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Biomass and carbon stocks of four vegetation types in the Llanos Orientales of Colombia (Mapiripán, Meta)

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ABSTRACT

Agricultural lands occupy 38% of global land surface and are expected to grow significantly in the next years, increasing the need for more sustainable practices, as well as better informed conservation practices of natural ecosystems. Carbon stocks are important estimates for the assessment of potential emissions caused by deforestation, and therefore widely used in strategies to mitigate climate change in agroforestry systems. Although research on biomass and carbon accumulation in agricultural lands is well documented, comparisons with adjacent natural forest areas are uncommon, mainly in tropical regions. Here, we used forest inventory data and allometric models to estimate biomass and carbon stocks of natural vegetation types (gallery forest-GF, morichal-MOR, and savanna-SAV) and oil palm (*Elaeis guineensis*) crops in the Orinoquía bioregion, in Eastern Colombia. We found that natural forests (GF and MOR) hold 542.45 Mg ha^{-1} of aboveground biomass, whereas oil palm plantations store 284.87 Mg ha^{-1}. Morichal vegetation, commonly known as peat swamp forests, accumulated the highest aboveground biomass and carbon per hectare among all vegetation types (natural and agricultural), with an estimate of 402.76 Mg ha^{-1}. Thus, although oil palm crops are great reservoirs of biomass and carbon at the landscape level, it is the combination of natural and agricultural lands which assure highest carbon sequestration in the study area. These results highlight the importance of preserving natural areas in agricultural landscapes for climate mitigation and conservation of biodiversity, which may jointly benefit plantations sustainable development.

1. Introduction

Forests play an important role for the environment and for humans, providing several goods and benefits such as food, timber, and climate regulation. They are major carbon sinks as well, in addition to being home to a great biodiversity and providing ecosystem services. However, forests can also be carbon sources due to deforestation (Baccini et al., 2019), adding more carbon to the atmosphere, and contributing to climate change (Pan et al., 2011). The quantification of biomass and carbon being held in such ecosystems is a challenging, but very informative and necessary for world-wide actions to mitigate climate change, such as the "Reduce emissions from deforestation and forest degradation in developing countries" (REDD+) initiative. REDD+ is an international framework that offers incentives for developing countries to reduce emissions from forested lands by preserving existing forest carbon stocks and incorporating sustainable forest management practices (Edwards et al., 2010).

Natural forests can benefit in many ways from incentive-driven projects like REDD+. In forest rich developing countries, they have shown great potential to slow forest loss and promote sustainable development. In fact, in some places they have been correlated with a reduction in forest fires and illegal logging, resulting in an improvement of ecological outcomes such as increases in vegetation cover and wildlife sightings (like the case of Nepal, Sharma et al., 2015). Because of this, quantification of carbon-related benefits is key to inform sustainable development, particularly related to pressures imposed by agricultural

Abbreviations: AGB, Aboveground Biomass; AGC, Aboveground Carbon; BGB, Belowground Biomass; BGC, Belowground Carbon; DBH, Diameter at breast height; GF, Gallery Forest; MOR, Morichal; OP, Oil Palm; SAV, Savanna.

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expansion.

Over the last 300 years, humans have accelerated the pace and extent of land use activities, and today, more than 38% of ice-free land is used for agriculture, with 10% covered by permanent crops (Ramankutty et al., 2008, 2018). For the past decades, most of the research on carbon emissions from agricultural lands have focused on carbon loss (Guo and Gifford, 2002; Johnson et al., 2014) although human-modified ecosystems can also be significant carbon sinks (Velarde et al., 2014). For instance, agricultural lands have the potential of removing and storing 42–90 Pg of C from the atmosphere during the next 50–100 years if they are properly managed (Albrecht and Kandji, 2003).

Among agricultural plantations, oil crops have had the biggest production increases during the past decades, especially oil palm (*Elaeis guineensis*), having an eightfold increase since 1961 (Ramankutty et al., 2018). In Southeast Asia, commercial oil-palm plantations have largely contributed to deforestation, biodiversity loss, and greenhouse gas emissions (Koh et al., 2011; Sodhi et al., 2010). By the early 2000s, almost 880,000 ha of peat-swamp forests were converted to oil palm plantations, resulting in the loss of ca 140 million metric tons (Mt) of aboveground carbon and annual emissions of ca 4.6 Mt of belowground carbon from peat oxidation (Koh et al., 2011). Such increases require that the agricultural industry commits to better sustainable practices and the conservation of biodiversity, as a higher demand for crop lands is expected in the near future (Laurance et al., 2014). Given that the impacts of oil palm expansion can be substantially mitigated if future plantations explicitly account for environmental and agricultural trade-offs (Koh and Ghazoul, 2010), the oil palm industry has committed to lessen their impact on the environment by establishing strict guidelines of sustainable practices.

In Colombia, *Fedepalma* (the national association of oil palm industry in Colombia) manages three environmental and social certifications: the Roundtable on Sustainable Palm Oil (RSPO), the International Sustainability & Carbon Certification (ISCC), and the Rainforest Alliance Certified (RAC) (Fedepalma, 2020). For acquiring these certifications, agricultural companies need to fulfill several requirements, including the implementation of practices such as using only natural pest controls, no-burn of waste at palm oil mills, and the delimitation and preservation of natural habitat patches recognized as High Conservation Value Areas (HCVAs) (Scriven et al., 2019). Additionally, in 2017, Fedepalma and several Latin American oil palm companies signed up a Zero Deforestation agreement, which was an important step towards preventing the loss of forest cover on biologically important regions such as the Amazon and Orinoquía (Fedepalma, 2020).

As of 2020, Colombia is the fourth largest producer of oil-palm in the world, with a planted area of 590,189 ha and ca 1600,000 tons of crude palm oil, 4% more than in 2019 (Fedepalma, 2020, 2021). 33 Colombian oil palm companies have received RSPO, ISCC or RAC certifications, tightening their commitment to zero deforestation and the protection of natural resources, as well as the incorporation of sustainable practices related to leveraging byproducts of the palm oil extraction process, the integral use of biomass by composting, and the proper planning and managing of water resources (Fedepalma, 2021). At the national level, the Orinoquía bioregion (eastern Colombia) has had the highest growth in oil palm planted area. This is a region of great interest due its large extension, a unique inter-annual biomass dynamic (Anaya et al., 2009), and for holding expansive savanna formations (Llanos Orientales) which cover approximately 17 million ha with a plain topography of great agronomical potential (Rippstein et al., 2001). Savannas in the Orinoquía have been historically impacted by human-induced fires for cattle production as well as logging for plantation expansion (Etter et al., 2010). Oil palm plantations in the Orinoquía cover large extensions of afforested land, and while they can be important carbon sinks, they may also protect native biodiversity if managed sustainably (Pilli et al., 2014).

In this study, we leverage allometric models and vegetation plot data to estimate above and belowground vegetation biomass and carbon stocks in four vegetation types: gallery forest (GF), morichal (MOR), savanna (SAV) and oil palm plantations (OP) in Mapiripán, Meta, Colombia. These four vegetation types are not discrete, but instead share several plant species, and co-occur within the same areas. Our purpose was to answer two research questions: (1) How do above- and belowground biomass and carbon stocks of dominating tree species vary across the four dominating vegetation types (GF, MOR, SAV, and OP)? (2) Which of these vegetation types hold higher biomass and carbon stocks at the local and at the landscape scale?

