Forest Ecology and Management 334 (2014) 28–42

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

# Ecological community traits and traditional knowledge shape palm ecosystem services in northwestern South America

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A R T I C L E   I N F O

*Article history:*
Received 6 June 2014
Received in revised form 22 August 2014
Accepted 23 August 2014
Available online 21 September 2014

*Keywords:*
Biodiversity
Cultural keystone species
Local ecological knowledge
Indigenous people
Natural resource management

## A B S T R A C T

Tropical rainforest ecosystems support the maximum expression of biocultural diversity on Earth and preserving them requires understanding and working with the needs of their inhabitants. Here, we combine traditional knowledge with ecological data to quantify cross-scale variation in the ecosystem services of palms (Arecaceae), the most useful plant family in northwestern South America. We sampled two very large datasets in northwestern South America: one on traditional knowledge ($n = 1494$ interviews) and one on palm ecology ($n = 197$; 0.25 ha-transects) collected in four countries and 47 communities inhabited by >10 Amerindian and non-Amerindian groups, spanning 21° latitude and 14° longitude. We grouped the 47 communities into 15 localities on the basis of geographic proximity and ethnic composition and grouped localities into four sub-regions: northwestern and southwestern Amazon basin, the Andes, and the Chocó. We asked which palm species are most important to villagers and how usefulness is related to the morphological traits of palms, about the cross-scale patterns in palm-based forest usefulness in different sub-regions, localities, and habitats, the relative contribution of different palm growth forms to forest usefulness, and the most valued use categories. We found that despite high geographical variation in traditional knowledge, only a few species were highly important at most localities. On all scales and in most areas, usefulness significantly correlated with stem height, mid-leaf length and fruit diameter, but not with palm abundance. Palm-based forest usefulness peaked in northwestern Amazon and was highest in the Amazon floodplain habitat, but there was large variation on all analyzed scales. Forest usefulness was significantly determined by three palm growth forms and by human food and construction uses. We conclude that palms are key ecosystem service providers that secure the well-being of thousands of inhabitants across northwestern South America. We advocate the need for alliances between forest-dependent people and conservation practitioners to manage these highly useful resources and the ecosystems where they grow.

## 1. Introduction

The livelihoods of tropical rainforest inhabitants are inextricably linked to the goods and services delivered by their ecosystems, also known as ecosystem services (Millennium Ecosystem Assessment, 2005). Tropical rainforest ecosystems support the maximum expression of biocultural diversity on the planet (Gorenflo et al., 2012), and preserving them requires understanding and working with the needs of their inhabitants. To a large extent, inhabitants' traditional knowledge (TK), which consists of past and present beliefs, traditions, practices, and views developed by indigenous and local communities (Huntington, 2000), is a key to accessing, using, and managing ecosystem services. This knowledge is diverse, dynamic, and place-specific. Still, it can also vary among communities and individuals, leading to different methods of obtaining benefits from the same resources (Byg and Balslev, 2004). The benefits that local communities obtain from their surrounding ecosystems are determined by the levels of TK about the classification, ecology, usefulness, and management of natural resources (Phillips et al., 1994), and on the richness, population size, and spatial distribution of species (Luck et al., 2003).

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http://dx.doi.org/10.1016/j.foreco.2014.08.019
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Much attention has been paid to understanding how the combination of social and ecological factors affects the production of ecosystem services (Reyers et al., 2013). Yet, the extent to which humans depend on ecosystem services across spatial scales and different population groups remains poorly understood (Yang et al., 2013). Scholars increasingly recognize the importance of integrating scientific knowledge and TK (Huntington, 2011). This approach bridges knowledge systems and facilitates processes of knowledge co-production to improve decision-making for management (Armitage et al., 2011).

Palms (Arecaceae) are an excellent model group for a study that integrates ecology and TK in order to determine the importance of ecosystem services on multiple spatial scales and with different population groups in South America. Palms are among the most abundant plant families in the tropical rainforests of South America. Some palm species are hyperdominant, and palms constitute a major proportion of the above ground biomass (ter Steege et al., 2013). In addition, many palms are “cultural keystone species” (Garibaldi and Turner, 2004) because they (i) have intense levels of use (Barfod and Balslev, 1988), (ii) have a multiplicity of uses (Balslev et al., 2008; Macía et al., 2011), (iii) have names and associated terminology in indigenous languages (Marmolejo et al., 2008), (iv) are prominent in narratives, ceremonies, and dances (Schultes, 1974), (v) are ubiquitous in the collective cultural consciousness (Cámara-Leret et al., 2014), (vi) are difficult to replace with other available native species, and (vii) are used as items of trade with other groups (Brokamp et al., 2011). Given their abundance, usefulness, and marketability, palms are intensely harvested, but mismanagement is common (Bernal et al., 2011).

Over the past few decades, scholars have sought to determine how useful plants influence native and non-native cultures (Prance et al., 1987; Phillips et al., 1994; Macía et al., 2001; Torre-Cuadros and Islebe, 2003), often to support conservation of South American rainforest habitats (Phillips et al., 1994). These studies have shown beyond a doubt that palms are the most useful plant family (Prance et al., 1987; Phillips et al., 1994). In the lowland *terra firme* forests of the Peruvian Amazon, a positive relationship exists between species usefulness and geographic range size (Ruokolainen and Vormisto, 2000). In lower montane forests (800–1000 m elevation) in south-eastern Ecuador, abundance and palm height positively correlate with usefulness (Byg et al., 2006). Another study using data from bibliographic references and herbarium specimens from the Ecuadorian Amazon (<500 m elevation) found that palm stem height, stem diameter, and fruit diameter positively correlate with the number of palm uses (de la Torre et al., 2009). Despite substantial advances, all of these studies employed different methods and were restricted in spatial scope, preventing conclusions on regional scales.

Here, we provide the first multiple-scale study on palm ethnoecology in the northwestern South American region, and possibly the world. Our study region ranks second in palm diversity globally (Dransfield et al., 2008) and is populated by a multiplicity of indigenous Amerindian groups and non-Amerindian groups of mixed ethnic origin (Lewis et al., 2013), whose livelihoods depend on forest-based products. As little is known about the ecosystem services of palms in other regions besides the Amazon, we included the tropical rainforests of the Andes and Chocó and investigated the TK of some of the human groups inhabiting them. Both of these regions are known to harbor hyper-diverse palm communities.

The overall objective of this study was to integrate TK about the usefulness of palms and ecological data to determine the distribution of palm-based ecosystem services on multiple spatial scales. Specifically, we asked the following questions: (1) Which palm species are most important to villagers and how is their usefulness related to their morphological attributes? (2) Are the patterns of forest usefulness similar across sub-regions, localities, and habitats? (3) What are the relative contributions of different palm growth forms to forest usefulness? (4) Which use categories are most important to villagers? Based on our findings, we evaluated the priorities necessary for future conservation plans in the region. To the best of our knowledge, this study is the first attempt to compare the ecosystem services of a keystone family across northwestern South America or any other region of the world.

Understanding large-scale spatial patterns in the distribution of palm-based ecosystem services on multiple scales will allow policymakers and managers to focus on species that make the greatest overall contribution to human livelihoods, prioritize conservation actions in habitats/sub-regions where palm ecosystem services are greatest, and direct more resources to areas where TK on palms is highest and, thus, where a danger of greater cultural erosion exists.

## 2. Methods

### 2.1. Study area

Our research was carried out in northwestern South America within the Amazon, Andes, and Chocó on three nested spatial scales: sub-regions, localities, and habitats (Fig. 1).

The four sub-regions were (i) northwestern Amazon, comprising areas in Colombia, Ecuador, and Peru east of the Andes at elevations below 1000 m and north of 5°S; (ii) southwestern Amazon, comprising areas in Peru and Bolivia east of the Andes at elevations below 1000 m and south of 5°S; (iii) the Andes, comprising the montane forests of Colombia and Peru above 1000 m; and (iv) the Chocó, comprising humid rainforests along the Pacific coast of Colombia and northwestern Ecuador (Fig. 1).

The 15 localities were defined on the basis of geographic proximity of communities with ethnobotanical interviews to the communities with palm transects (Table 1). Localities were inhabited by the following human groups: (i) Amerindian, dominated by one Amerindian group; (ii) multiethnic, mixed settlement of several Amerindian groups; (iii) mestizo, dominated by people of mixed origin whose parents were generally of European–Amerindian descendent; (iv) Afro-American, dominated by Black Americans of African ancestry; and (v) heterogeneous, mixed settlement of Amerindians and non-Amerindian groups (i.e., mestizos and/or Afro-Americans). The five sampled localities in the northwest Amazon sub-region are mostly inhabited and legally owned by Amerindians; they are vast and only accessible by rivers, and most are located far from markets. In contrast, the six localities in the southwest Amazon contain a greater proportion of non-Amerindian people and of private lands, access is mostly by roads and markets are close. Within the Chocó sub-region, the Colombian study locality is populated and owned by Afro-Americans. In the Ecuadorian Chocó, both Amerindians and non-Amerindians coexist in close proximity, and land tenure is a mixture between collectively owned Amerindian lands and private property. Both Chocó localities are accessible by roads and located close to markets. The remaining two Andean localities are inhabited by Amerindians and accessible by roads. The Colombian Andean site is located in a valley that harbors several large towns, has a mixture of private and indigenous lands, and is immersed in the market economy. In contrast, at the Bolivian site Amerindians are the exclusive owners of vast lands and villages are farther from markets.

