

Fundamental species traits explain provisioning services of tropical American palms

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The well-being of the global human population rests on provisioning services delivered by 12% of the Earth's ~400,000 plant species¹. Plant utilization by humans is influenced by species traits^{2–4}, but it is not well understood which traits underpin different human needs⁵. Here, we focus on palms (Arecaceae), one of the most economically important plant groups globally⁶, and demonstrate that provisioning services related to basic needs, such as food and medicine, show a strong link to fundamental functional and geographic traits. We integrate data from 2,201 interviews on plant utilization from three biomes in South America—spanning 68 communities, 43 ethnic groups and 2,221 plant uses—with a dataset of 4 traits (leaf length, stem volume, fruit volume, geographic range size) and a species-level phylogeny⁷. For all 208 palm species occurring in our study area, we test for relations between their traits and perceived value. We find that people preferentially use large, widespread species rather than small, narrow-ranged species, and that different traits are linked to different uses. Further, plant size and geographic range size are stronger predictors of ecosystem service realization for palm services related to basic human needs than less-basic needs (for example, ritual). These findings suggest that reliance on plant size and availability may have prevented our optimal realization of wild-plant services, since ecologically rare yet functionally important (for example, chemically) clades may have been overlooked. Beyond expanding our understanding of how local people use biodiversity in mega-diverse regions, our trait- and phylogeny-based approach helps to understand the processes that underpin ecosystem service realization, a necessary step to meet societal needs in a changing world with a growing human population^{5,8}.

Plant-based ecosystem services are crucial for satisfying human needs^{5,9}. These services, including provisioning services such as food and medicine, can be associated with particular species' traits that capture plant form and function¹⁰. For example, humans have selected plant species with traits that maximize crop yield, such as large fruits or height^{3,4}. Understanding which species' traits are linked to particular human needs is important for our efforts to maximize the resilience of ecosystem services in a changing world. Despite previous studies which address this question¹¹, the absence of large-scale approaches—spanning a variety of localities, biomes, cultures and biodiversity uses—has precluded our understanding of how species' traits govern the delivery of ecosystem services and fulfil human needs.

Here, we explore the association of species' traits with human plant utilization by integrating three large datasets on ethnobotany, traits and phylogeny. Our study area encompasses the western Amazon, and the Andes and Chocó biodiversity hotspots, which together also support a large ethnic diversity (Fig. 1). We focus on palms because they are one of the most useful and economically important plant families in the tropics⁶. The study area is exceptionally rich in palms and ranks second globally in palm diversity¹². For the ethnobotanical dataset, we interviewed forest inhabitants about the uses of palms following a standard protocol¹³ during 18 months of fieldwork, spanning a latitudinal gradient of 22°. This is the largest ethnobotanical documentation effort in the world for palms. We focus on the most important use categories that are key for the livelihoods of the rural population in our study area: Food, Construction, Culture and Medicine, as well as their respective use subcategories¹⁴ (Supplementary Table 1). For each use category and subcategory, we calculated species' relative frequency of citation (RFC)¹⁵, an index that quantitatively assesses people's consensus about a species' perceived value across our study region (Supplementary Table 2). Additionally, for all species in our study area, we compiled three functional traits that encapsulate the leaf-height-seed (LHS) strategy scheme¹⁶ (leaf length, stem volume and fruit volume), as well as a key geographic trait (range size), describing a species' availability.

We tested the relation between 208 palm species' traits and their RFC value for the different use categories using generalized linear modelling (GLM). We found that different traits correlate with different uses (Supplementary Table 3a). For instance, important species used for Culture have big leaves and fruits, whereas species used for Medicine have big leaves and are widespread. However, because each use category integrates information from various subcategories (Supplementary Table 1), and subcategories often contain different sets of species with different traits (for example, in Construction, not all species in the subcategory Thatch occur in the subcategory Houses), we further explored correlations between traits and the most important subcategories (Supplementary Fig. 1). We found that use subcategories were always related to fewer combinations of traits than use categories (for example, of the three traits significantly associated with the Construction category, only one trait was significantly related to either subcategory). Further, different subcategories within the same use category were often related to different traits (for example, Houses-geographic range versus Thatch-fruit volume in Construction), and many subcategories were never related to any trait (for example, Cosmetic and

