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Sustainable palm fruit harvesting as a pathway to conserve Amazon peatland forests

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Abstract

Sustainable management of intact tropical peatlands is crucial for climate change mitigation, biodiversity conservation and supporting the livelihoods of local communities. Here, we explore whether sustainable fruit harvesting from *Mauritia flexuosa* palms could support these linked goals by increasing fruit production and incomes across the 2.8 million ha of the most carbon-dense ecosystem in Amazonia: the lowland peatlands of north-eastern Peru. *M. flexuosa* is dioecious and fruits are typically harvested by felling female palms; the proportion of female palms therefore provides a good indicator of the health of a stand. Across 93 widely-distributed sites, we found that the proportion of female palms increases with travel time to the urban market and, overall, fruit harvesting has halved the current potential production and income from this resource. However, significantly more female palms are found where fruit are harvested by climbing. We estimate that region-wide uptake of climbing could eventually increase potential fruit production by 51 %, and increase its gross value to 62 ± 28.24 million USD a^{-1}. These findings demonstrate both the high cost of unsustainable resource extraction in Neotropical forests and outline a practical path to conserve and sustainably exploit one of the most carbon-rich landscapes on the planet.

Keywords: degradation, *Mauritia flexuosa*, tropical peatland, palm swamp forest, livelihoods, sustainable harvesting.

Introduction

Tropical peatlands store approximately 104 billion tonnes (Pg C) of carbon[1], harbour unique combinations of flora and fauna and provide a wide range of resources for indigenous and local communities[2-4]. Sustainable management of these ecosystems is therefore crucial for addressing three major interlinked challenges: climate change mitigation, biodiversity conservation and supporting livelihoods of forest-dwelling peoples. However, the integrity of these ecosystems is threatened by fragmentation from infrastructure development and agricultural expansion[5,6], while logging and unsustainable harvesting of non-timber forest products (NTFPs) are reducing the ability of peatland forests to supply resources that support local communities[7,8]. To support sustainable management and conserve the carbon stocks and biodiversity of tropical peatlands, it is important to quantify the services that these forests provide for people. In particular, it is crucial to understand how historical resource extraction has altered the abundance of economically important species and whether sustainable harvesting techniques can enhance the health of populations of these taxa.

We address these questions in the context of a key economic resource from Amazonian peatlands: the fruit of the palm *Mauritia flexuosa*, which is known in Peru as 'aguaje'. This palm is the most common species of tree in the forests on the extensive lowland tropical peatlands in northeastern Peru that store at least 3.14 Pg C, equivalent to >60 years of national fossil fuel emissions[1,9]. *Mauritia flexuosa* is characterized by many features that support successful large-scale NTFP use and commercialization[10,11]: the palm is a native and abundant component of Amazonian peatland ecosystems[12,13], there is a long-standing regional market for the product[11], and there are emerging, although far from comprehensively applied, legal mechanisms for communities to obtain land tenure along the major rivers[5] and rights to extract forest resources via government institutions. The resource is also already a significant component of community incomes and activities: where currently harvested, sale of its fruit represents 15–22 % of family incomes (USD 208–227 a^{-1})[14,15]. However, fruit harvesting is typically performed by felling the fruiting palms and as *Mauritia flexuosa* has a dioecious breeding system with separate male and female individuals, fruit harvesting reduces the density of female palms in these stands[16]. Although the negative impact of this activity has been recognised for more than 30 years[17], estimates of the magnitude of this activity are scarce: estimates of the number of stems of *Mauritia flexuosa* that are felled each year vary from 12,900 - 24,000 palms in 2007[18], to approximately 114,000 between 2012-2013[2]. There is also shown strong spatial and temporal variation in the origin of aguaje fruit arriving in the main city of Iquitos[2]. However, the overall drivers and cumulative impact of decades of tree felling on the spatial patterns of the proportion of female palms are unknown. It is also unclear whether sites where tree climbing has been introduced as an intervention to promote sustainable management have a higher proportion of female palms than sites where female palms continue to be felled. Evidence for a positive impact of tree climbing and an understanding of the spatial distribution of the resource base would enhance the justification for conservation action to expand the typically patchy and ephemeral sustainable management projects in this region.

Establishing a historical baseline of resource availability

Understanding how historical resource extraction has altered the abundance of species used by local communities requires us to address a key challenge in conservation science: how to quantify the impact of resource extraction on populations when we lack data on species abundance before harvesting. Establishing baselines is crucial for assessing the severity of declines in biodiversity and to stimulate conservation action. For example, long-term monitoring data have been used to estimate that 68 % of populations of vertebrate species have declined worldwide since the 1970s[19]. However, data on the long-term trajectory of plant populations, and tropical species in particular, remain scarce. Anecdotal reports, such as the disappearance of *Ceiba* trees from Amazonia in the 1970s – 80s[20], are susceptible to "shifting baseline syndrome" where successive generations assume that the state of resources that existed when they started to interact with the environment represents the baseline condition[21,22]. In contrast, qualitative assessments of extinction risk[23], and recent quantitative estimates of the impact of land-use change on population sizes of Amazonian tree species[24], do not provide sufficiently precise, species-level information on the trajectory of tree populations to design focussed interventions. Here, we tackle the lack of baseline data by measuring, mapping and analysing large-scale spatial variation in a direct indicator of the level of unsustainable extraction of the resource: the proportion of female palms in a stand. The sex ratio for unharvested stands and in plantations is 1:1[25,26] and therefore by comparing variation in the proportion of female palms within stands to a baseline value of 0.5, we can quantify the levels of resource extraction due to destructive harvesting.

