Received: 14 June 2023 | Accepted: 5 October 2025

DOI: 10.1002/pan3.70191

People and Nature

RESEARCH ARTICLE

Plant functional traits shape the provision of ecosystem services to Indigenous communities in western Amazonia

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Funding information
National Science Foundation, Grant/Award Number: DEB 0101775, DEB 0743457 and DEB 1836353; Directorate for Biological Sciences, Grant/Award Number: 1754647 and DEB 0743666; European Comission; National Geographic Society, Grant/Award Number: NGS 7754-04 and NGS 8047-06; Gordon and Betty Moore Foundation; Ministerio de Economía y Competitividad (2016) Ministerio de Ciencia, Innovacion y Universidades / Ministry of Science, Innovation and Universities, Grant/Award Number: CGL2016-75414-P and PID2019-105064GB-I00

Handling Editor: Rachel Carmenta

Abstract

1. *Context*. Exploring how Indigenous People interact with plants through their functional traits allows us to understand the ecological bases of plant selection. Functional traits can help explain why certain plants are consistently chosen for specific purposes across diverse cultural contexts. However, these relationships are complex and remain insufficiently explored. Here, we ask (1) which functional traits are most important in shaping different uses? and (2) do similarities in trait–use associations across Indigenous communities reflect patterns of knowledge convergence?
2. *Methods*. We conducted fieldwork across nine different Indigenous communities spanning a 1800 km distance in western Amazonia. In total, we sampled 115 0.1-ha plots, recording the abundance of 1856 woody plant species. For these species, we collected data on 13 different functional traits, primarily measured in the field, with additional values sourced from TRY and other databases, and conducted in situ ethnobotanical interviews with 25 Indigenous male participants, focusing on 14 distinct use categories. We analysed (1) trait–use relationships using generalized linear models and (2) the similarity in trait selection for each use across communities using generalized linear mixed models.
3. *Results*. Plants used for medicine or food were associated with multiple traits, including reproductive traits, exudates and life form. In contrast, culturally specific uses such as rituals, cosmetics or recreational were linked to more specific traits, particularly wood density and lianas. Across communities, we observed widespread convergence in trait–use associations, suggesting shared patterns of plant use despite cultural differences. However, 24% of the trait–use combinations showed divergence, indicating local adaptation or cultural specificity.

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4. *Synthesis and applications*. Plant selection by Indigenous communities is not random; rather, it is guided by functional traits that consistently support human well-being. We named this pattern 'functional selection convergence', highlighting how ecological function and traditional knowledge interact across distinct cultural contexts. This convergence shows the importance of functional ecology explaining traditional plant selection. Our findings are a call for a trait-based ethnobotanical approach to document and better preserve the ecosystem services essential to Indigenous livelihoods. Nevertheless, we emphasize the need for future research to involve broader and more diverse ethnobotanical participation.

KEYWORDS
biocultural conservation, ethnobotany, functional ecology, Indigenous Peoples, knowledge convergence, medicinal services, plant–human interaction, traditional ecological knowledge

1 | INTRODUCTION

Tropical forests provide important ecosystem services to humans that live in these areas and use their resources for their livelihood (Brandon, 2014). Ecosystem services are the benefits that people derive from natural ecosystems to ensure survival, quality of life and interactions (Millennium Ecosystem Assessment, 2005). Plant functional traits—defined as morpho-physio-phenological characteristics that influence plant fitness through growth, reproduction and survival (Violle et al., 2007)—are key to the delivery of these services (Cámara-Leret et al., 2017; Mokany et al., 2008), and increasingly essential in understanding their role in supporting human well-being (Díaz et al., 2006; Perrings et al., 2010; Faucon et al., 2017). Functional traits can explain complex ecological processes (Wright et al., 2004; Díaz et al., 2015), determining the quality, quantity and flow of resources within the ecosystem (Garnier et al., 2016). However, recent discussions argue that plant traits alone are poor predictors of ecosystem functioning (van der Plas et al., 2020), while others state that they are effective when used within appropriate contexts and suitable experimental designs (Chacón-Labella et al., 2023; Hagan et al., 2023). These contrasting viewpoints highlight the fact that the relationship between functional ecology, ecosystem services and human well-being is multiple, complex and still remains elusive (Pereira et al., 2005; Syrbe & Grunewald, 2017). Combining ethnobotany and functional ecology can provide a better understanding of these relationships. This joint field of study has gained importance in understanding the process behind the provision of ecosystem services to different ethnic groups (de Bello et al., 2010; Lavorel, 2013; Armstrong et al., 2021; Brown et al., 2013; Sellan et al., 2024; Cámara-Leret et al., 2014, 2017).

It is known that a sustainable provision of services depends on the combined action of multiple functional traits (de Bello et al., 2010; Garnier et al., 2016; Hanisch et al., 2020). For example, several traits related to competition strategies, such as large-stature or high wood density (WD) were found to be associated with the use of plants for construction materials (Brown et al., 2013). Reproductive and dispersal traits, such as seed mass (SM) or dispersal syndrome, were tightly related to important food resources (Thomson et al., 2010), while growth and defence traits (i.e. leave lifespan, latex and resin, leaf carbon–nitrogen ratio) were associated with medicinal uses (Hussein et al., 2018). Other studies have suggested that some ecosystem services are linked to specific functional traits, such as fine roots controlling soil erosion, and floral traits improving the landscape's aesthetic value (Hanisch et al., 2020). However, how different functional traits, individually and in combination, are linked to specific plant uses is understudied, and mostly so in tropical rainforests, where the increased biodiversity complicates the study of general patterns. Through time, Indigenous communities and local peoples have gathered intricate knowledge about plants and the different uses they provide. Their knowledge is considered an approximation of the relationships between plants, ecosystem services and well-being (Cámara-Leret & Bascompte, 2021). This traditional knowledge on woody plants and the livelihoods they provide, is acquired by long and complex knowledge transmission patterns (Reyes-García et al., 2009). It includes knowledge on plants for essential resources such as food, timber, tools, fuel, utensils and clothing. Also, beyond these tangible goods, woody plants also contribute to recreation, rituals, personal expression and cultural identity, influencing the aesthetic and spiritual dimensions of human life (Millennium Ecosystem Assessment, 2005).

The diversity of human groups, their history and languages, have driven the development of highly distinctive knowledge of plant species use (Junsongduang et al., 2014; Paniagua-Zambrana et al., 2016). Consequently, ethnobotanical knowledge may be widespread and shared among communities (Hawkins & Teixidor-Toneu, 2017), but it can also be specific and unique (Cámara-Leret et al., 2014; Paniagua-Zambrana et al., 2016; Vandebroek, 2010). There are factors that influence how plant knowledge is incorporated and developed in different cultures for a certain purpose (Gaoue et al., 2021). It is known that people use plants for the same purpose due to similarities in their morphological and functional characteristics (Pedrosa et al., 2021). Elements such as morphology, scent, taste, colour, texture, anatomy and life form influence human plant choice (Gonçalves et al., 2016). Thus, it is likely that functional traits play an important role in driving ethnobotanical convergence or divergence among communities. Studying the differences in the selection of functional traits among multiple Indigenous communities can help us identify which traits are more widely chosen and can be considered general drivers of human–plant selection (Lavorel, 2013).