The 15 localities covered eight habitats: (i) Amazon floodplain, including floodplain and swamp forests; (ii) Amazon non-inundated; (iii) Amazon pre-montane hills, located on the eastern flank of Andean foreland forests at elevations of 300–550 m; (iv) Chocó floodplain; (v) Chocó non-inundated; (vi) Chocó pre-montane hills, located on the western flank of Andean foreland forests at eleva-

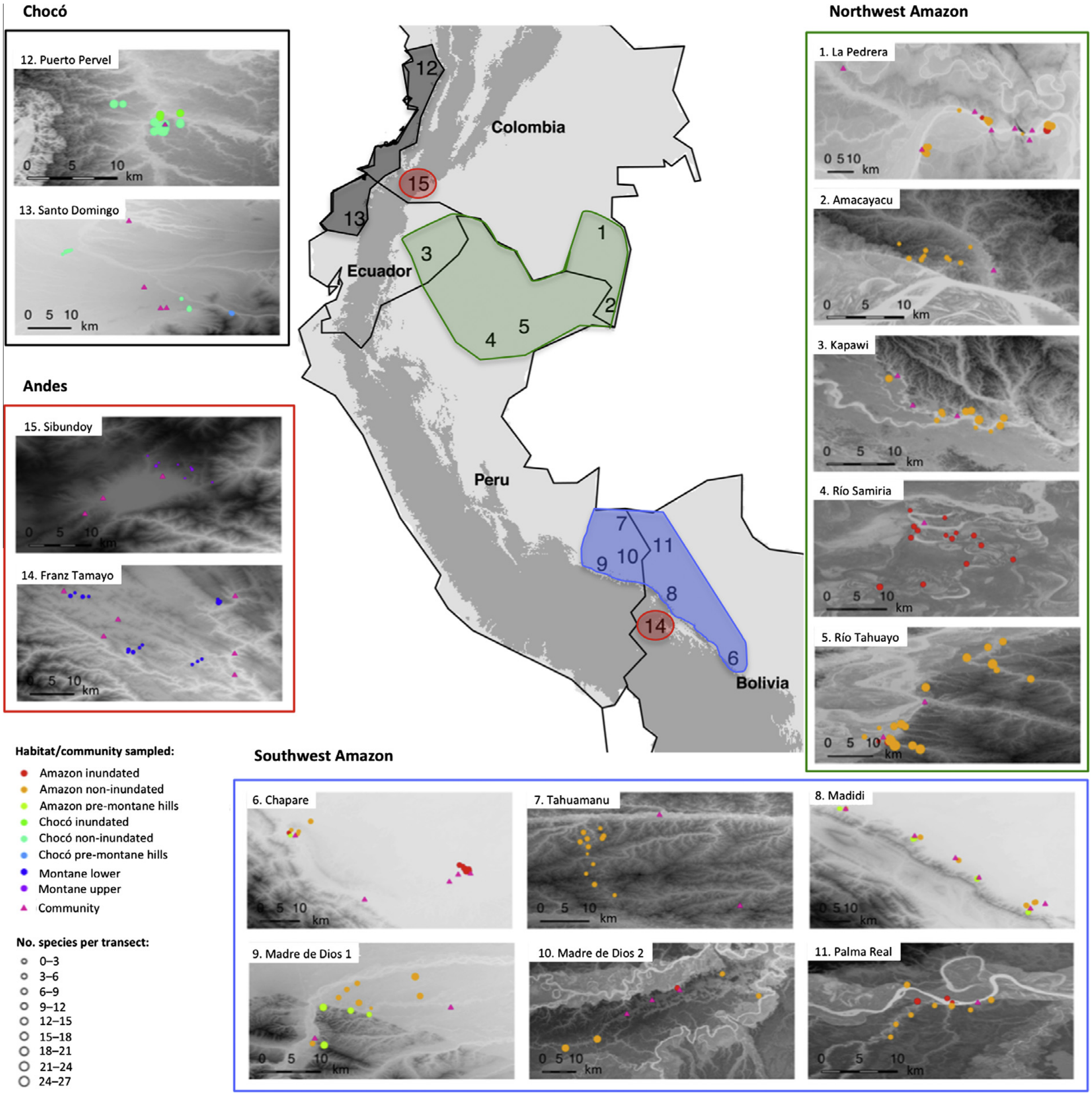

**Fig. 1.** Location of communities and transects sampled in 15 localities in northwestern South America, showing habitat type and local species richness for each transect. Symbol sizes indicate species richness, defined as the number of species per transect. The 90 m digital elevation images were obtained from the CGIAR-CSI Consortium for Spatial Information (http://srtm.csi.cgiar.org/).

tions ~800 m; (vii) lower montane, located at elevations of 1000–1900 m; and (viii) upper montane, located at elevations of 2500–2900 m (Table 1).

### 2.2. Ecological sampling

During 2005–2010, we assessed palm community composition in 197 transects using a standardized method (Balslev et al., 2010). These transects spanned 21° latitude and 14° longitude across the region (Table 1 and Fig. 1). Each transect was 5 × 500 m (0.25 ha) and divided into 100 subunits of 5 × 5 m. Within each subunit, we identified and counted all adult and sub-adult palm individuals, with sub-adults being fully grown individuals that did not show signs of having reproduced. The Puerto Nariño dataset from Colombia collected by J.C. Berrío differed from the standardized method in that transects were 4 × 500 m, and only adult palms with a diameter >1 cm at breast height were recorded. Transects were sampled from the eight habitat types, with 2–104 transects per habitat, located in 15 localities, with 5–25 transects per locality. Voucher specimens were deposited at AAU, AMAZ, CHOCO, COL, LPB, QCA, and USM (herbarium acronyms according to Thiers (2013)). Species were classified into palm growth forms following Balslev et al. (2011). Of the eight palm growth forms described for the Americas, medium/small palms with stout stems were absent from transects and ethnobotanical interviews. *Attalea plowmannii*, erroneously cited in the literature as being large tall-stemmed was corrected to acaulescent-large. Species absent in Balslev et al. (2011) were classified according to our field experience, namely *Attalea racemosa* (acaulescent-large), *Bactris gasipaes* var. *chichagui* (medium) and *Ceroxylon pityrophyllum* (medium). We followed the World Checklist of Palms to unify nomenclature (Govaerts and Dransfield, 2005).

**Table 1**
The 15 localities sampled in northwestern South America.

Ecological factors

| Sub-region/locality | Geographic coordinates[†] | N–S extent (km) | Min. and max. inter-transect distance (km) | Sample area (ha) | No. Species | Mean (±SD) no. species transect$^{-1}$ | No. transect/habitat | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | Total transects | Amazon inundated | Amazon non-inundated | Amazon pre-montane hills | Chocó inundated | Chocó non-inundated | Chocó pre-montane hills | Lower montane | Upper montane |
| Northwestern Amazon | | | | 17.25 | 78 | 11.6 ± 3.2 | 71 | 18 | 53 | 0 | 0 | 0 | 0 | 0 | 0 |
| 1 – La Pedrera | 1°13′19″S; 1°23′26″S | 19 | 0.7–51 | 4 | 41 | 11.6 | 16 | 2 | 14 | – | – | – | – | – | – |
| 2 – Amacayacu | 3°43′41″S; 3°45′45″S | 3 | 0.35–9 | 2 | 20 | 8 | 10 | – | 10 | – | – | – | – | – | – |
| 3 – Kapawi | 2°26′49″S; 2°34′38″S | 14 | 0.73–10 | 2.75 | 38 | 13.3 | 11 | – | 11 | – | – | – | – | – | – |
| 4 – Río Samiria | 4°38′53″S; 4°54′13″S | 29 | 1.62–29 | 3.5 | 17 | 9.2 | 14 | 14 | – | – | – | – | – | – | – |
| 5 – Río Tahuayo | 3°37′50″S; 4°23′8″S | 84 | 0.79–86 | 5 | 45 | 15.9 | 20 | 2 | 18 | – | – | – | – | – | – |
| Southwestern Amazon | | | | 19.625 | 40 | 10.2 ± 1.9 | 79 | 13 | 51 | 15 | 0 | 0 | 0 | 0 | 0 |
| 6 – Chapare | 16°21′34″S; 16°31′52″S | 19 | 0.45–48 | 3.5 | 16 | 8.9 | 14 | 9 | 4 | 1 | – | – | – | – | – |
| 7 – Tahuamanu | 10°59′58″S; 11°17′34″S | 32 | 1.23–32 | 3 | 20 | 8.6 | 12 | – | 12 | – | – | – | – | – | – |
| 8 – Madidi | 13°46′53″S; 14°25′16″S | 71 | 0.13–99 | 6.25 | 20 | 8.3 | 25 | – | 15 | 10 | – | – | – | – | – |
| 9 – Madre de Dios 1 | 12°50′0″S; 13°2′7″S | 23 | 2.11–27 | 2.875 | 25 | 11.8 | 12 | – | 8 | 4 | – | – | – | – | – |
| 10 – Madre de Dios 2 | 12°39′4″S; 12°53′24″S | 27 | 10.3–61 | 1.25 | 25 | 13 | 5 | 1 | 4 | – | – | – | – | – | – |
| 11 – Palma Real | 12°28′6″S; 12°35′33″S | 14 | 0.83–17 | 2.75 | 24 | 10.6 | 11 | 3 | 8 | – | – | – | – | – | – |
| Chocó | | | | 6 | 44 | 12.5 ± 7.3 | 24 | 0 | 0 | 0 | 3 | 19 | 2 | 0 | 0 |
| 12 – Puerto Pervel | 5°26′0″N; 5°22′59″N | 5 | 0.17–5 | 3.75 | 33 | 17.6 | 15 | – | – | – | 3 | 12 | – | – | – |
| 13 – Santo Domingo | 0°0′55″S; 0°18′24″S | 30 | 0.53–50 | 2.25 | 21 | 7.3 | 9 | – | – | – | – | 7 | 2 | – | – |
| Andes | | | | 5.75 | 22 | 3.8 ± 2.4 | 23 | 0 | 0 | 0 | 0 | 0 | 0 | 15 | 8 |
| 14 – Franz Tamayo | 14°47′8″S; 15°3′32″S | 30 | 0.41–40 | 3.75 | 17 | 5.5 | 15 | – | – | – | – | – | – | 15 | – |
| 15 – Sibundoy | 1°15′18″N; 1°11′13″N | 8 | 0.65–13 | 2 | 7 | 2.1 | 8 | – | – | – | – | – | – | – | 8 |