2. Materials and methods

2.1. Study area

This study was conducted in three farms (total of 10,000 ha) owned by Poligrow Colombia, one of the largest oil palm companies of the country, located in Mapiripán, Meta, in the Llanos Orientales (Orinoquía Region, eastern Colombia, Fig. 1). The region has mean annual temperatures of 26–30 °C and mean annual precipitation that ranges from 1500 mm to 3000 mm (IDEAM, 2015). The rainfall pattern is seasonal, with three months (December, January and February) of drought (rainfall of $<$100 mm), and high precipitation during the rest of the year (Veneklaas et al., 2005). The landscape has been shaped over millions of years by erosion, creating hills and valleys, where the latter is partly filled by colluvial wash, and the texture of the soil varies from clay to sand (Goosen, 1971). Ecosystems in the area include seasonal and flooded savannas, dominated by grasslands and riparian forests (Etter, 1997).

2.2. Field sampling

Vegetation plots were sampled in three farms owned by Poligrow Colombia (Barandales, Macondo and Toninas; Fig. 1), where two types of pre-classified natural vegetation occur: 1) gallery forest (GF), a woody vegetation and the most biological diverse, as well as structurally highest canopy (28 to 35 m) and most functionally heterogenous vegetation cover of the Colombian Orinoquía (Correa-Gómez and Stevenson, 2010), and 2) morichal (MOR), a vegetation dominated by the palm *Mauritia flexuosa*, also known as “moriche”, which is broadly known for inhabiting flooded peat swamps (Virapongse et al., 2017). In the three farms, transects of 100 m with five plots of 10 m × 10 m each (sample unit) were established in both natural vegetation types (Fig. 2, Table 1). A total of twenty transects were established and field vegetation inventories were conducted, manually collecting information on diameter at breast height (DBH) and height of all palms and trees with DBH $\geq$ 10 cm.

2.3. Selection of species and biomass/carbon stock estimations

In the forest vegetation data (GF and MOR) dominant species were selected based on the number of species that held at least 90% of the total basal area (estimated from the DBH) in each vegetation type. We also estimated the Importance Value Index (IVI) using BiodiversityR (Kindt and Coe, 2005), to have community-level information supporting our species selection. Although we did not sample savannas (hereby referred as SAV) in the field, we found data for this vegetation cover in the literature, and included it in our analyses of biomass and carbon stocks at the local (per area) and landscape levels. SAV has a predominant cover in our study area, as well as a large extension in the Orinoco Basin encompassing Venezuela and Colombia. It is a habitat dominated by herbaceous plants (grasses, forbs, etc.) with isolated trees and shrubs, which, due to the heterogeneity of the landscape, share woody species with GF. To identify the common tree species of SAV in our study site, we compared our list of GF species to the SAV species presented in San Jose et al. (1998) and found four species in common: *Cecropia sp., Protium heptaphyllum, Protium llanorum*, and *Xylopia aromatica*. These were

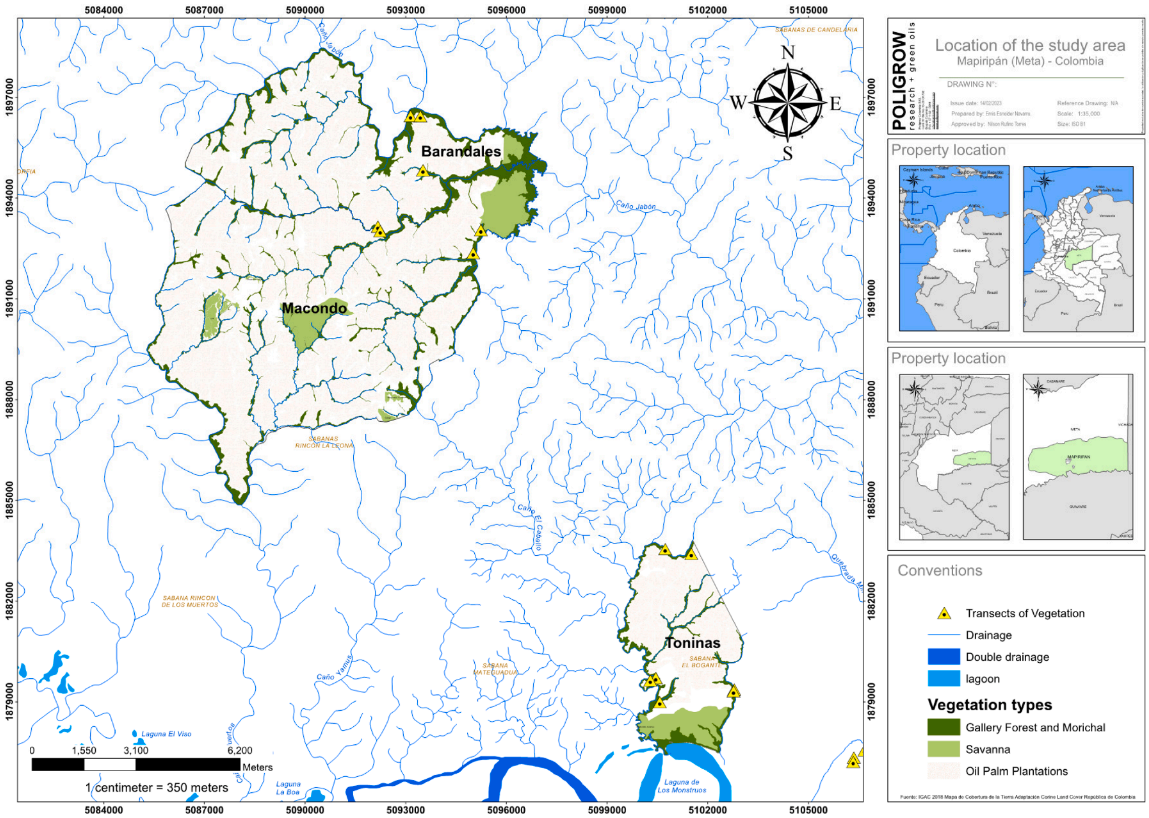

Fig. 1. Location of the study area in Mapiripán, Meta, Colombia, showing the three farms where the field work took place: Barandales, Macondo and Toninas. The yellow triangles indicate where the vegetation transects were located in the field. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 1
Sampling design.

Farm	Vegetation type	Number of transects
Barandales	GF	3
	MOR	3
Macondo	GF	3
	MOR	3
Toninas	GF	4
	MOR	4
Total		**20**

the result of floristic surveys described in Montes & San Jose (1995), which, similarly to our study, comprised transects of 5 m x 5 m to determine plant community profiles. Rippstein et al. (2001) also reported these four species in this type of vegetation in the Llanos Orientales. DBH and height measurements from our own floristic survey in GF were used for further quantitative analysis (i.e., biomass and carbon estimations) as these species are present in both vegetation types. Floristic surveys were performed in 2020.