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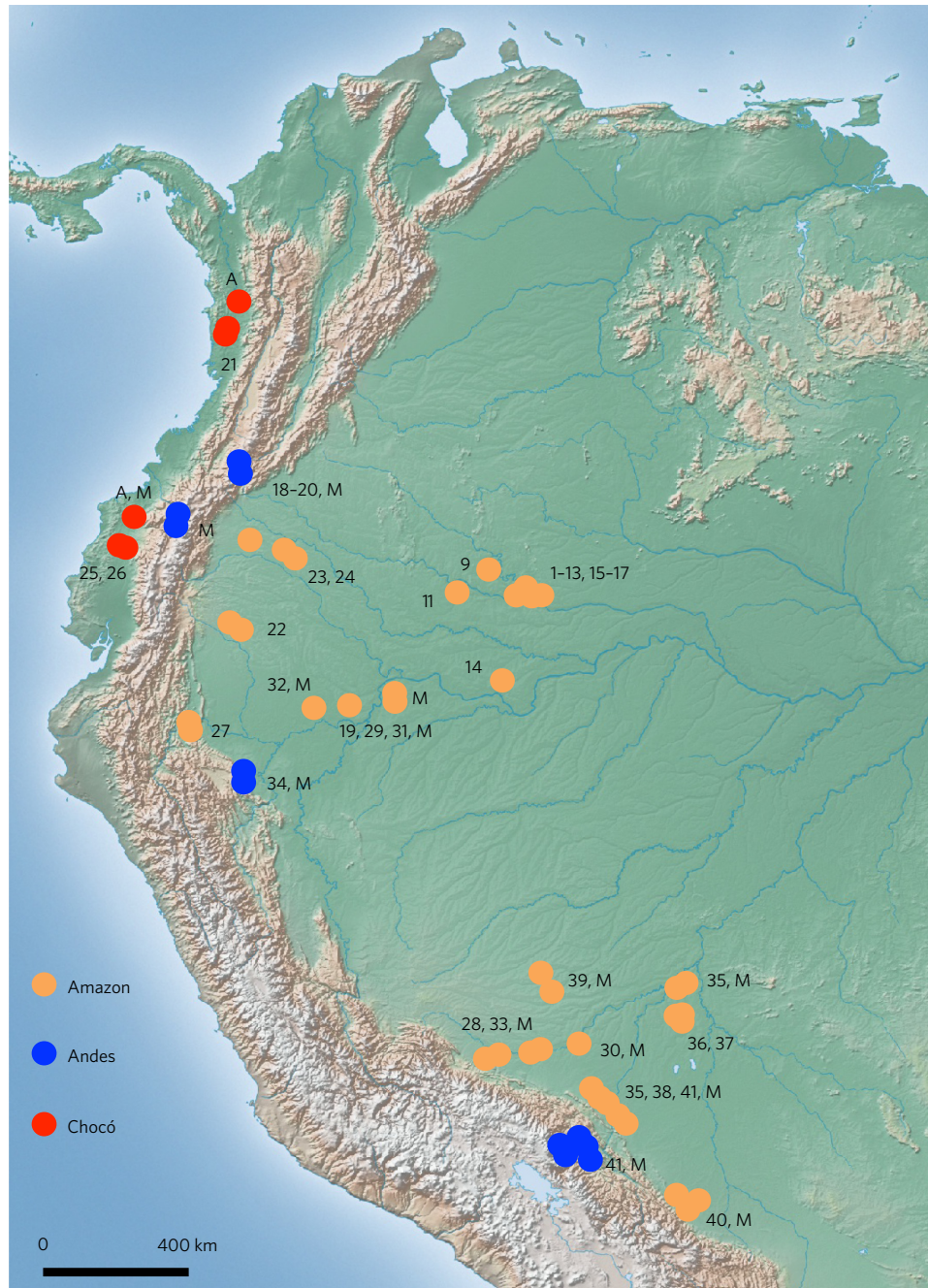


Figure 1 | Distribution of study communities. Map of northwestern South America showing the location of the 68 study communities and their ethnicity. Amerindian: 1, Bará; 2, Barasana; 3, Baré; 4, Bora; 5, Carijona; 6, Cubeo; 7, Desano; 8, Itano; 9, Macuna; 10, Matapi; 11, Miraña; 12, Tanimuca; 13, Tatuyo; 14, Ticuna; 15, Uitoto; 16, Yahuna; 17, Yucuna; 18, Camsá; 19, Inga; 20, Quillasinga; 21, Emberá; 22, Achuar; 23, Cofán; 24, Quichua; 25, Chachi; 26, Tsa'chila; 27, Aguaruna; 28, Amaraakaeri; 29, Cocama; 30, Ese Eja; 31, Shipibo; 32, Urarina; 33, Sapiteri; 34, Chanka; 35, Cavineña; 36, Chácobo; 37, Pacahuara; 38, Tacana; 39, Yaminahua; 40, Yuracaré; 41, Leco. Non-Amerindian: A, Afro-American; M, Mestizo.