We collected an extensive dataset of this novel indicator to explore the drivers of the intensity of historical resource extraction across the peatland complex of northern Peru. Given its regional importance as a food source, we expected levels of unsustainable extraction to be highest nearest the main urban centre of Iquitos, where transport costs are lowest, similar to other NTFPs with large regional markets[27]. We also explored the impacts of subsistence consumption by communities on the resource, by testing whether smaller palm swamps located near larger communities had a lower proportion of female palms independent of their proximity to Iquitos. Finally, we tested whether the sites where climbing techniques are now used have a higher proportion of female palms compared to sites where palms are cutting for fruit harvesting. We use insights from these analyses to model levels of unsustainable resource extraction from *M. flexuosa* populations across the Amazonian peatland complex and to estimate the decline in fruit production that has occurred as a result of felling palms. By demonstrating both the large cost that historical unsustainable resource extraction imposes on communities today and how sustainable management techniques could improve resource levels at large scales, our results open up a route to conserve one of the most carbon-rich landscapes in the Neotropics.

Results

Spatial variation in unsustainable resource extraction

The proportion of female palms of *M. flexuosa* among stands varied widely among the 93 sites, from three sites where less than 6 % of adult palms were female, to 24 sites with healthy populations where more than 40 % of adult individuals were female (Fig. 1). The total travel time to Iquitos from each site was significantly related to the variation in the proportion of female palms (GLMM; $z= 3.9$, $p<0.001$; Fig. 1, Supplementary Fig. 1): most of the sites with few female palms are located within four hours travel from Iquitos, whereas four sites located in the communities of Puerto Diaz and Nuevo Milagro which require >40 hours of travel from Iquitos, have stands with sex ratios approaching 0.5 (Figs. 1 & 2). However, neither the number of inhabitants (GLMM; $z= -0.77$, ns), nor the area of accessible palm swamp for each community (GLMM; $z= 0.71$, ns) were related to the proportion of female palms.

Crucially, sites where palms are climbed, rather than cut, for harvesting have a higher proportion of female palms (GLMM; $z= -2.1$, $p<0.05$; Fig. 1). This effect translates to an increase in the percentage of female palms from 26 % to 36 % in stands where palms are climbed, compared to cut, to harvest fruits. Variation in the proportion of female palms among sites harvested by climbing may be related to the timing of the transition from cutting to climbing the palms (Fig. 1). For example, in the community of Puerto Alegría, community members initiated tree climbing for harvesting in the 1980s; stands here currently have 52 % female adult palms. In contrast, in Pacaya Samiria National Reserve, the transition, overseen by SERNANP (the Peruvian National Parks Authority), was initiated in 2002 and some sites have less than 20 % female palms (Supplementary Table 1).

Modelling levels of unsustainable resource extraction of *M. flexuosa.*

The relationship between the proportion of female *M. flexuosa* palms and the total travel time to Iquitos was used to model variation in this indicator of forest health across the region (see Methods). Overall, the predicted level of unsustainable resource extraction declines markedly with distance from Iquitos (Fig. 2), but there are also stands close to the city, such as between the Marañón and Ucayali rivers, that have a high proportion of female palms because they are only accessible by small tributaries rather than via the main rivers (Fig. 2). The Tigre river basin, in the north of the study area also has *M. flexuosa* stands with an unexpectedly high proportion of female palms given its proximity to Iquitos (Fig. 2). This finding is consistent with the very low levels of aguaje fruit supply to Iquitos originating from the upper river Tigre in 2012/13[2]: although there were high levels of fruit supply from close to the mouth of the Tigre from the community of Nueva York, fruit supply diminished much more rapidly with distance along the river, compared to similar distances along the neighbouring river Marañón[2,28]. The healthy state of the stands alongside the upper river Tigre may be related to the lower frequency of transport along this river compared to other major rivers, as the Tigre river does not connect to other large regional centres or national transport links.