Social Factors

| Sub-region/locality (no. villages) | No. interviews (mean ± SD) | No. useful species (mean ± SD) | No. palm uses (mean ± SD) | Human group | Land tenure | Area (ha)[*] | Access | Remoteness | % Houses with palm thatch (mean ± SD) |
|---|---|---|---|---|---|---|---|---|---|
| Northwestern Amazon | 518 (104 ± 39) | 84 (40 ± 10) | 1114 (336 ± 198) | | | | | | 74 ± 21 |
| 1 – La Pedrera (*n* = 7) | 110 | 54 | 668 | Mu | Am | 280,000 | Fluvial | Remote | 46 |
| 2 – Amacayacu (*n* = 1) | 88 | 47 | 365 | Am | Am | 86,871 | Fluvial | Medium | 52 |
| 3 – Kapawi (*n* = 3) | 65 | 31 | 192 | Am | Am | 120,000 | Fluvial | Remote | 97 |
| 4 – Río Samiria (*n* = 1) | 87 | 36 | 195 | H | Am | 2000 | Fluvial | Remote | 86 |
| 5 – Río Tahuayo (*n* = 2) | 168 | 34 | 260 | Me | Pr | Pp | Fluvial | Remote | 89 |
| Southwestern Amazon | 404 (67 ± 37) | 37 (20 ± 3) | 351 (115 ± 47) | | | | | | 51 ± 26 |
| 6 – Chapare (*n* = 5) | 66 | 17 | 113 | Am | Am | 250,000 | Road | Close | 23 |
| 7 – Tahuamanu (*n* = 2) | 33 | 21 | 91 | H | Am/Pr | 26,675/Pp | Road | Medium | 39 |

(*continued on next page*)

**Table 1** (*continued*)

| Social Factors | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Sub-region/locality (no. villages) | No. interviews (mean ± SD) | No. useful species (mean ± SD) | No. palm uses (mean ± SD) | Human group | Land tenure | Area (ha)* | Access | Remoteness | % Houses with palm thatch (mean ± SD) |
| 8 – Madidi ($n = 6$) | 127 | 19 | 101 | H | Am | 198,400 | Road | Close | 97 |
| 9 – Madre de Dios 1 ($n = 2$) | 64 | 21 | 131 | H | Pr | Pp | Road | Close | 25 |
| 10 – Madre de Dios 2 ($n = 3$) | 25 | 16 | 58 | Me | Pr | Pp | Road | Close | 48 |
| 11 – Palma Real ($n = 1$) | 89 | 23 | 197 | Am | Am | 9491 | Fluvial | Medium | 73 |
| Chocó | 225 (113 ± 37) | 29 (19 ± 2) | 324 (180 ± 1) | | | | | | 0 |
| 12 – Puerto Pervel ($n = 1$) | 86 | 20 | 181 | Af | Af | Pp | Road | Close | 0 |
| 13 – Santo Domingo ($n = 4$) | 139 | 17 | 179 | H | Am/Pr | 19,119/Pp | Road | Close | 0 |
| Andes | 347 (174 ± 6) | 19 (11 ± 6) | 211 (107 ± 54) | | | | | | 15.5 |
| 14 – Franz Tamayo ($n = 6$) | 178 | 15 | 145 | Am | Am | 502,118 | Road | Medium | 31 |
| 15 – Sibundoy ($n = 3$) | 169 | 6 | 68 | Am | Am/Pr | 3252/Pp | Road | Close | 0 |

*Abbreviations*: *Human group*. Am: Amerindian, Af: Afro-American, H: Heterogeneous, Me: Mestizo, Mu: Multiethnic; *Land tenure*. Am: Amerindian lands; Pr: Private property; Af: Afro-American collective lands.

[*] *Area*: Pp: Private plots of 1–15 ha per person or family.

[†] Latitude of the northernmost and southernmost transects within a locality.

### 2.3. Ethnobotanical sampling

From May 2010 through December 2011, we collected ethnobotanical data on palm species using a standardized method (Paniagua-Zambrana et al., 2010; Cámara-Leret et al., 2012). We conducted 25–178 interviews in each of the 15 localities (in total $n = 1494$) where ecological data were gathered (Table 1). Ethnobotanical data were collected with two types of participants: expert informants, of whom we interviewed up to 15 in each locality (in total $n = 105$, mean = 7, SD = 4); and general informants, of whom we interviewed up to 165 in each locality (in total $n = 1389$, mean = 93, SD = 46). Selection of experts was through consensus during a community meeting. In localities with communities too large for gathering all villagers, such as in Andean sites with populations exceeding 1000 inhabitants, experts were recruited by asking several general informants to recommend their most knowledgeable peers. Walks in the field with each expert were performed to document palm uses and to compile a list of the vernacular names of as many palm species as possible. Once experts were interviewed, we used the list of compiled vernacular names as the basis for interviews with general informants. We selected general informants in each community (or group of communities belonging to one ethnic group when there were fewer than 87 informants in one community) in a stratified manner to have a representative sample of gender (women, $n = 758$; men, $n = 735$) and age classes (18–30 years, 28%; 31–40 years, 23%; 41–50 years, 20%; 51–60 years, 13%; over 60 years, 17%). Interviews were conducted in Spanish or when needed with a local interpreter.

### 2.4. Data analysis

We analyzed all data at the species level, with the exception of *Bactris gasipaes*, for which we differentiated the wild var. *chichagui* from the cultivated var. *gasipaes*. The latter was excluded from analyses, as were other cultivated species (i.e., *Cocos nucifera*, *Elaeis guineensis, Parajubaea cocoides*). Species cited by informants but absent from their locality (e.g., report of the Amazonian *Mauritia flexuosa* in a Chocó village) were excluded from the analyses because these reports do not contribute to local measures of forest usefulness.

#### 2.4.1. Which palm species are most important to stakeholders?

Palm use reports were classified into one of 10 use categories and subcategories following Cook (1995), with modifications proposed by Macía et al. (2011). Use categories include Animal food, Construction, Cultural, Environmental, Fuel, Human food, Medicinal and veterinary, Toxic, Utensils and tools, and Other uses. The category Cultural included clothes and accessories, cosmetics, dyes, personal adornment, recreational and ritual uses. The category Other uses included uses not classifiable within the previous categories and indirect use of palms (e.g. the use of beetle larvae that develop in rotting trunks). A subcategory is a more detailed classification of each use category. For instance, the Human food category is divided into four subcategories: Beverages, Food, Food additives and Oils. For a list of subcategories see Macía et al. (pp. 467–469) (2011). We defined each "palm use" as the use of a palm part from a given species associated with a use category and a use subcategory (Macía et al., 2011).

For each of the 15 localities, we created accumulation curves of the number of species per transect, the number of useful palm species cited by informants, and the number of palm uses cited by informants in 999 runs with a randomized order of transects and informants (Fig. A.1). The accumulation curves indicated that we had adequate ecological and ethnobotanical sampling at all localities. The usefulness of palms to locals at each locality was assessed by calculating use values ($UV_s$) for individual species as suggested by Phillips and Gentry (1993), with the simplification by Rossato et al. (1999). The use value of a species was defined by Eq. (1).

$$UV_s = \sum U_i/N \tag{1}$$

In the equation, $U_i$ is the number of uses mentioned by each informant $I$, and $N$ is the total number of informants interviewed in the locality.

To understand which of the morphological variables were underlying differences in use values for the whole study region we first conducted a Variation Inflation Factor analysis to assess for multicollinearity among the following predictor variables: maximum stem diameter, maximum stem height, max fruit diameter, maximum leaf number, maximum mid-leaf length, and abundance. We took out variables one at a time until all VIF values of the predictor variables set were less than 5. The result of the VIF analysis was the exclusion of maximum stem diameter (VIF = 6.32) from our predictor variable set. Using the new set of variables (maximum stem height, max fruit diameter, maximum leaf number, maximum mid-leaf length, and abundance), we examined a series of increasingly complex models. The best model was selected on the basis of the Akaike Information Criterion (AIC). AIC allows for choosing between competing models by testing all subsets of a model and is a measure of the relative goodness of fit between a data set and a given model (Akaike, 1974). When comparing models fitted by maximum likelihood to the same data, the model with the smallest AIC is generally considered as the best among all models under consideration. To assess how the predictor variables selected in the AIC best model acted on all sub-regions and localities, we performed non-parametric Spearman correlations between species use values and the predictor variables. Significance levels were assessed using 10,000 permutations for each test. Morphological data (i.e., maximum stem height, maximum stem diameter, maximum mid-leaf length, maximum leaf number, and maximum fruit diameter) were obtained from Borchsenius et al. (1998), Henderson (2002), Galeano and Bernal (2010), and the e-monocot website (http://e-monocot.org).