Ritual in Culture) (Supplementary Table 3a). The Thatch–fruit volume relationship is difficult to interpret from an ethnobotanical viewpoint (because thatching requires leaves, not fruits), unless palm fruit volume is significantly inter-related with palm leaf length. Indeed, both traits were significantly inter-related (Supplementary Fig. 3), and we account for this in the analysis below by applying a principal component analysis (PCA). Overall, these results illustrate the need for future trait-based studies to disaggregate ecosystem service categories to their constituent subcategories (where true biological meaning resides), which is not common practice.

The correlations we observed between species' traits and utility could arise from phylogenetic autocorrelation. That is, traits of utilized species might be more similar than expected by chance because closely related species are similar in both utility^{17,18} and traits^{19,20} (Fig. 2). To explore this, we used a new phylogeny of palm species⁷ and calculated the degree of phylogenetic clustering in plant utility and traits with Pagel's lambda (λ)¹⁹ for all species in our study region. We found that phylogenetic clustering was strong for species used for Construction ($\lambda = 0.91$), but weak for species used for Food, Culture and Medicine ($\lambda = 0.18$, $\lambda = 0.09$ and $\lambda = 0.00$, respectively) (Supplementary Table 3b). Specifically,

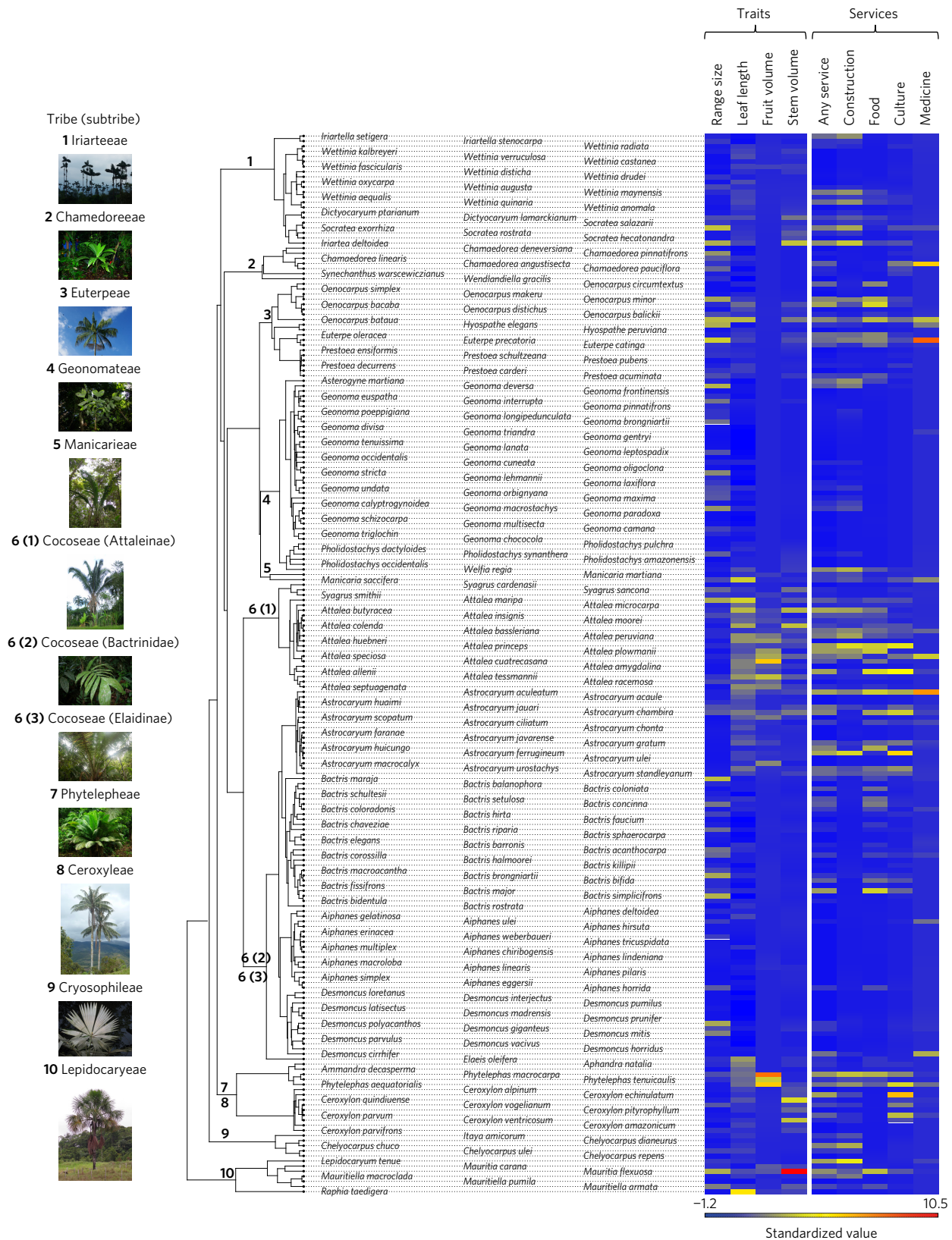


Figure 2 | Phylogenetic distribution of species' traits and of the contribution of 208 palm species to different ecosystem services in northwestern South America. Species' contribution to different ecosystem services is based on the RFC index (see Methods). All columns were standardized to have the same variance. Numbers 1-10 show palm tribes (subtribes in parentheses).

some palm tribes/subtribes (for example, Phytelpeae, *sensu* Dransfield *et al.*²¹) had a consistently higher RFC than average in all use categories, whereas others (for example, Cocoseae/

Bactrinidae *sensu* Dransfield *et al.*²¹) had a RFC below average in all use categories (Supplementary Fig. 2). Additionally, we assessed the degree of phylogenetic clustering in each subcategory, and found