The total potential production from harvesting fruits of *M. flexuosa* with the current spatial pattern in the proportion of female palms, estimated for palm swamps located within 5 km of the main rivers, is 298,581 Mg a^{-1}. This value equates to a gross potential value of 41 ± 20.13 million USD a^{-1} for the whole region, with per hectare values ranging from 45 to 333 USD $ha^{-1}a^{-1}$ based on current market prices (Fig. 4; see Methods). This large, overall potential value is comparable to the income from tax by oil extraction to the Loreto regional government (Fig. 4). However, historical removal of female palms means that this level of productivity is far lower than might be achieved if the stands of *M. flexuosa* were in their 'natural' state. If 50 % of the palms in the stands were female, the estimate of the potential production more than doubles to 829,315 Mg a^{-1}, with a potential gross value of 92 ± 38.27 million USD a^{-1} if prices are maintained as the market expands, similar to the gross declared value of timber to the Loreto regional government (Fig. 4). In other words, our estimates suggest that historical human extraction of palm fruits has led to a 55 % reduction of the productivity of the resource that is available to communities today.

More positively, the higher proportion of female palms in sites where tree climbing has been initiated suggests that some of this potential can be recovered over coming decades if this harvesting technique were to be introduced more widely. If the improvement in sex ratio found in the sites where fruit harvesting is carried out by climbing is applied across the region, productivity could rise to 656,384 Mg a^{-1} and the potential gross income could rise to 62 ± 28.24 million USD a^{-1}, which is an increase of 51 % compared to current values (Fig. 4).

Discussion

Our extensive dataset of the proportion of female palms in stands of *M. flexuosa* across the peat swamps of northwest Amazonia reveals multiple insights into the drivers and legacy of resource extraction, the impact of sustainable management practices and the economic potential of this resource. The link between levels of resource extraction of stands and their proximity to the main regional market likely reflects the overall importance of the commercial demand for this product as food source in Iquitos and beyond, rather than subsistence demand within communities, for driving resource extraction. The influence of the market extends approximately two days travel from Iquitos (Fig. 2), consistent with fruits remaining viable for sale up to five days following harvesting[14] and the distances of communities that supplied fruit to Iquitos during 2012/13[2]. Elsewhere in the tropics, shorter distances to the nearest urban centre have also been linked to variation in levels of biodiversity-based resources, such as lower population sizes of mammal, bird and timber species[27,29]. Our results, therefore, emphasise the importance of managing the impact of cities in tropical forest countries to reduce the impact of resource extraction on surrounding forests whilst maintaining the services that they provide.

Our finding that the total potential production and value of *M. flexuosa* fruits has halved due to cutting female palms (Fig. 4), provides an estimate of the often unrecognised but substantial cost that current and historical resource extraction places on communities. This impact is typically noted only anecdotally and at small spatial scales. For example, income from fruit extraction through cutting palms in the community of San Miguel diminished by 46 % over five years (1995–2000)[10], whilst the community of Dos de Mayo ultimately was forced to stop extraction as the resource became unavailable within the forests surrounding the community (G. Hidalgo, pers. comm.). In contrast, this study provides a quantitative estimate of the impact of resource extraction across a Neotropical forest landscape that spans nearly three million hectares. Our estimate of loss is similar to the magnitude of global declines in animal populations due to hunting since the 1970s[19] and demonstrates that the fingerprint of human resource extraction can also be strong in plant communities even in apparently intact forest landscapes.

The loss of potential production of *M. flexuosa* fruits reflects the historical management of this species as a common pool resource in these peatland landscapes[30,31]. Fortunately, recognition that intensively cutting trees for harvesting fruits is unsustainable is leading to the introduction of communal management systems that incorporate several aspects of successful adaptive governance schemes, particularly related to encouraging dialogue among stakeholders and defining the boundaries of the resource[32]. Sustainable management initiatives that promote tree climbing for fruit harvesting have been led by the communities themselves, such as in Puerto Alegría, NGOs (e.g. Amazonians for Amazonia; AMPA) and/or government institutions (e.g. the Peruvian Forest Service, SERFOR; the Peruvian Fund for Nature, PROFONANPE; SERNANP and the Loreto regional government, GOREL). Key components of all these initiatives have been the designation of land tenure and achieving sole legal access for communities over nearby palm swamps, and the establishment of community-led associations where a small number of families plan, extract and market the fruit. For communities inside national protected areas, harvesting activities are ultimately regulated by SERNANP, and there are attempts to regulate harvesting activities in communities outside protected areas as part of projects implemented by SERFOR and GOREL. Such regulation involves issuing permits to implement approved management and harvesting activities. However, in all sites, in practice, monitoring and active regulation of harvesting is at an early stage.

Cutting the palms for harvesting preceded the introduction of climbing in all sites, and the timescales of the start of the interventions and the demography of *M. flexuosa* suggests that the higher proportion of female palms in sites where palms are climbed today is due to recruitment of new adults since the intervention was introduced: *M. flexuosa* requires at least 6–10 years to become adult from seed[10], and these interventions were introduced 10–30 years ago. Of course, full recovery of these forests would require adequate levels of regeneration and in some sites, seed limitation may prove a barrier to recruitment of new individuals. However, demographic models of *M. flexuosa* suggest that recruitment can be maintained, up to harvesting rates of 50–90 % of fruit racemes[33].

