

The legacy of human use in Amazonian palm communities along environmental and accessibility gradients

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Abstract

Aim: Palms are iconic and dominant elements of neotropical forests. In the Amazon region, palms have been used and managed by humans for food, material, medicine and other purposes for millennia. It is, however, debated to what extent the structure of modern palm communities reflects long-term human modification. Here, we investigate the complex interplay of ecological and societal factors that influence the distributions of both human-used and non-used palms in western Amazonia.

Location: Amazonia.

Time period: Present.

Major taxa studied: Palms (Arecaceae).

Methods: We used Bayesian hierarchical joint species distribution models to predict the distributions and environmental niche dimensions of 78 western Amazonian species, and to explore their relationships with their diversity of human uses and with specific uses (food, construction and medicine). The models were parameterized with a comprehensive set of field- and satellite-derived environmental predictors.

Results: Our results suggest that a combination of ecological and anthropogenic factors drive the present-day distributions of Amazonian palms. The modelled ecological niches of the species revealed use-related species-sorting along soil, climatic, accessibility and drainage gradients. We found peaks in the proportions of useful palms and their diversity of uses in fertile soils, close to rivers, and on floodplains. These are habitats favourable for human settlement, although they harbour naturally restricted palm species pools. We also found a negative correlation between predicted palm species richness and number of human uses across western Amazonia.

Main conclusions: Soil characteristics, accessibility, and species pool size all contribute to defining palm–human relationships. At the basin scale, the signature of human use on palm communities was predicted to be stronger in the species-poor southwest than in central-western Amazonia. Overall, we conclude that environmental conditions have influenced modern Amazonian palm distributions both directly and indirectly, by regulating human settlement patterns and natural resource use over extended time periods.

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KEYWORDS

biodiversity, human footprint, plant communities, soil, tropical forests, vegetation

1 | INTRODUCTION

Management of wild plants has been practiced in lowland Amazonia for millennia (Bush et al., 1989; Bush & McMichael, 2016; Clement et al., 2015). Although the region was once considered pristine, the consensus now holds that Amazonian peoples have transformed their environments over extended periods (Heckenberger, 2003) and that modern forests reflect a mosaic of human and natural influences (Clement et al., 2015; Heckenberger, 2003; Heckenberger et al., 2007). However, the extent to which present-day Amazonian plant communities, and the distributions of species within these, have been directly shaped by pre- and post-Columbian peoples remains a topic of debate (Barlow et al., 2012; Bush et al., 2021; Levis et al., 2017; McMichael et al., 2012, 2017; Sander et al., 2018).

Amazonian peoples have both expanded and reduced species abundances and distributions by moving, planting and protecting useful species, and by cutting and practicing small-scale burning (Clement, 1999; Levis et al., 2017; Lévi-Strauss, 1952; Maezumi et al., 2018). There have also been periods of dramatic vegetation change, and reforestation that are likely to be associated with human population collapses (Koch et al., 2019; Maezumi et al., 2018) and changes in land use patterns (Bush et al., 2021). The arrival of Europeans in South America caused a continent-wide indigenous demographic bottleneck known as 'the Great Dying' (Koch et al., 2019; Wolf, 1982). The consequences included a 90% decline in indigenous population size and hence a drastic reduction in the intensity of land management (Nevle & Bird, 2008). One hypothesized result of this event was the regrowth of large forest areas (McMichael, 2021). This may, in turn, have favoured plant species managed by humans (Levis et al., 2012; ter Steege et al., 2013), resulting in forests with a species composition that is partially driven by past human presence.

Six of the top 10 top hyperdominant tree species in Amazonian forests are palms (ter Steege et al., 2013). Interestingly, these same six species are widely used by humans (Levis et al., 2017). Palms (Arecaceae) are iconic elements of neotropical forests, and their global economic importance is surpassed only by that of Poaceae, the grass family, which includes corn, rice and wheat (Balslev et al., 2016). Palm species richness increases regionally towards the equator (Bjorholm et al., 2005), likely due to high net diversification rates under climatically favourable and stable conditions (Svenning et al., 2008). Within Amazonia, environmental filtering further shapes the distributions of palm species along climatic, edaphic and hydrological gradients (Cámara-Leret et al., 2017; Costa et al., 2009). However, the strength of species–environment relationships varies widely among taxa (Cámara-Leret et al., 2017). Moreover, environmental determinism in palms is typically weaker than in other plant groups that are less used by humans, including melastomes, ferns

and gingers (Tuomisto et al., 2016; Zuquim et al., 2021). Relative to many other plant groups, palms are disproportionately abundant in lowland Amazonia (Muscarella et al., 2020). Thus, it has been hypothesized that humans have enriched palm communities historically and that natural reforestation may have further augmented the abundances of useful palms after the collapse of indigenous populations. Evidence of human settlements dating back to the late Pleistocene, and associated accumulations of palm seeds, are documented in northern Amazonia (Morcote-Ríos et al., 2021; Roosevelt et al., 1996). However, archaeological, palynological and botanical support for human-driven palm augmentation is limited and varies regionally (McMichael et al., 2012; Piperno et al., 2015). Anthropogenic and ecological drivers of palm distributions may furthermore be difficult to discern from each other since their spatial signatures may covary strongly. Environmental conditions synergistically influence the flora, human movements, settlement patterns and management practices.