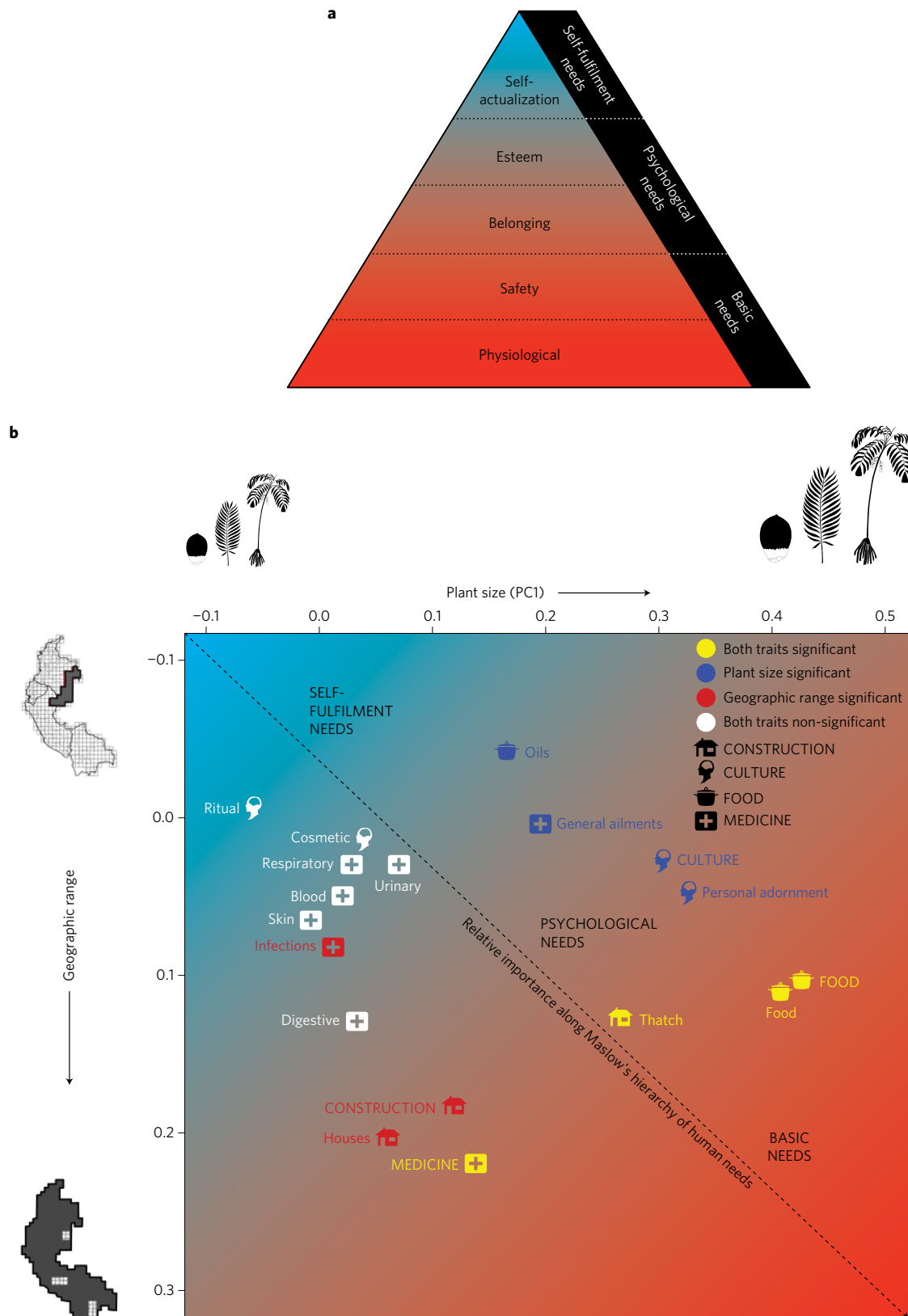


Figure 3 | The hierarchy of human needs, species' traits, and ecosystem services. **a**, Human needs can be organized hierarchically (*sensu* Maslow²⁵), from basic needs at the bottom of the pyramid to more existential or self-fulfilment needs at the top of the pyramid. **b**, Different combinations of plant size and geographic range (PGLS coefficients) underpin the benefits that people derive from nature and the hierarchy of human needs. Plant size is represented as axis one of a principal component analysis on the three functional traits—leaf length, fruit volume, and stem volume. Uses related to basic human needs (for example, Food) show a significant positive link with both plant size and geographic range (yellow symbols); uses related to psychological needs (for example, Culture) only show a significant link to one of the two traits (blue or red symbols); and uses related to self-fulfilment needs (for example, Ritual, Cosmetic) never show significant links to traits (white symbols).

that nine of the 14 subcategories (64%) showed strong phylogenetic clustering, including five of the seven Medicine subcategories (Supplementary Table 3b). We also recovered a degree of phylogenetic clustering for the species' traits: phylogenetic clustering was strong for leaf length and fruit volume ($\lambda = 0.89$ and $\lambda = 0.89$, respectively), moderate for stem volume ($\lambda = 0.46$) and weak for geographic range ($\lambda = 6.6 \times 10^{-5}$). Given the phylogenetic clustering of both species' utility and traits, we performed a phylogenetic generalized least-squares (PGLS) analysis²² to account for any effect of phylogenetic autocorrelation on our analyses. In the majority of cases, the PGLS and GLM analyses yielded qualitatively similar results (Supplementary Table 3) as expected because of the absence of phylogenetic clustering in ~50% of the uses in the dataset. However, the PGLS recovered different relations than the GLM between traits and utility in certain uses with strong phylogenetic clustering (for example, Construction, Thatch–Construction, and Infections–Medicine), which underscores the need to account for phylogenetic autocorrelation in ethnobotanical studies.

