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RESEARCH ARTICLE

# Net primary productivity and litter decomposition rates in two distinct Amazonian peatlands

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## Abstract

Measurements of net primary productivity (NPP) and litter decomposition from tropical peatlands are severely lacking, limiting our ability to parameterise and validate models of tropical peatland development and thereby make robust predictions of how these systems will respond to future environmental and climatic change. Here, we present total NPP (i.e., above- and below-ground) and decomposition data from two floristically and structurally distinct forested peatland sites within the Pastaza Marañón Foreland Basin, northern Peru, the largest tropical peatland area in Amazonia: (1) a palm (largely *Mauritia flexuosa*) dominated swamp forest and (2) a hardwood dominated swamp forest (known as 'pole forest', due to the abundance of thin-stemmed trees). Total NPP in the palm forest and hardwood-dominated forest (9.83 ± 1.43 and 7.34 ± 0.84 Mg C $ha^{-1}$ $year^{-1}$, respectively) was low compared with values reported for *terra firme* forest in the region (14.21–15.01 Mg C $ha^{-1}$ $year^{-1}$) and for tropical peatlands elsewhere (11.06 and 13.20 Mg C $ha^{-1}$ $year^{-1}$). Despite the similar total NPP of the two forest types, there were considerable differences in the distribution of NPP. Fine root NPP was seven times higher in the palm forest (4.56 ± 1.05 Mg C $ha^{-1}$ $year^{-1}$) than in the hardwood forest (0.61 ± 0.22 Mg C $ha^{-1}$ $year^{-1}$). Above-ground palm NPP, a frequently overlooked component, made large contributions to total NPP in the palm-dominated forest, accounting for 41% (14% in the hardwood-dominated forest). Conversely, *Mauritia flexuosa* litter decomposition rates were the same in both plots: highest for leaf material, followed by root and then stem material (21%, 77% and 86% of mass remaining after 1 year respectively for both plots). Our results suggest potential differences in these two peatland types' responses to climate and other environmental changes and will assist in future modelling studies of these systems.

G. C. Dargie and J. del Aguila-Pasquel should be considered joint first author.

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**KEYWORDS**
carbon, decomposition, *Mauritia flexuosa*, net primary productivity, palm swamp, peat, Peru, pole forest

## 1 | INTRODUCTION

Peatlands are among the Earth's most carbon-dense ecosystems (Page et al., 2011), thus, quantification of their carbon fluxes is essential to understanding the global carbon cycle (Loisel et al., 2021). Tropical peatlands are estimated to store 105 Pg of carbon (C) below-ground (Dargie et al., 2017), equivalent to the above-ground forest carbon stock of the entire Amazon basin and its contiguous forests (Mitchard et al., 2013). In recent decades, human-induced peatland destruction and degradation, mostly in Southeast Asia, has led to a decline in tropical peat carbon stocks (Miettinen et al., 2016, 2017). In Amazonia, the presence of extensive peatlands, particularly in Peru, has only come to light in the past 15 years (Draper et al., 2014; Hastie et al., 2022; Lähteenoja et al., 2009). So far, peatland degradation and disturbance have been limited there (Hastie et al., 2022). However, there is evidence that rates of peatland deforestation and degradation are increasing (Marcus et al., 2024); ongoing and future agricultural expansion, resource extraction, road-building and other infrastructure development may accelerate peat carbon loss further (Hastie et al., 2022; López Gonzales et al., 2020; Roucoux et al., 2017). In addition, Amazonian peatlands may be affected by 21st century climate change. For example, temperatures in Amazonia have increased by c. 0.7°C since the 1970s, precipitation appears to be declining in southern Amazonia and increasing in northern Amazonia (Marengo et al., 2018), extreme drought and flood events have increased throughout the region (Gloor et al., 2015), and parts of the Amazon are changing from a carbon sink to a carbon source (Gatti et al., 2021).

For Amazonian peatlands, changes in temperature and hydrology could affect peat accumulation because peat builds up under anaerobic conditions, that is, where waterlogging is near permanent, as these inhibit most microbial decomposers, allowing plant litter to accumulate over centuries to millennia. Increased dry season length or intensity may therefore increase peat decomposition via changes in water table level, leading to lower below-ground carbon stocks (Flores Llampazo et al., 2022; Young et al., 2023). Hydrology is also likely to affect vegetation composition and structure. Long-term lowering of the peatland water table may result in a change in species composition (Flores Llampazo et al., 2022), which in turn may result in an increase in above-ground biomass, if anaerobic conditions are reduced (Sousa et al., 2020). On the other hand, increased extreme flood events may lead to an increase in mortality events and a decrease in above-ground biomass (Flores Llampazo et al., 2022). Given the size of the peat carbon stock in Peruvian Amazonia, estimated at more than 5 Pg C (Hastie et al., 2022), the ongoing response of peatlands to human disturbance and climatic change is an important element of the changing carbon cycle in Amazonia.

Peat accumulation (or loss) primarily depends upon the balance between rates of plant litter production (i.e., the net primary productivity of the ecosystem) and organic matter loss through decomposition. For tropical peatlands, these rates are not well quantified. There is only one published study of the total net primary productivity (NPP) of a tropical peatland, from Micronesia (Chimner & Ewel, 2005), and data on litter and root productivity are available from just one peatland site within Peruvian Amazonia (Dezzeo et al., 2021; Hergoualc'h et al., 2023). Data on litter decomposition is available from five tropical peatland sites, in Peru (Dezzeo et al., 2021; Hergoualc'h et al., 2023), Micronesia (Chimner & Ewel, 2005; Ono et al., 2015), Malaysia (Yule & Gomez, 2009) and Panama (Hoyos-Santillan et al., 2015). NPP and decomposition data are not just of basic scientific value but are also crucial for quantitative peat accumulation simulation and forecasting (e.g., Kurnianto et al., 2015; Young et al., 2023).

Here, we address the knowledge gap by reporting NPP and decomposition data from two tropical peatland sites with contrasting vegetation, located in the Pastaza-Marañón Foreland Basin (PMFB) in northern Peruvian Amazonia. The PMFB peatlands are estimated to cover 43,600 $km^2$ and store a large proportion (4.1 Pg C) of the known lowland Amazonian peatland carbon stock (5 Pg C; Hastie et al., 2022). Of the major peatland ecosystems which have been identified in the PMFB, palm swamps dominated by the palm *Mauritia flexuosa*, known regionally as 'aguajales', are the most extensive, accounting for at least 75% of the peatland area (Draper et al., 2014; Hastie et al., 2022; Honorio Coronado et al., 2021). Owing to their large extent, palm swamps account for the largest proportion of the PMFB total peatland carbon stock (Draper et al., 2014; Hastie et al., 2022; Honorio Coronado et al., 2021), but the most carbon-dense peatlands known in the basin are hardwood tree-dominated swamp forests, known as pole forests, or 'varillales hidromórficos' (Draper et al., 2014; Hastie et al., 2022; Honorio Coronado et al., 2021) after the abundant thin-stemmed, often short-stature trees which characterise these forests (Draper et al., 2014; Lähteenoja & Page, 2011). Pole forest peatland covers only 11%–14% of the PMFB peatland area (Honorio Coronado et al., 2021), but yields the highest total carbon storage of any Amazonian forest, estimated at 1113 Mg C $ha^{-1}$ (compared to the c. 252 Mg C $ha^{-1}$ stored in the surrounding *terra firme* forests; Honorio Coronado et al., 2021), despite their relatively low above-ground biomass. This is owing to the tendency of pole forests to overlie deeper peat deposits.

We use *in situ* measurements of above-ground productivity and below-ground productivity of hardwood tree and arborescent palm species, and the results of litter bag experiments in two forest plots, a palm swamp peatland plot and a pole forest peatland plot, to estimate the net primary productivity and rates of

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decomposition in these two regionally important peatland forest types.

## 2 | MATERIALS AND METHODS

### 2.1 | Study sites

The two field sites in this study are both situated in the PMFB in northeast Peru and had pre-existing 0.5 ha permanent forest plots: plot NYO-03 in Nueva York (4.401° S, 74.271° W) and plot VEN-02 in Veinte de Enero (4.672° S, 73.819° W) (Figure 1). The climate of the region is tropical, ever-wet with mean annual temperatures and rainfall of 26°C and c. 3000 mm, respectively (Marengo, 1998).

Our site selection was based on ensuring we represented the most carbon-dense peatland type, pole forest peatland, and the most extensive peatland type, palm swamp peatland, in the PMFB, as well as the accessibility of the sites. Plot NYO-03 is located in an ombrotrophic pole forest peatland 3.5 km from the Tigre River, a black-water left-bank tributary of the Marañón. Pole forest peatlands are concentrated north of the Marañón River where the rivers appear to be relatively geomorphologically stable (Draper et al., 2014; Hastie et al., 2022; Honorio Coronado et al., 2021). Under these conditions of prolonged stability thick, domed peatlands have had time to develop (Draper et al., 2014; Lähteenoja & Page, 2011), with the oldest core recovered so far dating to 8650–8990 years Before Present at the base of the peat (Lähteenoja et al., 2012). The commonly domed structure of pole forest peatland areas means that they are predominantly rain-fed and, as a result, nutrient-depleted relative to minerotrophic swamps which, by contrast, can receive inputs of nutrients from rivers and ground water (Lähteenoja & Page, 2011). In plot NYO-03, the peat is 4.6 m thick; common tree species include *Pachira nitida*, *Platycarpum loretensis* and *Xylopia* sp. (Table S1). Plot NYO-03, for the remainder of the text, is referred to as the pole forest peatland plot.

Plot VEN-02 is located in a minerotrophic palm swamp peatland dominated by the arborescent palm *Mauritia flexuosa*, 2 km from the Yanayacu River, a black-water right-bank tributary of the Marañón River. Palm swamp peatlands are usually minerotrophic systems, that is, they receive water and nutrient inputs from a fluvial or groundwater source. Across the PMFB region, the peat underlying palm swamps is on average 1.6 m thick (Honorio Coronado et al., 2021) and is typically Mid- to Late Holocene in age at the base (Lähteenoja et al., 2012). Morphologically dynamic river systems, common in much of the PMFB, continuously rework their floodplains, which limits the age and thickness of peat deposits in the region south of the Marañón River (Draper et al., 2014; Lähteenoja et al., 2009). In plot VEN-02 the peat is 1.2 m thick. Although *Mauritia flexuosa* is by far the most abundant species, the palms *Socratea exorrhiza* and *Euterpe precatoria* are also common (Table S1). Plot VEN-02, for the remainder of the text, is referred to as the palm swamp peatland plot.

### 2.2 | Net primary productivity measurements

Methods for quantifying the components of forest NPP (tree stem, branch, canopy and root productivity) are well established and for consistency we followed the standardised methodology of the

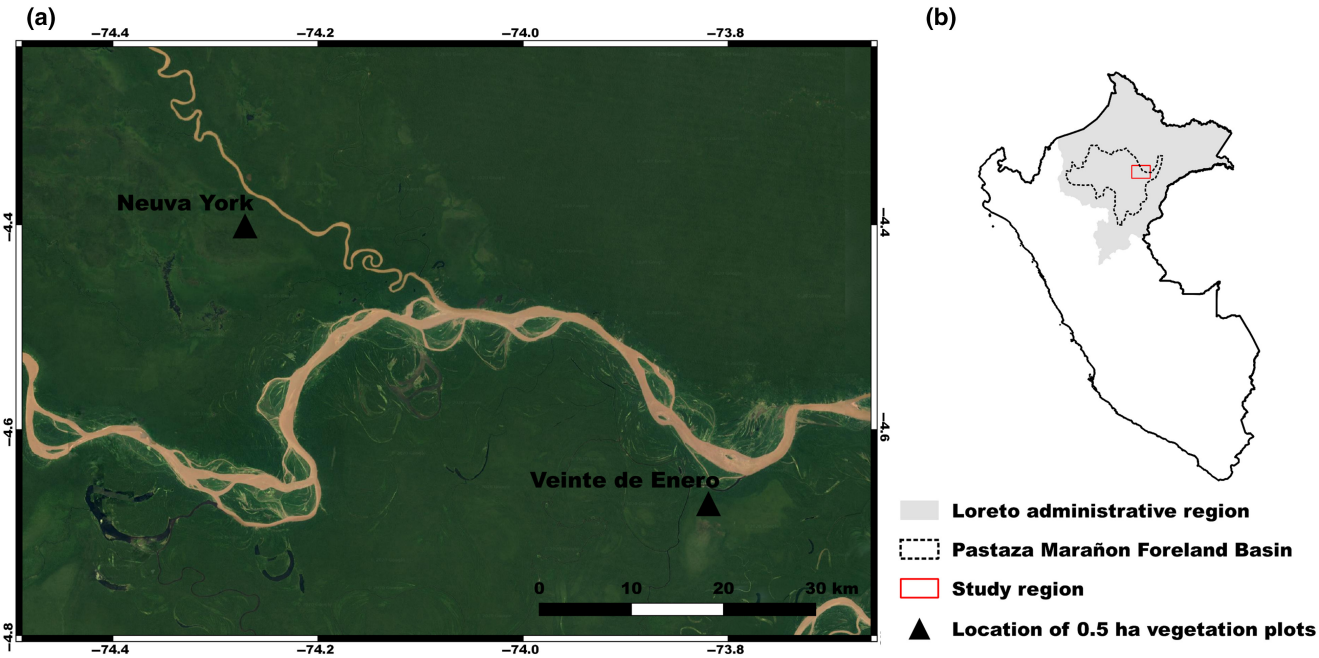


FIGURE 1 Fieldwork location maps showing: (a) the two 0.5 ha vegetation plots at the sites of Nueva York, a pole forest peatland, and Veinte de Enero, a palm swamp peatland, on Google Earth imagery; (b) the study region (i.e., the extent of (a), the Pastaza Marañón Foreland Basin and the administrative region of Loreto within Peru). Map created using the Free and Open Source QGIS. Map lines delineate study areas and do not necessarily depict accepted national boundaries.

