specialisation (Householder *et al.* 2012, Honorio *et al.* 2015). These palms and other woody species possess adaptations such as pneumatophores (*M. flexuosa*), strangler figs (*Ficus* and vines) and buttress roots (*Ceiba* sp.) that have allowed their distribution throughout the Amazon Basin (ter Steege *et al.* 2013, Pitman *et al.* 2014, Quinteros-Gómez *et al.* 2021a) with waterlogging causing variations in the composition (Costa *et al.* 2008), distribution and structure of forest types (Junk 1997, Eiserhardt *et al.* 2011). However, in the context of our research we must also consider factors such as the distance from seasonal rivers (which in times of higher rainfall usually flood both study localities) and the distance from local roads and national highways (Quinteros-Gómez *et al.* 2021a), which also influence the value of the BP index. BP was higher in areas with less anthropic influence and greater difficulty of access and tended to decrease when community richness increased, suggesting that BP worked better in comparisons between communities with similar richness regardless of total abundance.

Lower species richness in the Alto Mayo Valley is related to the altitude above sea level and anthropic activities such deforestation, species-selective extraction of trees, forest fire and wildlife hunting (Constantino 2016, Sander *et al.* 2018), in addition to the presence of hyperdominant species which form the foundation of tree communities in Amazonian territories (ter Steege *et al.* 2013).

The average density of *M. flexuosa* individuals in the Alto Mayo Valley (146 ha^{-1}) was similar to the values for adult individuals of 137 ha^{-1} (Horn *et al.* 2012) and 144 ha^{-1} reported in the Maijuna and

Parinari indigenous communities (Freitas Alvarado & Flores 2015) but lower than those found in Brazil (300 ha^{-1} and 667 ha^{-1}) by Sampaio *et al.* (2008). Using a similar method in Colombia, Galeano *et al.* (2015) reported 735 ha^{-1}. Differences in richness and abundance among sites and countries, for similar biomes, suggest that local environmental factors such as the period, timing and level of flooding (Casanova & Brock 2000), in addition to slope, altitude, soil type and anthropic activities, can be determinants of the forest structure (Rodrigues *et al.* 2014).

The management of territories with rare species is a topic of special interest in relation to assessments of the ecological impact of anthropic activities. Sometimes rare species are not reported in, or are removed from, species lists and inventory reports with the excuse that they do not help to answer the research questions posed (statistical analysis) and do not contribute to solving problems in the ecological community (Cao *et al.* 2001). If we considered only dominant species (excluding rare species) in the analysis, it would be assumed that anthropic influence affected the density of only the most abundant and hyper-dominant species and that observation of these species would reflect the response of the entire community. In our study, 47 % of the reported species were rare, so excluding them would amount to treating the Alto Mayo Valley swamp forests as scarcely diverse ecosystems with high dominance.

Woody species accounted for 58 % of the abundance but only 50.25 % of the biomass, as reported for the location (Loreto) of a Maijuna community in Peru (Endress *et al.* 2013). Most of the woody tree species had small diameters (< 20 cm) and low abundance in the emergent canopy, suggesting that the anaerobic and swampy soils could be differentially restricting the growth and survival of woody species relative to palms, which are the dominant group in both canopy and understorey in these ecosystems.

Cappelatti & Schmitt (2015) observed clumped distributions of *Euterpe*, *Bactris*, *Geonoma* and *Syagrus* palms in lowland dense humid forest in Brazil, and clumping is frequent in tropical palms (Souza & Martíns 2004, Cabrera & Wallace 2007). In our study, the palms *E. precatoria*, *M. armata* and *M. flexuosa* occurred in semi-dense and dense aggregations. This was corroborated by the standardised Morisita index values (Ip > 0) for palm trees in the plots with the highest palm densities. Cabrera & Wallace (2007) also observed a clumped distribution of *M. flexuosa*, which is adapted for survival in dense aggregations, in areas adjacent to the progenitors and with recruitment in all growth

categories (Cabrera & Wallace 2007, Assis & Wittmann 2011). Successful recruitment, distance from the parent tree and high seed predation are density-dependent factors; that is, the greater the aggregation, the more exposed are seedlings and seeds to predators (Romo *et al.* 2004). In this scenario, frugivorous animals (birds and larger mammals) play an important role in determining the spatial distribution of palms (Barroso *et al.* 2010). Indeed, in localities with less extensive swamp forest, such as Posic, the densities of vertebrates were reduced and this could be a limiting factor in seed dispersal, promoting aggregation. In contrast, in Tingana (conservation area) with a higher density of vertebrates there is a less aggregated distribution (Rojas-Robles *et al.* 2008) since the availability of fruits under the parent palm will always exceed the demand.

Our observations in the Alto Mayo Valley forests recorded the presence of late-successional species (*V. elongata*, *C. trinervia*, *P. aquatica*) with considerable basal area, biomass and carbon storage (Meister *et al.* 2012) compared to fast growing forests (Phillips *et al.* 2019). In Peru, there is no systematic scientific information on this subject, and the few previous studies in swamp forest were carried out on floodplains at 80–300 m a.s.l. in Loreto and Madre de Dios states (IIAP 2006, Honorio *et al.* 2015).

Forested wetlands have higher carbon stocks than other wetland types (Hernández & Moreno-Casasola 2018). The largest carbon reserves estimated from satellite images by Asner *et al.* (2014) were found on the Napo and Amazon rivers and, using the same method, the low Amazon swamp forest registered carbon stocks of 88.68 Mg ha^{-1} (García-Soria *et al.* 2012) and 76.53 Mg ha^{-1} (Hidalgo Ríos 2014). However, the carbon stock estimate for San Martín state (Asner *et al.* 2014) was similar to the average aerial biomass found in this study (61.7 Mg ha^{-1}), which suggests that biomass and carbon stock in conservation areas (low or no human impact) tend to increase as the diameter and DBH of forest individuals increases. Freitas Alvarado *et al.* (2006) state that swamp forests with a higher level of anthropic activity have a lower density of individuals, a lower biomass and consequently a lower carbon stock. In other words, the sustainable management of forests allows us to guarantee greater carbon reserves for the future and, furthermore, to increase carbon reserves in vegetation. This could be achieved by providing protection for the Posic forests and other degraded (low biomass and low carbon stock) contiguous forest, allowing the recovery of the ecosystem through natural regeneration and soil enrichment (Jobbágy & Jackson 2000).