We used previously developed allometric models to estimate aboveground (AGB) and belowground biomass (BGB) for all dominating species in the three dominating vegetation types (GF, MOR and OP) and the species shared by savanna and gallery forest (GF + SAV) (see Table 2 and **S1**). For dicot tropical trees allometric equation, we used wood density values (ρ) obtained from databases and published papers (**Appendix 1, Table S2**).

Oil palm (*Elaeis guineensis*) data was included to compare biomass and carbon stocks between natural and agricultural (afforested) habitats. For this purpose, we randomly selected 30 oil palm plots of 0.05 ha each, distributed across the three farms (Barandales, Macondo and Toninas) covering a total of 1.5 ha, and used inventory data that included values of palm abundance per ha, year of sowing and palm mean height. Palm plantations were divided into three categories according to age: 2009 – 2010 (OP Y1), 2011 – 2012 (OP Y2), and 2013 – 2014 (OP Y3) plantations, and they were sampled in 2020; belowground biomass (BGB) and aboveground biomass (AGB) were estimated using allometric equations specifically developed for *Elaeis guineensis*

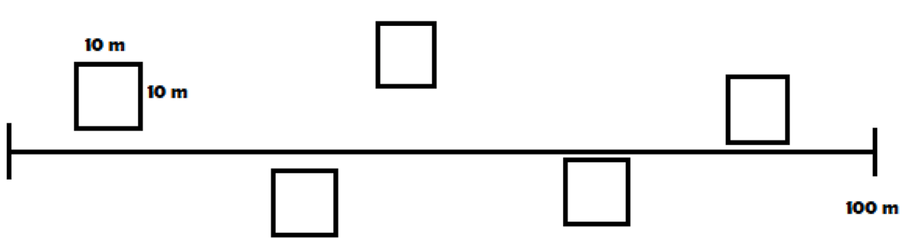

Fig. 2. Field sampling design, showing a transect of 100 m, with five subplots each covering an area of 0.01 ha (10 m × 10 m), with a total of 0.05 ha area in total per transect. All palms and trees with DBH ≥ 10 cm within the 10 m × 10 m subplots were measured (DBH and total height). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 2
Allometric models used to estimate above- and belowground biomass of palms and dicot trees (AGB and BGB; kg dry mass) using stem height (H_{stem}; m), diameter at breast height (D; cm) and wood density (ρ; $g\ cm^{-3}$). The Arecaceae equation is only valid for individuals with $H_{stem} > 3$ m and $6 \leq D < 40$ cm.

Taxa	Allometric equation	Reference
	Aboveground biomass (AGB)	
Mauritia	$Ln(AGB) = -2.4647 + 1.37777 \times ln(H\ stem)$	Goodman et al. (2013)
Mauritiella	$AGB = 2.8662 \times H\ stem$	
Astrocaryum	$AGB = 21.302 \times H\ stem$	
Attalea	$Ln(AGB) = 3.2579 + 1.1249 \times ln(H\ stem + 1)$	
Euterpe	$AGB = -108.81 + 13.589 \times (H\ stem)$	
Oenocarpus	$Ln(AGB) = 4.5496 + 0.1387 \times (H\ stem)$	
Socratea	$Ln(AGB) = -3.7965 + 1.0029 \times (\ln(D^2 \times H\ stem))$	
Arecaceae	$Ln(AGB) = -3{,}3488 + 2{,}7483 \times ln(D)$	
Dicot trees (all families)	$AGB = 0.0673 \times (\rho \times D^2 \times H\ stem)^{0.976}$	Chave et al. (2014)
Elaeis guineensis (oil palm)	$AGB = 1000 \times (0.0939 \times H\ stem + 0.0951)$	Kauffman et al. (2012)
	Belowground biomass (BGB)	
Dicot trees (all families)	$Ln(BGB) = -4.394 + 2.693 \times ln(D)$	Sierra et al. (2007)
Mauritia	$Ln(BGB) = -3.3488 + 2.0106 \times ln(H_{stem})$	Goodman et al. (2013)
Elaeis guineensis (oil palm)	$BGB = 0.489 \times AGB^{0.890}$	Kauffman et al. (2012)
All other palms	$Ln(BGB) = 1.0945 + 0.11086 \times (H_{stem})$	Goodman et al. (2013)

(Table 2). OP carbon stocks estimations were performed on a per hectare basis, as follows:

$$AGB\ per\ area\ \left(kg\ ha^{-1}\right) = \frac{AGB\ per\ palm\ (kg)\ \times\ Total\ palm\ abundance}{Total\ area\ (ha)} \quad (1)$$

Additionally, we estimated the maximum biomass and carbon that plantations would attain when they reach a height of 13 m, which represents oil palm harvest height, to compare the highest possible C sink of plantations on a per area basis versus that of natural habitats. We used average values of total palm abundance and total area across multiple years of measurement to estimate biomass and carbon per area. We then used conversion factors to estimate carbon content from biomass values across the three habitat types (Table 3).

2.4. Landscape biomass and carbon stock estimations

Biomass and carbon stocks of each of the three farms (Barandales, Macondo and Toninas) at the landscape level were estimated by multiplying the total area covered per vegetation type per farm by the estimated values of biomass and carbon per area of each vegetation type (GF and OP crops per year). MOR was excluded from the landscape analyses, as this vegetation type occupies small fractions of gallery forests which are very difficult to differentiate from, and for which it was impossible to estimate an area using satellite images.

Table 3
Above- and belowground carbon conversion factors used to estimate carbon content in vegetation biomass across three habitat types (GF, MOR and OP). GF and MOR held a combination of dicot trees and palm species, while OP contained only oil palms.

Taxa	Conversion factor	Reference
Aboveground carbon (AGC)		
Dicot trees	0.47	IPCC (2006)
Palms	0.418	Kauffman et al. (2012)
Mauritia	0.2461	Cabrera Mestanza and Rivas Mori (2014)
Oil palm	0.418	Kauffman et al. (2012)
Belowground carbon (BGC)		
Dicot trees	0.39	Kauffman et al. (2012)
Palms	0.418	Kauffman et al. (2012)
Mauritia	0.2461	Cabrera Mestanza and Rivas Mori (2014)
Oil palm	0.418	Kauffman et al. (2012)

We estimated biomass and carbon of SAV since they cover a significant amount of area of the studied farms. These estimations were performed using our own estimations of area covered by SAV per farm and incorporating values of AGB per area from Anaya et al. (2009) and AGC and BGC from San Jose et al. (1998). These estimations are comparable to our data for two reasons. First, in both studies, estimations of biomass and carbon were performed using allometric models and floristic surveys. Second, the Orinoco Basin savanna has a total area of 981,446 km^2 shared by Venezuela (65%) and Colombia (35%, 343,506 km^2) with different types of seasonally-flooded savannas across both countries (Jimenez et al., 2022). Thus, the Colombian savanna vegetation could be considered similar to the Venezuelan savanna measured by San Jose et al. (1998); as seen in (San Jose et al., 1998) where the same few tree species are the most common in different savanna ecosystems, being widely distributed in the Orinoco Basin. Moreover, San Jose et al. (1998) estimated carbon stocks using allometric models with vegetation census data (tree height). Finally, although we did an extensive literature search, we did not find any available BGB per area value for tropical savanna vegetation for the Llanos Orientales in Colombia, nor Orinoquía.