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global ecosystem monitoring (GEM) network (Marthews et al., 2014) where possible. However, the GEM NPP methodology was developed for *terra firme* forests and adaptions were required to measure fine root NPP in peat swamp conditions; additionally, we developed our own method to measure above-ground palm NPP, which is not considered in the GEM methodology. We follow the convention that palms are flowering monocots in the family Areceaceae within the order Arecales. We define trees as plants with an elongated stem comprising secondary woody growth, which excludes palms. We report NPP in $Mg\,C\,ha^{-1}\,year^{-1}$. Total NPP is the sum of all the component mean NPP measurements, as described in Table S2, where calculations of the mean and standard error for each NPP component are also presented.

### 2.2.1 | Tree stem net primary productivity

Tree stem NPP (palms excluded) was measured using dendrometer bands (following Marthews et al., 2014). In each plot, every stem with a diameter at breast height (DBH) of ≥10 cm was fitted with a dendrometer band. The dendrometer bands were placed close to, but not on, the point of measurement (typically 1.3 m) for DBH measurements. After installation in March 2018, the dendrometer bands were left for 1 month to settle before the measurement period commenced. At time zero, the DBH of each stem was measured using a diameter tape, then over the course of 12 months, circumference growth was measured from the dendrometer band every 3 months using callipers. In order to convert increments in tree stem circumference to increments in tree stem NPP, the above-ground biomass (AGB; kg) of each tree was estimated for each 3-month interval using the following equation (from Chave et al., 2014):

$$AGB = 0.0673 \times WD \times D^2 \times H^{0.976}, \quad (1)$$

where *WD* is wood density (g $cm^3$), *D* is tree stem diameter (cm), and *H* is tree height (m). WD was obtained from the Zanne et al. (2009) wood density database. Ideally, the mean species WD from the database was used; where species-level WD was not available, the genus, family or plot mean WD was used. Tree diameter was calculated from the dendrometer band-derived tree circumference. Tree height was not available for all trees, and so was estimated for all trees using modelled tree height from an asymptotic exponential model relating tree diameter to tree height fitted to pooled data from the palm swamp peatland plot and the pole forest peatland plot. The data were pooled, because the model using the 27 tree measurements from the palm swamp peatland plot did not converge. Tree heights were measured using a Nikon laser rangefinder (manufacturer: Nikon; model: Forestry Pro II Rangefinder) in 2009 in the palm swamp peatland plot (27 trees) and in 2019 in the pole forest peatland plot (52 trees). The model of best fit (residual standard error: 4.68 m; degrees of freedom: 76) for predicting tree height (*H*; m) from stem diameter (*D*; mm) was as follows:

$$H = 28.9298 - 47.2647 \times \exp^{(-0.0081 \times D)}. \quad (2)$$

The stand NPP for each census was then estimated as the sum of individual tree increments of all surviving trees between one census and the next:

$$\text{Stand NPP} = \Sigma\left(\text{individual AGB}_{\text{census } n+1} - \text{individual AGB}_{\text{census } n}\right). \quad (3)$$

Some dendrometer bands were damaged (largely owing to termites). The proportion of dendrometer bands which were damaged were 23% for the pole forest peatland plot and 16% for the palm-dominated peatland plot. A gap in the dendrometer band data for a tree was filled by interpolation, using data from previous and subsequent censuses or extrapolation if there were gaps at the beginning or end of the sequence of censuses. In the pole forest peatland plot there were individuals for which no growth measurement was available (3% of measurements). Therefore, a plot-level species-, genus- or family-DBH size class mean growth rate was used, as long as there were at least five measurements from which to calculate the mean. Where the number of measurements were fewer than five, a plot-level DBH size class mean growth rate was used (<1% of measurements). The DBH size classes were 10–19.9, 20–29.9, 30–39.9 and ≥40 cm. We assumed a carbon content of 45.6% of dry biomass, based on a mean value for tropical tree stems (Martin et al., 2018).

### 2.2.2 | Palm stem net primary productivity

At the time of field work, we were not aware of any study which measured palm stem NPP and therefore developed our own methodology. Given that mature palms do not exhibit secondary (diameter) growth, we estimated palm stem NPP by measuring changes in stem height over time, from the ground surface to the base of the lowest living frond. Members of the field team, in the year 2018, climbed the palm stems and measured stem height directly using a tape measure for all stems but one in the pole forest peatland plot ($n = 37$), and for a subsample of stems in the palm swamp peatland plot ($n = 46$). The physical nature of climbing the palms, which could only be done in dry weather, limited the number of individuals which could be physically measured for total palm height. The same palms were then remeasured in 2019 for the pole forest peatland plot and in 2020 for the palm swamp peatland plot.

To estimate the unmeasured palm heights for the year 2020 in the palm swamp peatland plot ($n = 209$), we used a regression between palm height data measured in the palm swamp peatland in 2019 using a Nikon laser rangefinder (manufacturer: Nikon; model: Forestry Pro II Rangefinder) and the 2020 directly measured height data ($p < .001$, $R^2 = .89$). To obtain estimates for 2018, we extrapolated back from the 2020 estimated heights using the mean palm stem height growth rate (0.06 m $year^{-1}$) of the directly measured palms. In the pole forest peatland plot, only one palm was not measured. For this, we estimated its height in 2019 using a regression between palm heights measured by laser in the pole forest peatland plot in 2019 and the 2019 directly measured palm heights ($p < .001$, $R^2 = .56$). To obtain an estimate for its height in

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2018, we extrapolated back from the 2019 height estimate using the mean palm stem height growth rate of the directly measured palms (0.13 m year$^{-1}$).

The AGB (kg) of each individual palm was then estimated using genus-specific palm allometric equations from Goodman et al. (2013), as follows:

$$\ln\left(\mathrm{AGB}_{\mathrm{Mauritia}}\right) = 2.4647 + (1.3777 \times \ln(H)), \quad (4)$$

$$\mathrm{AGB}_{\mathrm{Mauritiella}} = 2.8662 \times H, \quad (5)$$

$$\ln\left(\mathrm{AGB}_{\mathrm{Oenocarpus}}\right) = 4.5496 + (0.1387 \times H), \quad (6)$$

$$\ln\left(\mathrm{AGB}_{\mathrm{Socratea}}\right) = 3.7965 + \left(1.0029 \times \left(\ln\left(D^2 H\right)\right)\right), \quad (7)$$

$$\mathrm{AGB}_{\mathrm{Euterpe}} = -108.81 + (13.589 \times H), \quad (8)$$

where AGB is the above-ground biomass (kg) of the five genera present across the two plots, $H$ is the stem height of the palm (m) as measured in the field, and $D$ is the diameter at breast height (cm). For *Socratea* individuals ($n = 49$), the only genus for which diameter is a parameter in the AGB allometry, DBH was interpolated from DBH measurements made during forest inventories in 2017 and 2019, following the RAINFOR field protocol (Phillips et al., 2021). We assumed a carbon content 48.1% of dry biomass, based on the mean value measured for Amazonian palm stem tissue (Goodman et al., 2013).

To estimate the uncertainty associated with our palm stem NPP estimate we used a resampling approach. We estimated palm AGB increments, one for each stem, using resampled AGB increment data, to estimate palm stem NPP. We repeated the resampling 1000 times and calculated the standard error of palm NPP. This was necessary as we only have palm stem NPP estimated from one census interval.

### 2.2.3 | Branch net primary productivity

Branch shedding, which is assumed to be equal to branch NPP (Malhi et al., 2009), was measured by collecting all woody debris with a diameter ≥2 cm along four 1 × 100 m transects running parallel to the 0.5 ha plot boundaries (Marthews et al., 2014). Collections were made every 3 months (Marthews et al., 2014) and the woody debris was sorted into five classes of degree of decomposition and then into three diameter class sizes (2–5, >5–10 and >10 cm) (Baker & Chao, 2011). For each transect, the total fresh mass for each decomposition-diameter class was weighed in the field and a subsample was taken. Subsamples were weighed fresh and then dried to constant mass in an oven and weighed again to obtain the gravimetric water content. This water content of the subsample was used to estimate the total dry mass from the total fresh mass. We assumed a carbon content of 45.6% of dry biomass (Martin et al., 2018).

### 2.2.4 | Tree litter productivity

Tree litter production, which is assumed to be equal to canopy NPP (Malhi et al., 2009), was measured monthly. In both plots, a 0.25 m$^2$ litter trap was installed in the centre of 10 of the 15 subplots at a height of 1 m above the forest floor (Marthews et al., 2014). The monthly litter collections were dried to constant mass in an oven, separated into the categories of leaves, woody material, reproductive parts and miscellaneous material, then weighed. We assumed a carbon content 48.8% of dry biomass, based on a mean value for Amazonian tree litter (Hättenschwiler et al., 2008).

### 2.2.5 | Palm litter productivity

For the palm species, the large size of the palm fronds precluded the use of litter traps to measure this component of litter production. Palm litter production rates, assumed to be equal to the palm canopy NPP, were therefore measured using the same ground transects as were used for branch NPP. Palm litter was collected every 3 months and separated into the categories of petiole, leaflet and inflorescence (including any fruit). The total fresh mass of each category was weighed in the field and a subsample was taken to estimate the water content of each category for each transect. Subsamples were weighed fresh and then dried to constant mass in an oven and weighed again to obtain the gravimetric water content. We assumed a carbon content 51.2% of dry biomass, based on a mean value for Amazonian palm leaf tissue (Goodman et al., 2013).

### 2.2.6 | Root productivity

Fine root productivity was measured over 3-month intervals (following Marthews et al., 2014) from April 2018 to April 2019. In each plot, eight mesh cores measuring 6.5 cm in diameter and 50 cm in length, made up of a 15 mm outer rigid mesh lined with 2 mm flexible and root-penetrable mesh, were filled with root-free peat and installed in the ground at the eight interior intersections of the 15 subplots. Our cores were smaller in diameter and longer in length than the standard GEM methodology (Marthews et al., 2014): we used a smaller diameter to reduce disturbance of the peat profile (Laiho et al., 2014) and a longer depth to ensure we met the requirements of peat development models (Kurnianto et al., 2015). The root-free peat, which filled the cores, came from just outside each respective plot to ensure that the peat within the core was of a similar nutrient status to that of the surrounding peat. Roots were handpicked from the peat by a team of people over several days until no roots were visible in the peat. Once filled with root-free peat, the cores were wrapped and frozen to prevent the peat from running out of the core during transportation to the field. Every 3 months, the cores were replaced with new cores.

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The cores retrieved from the field were sieved using a 0.14 mm mesh sieve to recover all roots which had grown into the core over the 3-month period. The roots were then dried to constant mass in an oven before being weighed. The mass of carbon we assumed to be 45.9% of dry biomass for the pole forest plot and 48.3% for the palm-dominated plot, which is the weighted mean of tropical hardwood trees (45.6% C for tropical tree stem tissue; Martin et al., 2018) and palms (48.8% C for Amazonian palm root tissue; Goodman et al., 2013) in each plot.

The NPP of large structural tree roots, referred to here as coarse roots, are not captured by the root ingrowth core method. The logistical difficulty of measuring the NPP of such roots means that their NPP is usually estimated. Following Malhi et al. (2009), we assumed that the tree coarse root NPP was 21% of tree stem NPP. We assumed a carbon content 45.6% of dry biomass (Martin et al., 2018). Palm coarse root NPP was calculated as the difference between estimated below-ground biomass (BGB) at the start and end of the census period. The BGB (kg) of each individual palm was estimated using allometric equations from Goodman et al. (2013), as follows:

$$\ln\left(\mathrm{BGB}_{\mathrm{Mauritia}}\right) = -0.3688 + (2.0106 \times \ln(H)), \quad (9)$$

$$\ln\left(\mathrm{BGB}_{\mathrm{Mauritiella}}\right) = 1.0945 + (0.11086 \times H), \quad (10)$$

where $H$ is the height of the palm stem (m). In plot VEN 02, there were also *Socratea exorrhiza*, *Euterpe precatoria* and *Oenocarpus mapora* individuals. However, Goodman et al. (2013) do not present BGB allometric equations for these genera. Therefore, we applied the *Mauritia* BGB allometric equation to *Oenocarpus mapora* individuals and the *Mauritiella* BGB allometric equation to *Socratea exorrhiza* and *Euterpe precatoria* individuals, based on morphological similarities of these genera. We assumed a carbon content 48.8% of dry biomass (Goodman et al., 2013). The BGB palm allometric equations of Goodman et al. (2013) are not coarse root specific. However, the description of the destructive sampling behind these allometric equations (Freitas et al., 2006) suggests that it was only the vertical anchoring roots directly below the palm that were sampled, rather than horizontally growing roots. Therefore, we do not believe we have doubled accounted the root NPP captured in our root ingrowth cores. To estimate the uncertainty associated with our estimate of palm coarse NPP we used the same resampling approach described for palm stem NPP uncertainty.

## 2.3 | Litter decomposition

Litter bags were installed in each plot to measure decomposition rates. For both plots, mesh bags (material: polypropylene; dimensions: 26 cm × 30 cm; mesh size: 1.5 mm) were filled with either dried leaf (ca. 5 g), stem (ca. 5 g) or root (ca. 4 g) material collected from specimens of *Mauritia flexuosa* only. While this does not give us insight into whether tree species litter would follow a similar decomposition pathway, it does allow a direct comparison of decomposition rates between the ombrotrophic pole forest and minerotrophic palm swamp peatland sites. Note that the dried litter came from fresh rather than senesced leaves, and wood and roots from living trees, due to difficulty in collecting a sufficient quantity of dead but undecomposed material. 10 replicates of each litter type were placed in 10 different subplots within each plot. Decomposition bags containing leaf or stem material were left at the surface while decomposition bags containing roots were buried at a depth of 30 cm below the peat surface (a common treatment in decomposition studies, for example, Chimner & Ewel, 2005; Dezzeo et al., 2021; Hoyos-Santillan et al., 2015; Ono et al., 2015), to simulate where this litter category would typically enter the peat profile under natural conditions. A depth of 30 cm was chosen in order to be compatible with peat development models which have been adapted for tropical settings. One bag was recovered from each of the 10 locations after periods of approximately 1, 2, 3, 4, 6, 10 and 12 months. After collection, the bags were dried to constant mass in an oven and the content weighed.