Research in functional ecology has shown that plant functional traits are often inter-related²³, which is also the case between palm stem volume and leaf length ($R = 0.36$, $P = 6.12 \times 10^{-8}$) and between palm leaf length and fruit volume ($R = 0.42$, $P = 2.36 \times 10^{-10}$) (Supplementary Fig. 3). Because trait multicollinearity can obscure trait–use relationships, we performed a PCA on the three functional traits (leaf length, fruit volume, stem volume), selecting the first axis (PC1) to represent them jointly (accounting for 54% of their variability). As all three traits load positively on PC1, it represents overall plant size. We did not include geographic range size in the PCA because it represents a fundamentally different species characteristic and affects a different aspect of species' perceived utility, namely availability. In general, large and widely distributed palm species are the most conspicuous, more people and cultures are exposed to them, and they show the highest probability of human–plant interactions and cross-cultural knowledge transmission of perceived utility²⁴. We explored the association of PC1 ('plant size') and geographic range with different uses by means of GLM and PGLS analyses. Overall, we found that plant size was a stronger predictor than geographic range of a species' importance for Food and Culture (and their respective subcategories), whereas geographic range was a stronger predictor for Construction and Medicine (Supplementary Table 4). Some uses were not significantly related to either plant size and/or geographic range (for example, Ritual–Culture, Cosmetic–Culture, Respiratory–Medicine).