2.5. Statistical analysis

To elucidate how do above- and belowground biomass and carbon stocks of dominating tree species vary across species, we did a Kruskal-Wallis. We also compared the four dominating vegetation types ((GF, MOR, OP at 13 m (13 m), year one (OP Y1), year two (OP Y2) and year three (OP Y3)) with four sets of Generalized Linear Model (glm) with gamma fit to discern if they differed in terms of AGB, BGB, AGC and BGC. Additionally, to discern which of these vegetation types holds higher biomass and carbon stocks per area, we performed for each glm a set of Tukey tests to explore the degree of differences between vegetation types.

Biomass and carbon estimations were also analyzed with descriptive statistics at the species level (mean and total) and for all vegetation types to compare biomass and carbon stocks variation at the landscape level. All statistical analyses and figures were performed using the packages “car”, “multcomp”, “ggplot2”, “stats” and “tidyverse” of the software RStudio (RStudio Team, 2020).

3. Results

3.1. Individual tree species biomass and carbon contribution in gallery forests and oil palm plantations

In natural forests (GF and MOR), the dominant vegetation comprised 28 species belonging to 13 families. In GF, we found that 27 species, represented by 329 individuals held ca. 90% of the total basal area. *Macrolobium sp.* was the species that accumulated the second highest biomass and carbon per tree, besides having only one tree in our data, which had a significant large height and DBH compared to the rest of the trees (17.5 m and 49.0 cm, respectively). Unfortunately, we were not able to classify this individual to species since we did not find any flowers or fruits during field work. However, in more recent field inventories done in the same farm (Toninas), the species *Macrolobium acaciifolium* was identified, so it is possible that the unidentified individual corresponds to this species. Similar to this species, *Myrsine coriacea,* although represented by only 3 individuals, had the highest biomass and carbon per individual among all species in GF. In MOR, *Mauritia flexuosa* held ca 90% of the basal area with 942 individuals, hence being the only species in MOR included in the estimations. Additionally, we estimated biomass and carbon for tree species found in both GF (based on our field data) and SAV (*Cecropia sp., Protium heptaphyllum, Protium llanorum*, and *Xylopia aromatica*, based on the list of species presented on San Jose et al., 1998) (Fig. 3).

In terms of total biomass and carbon contribution per species (Fig. 4), *Mauritia flexuosa* in MOR is the species with the largest amounts of aboveground biomass and carbon, as well as the highest abundance per area, with 942 individuals, followed by *Xylopia aromatica* (Fig. 4; **Appendix 1, Table S5**). In contrast, we found species that despite having a considerable abundance, contribute with lower total stocks than less abundant species, e.g. *Socratea exorrhiza* with 69 individuals and 4.77 Mg of AGB versus *Caraipa llanorum* with 21 individuals and 8.65 Mg of AGB. Overall, our results show that species from natural vegetations (GF, GF+SAV, MOR) hold larger stocks than oil palm, even the oldest palms from 2009 – 2010 (*Elaeis guineensis* (Y1)).

3.2. Biomass and carbon per vegetation type per area

Biomass and carbon stocks of dominant vegetation types found in our study site were found to vary significantly. The aboveground biomass of natural forest (GF and MOR) and oil palm plantation (OP) were 542.45 Mg ha^{-1} and 284.87 Mg ha^{-1}, respectively. In natural forests, the highest biomass was contributed by *Mauritia flexuosa* (73.83%), the only species found dominating MOR, which in turn was the vegetation with the highest aboveground biomass per area (402.76 Mg ha^{-1}). In fact, this vegetation type had almost three-fold the biomass of GF, and young OP plantations (Fig. 4). However, it was the vegetation type with the least amount of belowground biomass per area (4.85 Mg ha^{-1}, Table 4 and Fig. 5).

Note that the values presented on Table 4 of SAV correspond to the estimates reported by Anaya et al. (2009) of AGB and San Jose et al. (1998) of AGC and BGC in similar savannas in the Orinoco. These were used only to estimate biomass and carbon at the landscape level (next section) and are not part of our analyses per area reported in this section, therefore, comparisons of these values to our estimations per area of GF, MOR, and OP should be interpreted carefully.

3.3. Biomass and carbon at the landscape level

We found that natural forests (GF including MOR) had an area of 3216.2 ha that extends within the three farms sampled (Macondo, Barandales, and Toninas), with a total biomass of 295.73 × 10^3 Mg and 109.86 × 10^3 Mg of carbon. OP plantations had twice the area of forests (6598.1 ha), and a total biomass of 816.2 × 10^3 Mg and 341.2 × 10^3 Mg of carbon. In natural forests, AGB and AGC were estimated as 242.39 × 10^3 Mg and 923.28 × 10^3 Mg, respectively, whereas in OP plantations, we estimated 643.64 × 10^3 Mg of AGB and 269.04 × 10^3 Mg of AGC.

At the belowground level, we estimated that natural forests have a BGB of 53.34 × 10^3 Mg and a BGC of 17.53 × 10^3 Mg. In contrast, OP plantations had a BGB of 172.56 × 10^3 Mg and a BGC of 72.13 × 10^3 Mg.

Despite of the fact that natural forests cover less area, they contribute significant amounts of biomass and carbon stocks. For example, in Macondo, even though OP covers 5 times more area than GF, they contribute only to 2.5 times more biomass/carbon than GF (Fig. 6).

4. Discussion

The present study addresses the importance of preserving natural vegetation and quantifying biomass and carbon accumulation in agricultural landscapes, specifically in the Orinoquía Region, a biome historically affected by extensive agriculture and cattle farming. We found that natural forests, gallery forest (GF) and morichal (MOR), as well as