Swamp forest management is an excellent environmental management tool, since a comparison of managed *versus* unmanaged treatments in the Peruvian Amazon indicated that carbon stocks in managed areas were 30 % higher (Guzmán 2004).

The contribution of *M. flexuosa* and *V. elongata* to the carbon stock in palm swamp forests is greater than 69 %. Mitidieri (2014) also identified *M. flexuosa* as the species with the highest carbon stock and palm trees as the most important group (63.5 % of the carbon stock of the forest). In the present investigation, the carbon stock of the six palm species recorded was also considerable (49.75 %), which suggests that in addition to being the most ecologically and culturally important plant group in the Amazon (Endress *et al.* 2013), palms are also important for climate change mitigation.

The carbon reserves in the Alta Mayo Valley swamp forests can be regarded as a baseline for future studies in this area, where there are still large areas of swamp forest that are being protected through the empowerment of communities by granting them conservation and ecotourism concessions. Therefore, in further assessments we recommend including density, forest structure, forest dynamics and conservation status (Meister *et al.* 2012, Hergoualc'h *et al.* 2017) to predict changes in above-ground carbon storage and carbon fluxes, since they vary greatly depending on the region and climate (Kayranli *et al.* 2009) and play a fundamental role in mitigating climate change due to the capture and storage of C.

ACKNOWLEDGEMENTS

AUTHOR CONTRIBUTIONS

The joint first authors YQG and OMV led the study, carried out the fieldwork and drafted the manuscript with MZG; AEA identified the species with YQG. MZG and AEA compiled and curated the data. DGT organised the database, designed and performed the data analysis, and prepared the statistical report. All authors were involved in the study and read, commented on and contributed to improvement of the manuscript.

REFERENCES

Alexandrov, G.A. (2007) Carbon stock growth in a forest stand: the power of age. *Carbon Balance and Management*, 2, 4, 5 pp.

Asner, G.P., Knapp, D.E., Martin, R.E., Tupayachi, R., Anderson, C.B., Mascaro, J., Sinca, F., Chadwick, K.D., Sousan, S., Higgins, M., Farfan, W., Silman, M.R., Llactayo, W.A., Neyra, A.F. (2014) *The High-Resolution Carbon Geography of Perú*. Minuteman Press, Berkeley CA, USA, 66 pp.

Assis, R.L., Wittmann, F. (2011) Forest structure and tree species composition of the understory of two central Amazonian várzea forests of contrasting flood heights. *Flora,* 206, 251–260.

Barroso, R.M., Reis, A., Hanazaki, N. (2010) Etnoecologia e etnobotânica da palmeira Juçara (*Euterpe edulis* Martius) em comunidades quilombolas do Vale do Ribeira, São Paulo (Ethnoecology and ethnobotany of the Juçara palm tree (*Euterpe edulis* Martius) in quilombola communities in Vale do Ribeira, São Paulo. *Acta Botânica Brasilica*, 24, 518–528 (in Portuguese).

Barthelmes, A., Ballhorn, U., Couwenberg, J. (2015) *Consulting Study 5: Practical Guidance on Locating and Delineating Peatlands and Other Organic Soils in the Tropics*. The High Carbon Stock (HCS) Science Study, CSIRO, Australia, 121 pp.

Bhatta, S., Poudel, A., Bahadur, Y. (2021) A comparative study of carbon stocks in the Sal Forest (*Shorea robusta*) in core and buffer zones of Shuklaphanta National Park, Nepal. *Forestry: Journal of Institute of Forestry, Nepal*, 18, 52–60.

Bijos, N.R., Eugenio, C., Mello, T.R., Souza, G., Munhoz, C. (2017) Plant species composition, richness, and diversity in the palm swamps (veredas) of Central Brazil. *Flora,* 236–237, 94–99.

Börner, A., Zimmermann, R. (2003) Classification of East-Andean Forest Amphibiomes in the Río Avisado Watershed, Alto Mayo Region, Perú. *Lyonia*, 3, 29–36.

Cabrera, W.H., Wallace, R.B. (2007) Densidad, composición y patrón de distribución espacial de palmeras arborescentes en un bosque amazónico de Bolivia (Density, composition and spatial distribution pattern of arborescent palms in an Amazonian forest of Bolivia). *Ecología en Bolivia*, 42, 131–135 (in Spanish).

Cao, Y., Larsen, D.P., Thorne, R. (2001) Rare species in multivariate analysis for bioassessment: some considerations. *Journal of the North American Benthological Society*, 20, 144–153.

Cappelatti, L., Schmitt, J.L. (2015) Spatial distribution and population structure of palms (Arecaceae) in a forest fragment of lowland dense

humid forest in South Brazil. *Ciência Florestal Santa Maria*, 25, 817–825.

Casanova, M.T., Brock, M.A. (2000) How do depth, duration and frequency of flooding influence the establishment of wetland plant communities? *Plant Ecology*, 147, 237–250.

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.

Chave, J., Réjou-Méchain, M., Búrquez, A., Chidumayo, E., Colgan, M.S., Delitti, W.B., 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. *Global Change Biology*, 20, 3177–3190.

Constantino, P.A.L. (2016) Deforestation and hunting effects on wildlife across Amazonian indigenous lands. *Ecology and Society*, 21(2), 3, 10 pp.