### *2.4.2. What are the cross-scale patterns in forest usefulness in different sub-regions, localities, and habitats?*

To determine the usefulness of forests, we only included adult and subadult palm individuals in our analyses because seedlings and juveniles are rarely used in the study area. On each scale, we quantified the use value of a forest hectare ($UV_f$) (cf. Thomas et al., 2009). $UV_f$ represents the summed use value of stems per forest hectare and is defined by Eq. (2).

$$UV_f = \frac{\sum UV_s * n}{a} \tag{2}$$

In this equation, $UV_s$ is the use value of each species, $n$ is the number of individuals belonging to that species, and $a$ is the total number of hectares. On each scale (i.e., habitat, locality, sub-region), a Kruskal–Wallis analysis was conducted to test for significant differences in $UV_f$. Pairwise Wilcoxon rank sum comparisons with a Bonferroni correction were performed as a post hoc test on the different scales.

### *2.4.3. What is the contribution of different palm growth forms and use categories to forest usefulness?*

In each locality, we assessed how much of the total summed use value of a forest hectare (Eq. (2)) was accounted for by the different palm growth forms and use categories using two-way ANOVA. For growth forms identified in the ANOVA as having a significantly higher contribution to forest usefulness, we performed a MANOVA to determine whether they differed significantly in their contribution to the five most important use categories. Finally, pairwise Wilcoxon rank sum comparisons with a Bonferroni correction were performed as a post hoc test of significant differences among each growth form. All analyses were performed using R 3.0.1 (R Development Core Team, 2013).

### *2.5. Ethics statement*

Approval for this study was granted by the Committee for Ethical Research of the Autonomous University of Madrid (#48-922; PI Manuel J. Macía). We conducted our research in association with the following local institutions: Universidad Nacional de Colombia (Colombia); Pontificia Universidad Cátolica del Ecuador (Ecuador); Universidad Nacional Mayor de San Marcos (Peru); and Universidad Mayor de San Andrés (Bolivia). Before initiating in situ data collection, we obtained oral informed consent on the village level and then individually prior to each interview out of respect for the fact that some interviewees lack reading or writing skills. The ethics committee of the Autonomous University of Madrid approved this procedure. The consent of participation was acknowledged by writing the date and name of the informant on the interview questionnaire. Informants were informed of their right to discontinue the interviews at any time and that all information that they provided would be anonymized.

Palm collection 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 Areas Protegidas (Bolivia). The field studies did not involve endangered or protected species.

## 3. Results

### *3.1. Traditional knowledge patterns*

A total of 1656 different palm uses were mentioned in 1494 interviews, and they derived from 120 species of palms. Overall TK peaked in northwestern Amazon, with 70% of all the registered useful palm species and 67% of all uses represented. The percentage of houses thatched with palms varied greatly between sub-regions (Table 1). The higher levels of TK in the northwestern Amazon sub-region were associated with poor road access, greater remoteness, and higher mean percentage of houses thatched with palm leaves. Of all localities, the multi-ethnic La Pedrera in northwestern Amazon had the highest levels of TK as indicated by the number of useful palm species and number of uses known by informants. Traditional knowledge of Amerindian localities was similar to that of non-Amerindian localities in the Peruvian Amazon and to heterogeneous localities in the Chocó. In the Andes, the upper montane Amerindian locality (Sibundoy) had substantially lower levels of TK than the lower montane locality (Franz Tamayo).

### *3.2. Palm species richness*

Altogether, we found 130 palm species and counted 35,890 adult and subadult palm individuals in the 197 transects, covering 49.25 ha. Palm species richness peaked in the northwestern Amazon sub-region (up to 45 species in locality 5, Río Tahuayo; Table 1). In contrast, the southwestern Amazon sub-region had a similar number of species as the Chocó, and species richness was lowest in the Andes (seven species in locality 15, Sibundoy). Thirty-seven species occurred in more than one sub-region, and six species were present in all four sub-regions (Table A.1). Regarding habitats, Amazon non-inundated forests had the highest species richness (81 species), and Chocó floodplain forests had the highest mean number of species per transect (Table 2). The mean density of palms per hectare peaked in the Amazon floodplain and Amazon pre-montane hills, and it was lowest in the Andean upper montane habitat. As for the mean number of species per transect, the highest values were found in Chocó (Puerto Pervel) and the lowest values in both Andean localities. Locally, species showed signs of non-random distribution patterns, with 63 species (or 48% of all species) occurring in only one locality (Table A.1).

### 3.3. Most useful palm species

Overall, 90 species (69%) and 24,194 individuals (67%) found in the transects were useful to the people in our study localities (see Table A.1 for complete species list). However, the use values of species in the 15 localities varied greatly (Fig. 2). A small group of species (*Attalea phalerata, Euterpe precatoria, Iriartea deltoidea, Oenocarpus bataua,* and *Socratea exorrhiza*) were highly important locally but exhibited marked variation across localities (Fig. 3). Thus, some species were highly useful within one locality (e.g., *Aphandra natalia* in locality 3, Kapawi), but other species, such as *O. bataua*, were highly useful in 14 of the 15 localities (Fig. 3). The species that were highly useful at multiple localities varied in their abundance, but the variation in abundance was unrelated to variation in use value. Furthermore, on all analyzed scales, no correlation was found between the use value and the abundance of palm species (Table 3 and Table A.2).

By and large, species with the highest use values were largely concentrated in the growth form large tall-stemmed palms ($UV_s$ range = 0.8–10.8, mean = 3.8 ± 2.2 SD) (Fig. 3). For the whole study area, we found that species' use values were best predicted by maximum stem height, maximum fruit diameter and maximum mid-leaf length as predictor variables (model 7, AIC = 1313) (Table 3). A similar trend was observed on the local scale, and $UV_s$ significantly correlated with maximum stem height, maximum fruit diameter, and maximum mid-leaf length in most sub-regions and localities, but not with abundance (Table A.2).

### 3.4. Cross-scale patterns in forest usefulness

At the sub-region scale, we found that all between-subregion comparisons of $UV_f$ were not significant (Fig. 4). In contrast, at the local scale all between-locality comparisons of $UV_f$ were significant (Kruskal–Wallis test: H = 99.67, $P < 0.001$; Table A.3). The density of highly useful species exhibited large within-locality and between-locality variation (Table A.4). In addition, some species, even highly important ones, were not present everywhere and, thus, did not contribute to local-scale measures of forest usefulness. Species absences peaked in Amazonian localities and were most common in the larger palm growth forms.

At the habitat scale, we found that forest usefulness differed according to the measure of usefulness used. According to the percentage of useful species, the Amazon floodplain and Amazon non-inundated forests were the most useful, but according to the percentage of useful individuals lower montane and the Chocó floodplain were the most useful habitats (Table 2). Based on use value data, the habitats differed significantly in the grand total of their use values or $UV_f$ (Kruskal–Wallis test: H = 34.08, $P < 0.001$). Post-hoc pairwise between-habitat comparisons revealed that the Amazon floodplain was the most useful habitat (Fig. 4 and Table A.5).

### 3.5. Importance of use categories and growth forms

A breakdown of the proportion of summed use value according to the nine use categories is shown in Table A.6. Overall, 'human food' ($F = 5.848$, $P < 0.001$) and 'construction' ($F = 7.770$, $P < 0.001$) accounted for significantly higher proportions of $UV_f$, both within and between localities. 'Construction' was the most important use category in all sub-regions, accounting for an average of 47% of forest usefulness (±20% SD). The second most important category in the northwestern Amazon, the southwestern Amazon, and the Chocó was 'human food'; in the Andes it was 'cultural uses'. However, large variation was found in the importance of use categories within localities. Thus, 'construction' scored highest in ten localities (3, 5, 6, 7, 8, 9, 10, 11, 13, and 14), 'human food' in three localities (1, 4, and 12), and 'cultural' in two (2 and 15). 'Utensils and tools' ranked among the three most important use categories in seven localities (1, 4, 6, 12, 13, 14, and 15). In contrast, 'medicinal and veterinary' and 'other' accounted for very low proportions of forest usefulness, and 'animal food', 'environmental', and 'fuel' were the least important use categories in all sub-regions and localities, with an average contribution of <1%.

Three growth forms presented a significantly higher contribution to overall forest usefulness within localities: large tall-stemmed palms ($F = 3.975$, $P < 0.001$), large-leaved medium-short stemmed ($F = 2.221$, $P = 0.03$), and small palms ($F = 4.244$, $P < 0.001$; Figs. 5 and 6). Large tall-stemmed palms constituted the most important growth form in six localities (1, 3, 7, 9, 13, and 14), small palms in six localities (4, 5, 6, 8, 10, and 11), and large-leaved medium-short stemmed in one locality (2) (Fig. 5). The three growth forms differed significantly in their contribution to 'cultural' ($F = -2.856$, $P = 0.005$) and 'medicinal and veterinary' ($F = -3.808$, $P = 0.0003$), with large tall-stemmed palms accounting for a significantly higher contribution to both 'cultural' and 'medicinal and veterinary' uses than the other growth forms ($P < 0.05$ in both comparisons; Fig. 6).