In the statistical analysis, we treat the stem, branch and root litter independently to obtain the most robust decomposition model for each (see Table 1). For all three litter types, we used non-linear least squares analyses, with forest plot fitted as a factor. For both stem and root litter, we weighted the models to reduce the heteroscedasticity (see Table 1). To assess whether decomposition patterns were different between the palm swamp peatland and the pole forest peatland for the three litter types, we also fitted a nested model,

**TABLE 1** Model parameters and applied weightings for the model of best fit describing litter decomposition (the fraction of initial mass remaining) as a function of time (number of days; represented by ***x***), for each litter type (stem, roots and leaves) in plots NYO-03, a pole forest peatland, and VEN-02, a palm swamp peatland.

| | | Parameter values (±SE) for the model form: $y = a + (b - a) \times e^{(-e^{c} \times x)}$ | | | |
|---|---|---|---|---|---|
| **Litter type** | **Site** | ***a*** | ***b*** | ***c*** | **Weighting applied** |
| Stem | Pole forest peatland | 0.844 ± 0.038*** | 0.992 ± 0.007*** | −5.025 ± 0.453*** | $1/x^2$ |
| | Palm swamp peatland | 0.862 ± 0.018*** | 1.007 ± 0.015*** | −4.257 ± 0.328*** | $1/x^2$ |
| Roots | Both | 0.759 ± 0.028*** | 1.024 ± 0.012*** | −4.584 ± 0.232*** | $1/x^2$ |
| Leaves | Both | 0.150 ± 0.054** | 0.948 ± 0.045*** | −4.949 ± 0.199*** | NA |

*Note*: For root and leaf litter, the inclusion of forest plot as factor was non-significant ($p > .05$); therefore, we present a single model for both plots. All model parameters shown are significant; ** denotes a $p$-value <.01, *** denotes a $p$-value <.001.

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where plot was not fitted as a factor, and compared the nested models to the originals using ANOVA. If models were not significantly different ($p > .05$) we selected the simpler model. Model fit was assessed using residual quantile-quantile plots, residuals plotted against fitted values, and histograms of the residuals. From the models of best fit, we predict the mass remaining after 1 year for each litter type and the 95% confidence intervals. Confidence intervals were calculated using the 'predFit' function of the R package investr (Greenwell & Schubert Kabban, 2014).

### 2.4 | Data processing and analysis software

All analysis was carried out in R (R Core Team, 2022). The tidyr (Wickham, 2001), dplyr (Wickham et al., 2021), lubridate (Grolemund & Wickham, 2011), nls2 (Grothendieck, 2013) and investr (Greenwell & Schubert Kabban, 2014) packages were used in data processing and analysis.

## 3 | RESULTS

### 3.1 | Net primary productivity

Total mean (± SE) NPP was similar in the two peatland plots: $9.83 \pm 1.43$ Mg C $ha^{-1} year^{-1}$ in the palm swamp peatland and $7.34 \pm 0.84$ Mg C $ha^{-1} year^{-1}$ in the pole forest peatland. This similarity masks considerable differences between the different NPP components for the two plots (Figure 2) and their proportional contribution to the total NPP (Table 2). Given the different vegetation composition of the two plots, it was to be expected that they would differ in terms of the proportional contribution of the different plant components to total NPP. The low stem, litter and branch NPP in the palm swamp peatland plot reflects the lower tree stem numbers in the plot (55 surviving stems vs. 375 in the pole forest peatland). The palm swamp peatland plot had a higher number of palm individuals than the pole forest peatland plot (275 vs. 38 surviving individuals) and therefore palm NPP, both in absolute values and proportional contribution, was much higher in the palm swamp.

The palm swamp peatland plot fine root NPP was $4.56 \pm 1.05$ Mg C $ha^{-1} year^{-1}$, which was much higher than the fine root NPP of the pole forest peatland plot at $0.61 \pm 0.22$ Mg C $ha^{-1} year^{-1}$. In the palm swamp, roots (fine and coarse root NPP combined) were the largest contributor (49%) to total NPP, followed by palm above-ground NPP (palm stem and palm litter NPP combined; 41%), with hardwood above-ground NPP (tree branch, stem and litter NPP combined) contributing just 10% (Table 2). In the pole forest peatland, however, hardwood above-ground NPP contributed 74% of total NPP, mostly through litter (56% of total NPP). Roots and palms contributed just 13% and 14% to total NPP respectively (Table 2).

The two forest types appear aseasonal in terms of NPP. There are no clear seasonal or other temporal patterns in the tree litter NPP data from the palm swamp peatland plot, nor in the quarterly measurements of tree stem NPP, branch NPP, palm litter NPP and root NPP from both sites (Figure 3; Figures S2–S5). There are no clear season patterns in the pole forest peatland plot except possibly for tree litter NPP, which was highest in July to October 2018 when the water table was at its lowest level over the measurement period, and in March and April 2019 following a short-lived rise in water table (Figure 3; Figures S2–S5).

### 3.2 | Litter decomposition

Leaf litter decomposed at the fastest rate in both the palm and pole forest peatland plots, with 21% (95% CI: 16%–26%) mass remaining after 1 year for both plots (Figure 4; Table 4). This was followed by much slower rates for stem material, with 77% (95% CI: 72%–81%) mass remaining after 1 year for both plots (Figure 4; Table 4). The slowest rates were for root litter, with 86% (95% CI pole forest peatland: 82%–89%; 95% CI palm swamp peatland: 83%–90%) of mass remaining after 1 year for both plots. For stem litter, decomposition was initially significantly faster in the pole forest peatland plot than in palm swamp peatland plot, driven by modest differences in the first 6 months, shown by the original model being a significantly better fit than the nested model ($p < .001$). Root and leaf litter decomposition patterns were not different between the palm swamp and the pole forest peatlands, shown by there being no significant difference between the original and nested models (roots: $p = .93$; leaves: $p = .95$).

## 4 | DISCUSSION

### 4.1 | Net primary productivity

Our results underline the importance of considering the contribution of palms to productivity and carbon cycling in peatlands. Few previous studies have considered the NPP of palm species outside of plantation agriculture settings (Avalos et al., 2022; Bocko et al., 2023; Goodman et al., 2013) and this omission may lead to considerable underestimations of forest NPP, particularly in tropical peatland settings where palms frequently dominate the canopy (Bocko et al., 2023). We found NPP in the palm swamp peatland ($9.83 \pm 1.43$ Mg C $ha^{-1} year^{-1}$) to be non-significantly different to NPP in the pole forest peatland ($7.34 \pm 0.84$ Mg C $ha^{-1} year^{-1}$). It is likely that palms account for the majority of the palm swamp peatland total NPP; when we combine palm above-ground NPP (41% of total NPP) with root NPP (49% of total NPP), the majority of which is likely palm roots, it seems that palms could account for more than >80% of total NPP. Even in the pole forest peatland palm above-ground NPP accounted for 14% of total NPP, still a significant proportion of NPP even though this site was dominated by hardwood trees.

At a regional level our results suggest that Peruvian lowland peatlands are substantially less productive than the region's *terra firme* forests, with values between 14.21 and 15.01 Mg C $ha^{-1} year^{-1}$

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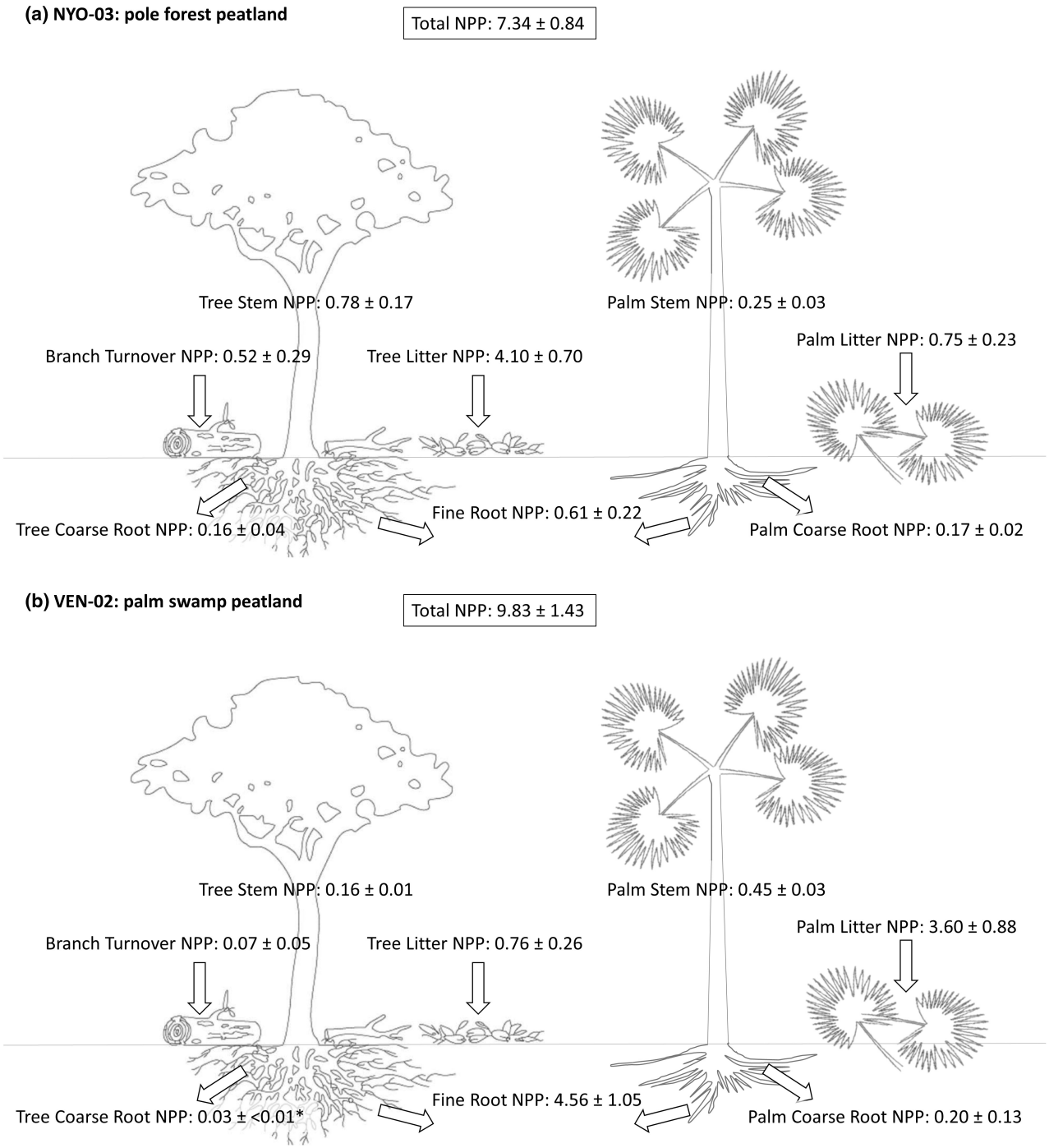


**FIGURE 2** Net primary productivity for (a) a pole forest ombrotrophic peatland (NYO-03) and (b) a palm swamp minerotrophic peatland (VEN-02) in the Pastaza Marañón Foreland Basin. Values of the mean and standard error are presented in Mg C $ha^{-1}$ $year^{-1}$. *Tree coarse root NPP standard error for plot VEN-02 is equal to 0.003.

reported for Peruvian lowland *terra firme* forests (del Aguila-Pasquel et al., 2014; Malhi et al., 2014; Table 3), although it should be noted that these *terra firme* values are higher than in many other tropical forest settings, which are typically <10 Mg C $ha^{-1}$ $year^{-1}$ (Clark et al., 2001). The comparatively low productivity of the peatlands is consistent with the anaerobic soil conditions, which are known to adversely affect tree photosynthetic rate and respiration efficiency (Kozlowski, 2002). These peatland sites also have much lower stem productivity than nearby seasonally flooded forests on alluvial floodplains (average of 8.5 Mg C $ha^{-1}$ $year^{-1}$; Nebel et al., 2001) which, despite annual flooding, can have a higher NPP than the surrounding *terra firme* forests. It has been suggested that the location of the seasonally flooded forests, on alluvial floodplains inundated by white-water rivers with relatively high nutrient levels, explains this high productivity (Malhi et al., 2004; Nebel et al., 2001). In the PMFB peatlands, however, the near year-round waterlogged

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**TABLE 2** Absolute and proportional contribution of different net primary productivity (NPP) components to total NPP from this study and from studies in the literature which report the breakdown of total NPP for Peruvian forests and peatland forests in other tropical regions.