Here, we provide a new perspective on the complex interplay described above by systematically combining information on palm species environmental niches with their known uses. We use an extensive field dataset on palm community composition across western Amazonia combined with field and satellite observations to shed light on palm species distributions and possible human use footprints. We hypothesize that: (a) palm species of different habitats will vary in their human use potential, and their number of uses will vary along environmental and human accessibility gradients; (b) palm species that humans intensively use are most likely to show spatial structure that is unrelated to present-day environmental conditions; (c) within palm communities, the proportions of useful species and their diversity of uses will shift as a function of palm resource diversity (defined as species richness) and along habitat and accessibility gradients.

To address these questions, we first model the environmental distributions ('niches') of each species and test whether niche positions along environmental gradients vary as a function of their diversity of uses. Second, we analyse covariance between residual spatial structure in palm species distributions (i.e., variance unexplained by environmental covariates) and human use variables to test if palm species more intensively used by humans are more likely to show spatial structure that is unexplained by current environmental conditions. Third, we evaluate the proportions of useful palms in the communities and their mean number of uses as a function of species richness and environmental and accessibility gradients. Finally, we map spatial predictions of (a) palm species richness, (b) the proportions of useful palm species with known food, construction and medicinal uses, and (c) palm use diversity across the entire western Amazonian region.

2 | MATERIALS AND METHODS

2.1 | Study area

This study analysed palm communities of mature forests of the western Amazonian lowlands (<600 m a.s.l.), which cover a wide range of edaphic, topographic and climatic conditions.

2.2 | Palm data

We obtained palm species data from inventories in 430 transects (each 500 m × 5 m) collected across the study region between 1995 and 2012 (details in Balslev et al., 2019). In each transect, all palm individuals were counted and identified to the species or variety level. The original dataset was quantitative, and classified individuals into seedling, juvenile, adult and sub-adult categories. Here, we transformed the original dataset from abundance to presence-absence data. Moreover, we included only adults and sub-adults, which were combined into a single category. Juveniles and seedlings were excluded from the analysis. Vouchers of collected specimens are deposited at the Aarhus University herbarium (AAU) and in at least one herbarium in the countries of origin of the specimens (COL, QCA, AMAZ, USZ, LPB, INPA).

2.3 | Environmental characteristics

Local environmental variables for each transect were obtained from the same published dataset (Balslev et al., 2019). Soil nutrient concentrations (SOIL; the sum of the exchangeable cations Na, Ca, Mg and K) were measured in the laboratory from topsoil (0–10 cm) samples typically taken at the beginning, middle and end of each transect. We used a single soil value, the log-transformed exchangeable cation sum averaged over all samples within each transect, to represent its soil fertility in subsequent analyses. Habitat types (HABITAT) were defined based on field observations, interviews with local guides, and visual examination of satellite images. The original classification included seven categories, which were condensed into two for analysis. The categories were coded as inundated forests, which include floodplains, backswamps and restingas (1), and terra-firme forests, which include pre-montane hills, terra-firme and white-sand forests and terraces (2). Anthropogenic soil areas (Amazonian Dark Earth, ADE) were not sampled.

Hydrological conditions (HAND) were coded as the vertical height of each transect above the nearest drainage (Nobre et al., 2011; Rennó et al., 2008). HAND values were extracted from a publicly available GIS layer at 90-m resolution and based on a 50-pixel drainage area contribution threshold designed to include smaller drainages (<http://www.dpi.inpe.br/Ambdata/English/download.php>). Nineteen bioclimatic variables were extracted at 30-arcsec resolution (approximately 1 km) from the Climatologies at High Resolution for the

Earth's Land Surface Areas (CHELSA) database (Karger et al., 2017). As a measure of site accessibility, we calculated the shortest log-transformed distance from each transect to the nearest river (DISTRIVER) as estimated from the HydroRivers GIS-layer (<https://www.hydrosheds.org/page/hydrorivers>). Watercourses of orders 1–5 were considered rivers.

Landsat TM/ETM+ reflectance values (LANDSAT) were extracted from a 30-m-resolution composite of Landsat images based on over 16,000 relatively cloud-free acquisitions for 2000–2009 (Van Doninck & Tuomisto, 2018). We obtained a single value for each band to represent the whole transect by calculating the median value of all the pixels in a 15 × 15 pixel window centred on the transect. This was done separately for each of the three spectral bands (bands 3, 4 and 7) analysed in this study.

Regional predictions of palm community attributes across the western Amazon required a regional soil raster as input. To generate a high-quality soil raster, we retrieved field-sampled soil exchangeable base cation values from the Harmonized World Soil Database, from databases maintained by the Amazon Research Team of University of Turku (<http://utu.fi/amazon>), Brazilian Program from Biodiversity Research (<https://ppbio.inpa.gov.br/en>) and Balslev et al. (2019). The Sum of Exchangeable Base Cations (SB) values were also indirectly estimated using SB-indicator fern species occurrences for the entire region generated following the methods described by Zuquim et al. (2019). The georeferenced soil SB estimates served as input values in random forest (RF) models using median Landsat band 2, 3, 4, 5 and 7 values within a 200-m buffer as predictors. The models were evaluated using random 10-fold cross-validation. The best RF model ($R^2 = .32$) was then projected to generate a predicted SB raster covering the whole study region using Landsat band values at a 450-m resolution.