On a per hectare basis, based on the current pattern of the proportion of female palms across the region, our analysis indicates a current potential annual gross income of 45-333 USD $ha^{-1}a^{-1}$ which is similar to published values for sustainably harvested stands in the community of Veinte de Enero[10,34]. These values are of course lower than equivalent per hectare values of large-scale plantations of *Elaeis guineensis* for palm oil which can rise to several thousand dollars per hectare[35]. However, sustainable harvesting of *M. flexuosa* fruits provides a wider and more evenly-distributed range of benefits than plantation development[15,17]: it could provide a foundation for a regional economy that substantially improves incomes to local communities whilst also protecting the high carbon stocks and unique biodiversity of these ecosystems. It is also more ecologically appropriate within the dynamic Amazonian peatlands where drainage is not possible. This approach of using community-led, sustainable management of existing stands of a native palm species contrasts strongly with that of deforestation and conversion to intensive agriculture of a non-native palm species which has been the predominant development pathway for tropical peatlands in SE Asia in recent decades[36]. As the debate opens up on the nature of economic development in Amazonia following the COVID-19 pandemic, it is crucial that the full potential of sustainable, climate-friendly development options such as *M. flexuosa* fruit extraction are explored.

Our estimate of the economic potential of *M. flexuosa* fruit harvesting is broadly comparable to revenue levels from other important NTFPs in Amazonian such as açaí fruit (*Euterpe sp*.) which had a gross value of approximately 200 million USD in 2019 in Brazil[37], and Brazil nut extraction which was worth 75, 25 and 19 million USD for Bolivia, Brazil and Peru respectively in 2005[38]. Intriguingly, the current potential value of *M. flexuosa* fruit is equivalent to 39 % of the annual declared value of timber in 2015 (106.6 million USD) and almost double the average annual value (USD 21.6 million USD) of tax revenue from oil extraction from 2015–2018[39,40] for the region of Loreto in northeastern Peru (Fig. 4). Overall, even with uncertainty about how prices would change as markets develop, these comparisons indicate that sustainable fruit harvesting has similar potential for generating economic benefits for communities to existing major Amazonian NTFPs, and could provide benefits that are comparable to redistributing tax revenues from oil extraction or deriving income from logging.

Realising the potential of sustainable *M. flexuosa* fruit harvesting will be challenging and need to heed lessons about the potentially illusory nature of the high value of NTFPs within intact tropical forests[41-43]. *M. flexuosa* fruit does broadly meet criteria associated with successful expansion of NTFP use[8,43]: for example, development of this product is closely aligned with national environmental policy, in this case related to enhancing sustainable management of tropical peatlands as part of the Nationally Determined Contributions (NDCs) of Peru to the Paris Agreement[44], increases in production and income can be closely linked to improving livelihoods given the widespread presence of extensive palm swamps close to communities across the region, and demographic models suggest ecological sustainability is possible in stands with fruit harvesting[33]. However, expansion of national and international markets will be crucial to drive increases in the overall value of this product, and maintain prices as production increases[42]. In this context, support for using fruit of *M. flexuosa* as the basis for juices and food supplements by national and international companies (e.g. RAFSAC, Aje Group, Inkanatura)[11] will be vital.

A range of steps needs to be taken to support communities that engage in palm fruit harvesting. Currently, uptake of climbing as a sustainable management technique has been limited because of a lack of training, equipment and information about the ease of harvesting by climbing. For example, there is often a perception that cutting down the palm is faster than climbing. However, in practice, both cutting and climbing take similar lengths of time - cutting an adult *Mauritia* palm takes around 20–25 minutes, whilst climbing takes 17–30 minutes[12]. A particular challenge is to develop effective community-led monitoring schemes to achieve successful, long-term management[32], and long-term support must be offered to communities to ensure that sustainable harvesting techniques are maintained even if demand increases. For example, the Maijunas, an indigenous group in the northern Peruvian Amazon, harvested this resource for their consumption using the mainly sustainable method of collecting ripe fruit from the ground, but as demand increased, the use of destructive techniques became common[45]. Legal land tenure needs to be expanded to all communities with access to palm swamps, and harvesting areas must be demarcated. More precise maps of the abundance *M. flexuosa* palms would also support the expansion of the management of this resource: high-resolution spectral data obtained using UAVs offers one way to map the distribution of palms accessible to communities, as *M. flexuosa* palms are readily distinguished from the surrounding trees[46]. Finally, safeguards are required to ensure that communities continue to be the primary beneficiaries of fruit harvesting as the market expands, and to avoid the benefits and resource being appropriated solely by private interests[47]. Overall, careful monitoring of the effects of harvesting on both the social and ecological aspects of these systems is required to ensure that there are not negative impacts[37], and support the drive to develop a sustainable and equitable biodiversity-based economy across Amazonia[48].