Thereby, to explore the relationship between the woody plants of Amazonian rainforests and its contributions to human well-being, we worked with nine Indigenous communities in western Amazonia along an 1800 km distance spanning Ecuador, Peru and Bolivia (Figure 1). Our specific questions are as follows: (1) which plant functional traits are associated with different traditional plant uses? and (2) do different Indigenous communities use similar plant traits to fulfil similar needs? Although we cannot predict every specific relationship of all trait–use combinations, we expect that, as a general pattern, the services provided to Indigenous peoples are supported by multiple functional traits acting in concert. This redundancy many enhance the resilience of both ecosystems and human practices to species loss, overexploitation or environmental change. As well, we expect finding similarities among Indigenous communities, since similarities in the morphological and functional characteristics of their surrounding forests lead to similar uses. These questions can be answered by our integrated dataset compiled in situ, which includes species identity, their functional traits and individual-level ethnobotanical uses. We consider Indigenous knowledge on plants as plural, emerging from both ecological processes and cultural traditions. Our work aims to reflect this duality, contributing to a better understanding of forest functioning and resilience.

2 | METHODS

2.1 | Study area

From 1997 to 2019, different floristic and ethnobotanical field expeditions were conducted at nine sites in old-growth rainforests of western Amazonian (Bolivia, Peru and Ecuador). Sites were selected considering their proximity to Indigenous communities. At each site, between nine and 25 0.1-ha plots (50 × 20 m), located at least 300 m apart, were established relatively close to the communities following a standardized sampling protocol (Arellano et al., 2016), but avoiding natural gaps and human disturbances. In total, 115 plots were surveyed. Within each plot, all woody plant individuals (trees, lianas, tree, palms and hemiepiphytes) with a diameter at breast height (DBH) ≥2.5 cm and rooted within the plot boundaries, were

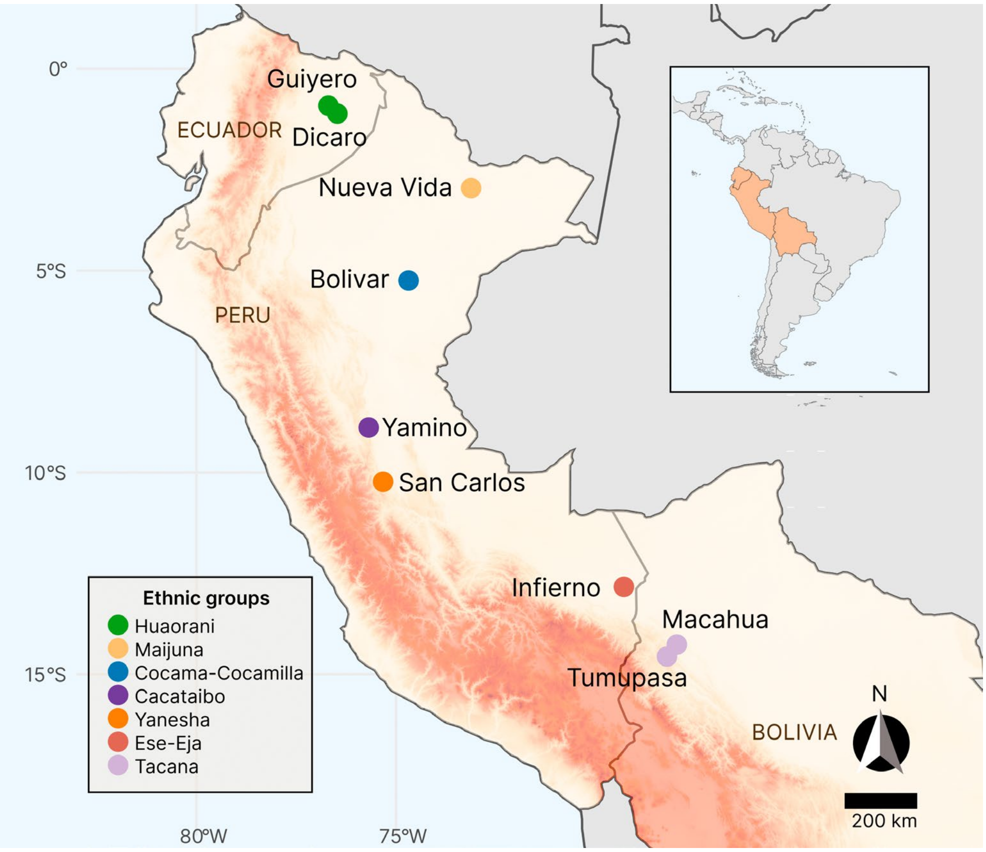

FIGURE 1 Locations of the nine studied Indigenous communities in western Amazonia (Ecuador, Peru and Bolivia) plotted on a digital elevation model (Shuttle Radar Topography Mission [SRTM]) in WGS84 datum, latitude-longitude coordinate reference system. At each community, 9–25 50 × 20 m plots were established at least 300 m apart from each other. Points' colours indicate the ethnic group of each Indigenous community.

measured and recorded. This approach allowed us to compile data on the identity and abundance of all woody plant species present. Botanical experts specialized in tropical flora and local Indigenous participants, helped with the recognition of key morphological traits and actively collaborated in specimen identification. Preliminary identifications were made in the field, and specimens were collected for further verification in regional herbaria. Approximately 4000 voucher specimens were gathered, then pressed, dried and taxonomically assessed. Because approximately 85% of the samples were infertile, species identification relied on comparisons with existing herbarium vouchers. We acknowledge that identifying vegetative samples might introduce some bias, either by splitting morphologically similar species or erroneously merging different species (Dexter et al., 2010). However, we remain confident in our results, as analyses at the community level are typically robust to such misidentifications. Specimens were identified to the finest taxonomic level possible; still, 12% of morphospecies could only be identified to genus or family level due to their rarity, scarcity of comparative herbarium material or poor specimen condition. These unresolved samples were excluded from the analysis. Voucher specimens were classified and stored at different herbaria in Ecuador (QCA, QCNE), Peru (USM, MOL) and Bolivia (LPB). Taxonomic standardization of species names was carried out using the R package 'WorldFlora' (Kindt, 2020) with the backbone species list retrieved in July 2025.