2.4 | Human uses

We recorded each palm species' types and diversity of known human uses, if any, from the World Checklist of Useful Plant Species (Diazgranados et al., 2020). The three main human use categories included were food, building material (e.g., housing, thatch), and medicine. For each of these uses, species received a binary classification of used (1) or not used (0). We also assigned a 'use diversity' value to each species based on eight types of use, including human food, animal food, material (e.g., housing, thatch), medicine, environmental uses (e.g., ornamental, shading other plants, soil improvers), fuel, genetic, and social uses. These values could range from 0 to 8, but no species was found to be used for all the eight categories, the maximum number of uses was seven. The underlying assumption is that a higher use diversity indicates that a species is, or has historically been, more intensively used by humans (Macía et al., 2011). These human use values were used in subsequent analyses to explore whether species with more uses differed in their realized environmental niches or spatial distributions from species with fewer uses.

2.5 | Phylogeny

We obtained a genus-level phylogenetic tree based on 1,000 palm phylogenies (Faurby et al., 2016; Phylogeny_Con_Checklist.nex). The original 1,000 trees were reduced to include only the species of interest using the ape (Paradis & Schliep, 2019) and phytools (Revell, 2012) packages in R (R Core Team, 2020). A maximum clade credibility (MCC) tree for the 1,000 trees was calculated using TREEANNOTATOR v2.6.3 (BEAST 2 package; Bouckaert et al., 2014). All branches with a posterior support below 95% were collapsed using TREEGRAPH 2 (Stöver & Müller, 2010). All MCC tree nodes showed good support at the genus level but not at the species level. We, therefore, used a genus-level tree in the analysis.

2.6 | Statistical analyses

We used the hierarchical modelling of species communities (HMSC; Ovaskainen & Abrego, 2020; Ovaskainen et al., 2017) joint species distribution modelling approach (Warton et al., 2015) to model the occurrence of each palm species. Species occurring in fewer than 10 transects were excluded from the analysis. The response variables in HMSC were vectors representing the occurrences of 78 selected palm species across 430 transects. As we used presence-absence data, species were modelled using a Bernoulli distribution with a probit link function. Eight continuous environmental covariates and the binary habitat class variable were included in the model as fixed effects. The minimum temperature of coldest month (CHELSA6), and precipitation seasonality (CHELSA15) were included to represent the main gradients in temperature and precipitation seasonality across the study region. These were the two CHELSA bioclimatic variables with the strongest correlations with axes 1 and 2 of a principal coordinates analysis of the palm community data. The other model covariates were SOIL, HAND, DISTRIVER, HABITAT and LANDSAT bands 3, 4 and 7, as defined above. SOIL was modelled as a second-order polynomial to allow for hump-shaped or curvilinear responses to the long soil SB gradient encompassed by the transects. We furthermore assumed phylogenetically structured residuals in species responses to these fixed effects to account for any phylogenetic structure in species environmental responses.

Spatial autocorrelation among transects might arise from dispersal processes, as a result of human use patterns, or due to other undetected factors in species distributions. To account for autocorrelation, we included community-level random effects implemented through spatial latent variables based on the transect coordinates following Ovaskainen et al. (2016). We fitted the model with the R package HMSC (Tikhonov et al., 2020), assuming the default prior distributions. We sampled the posterior distribution with four Markov chain Monte Carlo (MCMC) chains over runs of 375,000 iterations, of which the first 125,000 were removed as burn-in. Iterations were then thinned by 1,000 to yield 250 posterior samples per chain and thus 1,000 posterior samples in total.

The explanatory performance of the models for each species was evaluated using Tjur's R^2 (Tjur, 2009). To evaluate the predictive power of the HMSC models, we used random four-fold cross-validation. We fitted the model using one set as training data and the other three as validation data. Due to long runtimes for this large dataset, cross-validations only used 10% of the iterations used to fit the full models.

To explore the main drivers of palm species distributions, we quantified the proportions of variation explained by climate, soils, hydrology, distance from rivers, habitat type, and Landsat reflectance values for each palm species (Ovaskainen et al., 2017). We tested if species environmental responses, as represented by their standardized beta coefficients per environmental covariate, varied between taxa as a function of their total number of known human uses. We furthermore generated marginal effects predictions for each environmental gradient of the overall species richness of local palm communities, the proportions of taxa with particular human uses, and the mean number of human uses per species.