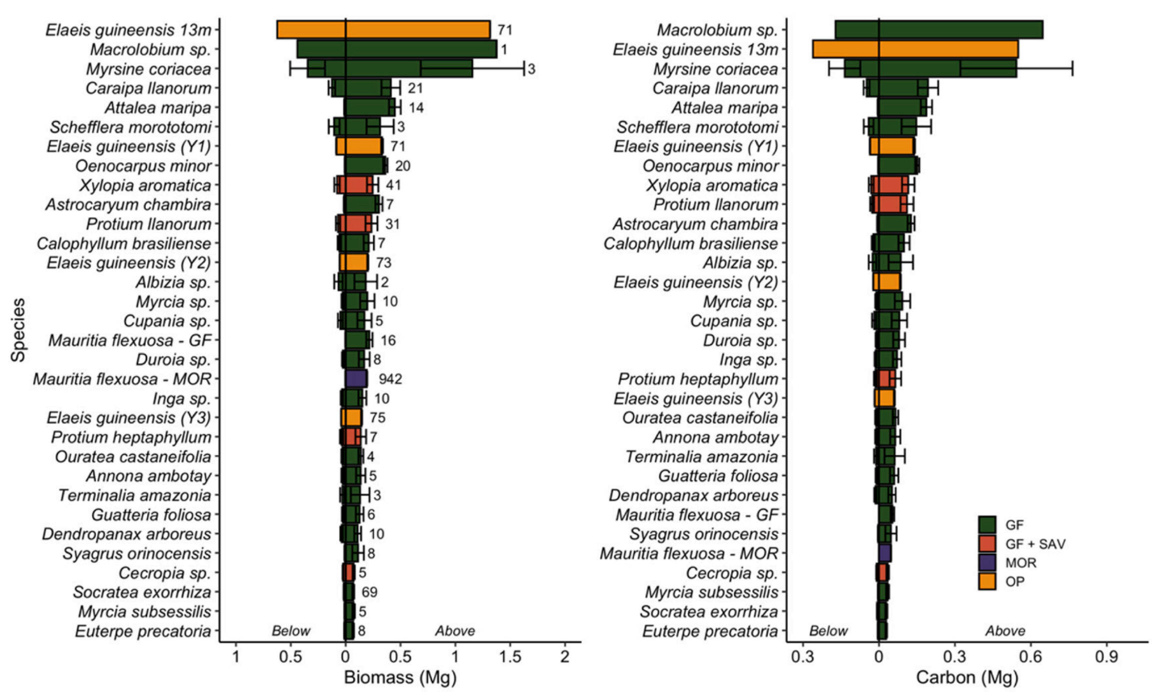

Fig. 3. Average biomass (left) and carbon (right) per individual per species found in 20 vegetation plots in natural vegetation types (gallery forest (GF), gallery forest and savanna (GF + SAV), morichal (MOR)) and oil palm plantation (OP) per year (from 2009 – 2010 – *Elaeis guineensis* (Y1), from 2011 – 2012 – *Elaeis guineensis* (Y2), and from 2013 – 2014 – *Elaeis guineensis* (Y3)), and at a height of 13 m (a hypothetical value estimated with an allometric equation and carbon conversion factors (See Tables 2 and 3, respectively)). OP abundance was drawn from plot survey data in three farms in Mapiripán, Meta, Colombia. Belowground estimates are shown to the left of each panel, and aboveground to the right. Numbers on each bar in the left panel indicate the abundance of each species in vegetation plots established in the field– GF + SAV species were found in our floristic surveys in GF and reported in the literature by San Jose et al. (1998); their abundance values correspond only to data from our study plots. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

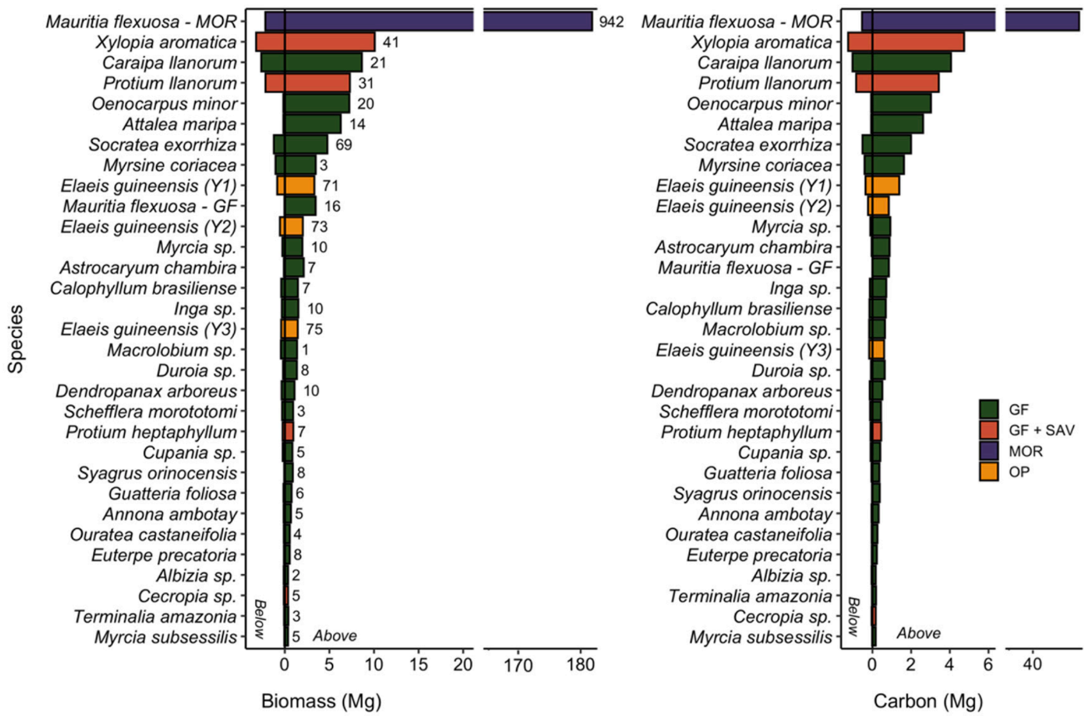

Fig. 4. Total biomass (left) and carbon (right) contribution per species found in 20 vegetation plots in three vegetation types in Mapiripán, Meta, Colombia: gallery forest (GF), gallery forest and savanna (GF + SAV), morichal (MOR), and oil palm plantation (OP) per year (from 2009 – 2010 – *Elaeis guineensis* (Y1), from 2011 – 2012 – *Elaeis guineensis* (Y2), and from 2013 – 2014 – *Elaeis guineensis* (Y3)). Belowground estimates are shown to the left of each panel, and aboveground to the right. The total sampled area of gallery forests was 0.5 ha, therefore estimates for OP, MOR, and SAV, were scaled to 0.5 ha. Numbers on each bar in the left panel indicate the abundance per species. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 4
Biomass and carbon per area (ha) in tropical natural and agricultural habitats in the Llanos Orientales of Colombia (Mapiripán, Meta). AGB: aboveground biomass, BGB: belowground biomass, AGC: aboveground carbon, and BGC: belowground carbon.

Vegetation type	Sampled area (ha)	Biomass and carbon density (Mg ha^{-1})				Number of species	Abundance
		AGB	BGB	AGC	BGC		
GF	0.5	139.69	29.32	61.83	11.53	27 (90% of dbh)	329
MOR	0.45	402.76	4.85	99.12	1.19	1 (90% of dbh)	942
SAV	3.60×10^{7}†, 3‡	21.00†	–	0.71‡	0.31‡	3*	–
OP 13m	17	186.84	88.65	78.1	37.06	1	2449**
OP Y1	195.7	46.81	12.08	19.56	5.05	1	27,681
OP Y2	150.3	29.24	7.97	12.22	3.33	1	21,985
OP Y3	158.7	21.98	6.21	9.19	2.60	1	23,800

† AGB value taken from Anaya et al. (2009).
‡ AGC and BGC values taken from San Jose et al. (1998).
* Number of species shared by GF and SAV, found in our floristic survey and reported in savanna by San Jose et al. (1998).
** Hypothetical value.

oil palm agroforestry systems in the Orinoquía hold large reservoirs of biomass and carbon. Our results suggest that 1) the trees *Macrolobium sp.* and *Myrsine coriacea* hold the highest biomass and carbon stocks per individual, followed by theoretical estimates for *Elaeis guineensis* (oil palm) at 13 m of height (maximum productivity), 2) MOR has the largest AGB stocks per area despite being dominated by one species of palm, and 3) OP plantations have the largest amounts of biomass and carbon at the landscape level due to their extension, but GF have comparable stocks despite having a much smaller area. Results from this research shed light on the importance of incorporating carbon-based policies in agriculture in the context of climate change mitigation and protection of biodiversity, as well as highlighting the need of developing further research related to the estimation of above and belowground biomass and carbon stocks using more direct methods such as plant inventories across all vegetation types, and field measurements of wood density.