2.2 | Ethnobotanical data

Before initiating in situ data collection, prior informed consent was agreed and signed with the communities and the participants. The participants were selected as experts by their peers in the local communities as the individuals with larger traditional knowledge which were still active in forest utilization (Corroto & Macía, 2021). Before the start of the interviews, participants were aware of their right to discontinue the interviews at any time and that all the provided information would remain anonymous. The ethic statement and approval for this study were granted by the Committee for Ethical Research of the Autonomous University of Madrid (#48-922 and #103-1970, PI Manuel J. Macía). The nine communities belonged to seven different ethnic groups. A total of 24 experienced male participants (>40 years old) were interviewed using semi-structured ethnobotanical surveys across nine communities (Figure 1). The number of participants per community ranged from 2 to 4: in Ecuador, Dicaro (3) and Guiyero (3), both from the Huaorani ethnic group; in Peru, Nueva Vida (2) from the Maijuna-Kichwa, San Carlos (3) from the Yanesha, Bolívar (2) from the Cocama-Cocamilla, Yamino (2) from the Cacataibo, and Infierno (2) from the Ese-Eja; and in Bolivia, Tumupasa (4) and Macahua (3) from the Tacana ethnic group. The number of participants per community was limited due to logistic difficulties, since reaching these remote areas, more than a day's travel was needed, and the fieldwork itself involved a month stay with daily walks to forest plots, making it difficult to accommodate large groups under such conditions. Additionally, there was a trade-off between the number of participants and the depth of ethnobotanical data collection: with our methodology, each individual plant was discussed in detail, allowing us to capture the full range of local knowledge about a species, even when its morphological features (such as shape, size or colour) varied between individuals. Moreover, each woody plant encountered and inventoried could be examined in full by the participants, studying their leaves, roots, fruits, flowers, smell or slash of the bark. The ethnobotanical questions were of the kind: 'do you know this stem?', 'what are the possible uses for it?' (Macía et al., 2011). This methodology also incorporated validation of participants' knowledge by repeating ethnobotanical questions across different plots containing the same species. The traditional uses of all inventoried stems were noted down into notebooks. Then, uses were transcribed and classified by their plant parts, use categories and subcategories and grouped by species and community, following Cook's (1995) ethnobotanical classification, modified by Macía et al. (2011). This classification was made based on an existing ethnobotanical classification (Macía 2004; Macía et al., 2011; Pardo-de-Santayana et al., 2014; Cámara-Leret et al., 2014), coupled with ecosystem services literature (Barraclough et al., 2022; Garnier et al., 2016; Haines-Yough & Potschin, 2010; Power, 2010), personal experience and observation (Table S1). We included the 14 categories: timber, firewood, medicinal and utensils, along with the subcategories thatch, rope, beverages, food, ritual, recreational, dyes, toxic, clothing and accessories, and cosmetics at the same hierarchical level, to facilitate their interpretation in relation to functional traits. The data were collected at the individual level and then aggregated per species, preserving variability and capturing the heterogeneity of knowledge in plant size and form.

2.3 | Functional trait data

We considered 13 functional traits commonly used as indicators of plant functional strategies (Lavorel & Garnier, 2002; Wright et al., 2004) (details in Table S2). We measured them using both field data and existing databases. We compiled field data for the following traits: life form, maximum DBH, specific WD, leaf area (LA), specific leaf area (SLA), and leaf thickness (LT), latex presence (LX), resin presence (RS), fruit fleshiness (FF) and seed mass (SM). These functional traits are widely employed to assess the fundamental strategic dimensions of woody plants (Cornelissen et al., 2003).

Functional data were obtained by classifying life forms as trees, palms, lianas or hemiepiphytes, based on species identification. We measured DBH of all individuals with a diameter tape at 1.5 m above the rooting point and we calculated the maximum DBH per species. For WD, SLA and LT, we collected three replicates from separate individuals in different plots for every species present at each study site (Ben Saadi et al., 2022). WD was determined with the geometric method (Fearnside, 1997; Baker et al., 2004). A small fraction from the branch (around 10 cm) was taken. The external bark was removed and with a calliper the length and the diameter of both sides were measured while fresh, to obtain the green volume. In the laboratory, samples were oven-dried at 100° for 48 h and weighed (Cornelissen et al., 2003). WD was then expressed as dry weight over green volume. For LA, we sampled five leaves per individual measured. The selection avoided leaves with a great degree of herbivory or disease. These leaves were kept in newspaper saturated with 70% alcohol, similarly to the floristic samples. In the laboratory, leaf fresh area was measured with a scanner CI-202 Portable Laser Leaf Area Meter. The mean of the five measures was calculated per individual. To measure SLA, these same leaves were oven-dried (80° for 48 h) and weighed immediately after. SLA was calculated as the ratio between fresh area and dry weight for each leaf and then averaged per individual. Lastly for LT, two mature leaves were taken from every individual measured. A total of three measurements were done per leaf with a calliper, needing to cut off the margin and avoiding the main nerves. The mean of the six measures was calculated per individual. Then, mean trait values were calculated for each species. Additionally, we obtained information on certain traits, such as the presence of latex, resin, SM and FF, out of other databases (ter Steege et al., 2025; ter Steege & Hammond, 2001). Correlation between functional traits was low to moderate (maximum Pearson's correlation $r = -0.46$; Tables S3 and S4; Figure S1).

Out of the 13 traits analysed in this study: (i) six were continuous (WD, LA, SLA, LT, DBH and SM) and normally distributed, except for LA, which was converted to a log scale (Table S2); and (ii) seven were binary (latex, resin, FF, tree, palm, liana, hemiepiphyte). For all the species present in the sampled plots, some traits were obtained entirely from in-field measurements, as maximum DBH and life form. LA, SLA, LT and WD were measured in the field for 64% of all the species included in our study (measured in 50 of our study plots). Mean trait values were calculated for each species. For those species for which field data was not available, trait values were obtained from existing databases, including TRY (Kattge et al., 2020) and FunAndes (Báez et al., 2022).

2.4 | Data analyses

2.4.1 | Trait–use relationships

To test which plant functional traits are associated with each use category, we used generalized linear models (GLMs) with a binomial error distribution. The response variable represented the probability that a species provides a particular use (1) and (0) the species is not used for that purpose (e.g. *Socratea exorrhiza* for medicine = 1; *Hirtella elongata* for medicine = 0). The use was tested against the corresponding trait value (e.g. *S. exorrhiza* LT = 0.2 mm, *H. elongata* LT = 0.6 mm), which served as the predictor. When traits were associated with a particular part of the plant (stem, leaves or fruits), we selected only those species for which that part of the plant was used. For instance, to test whether LT was linked to medicinal uses, those species whose leaves were reported to be medicinal by local communities were tested against the LT of the rest of the species. Note that some traits were not associated with any particular part of the plant, such as the presence of latex, resin or the life form (Table 1). We fitted one GLM for each combination of the use categories and traits associated with a given part of the plant, resulting in 182 models. We used the chi-squared statistic to test the significance of each variable using a significance level of $\alpha \le 0.05$. We calculated the squared deviance (D^2) as a measure of the amount of deviance explained by each trait. Slope coefficients of the models were used to determine the direction of the relationship (either positive or negative). To assess the potential phylogenetic clustering of species associated with each use category, we calculated mean nearest taxon distance (MNTD) and mean pairwise distance (MPD) using the 'picante' R package (Kembel et al., 2010). These metrics quantify phylogenetic clustering or overdispersion: MNTD shows the clustering among closely related species, while MPD indicates deeper phylogenetic relationships. Significance was determined using z-scores and p-values. To obtain the phylogenetic tree, we used the V.Phylomaker package (Jin & Qian, 2019), scenario 1, with the updated World Flora Online species list (Kindt, 2020). To evaluate the extent to which phylogenetic relatedness explains variation in each trait–use associations, we fit phylogenetic generalized linear mixed models (PGLMM) with the 'phyr' R package, version 1.1.0 (Ives et al., 2019), specifying the trait as the predictor and the use as the response variable. Species identity was included as a random effect, which phylogenetic covariance informed by the same phylogenetic tree used on the MNTD analysis. Significance of each model was determined with p-values and fitness with the predicted R^2 (Ives, 2019), of the 'rr2' package, version 1.1.1 (Ives, 2018).