| | | | | NPP (Mg C ha$^{-1}$year$^{-1}$) | | | | | Proportional contribution to total NPP (%) | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Forest type | Region | Country | Plot code | Tree litter | Tree woody AG | Total roots | Palm AG | Total | Tree litter | Tree woody AG | Total roots | Palm AG | Source |
| Pole forest peatland | Loreto | Peru | NYO-03 | 4.10 | 1.30 | 0.94 | 1.00 | 7.34 | 56 | 18 | 13 | 14 | This study |
| Palm swamp peatland | Loreto | Peru | VEN-02 | 0.76 | 0.23 | 4.79 | 4.05 | 9.83 | 8 | 2 | 49 | 41 | This study |
| Cloud forest-Upper montane | Cuzco | Peru | WAY | 1.92 | 1.70 | 1.48 | NA | 5.09 | 38 | 33 | 29 | NA | Girardin et al. (2010) |
| Cloud forest-Upper montane | Cuzco | Peru | TU3 | 1.19 | 1.40 | 1.52 | NA | 4.11 | 29 | 34 | 37 | NA | Girardin et al. (2010) |
| Cloud forest-Upper montane | Cuzco | Peru | TU4 | 1.83 | 2.17 | 1.96 | NA | 5.98 | 31 | 36 | 33 | NA | Girardin et al. (2010) |
| Cloud forest-Lower montane | Cuzco | Peru | TU7 | 1.44 | 1.09 | 1.96 | NA | 4.50 | 32 | 24 | 44 | NA | Girardin et al. (2010) |
| Cloud forest-Lower montane | Cuzco | Peru | TU8 | 1.44 | 1.09 | 3.43 | NA | 5.97 | 24 | 18 | 57 | NA | Girardin et al. (2010) |
| Cloud forest-Lower montane | Cuzco | Peru | SPD | 2.76 | 2.22 | 2.04 | NA | 7.06 | 39 | 31 | 29 | NA | Girardin et al. (2010) |
| Premontane Tropical Forest | Cuzco | Peru | TON | 2.49 | 1.84 | 2.70 | NA | 7.07 | 35 | 26 | 38 | NA | Girardin et al. (2010) |
| *Terra firme* | Madre de Dios | Peru | TAM05 | 5.39 | 3.36 | 5.05 | 0.22 | 15.01 | 36 | 22 | 34 | 1 | Malhi et al. (2014) |
| *Terra firme*. Palms make up >30% of stems. | Madre de Dios | Peru | TAM06 | 4.94 | 2.99 | 2.63 | 2.81 | 14.21 | 35 | 21 | 19 | 20 | Malhi et al. (2014) |
| *Terra firme* | Loreto | Peru | Alp-A | 4.20 | 4.87 | 3.71 | NA | 14.14 | 30 | 34 | 26 | NA | del Aguila-Pasquel et al. (2013) |
| Seasonally flooded/*terra firme* mix | Loreto | Peru | Alp-C | 5.66 | 3.74 | 4.05 | NA | 14.41 | 39 | 26 | 28 | NA | del Aguila-Pasquel et al. (2013) |
| Hardwood dominated wetland | Western Pacific | Micronesia | Yela | 7.55 | 2.83 | 3.00 | NA | 11.37 | 66 | 25 | 26 | NA | Chimner and Ewel (2005) |
| Hardwood dominated peatland | Western Pacific | Micronesia | Yewak | 7.45 | 3.70 | 3.00 | NA | 11.06 | 67 | 33 | 27 | NA | Chimner and Ewel (2005) |

*Note*: For comparability with other studies some components presented in Figure 2 have been grouped together; branch and stem NPP are grouped as 'Tree Woody AG' (AG = above-ground), coarse (both palm and tree) and fine root NPP are grouped as 'Total Roots', and palm litter and palm stem NPP are grouped as 'Palm AG'.

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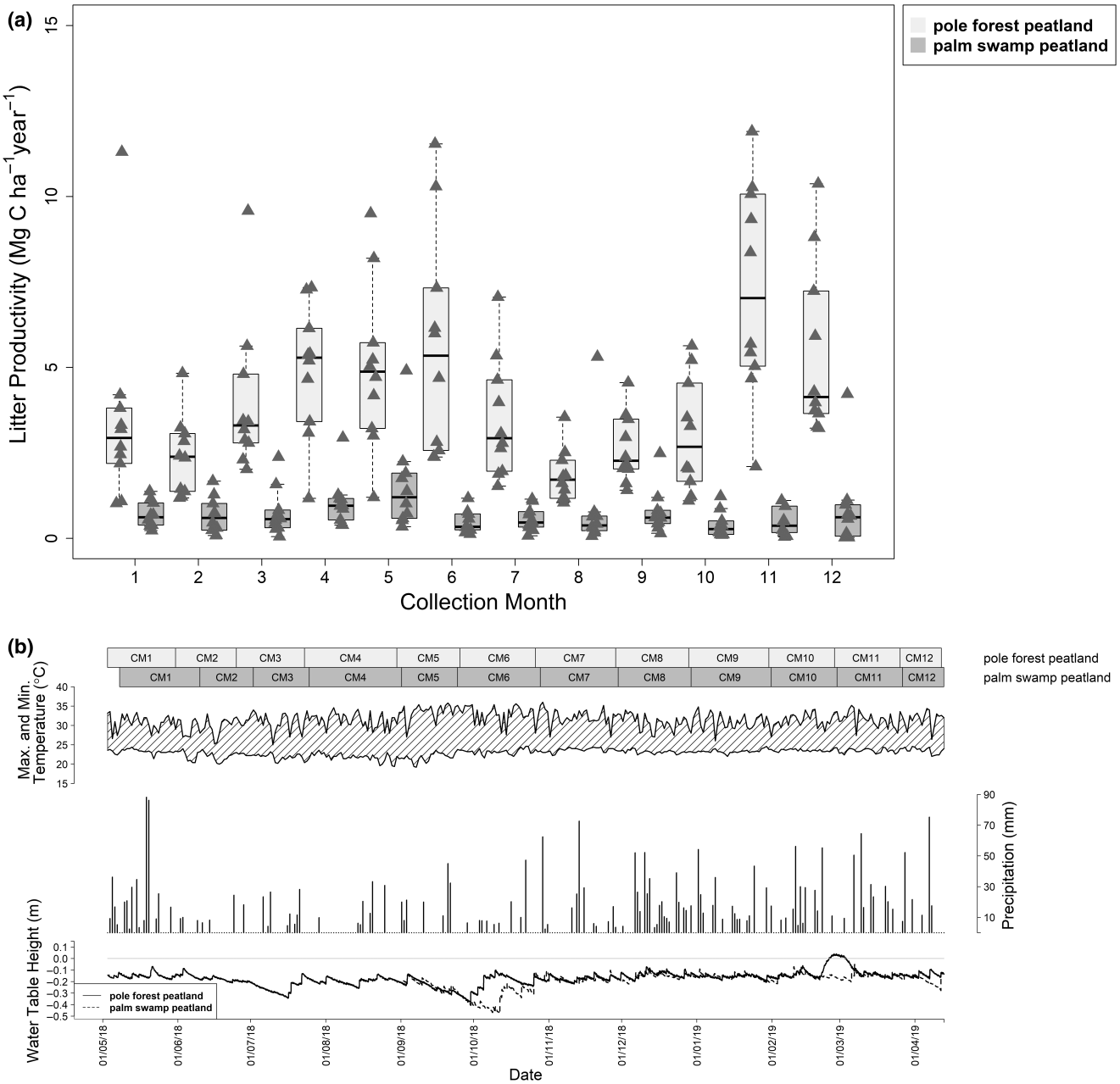


**FIGURE 3** (a) Boxplot and stripchart (triangles) of total litter productivity for the pole forest peatland plot (light grey) and palm swamp peatland plot (dark grey) across the 12 one-month census periods (starting in May 2018). The box represents the interquartile range, and the middle line represents the median and the whiskers represent the minimum and maximum values. (b) Minimum and maximum daily air temperature time series (top panel), daily precipitation time series (middle panel) and *in situ* water table time series (with the peatland surface represented by the grey solid line) recorded in the pole forest peatland plot (solid line) and palm swamp peatland plot (dashed line; time series available only since 09/2018), during the 12 collection months (CM) of the two plots, shown at the top of the figure. The air temperature and precipitation times series were recorded at Puerto Almendra meteorological station (3.829° S, 73.377° W; ca. 100–120 km from the two plots; data available from the Servicio Nacional de Meteorología e Hidrología del Perú: http S://www.senamhi.gob.pe/?p=estaciones).

conditions may counteract any productivity benefit that comes from any influx of nutrients in floodwaters. Furthermore, as is the case for our sites, many PMFB peatlands are either ombrotrophic (the pole forest peatland plot) or are likely only flooded by nutrient-poor black-water rivers (the palm swamp peatland plot) and so are unlikely to receive large fluxes of nutrients from flooding. In fact, PMFB peatlands have similar NPP values to montane forests: the NPP of the pole forest peatland plot is comparable to NPP values reported for lower montane cloud forests (Girardin et al., 2010; Table 3). Like the PMFB peatlands, cloud forests often have high soil moisture content and low pH, but unlike the lowland peatlands, they are also subjected to low temperatures (Bruijnzeel & Veneklaas, 1998), which is thought to limit soil N mineralisation and therefore N availability (Fisher et al., 2013).

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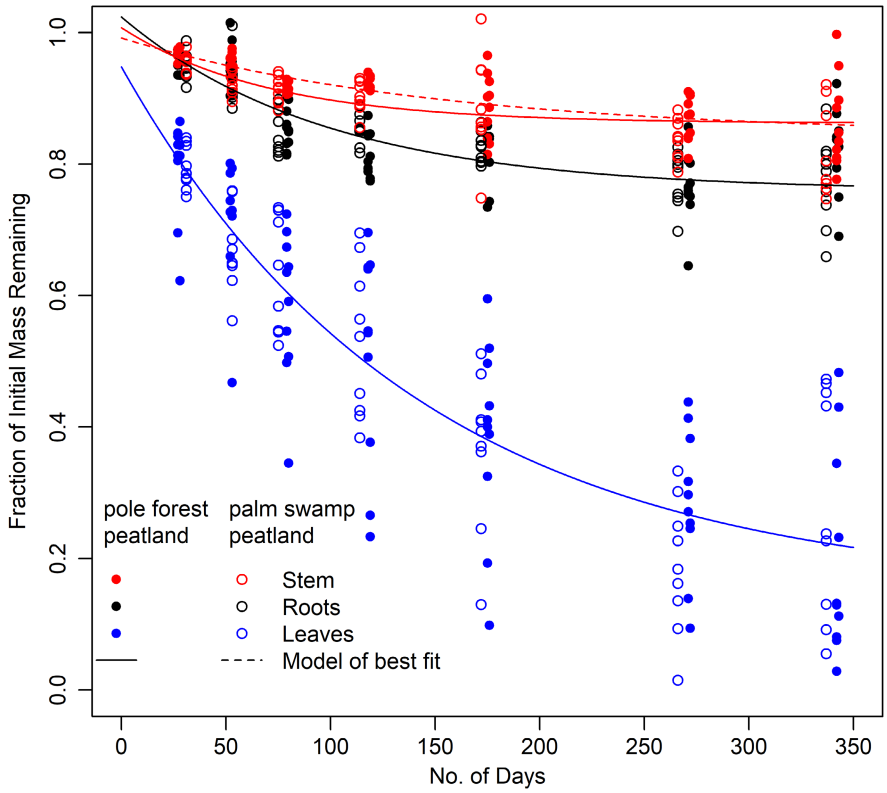


**FIGURE 4** *Mauritia flexuosa* litter decomposition through time. The fraction of the initial mass remaining plotted against the number of days the decomposition bags were left in the field for stem, root and leaf litter in the pole forest peatland plot and the palm swamp peatland plot. The models of best fit from non-linear least squares regression analyses (described in Table 1) are also shown. For root and leaf litter, the inclusion of forest plot as a factor was non-significant ($p > .05$) and therefore the lines represent decomposition through time for both plots. However, for stem litter, the inclusion of forest plot as a factor was significant ($p < .05$). Therefore, a model of best fit for the pole forest peatland and palm swamp peatland plots are shown separately.

Both the palm swamp and pole forest peatland plots had a total NPP lower than the total NPP estimates reported in the literature for peatlands in Indonesia (13.2 Mg C $ha^{-1}$ $year^{-1}$; Basuki et al., 2019) and Micronesia (11.06 Mg C $ha^{-1}$ $year^{-1}$; Chimner & Ewel, 2005; Table 3). Tree stem NPP in the pole forest peatland plot was considerably lower than stem NPP in Micronesian peatlands (Chimner & Ewel, 2005). In our search of the literature, we did not find a study which reported branch NPP for another tropical peatland. Drier conditions at the Indonesian site may explain the higher NPP compared to PMFB peatlands. The water table at the Indonesian site was reported to be on average 40 cm below the peatland surface (Basuki et al., 2019), similar to the lowest water table depth recorded within our plots (Figure 3). Increased soil aeration could increase productivity through an increase in root respiration, as well as litter mineralisation, potentially increasing plant nutrient availability. This, however, cannot explain the difference between NPP at the PMFB peatlands and the Micronesian peatland site since, like our sites, the authors report a mean water table level close to the surface (Chimner & Ewel, 2005).

Within the PMFB, Hergoualc'h et al. (2023) report litter NPP for another *Mauritia flexuosa*-dominated palm swamp peatland, Quistococha. Comparing our result to theirs, it appears that variation in the density of palms determines variation in NPP among different palm swamps in the region. Quistococha has 170 *Mauritia flexuosa* stems and 1846 tree stems per hectare (Hergoualc'h et al., 2023), while our palm swamp peatland plot has density of 548 palm (358 *Mauritia flexuosa*) stems and 118 tree stems per hectare. Therefore, it is not surprising that Hergoualc'h et al. (2023) found tree litter NPP to be almost five times higher at Quistococha than tree litter NPP in our palm swamp peatland. Furthermore, *Mauritia flexuosa* litter NPP was an order of magnitude lower than tree litter NPP at Quistococha (Hergoualc'h et al., 2023), whereas in our palm swamp peatland palm litter NPP is over four times as high as the tree litter NPP. The high palm stem density of our plot suggests that the Veinte de Enero palm swamp has been subjected to relatively low levels of human disturbance (Hidalgo Pizango et al., 2022). Although the palm swamp peatland studied by Hergoualc'h et al. (2023) is inside a reserve, its close proximity to the urban centre of Iquitos, means it has likely been subjected to more human disturbance than the more remote palm swamp peatland at Veinte de Enero. This is supported by the *Mauritia flexuosa* male/female ratios of the two plots (Quistococha: 4.1; VEN-02: 1.5); the destructive harvesting of female *Mauritia flexuosa* for their fruit can leave palm swamp forests with high *Mauritia flexuosa* male to female ratios (Hidalgo Pizango et al., 2022).