Our map of variation in the proportion of female trees of *Mauritia flexuosa* across the basin is also important for understanding where greenhouse gas emissions from peatland degradation may occur in the future. Although cutting removes female palms and reduces the abundance of *M. flexuosa* (Supplementary Fig. 2), the current impact on above- and below-ground carbon stocks and greenhouse gas emissions is likely to be small across the gradient of resource extraction that we studied here. Highly degraded sites, where palm swamps become dominated by pioneer trees are associated with significant carbon emissions due to higher respiration rates derived from the remaining organic matter[49]. However, the sites we studied here still have substantially higher densities of *Mauritia flexuosa* than the 16 stems ha^{-1} that were found in one highly-degraded site where significant carbon emissions were reported[49] (Supplementary Fig. 4). The sites in our study have therefore been modified, but currently likely not degraded and damaged to an extent that substantially affects their carbon balance. The challenge for the future is to ensure that these sites are not subsequently converted to secondary forest and other land uses, which is a pathway that may follow the removal of female palms and resulting loss of value of the standing forest. In this context, our map of the proportion of females across this region is an 'early warning' signal of where interventions are required to prevent more substantial modification of the landscape and greenhouse gas emissions. The higher proportion of female palms in sites where trees are climbed for harvesting and increase in the potential economic value of stands where this value approaches 0.5, indicates that introducing climbing techniques is a means to increase the value of standing forest, and as a result, help to conserve the carbon-rich peat deposits below these forests.

Our findings that historical resource extraction has halved the potential production of harvesting *M. flexuosa* fruit and that this can be reversed by tree climbing provides a powerful incentive to introduce and maintain sustainable management practices. This study therefore provides strong support for using sustainable harvesting of *M. flexuosa* fruits as a focus of Amazonian peatland conservation[5,50]. For local communities, the demonstrable success of using climbing to harvest fruits for maintaining the health of *M. flexuosa* populations will help to encourage uptake this technique across the region. For regional and national government institutions and NGOs, our findings will help to promote coordinated, region-wide initiatives to support the introduction of sustainable management programmes and support efforts to increase the market for *M. flexuosa* fruits. For the international conservation community, these results demonstrate the viability of sustainable palm swamp management for preserving Amazonian peatlands and the substantial carbon stocks that they hold below ground. Finally, the results demonstrate how apparently intact tropical forests have been affected by resource extraction, and how developing a precise understanding of how ecosystems have been modified can be used to define a pathway for conservation action.

Methods

Study area and species description

The study was carried out across the extensive peatlands of the Pastaza-Marañón foreland basin in the region of Loreto in northern Peruvian Amazonia. This basin is a geological depression formed in reaction to the uplift and eastern movement of the Andes and today acts as collecting point for water from tributaries of the upper Amazon[50]. This region is characterised by a warm, humid tropical climate with a mean temperature of 26 °C and a daily range of 22 °C – 30 °C[51,52]. The average annual rainfall of the region is around 3000 mm and there is no regular dry season[52].

Peatlands cover 35,600 km^2 of the basin and palm swamps, the most extensive vegetation type, cover 2.8 million hectares or 78 % of this area[9]. These stands are located along the Marañón, Ucayali and Amazon rivers and their tributaries: the Samiria, Tigrillo, Tigre, Itaya and Nanay rivers (Fig. 3). The palm swamps have an average peat depth of 1.7 m (range 0 – 5.4 m) and in total contain 2.3 Pg C (95% confidence limits: 0.27 – 6.00)[9].

The dominant species of these peatlands is the palm tree *Mauritia flexuosa*[13] which is locally called "aguaje" ("burití" in Brazil, "canangucho" in Amazonian Colombia, "moriche" in Venezuela[53]). Palm swamps are locally named "aguajales" due to the dominance of *M. flexuosa* in this type of forest[54]. *M. flexuosa* is a large native palm tree of the neotropics, reaching 35 – 40 m height and 50 cm diameter[12,55]. The fruit is an elliptical-globular drupe, 3 – 7 cm long, with a mean weight of 40 to 85 g [14]. Its phenology varies across the region, as the peak of the fruit season is linked to variation in the water level of the river[56] and as a result there is a continuous supply of fruit to the market[2].

This species is dioecious and thus has separate male and female individuals[55,57]. The proportion of female palms is therefore a good indicator of levels of unsustainable resource extraction in palm swamp ecosystems as female individuals of *M. flexuosa* bearing fruit are typically harvested by cutting down the palms[16,58] (Supplementary Fig. 6). The sex ratio of *M. flexuosa* in an undisturbed stand was reported as 1:1 (50 % male and 50 % female palms) in the Colombian Amazon[25] and a similar ratio (1.1 : 1) was found in two experimental plantations of this species in Jenaro Herrera in the Peruvian Amazon[12,26]. For this study, we, therefore, assess the level of unsustainable resource extraction as the reduction in the proportion of female palms compared to a baseline of 50 %. This knowledge of the baseline gender ratio under natural conditions allows us to estimate the impact of historical resource extraction on the health of *M. flexuosa* populations.