2.4.2 | Trait selection by Indigenous communities

To investigate whether trait selection for each service was similar across communities, we used generalized linear mixed models (GLMMs) with a Gaussian error distribution for the continuous traits and with a binomial error distribution for the binary traits. As in the previous research question, species for which a specific part of the plant was used were tested against traits associated with a particular part of the plant (stem, leaves or fruits). The response variable was the trait value for those species committed to a particular service for a certain Indigenous community and the explanatory variable was the community, which was introduced in the model as a random factor. By modelling random effects, we can generalize results beyond the specific levels of the random factor present in the data, helping to understand results to other communities not included in the study. Moreover, the results are more stable and produce reliable estimates, particularly for use categories with small sample sizes or unbalanced data, resulting in more parsimonious models. Since our field methodology included data on the abundance of woody plants, we incorporated prior weights reflecting the relative abundance of each species in each community into the models, to account for differences in species

TABLE 1 Analysis flow on the trait–use relationship.

Use category	Part of the plant	Traits tested	Analysis
Classification of each species into the use or uses they provide (medicinal, construction, rituals, recreation, food, etc.)	Stem (trunk, branches, spines and/or bark)	WD	GLM with binomial error distribution: Response variable: species providing a use category (1) the rest of species (0)~Predictor variable: trait
	Leaves (leaf, petiole, leaflet, palm heart, bract and rachis)	LA+SLA+LT	
	Fruits (seed, fruit, flower, inflorescence and infructescence)	Seed mass+fruit fleshiness	
	All plant parts (stem, leaves, fruits)	Latex+resin	
		Life form (tree, liana, palm, hemiepiphyte)	
		DBH	

Note: First, the classification of the species into the use they provide, and the part of the plant used, tested against each of the traits with a GLM with binomial error distribution. For instance, the probability that the leaves of the species provide medicinal services is higher with increasing LA.

availability across 'communities' (number of individuals each woody plant species/total individuals in the community). They were incorporated in the models to account for differences in species availability across communities. We then compared models with and without the random factor using Akaike's information criterion corrected for small sample sizes (AICc). Models with a difference in AICc >2 indicated that the worst model had virtually no support and could be omitted. When the best model included the community, we calculated the conditional coefficient of determination to calculate the goodness-of-fit (R^2) (Nakagawa & Schielzeth, 2013). We used the R packages 'MuMIn' version 1.43.17 (Barton, 2022) and lme4 version 1.1-27.1 (Bates, Mächler, Bolker & Walker, 2015). All analyses were conducted in R v4.1.1 (R Core Team, 2025).

2.5 | Study limitations and perspectives

By analysing 1856 plant species across forests in western Amazonia, we found that functional and morphological traits are key drivers of ecosystem services that support human well-being. However, there is significant room for future exploration and improvement. We acknowledge some limitations in our study, mostly resulting from the experimental design. First, we did not account for intraspecific variation in functional traits. While we recognize that analysing trait variation at the individual level would have enriched the analysis, collecting such detailed data for 1856 species in the field was logistically unfeasible. Additionally, other potentially relevant traits, such as bark thickness and leaf C:N ratio, were not measured and could have enhanced our understanding of the traits associated with medicinal properties. Second, our ethnobotanical data were based on interviews with only two to four participants per community. These individuals were selected as experts and accompanied the research team throughout the entire fieldwork campaign. Expanding participation was constrained by the logistical challenges of working in undisturbed and remote areas, far from the Indigenous communities themselves. Furthermore, this study captured only male knowledge, as participants were identified by their peers as the most knowledgeable individuals (Corroto & Macía, 2021). We acknowledge that this limits the scope of the study and may not fully represent the breadth of knowledge present within Indigenous communities. It is essential to recognize intracultural variation in plant knowledge, particularly gendered dimensions. Gender bias in ethnobotanical research often stems from culturally embedded cognitive models, which can lead to systematic exclusion and biased interpretations (Howard, 2006). Women are frequently overlooked as informants (Ladio, 2021), unless gender differences in plant knowledge are explicitly studied (e.g. Paniagua-Zambrana et al., 2014). However, numerous studies have shown that women, particularly in relation to medicinal uses, often hold more extensive plant knowledge than men (Voeks, 2007; Garibay-Orijel et al., 2012; Srithi et al., 2012; Corroto et al., 2019). We recommend increasing participant numbers and incorporating greater diversity in gender and social roles to better capture the full dimensions of local knowledge systems and their transmission. Additionally, integrating additional cultural variables such as belief systems, land–use patterns, knowledge transmission and linguistic evolution, will be essential for explaining patterns of ethnobotanical convergence and divergence. We also emphasize the value of jointly analysing both evolutionary and functional influences to better define the phenomenon of selection patterns. Finally, coupling ecological data with research led by the community would strengthen co-produced knowledge frameworks and reinforce biocultural conservation efforts throughout the Amazon.

3 | RESULTS

3.1 | Trait–use relationships

The 13 plant functional traits included in this study related to 14 use categories (Figure 2). Of all 182 trait–service associations, we found 67 statistically significant relationships (37%). Some services such as food, timber, medicinal, rope, thatch and firewood showed significant relationships with multiple traits (we assumed independence of