## 4. Discussion

### 4.1. Traditional knowledge patterns

Tropical rainforest inhabitants possess high levels of TK about palms. Our study revealed that, the people of the northwestern

**Table 2**
Habitat type usefulness based on use value techniques and percentage of useful species and individuals.

| Habitat | No. transects | No. species inventoried | Mean no. species transect$^{-1}$ | No. individuals inventoried | Mean density (palms ha$^{-1}$) | % useful species | % useful individuals | Average use value individual$^{-1}$ | Summed use values of stems |
|---|---|---|---|---|---|---|---|---|---|
| Amazon floodplain | 31 | 50 | 10.11 | 7935 | 1024 | 80 | 69 | 1.04 | 265.3 |
| Amazon non-inundated | 104 | 81 | 10.39 | 20,114 | 794 | 75 | 70 | 0.89 | 173.2 |
| Amazon pre-montane hills | 15 | 25 | 10.42 | 3826 | 1020 | 48 | 41 | 0.46 | 117.3 |
| Chocó floodplain | 3 | 27 | 17.67 | 392 | n.a. | 63 | 91 | 1.70 | 222.5 |
| Chocó non-inundated | 19 | 39 | 13.63 | 1793 | 377 | 62 | 80 | 1.43 | 135.1 |
| Chocó pre-montane hills | 2 | 13 | 8.5 | 196 | n.a. | 62 | 76 | 0.40 | 39.4 |
| Lower montane | 15 | 17 | 5.47 | 1413 | 377 | 65 | 97 | 1.52 | 142.7 |
| Upper montane | 8 | 7 | 2.13 | 221 | 111 | 50 | 66 | 1.76 | 48.5 |

Amazon basin have the highest levels of overall TK about palms. Amerindian groups in the northwestern Amazon reported >1000 different palm uses, almost twice as many uses as the rest of our study area combined (Colombia, Ecuador, Peru, Bolivia). The drivers of the high levels of TK in the northwest Amazon are most likely the predominantly Amerindian population of the sub-region, the exclusive fluvial access to most villages (versus road access in the other sub-regions), and the greater remoteness of its villages from markets. On smaller scales, we found that locality 1 (La Pedrera), where over five different Amerindian tribes coexist near their traditional lands, had the highest levels of knowledge among all study sites. Such findings are congruent with the cultural edge hypothesis of Turner et al. (2003), which states that, in areas where multiple cultures interact, a broader range of TK exists compared to areas inhabited by a single group. In contrast, our local scale findings in the Peruvian Amazon and Chocó, that the TK of non-Amerindian and heterogeneous villages reached similar levels as Amerindian villages, contradicts past findings in the Brazilian and Ecuadorian Amazon (Campos and Ehringhaus, 2003; Byg and Balslev, 2004). Though much of this folk knowledge may have grown by information exchange with Amerindians (Caballero, 1995), novel methods of using palms may also have been discovered by non-Amerindians. However, when interpreting our results, four components of TK can be recognized (Berkes et al., 2000): names of the living (e.g., plants), the functions and uses of each component, the land-resource management systems and institutions that govern them, and the world views-cosmologies that guide people's ethics. Because our study only captures the first two components in detail, our findings should not be extrapolated to the other levels.

### 4.2. Most useful species

Although multiple species may contribute to a particular ecosystem service, some palm species are overwhelmingly more important than others to local people. Even some ethnic groups

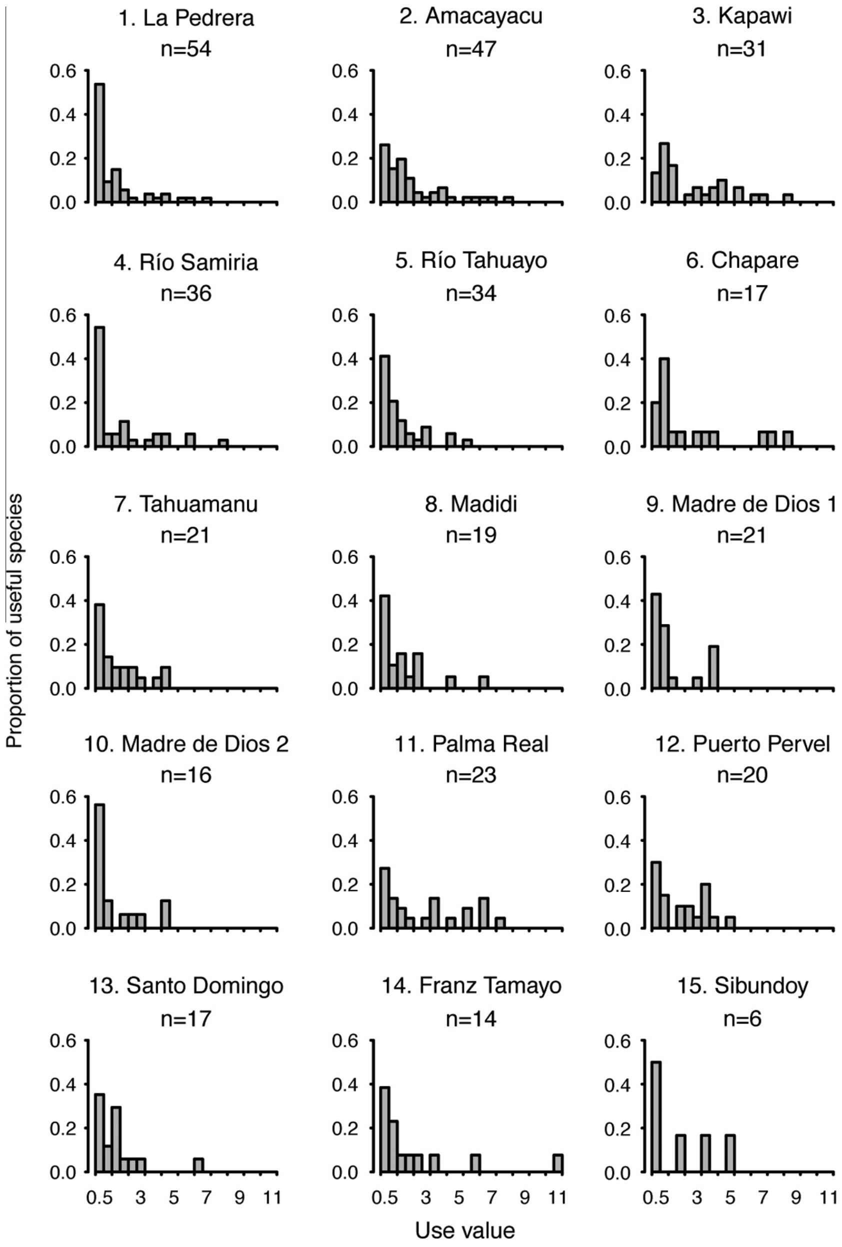

**Fig. 2.** Frequency distribution of the use values for palm species in 15 localities of northwestern South America. The value of n indicates the number of useful species.