Costa, F.R.C., Guillaumet, J.L., Lima, A.P., Pereira, O.S. (2008) Gradients within gradients: the mesoscale distribution patterns of palms in a central Amazonian Forest. *Journal of Vegetation Science*, 20, 69–78.

Crowther, T.W., Glick, H.B., Covey, K.R., Bettigole, C. and 34 others (2015) Mapping tree density at a global scale. *Nature*, 525, 201–205.

Draper, F.C., Roucoux, K.H., Lawson, I.T., Mitchard, E.T.A., Honorio, E.N.H., Lähteenoja, O., Torres, L.M., Valderrama, E.S., Zarate, R., Baker, T.R. (2014) The distribution and amount of carbon in the largest peatland complex in Amazonia. *Environmental Research Letters*, 9, 124017, 12 pp.

Draper, F.C., Honorio, E.N.C., Roucoux, K.H., Lawson, I.T., Pitman, N.C.A., Fine, P.V.A., Phillips, O.L., Torres, L.A., Valderrama, E.S., Mesones, I., García-Villacorta, R., Ramirez, F.R.A., Baker, T.R. (2018) Peatland forests are the least diverse tree communities documented in Amazonia but contribute to high regional beta-diversity. *Ecography*, 41, 1256–1269.

Eiserhardt, W.L., Svenning, J.C., Kissling, W.D., Balslev, H. (2011) Geographical ecology of the palms (Arecaceae): determinants of diversity and distributions across spatial scales. *Annals of Botany*, 108, 1391–1416.

Endress, B.A., Horn, C.M., Gilmore, M.P. (2013) *Mauritia flexuosa* palm swamps: composition, structure and implications for conservation and management. *Forest Ecology and Management*, 302, 346–353.

Fagundes, N.C.A., Ferreira, E.F. (2016) Veredas (*Mauritia flexuosa* palm swamps) in the Southeast Brazilian savanna: Floristic and structural peculiarities and conservation status. *Neotropical Biology and Conservation*, 11, 178–183.

Finn, D.R., Ziv-El, M., van Haren, J., Park, J.G., Del Aguila-Pasquel, J., Urquiza-Muñoz, J.D., Cadillo-Quiroz, H. (2020) Methanogens and methanotrophs show nutrient-dependent community assemblage patterns across tropical peatlands of the Pastaza-Marañón Basin, Peruvian Amazonia. *Frontiers in Microbiology*, 11, 15 pp.

Fittkau, E.J., Klinge, H. (1973) On biomass and trophic structure of the Central Amazonian rain forest ecosystem. *Biotropica,* 5, 2–14.

Fonseca, W., Ruíz, L., Rojas, M., Alice, F. (2013) Modelos alométricos para la estimación de biomasa y carbono en *Alnus acuminata* (Allometric models for the estimation of biomass and carbon in *Alnus acuminata*). *Revista de Ciencias Ambientales,* 46, 37–50 (in Spanish).

Freitas Alvarado, L., Flores, H. (2015) Condición silvicultural de la palmera *Mauritia flexuosa* L.f. en el ecosistema "aguajal" de Parinari, Loreto, Perú (Silvicultural condition of *Mauritia flexuosa* L.f. in the "aguajal" ecosystem of Parinari, Loreto, Peru). *Folia Amazónica*, 242, 155–162 (in Spanish).

Freitas Alvarado, L., Otárola Acevedo, E., del Castillo Torres, D., Linares Bensimón, C., Martínez Dávila, P., Malca Salas, G.A. (2006) Servicios ambientales de almacenamiento y secuestro de carbono del ecosistema aguajal en la Reserva Nacional Pacaya Samiria, Loreto-Perú (*Environmental Services of Carbon Storage and Sequestration of the Aguajal Ecosystem in the Pacaya Samiria National Reserve, Loreto-Peru*). Documento Técnico N° 29, Instituto de Investigaciones de la Amazonía Peruana (IAAP), Iquitos-Perú, 62 pp. (in Spanish).

Galeano, A., Urrego, L.E., Sánchez, M., Peñuela, M.C. (2015) Environmental drivers for regeneration of *Mauritia flexuosa* L.f. in Colombian Amazon swamp forest. *Aquatic Botany*, 123, 47–53.

García-Soria, D., Honorio, E., Del Castillo, D. (2012) Determinación del stock de Carbono en Aguajales de la cuenca del río Aguaytía, Ucayali, Perú (Determination of the carbon stock in Aguajales of the Aguaytía river basin, Ucayali, Peru). *Folia*

11

Amazónica, 21, 153–160 (in Spanish).

Gaya, T.R.L.M. (2014) *A floresta inundável do norte de Minas Gerais: identidade florística e estrutura de comunidades arbustivo-arbóreas* (*A Flooded Forest in the North of Minas Gerais: Floristic Identity and Structure of Shrub-Tree Communities*). Masters dissertation, Universidade Federal de Lavras, Lavras MG, Brazil, 225 pp. (in Portuguese).

Gentry, A.H., Ortiz, R. (1993) Patrones de composición florística en la Amazonía Peruana (Floristic composition patterns in the Peruvian Amazon). In: Kalliolla, R., Puhakka, M., Danjoy, W. (eds.) *Amazonia Peruana: Vegetación húmeda tropical en el llano subandino*, Proyecto Amazonia Universidad de Turku (PAUT) y Oficina Nacional de Evaluación de Recursos Naturales (ONERN), Jyväskylä, 155–166 (in Spanish).

Gilmore, M.P., Endress, B.A., Horn, C.M. (2013) The socio-cultural importance of *Mauritia flexuosa* palm swamps (*aguajales*) and implications for multi-use management in two Maijuna communities of the Peruvian Amazon. *Journal of Ethnobiology and Ethnomedicine*, 9, 29, 23 pp.