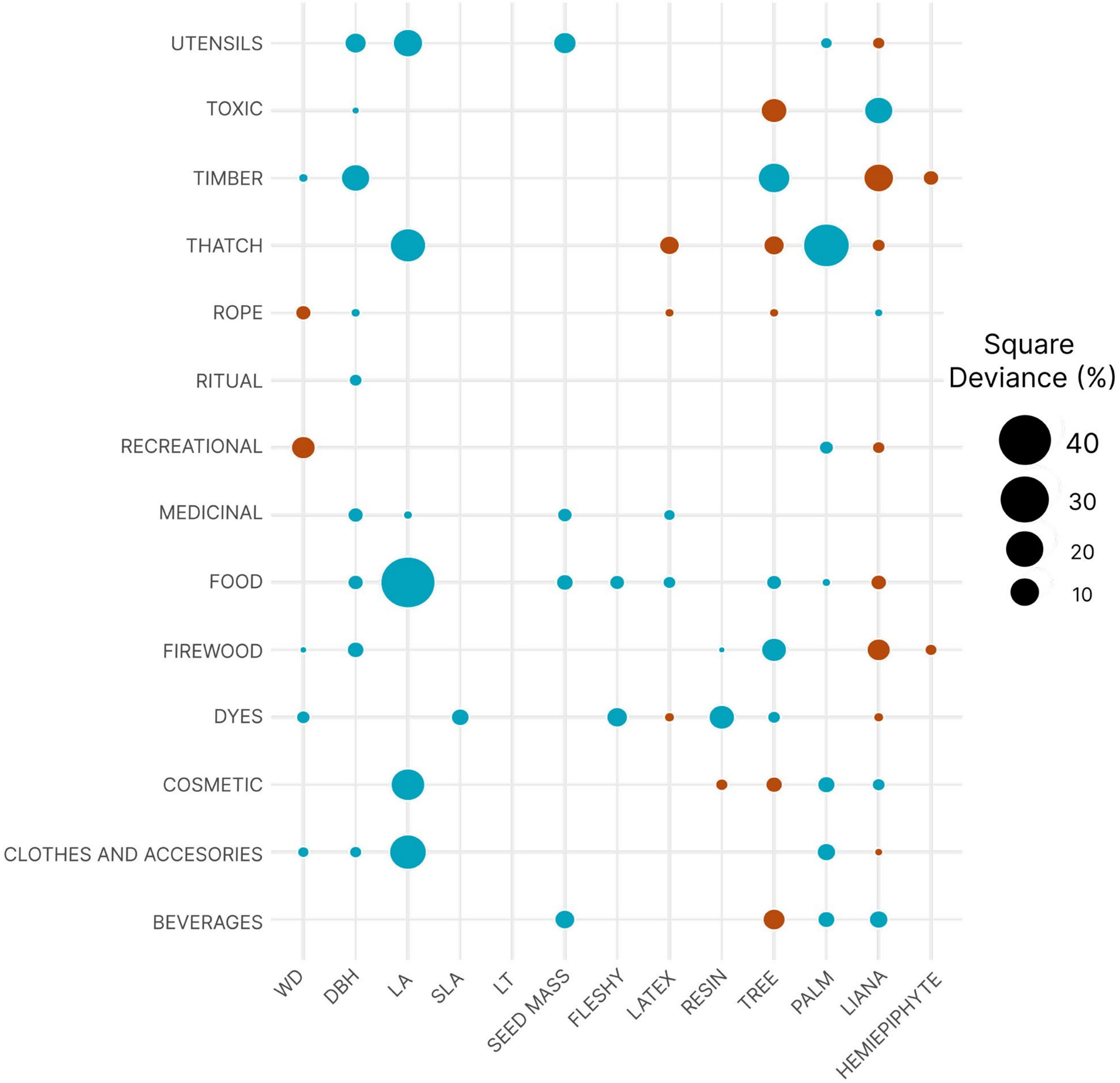

FIGURE 2 Dot diagram showing associations among woody plant functional traits and ecosystem services in western Amazonia. Each reported trait–service association is displayed with a circle: Colours show the direction (blue, positive; red, negative) and size show the strength of associations by the D^2 (%) of each of the best fit of the generalized linear models. WD (wood density), DBH (maximum diameter at breast height), LA (leaf area), SLA (specific leaf area), LT (leaf thickness) and FLESHY (fleshy fruits).

the traits due to their low correlations [Table S3]). Food was positively related to SM, fleshy fruits, maximum DBH, LA, LX and the tree and palm life forms (Figure 2). Timber use was linked to trees, maximum DBH and high WD. Medicinal uses were associated with large DBH, high SM, large LA and latex. Firewood was related to traits promoting long burning, such as resin, large DBH and high WD. Rope was associated with low WD, high DBH, lianas, while thatch was related to LA and palms.

Other services, such as cosmetics, clothes and accessories, recreation and toxic uses were generally linked to fewer traits (Figure 2), except for dyes that were linked to multiple traits (high WD, high SLA, fleshy fruits, resin and trees). Cosmetics showed positive relationships with LA, palms and lianas, and negative relationships with resin and trees. Clothing was linked to high LA, large DBH and palms. Recreational uses were linked to low WD and palms. Toxic uses were associated with increasing DBH and lianas, and rituals to high DBH as well. We did not find any service associated with LT. There is a general pattern in which the uses that are positively associated with trees tend to be negatively associated with lianas and vice versa. This inverse relationship arises because the two growth forms are mutually exclusive (being a tree precludes being a liana). Consequently, a positive association with one implies a negative association with the other, reflecting their different ecological strategies. The liana life form showed multiple associations with various services, most of which were negative, indicating a lower probability of providing timber, thatch, recreation, food, firewood, dyes or clothing when the growth form was a liana. However, positive associations were observed for beverages, cosmetics, ropes and toxic uses.

Phylogenetic analysis showed consistent patterns. On the one hand, the phylogenetic aggregation of the species associated with each use category, assessed with MNTD and MPD, revealed significant clustering for several uses (Tables S5 and S6). MNTD results indicated that species used for dyes, firewood, food, beverages, thatch, timber and toxic purposes were more closely related than expected by chance ($p < 0.05$), suggesting terminal phylogenetic clustering and potential trait similarity among closely related species. MPD revealed significant clustering for clothes and accessories, firewood and food, showing deeper phylogenetic patterns. The overlap of significant results in firewood and food for both MNTD and MPD suggests that both uses have recent and ancient phylogenetic convergence. On the other hand, PGLMMs supported most significant relationships found in the original GLMs. Among the fitted models that could be fitted, a few previously significant GLMs became non-significant in the PGLMMs, specifically: toxic-DBH, fleshy fruits-dyes, latex-dyes and thatch-lianas, indicating that the variance explained by these relationships was mainly due to phylogenetic clustering. This relation is congruent with some of the results of the MNTD, since toxic, dyes and thatch, were found to have a strong influence of phylogenetic clustering calculated with both methods.

3.2 | Trait selection by Indigenous communities

Out of the 182 trait–use combinations analysed, 46 (24%) showed significant differences in trait values associated with a given use among Indigenous communities, suggesting that trait selection varies across communities. Comparing this result with the previous one, when the overall trait–use combinations were not significant and showed significant differences among the Indigenous communities, this indicates that the high trait variability does not translate into selection patterns. In contrast, when a trait–use combination was significant and the selection among communities showed differences as well, is understood as the trait is generally important for the use but subject to differences among the selection patterns of the Indigenous communities. Notable examples of this last case include selection for species for timber differing by DBH across communities; medicinal uses showing variation in both DBH and LA; food uses involving differences in DBH, SM or the presence of fleshy fruits; and beverages differing in their SM.