| Sub-region | Northwest Amazon | | | | | Southwest Amazon | | | | | | Chocó | | Andes | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Locality | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 |
| **Large tall-stemmed** | | | | | | | | | | | | | | | |
| *Astrocaryum chambira* Burret | ● | ● | ● | ◐ | ● | | | | | | | | | | |
| *Astrocaryum jauari* Mart. | | | | ○ | | | | | | | | | | | |
| *Astrocaryum standleyanum* L.H.Bailey | | | | | | | | | | | | | ◐ | | |
| *Attalea butyracea* (Mutis ex L.f.) Wess.Boer | | ◐ | ◐ | ● | ○ | ● | ● | | | | ● | | | | |
| *Attalea colenda* (O.F.Cook) Balslev & A.J.Hend. | | | | | | | | | | | | | ● | | |
| *Attalea maripa* (Aubl.) Mart. | ● | ○ | ◐ | | ○ | | | | ◐ | | ○ | | | | |
| *Attalea phalerata* Mart. ex Spreng. | | | ○ | ● | ○ | ● | ○ | ● | ● | ◐ | ● | | | ● | |
| *Ceroxylon ventricosum* Burret | | | | | | | | | | | | | | | ● |
| *Dictyocaryum lamarckianum* (Mart.) H.Wendl. | | | | | | | | | | | | | | ● | |
| *Euterpe oleracea* Mart. | | ◐ | | | | | | | | | | ● | | | |
| *Euterpe precatoria* Mart. | ● | ● | ○ | ● | ● | | ● | ● | ◐ | ● | ● | | | ◐ | |
| *Iriartea deltoidea* Ruiz & Pav. | ◐ | ◐ | ● | ○ | ◐ | ● | ◐ | ● | ● | ● | ○ | | ● | ● | |
| *Mauritia flexuosa* L.f. | ◐ | ● | ● | ● | ● | | ◐ | ◐ | ● | ● | ◐ | | | | |
| *Oenocarpus bacaba* Mart. | ◐ | | | | | | | | | | | | | | |
| *Oenocarpus bataua* Mart. | ● | ● | ● | ○ | ◐ | ● | ● | ● | ● | ● | ● | ● | ◐ | ● | |
| *Socratea exorrhiza* (Mart.) H.Wendl. | ◐ | ◐ | | ◐ | ◐ | ◐ | ● | ○ | ◐ | | ○ | ◐ | ○ | ◐ | |
| **Large-leaved Medium-short stemmed** | | | | | | | | | | | | | | | |
| *Aphandra natalia* (Balslev & A.J.Hend.) Barfod | | | ◐ | | | | | | | | | | | | |
| *Astrocaryum ferrugineum* F.Kahn & B.Millán | | ○ | | | | | | | | | | | | | |
| *Astrocaryum gratum* F.Kahn & B.Millán | | | | | | | | | ◐ | | ◐ | | | | |
| *Astrocaryum murumuru* Mart. | | | | | | ◐ | ○ | ◐ | | | | | | ○ | |
| *Astrocaryum urostachys* Burret | | | ◐ | | | | | | | | | | | | |
| *Manicaria saccifera* Gaertn. | | | | | | | | | | | | ● | | | |
| *Phytelephas aequatorialis* Spruce | | | | | | | | | | | | | ● | | |
| *Phytelephas macrocarpa* Ruiz & Pav. | | ○ | | ◐ | ● | | ◐ | ◐ | ○ | | ○ | | ◐ | | |
| *Phytelephas tenuicaulis* (Barfod) A.J.Hend. | | | ○ | | | | | | | | | | | | |
| **Medium** | | | | | | | | | | | | | | | |
| *Bactris gasipaes var. chichagui* (H.Karst.) A.J.Hend. | | | | | | | ◐ | | | | ◐ | | ○ | | |
| *Ceroxylon parvum* Galeano | | | | | | | | | | | | | | ◐ | |
| *Ceroxylon vogelianum* (Engel) H.Wendl. | | | | | | | | | | | | | | | ● |
| *Oenocarpus mapora* H.Karst. | ○ | ○ | ○ | ◐ | ◐ | | | ◐ | ○ | ◐ | ◐ | ● | | | |
| *Prestoea acuminata* (Willd.) H.E.Moore | | | | | | | | | | | | | | | ● |
| *Welfia regia* H.Wendl. | | | | | | | | | | | | ○ | | | |
| *Wettinia quinaria* (O.F.Cook & Doyle) Burret | | | | | | | | | | | | ◐ | ● | | |
| **Small** | | | | | | | | | | | | | | | |
| *Aiphanes horrida* (Jacq.) Burret | | | | | | ○ | | | | | | | | ◐ | |
| *Asterogyne martiana* (H.Wendl.) H.Wendl. ex. Drude | | | | | | | | | | | | ○ | | | |
| *Astrocaryum huaimi* Mart. | | | | ○ | | | | | | | | | | | |
| *Bactris chaveziae* A.J.Hend. | | | | | | ○ | | | | | | | | | |
| *Bactris coloniata* L.H.Bailey | | | | | | | | | | | | ○ | | | |
| *Bactris major* Jacq. | | | | | | ◐ | | | ○ | | | | | | |
| *Bactris concinna* Mart. | | | | | | | ○ | ○ | | | | | | | |
| *Bactris setulosa* H.Karst. | | | | | | | | | | | | | ◐ | | |
| *Chamaedorea angustisecta* Burret | | | | | | | | ○ | | | | | | ○ | |
| *Geonoma brongniartii* Mart. | | | | | | ○ | | | | | | | | | |
| *Geonoma deversa* (Poit.) Kunth | | | | | | ◐ | ○ | ○ | ○ | ◐ | | | | | |
| *Geonoma undata* Klotzsch | | | | | | | | | | | | | | ○ | |
| *Hyospathe elegans* Mart. | | | | | | ○ | | | | | | | | | |
| *Iriartella setigera* (Mart.) H.Wendl. | ○ | | | | | | | | | | | | | | |
| *Lepidocaryum tenue* Mart. | ○ | | | | | | | | | | | | | | |
| *Mauritiella macroclada* (Burret) Burret | | | | | | | | | | | | ◐ | | | |
| *Wettinia aequalis* (O.F.Cook & Doyle) R.Bernal | | | | | | | | | | | | | ○ | | |
| **Acaulescent large** | | | | | | | | | | | | | | | |
| *Attalea allenii* H.E.Moore | | | | | | | | | | | | ◐ | | | |
| *Attalea insignis* (Mart.) Drude | | | | | ○ | | | | | | | | | | |
| *Attalea microcarpa* Mart. | ○ | | | | | | | | | | | | | | |
| **Climbing** | | | | | | | | | | | | | | | |
| *Desmoncus cirrhiferus* A.H.Gentry & Zardini | | | | | | | | | | | | ○ | | | |

● very high use value, ◐ high use value, ○ medium use value

**Fig. 3.** The 12 most important species of each locality with a use value ⩾0.5 divided into three classes of importance and grouped by their respective growth form. For names of the 15 localities see Table 1.

**Table 3**
The increasingly complex models (1–9) used to evaluate the relationship between species UV (dependent variable) versus palm morphology as well as palm abundance.

| Model | Independent variables | Akaike information criterion (AIC) |
|---|---|---|
| 1 | Abundance | 1524 |
| 2 | Max.fruit diameter | 1462 |
| 3 | Max.mid-leaf.length | 1388 |
| 4 | Max.stem height | 1372 |
| 5 | Max.stem height + Max.fruit diameter | 1325 |
| 6 | Max.stem height + Max.mid-leaf length | 1342 |
| **7** | **Max.stem height + Max.fruit diameter + Max. mid-leaf length** | **1313** |
| 8 | Max.stem height + Max.fruit diameter + Max. mid-leaf length + Abundance | 1314 |
| 9 | Max.stem height + Max.fruit diameter + Max. mid-leaf length + Max.leaf number | 1315 |

Bold AIC value is the lowest and therefore judged the best model.

interviewed in our study are named after some of these highly useful palms. For example, the term *achuar* referring to the Amerindian tribe is a contraction of the two words *achu shuar*, which translates as the *M. flexuosa people* (Descola, 1986). Interestingly, our finding that usefulness in most sub-regions positively correlates with maximum stem height, maximum mid-leaf length and maximum fruit diameter suggests that the structural properties of palms strongly determine local preferences. This result agrees with past studies conducted on smaller scales, based on different methods, and restricted to the Amazon (Ruokolainen and Vormisto, 2000; de la Torre et al., 2009), and lends support to the idea that plant salience is positively correlated with usefulness (Phillips and Gentry, 1993). A positive relationship between a species' maximum mid-leaf length and its usefulness has not, to our knowledge, been reported in previous studies. Yet, the fact that these correlations were not always significant on local scales indicates that additional factors affect local perceptions.

The absence of a significant relationship between palm abundance and usefulness partially contradicts results from a study in the pre-montane habitat of southern Ecuador, where significant relationships were detected for some villages characterized by intermediate to low knowledge levels (Byg et al., 2006). A lack of correlation in our study at all analyzed scales may be due to the omission of seedlings from the analyses. Had we included seedlings, we would likely have overestimated the abundance of large-tall stemmed palms because this growth form is characterized by a greater proportion of seedlings than adults in tropical rainforests (Kristiansen et al., 2009). And because large tall-stemmed palms were the most useful growth form in our study, abundance and usefulness would likely have been correlated. However, the high mortality rates of seedlings in tropical rainforests combined with the extremely slow growth rates of many palms (Henderson, 2002) makes the inclusion of seedlings in ecosystem service studies irrelevant because seedlings do not reflect a harvestable resource.

In contrast to abundance, geographic range was an important determinant of palm species usefulness. Regionally, seven geographically widespread species were highly useful to locals in three or more sub-regions: *A. phalerata, E. precatoria, I. deltoidea, O. bataua, Oenocarpus mapora, Phytelephas macrocarpa,* and *Socratea exhorriza*. Other studies limited to Amazonian palms have also reported positive correlations between geographic range and usefulness (Ruokolainen and Vormisto, 2000), but we confirmed this pattern based on interview data and extended it to the Chocó and Andes sub-regions. The consensus between informants across our study area underscores just how many livelihoods are supported by a few widespread palm species, and demonstrates how important it is to understand local preferences that drive humans to select certain species over others. This understanding requires linking cultural, morphological, and ecological factors, all of which can only be analyzed together through an interdisciplinary lens.

### 4.3. Usefulness of forest types

A greater usefulness of Amazon floodplain forests compared to other habitats of the Amazon, Chocó, and Andes has not, to the best of our knowledge, been reported in the literature. Although inventories on smaller scales in the Peruvian and Bolivian Amazon have shown the Amazon floodplain to be more useful than Amazon non-inundated habitats (Phillips et al., 1994; Macía et al., 2001; Thomas et al., 2009), our findings are novel because they consider comparisons with other habitats beyond those found in the Amazon. Our conclusions are also based on data from not just large-diameter palms, but also smaller palm growth forms not included in past studies. Although Amazon non-inundated forests had the highest total number of useful palm species, their lower mean summed use value can be explained by a lower density of very useful palms compared to Amazon floodplain forests. Despite the lower usefulness of Amazon non-inundated forests, these forests are important to livelihoods because they provide highly useful species that are absent from floodplain forests, such as *Astrocaryum chambira* (Table A.1). At least three other reasons exist for making the Amazon floodplain a priority habitat: (i) it has a much smaller area than upland terra firme forests, (ii) it is closer to urban areas and river settlements, and is being deforested faster than other habitats, and (iii) it is indispensable for managing Amazon fish stocks (Barthem and Goulding, 2007).