Gonçalves-Souza, D., Vilela, B., Phalan, B., Dobrovolski, R. (2021) The role of protected areas in maintaining natural vegetation in Brazil. *Science Advances*, 7, eabh2932, 9 pp.

Goodman, R.C., Phillips, O.L., del Castillo, D.T., Freitas, L., Tapia, S.C., Monteagudo, A., Baker, T.R. (2013) Amazon palm biomass and allometry. *Forest Ecology and Management*, 310, 994–1004.

Guzmán, W. (2004) Valoración económica de beneficios ambientales en el manejo sostenible de humedales: estudio del caso del manejo sostenible de sistemas de aguajal en la comunidad de Parinari, Reserva Nacional Pacaya Samiria (RNPS) (Economic valuation of environmental benefits in the sustainable management of wetlands: a case study of the sustainable management of aguajal systems in the community of Parinari, Pacaya Samiria National Reserve (RNPS)). In: Loyola, R., García-Zamora, E. (eds.) *Valoración Económica de los bienes y servicios ambientales: resultados del segundo programa de becas 2002–2003* (*Economic Valuation of Environmental Goods and Services: Results of the Second Scholarship Programme 2002–2003*), INRENA-USAID, Lima, 269–302 (in Spanish).

Hammer, Ø., Harper, D.A.T., Ryan, P.D. (2001) PAST: Paleontological statistics software package for education and data analysis. *Palaeontologia Electronica*, 4(1), 4, 9 pp.

Hergoualc'h, K., Gutiérrez-Vélez, V.H., Menton, M., Verchot, L.V. (2017) Characterizing degradation of palm swamp peatlands from space and on the ground: An exploratory study in the Peruvian Amazon. *Forest Ecology and Management*, 393, 63–73.

Hernández, M., Moreno-Casasola, P. (2018) Almacenes y flujos de carbono en humedales de agua dulce en México (Carbon stocks and fluxes in freshwater wetlands in Mexico). *Madera y Bosques*, 24, e2401881, 12 pp. (in Spanish).

Hidalgo Ríos, R.G. (2014) *Almacenamiento de carbono en la biomasa aerea y del suelo del bosque Yungueño Montano pluviestacional de la concesión para conservación, Alto Huayabamba - San Martín* (*Carbon Storage in the Aerial and Soil Biomass of the Yungueño Montano Pluviseasonal Forest of the Conservation Concession Alto Huayabamba - San Martín*). Thesis, Universidad Nacional Agraria de la Selva, Tingo María, Peru, 197 pp. (in Spanish).

Honorio, C.E., Vega, A.J., Corrales, M.N. (2015) Diversidad, estructura y carbono de los bosques aluviales del noreste peruano (Diversity, structure and carbon of the alluvial forests of northeastern Peru). *Folia Amazónica*, 24, 55–70 (in Spanish).

Horn, C.M., Gilmore, M.P., Endress, B.A. (2012) Ecological and socio-economic factors influencing aguaje (*Mauritia flexuosa*) resource management in two indigenous communities in the Peruvian Amazon. *Forest Ecology and Management*, 267, 93–103.

Householder, J.E., Janovec, J.P., Tobler, M.W., Page, S., Lähteenoja, O. (2012) Peatlands of the Madre de Dios River of Peru: Distribution, geomorphology, and habitat diversity. *Wetlands*, 32, 359–368.

IIAP (2006) *Servicios ambientales de almacenamiento y secuestro de carbono del ecosistema aguajal en la Reserva Nacional Pacaya Samiria* (*Environmental Storage and Carbon Sequestration Services of the Aguajal Ecosystem in the Pacaya Samiria National Reserve*). Technical Document 29, Instituto de Investigaciones de la Amazonía Peruana (IIAP), Loreto-Perú, 65 pp. (in Spanish).

IPCC (2003) *Good Practice Guidance for Land Use, Land-Use Change and Forestry*. Intergovernmental Panel on Climate Change (IPCC), Kanagawa-Japan, 570 pp.

IPCC (2008) *2006 IPCC Guidelines for National Greenhouse Gas Inventories - A Primer, Prepared by the National Greenhouse Gas Inventories Programme*. Intergovernmental Panel on Climate Change (IPCC): Eggleston, H.S., Miwa, K., Srivastava, N., Tanabe, K. (eds.), IGES, Japan.

Jobbágy, E.G., Jackson, R.B. (2000) The vertical distribution of soil organic carbon and its relation to climate and vegetation. *Ecological*

Applications, 10, 423–436.

Junk, W.J. (1997) General aspects of floodplain ecology with special reference to Amazonian floodplains. In: Junk, W.J. (ed.) *The Central Amazon Floodplain: Ecology of a Pulsing System*, Ecological Studies 126, Springer-Verlag, Berlin-Heidelberg, 3–20.

Kayranli, B., Scholz, M., Mustafa, A., Hedmark, Å. (2009) Carbon storage and fluxes within freshwater wetlands: A critical review. *Wetlands*, 30, 111–124.

Krebs, C.J. (1999) *Ecological Methodology*. Second Edition, Pearson Education, New York, 620 pp.

Lähteenoja, O., Ruokolainen, K., Schulmanw, L., Oinonenz, M. (2009) Amazonian peatlands: an ignored C sink and potential source. *Global Change Biology*, 15, 2311–2320.

Lähteenoja, O., Rojas, Y.R., Rasanen, M., del Castillo, D., Oinonen, M., Page, S. (2011) The large Amazonian peatland carbon sink in the subsiding Pastaza-Marañón foreland basin, Peru. *Global Change Biology*, 18, 164–178.