Sampling sites and field methods

Data on the proportion of female palms in different palm swamps was collected from sites across the region that encompass the full gradient of human use, including largely undisturbed forests, abandoned areas where harvesting stopped 3 – 15 years ago and areas that are actively harvested every fruiting season (Supplementary Table 1). Stands were selected based on covering a wide range of distances to Iquitos and prioritising data gaps. In all sites, estimates of the proportion of female palms were based on evaluating the gender of adult palms based on the presence of floral organs, by carefully observing flowers/fruits either on the palm using binoculars or on the ground next to the corresponding palm stem (Supplementary Fig. 5).

Data on the variation in the proportion of females of *M. flexuosa* in the largely undisturbed forests in the eastern portion of the basin was obtained from sixteen, 0.5 ha plots established by the Instituto de Investigaciones de la Amazonía Peruana (IIAP) and the Amazon Forest Inventory Network (RAINFOR) between February 2017 to October 2019[59]. These data were augmented by information from six transects located adjacent to the plots and sampled between June 2008 and July 2009 - these transects represent 6.5 % of total sampling sites and the values were validated by new transects established under this study in the surrounding area - also, fourteen transects between February 2017 to October 2019 and 10 transects in January and February 2020. In each of these transects, the gender of 100 –200 adult palms was recorded. Data on variation in the proportion of female palms of *M. flexuosa* in the undisturbed forests in the western portion of the region in Datem del Marañón province were collected using sixteen plots varying from 0.36 – 0.72 ha in size (Supplementary Table 1), in August and September 2018[60].

Finally, thirty-one transects were established as part of this study in June and July 2019 to understand how the proportion of female palms varies among areas that have been harvested in the past but since abandoned, and in areas that are being harvested today. Sampling sites were located in accessible areas along the rivers, which is the most important area for fruit sold in the main regional market. For each of these transects, the gender was recorded for 200 individuals and the transects were extended if necessary until the sample included at least 20 female palms. This sample size and design was chosen based on how uncertainty in estimates of the proportion of female palms varies with the level of the unsustainable resource use using simulations based on the binomial distribution (Supplementary Fig. 7). Sampling 200 individuals provided reasonable levels of confidence in estimates of the proportion of female palms across three levels of harvesting - the baseline proportion (50 %), half the "natural" female proportion (25 %) and where there is a low proportion of female palms (10 %). Semi-structured interviews with harvesters during fieldwork were used to obtain information about harvesting techniques, the time and distances to harvesting sites and the sale price of a sack of aguaje fruit in each community.

Explanatory variables

Variation in the proportion of female palms associated with different communities was broadly related to variation in the amount of aguaje fruit that each community supplied to Iquitos in 2012/13[28] (Spearman rank correlation, $p<0.001$; Supplementary Fig. 3). To identify the ultimate causes of spatial variation in unsustainable resource use of palm swamp forests, we analysed whether a range of variables associated with drivers of the intensity of harvesting activities were associated with variation in the proportion of female palms. We assessed the influence of the urban market by comparing the travel time to the main market (Iquitos) from each sampling site with the proportion of female palms. In Iquitos, the fruits are commercialised as fruits and also transformed into a paste for use in other products. The total travel time (hrs) from each sampling site to Iquitos was estimated as the sum of the travel time from Iquitos to the nearest community by river, the travel time from the community by river to the nearest access point for each site, and the walking time from the river to the site. The estimate of the travel time from Iquitos to each community was based on a boat speed of 15 km hr^{-1} (by "lancha")[61] for routes via the Marañón, Ucayali and Amazon rivers and 4 km hr^{-1} (by "peque peque") for boats travelling during the fieldwork on the Nanay, Itaya, Tigre, Tigrillo and Samiria rivers. Each palm swamp was allocated to its nearest community, and the travel time from the community to the nearest access point was estimated based on the distance by river, and the travel speed by "peque peque". Finally, the walking time from the nearest access point to the sampling site was estimated based on the straight-line distance and a walking speed of 1.5 km hr^{-1} within the forest recorded during fieldwork in palm swamps in this study, the speeds values were registered by a GPS device. Spatial modelling was performed using the cost distance, Euclidean allocation and Euclidean distance functions in ArcGIS v. 10.4.1[62]. The modelled travel times closely matched times to reach Iquitos estimated by community members during fieldwork (Supplementary Fig. 8).

The importance of variation in the intensity of harvesting by local communities for determining levels of unsustainable resource use was assessed by exploring whether variation in the number of inhabitants among communities (population size varies from 10 to 3500 members[63]) and the area of palm swamp within 5 km of each community explains variation in the proportion of females among sites. The effect of management technique was assessed by comparing the difference in the proportion of female palms among palm swamps where communities cut the palms to harvest the fruits, with those where communities climb the palms without damaging the trees[12]. Information on the technique that has predominately been used at each site during the previous decade was obtained by a semi-structured interview to harvesters during the fieldwork and verified during the census of the transects by noting the presence/absence of cut trunks.