Tree litter NPP as a proportion of total NPP in the pole forest peatland was much higher than is typical of tropical forests (Malhi et al., 2011). The high proportional contribution of tree litter to total NPP is in part the result of the low root NPP in the pole forest peatland, but nonetheless the ratio of litter to stem NPP of both the palm swamp and pole forest peatland plots (4.8 and 5.3, respectively) is higher than is typical for forests across the region (0.7–2.2; Table S3). Similarly high NPP allocation to tree litter, and high litter-to-stem ratios, have been reported by Chimner and Ewel (2005) for Micronesian wetlands (Table 3). A finding of high NPP allocation to tree litter in a tropical peatland is perhaps surprising, as one might expect the nutrient-poor conditions to limit leaf turnover (Poorter et al., 2009), and indeed there is evidence from tropical peatlands elsewhere that peatland species

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**TABLE 3** Net primary productivity (NPP) values reported in the literature for Peruvian forests and peatland forest in other tropical regions.

| | | | | NPP (Mg C ha$^{-1}$ year$^{-1}$) | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Forest type | Region | Country | Plot code | Tree stem | Tree litter | Branch | Palm stem | Palm litter | Palm AG | Tree coarse roots | Palm coarse roots | Fine roots | Total roots | Total | Source |
| Pole forest peatland | Loreto | Peru | NYO-03 | 0.78 | 4.10 | 0.52 | 0.25 | 0.75 | 1.00 | 0.16 | 0.17 | 0.61 | 0.94 | 7.34 | This study |
| Palm swamp peatland | Loreto | Peru | VEN-02 | 0.16 | 0.76 | 0.07 | 0.45 | 3.60 | 4.05 | 0.03 | 0.20 | 4.56 | 4.79 | 9.83 | This study |
| Palm swamp peatland | Loreto | Peru | Quistococha Intact | | 3.9 | | | | | | | 3.72 | | | Dezzeo et al. (2021); Hergoualc'h et al. (2023) |
| *Terra firme* | Loreto | Peru | ALP-11 | 2.59 | | | | | | | | | | | Malhi et al. (2004) |
| *Terra firme* | Loreto | Peru | ALP-12 | 3.24 | | | | | | | | | | | Malhi et al. (2004) |
| *Terra firme* | Loreto | Peru | ALP-21 | 3.64 | | | | | | | | | | | Malhi et al. (2004) |
| *Terra firme* | Loreto | Peru | ALP-22 | 3.11 | | | | | | | | | | | Malhi et al. (2004) |
| Seasonally flooded (~1 month per annum) | Loreto | Peru | JEN-03 | 5.09 | 3.51 | | | | | | | | | | Malhi et al. (2004) |
| Seasonally flooded (~2 month per annum) | Loreto | Peru | JEN-06 | 5.43 | 3.57 | | | | | | | | | | Malhi et al. (2004) |
| Seasonally flooded (~4 month per annum) | Loreto | Peru | JEN-09 | 5.09 | 3.47 | | | | | | | | | | Malhi et al. (2004) |
| *Terra firme* | Loreto | Peru | MSH-01 | 2.61 | | | | | | | | | | | Malhi et al. (2004) |
| *Terra firme* | Loreto | Peru | SUC-01 | 3.12 | | | | | | | | | | | Malhi et al. (2004) |
| *Terra firme* | Loreto | Peru | SUC-02 | 3.39 | | | | | | | | | | | Malhi et al. (2004) |
| *Terra firme* | Loreto | Peru | YAN-01 | 3.91 | | | | | | | | | | | Malhi et al. (2004) |
| Cloud forest-upper montane | Cuzco | Peru | WAY | 1.20 | 1.92 | 0.50 | | | | 0.25 | | 1.23 | 1.48 | 5.09 | Girardin et al. (2010) |
| Cloud forest-upper montane | Cuzco | Peru | TU3 | 1.00 | 1.19 | 0.40 | | | | 0.21 | | 1.31 | 1.52 | 4.11 | Girardin et al. (2010) |
| Cloud forest-upper montane | Cuzco | Peru | TU4 | 1.57 | 1.83 | 0.60 | | | | 0.33 | | 1.63 | 1.96 | 5.98 | Girardin et al. (2010) |
| Cloud forest-lower montane | Cuzco | Peru | TU7 | 0.79 | 1.44 | 0.30 | | | | 0.16 | | 1.80 | 1.96 | 4.50 | Girardin et al. (2010) |
| Cloud forest-lower montane | Cuzco | Peru | TU8 | 0.79 | 1.44 | 0.30 | | | | 0.17 | | 3.26 | 3.43 | 5.97 | Girardin et al. (2010) |
| Cloud forest-lower montane | Cuzco | Peru | SPD | 1.62 | 2.76 | 0.60 | | | | 0.34 | | 1.70 | 2.04 | 7.06 | Girardin et al. (2010) |
| Premontane tropical forest | Cuzco | Peru | TON | 1.34 | 2.49 | 0.50 | | | | 0.28 | | 2.42 | 2.70 | 7.07 | Girardin et al. (2010) |
| *Terra firme* | Madre de Dios | Peru | TAM05 | 2.41 | 5.39 | 0.95 | | | 0.22 | 0.51 | | 4.54 | 5.05 | 15.01 | Malhi et al. (2014) |
| *Terra firme*. Palms make up >30% of stems. | Madre de Dios | Peru | TAM06 | 2.49 | 4.94 | 0.50 | | | 2.81 | 0.52 | | 2.11 | 2.63 | 14.21 | Malhi et al. (2014) |
| *Terra firme* | Loreto | Peru | ALP-A | 3.45 | 4.20 | 1.42 | | | | 0.69 | | 3.02 | | 14.14 | del Aguila-Pasquel et al. (2014) |

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TABLE 3 (Continued)

| Forest type | Region | Country | Plot code | NPP (Mg C ha$^{-1}$ year$^{-1}$) | | | | | | | | | | | Source |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | Tree stem | Tree litter | Branch | Palm stem | Palm litter | Palm AG | Tree coarse roots | Palm coarse roots | Fine roots | Total roots | Total | |
| Seasonally flooded/*terra firme* mix | Loreto | Peru | ALP-C | 2.73 | 5.66 | 1.01 | | | | 0.55 | | 3.50 | | 14.41 | del Aguila-Pasquel et al. (2014) |
| Peat swamp forest | West Kalimantan | Indonesia | | | | | | | | | | | | 13.20 | Basuki et al. (2019) |
| Hardwood dominated wetland | Kosrae | Micronesia | Yela | 2.83 | 7.55 | | | | | | | 3.00 | | 11.37 | Chimner and Ewel (2005) |
| Hardwood dominated peatland | Kosrae | Micronesia | Yewak | 3.70 | 7.45 | | | | | | | 3.00 | | 11.06 | Chimner and Ewel (2005) |
| Hardwood dominated peat swamp forest | Likouala Department | Congo | EKG-02 | | | | | | | | | 1.90 | | | Sciumbata et al. (2023) |
| Palm-dominated peat swamp forest | Likouala Department | Congo | EKG-03 | | | | | | | | | 2.60 | | | Sciumbata et al. (2023) |

*Note*: 'Palm AG' (AG = above-ground) is palm litter and palm stem NPP grouped together. 'Total Roots' is coarse (both palm and tree) and fine root NPP grouped together.

have a higher investment in leaf preservation than non-peatland species (Yule & Gomez, 2009), which presumably leads to longer leaf lifespans (Wright et al., 2004). However, at least one species, *Platycarpum loretense*, particularly abundant in the pole forest peatland plot (Table S1), has been observed to have high levels of leaf turnover (authors' personal observation).

Root NPP in the palm swamp peatland plot was high compared with other tropical peatlands (Table 3): asround a third higher than has been reported for Quistococha (Dezzeo et al., 2021), and higher still than root NPP reported for a Micronesian peatland (Chimner & Ewel, 2005; Table 3) and Congolese peatlands (Sciumbata et al., 2023). Given the low number of tree stems in the palm swamp peatland plot, it can reasonably be assumed that this higher root productivity is the result of palm root productivity specifically, which would explain the lower root productivity at the Quistococha site where (despite still being classed as a palm swamp) the density of palms is lower (Hergoualc'h et al., 2023). Hardwood tree root productivity at our sites appears to be very low, as root NPP in the pole forest peatland was considerably lower than any root NPP values reported in the literature for tropical forests, both in terms of proportional contribution to total NPP (13%) and in absolute value (0.94 Mg C ha$^{-1}$ year$^{-1}$). Dezzeo et al. (2021), however, found no significant difference between tree and palm root productivity at Quistococha. While methodological effects, such as root disturbance during ingrowth core installation, higher substrate bulk density inside root ingrowth cores, and excessively large core volumes can artificially reduce measurements of root productivity (Laiho et al., 2014), we took steps to reduce the possibility of such scenarios (see Section 2) and would expect these effects to act equally on both plots. A root productivity study in lowland Congolese peatlands which used a mini-rhizotron method also found higher root productivity in their palm-dominated peatland site compared to their tree-dominated peatland site (Sciumbata et al., 2023; Table 3). It could be, therefore, that the non-woody nature of palm roots means that palms have a more prolific rooting system than trees and/or have a faster regeneration rate following severing (Hodel, 2009). Further research on the contribution of roots to peat carbon accumulation should be a priority.

It is becoming increasingly apparent that different forest types can have very different NPP allocation patterns (e.g., Zhang-Zheng et al., 2024), and Malhi et al. (2021) make the point that using tree stem growth alone as an indicator of ecosystem NPP can not only lead to these differences being overlooked, but also can lead to considerable underestimations of total NPP. The two peatland plots, with their low tree stem NPP, but relatively high leaf NPP in the pole forest peatland and high root and palm NPP in the palm swamp peatland, are good examples of where this NPP underestimation would occur.

It is notable that only litter productivity showed a slight seasonal pattern, with higher productivity coinciding with the drier months in the pole forest peatland (Figure 3). This is a common finding for tropical forests, as many trees shed their leaves in the dry season (Zhang et al., 2014). In the pole forest peatland there was an additional, higher peak in litter productivity following a short, sharp

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**TABLE 4** Comparison of decomposition rates of palm and hardwood litter in tropical wetlands from this study and other studies in the literature[a].

| Forest type | Region | Country/ territory | Plot/site code/ name | Litter type | Mass remaining (%) after 1 year[b] | | | Notes | Source |
|---|---|---|---|---|---|---|---|---|---|
| | | | | | Leaves | Stem | Roots | | |
| Pole forest peatland | Loreto | Peru | NYO-03 | Palm | 21 | 86 | 77 | *Mauritia flexuosa* litter. Palm leaflet and stem material left to decompose at surface. Roots buried 30 cm below the surface. | This study |
| Palm swamp peatland | Loreto | Peru | VEN-02 | Palm | 21 | 86 | 77 | *Mauritia flexuosa* litter. Palm leaflet and stem material left to decompose at surface. Roots buried 30 cm below the surface. | This study |
| Palm-dominated peatland | Central America | Panama | SSPS1 | Palm | 49 | 34 | 86 | *Raphia taedigera* litter. Palm leaf and stem material left to decompose at surface. Roots buried to 50 cm below the surface. | Hoyos-Santillan et al. (2015) |
| Palm-dominated peatland | Central America | Panama | Chiriquí Grande | Palm | 55 | 48 | 89 | *Raphia taedigera* litter. Palm leaf and stem material left to decompose at surface. Roots buried to 50 cm below the surface. | Hoyos-Santillan et al. (2015) |
| Montane (750 m a.s.l.) palm-dominated floodplain forest | Caribbean | Puerto Rico | Luquillo Experimental Forest | Palm | 46 | 62 | NA | *Prestoea acuminata* var. montana litter. Palm leaf and stem material left to decompose at surface. | Frangi and Lugo (1985) |
| Palm-dominated peatland | Loreto | Peru | Quistacocha Intact | Palm | NA | NA | 60 | *Mauritia flexuosa* litter. Root material buried to 15 cm below the surface. | Dezzeo et al. (2021) |
| Palm-dominated peatland | Loreto | Peru | Quistacocha Intact | Hardwood | 37 | NA | 69 | Hardwood litter from multiple species. Leaf material left to decompose at surface. Root material buried to 15 cm below the surface. | Dezzeo et al. (2021); Hergoualc'h et al. (2023) |
| Seasonally flooded forest | South America | Ecuador | Tiputini Biodiversity Station | Hardwood | 20 | NA | NA | *Inga punctatalitter* litter left at the surface to decompose. | Capps et al. (2011) |
| Seasonally flooded forest | South America | Ecuador | Tiputini Biodiversity Station | Hardwood | 11 | NA | NA | *Triplaris dugandii* litter left at the surface to decompose. | Capps et al. (2011) |
| Mixed hardwood and palm peatland | Central America | Panama | SSPS2 | Hardwood | 54 | 50 | 84 | *Campnosperma panamensis* litter. Leaf and stem material left to decompose at surface. Roots buried to 50 cm below the surface. | Hoyos-Santillan et al. (2015) |
| Mixed hardwood and palm peatland | Central America | Panama | Almirante | Hardwood | 44 | 71 | 85 | *Campnosperma panamensis* litter. Leaves and stem material left to decompose at surface. Roots buried to 50 cm | Hoyos-Santillan et al. (2015) |

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TABLE 3 (Continued)

| Forest type | Region | Country/ territory | Plot/site code/ name | Litter type | Mass remaining (%) after 1 year[b] | | | Notes | Source |
|---|---|---|---|---|---|---|---|---|---|
| | | | | | Leaves | Stem | Roots | | |
| Montane (750 m a.s.l.) palm-dominated floodplain forest | Caribbean | Puerto Rico | Luquillo Experimental Forest | Hardwood | 40 | NA | NA | Hardwood litter from multiple species left to decompose at surface. | Frangi and Lugo (1985) |
| Hardwood dominated wetland | Western Pacific | Micronesia | Yela | Hardwood | 13 | 28 | 62 | Hardwood litter from multiple species. Leaf and stem material left to decompose at surface. Roots buried to 5 cm below the surface. | Chimner and Ewel (2005) |
| Hardwood dominated peatland | Western Pacific | Micronesia | Yewak | Hardwood | 10 | 67 | 69 | Hardwood litter from multiple species. Leaf and stem material left to decompose at surface. Roots buried to 5 cm below the surface. | Chimner and Ewel (2005) |
| Mangrove peatland | Western Pacific | Micronesia | PC | Hardwood | 5 | NA | 32 | *Rhizophora stylosa* litter. Leaf material was left to decompose at the surface. Roots buried to 30 cm below the surface. | Ono et al. (2015) |
| Secondary swamp forest | Southeast Asia | Malaysia | North Selangor Peat swamp Forest Reserve | Hardwood | 52 | NA | NA | *Macaranga pruinosa* litter. Leaf material was left to decompose at the surface. | Yule and Gomez (2009) |
| Secondary swamp forest | Southeast Asia | Malaysia | North Selangor Peat swamp Forest Reserve | Hardwood | 60 | NA | NA | *Campnosperma coriaceum* litter. Leaf material was left to decompose at the surface. | Yule and Gomez (2009) |
| Secondary swamp forest | Southeast Asia | Malaysia | North Selangor Peat swamp Forest Reserve | Hardwood | 75 | NA | NA | *Pandanus atrocarpus* litter. Leaf material was left to decompose at the surface. | Yule and Gomez (2009) |
| Secondary swamp forest | Southeast Asia | Malaysia | North Selangor Peat swamp Forest Reserve | Hardwood | 78 | NA | NA | *Stenochlaena palustris* litter. Leaf material was left to decompose at the surface. | Yule and Gomez (2009) |

[a]Many of the studies cited here applied multiple treatments (e.g., different litter types, different environmental conditions) in their decomposition experiments. For brevity and relevance, we present the treatments which most closely resemble our study. For example, if a study has reported decomposition rates for root material left at the surface and root materiel buried, we only present the buried root material decomposition rate. Likewise, results from a non-wetland setting have been excluded.