Lamprecht, H. (1990) *Silvicultura en los Trópicos: los ecosistemas forestales en los bosques tropicales y sus especies arbóreas; posibilidades y métodos para un aprovechamiento sostenido* (*Silviculture in the Tropics: Forest Ecosystems in Tropical Forests and their Arboreal Species; Possibilities and Methods for Sustained Use*). GTZ, Eschborn, Germany, 360 pp. (in Spanish).

Lilleskov, E., McCullough, K., Hergoualc'h, K., del Castillo, D., Chimner, R., Murdiyarso, D., Kolka, R., Bourgeau-Chavez, L., Hribljan, J., del Aguila, P.J., Wayson, C. (2019) Is Indonesian peatland loss a cautionary tale for Peru? A two-country comparison of the magnitude and causes of tropical peatland degradation. *Mitigation and Adaptation Strategies for Global Change*, 24, 591–623.

Magurran, A.E. (2004) *Measuring Biological Diversity*. Blackwell Publishing, Oxford, UK, 266 pp.

Mangwale, K., Shackleton, C.M., Sigwela, A. (2017) Changes in forest cover and carbon stocks of the coastal scarp forests of the Wild Coast, South Africa. *Southern Forests*, 79, 305–315.

Meister, K., Ashton, M.S., Craven, D., Griscom, H. (2012) Carbon dynamics of tropical forests. In: Ashton, M.S., Tyrrell, M.L., Spalding, D., Gentry, B. (eds.) *Managing Forest Carbon in a Changing Climate*, Springer-Verlag, New York, 51–75.

Mitidieri, N. (2014) *Reservas de Carbono y composición florística en dos parcelas de 0,5 ha en bosques pantanosos "aguajales" cercanos a las comunidades Quistococha y San Jorge en Loreto, Perú* (*Carbon Reserves and Floristic Composition in two 0.5 ha Plots in "Aguajales" Swamp Forests near the Quistococha and San Jorge Communities in Loreto, Peru*). Batchelor thesis, Universidad Nacional de la Amazonía Peruana, 110 pp. (in Spanish).

Morales, G., Kemper, G., Sevillano, G., Arteaga, D., Ortega, I., Telles, J. (2018) Automatic segmentation of *Mauritia flexuosa* in Unmanned Aerial Vehicle (UAV) imagery using deep learning. *Forests*, 9, 736, 14 pp.

Morisita, M. (1959) Measuring of the dispersion and analysis of distribution patterns. *Memoirs of the Faculty of Science, Kyushu University, Series E Biology*, 2, 215–235.

Mund, M., Schulze, E.D. (2006) Impacts of forest management on the carbon budget of European Beech (*Fagus sylvatica*). *Allgemeine Forst und Jagdzeitung*, 177(3), 47–63.

Nebel, G., Kvist, L.P., Vanclay, J.K., Christensen, H., Freitas, L., Ruiz, J. (2001) Structure and floristic composition of flood plain forests in the Peruvian Amazon: I. Overstorey. *Forest Ecology and Management*, 150, 27–57.

Page, S.E., Rieley, J.O., Banks, C.J. (2011) Global and regional importance of the tropical peatland carbon pool. *Global Change Biology*, 17, 798–818.

PEAM (2004) *Boletín Meteorológico e Hidrológico del Alto Mayo, 1996–2004* (*Meteorological and Hydrological Bulletin of Alto Mayo, 1996–2004*). Proyecto Especial Alto Mayo (PEAM), Moyobamba, Región San Martín, Perú, 57 pp. (in Spanish).

Pereira, L.D., Schröder, T., Chies, J., Zanchetti, F., Fleig, F.D. (2015) Influence of plot size on distribution analyses and effects of altitude on spatial patterns of palm heart in submontane tropical rainforest, Ibirama, Brazil. *Bosque*, 36, 323–329.

Petersson, H., Holm, S., Stahl, G. Alger, D., Fridman, J., Lehtonen, A., Lundström, A., Mäkipää, R. (2012) Individual tree biomass equations or biomass expansion factors for assessment of carbon stock changes in living biomass - a comparative study. *Forest Ecology and Management*, 270, 78–84.

Phillips, O.L., Sullivan, M.J.P., Baker, T.R., Monteagudo, A., Núnez, P., Vásquez, R. (2019) Species matter: Wood density influences tropical forest biomass at multiple scales. *Surveys in Geophysics*, 40, 913–935.

Pitman, N., Terborgh, J., Silman, M.R., Nuñez, P. (1999) Tree species distributions in an upper Amazonian Forest. *Ecology*, 80, 2651–2661.

Pitman, N.C., Andino, J.E.G., Aulestia, M., Cerón, C.E., Neill, D.A., Palacios, W., Rivas-Torres, G., Silman, M.R., Terborgh, J.W. (2014) Distribution and abundance of tree species in swamp forests of Amazonian Ecuador. *Ecography*, 37, 902–915.

13

Quinteros-Gómez, Y., Monroy-Vilchis, O., Zarco-González, M. (2021a) Turberas en Valle del Alto Mayo, Perú: importancia, amenazas y perspectivas de conservación (Peatlands in the Alto Mayo Valley, Peru: Importance, threats and conservation perspectives). *CIENCIA ergo-sum*, 28(1), 1, 11 pp. (in Spanish).

Quinteros-Gómez, Y., Monroy-Vilchis, O., Zarco-González, M., Endara-Agramont, A., Pacheco, X. (2021b) Floristic composition, structure, and species conservation status of *Mauritia flexuosa* palm swamps in Andean-Amazonian piedmont in the Department of San Martín, Peru. *Revista Mexicana de Biodiversidad*, 92, e923186, 17 pp.

Riemann, J.C., Ndriantsoa, S.H., Rödel, M.O., Glos, J. (2017) Functional diversity in a fragmented landscape - habitat alterations affect functional trait composition of frog assemblages in Madagascar. *Global Ecology and Conservation*, 10, 173–183.