Finally, we mapped predictions of these same community characteristics over the entire western Amazon at a c. 1.5-km spatial resolution (0.017 decimal degrees). For regional mapping, the underlying models differed in three ways from those used in the detailed transect-level analyses. First, the field-derived SOIL covariate was replaced with predicted SB soil values from the western Amazonian soil raster described above. Second, the variables HABITAT and DISTRIVER were excluded from the model because these could not be reliably derived for the entire region. Third, regional predictions were based on a non-spatial model to make the model computationally feasible for 867,709 pixels. These choices did not likely significantly alter model predictions because contributions of the spatial random effect, HABITAT and DISTRIVER to explained variation were minor in the full models relative to contributions of the climatic, soil, and satellite reflectance variables. The regional-scale model was first fitted to the transect palm data using the original CHELSA, LANDSAT, HAND covariates, and the SB soil values. The fitted model parameters were then used to project palm species occurrences and community attributes derived from transects across the entire region.

3 | RESULTS

3.1 | Environmental drivers of western Amazonian palm distributions

Many palm species distributions covary with climate and soil fertility (Figure 3), as previously reported (Cámara-Leret et al., 2017; Eiserhardt et al., 2011; Tuomisto et al., 2016). The distributions of some species, such as *Attalea phalerata*, *Bactris simplicifrons*, *Geonoma maxima* and *Phytelephas macrocarpa*, depend primarily on soil fertility, defined as the concentration of exchangeable bases in soil. The distributions of other species, such as *Astrocaryum aculeatum*, *Bactris brongniartii* and *Aiphanes ulei*, depend primarily on climate. Landsat 7 ETM+ satellite reflectance values provide basin-wide measures of

habitat variability and emerged as particularly useful predictors of *Prestoea schultzeana*, *Ammandra decasperma*, *Mauritia flexuosa* and *Aiphanes ulei* distributions. The explanatory power and the quality of the models varied among species [mean Tjur $R^2 = .34$, range .05–.71; mean area under the curve (AUC) = .92, range .68–.99;

Figure 1, Supporting Information Table S1]. The mean predictive power based on fourfold cross-validation was somewhat lower (mean Tjur $R^2 = .23$, range 0–.57; mean AUC = .85, range = .42–.99; Supporting Information Table S1). We did not find evidence of phylogenetic effects in species' responses to the environmental