For the remaining 136 (76% of the cases), there were no differences in the trait values selected for a certain use, indicating trait selection tended to be similar across communities. Focusing on the 72 trait–service combinations that were significant in the previous research question, the similarity in trait choice was found for dyes and fleshy fruits, medicine and latex, toxic uses and lianas, utensils and LA, clothes and palms, rituals and DBH, and recreation and SM (Figure 3).

4 | DISCUSSION

4.1 | Trait–use relationship

We found that the traditional uses of plants by Indigenous people in western Amazonian forests were associated with different functional traits. Among the various trait–use relationships identified, a few specific cases merit particular attention. The species that were linked to medicinal services were mainly associated with traits related to leaf and plant size (LA and DBH) and to the presence of latex. Higher DBH is usually linked to a more extensive root system (Ledo et al., 2017), and a greater crown volume and light interception capacity, which typically leads to increased photosynthetic productivity and higher nutrient and water demands (Poorter et al., 2010) that can enhance nutrient uptake, which in turn can influence the concentration of bioactive compounds in plants, potentially increasing their medicinal value. Aside, plant exudates are a plant defence mechanism (being toxic or sticky), and can be sometimes beneficial for human health due to their pharmacologic compounds (alkaloids and proteins) (Gracz-Bernaciak et al., 2021). Accordingly, here we report a strong relationship between medicinal uses and latex, confirming this hypothesis. The provision of food was shaped by SM and fleshy fruits, which are dispersal syndromes suited for human dispersal, aligning with the importance of human as dispersals agents in Amazonia—both deliberately and incidentally (Levis et al., 2018). Moreover, we suggest that is in fact the association between these two traits (i.e. large and fleshy fruits) what determines the selection pattern. Food was as well influenced by LX, since many latex-yielding plants were important providers of edible fruits.

Timber was directly related to trees with high WD, DBH, coinciding with general knowledge and earlier research (Berenguer et al., 2018), and indicating that people are actively selecting wood with high durability, splitting resistance and elasticity to bend (Chave et al., 2009). The stems of large palms are often reported as building materials, yet here did not show any relationship, which contrast with previous studies (e.g. Macía, 2004). We interpret this difference as a result of the broad scope of our analysis: While palms are ecologically and culturally important for many uses, they are underrepresented in the timber category when all woody species are considered. We suggest that high WD and large size likely overshadow the contribution of palms in timber selection. Fuel wood was related to tree size, resins and high WD, traits providing longer burning times (Brown et al., 2013; Cardoso et al., 2015). To sum up, we found a high number of traits associated with important services providing direct goods, mostly related to size and dispersal traits. However, we acknowledge that to some categories, such as medicinal services, the elevated number of traits associated could be related to the wide variety of products they provide (ointments, intangible products, drinks and baths), while other services, such as timber, firewood,

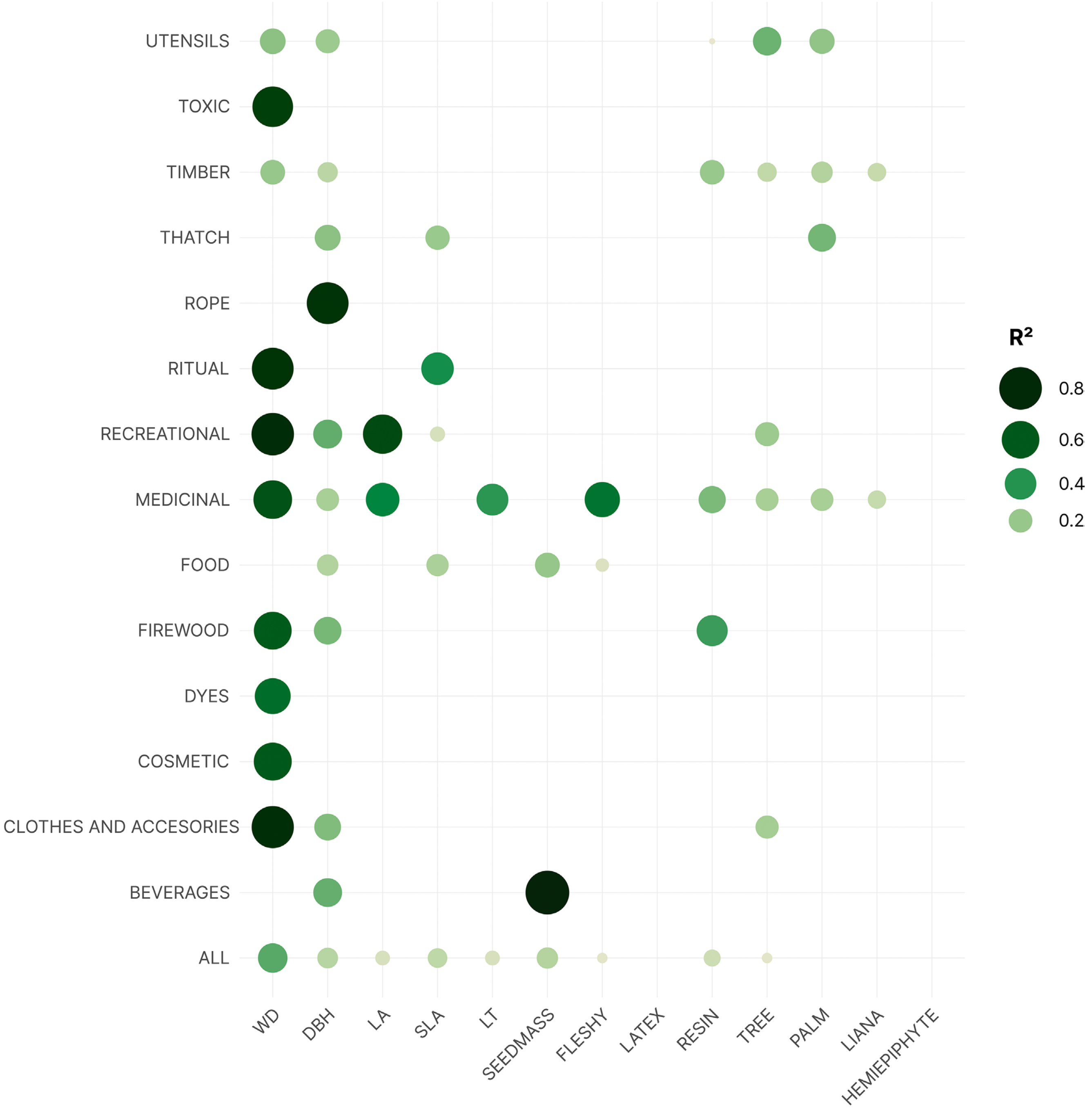

FIGURE 3 Dot diagram showing the R^2 obtained from the generalized linear mixed models. R^2 was a proxy of the significance of the Indigenous community (included as a random factor) shaping the differences in the trait selection for the different categories of uses. An elevated R^2 indicates that Indigenous communities significantly influence the differences in the functional traits of species providing a particular ecosystem service. Each reported trait–service association is displayed with a circle: Colours and size showed the strength of associations by the R^2 of each of the best fit of the generalized linear mixed models. WD (wood density), DBH (maximum diameter at breast height), LA (leaf area), SLA (specific leaf area), LT (leaf thickness) and FLESHY (fleshy fruits).

thatch and rope, involved fewer or even single products, still exhibited a high number of associated traits, that can also be explained by the high number of different species providing these services.