Data analysis

The proportion of females for each sampling site was obtained by dividing the number of female palms by the total number of adult trees. We used generalised linear mixed models implemented using the *glmer* function within the lme4 package[64] in R v.3.5.3[65] to assess if the explanatory variables were significantly related to the variation in the proportion of female palms. Our statistical model was:

$$y = \beta_0 + \beta_1 * Time + \beta_2 * Inhabitants + \beta_3 * Area + \beta_4 * Technique + (1|Community) + (1|River) + \varepsilon$$

where y is the proportion of female palms within the stand, $\beta_0 - \beta_4$ represent the model coefficients, *Time, Inhabitants, Area and Technique* are the travel time to the urban market of Iquitos, the number of inhabitants per community, the area of palm swamp within 5 km of each community and the harvesting technique, respectively. *Community* and *River* are nested, random factors which reflect that multiple palm swamps may be accessed by any given community, and multiple communities are found along each river. River was included as a random factor as each watershed has different characteristics in terms of river size and transport frequency that may influence how the other factors relate to the proportion of female trees (Supplementary Fig. 1). All continuous variables were scaled prior to analysis and each data point was weighted by number of palms sampled at each site.

The analysis was subjected to k-fold, cross-fold validation to test if the predictions of the mixed model were robust to omitting subsets of the underlying data (Supplementary Fig. 9). Spatial auto-correlation was explicitly incorporated in the original statistical model through the nested, random factors of community and river basin, so we used a random cross-fold approach to validate the predictions with the same underlying model structure. Predicted values of the proportion of female palms for each site, based on running a mixed model with 80 % of the original data, were significantly correlated with the observed values (Supplementary Fig. 9). This result demonstrates that the relationships are not unduly influenced by a small subset of the data and the model can be used to describe variation in the proportion of female palms across the range of the explanatory variables that are found in this region.

Modelling variation in the proportion of female palms of *M. flexuosa*.

The finding that travel time explains a significant amount of variation in the proportion of female palms of *M. flexuosa* among sites, was used to model this parameter across the region of Loreto (Fig. 2). Travel time to Iquitos was estimated across Loreto at a 1 km^2 pixel size (Fig. 3), following the methods above. All pixels representing *M. flexuosa* stands were then extracted using a map of the distribution of palm swamps across the Pastaza-Marañón basin[9]. The coefficients from the mixed model (Fig. 1, Supplementary Fig. 1) were used to estimate the proportion of female palms of *M. flexuosa* across the palm swamps of Loreto based on the travel time to Iquitos from each pixel. The proportion of female palms was estimated independently for palm swamps in each river basin, as the proportion of female palms varies significantly among watersheds (Supplementary Fig. 1).

Estimating the potential value of *M. flexuosa* to local communities

The potential area of fruit harvesting was defined as all palm swamps within 5 km from a main river, based on information from harvesters obtained during fieldwork. This area was delimited based on the information recorded about the distance they walk to the extraction zones and the distance of the sampling sites from the communities. Palm swamps within this area cover 331,900 ha (Fig. 2; area indicated by the black solid line).

The proportion of females across this harvesting area was used to estimate the gross potential income of fruit sale. Firstly, the density of female palms was estimated based on the estimated proportion of females for each pixel. Our field data demonstrates that the density of males remains constant as the proportion of females declines in the sampled stands; within our dataset, there is no evidence of substantial felling of males even where the females have been almost entirely harvested (Supplementary Fig. 2), even though in some communities, a few male palms are occasionally felled for making walkways or cultivating the palm weevil (*Rhynchophorus palmarum*[3,4]). We therefore estimated the density of females as:

$$D_{fem,i} = \frac{(F_i * D_{male})}{1 - F_i}$$

where $D_{fem,i}$ is the estimated number of adult female palms of *M. flexuosa* of each pixel, i, in the harvesting area, F_i is the estimated proportion of females of each pixel, and D_{male} is the average density of male palms across all sites (86 ind/ha). This model of how female harvesting affects the density of populations of *M. flexuosa* fits the observed data closely (Supplementary Fig. 2).

The total potential current income was then estimated as:

$$Income_t = \sum_{i=0}^{n} D_{fem,i} * A * R_i * S_i * P_i$$

where $D_{fem,i}$ is the density of female palms in each pixel, *i,* in the harvesting area and A is the area in hectares per pixel (100 ha). R is the average number of racemes harvested per palm (1.3 ± 0.03 racemes); this value was calculated from data on the number of racemes of 3,567 female palms recorded during fieldwork across all sites and integrates across the temporal and spatial variation in fruit production among individual palms. S is the factor (0.6 ± 0.1 sack/raceme) used to convert the number of racemes into the number of sacks of fruit of aguaje; this value was calculated from measurements of fruit production from 16 *M. flexuosa* palms in Jenaro Herrera in 2018[12]. P is the average price of USD 5 ± 0.32 (17 PEN) per sack recorded in the fieldwork from 13 communities during the interviews with harvesters. The overall projected income for the total harvesting area, $Income_t$, was calculated as the sum of the value across all pixels and represents a potential, maximum gross value of this resource in this region.