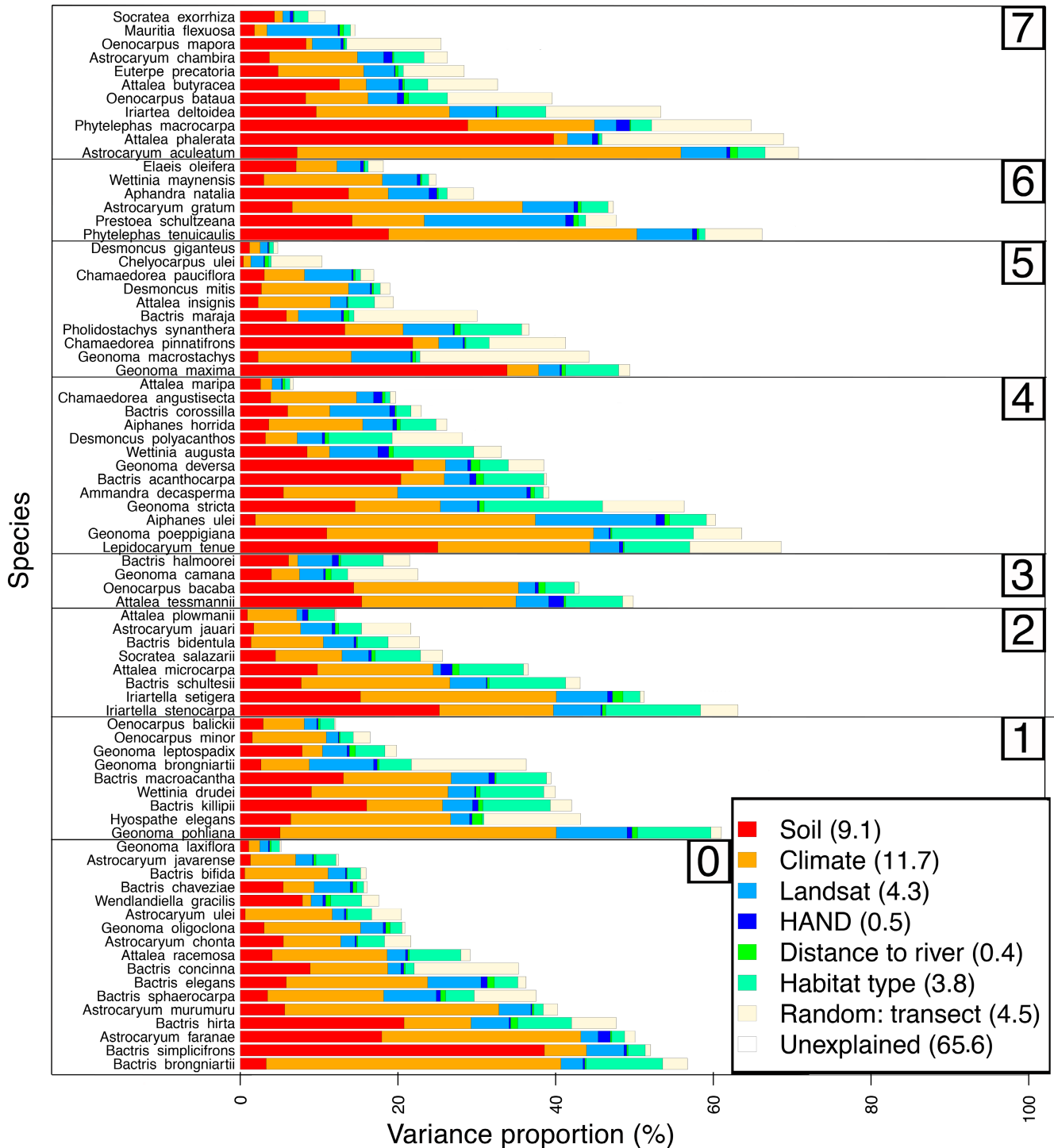


FIGURE 1 Horizontal bars illustrating variation (%) in the occurrences of 78 western Amazonian palm species across 430 transects that can be explained according to soil fertility, climate, Landsat reflectance, hydrology (HAND), distance from rivers, habitat type and a spatial random effect. Species are sorted in ascending order according to their known number of human uses (0–7) and within each category of human use diversity by total variance explained. Number of uses is indicated in small boxes at the upper right of each rectangle. The average variation explained by each predictor is given in parentheses in the legend (larger box at lower right).

covariates ($\text{Pr}(\rho > 0) = .15$) or of spatial correlation at the community level ($\text{Pr}(\alpha > 0) = 0$).

3.2 | Human use potential versus environmental distributions of palms

Seventy-eight percent of the studied species exhibited at least one recorded form of human use. We found a clear relationship between species' known numbers of uses and their niche positions along several environmental axes (Figure 2). Species that tended to show higher diversity of uses were those occupying more fertile soils (Figure 2a), sites closer to rivers (Figure 2b), areas with shallower water-tables (Figure 2c), and floodplains (Figure 2d). Species' numbers of uses and

niche positions were not clearly associated along climatic (Figure 2e-f) or Landsat reflectance gradients (Figure 2g-i). The predicted niche positions of non-used species varied and did not align with trends among used species.

3.3 | Residual spatial structure and human use

We quantified residual structure in the occurrences of palm species (i.e., spatial structure unexplained by environmental covariates) via a spatial random effect based on transect coordinates. The proportion of total variance in species' occurrences captured by the spatial random effect averaged 4.5% and varied widely (range 0.2–23.0%, Figure 1). Among palm species, the fraction of variance that was