What do these findings reveal about the processes that underpin ecosystem service realization? Psychologists have ranked human needs—based on importance for survival—from basic human needs (for example, food and health) to less-basic needs (for example, self-esteem and self-actualization)²⁵ (Fig. 3a). Typically, one would expect basic needs to show a strong link to species' traits because species that satisfy basic physiological needs must possess particular traits and be cost-effective to gather. In contrast, species used for non-basic needs could possess diverse traits because of idiosyncratic cultural preferences. We investigated how different plant uses position along the plant size and geographic range axes (PGLS coefficients), and how this relates to the hierarchy of human needs (Fig. 3b). Our findings show that different combinations of species' traits drive which benefits people obtain from biodiversity. We hypothesize that the strong coupling of plant size and Food is consistent with a need for constantly high yields in subsistence livelihoods that rely on local resources for food security. The weaker link between Medicine and plant size and a strong link to geographic range is consistent with availability as key for the selection of medicinal resources. This suggests that the traits selected for do not really reflect a specific need for efficacy because general and specific medical conditions correlate with availability. Efficacy as medicine should be the underlying trait, but the pharmacological

tests needed to verify this are largely inexistent. In principle, a high Pagel's λ would be expected for working medicines because the concentration (and existence of) any chemical compound is expected to be phylogenetically conserved. That certain palm tribes (Manicarieae, Chamaedoreae and Euterpeae) had very high RFC scores for Medicine (Supplementary Fig. 2) and that five of seven medical subcategories were strongly phylogenetically clustered is a noteworthy lead for future ethnopharmacological work. Construction's intermediate position along the plant size and geographic range axes highlights that both quantity (for example, leaf or stem biomass) and especially availability influence people's selection of species as housing material. At the other extreme, higher-level human needs such as Ritual–Culture uses do not necessarily reflect physical or chemical properties of plants, and hence need not be strongly linked to plant traits. Ritual–Culture uses in South America include far more uses than psychotropic ones (for example, uses related to myth–religious aspects, festivals and feasts, construction of coffins, sorcery), and we propose that this is why Ritual–Culture uses showed no clear relation to phylogeny, and potentially underlying plant chemistry. This would be consistent with numerous cases in Africa and Asia where idiosyncratic cultural preferences for various traits, and not plant chemistry, strongly determine human selection of plants for Ritual–Culture²⁶.

By integrating local stakeholders' views, ecology and phylogeny, we provide a novel interdisciplinary perspective on the linkages between ecosystem services, human needs and species' traits. Typically, these relationships are explored at local scales²⁷, but taking advantage of large-scale, cross-cultural ethnobotanical datasets can shed new light on these linkages. Our study highlights the importance of ethnobotanical research documenting how cultural heritage is linked to biodiversity resources, particularly in areas where this is understudied, such as South America²⁸. We demonstrate that this research can help us better understand the processes that underpin ecosystem service realization, which will be crucial to meet current and future societal needs under strong human population growth and environmental changes. Our findings on New World palms may not reflect global trends across other societies and plant families, and further trait-based research on the full spectrum of human-associated plants is therefore urgently needed. Given our reliance on a limited number of food crops²⁹, the use of similar interdisciplinary approaches to predict which lineages of the tree of life are likely to yield novel food crops and medicines could be highly rewarding. Still, the traditional importance of plant size and availability may also have prevented our complete understanding of wild-plant services. This may be so because ecologically rare yet functionally (for example, chemically) important clades may have been overlooked, even by local communities with great knowledge about biodiversity. Previous studies have shown that imminent global change may cause a shift in community functional traits³⁰ and our findings indicate that such shifts are bound to directly affect provisioning services—particularly covering food—that is directly linked to species' traits. Hence, efforts looking to enhance the resilience of ecosystem services for human well-being⁸ should consider the linkages between species' traits, evolutionary history and human needs.