Rodrigues, L.F., Cintra, R., Castilho, C.V., Pereira, O.S., Pimentel, T.P. (2014) Influences of forest structure and landscape features on spatial variation in species composition in a palm community in central Amazonia. *Journal of Tropical Ecology*, 30, 565–578.

Rojas-Robles, R., Correa, A., Serna-Sánchez, E. (2008) Seed shadows, seedling survival and spatial distribution of the palm *Oenocarpus bataua*, in a forest of the Colombian Andes. *Actualidades Biológicas*, 30, 135–150.

Román-Cuesta, R.M., Salinas, N., Asbjornsen, H., Oliveras, I., Huaman V., Gutiérrez, Y., Puelles, L., Kala, J., Yabar, D., Rojas, M., Astete, R., Jordán, D.Y., Silman, M., Mosandl, R., Weber, M., Stimm, B., Günter, S., Knoke, T., Malhi, Y. (2011) Implications of fires on carbon budgets in Andean cloud montane forest: the importance of peat soils and tree resprouting. *Forest Ecology and Management*, 261, 1987–1997.

Romo, M., Tuomisto, H., Loiselle, B.A. (2004) On the density-dependence of seed predation in *Dipteryx micrantha*, a bat-dispersed rain forest tree. *Oecologia*, 140, 76–85.

Romulo, C., Gilmore, M., Endress, B., Horn, C. (2022) *Mauritia flexuosa* fruit production increases with increasing palm height in the Peruvian Amazon. *Plants People Planet*, 4, 599–604.

Sampaio, M.B., Schmidt, I.B., Figueiredo, I.B. (2008) Harvesting effects and population ecology of the Buriti Palm (*Mauritia flexuosa* L.f., Arecaceae) in the Jalapão Region, Central Brazil. *Economic Botany*, 62, 171–181.

Sander, N., Pérez-Zavala, F., da Silva, C., Pulido, M.T. (2018) Rivers shape population genetic structure in *Mauritia flexuosa* (Arecaceae). *Ecology and Evolution*, 8, 6589–6598.

Somogyi, Z., Teobaldelli, M., Federici, S., Matteucci, G., Pagliari, V., Grassi, G., Seufert, G. (2008) Allometric biomass and carbon factors database. *iForest,* 1, 107–113.

Souza, A.F., Martíns, F.R. (2004) Microsite specialization and spatial distribution of *Geonoma brevispatha*, a clonal palm in south-eastern Brazil. *Ecological Research*, 19, 521–532.

Terborgh, J., Nuñez-Iturri, G., Pitman, N.C.A., Valverde, F.H.C., Alvarez, P., Swamy, V., Pringle, E.G., Paine, C.E.T. (2008) Tree recruitment in an empty forest. *Ecology*, 89, 1757–1768.

ter Steege, H., Pitman, N.C.A., Sabatier, D., Baraloto, C. and 116 others (2013) Hyperdominance in the Amazonian tree flora. *Science*, 342, 1243092, 10 pp.

Trujillo-González, J.M., Torres, M.A.M., Santana, E.C. (2011) La palma de Moriche (*Mauritia flexuosa* L.f.) un ecosistema estratégico (The Moriche palm (*Mauritia flexuosa* L.f.) a strategic ecosystem). *Orinoquia*, 15, 62–70 (in Spanish).

Vieira, S., Alves, L.F., Aidar, M., Araújo, S.L., Baker, T., Batista, J.L.F., Campos, M.C., Camargo, P.B., Chave, J., Delitti, W.B.C., Higuchi, N., Honorio, E., Joly, C.A., Keller, M., Martinelli, L.A., de Mattos, E.A., Metzker, T., Phillips, O., dos Santos, F.A.M., Shimabukuro, M.T., Silveira, M., Trumbore, S.E. (2008) Estimation of biomass and carbon stocks: the case of the Atlantic Forest. *Biota Neotropica*, 8(2), 21–29.

Virapongse, A., Endress, B.A., Gilmore, M.P., Horn, C., Romulo, C. (2017) Ecology, livelihoods, and management of the *Mauritia flexuosa* palm in South America. *Global Ecology and Conservation*, 10, 70–92.

Zanne, A.E., Lopez-González, G., Coomes, D.A., Ilic, J., Jansen, S., Lewis, S.L., Miller, R.B., Swenson, N.G., Wiemann, M.C., Chave, J. (2009) Data from: Towards a worldwide wood economics spectrum. Dryad, Dataset, https://doi.org/10.5061/dryad.234.

Submitted 04 Sep 2021, final revision 12 Apr 2023
Editors: Mark Harrison and Olivia Bragg

_____

Author for correspondence:
Dr Octavio Monroy-Vilchis, Universidad Autónoma del Estado de México (UAEMex), Instituto Literario 100, Centro, C.P. 50000, Toluca, México. Tel: +52 72240 31970; E-mail: tavomonroyvilchis@gmail.com

Appendix

Derivation of the standardised Morisita index

The standardised Morisita index (I_p) is based on the Morisita dispersion index (I_d) (Morisita 1959), which is calculated by the following expression:

$$I_d = n\left[\frac{\sum x^2 - \sum x}{(\sum x)^2 - \sum x}\right]$$

where:

n = number of units in the sample;

$\sum x$ = sum of the counts of the sample units = $x_1 + x_2 + x_3 \ldots$; and

$\sum x^2$ = sum of the squares of the counts = $x_1^2 + x_2^2 + x_3^2 \ldots$

To calculate the standardised Morisita index it is necessary to determine two extreme critical values, the uniformity index (M_u) and the clustering index (M_c) from the following formulae:

$$M_u = \frac{\chi^2_{0.975} - n + \sum x_i}{(\sum x_i) - 1} \qquad M_c = \frac{\chi^2_{0.25} - n + \sum x_i}{(\sum x_i) - 1}$$

where:

$\chi^2_{0.975}$ = ji squared test with $(n - 1)$ degrees of freedom and 97.5 % from the area to the right;

$\chi^2_{0.025}$ = ji squared test with $(n - 1)$ degrees of freedom and 2.5 % from the area to the right;

x_i = number of individuals in sample unit i $(i = 1, \ldots . n)$; and

n = sample unit number.