4.1. Effect of species identity and abundance on biomass and carbon accumulation

Our results show that multiple vegetation types in the Orinoquía region are key for the conservation of plant diversity, having ca. 17% of Colombia's plant species (4500 vascular plants) (Rangel-Ch. and Orlando, 2015), and also large reservoirs of biomass and carbon accumulated in native tree and palm species. Our estimations of above (AGB) and belowground biomass (BGB) and carbon (AGC + BGC) stocks varied widely across species in the studied vegetation types. For instance, native species like *Macrolobium sp.* (probably *Macrolobium acaciifolium*) and *Myrsine coriacea,* albeit represented by few individuals, had the highest biomass and carbon per individual among all species in GF, followed by the theoretical estimates for individual oil palms of 13 m in height. In addition to this study presenting evidence on the contribution of biomass and carbon stocks by these species in the Orinoquía, both

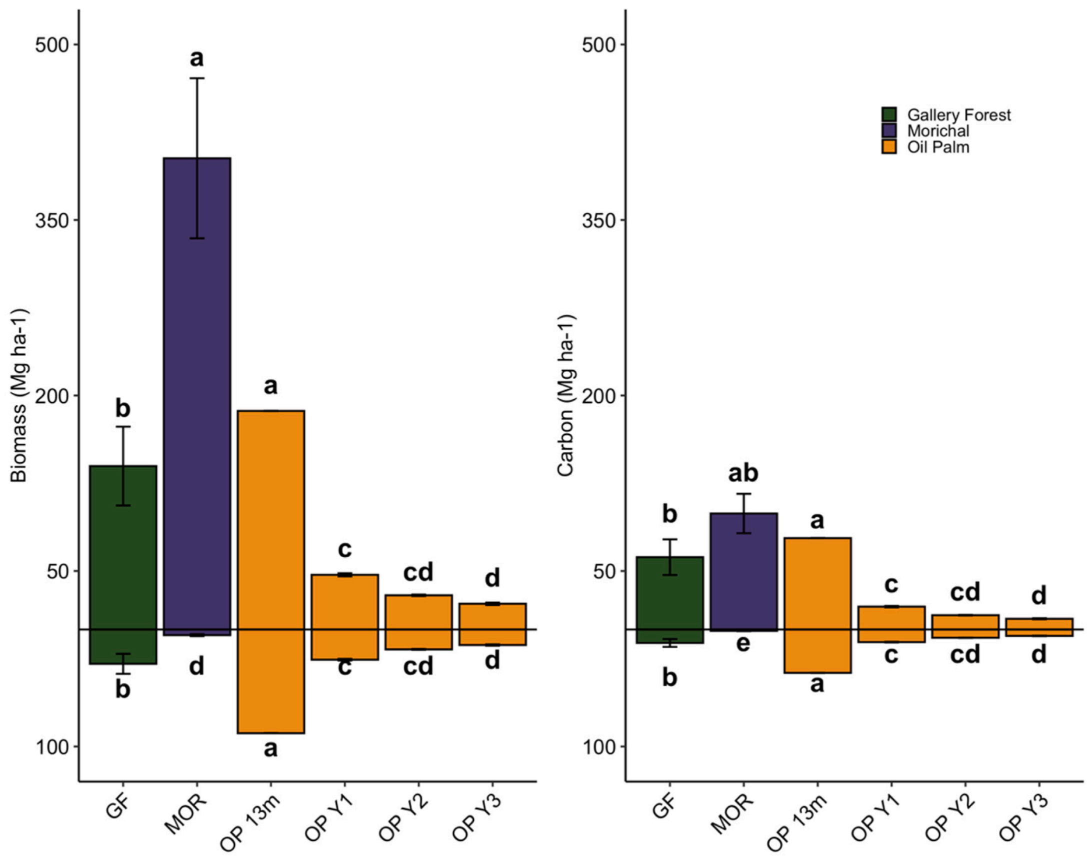

Fig. 5. Mean above- (positive bars) and belowground (negative bars) biomass and carbon per area estimated from 10 vegetation plots in each of two natural vegetation types in Mapiripán, Meta, Colombia: gallery forest (GF) and morichal (MOR), and from oil palm plantations (OP) of different age (planted in 2009 – 2010 (OP Y1), 2011 – 2012 (OP Y2), or 2013 – 2014 (OP Y3)) and at 13 m of height (OP 13 m). Different letters on top of each bar show significant differences based on GLM analyses. Oil Palm (OP) vegetation had little data variability, and no standard deviation is illustrated for OP 13 m as it is a hypothetical estimation. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Macrolobium sp. and *Myrsine coriacea* have been listed as useful plants with uses for animal food, medicine, fuel and/or human consumption (ColPlantA, 2022; Nogueira Lima et al., 2012; Roucoux et al., 2013).

Forest inventory data has provided inconsistent support for a relationship between diversity/abundance of species and function, and there is evidence for both a positive (Caspersen and Pacala, 2001) and no relationship between productivity and biodiversity (Enquist and Niklas, 2001). The identity of plant species influences their relative contribution to stocks, whereby some species can accumulate more than others depending on their functional traits (e.g., DBH and wood density) and use of resources, but as discussed in Kirby & Potvin (2007), the magnitude of the effects of functional traits differences across species on carbon storage is rarely emphasized in the context of biomass or carbon uptake (see Balvanera et al., 2005).

In the case of oil palm, a well established crop species with large productivity (Corley and Tinker, 2016), our estimates suggests it is a large biomass and carbon storage. We estimated that one palm of *E. guineensis* at 13 m has 1.32 Mg of AGB, 0.62 Mg of BGB, 0.55 Mg of AGC and 0.26 Mg of BGC. This is a theoretical estimation made based on the fact that palms are harvested and replaced at a maximum height of 13 m at Poligrow Colombia (E. Fandiño, *pers. comm.*, 2021). Rivera-Méndez et al. (2017) reported that in a different OP plantation in Barrancabermeja – Santander (Colombia) a palm at its maximum biomass accumulation (after 22 years) has 113 Mg of C ha^{-1}. In their analysis, OP abundance was 143 palms ha^{-1}, therefore we estimate that each palm would have ca. 0.79 Mg of C in total, a value comparable to our total estimation per individual (AGC + BGC = 0.76 Mg). Another study in the Philippines found that aboveground and belowground biomass per individual oil palm ranged from 0.023 - 0.99 Mg, where nine-year-old plants held the largest biomass (Pulhin et al., 2014), which is also consistent with our estimates. Besides methodological differences, variability in biomass and carbon content might be explained by multiple variables like the age of palms, the oil palm genotype used in each plantation, soil conditions, etc. (Rivera-Méndez et al., 2017).