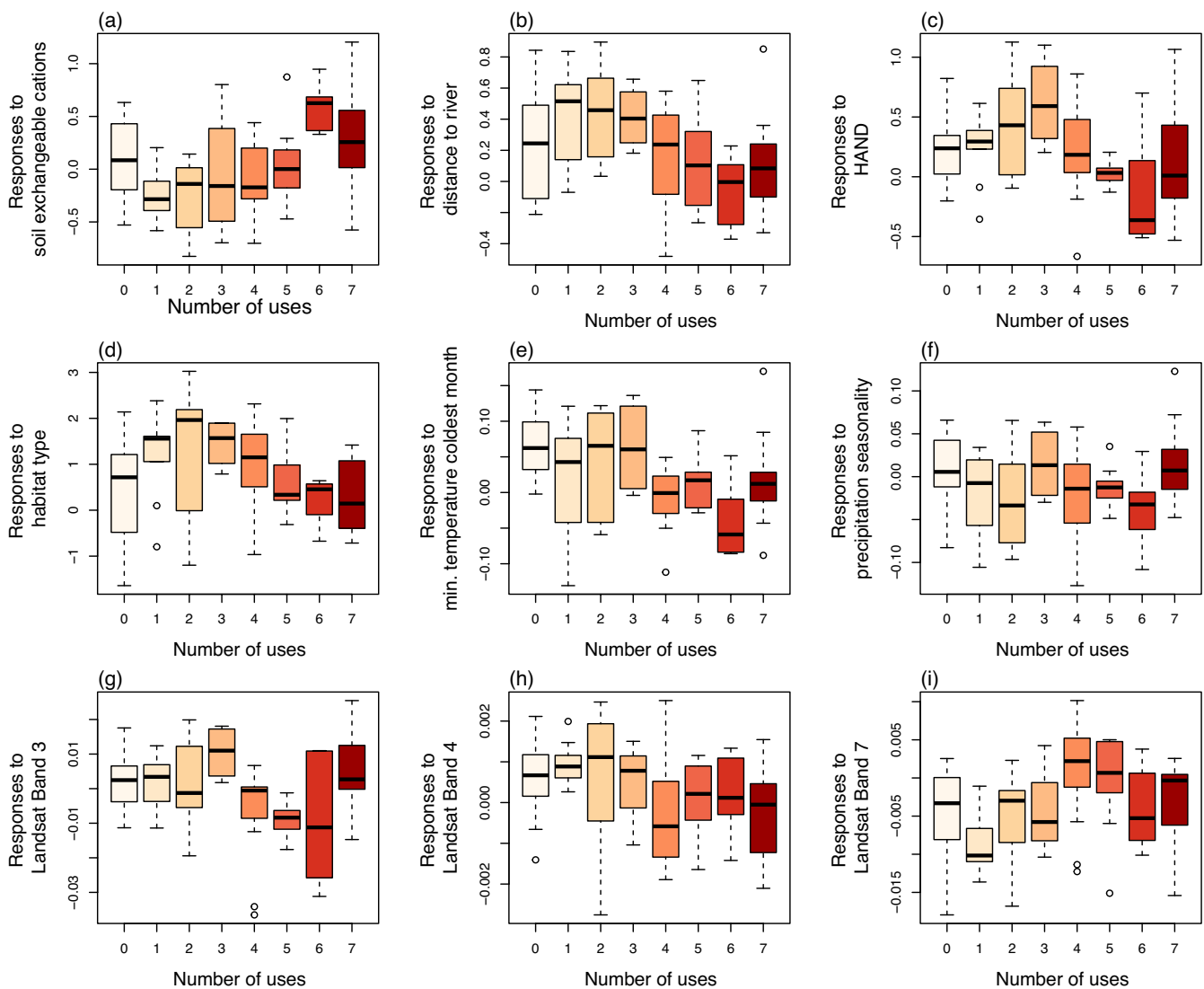


FIGURE 2 Estimated niche positions of western Amazonian palm species along nine environmental gradients with species grouped in ascending order according to their recorded number of human uses. Niche positions were quantified for each species as the posterior mean of their beta parameter estimates per gradient. Habitat type was a binary variable where 0 = floodplain and 1 = terra-firme, including white-sand forest. The other eight gradients are continuous variables. HAND, height above the nearest drainage which is an indicator of the distance to water table.