Based on the values obtained for the Morisita dispersion index (I_d) and the extreme values (M_u) and (M_c), the standardised Morisita index is calculated from the following formulae:

when:

$I_d \geq M_c > 1,$ $\qquad\qquad I_p = 0.5 + 0.5\left(\dfrac{I_d - M_c}{n - M_c}\right)$

$M_c > I_d \geq 1,$ $\qquad\qquad I_p = 0.5\left(\dfrac{I_d - 1}{M_u - 1}\right)$

$1 > I_d > M_u,$ $\qquad\qquad I_p = -0.5\left(\dfrac{I_d - 1}{M_u - 1}\right)$

$1 > M_u > I_d,$ $\qquad\qquad I_p = -0.5 + 0.5\left(\dfrac{I_d - M_u}{M_u}\right)$

Table A1. List of species recorded, their conservation status, number of individuals, wood density (from Zanne *et al.* 2009), biomass and average carbon stocks in the four aguajales of *M. flexuosa* palm peat swamp forest in the Alto Mayo Valley (DBH ≥ 10 cm). Origin: N = Native, E = Endemic. Aguajales: Tingana (SA: Semi-dense aguajal, MI: Mixed-aguajal), Posic (SD: Semi-dense aguajal, MA: Mixed aguajal). * To estimate biomass of palms, we used the models proposed by Goodman *et al.* (2013) which do not require wood density values.

Family	Species	Origin	Tingana		Posic		Wood density	Biomass	Carbon
			SA	MI	SD	MA	(g cm^{-3})	(Mg ha^{-1})	(Mg ha^{-1})
Annonaceae	*Guatteria blepharophylla* Mart.		0	2	1	4	0.450	1.2310	0.5537
	Oxandra sphaerocarpa R.E.Fr.	N	9	7	0	0	0.770	1.6798	0.7557
	Xylopia ligustrifolia Dunal	N	1	4	0	0	0.600	0.5060	0.2276
Araceae	*Anthurium clavigerum* Poepp.		0	1	0	0	0.500	0.1067	0.0480
Araliaceae	*Schefflera morototoni* (Aubl.) Maguire, Steyerm. & Frodin	N	0	0	6	12	0.470	1.6497	0.7421
Arecaceae	*Euterpe precatoria* Mart.	N	56	11	0	0	*	6.5321	2.9384
	Mauritia flexuosa L.f.	N	184	121	156	123	*	248.7578	111.9009
	Mauritiella armata (Mart.) Burret	N	3	0	85	76	*	4.4569	2.0049
	Oenocarpus bataua Mart.	N	0	0	3	0	*	1.0944	0.4923
	Oenocarpus mapora H.Karst.	N	15	5	1	6	*	10.8515	4.8814
	Socratea exorrhiza (Mart.) H. Wendl.	N	2	3	0	13	*	1.1856	0.5333
Asteraceae	*Vernonanthura patens* (Kunth) H. Rob.		0	0	1	0	0.540	0.0182	0.0082
Burseraceae	*Protium sagotianum* Marchand		0	0	1	0	0.610	0.0569	0.0256
	Tetragastris panamensis (Engl.) Kuntze cf.	N	0	0	0	2	0.710	0.2078	0.0935
Celastraceae	*Cheiloclinium cognatum* (Miers) A.C. Sm.	N	0	0	0	1	0.500	0.0575	0.0259
Clusiaceae	*Calophyllum longifolium* Willd.		0	0	1	10	0.720	0.5284	0.2377
	Clusia loretensis Engl.	E	0	0	7	7	0.560	0.8556	0.3849
	Symphonia globulifera L.f.	N	90	1	10	5	0.580	19.7762	8.8961
Combretaceae	*Buchenavia sericocarpa* Ducke		0	2	0	0	0.720	0.1033	0.0465

Family	Species	Origin	Tingana		Posic		Wood density	Biomass	Carbon
			SA	MI	SD	MA	(g cm^{-3})	(Mg ha^{-1})	(Mg ha^{-1})
Cyatheaceae	*Cyathea pilosissima* (Baker) Domin		0	0	1	0	0.312	0.0059	0.0027
Elaeocarpaceae	*Sloanea robusta* Uittien	N	2	3	0	0	0.860	3.8237	1.7201
Euphorbiaceae	*Alchornea glandulosa* Poepp.	N	0	0	0	2	0.400	0.1194	0.0537
	Hura crepitans L.	N	1	9	0	0	0.370	0.4270	0.1921
Hypericaceae	*Vismia baccifera* (L.) Triana & Planch.	N	5	0	0	0	0.430	0.1550	0.0697
	Vismia pozuzoensis Engl.	N	0	0	2	0	0.480	0.1545	0.0695
Lauraceae	*Aiouea grandifolia* van der Werff	N	0	0	0	3	0.370	0.6028	0.2712
	Nectandra acuminata (Nees & Mart.) J.F.Macbr.	N	1	0	0	0	0.590	0.0369	0.0166
	Nectandra pseudocotea C.K. Allen & Barneby ex Rohwer	N	0	0	1	0	0.590	0.0944	0.0425
	Nectandra pulverulenta Nees	E	0	4	0	0	0.590	1.6959	0.7629
Leguminosae	*Clitoria javitensis* (Kunth) Benth.	N	0	0	2	1	0.670	0.1190	0.0535
	Hymenaea oblongifolia Huber	N	2	0	0	6	0.670	0.4292	0.1931
	Inga cayennensis Benth.		2	10	0	0	0.530	1.2035	0.5414
	Inga oerstediana Benth.	N	0	4	0	0	0.420	0.0755	0.0340
	Inga stenoptera Benth.	N	0	12	0	0	0.420	0.3971	0.1786
	Machaerium floribundum Benth.	N	164	0	0	0	0.700	26.0710	11.7277
	Macrolobium bifolium (Aubl.) Pers	N	4	0	0	0	0.540	0.2937	0.1321
	Senna quinquangulata (Rich.) H.S. Irwin & Barneby	N	2	2	0	0	0.570	0.4615	0.2076
Malvaceae	*Ceiba samauma* (Mart. & Zucc.) K.Schum.		0	0	0	1	0.570	0.0291	0.0131
	Matisia bracteolosa Ducke	N	1	0	185	78	0.410	35.6875	16.0536
	Pachira aquatica Aubl.	N	0	5	0	0	0.370	8.1683	3.6744