Plants associated with rituals, use of toxins, clothes, accessories and cosmetics, were generally linked to fewer traits, mainly due to the lower number of species associated with these services, suggesting a more trait-specific service relationship. These uses are generally related to cultural expression and practices, which are influenced by the unique beliefs of each community, developed regardless their morphology or functionality, and not being associated with any specific trait (Cámara-Leret et al., 2017). However, our results showed that some cultural species are tightly related to structural and defence traits. For example, ritual practices are more likely to be developed with plants with a larger diameter. This can be attributed to the fact that plants with aromatic barks are often burned in sanctuaries or used to banish negative energy during rituals. Consequently, these culturally important plants made DBH a significant trait, due to the thicker bark of larger trees (Maynard et al., 2022).

Lianas were important providers of rope and custom fibres, since their stems with wide vessels result in high bending capacity and fissure resistance (Angyalossy et al., 2014; Carlquist & Hoekman, 1985). Also, many lianas were reported in our study as culturally important (e.g. *Paullinia alsmithii* and *Curarea tecunarum*) since they contain active saponins or alkaloids, which are toxins effective for fishing or hunting (de la Torre et al., 2008). Negative links between lianas and other uses were also found, showing the unsuitability of this life form for certain services related to the provision of dyes, materials, utensils or fuel. Other important negative relationships were found, for example for toys and instruments were associated with lower WD for ease of manipulation. This last finding shows that a single functional trait can have trade-offs: it is important to maintain both high and low values of WD in forests to provide simultaneously timber and recreational services. Then, reducing functional diversity or changing its composition can trigger substantial changes in the ecosystem service balance and affect well-being (Sharafatmandrad & Khosravi Mashizi, 2021).

4.2 | Trait selection by Indigenous communities

Our results showed that in 76% of the cases the plants with morphologic and functional similarity are chosen for the same purposes among different Indigenous communities. Previous studies have found that people often use the same or closely phylogenetically related species for similar purposes (Saslis-Lagoudakis et al., 2011; De-Nova et al., 2024). Ethnobotanical convergence has been originally defined as different ethnic groups giving similar uses to closely related plants (Garnatje et al., 2017a). When this occurs by unrelated cultural groups, and it may indicate independent acquisition of knowledge (but see Garnatje et al., 2017b; Hawkins & Teixidor-Toneu, 2017). Here we show, for the first time, that this phenomenon also arises when being analysed from a functional perspective. As such, we name this strategy ‘functional selection convergence’, defined as the similarity of knowledge between different groups on the use of traits, regardless of the species taxonomic identity, since floristic composition was not shared among the research sites (de Aledo et al., 2023).

Similar use of traits might result from either independent learning or cross-cultural knowledge transmission. For example, lianas were consistently sought for preparing beverages, regardless of the Indigenous community. However, mean phylogenetic distance results (Table S5) revealed phylogenetic clustering among species with certain uses (beverages, among them), suggesting that relatedness plays a role in some trait–use combinations. SM emerged as another trait consistently associated with various uses across communities, such as rituals, recreation, crafts and cosmetics. This pattern highlights the importance of SM related to cultural well-being, reflecting both utility and a long history of selection by Indigenous peoples. Other dispersal traits, such as fleshy fruits, were also selected for dyeing and as food across communities. Notably, the species used for these services were phylogenetically clustered, underscoring the influence of evolutionary lineage on trait selection. Latex-bearing plants were frequently chosen for medicinal uses in all communities, but in contrast to food and dyes, these medicinal species did not show any phylogenetic clustering (Tables S5 and S6). This suggests that latex itself is a strong indicator of medicinal potential, supporting its role in bioprospecting. Importantly, in all these cases, the convergence in trait–use (i.e. functional selection convergence) appeared to be independent of species availability, as functional composition and species abundance varied across communities (Figure 3—ALL).

We here hypothesize that this pattern reflects both shared experiences and historical interactions among Indigenous groups, possibly rooted in long-term human engagement with and management of Amazonian forests. Human societies have modified the Amazonian landscape (Levis et al., 2018; Peripato et al., 2023), vegetation structure (Maezumi et al., 2018), species composition (Jones et al., 2016; Levis et al., 2017; Ross, 2011), and functional diversity (Armstrong et al., 2021; Brown et al., 2013), and likely also functional composition. Similar patterns in human plant selection may point to active, long-term selection processes (Armstrong et al., 2021; Roberts et al., 2017), with cascading effects on the functional makeup of today's tropical ecosystems. These processes may have favoured traits such as large, fleshy fruits (Clement et al., 2017), the prevalence of palms and the presence of latex, which are traits that appeared consistently across multiple use categories in our study. However, in 24% of the cases, we found differences in the selection of traits for specific needs. This dissimilar use is therefore opposite to the functional selection convergence, and accordingly, we have named it ‘functional selection divergence’. This phenomenon is defined as the divergence of knowledge regarding species traits among different ethnic groups for a particular service. While the functional characteristics of these plants are crucial for their use, this knowledge is not uniformly shared across communities. Functional selection divergence has been observed for the trait–use combinations that were significant in the previous analysis, suggesting that the trait is generally important for the use, but subjected to local preferences or availability. For example, medicinal uses showed high variability in the plant size selected (DBH and LA) across communities. In this case, the idiosyncrasy of these communities shapes the learning process of plants providing medicines. Another example is the SM seed mass selected for beverages, that although is a trait positively related to this use, different seed weights were selected among communities. Additionally, as mentioned, the differences in choice might be as well caused by differences in the availability of functional traits in the forests belonging to each Indigenous community. For example, the species that are selected for timber by different communities differ in their DBH and WD, due to the differences in the availability of this trait in the forests. It is known that people adapt their knowledge to plants' abundance, frequency and salience. Common species are often more extensively tested and thus have more practical uses (Gonçalves et al., 2016; de Lucena et al., 2012; Phillips & Gentry, 1993; Soldati et al., 2017). Here, we show that the selection of plants among communities could be explained not only by the species identity but by their availability of functional attributes, such as large size, diameter and high WD.