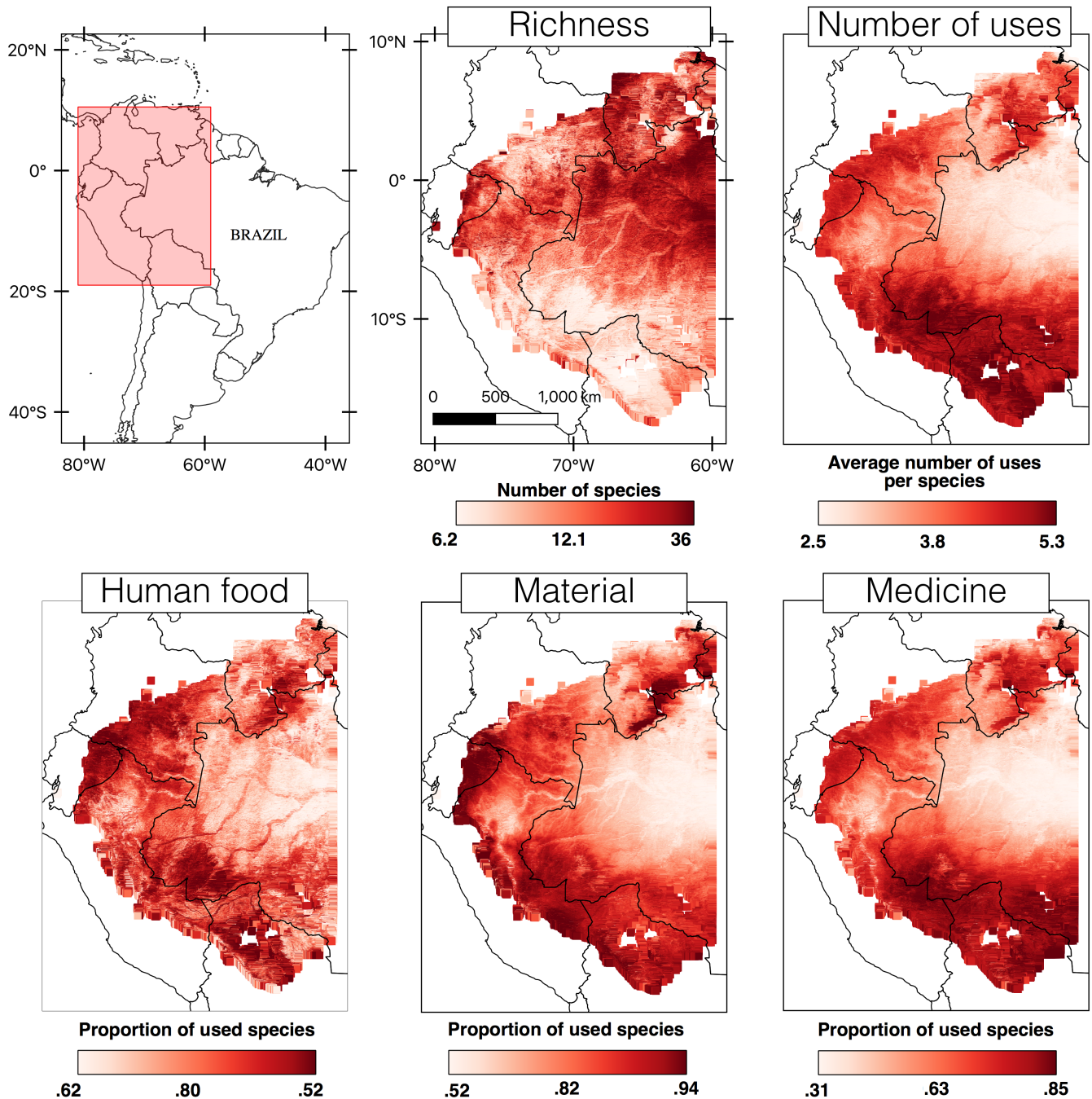


FIGURE 3 Predicted species richness of palm communities, proportions of palms used by humans for food, materials and medicines, and average number of uses per species across western Amazonia. Species richness correlates negatively with the proportions of food ($r = -.57$), material ($r = -.53$) and medicinal species ($r = -.66$), and with overall use diversity ($r = -.78$). The red rectangle in the first map indicates the area represented in other maps.

spatially structured correlated positively with their known number of human uses ($r = .32$, $p < .05$).

3.4 | Palm species richness and human use across western Amazonia

Intriguingly, predicted palm species richness correlated inversely with predicted use diversity ($r = -.78$) and with the

proportional representation of each of the major palm uses (food: $r = -.57$; material: $r = -.53$, medicine: $r = -.66$). This negative relationship implies that relatively species-poor habitats in western Amazonia tend to harbour palm species with many uses. Divergent richness–human use trends were evident along most environmental gradients (Supporting Information Figure S1). This pattern held especially true for food and medicinal palms and for overall use intensity. The effect was less consistent for palms with material uses. Sites near rivers, associated with

shallower water-tables, and in areas with greater seasonal climate variation were found to harbour relatively species-poor palm communities but with a high mean number of uses and representation of food and medicinal species. Along soil gradients, species richness peaked in moderately nutrient-poor habitats, whereas the number of uses of a species tended to be higher in more fertile soils.

Our mapped predictions illustrate these contrasting patterns between species richness and human use intensity across western Amazonia (Figure 3). Human use diversity and the proportions of palm species used for food, materials and medicine were predicted to be consistently higher in relatively species-poor habitats across the region. For example, central Amazonia was predicted to harbour the highest palm species richness but relatively low proportions of species used for food, materials, medicines, and lower average use diversity per species. In contrast, a low species richness but a high proportion of used palm species was predicted in the seasonal and fertile southern periphery. The maps also reflect that near rivers, there is a higher proportion of species used for food and overall use diversity, while palm species richness is reduced in these areas.

4 | DISCUSSION

The historical use and domestication of palms reflect ecological, cultural and environmental factors. Amazonian peoples have managed plants by removing non-useful species and planting, pruning, encouraging or conserving useful species at different spatial scales (Levis et al., 2018; Morcote-Ríos et al., 2021). The discussion below addresses how humans, interacting with the environment, may have thereby shaped palm distributions and uses at regional to continental scales.

4.1 | Rivers and soil fertility shape human use of palms

Palm species along rivers, on floodplains and within fertile soils were predicted to have the highest numbers of uses. These may also be the most favourable habitats for human access and settlement. Therefore, the patterns that we have detected in the diversity of uses suggest that environmental conditions have shaped Amazonian palm species uses and distributions directly by filtering species according to their ecological niche preferences, and indirectly by regulating human settlement patterns and human use of palm resources. This accords with paradigms of a widespread, long-term human influence within the Amazonian riverscape (Clement et al., 2015; McMichael et al., 2014) and also highlights the added importance of soil fertility in defining human use of palms and other forest resources.

Amazonian forests on more fertile soils tend to have higher productivity and turnover (Quesada et al., 2012), higher game animal densities (Palacios & Peres, 2005; Peres, 2008) and plants with a

greater range of chemical and structural characteristics (Asner et al., 2016; Fine et al., 2006), and perhaps nutritional quality and palatability, than forests on nutrient-poor soils. Thus, naturally more fertile soils in Amazonia may favour cultivation, hunting and gathering activities. Our results support a hypothesis that such soil-related 'bottom up' control of plant and animal populations has also modulated the long-term structure of human populations within Amazonia and the diversity of palm uses seen in these habitats today. This finding does not preclude management-related augmentation or reduction of the distributions of particular palm species.

In addition, we found that the greater the human use potential of a palm species, the more likely its distribution was to show spatial structure that was unexplained by the environmental characteristics considered. Human use intensity of natural resources is likely to decline as a function of distance from settlements, which could, over time, generate such spatial structure. The residual spatial structure detected is hence congruent with imprints of forest management by pre- or post-Columbian peoples (including the present-day inhabitants), or their sequential combination. An alternative interpretation of the correlation between unexplained spatial structure in palm distributions and their human use potential is the influence of unmeasured, spatially structured environmental gradients that modulate the properties of palms, and thereby their human use potential.