| Family | Species | Origin | Tingana | | Posic | | Wood density | Biomass | Carbon |
			SA	MI	SD	MA	(g cm^{-3})	(Mg ha^{-1})	(Mg ha^{-1})
Melastomataceae	*Miconia poeppigii* Triana	N	0	1	0	0	0.650	0.0904	0.0406
	Miconia ternatifolia Triana	N	1	0	0	0	0.620	0.0364	0.0164
	Tococa guianensis Aubl.	N	0	0	1	0	0.550	0.1396	0.0628
Meliaceae	*Cedrela montana* Moritz ex Turcz.	N	1	0	0	0	0.340	0.0164	0.0074
	Cedrela odorata L.		1	0	0	0	0.440	0.0308	0.0139
	Guarea guidonia (L.) Sleumer	N	0	0	0	1	0.660	0.0791	0.0356
Moraceae	*Ficus castellviana* Dugand	N	0	0	3	4	0.390	0.4107	0.1848
	Ficus maxima Mill.	N	0	2	1	10	0.330	1.7810	0.8012
	Ficus pertusa L.f.	N	2	0	0	0	0.420	0.1018	0.0458
	Ficus tonduzii Standl.	N	0	0	0	2	0.390	0.2641	0.1188
	Ficus trigona L.f.	N	0	12	0	0	0.470	2.2984	1.0339
	Sorocea muriculata Miq	N	1	0	0	0	0.560	0.0310	0.0140
Myristicaceae	*Iryanthera juruensis* Warb.		1	0	0	0	0.610	0.1083	0.0487
	Virola elongata (Benth.) Warb.	N	105	76	22	21	0.620	128.4570	57.7850
	Virola pavonis (A. DC.) A.C. Sm.	N	1	4	0	0	0.610	7.8740	3.5420
	Virola surinamensis (Rol. ex Rottb.) Warb.	N	0	0	5	6	0.480	3.7465	1.6853
Olacaceae	*Aptandra tubicina* (Poepp.) Benth. ex Miers	N	0	0	1	0	0.800	0.0600	0.0270
Phyllanthaceae	*Hieronyma alchorneoides* Allemão		10	0	10	13	0.630	3.2368	1.4560
Picramniaceae	*Picramnia sellowii* Planch.	E	3	0	0	0	0.360	0.0433	0.0195
Polygonaceae	*Triplaris longifolia* Huber	E	3	0	0	5	0.560	2.7628	1.2428
	Triplaris poeppigiana Wedd	N	1	0	0	0	0.490	0.2020	0.0909

Family	Species	Origin	Tingana		Posic		Wood density	Biomass	Carbon
			SA	MI	SD	MA	(g cm^{-3})	(Mg ha^{-1})	(Mg ha^{-1})
	Ardisia huallagae Mez	N	2	0	0	0	0.620	0.1589	0.0715
	Cybianthus spichigeri Pipoly	E	0	0	1	0	0.580	0.0346	0.0156
Primulaceae	*Myrsine coriacea* (Sw.) R. Br. ex Roem. & Schult.	N	1	0	0	0	0.590	0.0372	0.0168
	Myrsine oligophylla Zahlbr.	N	0	0	1	0	0.700	0.0423	0.0190
	Myrsine pellucida (Ruiz & Pav.) Spreng.	N	1	2	0	0	0.700	0.3286	0.1478
Rhamnaceae	*Colubrina spinosa* Donn. Sm.		1	0	0	0	0.490	0.0374	0.0168
	Elaeagia pastoensis L.E.Mora		0	1	0	0	0.560	0.0226	0.0102
	Ferdinandusa chlorantha (Wedd.) Standl.	N	0	0	19	74	0.650	7.5633	3.4023
	Ferdinandusa loretensis Standl.	N	0	2	0	0	0.650	0.6402	0.2880
Rubiaceae	*Ladenbergia macrocarpa* (Vahl) Klotzsch		0	0	0	2	0.510	0.0662	0.0298
	Palicourea conferta (Benth.) Sandwith		0	0	0	1	0.560	1.4781	0.6649
	Psychotria alba Ruiz & Pav.		1	3	0	0	0.520	0.2201	0.0990
	Psychotria ernestii K. Krause	N	1	0	0	0	0.520	0.0168	0.0075
	Allophylus floribundus (Poepp.) Radlk.	N	0	2	0	0	0.390	0.8273	0.3722
Sapindaceae	*Matayba purgans* (Poepp.) Radlk.	N	0	0	1	0	0.730	0.0404	0.0182
	Serjania membranacea Splitg.	N	0	2	0	0	0.490	0.0845	0.0380
Urticaceae	*Coussapoa trinervia* Spruce ex Mildbr.	N	2	19	14	9	0.490	4.5326	2.0389
Violaceae	*Leonia glycycarpa* Ruiz & Pavon	N	0	0	5	5	0.650	0.8521	0.3833