[b]The mass remaining after 1 year was calculated for each study using their reported model of best fit for the respective treatment.

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rise in water table levels. Peaks in leaf shedding have been observed during flood pulses in other flooded forest types in Amazonia, including the Quistococha peatland, as the anoxic conditions limit canopy growth and leaves are abscised (Hergoualc'h et al., 2023; Nebel et al., 2001; Schöngart et al., 2002). However, seasonally flooded forests experience much larger water table level changes than pole forest peatlands (Flores Llampazo et al., 2022), and the leaf shedding event in response to flooding observed by Hergoualc'h et al. (2023) in a palm swamp peatland was during an El Niño event, when water table levels were exceptionally high. The rather modest rise in water table level in our pole forest peatland plot, along with the asynchronicity of the peaks in litter productivity and water table levels, may indicate that the higher water table was not responsible for the higher litter productivity at this time. The absence of any apparent seasonal variation in the other NPP components may prove to be a distinctive feature, given that both climate and water table position often do not vary substantially in PMFB peatlands (Flores Llampazo et al., 2022), but longer records of NPP from more peatland sites are needed in order to properly assess the importance of seasonality in these ecosystems.

## 4.2 | Litter decomposition

We found that, for the three different *Mauritia flexuosa* litter types, stem material decomposed at the slowest rate, followed by root material, followed by leaf material. The fast decomposition of palm leaves is consistent with the findings of the limited number of studies which have measured palm litter decomposition in a tropical wetland setting (Frangi & Lugo, 1985; Hoyos-Santillan et al., 2015). Our palm leaf decomposition rates are higher than the values published for the other palm litter decomposition studies (Table 4), and slightly higher than decomposition rates reported for hardwood litter at another PMFB palm-dominated peatland site (Hergoualc'h et al., 2023). This could be in part owing to our use of fresh, rather than senesced litter, which may mean that the leaf material was higher in nutrients and non-structural carbohydrates, which can have a priming effect on microbial populations (Hättenschwiler et al., 2011). However, our palm leaf decomposition rates are within the range of decomposition rates published for hardwood leaf litter at other tropical wetland sites (Table 4). Unlike the leaf litter, root litter at both our sites had slightly slower rates of decomposition compared with palm and tree root decomposition observed at the other published PMFB palm-dominated peatland site (Dezzeo et al., 2021; Table 4). Our finding of higher decomposition rates for palm root material compared to palm stem material is in contrast to the findings of Hoyos-Santillan et al. (2015), who found root material, both for palms and hardwood species, to decompose slower than stem material in Panamanian peatlands. In general, looking across a range of decomposition studies in tropical wetlands, the emerging pattern is one of leaf litter decomposing fastest, followed by much slower decomposition of stem material and then root material (Table 4).

Decomposition rates are either determined by environmental factors, such as temperature, pH and degree of anaerobicity, or by litter traits, such as the degree of recalcitrance of the carbon compounds, the presence of priming compounds and nutrient levels within the litter (Hättenschwiler et al., 2011). The use of litter from a single species, *Mauritia flexuosa*, provides insight into how the different environmental conditions in the ombrotrophic pole forest and the minerotrophic palm swamp peatland affect decomposition rates. The comparable decomposition rates between the two plots suggest that the differences in hydrology do not result in different decomposition rates directly. However, interspecific variations in litter quality can be high (Hättenschwiler et al., 2008, 2011) and it is possibly that differences in species composition between the two plots, likely driven by hydrology (Flores Llampazo et al., 2022), may result in differences in plot-level decomposition rates that have not been detected by our use of a single species.

Similarly, differences in hydrological conditions within the plots did not seem to be the principal factor determining decomposition rates between litter types; root material, buried below the surface decomposed at a faster rate than the stem material at the surface. It is likely that the aerobic conditions at the surface would have had a positive influence on decomposition rates. Therefore, our results suggest that it is the difference in litter traits between the three litter types that drives the differences in decomposition rates. As most other studies find that roots decompose more slowly than stem material (Table 4), contrary to our results, it suggests that the structural composition of *Mauritia flexuosa* roots, or indeed stem, may be atypical. This is supported by the findings of Dezzeo et al. (2021) who found *Mauritia flexuosa* roots to decompose faster than hardwood species, despite similar C/N ratios. This is an important topic for further research, given the abundance of *Mauritia flexuosa* roots in many PMFB peat profiles, which would suggest they play a key role in peat accumulation.

## 4.3 | Potential future changes in NPP and decomposition

Estimating tropical peatland NPP is a first step in understanding these systems. We then need to know what the principal controlling factors of forest NPP in a tropical peatland setting are and how that differs from non-peatland tropical forest. For example, while climatic drying can reduce tropical forest NPP (Clark et al., 2013) if drying is sufficient to induce water stress, within a peatland it may result in an increase in NPP, as anoxic conditions are reduced. Our results begin this process of increasing understanding of tropical peatland NPP dynamics.

In the northwestern Amazon, where our two peatland plots are located, increased precipitation and floodplain inundation has been observed over the last few decades (Gloor et al., 2015). Peatland forests, which tend not to experience water deficits even in the dry season, are unlikely to experience increases in NPP in response to wetter conditions. In fact, increased precipitation

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could have a negative impact on peatland NPP if there is an associated increase in cloudiness, reducing solar radiation (Graham et al., 2003; Schuur, 2003), or if there is an increase in inundation levels or their duration this may impede respiration, limiting plant growth (Fonseca et al., 2019; Schöngart et al., 2002). Indeed, inundation events which exceed the vegetation tolerance to flooding can result in mortality events (Kalliola et al., 1991), which may change the structure and function of the system. Even more modest changes in hydrology could, over long time periods, result in a change in NPP if there is a change in vegetation community composition (Flores Llampazo et al., 2022). Although palm swamp peatlands tend to receive flood waters, more extreme flood regimes may force a shift in vegetation community towards to seasonally flooded forest communities more tolerant of larger fluctuations in water table levels (Flores Llampazo et al., 2022), which may result in an increase in forest NPP, depending on the nutrient content of the flood water (del Aguila-Pasquel et al., 2014; Malhi et al., 2004; Table 3).

Whether changes in peatland NPP would lead to changes in peat accumulation rates in the PMFB would depend on the degree to which NPP changes were reinforced or counteracted by changes in decomposition rates. If precipitation/flooding increased in the region and water table levels increased as a result, one would expect a reduction in decomposition rates. However, this could be counteracted to a degree if changes in vegetation community lead to a change in litter quality and therefore lability (Wang et al., 2015; Wright et al., 2013) or if increased flooding were accompanied by an increase in mineral load into the peatlands (Kalliola et al., 1991) leading to increased microbial activity or changes in the microbial population (Andersen et al., 2013). Processes of peat accumulation are complex, and even with high initial rates of decomposition, a negative feedback can occur whereby the organic matter remaining is highly recalcitrant, protecting it from further decomposition (Hodgkins et al., 2018; Leifeld et al., 2012).

In order to make quantitative predications of future change in peat accumulation, processed based mathematical models of peatland development are required. While at present there is perhaps not sufficient data to adequately represent some of the more complex processes influencing peat accumulation rates, two models, HMPTrop (Kurnianto et al., 2015) and Digibog (Young et al., 2023) have successfully simulated historical variations in peat accumulation rates in Southeast Asia and the Congo Basin respectively, using limited data on plant litter production (i.e., NPP) and decomposition. Our data could be used as the basis for similar modelling work in the PMFB, eventually leading to forecasting of peat accumulation rates under different land use change and climate change scenarios in the PMFB.

## 5 | CONCLUSIONS

We have presented data on total net primary production and litter decomposition from two types of Amazonian peatlands, a palm swamp peatland and a pole forest peatland. These data will be important for parameterising and validating process-based models of peat accumulation, but they also provide insights into ecosystem functioning in Amazonian peatlands that have, until now, been lacking.

Total NPP is similar at both sites and is low compared to *terra firme* and seasonally flooded forests in the lowland tropics, but similar to NPP estimates from the very limited data from other tropical peatlands. However, despite the similar total NPP, there are strong differences between our two sites, particularly in the contribution of roots to overall productivity, which was very high (49%) in the palm swamp peatland and much less important in the pole forest peatland (13%). This suggests that palm swamp peatlands may be more inclined to produce 'replacement peat'—, that is, mostly made from roots, below-ground—than other vegetation types, which would affect the bulk radiocarbon age of the peat and other properties of relevance to palaeoenvironmental reconstruction, because the different components of a peat sample, for example, pollen versus roots, will represent material produced at different times and potentially under different environmental conditions.

We find that there is little difference in litter decomposition rates at our two sites. Our estimates are broadly comparable to data from other tropical peatlands, with faster decomposition of leaves compared to stem and root material. A possible explanation is that the roots of *Mauritia flexuosa*, the species studied here, may be composed of less recalcitrant material than hardwood roots (Dezzeo et al., 2021). Further investigation of the properties of *Mauritia flexuosa*, which dominates large areas of peatland in the PMFB, would help to understand the extent to which it plays a particular role in peat formation in this region.

Clearly, data from just two sites are insufficient to fully characterise the likely variability in ecosystem function within PMFB peatlands, which are known to include other vegetation types such as seasonally flooded and open (herbaceous) peatlands (Honorio Coronado et al., 2021). Similarly, it is not possible to draw firm conclusions on seasonality from our short study, but indications of possible seasonality in litter production at the pole forest peatland plot (but not the palm swamp peatland plot) suggest an avenue for future research.

Finally, our study points to the need for standardised methods for measuring forest NPP in tropical peatland settings. Peatland fine root NPP is particularly challenging to measure: obtaining root-free medium to fill ingrowth cores with is extremely difficult, given that tropical peats can be largely composed of root material (Hoyos-Santillan et al., 2015). Furthermore, flooding and the tendency of the peat to collapse upon excavation prevent the use of traditional rhizotrons. Although mini-rhizotrons have been developed for and deployed in peatlands (Arnaud et al., 2019, 2021; Sciumbata et al., 2023), the method requires the conversion of root length, observed in photographs taken from inside the mini-rhizotron, to root mass, and requires a number of assumptions which have yet to be clearly quantified (Sciumbata et al., 2023). Furthermore, the assumption that coarse root NPP amounts to 21% of stem NPP,

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based on very limited data, is very possibly an underestimation in a forested peatland setting, where many tree species show root adaptations for the flooded conditions such as stilt roots and pneumatophores. Similar methodological developments will be needed to better account for the contribution of palms to peatland canopy and stem NPP, building on the methods pioneered here.

## AUTHOR CONTRIBUTIONS

**G. C. Dargie:** Data curation; formal analysis; investigation; methodology; writing – original draft. **J. del Aguila-Pasquel:** Data curation; methodology; supervision; writing – review and editing. **C. J. Córdova Oroche:** Data curation; investigation; writing – review and editing. **J. Irarica Pacaya:** Data curation; investigation. **J. Reyna Huaymacari:** Data curation; investigation; writing – review and editing. **T. R. Baker:** Formal analysis; methodology; writing – review and editing. **A. Hastie:** Methodology; writing – review and editing. **E. N. Honorio Coronado:** Methodology; writing – review and editing. **S. L. Lewis:** Formal analysis; writing – review and editing. **K. H. Roucoux:** Conceptualization; formal analysis; methodology; supervision; writing – review and editing. **E. T. Mitchard:** Writing – review and editing. **M. Williams:** Writing – review and editing. **F. C. H. Draper:** Writing – review and editing. **I. T. Lawson:** Conceptualization; methodology; project administration; supervision; writing – review and editing.

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## CONFLICT OF INTEREST STATEMENT

The authors are not aware of any conflict of interest.

## DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in NERC Environmental Information Data Centre at https://doi.org/10.5285/e34dc4c7-57d8-4120-921b-06d2f25d5e04.