### 4.4. Importance of growth forms and use categories

To the best of our knowledge, this study is the first to show that palm-based ecosystem services are largely driven by the contribution of three functional groups: large tall-stemmed, large-leaved medium-short stemmed, and small palms. Therefore, palm-based

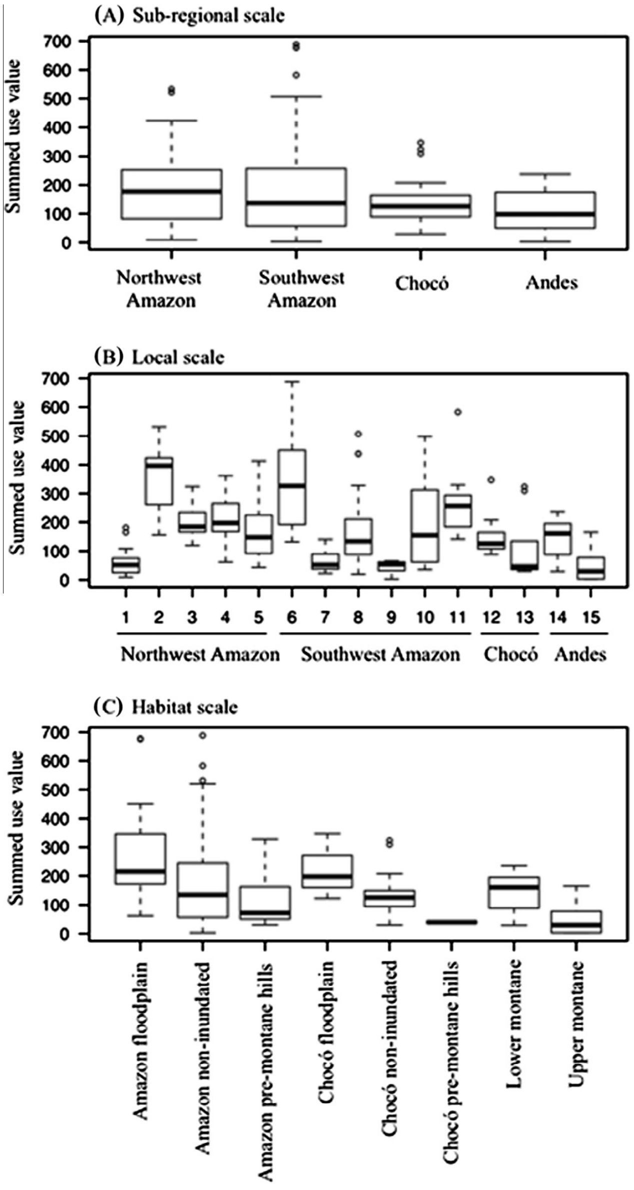

**Fig. 4.** Multi-scale comparison of forest usefulness showing the range and mean of transect summed use values. Whiskers extend to the most extreme data point which is no more than 1.5 times the interquartile range from the box; more extreme values are displayed as circles.

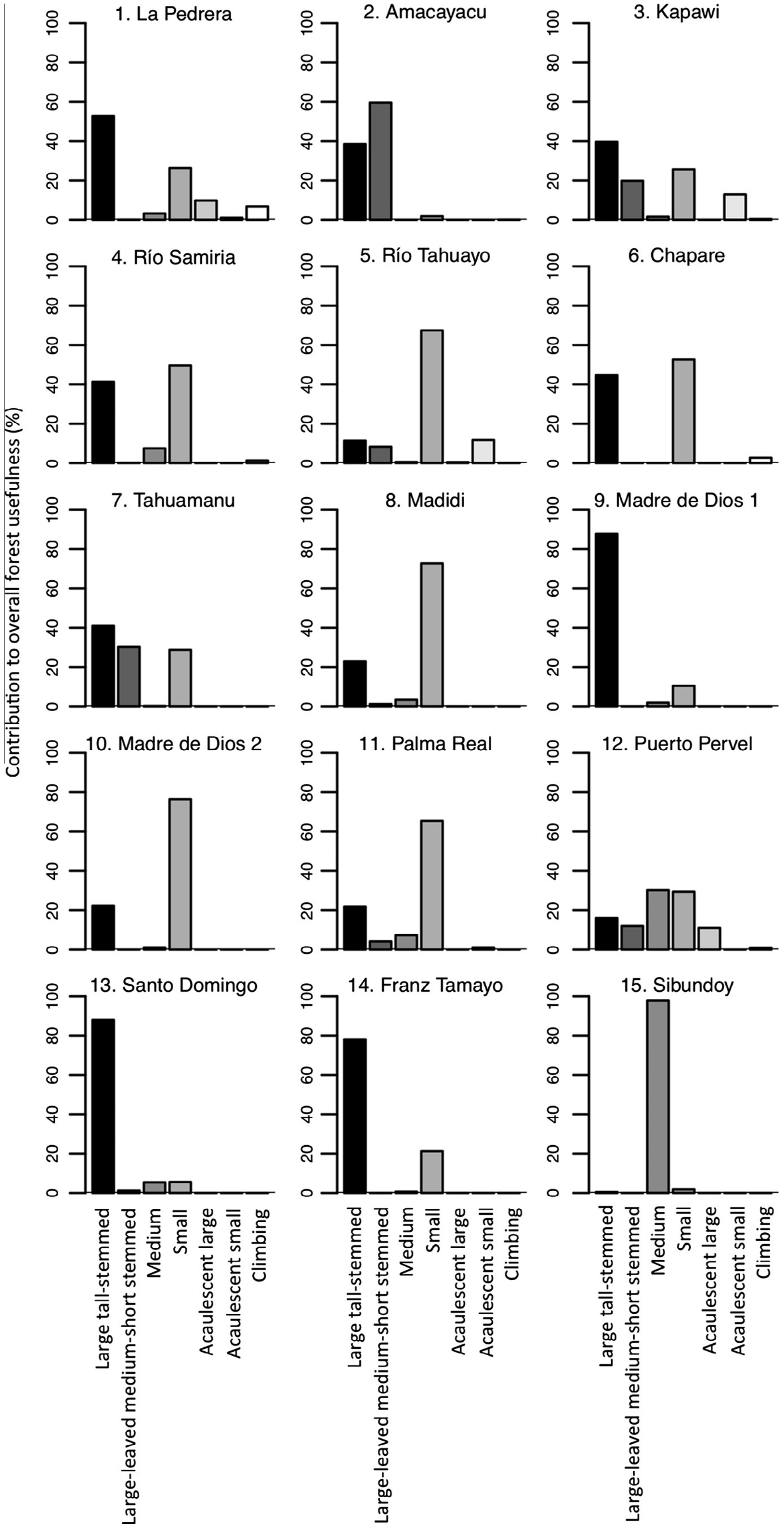

**Fig. 5.** Contribution of seven palm growth forms to overall forest usefulness in 15 localities of northwestern South America.

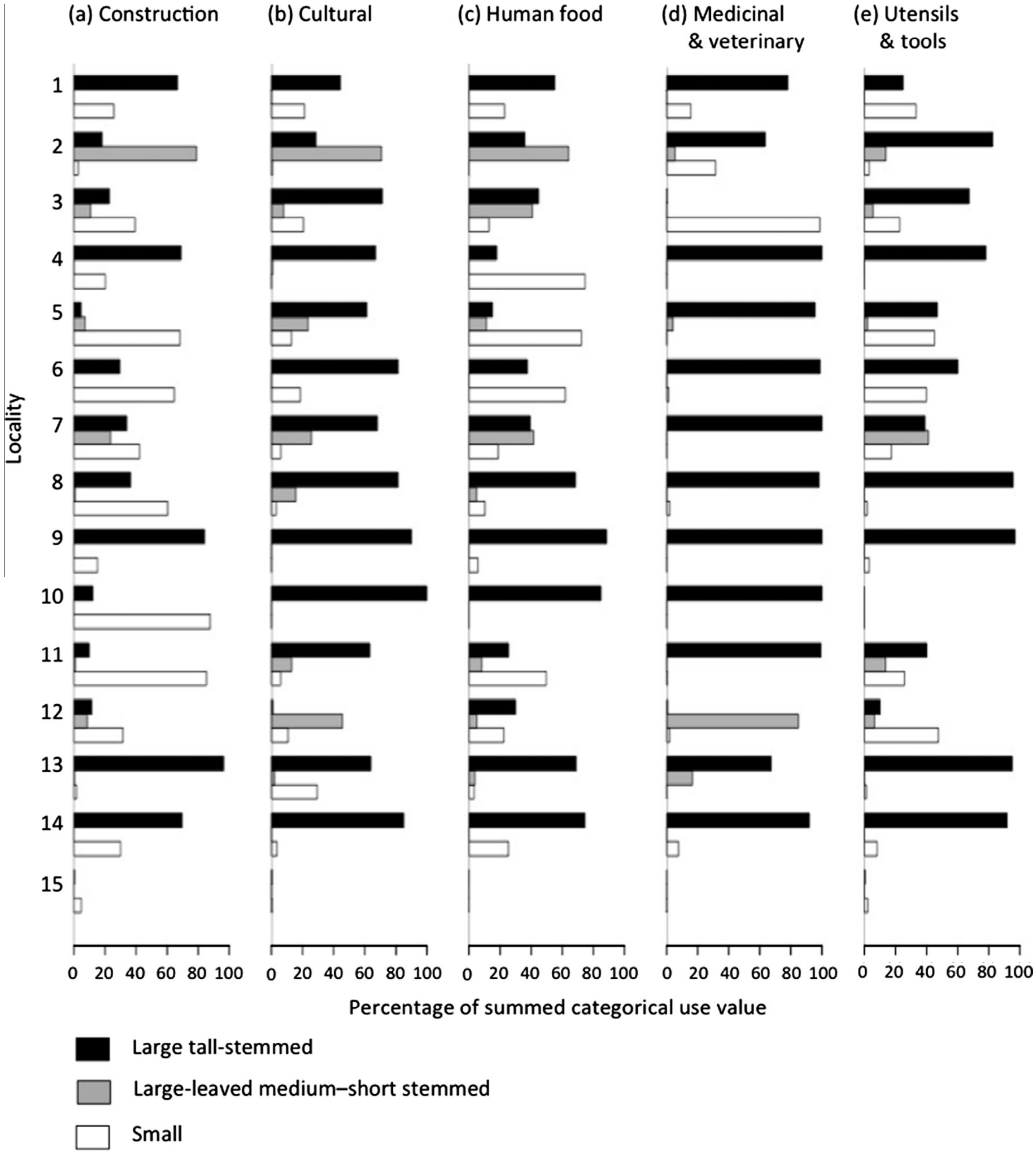

**Fig. 6.** Percentage of the summed categorical use values attributed to the three most useful palm growth forms in the 15 study localities.