The potential income from harvesting area was also estimated for 'natural' forests, assuming a uniform proportion of 50 % female palms across all pixels. Finally, to estimate the potential income if the fruits were harvested by climbing and the forests began to recover, the estimates of the proportion of female palms across all pixels from the current scenario were modified by adding the estimated impact of climbing from the mixed model (an absolute increase of 0.1 in the proportion of female palms up to a maximum value of 0.5). This scenario represents the potential value of the stand after approximately one to two decades if cutting trees down for harvesting ceases today.

The density of palms, number of racemes per palm, the sack/racemes factor and price of sacks all vary due to natural variation among stands and variation in market conditions. To estimate the standard error of the overall potential income, the standard errors of each component were propagated conservatively as the sum of the fractional errors of each term[66] as:

$$SE\ (Income_t) = \sum_{i=0}^{n} |Income_t| * \left(\frac{SE(D_{fem,i})}{D_{fem,i}} + \frac{SE(R_i)}{R_i} + \frac{SE(S_i)}{S_i} + \frac{SE(P_i)}{P_i}\right)$$

Data availability statement: The datasets used in the analysis in the current study are available within the article and supplementary information file.

Consent for publication: The authors affirm that human research participants provided informed consent for publication of the images in Supplementary Figure 6.

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Author contributions

C.G.H.P., E.N.H.C and T.R.B conceived the study, C.G.H.P., T.R.B., O.L.P and E.N.H.C designed the study. C.G.H.P and T.R.B analysed the data, C.G.H.P. created the maps and wrote the paper; J.D.P., J.D.J., J.M.R.H, C.J.C.O., G.G.M., G.F.L., E.R.P., J.I.P., L.G.S. and M.M.B. led or took part in the field data collection and D.D.C.T, K.H.R., S.J.C., F.C.D., S.D.B., M.P.C., M.V.D.Z., G.M. and J.L. contributed funding or provided materials for mapping the proportion of female *M. flexuosa* trees in palm swamp forests. All co-authors commented on and approved the manuscript.

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Figure legends

Figure 1. Relationship between the proportion of female palms and travel time to Iquitos, for 93 palm swamp forest stands across the Pastaza Marañón basin. Sites where trees are cut down to harvest fruits are shown with filled circles and sites where palms are climbed for harvesting are shown using open circles. The black line indicates the predicted relationship from the mixed model between travel time and the proportion of female palms for sites where trees are cut down to harvest the fruits; the shaded area indicates the 95 % confidence limits of this relationship. This relationship was used to predict and map the proportion of female palms across the palm swamps of Loreto.

Figure 2. Map showing modelled variation in the proportion of female *Mauritia flexuosa* trees in palm swamp forests in the northern Peruvian Amazon. The estimated proportion of female *M. flexuosa* trees varies more than four-fold across the palm swamps of the region. The solid black line delineates *M. flexuosa* stands within 5 km of the main rivers and is used for calculating the total area of accessible palm swamps for estimating the maximum potential income from fruit harvesting. Sampling sites evaluated for this study are also shown. Inset highlights the location of Iquitos within Loreto, Peru.

Source: this study

Figure 3. Map of estimated travel time to Iquitos from across Loreto. Estimates are calculated for each 1 km^2 pixel based on river transport times from Iquitos to the nearest point on a river, plus walking times to the centre of each pixel. River transport

is the main method of transportation in Loreto, with boat speed varying according by route and load capacity. Here, we used a speed of 15 km hr^{-1} for “lanchas” that ply the main rivers and 4 km hr^{-1} for “peque peques” that are used on the tributaries (see Methods).

Source: this study

Figure 4. Estimated total potential regional income based on different land uses for northern Amazon Peruvian forests. Left hand bar shows total potential estimated value for accessible palm swamps <5km from a main river of (1) *M. flexuosa* fruit harvesting today (± standard error), (2) *M. flexuosa* fruit harvesting where sustainable harvesting techniques are employed across the whole area and the proportion of females has increased in absolute terms by 0.1, up to a maximum value of 0.5, consistent with the state of palm swamps today where fruits are harvested by climbing the trees, and (3) under baseline, ‘natural’ conditions assuming a 1:1 sex ratio. Also shown are the average annual value of taxes to the regional government of Loreto for the period 2015 – 2018 for oil exploitation (central bar), and the total declared value of timber by forestry companies for 2015 (right hand bar). Timber and oil tax revenue values were adjusted to 2019 values using the World Bank consumer price index[67].

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