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## REFERENCES

Andersen, R., Chapman, S. J., & Artz, R. R. E. (2013). Microbial communities in natural and disturbed peatlands: A review. *Soil Biology and Biochemistry*, *57*, 979–994. https://doi.org/10.1016/j.soilbio.2012.10.003

Arnaud, M., Baird, A. J., Morris, P. J., Harris, A., & Huck, J. J. (2019). EnRoot: A narrow-diameter, inexpensive and partially 3D-printable minirhizotron for imaging fine root production. *Plant Methods*, *15*, 101. https://doi.org/10.1186/s13007-019-0489-6

Arnaud, M., Morris, P. J., Baird, A. J., Dang, H., & Nguyen, T. T. (2021). Fine root production in a chronosequence of mature reforested mangroves. *New Phytologist*, *232*, 1591–1602. https://doi.org/10.1111/nph.17480

Avalos, G., Cambronero, M., & Alvarez-Vergnani, C. (2022). Allometric models to estimate carbon content in Arecaceae based on seven species of Neotropical palms. *Frontiers in Forests and Global Change*, *5*. https://doi.org/10.3389/ffgc.2022.867912

Baker, T., & Chao, K. (2011). *Manual for coarse woody debris measurement in RAINFOR plots*. https://rainfor.org/wp-content/uploads/sites/129/2022/06/CWD_protocol_RAINFOR_2011_EN.pdf

Basuki, I., Kauffman, J. B., Peterson, J., Anshari, G., & Murdiyarso, D. (2019). Land cover changes reduce net primary production in tropical coastal peatlands of West Kalimantan, Indonesia. *Mitigation and Adaptation Strategies for Global Change*, *24*, 557–573. https://doi.org/10.1007/s11027-018-9811-2

Bocko, Y. E., Panzou, G. J. L., Dargie, G. C., Mampouya, Y. E. W., Mbemba, M., Loumeto, J. J., & Lewis, S. L. (2023). Allometric equation for Raphia laurentii De wild, the commonest palm in the central Congo peatlands. *PLoS One*, *18*, e0273591. https://doi.org/10.1371/journal.pone.0273591

Bruijnzeel, L. A., & Veneklaas, E. J. (1998). Climatic conditions and tropical montane forest productivity: The fog has not lifted yet. *Ecology*, *79*, 3–9. https://doi.org/10.2307/176859

Capps, K. A., Graça, M. A. S., Encalada, A. C., & Flecker, A. S. (2011). Leaf-litter decomposition across three flooding regimes in a seasonally flooded Amazonian watershed. *Journal of Tropical Ecology*, *27*, 205–210. https://doi.org/10.1017/S0266467410000635

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

Chimner, R. A., & Ewel, K. C. (2005). A tropical freshwater wetland: II. Production, decomposition, and peat formation. *Wetlands Ecology*

13652486, 2024, 8, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/gcb.17436 by Cochrane Peru, Wiley Online Library on [04/10/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

*and Management*, *13*, 671–684. https://doi.org/10.1007/s11273-005-0965-9

Clark, D. A., Brown, S., Kicklighter, D. W., Chambers, J. Q., Thomlinson, J. R., Ni, J., & Holland, E. A. (2001). Net primary production in tropical forests: An evaluation and synthesis of existing field data. *Ecological Applications*, *11*, 371–384. https://doi.org/10.2307/3060895

Clark, D. A., Clark, D. B., & Oberbauer, S. F. (2013). Field-quantified responses of tropical rainforest aboveground productivity to increasing $CO_2$ and climatic stress, 1997–2009. *Journal of Geophysical Research: Biogeosciences*, *118*, 783–794. https://doi.org/10.1002/jgrg.20067

Dargie, G. C., Lewis, S. L., Lawson, I. T., Mitchard, E. T. A., Page, S. E., Bocko, Y. E., & Ifo, S. A. (2017). Age, extent and carbon storage of the central Congo Basin peatland complex. *Nature*, *542*, 86–90. https://doi.org/10.1038/nature21048

del Aguila-Pasquel, J., Doughty, C. E., Metcalfe, D. B., Silva-Espejo, J. E., Girardin, C. A. J., Chung Gutierrez, J. A., Navarro-Aguilar, G. E., Quesada, C. A., Hidalgo, C. G., Reyna Huaymacari, J. M., Halladay, K., del Castillo Torres, D., Phillips, O., & Malhi, Y. (2014). The seasonal cycle of productivity, metabolism and carbon dynamics in a wet aseasonal forest in north-west Amazonia (Iquitos, Peru). *Plant Ecology and Diversity*, *7*, 71–83. https://doi.org/10.1080/17550874.2013.798365

Dezzeo, N., Grandez-Rios, J., Martius, C., & Hergoualc'h, K. (2021). Degradation-driven changes in fine root carbon stocks, productivity, mortality, and decomposition rates in a palm swamp peat forest of the Peruvian Amazon. *Carbon Balance and Management*, *16*, 33. https://doi.org/10.1186/s13021-021-00197-0

Draper, F. C., Roucoux, K. H., Lawson, I. T., Mitchard, E. T. A., Coronado, E. N. H., Lähteenoja, O., Montenegro, L. T., Sandoval, E. V., Zaráte, R., & Baker, T. R. (2014). The distribution and amount of carbon in the largest peatland complex in Amazonia. *Environmental Research Letters*, *9*, 124017. https://doi.org/10.1088/1748-9326/9/12/124017

Fisher, J. B., Malhi, Y., Torres, I. C., Metcalfe, D. B., van de Weg, M. J., Meir, P., Silva-Espejo, J. E., & Huasco, W. H. (2013). Nutrient limitation in rainforests and cloud forests along a 3,000-m elevation gradient in the Peruvian Andes. *Oecologia*, *172*, 889–902. https://doi.org/10.1007/s00442-012-2522-6

Flores Llampazo, G., Honorio Coronado, E. N., del Aguila-Pasquel, J., Cordova Oroche, C. J., Díaz Narvaez, A., Reyna Huaymacari, J., Grandez Ríos, J., Lawson, I. T., Hastie, A., Baird, A. J., & Baker, T. R. (2022). The presence of peat and variation in tree species composition are under different hydrological controls in Amazonian wetland forests. *Hydrological Processes*, *36*, e14690. https://doi.org/10.1002/hyp.14690

Fonseca, L. D. M., Dalagnol, R., Malhi, Y., Rifai, S. W., Costa, G. B., Silva, T. S. F., Da Rocha, H. R., Tavares, I. B., & Borma, L. S. (2019). Phenology and seasonal ecosystem productivity in an Amazonian floodplain forest. *Remote Sensing*, *11*, 1530. https://doi.org/10.3390/rs11131530

Frangi, J. L., & Lugo, A. E. (1985). Ecosystem dynamics of a subtropical floodplain forest. *Ecological Monographs*, *55*, 351–369. https://doi.org/10.2307/1942582

Freitas, L., Otárola, E., del Castillo Torres, D., Linares, C., Martínez, C., & Malca, G. A. (2006). *Servicios Ambientales de Carbono y Secuestro de Carbono de Ecosistema Aguajal en la Reserva Nacional Pacaya Samiria, Loreto – Perú* (Documento Técnico No. 29). Investigaciones de la Amazonía Peruana (IIAP). https://hdl.handle.net/20.500.12921/228

Gatti, L. V., Basso, L. S., Miller, J. B., Gloor, M., Gatti Domingues, L., Cassol, H. L. G., Tejada, G., Aragão, L. E. O. C., Nobre, C., Peters, W., Marani, L., Arai, E., Sanches, A. H., Corrêa, S. M., Anderson, L., Von Randow, C., Correia, C. S. C., Crispim, S. P., & Neves, R. A. L. (2021). Amazonia as a carbon source linked to deforestation and climate change. *Nature*, *595*, 388–393. https://doi.org/10.1038/s41586-021-03629-6

Girardin, C. A. J., Malhi, Y., Aragão, L. E. O. C., Mamani, M., Huaraca Huasco, W., Durand, L., Feeley, K. J., Rapp, J., Silva-Espejo, J. E., Silman, M., Salinas, N., & Whittaker, R. J. (2010). Net primary productivity allocation and cycling of carbon along a tropical forest elevational transect in the Peruvian Andes. *Global Change Biology*, *16*, 3176–3192. https://doi.org/10.1111/j.1365-2486.2010.02235.x

Gloor, M., Barichivich, J., Ziv, G., Brienen, R., Schöngart, J., Peylin, P., Ladvocat Cintra, B. B., Feldpausch, T., Phillips, O., & Baker, J. (2015). Recent Amazon climate as background for possible ongoing and future changes of Amazon humid forests. *Global Biogeochemical Cycles*, *29*, 1384–1399. https://doi.org/10.1002/2014GB005080

Goodman, R. C., Phillips, O. L., del Castillo Torres, D., Freitas, L., Cortese, S. T., Monteagudo, A., & Baker, T. R. (2013). Amazon palm biomass and allometry. *Forest Ecology and Management*, *310*, 994–1004. https://doi.org/10.1016/j.foreco.2013.09.045

Graham, E. A., Mulkey, S. S., Kitajima, K., Phillips, N. G., & Wright, S. J. (2003). Cloud cover limits net $CO_2$ uptake and growth of a rainforest tree during tropical rainy seasons. *Proceedings of the National Academy of Sciences of the United States of America*, *100*, 572–576. https://doi.org/10.1073/pnas.0133045100

Greenwell, B. M., & Schubert Kabban, C. M. (2014). investr: An R package for inverse estimation. *The R Journal*, *6*, 90–100. https://doi.org/10.32614/RJ-2014-009

Grolemund, G., & Wickham, H. (2011). Dates and times made easy with lubridate. *Journal of Statistical Software*, *40*, 1–25. https://doi.org/10.18637/jss.v040.i03

Grothendieck, G. (2013). *nls2: Non-linear regression with brute force*. https://cran.r-project.org/package=nls2

Hastie, A., Honorio Coronado, E. N., Reyna, J., Mitchard, E. T. A., Åkesson, C. M., Baker, T. R., Cole, L. E. S., Oroche, C. J. C., Dargie, G., Dávila, N., De Grandi, E. C., Del Águila, J., Del Castillo Torres, D., De La Cruz Paiva, R., Draper, F. C., Flores, G., Grández, J., Hergoualc'h, K., Householder, J. E., … Lawson, I. T. (2022). Risks to carbon storage from land-use change revealed by peat thickness maps of Peru. *Nature Geoscience*, *15*, 369–374. https://doi.org/10.1038/s41561-022-00923-4

Hättenschwiler, S., Aeschlimann, B., Coûteaux, M.-M., Roy, J., & Bonal, D. (2008). High variation in foliage and leaf litter chemistry among 45 tree species of a neotropical rainforest community. *New Phytologist*, *179*, 165–175. https://doi.org/10.1111/j.1469-8137.2008.02438.x

Hättenschwiler, S., Coq, S., Barantal, S., & Handa, I. T. (2011). Leaf traits and decomposition in tropical rainforests: Revisiting some commonly held views and towards a new hypothesis. *New Phytologist*, *189*, 950–965. https://doi.org/10.1111/j.1469-8137.2010.03483.x

Hergoualc'h, K., van Lent, J., Dezzeo, N., Verchot, L. V., van Groenigen, J. W., López Gonzales, M., & Grandez-Rios, J. (2023). Major carbon losses from degradation of *Mauritia flexuosa* peat swamp forests in western Amazonia. *Biogeochemistry*, *167*, 327–345. https://doi.org/10.1007/s10533-023-01057-4

Hidalgo Pizango, C. G., Honorio Coronado, E. N., del Águila-Pasquel, J., Flores Llampazo, G., de Jong, J., Córdova Oroche, C. J., Reyna Huaymacari, J. M., Carver, S. J., del Castillo Torres, D., Draper, F. C., Phillips, O. L., Roucoux, K. H., de Bruin, S., Peña-Claros, M., van der Zon, M., Mitchell, G., Lovett, J., García Mendoza, G., Gatica Saboya, L., … Baker, T. R. (2022). Sustainable palm fruit harvesting as a pathway to conserve Amazon peatland forests. *Nature Sustainability*, *5*, 479–487. https://doi.org/10.1038/s41893-022-00858-z

Hodel, D. R. (2009). Biology of palms and implications for management in the landscape. *HortTechnology*, *19*, 676–681. https://doi.org/10.21273/HORTSCI.19.4.676

Hodgkins, S. B., Richardson, C. J., Dommain, R., Wang, H., Glaser, P. H., Verbeke, B., Winkler, B. R., Cobb, A. R., Rich, V. I., Missilmani,

13652486, 2024, 8, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/gcb.17436 by Cochrane Peru, Wiley Online Library on [04/10/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

M., Flanagan, N., Ho, M., Hoyt, A. M., Harvey, C. F., Vining, S. R., Hough, M. A., Moore, T. R., Richard, P. J. H., De La Cruz, F. B., … Chanton, J. P. (2018). Tropical peatland carbon storage linked to global latitudinal trends in peat recalcitrance. *Nature Communications*, *9*, 3640. https://doi.org/10.1038/s41467-018-06050-2

Honorio Coronado, E. N., Hastie, A., Reyna, J., Flores, G., Grández, J., Lähteenoja, O., Draper, F. C., Åkesson, C. M., Baker, T. R., Bhomia, R. K., Cole, L. E. S., Dávila, N., Águila, J. D., Águila, M. D., Torres, D. D. C., Lawson, I. T., Brañas, M. M., Mitchard, E. T. A., Monteagudo, A., … Montoya, M. (2021). Intensive field sampling increases the known extent of carbon-rich Amazonian peatland pole forests. *Environmental Research Letters*, *16*, 074048. https://doi.org/10.1088/1748-9326/ac0e65

Hoyos-Santillan, J., Lomax, B. H., Large, D., Turner, B. L., Boom, A., Lopez, O. R., & Sjögersten, S. (2015). Getting to the root of the problem: Litter decomposition and peat formation in lowland Neotropical peatlands. *Biogeochemistry*, *126*, 115–129. https://doi.org/10.1007/s10533-015-0147-7

Kalliola, R., Puhakka, M., Salo, J., Tuomisto, H., & Ruokolainen, K. (1991). The dynamics, distribution and classification of swamp vegetation in Peruvian Amazonia. *Annales Botanici Fennici*, *28*, 225–239.