4.2. Biomass and carbon contrast across vegetation types

We found that MOR, a vegetation type dominated by a single palm species (M*auritia flexuosa*), had greater carbon stocks than GF, a more diverse forest type. As discussed above, the link between species diversity and carbon storage in natural forest systems is not always straight forward, but there is a clear correlation across several biodiversity attributes (i.e., taxonomic diversity, trait diversity, community-mean traits, and structural attributes) (Ruiz-Jaen and Potvin, 2011), and generally speaking, carbon stocks are highly dependent on forest maturity and levels of disturbance (Chazdon et al., 2016). For example, biodiversity appears to be less significantly correlated to carbon storage and carbon uptake (CSU) in plantations and disturbed forests than in mature forests (van der Sande et al., 2017). The relationship between carbon storage and species richness has been a subject of debate, and there is contrasting evidence on a correlation between these attributes (Martinez-Sanchez and Cámara, 2012; Ruiz-Jaen and Potvin, 2010; Strassburg et al., 2010) but it appears to vary with scale (Soto-Navarro et al., 2020).

Forest architecture also plays an important role in biomass and carbon accumulation across different ecosystem types. In our study,

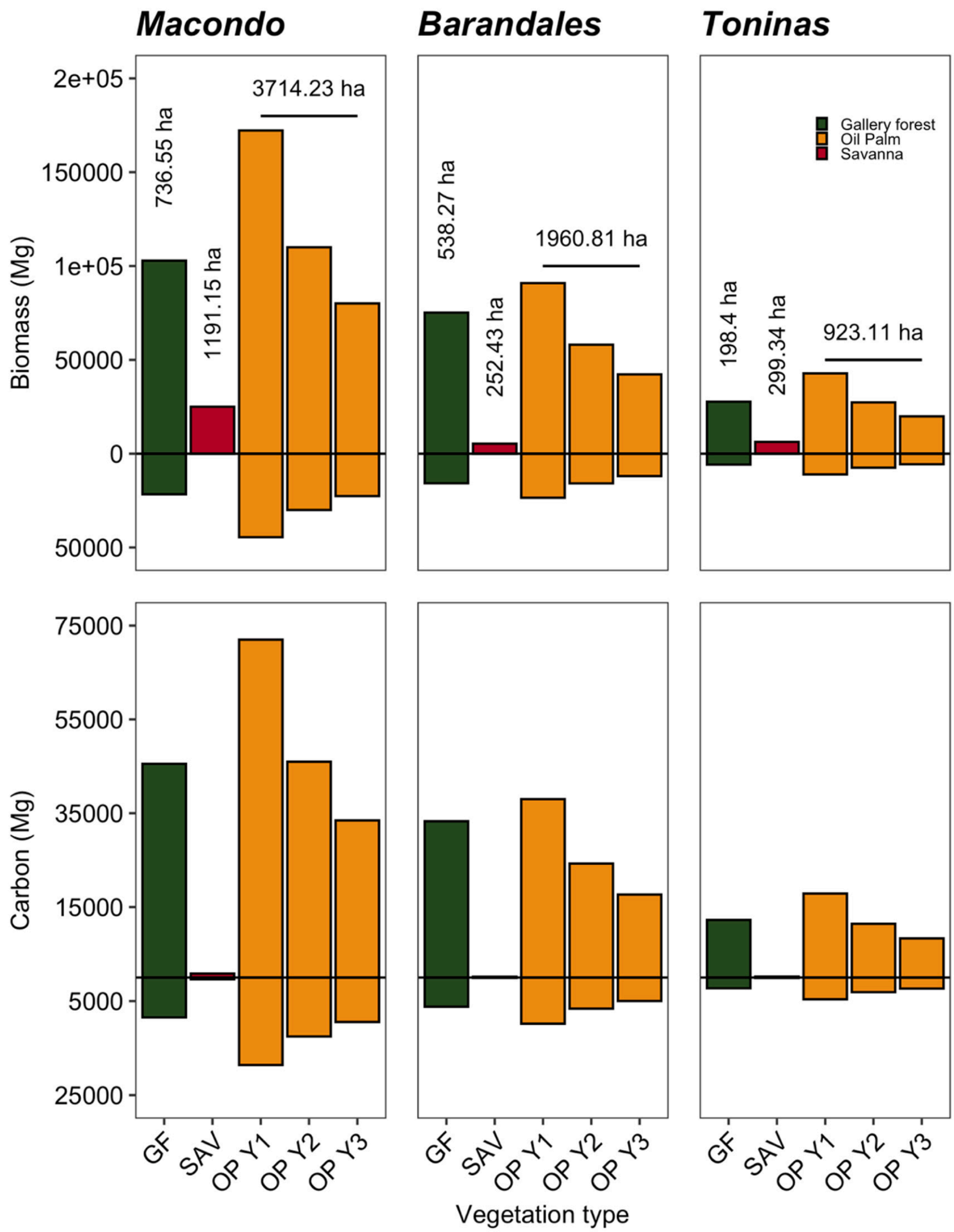

Fig. 6. Contributions of above- (positive bars) and belowground (negative bars) biomass and carbon of each of three vegetation types in Mapiripán, Meta, Colombia: gallery forest (GF), savanna (SAV), and oil palm plantations (OP) of different age. Area (ha) covered by each vegetation type is shown above the bars. Belowground carbon was not estimated for SAV because an average value of carbon at this level is lacking for the study region. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

MOR was entirely dominated by *M. flexuosa*, palms with a single growing point in the apex which are resistant to flooding. Their relatively slim apex allows for them to occur in high density in swamps. This means that in addition to lacking lateral growth in the canopy, a high stem density can be reached on a per area basis (more than 150 individuals ha^{-1}, see Draper et al., 2014). Poorter & Sande (2015) suggest that forests with higher tree density may have larger and more stems, and because most carbon is stored in stems, more biomass and carbon can potentially be accumulated (Poorter and Sande, 2015), as we found to be true for MOR. It is worth noting that height is a trait that tends to be under- and/or overestimated, and since estimations of biomass and carbon for *M. flexuosa* were made with allometric equations that depended only on stem height, our results for this vegetation type should be interpreted carefully.

Following MOR, GF also held high carbon stocks per area, surpassing oil palm plantations, despite OP having approximately 74 times more individuals than GF (see Table 4). Furthermore, it is remarkable that these forests account for such great biomass and carbon stocks, as they don't have a continuous cover in the landscape and occur only on the borders of water streams and rivers in the savanna. Moreover, gallery forests had the highest tree and palm diversity, which translates into a high variation in architecture compared to other vegetation types. These results highlight the importance of assuring the conservation of species-rich vegetation types such as GF, not only because they contain a high species diversity, but also because they hold massive carbon stocks that contribute to climate mitigation, in addition to providing other ecosystem services. Nevertheless, there are vegetation types that despite being dominated by few species, they provide a great deal of these ecosystem services such as MOR forests, ground-flooded palm-swamps key for the sequestration of atmospheric carbon (Lähteenoja et al., 2009; Vegas-Vilarrúbia et al., 2010). In addition to carbon uptake, van der Hoek et al. (2019) proposed *M. flexuosa* as a hyperkeystone species, because it provides key plant resources (such as habitat, nest and food) to multiple different species (e.g., ca 940 vertebrate species, 19 of which are keystone species themselves).