To sum up, comparing trait selection among communities revealed that for some needs similar traits were selected (convergence) and to fulfil other needs, the selection of traits was different (divergence) across different Indigenous communities. However, we acknowledge that these communities are not completely isolated. Historical connections, cultural exchanges and shared ancestral ties have likely played a major role in shaping plant–use convergence (Hawkins & Teixidor-Toneu, 2017). Linguistic affinities can influence use patterns and may serve as proxies for shared ancestry, migration routes and community interactions (Menendez-Baceta et al., 2015). Conversely, divergences in knowledge may result from distinct cultural trajectories, including differences in belief systems, educational practices, oral traditions or social organization (Quave & Pieroni, 2015), as well as from differences in local trait availability, promoting functional adaptive choices. While cultural variables were not directly tested in this study, we recognize their relevance and need to incorporate them into future analyses. This study highlights the value of studying patterns of ethnobotanical convergence in different contexts to understand how plants are selected and how traditional knowledge is transmitted. We highlight the importance of ethnobotany as a means to join scientific and Indigenous knowledge, parallellysupporting the maintenance of the continuous flow of functional traits, critical for Indigenous well-being.

AUTHOR CONTRIBUTIONS

Julia G. de Aledo, Luis Cayuela and Manuel J. Macía conceived the ideas; Julia G. de Aledo, Hans ter Steege, Luis Cayuela analysed the data; Julia G. de Aledo led the writing; Julia G. de Aledo, Celina Ben Saadi and Manuel J. Macía collected the ethnobotanical and functional data; Selene Báez, Guillermo Bañares-de-Dios, Leslie Cayola, Belén Fadrique, William Farfán-Rios, Alfredo Fuentes, Jürgen Homeier, Oswaldo Jadán, J. Sebastián Tello and Hans ter Steege collected the functional data and collaborated with the reviewing process. Norma Salinas and María de los Ángeles La Torre-Cuadros provided bureaucratic, logistic and field support and collaborate with the reviewing process; Hans ter Steege, Luis Cayuela, Laura Matas-Granados, Celina Ben Saadi and Manuel J. Macía gave continuous input to the writing and comments on the analyses. All authors approved the final version.

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ACKNOWLEDGEMENTS

We thank the native communities that received and assisted us in their forests (Dicaro and Guiyero in Ecuador; Nueva Vida, Leoncio Prado, San Carlos, Yamino, and Infierno in Peru; and Tumupasa and Macahua in Bolivia). We thank the field assistance from Luis Torres Montenegro, Piher Maceda, Manuel Marca, Alex Nina, Iñigo Gomez, Maaike Pyck, Silvia Aguado and Mara Paneghel. We thank the local authorities for supporting and allowing our work in their protected areas: Servicio Nacional de Áreas Naturales Protegidas por el Estado (SERNANP) and Servicio Nacional Forestal (SERFOR) in Peru, Ministerio de Medio Ambiente y Agua and Ministerio de Desarrollo Rural, Agropecuario y Medio Ambiente in Bolivia and Organización de Nacionalidades Huaorani de la Amazonia Ecuatoriana (ONHAE) in Ecuador. Fieldwork permissions were obtained to access the areas and collect the samples. Peru: Reserva Nacional Tambopata: N° 35-2017-SERNANP-DGANP, Reserva Nacional Pacaya-Samiria: N° 037-2018-SERNANP-JEF, Zona de Amortiguamiento Parque Nacional Cordillera Azul: N° 315-2017-SERFOR-DGGSPFFS, Zona de Amortiguamiento Reserva Comunal Yanesha: N° 401-2018-MINAGRI-SERFOR-DGGSPFFS, Área de Conservación Regional Maijuna-Kichwa: N° 003-2019-GLR-GGR-ARA. Bolivia: Parque Nacional Madidi: MDRAyMA—VBRFMA—DGBAP—UAPVS N° 2869/08. Funding for plot data collection came from different sources: J.G.A., L.C., L.M.-G., C.B.S. and M.J.M. acknowledge support from Ministerio de Economía y Competitividad (2016) Ministerio de Ciencia, Innovacion y Universidades / Ministry of Science, Innovation and Universities under grant numbers CGL2016–75414–P and PID2019-105064GB-I00, the European Union grant contract INCO-DC, IC18-CT960038 and the Nextgeneration EU, the Education Department of Madrid (Spain) and the Universidad Autónoma de Madrid. J.S.T. acknowledges support to the National Science Foundation (DEB 0101775, DEB 0743457, DEB 1836353), National Geographic Society (NGS 7754-04 and NGS 8047-06), Taylor and Davidson families. B.F. was supported by the EU Marie Curie-IF 892383 (RESCATA). W.F.-R. acknowledges the funding for the Andes Biodiversity and Ecosystem Research Group (ABERG) plot network coming from the Gordon and Betty Moore Foundation's Andes to Amazon initiative and the US National Science Foundation (NSF) DEB 0743666 and NSF Long-Term Research in Environmental Biology (LTREB) 1754647.

CONFLICT OF INTEREST STATEMENT

The authors have no conflicts of interest to declare.

DATA AVAILABILITY STATEMENT

Raw data are not publicly available because the ethnobotanical data are subject to intellectual property rights. The processed data associated (i.e. species' mean functional traits and whether they are useful for the communities of this study) are available in Zenodo (de Aledo et al., 2025) and in the following link: https://doi.org/10.5281/zenodo.17315311.

POSITIONALITY STATEMENT

This study includes authors from different countries, including scientists based in the countries where the study was carried out. The authors are aware of current research inequities, legacies of colonialism and ethical considerations of working with Indigenous communities. The authors acknowledge the complexity of concepts like Indigenous Peoples, Indigenous communities, ethnicity, as well as the challenge of explaining across disciplines and different belief systems than those of the authors. They acknowledge their non-Indigenous position, which may introduce biases in the writing and interpretation of the manuscript's results.

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SUPPORTING INFORMATION

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

Table S1. Use categories of in this study (modified from Macía et al. (2011)), their description and the number of species used for each use category.

Table S2. Description of the functional traits analysed in this study, their ecological meaning, source, type of variable, data transformation and number of species compiled for each trait.

Table S3. Pearson correlation between functional traits of woody plants in western Amazonia.

Table S4. Mean, min and max of each functional trait.

Table S5. Mean nearest taxon distance (MNTD) for species used in each use category.

Table S6. Mean pairwise distance (MPD) for species used in each use category.

Table S7. Results from the PGLMM analysis for each trait–use combination.

Figure S1. Principal component analysis (PCA) relating the functional traits studied in this research.

Figure S2. Visualization of regression model fits for each trait–use combination using *visreg* R package.

Figure S3. Dot diagram showing associations among woody plant functional traits and ecosystem services in western Amazonia.

How to cite this article: de Aledo, J. G., ter Steege, H., Cayuela, L., Matas-Granados, L., Ben Saadi, C., Salinas, N., La Torre-Cuadros, M. d. l. Á., Báez, S., Bañares-de-Dios, G., Cayola, L., Fadrique, B., Farfán-Rios, W., Fuentes, A., Homeier, J., Jadán, O., Tello, J. S., & Macía, M. J. (2025). Plant functional traits shape the provision of ecosystem services to Indigenous communities in western Amazonia. *People and Nature*, *7*, 3313–3329. https://doi.org/10.1002/pan3.70191