Methods

Species' traits. For all species in our study area we obtained five morphological measurements: maximum stem height, maximum stem diameter, maximum leaf length, average fruit length and average fruit diameter from Henderson³¹, and complemented it with data from recent taxonomic revisions^{32–39}. For the few species lacking some measurements (stem height, $N = 8$ species; maximum stem diameter, $N = 4$; maximum leaf length, $N = 2$; maximum rachis length, $N = 1$; maximum petiole length, $N = 4$; average fruit length, $N = 7$; average fruit diameter, $N = 6$), we assigned the average value of all congeneric species. For our analyses, we selected three functional traits following Westoby's LHS plant ecology strategy scheme¹⁶: maximum leaf length, stem volume ($V_{\text{stem}} = \pi \times r^2 \times h$; r , stem radius, derived from maximum stem diameter; h , maximum stem height) and fruit volume

($V_{\text{fruit}} = 4/3 \times \pi \times a \times b \times c$; a , average fruit length/2; b , fruit height/2; c , average fruit width/2). Leaf length and fruit volume reflect specific leaf area and seed size in Westoby's scheme, respectively. Further, seed size and fruit volume are closely related in palms (many palm genera are one-seeded)⁴⁰. Together, leaf length and fruit volume represent the best available data for New World palms⁴⁰. We used stem volume instead of maximum stem height to better correct for the size of the relatively small overall size of climbing palms, which are tall but thin.

Geographic range. We derived a list of all palm species growing in our study area from Balslev *et al.*⁴¹ and followed The Plant List⁴² to unify nomenclature. This resulted in a total regional pool of 291 native palm species, 208 of which were present in our study communities, and which we subsequently analysed. For these 208 species, we compiled 1° grid square resolution distribution maps from Bjorholm *et al.*⁴³ Because the distribution maps of Bjorholm *et al.* were based on taxonomic knowledge from 1995⁴⁴, we made additional distribution maps for newly described species and for genera with more recent taxonomic treatments (for example, *Aiphanes*⁴⁵, *Astrocaryum*^{46,47}, *Attalea* (J.-C. Pintaud, personal communication), *Bactris*⁴⁸, *Calyptrogyne*³³, *Ceroxylon*³⁹, *Desmoncus*³⁵, *Geonoma*³⁴, *Hyospathe*³², *Pholidostachys*³⁶ and *Welfia*³⁷). We first mapped known collection localities into a grid with unit cells of 1° in latitude and longitude, and subsequently added new grid cells where we expect species to occur based on our field experience in the region, or that of other experts (Jean-Christophe Pintaud, *Attalea*). Thus, these new distribution maps are expert geographic range maps, as those that Bjorholm *et al.*⁴³ derived from Henderson *et al.*⁴⁴. For species with updated geographic ranges in Colombia, we geo-referenced the expected geographic range maps of Galeano & Bernal³⁸. In combination, these distribution maps represent the most up-to-date geographic ranges available for all species in our study area. All distribution maps were made using ArcGIS 10.1 (ESRI Inc.). From these maps, we quantified the geographic range size of each of the palm species in our study area by counting the number of 1° grid squares in which it is present. We refer to this number as 'geographic range' in our study.

Ethnobotany. Approval for this study was granted by the Committee for Ethical Research of the Autonomous University of Madrid (no. 48-922; Principal Investigator M.J. Macía). Before initiating data collection *in situ*, we obtained oral informed consent at the community level and then from the individual before each interview. Informants were made aware of their right to discontinue the interviews at any time and that all of the information provided would be anonymized. We collected ethnobotanical information about palms making 2,201 interviews over 18 months of fieldwork (May 2010 to December 2011) using a standardized method^{13,49}, developed to address the void in large-scale ethnobotanical efforts and comparative analyses¹⁴ (Fig. 1). We collected ethnobotanical data with two types of participants: expert informants and general informants. Experts were selected through consensus during community meetings. In communities too large for gathering all villagers, we asked general informants to recommend their most knowledgeable peers. Walks in the field with each expert were performed to identify all palm species growing in the surrounding forest, register their vernacular names and document their uses. Once experts were interviewed, we used the list of compiled vernacular names as the basis for interviews with general informants. General informants were selected in each community in a stratified manner to have a representative sample of age classes (18–30 years, 28%; 31–40 years, 23%; 41–50 years, 20%; 51–60 years, 13%; >60 years, 16%) and gender (women, $n = 1107$; men, $n = 1094$). Interviews were generally conducted in Spanish or with a local interpreter when needed. Palm species were identified in the field using Galeano & Bernal³⁸, Borchsenius *et al.*⁵⁰ and Moraes⁵¹, and specimens collected when our field identification needed confirmation. Palm-collecting permits were obtained through the following authorities: Instituto Amazónico de Investigaciones Científicas Sinchi (Colombia); the Ministry of Environment (Ecuador); the Instituto Nacional de Recursos Naturales (Peru); and the Dirección General de Biodiversidad y Áreas Protegidas (Bolivia). Field studies did not involve endangered or protected species. Voucher specimens ($N = 203$) are deposited in the herbaria of AAU, AMAZ, COL, LPB, QCA and USM, acronyms according to Thiers⁵². We classified use reports from interviews into one of ten use categories following the Economic Botany Data Collection Standard⁵³, with recently proposed modifications¹⁴. Our analyses focus on the most important palm-based ecosystem services in our study area, which correspond to the use categories Food ('Human food' in ref. 14), Construction, Culture ('Cultural' in ref. 14) and Medicine ('Medicinal and veterinary' in ref. 14) and their respective subcategories^{14,54} (for a description refer to Supplementary Table 1). In addition, we include a broad measure of usefulness in our analyses, which we here term 'Any service'. This measure contains information on whether a species has use reports associated to the four important palm-based ecosystem services or to any of the other less-important^{14,54} services (Animal food, Environmental, Fuel, Toxic, Utensils and tools, and Other uses) (Supplementary Table 1). For each of these classifications of palm-based ecosystem services (four use categories, 14 subcategories and Any service), we calculated a modified version of the RFC, an index that has been recommended for comparative studies that assess the perceived value of species¹⁵. To obtain the RFC we first counted the number of informants that mentioned a given species in a use category (or subcategory, or any service) and then counted the number of informants across the geographic range of