ecosystem service assessments must incorporate different growth forms, even the smallest ones. The small palms growth form makes up 68% of all inventoried individuals in our study (Table A.4), accounts for the greatest proportion of forest value in 40% of our study localities (Fig. 5), and is essential for construction uses.

Our finding that human food and construction dominate forest use irrespective of sociocultural background highlights how much local people rely on palms for subsistence livelihoods (Phillips et al., 1994; Macía et al., 2001; Macía, 2004). However, one of the shortcomings of the use value index is its inability to distinguish between 'real use' and TK (Torre-Cuadros and Islebe, 2003). For example, we found that this was the case for construction uses. Despite the high categorical use values for construction in both Chocó study sites, palm thatch was absent in all homes. Local people in the Chocó explained that this shift had occurred over the past few decades because of better economic opportunities and industrial materials becoming increasingly available. In the Andean upper montane habitat (Sibundoy), the wood from *Ceroxylon ventricosum* was replaced in the 1960s by sawed boards for house walls (Bristol, 1965), and the use of *Prestoea acuminata* leaves for thatch in the 1960s is no longer present. In contrast, in the Amazon localities we visited, over 50% of homes were still thatched with palms. In the southwestern Amazon, *Genoma deversa* is highly esteemed (Zuidema, 2000), whereas in the northwestern Amazon, *Lepidocaryum tenue* is irreplaceable in the construction of traditional roundhouses (Galeano and Bernal, 2010) (Fig. 7).

Although past studies show that smaller life forms (e.g., herbs) have a higher medicinal value than larger woody forms (Thomas et al., 2011), we found that this was not applicable to palms because large tall-stemmed palms were the most important growth form in this use category. The medicinal importance of palms has been increasingly recognized over the last few decades (Macía et al., 2011), and experimental confirmation on the

**Fig. 7.** Many palms are cultural keystone species with a fundamental influence on culture. This is the case of (A) *Lepidocaryum tenue* for numerous Amerindian tribes of the Colombian Amazon, (B) *Ceroxylon ventricosum* for the Kamsá of the Colombian Andes, and (C) *Manicaria saccifera* for Afro-Colombians in the Chocó. (Photos: Rodrigo Cámara-Leret, Juan C. Copete, Dennis Pedersen, and Marybel Soto).

medicinal properties of some large tall-stemmed palm species already exists (Maia and Rao, 1989). Finally, our finding that large tall-stemmed palms make a significantly higher contribution to cultural uses provides additional support to our statement that cultural keystone species are generally large tall-stemmed palms with a multiplicity of uses and a set of attached myths and rituals. In this regard, ritual use of towering palms constitutes the most important palm-based ecosystem service for Amerindians in the Colombian Andes (Sibundoy) (Fig. 7). Similarly, in the northwest Amazon locality 2 (Amacayacu), large tall-stemmed palms play an overwhelming role in cultural uses because this growth form provides the best materials for palm-based souvenirs that are sold to tourists to complement local economies.

## 5. Implications for conservation and recommendations

In the coming decades, the sustainable use of palms will be critical for biocultural conservation given the rapid demographic growth of indigenous populations in Latin America (McSweeney, 2005), the rapid increase in household numbers in biodiversity hotspots (Liu et al., 2003), and the increasing encroachment by oil and gas projects (Finer et al., 2008), and industrial plantations of African oil palm (Butler and Laurance, 2009), all of which open the doors for colonists and markets. Our work shows that thousands of tropical rainforest dwellers rely on palm-based ecosystem services in northwestern South America and calls for management of palm populations wisely to sustain the flow of palm-based goods. The conservation and management of palm species with widespread importance is essential for all Andean Community member states programs that seek to benefit rainforest dwellers, and highly useful palm species should be introduced in regional biodiversity strategies (e.g., Amazon Cooperation Treaty Organization, Andean regional biodiversity strategy). However, in addition to provisioning ecosystem services from palms, the cultural non-material benefits further highlight the roles of palms in human well-being. Despite the fact that cultural services are weakly integrated into the ecosystem service research and policy framework (Daniel et al., 2012), the non-material appreciation of palms by forest cultures could facilitate the development of socioecological models for these cultural services across multiple regions.

Because Amerindian and Afro-Americans have full autonomy to manage resources within their territories in many of our study sites, top-down single-sector management may be of limited efficacy and other complementary measures are needed. Conservation programs that focus on a set of key palms could be implemented directly through partnerships between NGOs, scientists, Amerindian organizations, and non-Amerindian collective groups. Some promising examples already exist. For example, the sustainable management of *M. flexuosa* was achieved in a remote river community of the Peruvian Amazon by the active engagement of villagers in an NGO-sponsored project. This project had a broad outlook and contributed to securing communal tenure, participatory inventories of palm resources, setting aside a protected area, establishing a palm nursery, and purchasing tree-climbing devices (Manzi and Coomes, 2009). Our results provide a working list of locally valued species for NGOs, environmental agencies, and communities, and the list can be further refined through on-the-ground discussions in order to establish immediate priorities for multi-species management plans. Management practices are particularly important for small palm species used for thatch given the number of individuals needed to thatch a house (Galeano and Bernal, 2010), but also for large tall-stemmed palms whose towering stems are often felled to harvest fruits for human food and wood for construction. Furthermore, many of these widespread, highly useful palms are important in local markets, and some reach international markets; thus, their strong harvest imposes pressure on the populations in all four Andean countries (Brokamp et al., 2011).

While scientists can inform policymakers and locals, the ultimate decision to contribute to these goals rests upon stakeholders, especially at remote sites where law enforcement is weak. The widespread existence of Amerindian and local communities' property rights in the study area (cf. Decree 2164, Constitution 1991, Colombia; Ministerial Agreement 265, Ecuador; Law 22175, Peru; Law 3545, Constitution 2009, Bolivia) provides ideal conditions for translating the findings of our study into future community-based resource management initiatives. Although TK, with its place-based, fine-scale spatiotemporal information and institutions, has allowed for the conservation of vast tracts of tropical rainforests, its erosion may lead to negative conservation outcomes. Spearheaded by local institutions, village-wide adoption of conservation measures could substantially reduce the deleterious impacts of harvest on palm populations. Gaining insight into TK and developing alliances with Amerindian and non-Amerindian organizations represent challenges that must be overcome in order to promote conservation in one of the most valuable places on Earth in terms of biocultural diversity and human knowledge about palm ecosystem services.

## Author contributions

Conceived and designed the study: RCL, MJM, AB, HB. Performed the fieldwork: RCL, NPZ, HB, JCC, MJM. Analyzed the data: RCL, AB. Wrote the paper: RCL, HB, AB, MJM.

## Acknowledgements

We warmly thank the 1494 informants in our fieldwork interviews, whose names are too many to list here. We are grateful to the many institutions and research teams that facilitated our research. We would especially like to thank Gloria Galeano, Rodrigo Bernal, Laura Mesa, Eva Ledezma, Alicia Mena, Gaspar Morcote, Julio Betancur, Juan Alvaro Echeverri, Dairon Cardenas, Erwin Palacios, Henry Yucuna, Renato Valencia, Rommel Montúfar, Roberto Carrillo, Hugo Navarrete, Lucía de la Torre, the William L. Brown Center, INBIA Peru, Betty Millán, Cesar Grández, Monica Moraes, Alejandro Ordoñez, Ziyu Ma, and the Ecoinformatics and Biodiversity Group at Aarhus University for their support and discussions. We also wish to extend our gratitude to Marybel Soto, Armando Nacimiento, Amancio Perea, Jailer Macuna, Mateo Jaimes, Lina Camelo, Rainer Bussmann, and Erika Blacutt for assistance with the fieldwork. Juan Carlos Berrío kindly provided ecological data for the Leticia locality. This study was funded by the European Union, 7th Framework Programme (Contract No. 212631), the Russel E. Train Education for Nature Program of the WWF, and the Anne S. Chatham fellowship of the Garden Club of America (to NPZ), as well as the Universidad Autónoma de Madrid travel grants program and the GSST fellowship of Aarhus University (to RCL).

## Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2014.08.019.

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