4.2 | Fewer species, more uses

We also observed contrasting relationships between predicted palm species richness and human use at the basin-wide scale. In more species-poor communities, the average number of uses per species and the proportions of useful species in the community were higher. Palm species richness tends to peak further from rivers and in poorer soils. Differences in human use were also associated with river proximity and along soil gradients. Useful palm species were disproportionately represented, and their uses were more diversified near rivers and in areas with more fertile soils. The species-poor palm communities of south-western Amazonia, with their high average number of uses, contrast with the species-rich central and western forests, where proportionately fewer species are used and species, on average, have a smaller number of uses.

It is likely that our findings predominantly reflect the efficient use of palms for various purposes in naturally less species-rich habitats rather than the direct reduction of palm species richness arising from overuse. In environments where the palm species pool is smaller, this means using the same species in numerous ways (Diazgranados et al., 2020; Macía et al., 2011), even if the characteristics of the species are not ideal for all uses. For example, if the fruit of a species is not particularly nutritious or tasty, but the leaf is good for thatch, the fruit may be used anyway, given its availability and the lack of alternatives. In this context, Amazonian Dark Earth anthropogenic soils (ADEs) in eastern Amazonia should also be mentioned as a unique but similar case. While the less fertile and less managed surroundings of ADE sites have a higher palm

species richness than the ADEs themselves, the proportions of used palm species within ADEs are higher (Maezumi et al., 2018). It is well documented that these patterns arose from active management favouring useful species within ADEs (Piperno et al., 2019).

4.3 | Biogeographical patterns in the use of palms

These broad-scale patterns might reflect a more substantial influence of pre- and post-Columbian peoples on palm communities in the fertile, seasonal south-west of Amazonia. Levis et al. (2017) similarly found high proportions of useful tree species in south-western Amazonia and Clement et al. (2015) reported a high concentration of Brazil nut stands (interpreted as indicators of historical human settlements) and several other domesticated species in this region. These findings could reflect the impacts of relatively large historical human populations in the region and intensive past management of plant resources. However, knowledge of population sizes and the geographical distribution of past human settlements in western Amazonia remains very limited. While pre-European evidence of human activity, including geoglyphs, raised fields and other earthworks is abundant (de Souza et al., 2018; WinklerPrins & Levis, 2021), some studies have predicted only sparse landscape transformation and low probabilities of human settlements in south-western Amazonia from 2,500–500 years ago (McMichael et al., 2012; Piperno et al., 2019).

Palaeoecological evidence of the community-level dominance of edible plants and their enduring legacy in modern forests has been reported for some parts of the Amazon. Abrupt pre-Columbian enrichment of edible plant species has for example, been reported in eastern Amazonia (Maezumi et al., 2018). On the other hand, little evidence of human-induced enrichment of three palm species was found at study sites in central and south-west Amazonia (Piperno et al., 2019). The widespread, severely weathered and nutrient-poor soils within Amazonia (Quesada et al., 2011) were thought to have precluded the establishment of large, dense and sedentary human populations in the past (Meggers, 1971). The proportion of used species was in fact, lower in poorer soils. More research is needed to clarify if, in fact, the relatively fertile arc of south-western Amazonia (Quesada et al., 2011) had higher past population densities. Nevertheless, even in the poor soil areas, at least half of the palms in the species pool were used. Therefore, we conclude that the use of palms has been widespread in Amazonia, with different levels of intensity. This confirms that humans living in the Amazonian region had a strong knowledge of the benefits of palm species for their livelihoods and developed multiple ways of using them.

Besides the known effects of accessibility, our results show that soil nutrients can also contribute to spatial heterogeneity in the human use of plant communities. Soils affect the natural distributions of palm species, as well as human settlement patterns (McMichael et al., 2012) and management practices. It remains to be investigated how soils and other environmental characteristics that shape palm traits, such as sugar concentration and leaf and trunk structure, interact with human choices in the harvesting and management of palm species.

4.4 | Final message

Humans have been a part of the Amazon forest system for millennia and have likely contributed to shaping present-day species distributions. Amazonian peoples have sustainably managed and domesticated plant species for the past 6,000 years (Clement et al., 2015) and at least half of the palm species found in Amazonia are used by humans to varying degrees (Smith, 2015). The proportion of palms with known uses, and their diversity of uses, are unevenly distributed throughout the Amazon and strongly associated with river proximity and soil fertility. Regionally, more diversity in the use of individual palm species is found in the species-poor palm communities of the fertile and seasonal south-west relative to central-western Amazonia. The observed connections between palm species distributions, environmental conditions, and human resource use highlight the importance of Amazonian peoples' cultural practices in managing species and forests over long timeframes (FAO & FILAC, 2021).

AUTHOR CONTRIBUTIONS

GZ, MJ, HB designed the study, GZ, MJ and OO performed the analysis, HB collected data, GZ wrote the first draft with significant contributions from all the authors.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

All input data came from publically available sources and are cited in the Materials and methods section. The formatted input data tables and the codes for fitting HMSC models are available at https://github.com/gabizuquim/HMSC_AmazonPalmUses (DOI: [10.5281/zenodo.7683941](https://doi.org/10.5281/zenodo.7683941)). Given that the models are computationally heavy, we also made the fitted models available at <https://doi.org/10.23729/9e2da5a5-5c6c-45a6-b23a-e7af08aface2>.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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