each species, by counting the number of interviews performed per 1° grid cell in our study region. The RFC is thus the number of informants that cite a given species for a particular use category or subcategory divided by the total number of informants interviewed across the species' geographic range. Given our large-scale analyses, our approach to compute the RFC limits the number of informants for computing the RFC to those interviewed in the grid cells where the particular species occurs. This was done to ensure that widespread species, to which more informants are exposed, did not necessarily receive higher RFC values.

Data analysis. For each use classification we performed separate GLM analyses, selecting the RFC as the response variable and species' geographic range and traits as the explanatory variables. Before analyses, we normalized all species' morphological traits and geographic range to a mean of 0 and a standard deviation of 1. The response variable was arcsin transformed and normalized to a mean of 0 and a standard deviation of 1. Plant morphological traits are often significantly correlated²³, and this was also the case in our trait dataset (Supplementary Fig. 2). To ease interpretation and avoid potential multicollinearity problems in our analyses, we performed a PCA on the three morphological traits (leaf length, fruit volume and stem volume). We selected PC1 (accounting for 54% of the variability in the data) and ran additional GLM analyses with the RFC values as response variables and PC1 and geographic range as explanatory variables (Supplementary Table 3).

We also reanalysed all data incorporating phylogenetic autocorrelation into our analysis. All phylogenetic analyses were based on the 1,000 constraint trees from the species level phylogeny of palms of Faurby *et al.*⁷. The trees were trimmed to only include species present in the study region. Before analyses, we normalized all species' morphological traits and geographic range to a mean of 0 and a standard deviation of 1. The response variable was arcsin transformed and normalized to a mean of 0 and a standard deviation of 1. To calculate the degree of phylogenetic clustering of uses and traits, we used Pagel's lambda¹⁹ (hereafter λ). Values of λ close to 0 are found for data without phylogenetic dependence, whereas values close to 1 indicate strong phylogenetic clustering. We assessed correlations between species' traits and uses while accounting for phylogenetic autocorrelation using a PGLS²² analysis. The results from 1,000 trees were then combined as the weighted mean (by Akaike information criterion weight) of the point estimates, standard errors and P -values from the analysis of each tree. Additional PGLS analyses were made to assess the correlation between PC1 and geographic range values with uses. All analyses were performed in R⁵⁵ using commands from the libraries *phylom*⁵⁶ *phytools*⁵⁷, *ape*⁵⁸ and quantitative PCR (qPCR)⁵⁹.

Data availability. The data that support the findings of this study are available from the corresponding author upon request.

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Author contributions

R.C.-L. and C.H.S.-L. conceived and designed the study. R.C.-L. and M.J.M. did the ethnobotanical fieldwork. R.C.-L., M.J.M., H.B., S.F., B.G. and W.D.K. provided data. R.C.-L., B.G. and H.B. built new geographic range maps. R.C.-L., C.H.S.-L. and S.F. analysed the data. R.C.-L. and C.H.S.-L. wrote the paper. All authors discussed the results and commented on the manuscript.

Additional information

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Competing interests

The authors declare no competing financial interests.