Kozlowski, T. T. (2002). Physiological-ecological impacts of flooding on riparian forest ecosystems. *Wetlands*, *22*, 550–561. https://doi.org/10.1672/0277-5212(2002)022[0550:PEIOFO]2.0.CO;2

Kurnianto, S., Warren, M., Talbot, J., Kauffman, B., Murdiyarso, D., & Frolking, S. (2015). Carbon accumulation of tropical peatlands over millennia: A modeling approach. *Global Change Biology*, *21*, 431–444. https://doi.org/10.1111/gcb.12672

Lähteenoja, O., & Page, S. (2011). High diversity of tropical peatland ecosystem types in the Pastaza-Marañón basin, Peruvian Amazonia. *Journal of Geophysical Research*, *116*, G02025. https://doi.org/10.1029/2010JG001508

Lähteenoja, O., Reátegui, Y. R., Räsänen, M., Torres, D. D. C., Oinonen, M., & Page, S. (2012). The large Amazonian peatland carbon sink in the subsiding Pastaza-Marañón foreland basin, Peru. *Global Change Biology*, *18*, 164–178. https://doi.org/10.1111/j.1365-2486.2011.02504.x

Lähteenoja, O., Ruokolainen, K., Schulman, L., & Alvarez, J. (2009). Amazonian floodplains harbour minerotrophic and ombrotrophic peatlands. *CATENA*, *79*, 140–145. https://doi.org/10.1016/j.catena.2009.06.006

Laiho, R., Bhuiyan, R., Straková, P., Mäkiranta, P., Badorek, T., & Penttilä, T. (2014). Modified ingrowth core method plus infrared calibration models for estimating fine root production in peatlands. *Plant and Soil*, *385*, 311–327. https://doi.org/10.1007/s11104-014-2225-3

Leifeld, J., Steffens, M., & Galego-Sala, A. (2012). Sensitivity of peatland carbon loss to organic matter quality. *Geophysical Research Letters*, *39*, L14704. https://doi.org/10.1029/2012GL051856

Loisel, J., Gallego-Sala, A. V., Amesbury, M. J., Magnan, G., Anshari, G., Beilman, D. W., Benavides, J. C., Blewett, J., Camill, P., Charman, D. J., Chawchai, S., Hedgpeth, A., Kleinen, T., Korhola, A., Large, D., Mansilla, C. A., Müller, J., van Bellen, S., West, J. B., … Wu, J. (2021). Expert assessment of future vulnerability of the global peatland carbon sink. *Nature Climate Change*, *11*, 70–77. https://doi.org/10.1038/s41558-020-00944-0

López Gonzales, M., Hergoualc'h, K., Angulo Núñez, Ó., Baker, T., Chimner, R., del Águila Pasquel, J., del Castillo Torres, D., Freitas Alvarado, L., Fuentealba Durand, B., & García Gonzales, E. (2020). *What do we know about Peruvian peatlands? Occasional paper 210*. CIFOR. https://doi.org/10.17528/cifor/007848

Malhi, Y., Aragão, L. E. O. C., Metcalfe, D. B., Paiva, R., Quesada, C. A., Almeida, S., Anderson, L., Brando, P., Chambers, J. Q., Da Costa, A. C. L., Hutyra, L. R., Oliveira, P., Patiño, S., Pyle, E. H., Robertson, A. L., & Teixeira, L. M. (2009). Comprehensive assessment of carbon productivity, allocation and storage in three Amazonian forests. *Global Change Biology*, *15*, 1255–1274. https://doi.org/10.1111/j.1365-2486.2008.01780.x

Malhi, Y., Baker, T. R., Phillips, O. L., Almeida, S., Alvarez, E., Arroyo, L., Chave, J., Czimczik, C. I., Fiore, A. D., Higuchi, N., Killeen, T. J., Laurance, S. G., Laurance, W. F., Lewis, S. L., Montoya, L. M. M., Monteagudo, A., Neill, D. A., Vargas, P. N., Patiño, S., … Lloyd, J. (2004). The above-ground coarse wood productivity of 104 Neotropical forest plots. *Global Change Biology*, *10*, 563–591. https://doi.org/10.1111/j.1529-8817.2003.00778.x

Malhi, Y., Doughty, C., & Galbraith, D. (2011). The allocation of ecosystem net primary productivity in tropical forests. *Philosophical Transactions of the Royal Society, B: Biological Sciences*, *366*, 3225–3245. https://doi.org/10.1098/rstb.2011.0062

Malhi, Y., Farfán Amézquita, F., Doughty, C. E., Silva-Espejo, J. E., Girardin, C. A. J., Metcalfe, D. B., Aragão, L. E. O. C., Huaraca-Quispe, L. P., Alzamora-Taype, I., Eguiluz-Mora, L., Marthews, T. R., Halladay, K., Quesada, C. A., Robertson, A. L., Fisher, J. B., Zaragoza-Castells, J., Rojas-Villagra, C. M., Pelaez-Tapia, Y., Salinas, N., … Phillips, O. L. (2014). The productivity, metabolism and carbon cycle of two lowland tropical forest plots in south-western Amazonia, Peru. *Plant Ecology and Diversity*, *7*, 85–105. https://doi.org/10.1080/17550874.2013.820805

Malhi, Y., Girardin, C., Metcalfe, D. B., Doughty, C. E., Aragão, L. E. O. C., Rifai, S. W., Oliveras, I., Shenkin, A., Aguirre-Gutiérrez, J., Dahlsjö, C. A. L., Riutta, T., Berenguer, E., Moore, S., Huasco, W. H., Salinas, N., da Costa, A. C. L., Bentley, L. P., Adu-Bredu, S., Marthews, T. R., … Phillips, O. L. (2021). The global ecosystems monitoring network: Monitoring ecosystem productivity and carbon cycling across the tropics. *Biological Conservation*, *253*, 108889. https://doi.org/10.1016/j.biocon.2020.108889

Marcus, M. S., Hergoualc'h, K., Honorio Coronado, E. N., & Gutiérrez-Vélez, V. H. (2024). Spatial distribution of degradation and deforestation of palm swamp peatlands and associated carbon emissions in the Peruvian Amazon. *Journal of Environmental Management*, *351*, 119665. https://doi.org/10.1016/j.jenvman.2023.119665

Marengo, J. (1998). Climatología de la zona de Iquitos, Perú. In R. Kalliola & S. Flores Paitán (Eds.), *Geoecología y desarrolloamazónico: estudio integrado en la zona de Iquitos, Perú* (pp. 35–57). Annales Universitatis Turkuensis Ser A II 114. Finland: University of Turku.

Marengo, J. A., Souza, C. M., Thonicke, K., Burton, C., Halladay, K., Betts, R. A., Alves, L. M., & Soares, W. R. (2018). Changes in climate and land use over the Amazon region: Current and future variability and trends. *Frontiers in Earth Science*, *6*. https://doi.org/10.3389/feart.2018.00228

Marthews, T., Riutta, T., Oliveras Menor, I., Urrutia, R., Moore, S., Metcalfe, D., Malhi, Y., Phillips, O., Huaraca Huasco, W., Ruiz Jaén, M., Girardin, C., Butt, M., Cain, R., & colleagues from the RAINFOR and GEM networks. (2014). *Measuring Tropical Forest Carbon Allocation and Cycling: A RAINFOR-GEM Field Manual for Intensive Census Plots* (v3.0). https://ora.ox.ac.uk/objects/uuid:f33a0929-4675-43c6-91a3-8cbcda962775/files/m1844bb29c06f7d69207569648142e020

Martin, A. R., Doraisami, M., & Thomas, S. C. (2018). Global patterns in wood carbon concentration across the world's trees and forests. *Nature Geoscience*, *11*, 915–920. https://doi.org/10.1038/s41561-018-0246-x

Miettinen, J., Hooijer, A., Vernimmen, R., Liew, S. C., & Page, S. E. (2017). From carbon sink to carbon source: Extensive peat oxidation in insular Southeast Asia since 1990. *Environmental Research Letters*, *12*, 024014. https://doi.org/10.1088/1748-9326/aa5b6f

Miettinen, J., Shi, C., & Liew, S. C. (2016). Land cover distribution in the peatlands of peninsular Malaysia, Sumatra and Borneo in 2015 with changes since 1990. *Global Ecology and Conservation*, *6*, 67–78. https://doi.org/10.1016/j.gecco.2016.02.004

Mitchard, E. T., Saatchi, S. S., Baccini, A., Asner, G. P., Goetz, S. J., Harris, N. L., & Brown, S. (2013). Uncertainty in the spatial distribution

13652486, 2024, 8, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/gcb.17436 by Cochrane Peru, Wiley Online Library on [04/10/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

of tropical forest biomass: A comparison of pan-tropical maps. *Carbon Balance and Management*, *8*, 10. https://doi.org/10.1186/1750-0680-8-10

Nebel, G., Dragsted, J., & Vega, A. S. (2001). Litter fall, biomass and net primary production in flood plain forests in the Peruvian Amazon. *Forest Ecology and Management*, *150*, 93–102. https://doi.org/10.1016/S0378-1127(00)00683-6

Ono, K., Hiradate, S., Morita, S., Hiraide, M., Hirata, Y., Fujimoto, K., Tabuchi, R., & Lihpai, S. (2015). Assessing the carbon compositions and sources of mangrove peat in a tropical mangrove forest on Pohnpei Island, Federated States of Micronesia. *Geoderma*, *245–246*, 11–20. https://doi.org/10.1016/j.geoderma.2015.01.008

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. https://doi.org/10.1111/j.1365-2486.2010.02279.x

Phillips, O., Baker, T., Feldpausch, T., & Brienen, R. (2021). *RAINFOR field manual for plot establishment and remeasurement*. https://forestplots.net/upload/ManualsEnglish/RAINFOR_field_manual_EN.pdf

Poorter, H., Niinemets, Ü., Poorter, L., Wright, I. J., & Villar, R. (2009). Causes and consequences of variation in leaf mass per area (LMA): A meta-analysis. *New Phytologist*, *182*, 565–588. https://doi.org/10.1111/j.1469-8137.2009.02830.x

R Core Team. (2022). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. https://www.R-project.org/

Roucoux, K. H., Lawson, I. T., Baker, T. R., Del Castillo Torres, D., Draper, F. C., Lähteenoja, O., Gilmore, M. P., Honorio Coronado, E. N., Kelly, T. J., Mitchard, E. T. A., & Vriesendorp, C. F. (2017). Threats to intact tropical peatlands and opportunities for their conservation. *Conservation Biology*, *31*, 1283–1292. https://doi.org/10.1111/cobi.12925

Schöngart, J., Piedade, M. T. F., Ludwigshausen, S., Horna, V., & Worbes, M. (2002). Phenology and stem-growth periodicity of tree species in Amazonian floodplain forests. *Journal of Tropical Ecology*, *18*, 581–597. https://doi.org/10.1017/S0266467402002389

Schuur, E. A. G. (2003). Productivity and global climate revisited: The sensitivity of tropical forest growth to precipitation. *Ecology*, *84*, 1165–1170.

Sciumbata, M., Wenina, Y. E. M., Mbemba, M., Dargie, G. C., Baird, A. J., Morris, P. J., Ifo, S. A., Aerts, R., & Lewis, S. L. (2023). First estimates of fine root production in tropical peat swamp and terra firme forests of the central Congo Basin. *Scientific Reports*, *13*, 12315. https://doi.org/10.1038/s41598-023-38409-x

Sousa, T. R., Schietti, J., Coelho de Souza, F., Esquivel-Muelbert, A., Ribeiro, I. O., Emílio, T., Pequeno, P. A. C. L., Phillips, O., & Costa, F. R. C. (2020). Palms and trees resist extreme drought in Amazon forests with shallow water tables. *Journal of Ecology*, *108*, 2070–2082. https://doi.org/10.1111/1365-2745.13377

Wang, H., Richardson, C. J., & Ho, M. (2015). Dual controls on carbon loss during drought in peatlands. *Nature Climate Change*, *5*, 584–587. https://doi.org/10.1038/nclimate2643

Wickham, H. (2001). *tidyr: Tidy messy data*. https://cran.r-project.org/web/packages/tidyr/index.html

Wickham, H., François, R., Henry, L., & Müller, K. (2021). *dplyr: A grammar of data manipulation*. https://cran.r-project.org/web/packages/dplyr/index.html

Wright, E. L., Black, C. R., Cheesman, A. W., Turner, B. L., & Sjögersten, S. (2013). Impact of simulated changes in water table depth on ex situ decomposition of leaf litter from a neotropical peatland. *Wetlands*, *33*, 217–226. https://doi.org/10.1007/s13157-012-0369-6

Wright, I. J., Reich, P. B., Westoby, M., Ackerly, D. D., Baruch, Z., Bongers, F., Cavender-Bares, J., Chapin, T., Cornelissen, J. H. C., Diemer, M., Flexas, J., Garnier, E., Groom, P. K., Gulias, J., Hikosaka, K., Lamont, B. B., Lee, T., Lee, W., Lusk, C., … Villar, R. (2004). The worldwide leaf economics spectrum. *Nature*, *428*, 821–827. https://doi.org/10.1038/nature02403

Young, D. M., Baird, A. J., Morris, P. J., Dargie, G. C., Mampouya Wenina, Y. E., Mbemba, M., Boom, A., Cook, P., Betts, R., Burke, E., Bocko, Y. E., Chadburn, S., Crabtree, D. E., Crezee, B., Ewango, C. E. N., Garcin, Y., Georgiou, S., Girkin, N. T., Gulliver, P., … Lewis, S. L. (2023). Simulating carbon accumulation and loss in the central Congo peatlands. *Global Change Biology*, *29*, 6812–6827. https://doi.org/10.1111/gcb.16966

Yule, C. M., & Gomez, L. N. (2009). Leaf litter decomposition in a tropical peat swamp forest in Peninsular Malaysia. *Wetlands Ecology and Management*, *17*, 231–241. https://doi.org/10.1007/s11273-008-9103-9

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

Zhang, H., Yuan, W., Dong, W., & Liu, S. (2014). Seasonal patterns of litterfall in forest ecosystem worldwide. *Ecological Complexity*, *20*, 240–247. https://doi.org/10.1016/j.ecocom.2014.01.003

Zhang-Zheng, H., Adu-Bredu, S., Duah-Gyamfi, A., Moore, S., Addo-Danso, S. D., Amissah, L., Valentini, R., Djagbletey, G., Anim-Adjei, K., Quansah, J., Sarpong, B., Owusu-Afriyie, K., Gvozdevaite, A., Tang, M., Ruiz-Jaen, M. C., Ibrahim, F., Girardin, C. A. J., Rifai, S., Dahlsjö, C. A. L., … Malhi, Y. (2024). Contrasting carbon cycle along tropical forest aridity gradients in West Africa and Amazonia. *Nature Communications*, *15*, 3158. https://doi.org/10.1038/s41467-024-47202-x

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