4.3. Similar accumulation of biomass and carbon across natural and afforested vegetation types at the landscape level

Large-scale spatial patterns of carbon stocks across vegetation types can be predicted by a number of factors often related to taxonomic or functional diversity, as previously discussed. Knowledge on carbon stocks at the landscape level is relevant for the implementation of strategies that maximize co-benefits for climate change mitigation and tropical forest conservation, especially in agricultural landscapes. Our quantifications of biomass and carbon stocks in natural vegetation types (GF, in particular) yielded comparable values even though they have significantly smaller extension when compared to OP. For example, Kho & Jepsen (2015) estimated 156.9 $\pm$ 22.7 Mg C ha^{-1} of total aboveground carbon stock in undisturbed (primary) peatswamp forests in Malasya, and 58.7 $\pm$ 10.7 Mg C ha^{-1} in secondary peatswamp forest, which are similar to our estimates for GF (61.83 Mg C ha^{-1}) and MOR (99.12 Mg C ha^{-1}). Similarly, Kho and Jepsen (2015) estimated mature oil palm has between 20.0 and 50.0 Mg C ha^{-1} of aboveground carbon, which is a bit lower than our estimates of 78.1 Mg C ha^{-1} for 13-year OP plantation, probably due to differences in plantation age or palm density per area.

For savannas, we were only able estimate AGB, AGC, and BGC with values found in the literature (Anaya et al., 2009; San Jose et al., 1998) and not based on field inventory data from our study site. The literature suggests great variation of biomass and carbon stocks in the Orinoco's savanna. Rüegg (2017) conducted a study in oil palm plantations and savannas in an oil palm farm in Puerto Gaitan, Meta (Colombia), another location of the Orinoco, and found an aboveground biomass of ca. 2.98 Mg ha^{-1} in savannas, while the one estimated by Anaya et al. (2009) was 21 Mg ha^{-1}. The estimate of 0.31 Mg ha^{-1} belowground carbon reported by San Jose et al. (1998) is also way smaller than to those reported by Martín-López et al. (2022) for soil organic carbon stocks of 83.13 Mg ha^{-1} to a depth of 30 cm in Casanare flooded savannas (Colombia). In contrast, Rüegg (2017) reported a belowground carbon stock of 0.8 Mg ha^{-1} in savanna, closer to the estimate reported by San Jose et al. (1998). Seasonality in the savannas could play a role driving this variation. For example, Rao et al. (2001) reported 3.84 Mg dry mass ha^{-1} in the wet season, and 0.24 Mg ha^{-1} in the dry season. Different approaches used in estimating carbon stocks could potentially influence variability, where some studies include only plant root to estimate belowground stocks, while Martín-López et al. (2022) estimates are for soils as a whole (organic matter, roots, and mineral soils). Thus, we recommend undertaking thorough vegetation and soil surveys in the Orinoco savanna in proximity to OP plantations, as this will better inform biomass and carbon estimations at the landscape level in eastern Colombia. Systematic efforts to quantify biomass and carbon stocks both above- and belowground, and at multiple scales in the Orinoco savanna are needed.

We found that OP plantations had the largest biomass and carbon stocks at the landscape level due to their large extension in the study site, although previous studies have shown that OP carbon stocks are variable and depend on ecosystem type and location (Carlson et al., 2012; Kho and Jepsen, 2015; Quezada et al., 2019; Zhao et al., 2022). In fact, most of the research on OP carbon stocks has been conducted in Southeast Asia, being fundamentally different from plantations in African and Neotropical regions (Kho and Jepsen, 2015). In Southeast Asia, oil palm aboveground carbon stocks can range from 17 – 69 ha^{-1} (Ziegler et al., 2012), comparable to our estimate of 19.56 Mg ha^{-1} in the oldest crops (OP Y1). OP plantations cover 559,583 ha in the Orinoco, making Colombia the fourth largest producer of this crop and its byproducts (Fedepalma, 2021). We estimate that a total of ca 10 million Mg of aboveground carbon could be stored in this afforested land (using the value of AGC per ha of OP Y1 as reference); in Southeast Asia, there is almost 17.5 Mha (million of hectares) (Meijaard et al., 2020) under production of oil palm, so the total amount of aboveground carbon in this region could be a minimum of ca. 297.5 million Mg.

In addition to afforestation of savannas when replaced with tree or palm plantations, historically, human-induced fires are a common and frequent practice in the Orinoquía region. These two types of landcover transformation which result in a loss of biodiversity, occur across the landscape in an interchangeable manner. Traditional landowners use fire to renew pastures for feeding cattle with fresh regrowth due to the low palatability and forage quality of adult grasses in addition to controlling woody plants (Romero-Ruiz et al., 2010). Although some plant species in this vegetation type have positive interactions with fire (e.g. increased germination rates) (Dairel and Fidelis, 2020), uncontrolled burning with short time intervals has negative effects on seed germination and viability, as it can promote the domination of fire-resistant species such as grasses (Zhou et al., 2013), resulting in a significant loss of species richness in neotropical savannas (Armenteras et al., 2021). At the same time, agricultural companies have taken over part of these heavily burned savannas over the past years, transforming them into mostly afforested lands with extensive monocultures such as rubber or oil palm plantations. For instance, almost all land use change associated to oil palm expansion area in Colombia that took place between 1990 and 2009 was on previous shrub land, savanna, and/or cropland (Geraldes-Castanheira et al., 2014). While oil palm plantations can offer benefits for climate regulation to some extent, this type of land use change is not comparable to the restoration or protection of lowland tropical forests, which is a pressing need in Colombia (Jimenez et al., 2022). Thus, agricultural plantations will only contribute to both climate regulation and biodiversity conservation if natural habitats such as GF and MOR are preserved in the landscape. Correspondingly, some companies have committed to the protection of existing forest land nearby agricultural land, implementing strategies such as "Reducing emissions from deforestation and forest degradation (REDD)", a world-wide framework that provides economic benefits to landowners that preserve forest cover. Biomass and carbon estimates like those provided by this study are scarce, but fundamental for implementing these types of initiatives.

REDD+ is largely implemented in several countries, as it provides a framework within which landowners can be compensated for leaving their forests untouched. Since 2017, Fedepalma and a number of palm companies have joined the Zero Deforestation in the Palm Oil Supply Chain Memorandum of Understanding, which aims to eradicate the effects of deforestation in this industry (Fedepalma, 2021). Above- and belowground biomass and carbon stocks estimations are of high importance to inform practices for companies when implementing No Deforestation commitments, especially in tropical secondary forests (Rosoman et al., 2017). Similarly, the High Carbon Stock (HCS) approach is a framework established to identify forest areas that need to be protected from degradation through an integrated land use approach. In general, HCS uses field data (i.e., levels of biomass, vegetation structure and composition) in combination with satellite images, to make HCS classifications that range from high density areas to open land (Rosoman et al., 2017). We recommend RSPO plantations to not only increase their participation in REDD, but also incorporate strategies such as HCS, since as of 2020, Fedepalma has focused on providing certifications based on HCVAs (High Conservation Value Areas) (Fedepalma, 2021). Thus, the results provided in this study may contribute to an improvement in above- and belowground biomass and carbon stock estimates, and an increase in field studies, which are all necessary for the successful implementation of these environmentally sound agricultural schemes.

Declaration of Competing Interest

The authors have declared no competing interests.

Data availability

Data will be made available on request.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.tfp.2023.100380.

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