Are Ecologically Important Tree Species the Most Useful? A Case Study from Indigenous People in the Bolivian Amazon[1]

Maximilien Guèze[2], Ana Catarina Luz[2], Jaime Paneque-Gálvez[2], Manuel J. Macía[3], Martí Orta-Martínez[2], Joan Pino[4], and Victoria Reyes-García*,[5]

[2]Institut de Ciència i Tecnologia Ambientals (ICTA), Universitat Autònoma de Barcelona, 08193 Bellaterra, Spain
[3]Departamento de Biología, Área de Botánica, Universidad Autónoma de Madrid, Calle Darwin 2, 28049 Madrid, Spain
[4]Centre de Recerca Ecològica i Aplicacions Forestals (CREAF), Universitat Autònoma de Barcelona, 08193 Barcelona, Spain
[5]ICREA at the Institut de Ciència i Tecnologia Ambientals (ICTA), Universitat Autònoma de Barcelona, 08193 Bellaterra, Spain
*Corresponding author; e-mail: Victoria.reyes@uab.cat

Are Ecologically Important Tree Species the Most Useful? A Case Study from Indigenous People in the Bolivian Amazon. Researchers have argued that indigenous peoples prefer to use the most apparent plant species, particularly for medicinal uses. However, the association between the ecological importance of a species and its usefulness remains unclear. In this paper we quantify such association for six use categories (firewood, construction, materials, food, medicines, and other uses). We collected data on the uses of 58 tree species, as reported by 93 informants in 22 villages in the Tsimane' territory (Bolivian Amazon). We calculated the ecological importance of the same species by deriving their importance value index (IVI) in 48 0.1-ha old-growth forest plots. Matching both data sets, we found a positive relation between the IVI of a species and its overall use value (UV) as well as with its UV for construction and materials. We found a negative relation between IVI and UV for species that were reportedly used for medicine and food uses, and no clear pattern for the other categories. We hypothesize that species used for construction or crafting purposes because of their physical properties are more easily substitutable than species used for medicinal or edible purposes because of their chemical properties.

Las especies de árboles de mayor importancia ecológica ¿son también las más útiles? Estudio de caso en un pueblo indígena de la Amazonia boliviana. Se ha argumentado que las poblaciones indígenas usan más las especies de plantas más comunes, especialmente para fines medicinales. Sin embargo, los patrones de asociación entre la importancia ecológica de una especie y su utilidad no son totalmente consistentes. En este estudio cuantificamos esta asociación para seis categorías de usos (leña, construcción, materiales, comestible, medicinal, y otros usos) en el territorio Tsimane' (Amazonía boliviana). Recogimos datos de usos de 58 especies de árboles, reportados por 93 informantes en 22 comunidades, y combinamos estos datos con la importancia ecológica de las especies, estimada por su índice de importancia ecológica (IVI) en 48 parcelas de 0.1 ha establecidas en bosque maduro. Encontramos una relación positiva entre el IVI de las especies y su valor de uso (UV) general, además de su UV en construcción y materiales. Encontramos una relación negativa entre el IVI y el UV para las plantas medicinales y comestibles, y ningún patrón claro para las otras categorías. Nuestros datos sugieren que las especies usadas para construcción o materiales por sus propiedades físicas son más fácilmente sustituibles que las especies usadas como medicinales o comestibles por sus propiedades químicas.

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Introduction

The ethnobotanical knowledge of people living in tropical forests has been increasingly well documented in the last decades (Albuquerque and Lucena 2005; Bennett 1992). However, little is known about why people use some species more than others and particularly whether spatial distribution patterns of species relate to patterns of use. Ethnobotanists have addressed this question through the "ecological apparency" hypothesis (Lucena et al. 2007; Phillips and Gentry 1993a, b). The hypothesis, first developed to explain plant-herbivores relations, considers that the visibility (or apparency) of the plant, together with its chemical composition, will influence herbivores' behavior. When applied to human uses of plant species, researchers have hypothesized that most apparent species (i.e., most visible) have more known uses, and therefore a greater use value (UV) (*sensu* Phillips and Gentry 1993a), because they are readily available.

Some studies have tested this hypothesis mostly by relating the number of uses of species to their apparency, proxied by different ecological measures. For example, some authors have related the overall UV of a species with its density, dominance, and frequency (Galeano 2000; Lawrence et al. 2005; Phillips and Gentry 1993b) or with its importance value index (IVI) (Lucena et al. 2007; Thomas et al. 2009a; Torre-Cuadros and Islebe 2003). Particularly, the IVI of a species seems to be a good indicator of apparency because it provides information on basal area, frequency, and abundance, and therefore on the saliency of the species (Thomas et al. 2009a). Another study has related the UV to the accessibility of plant communities, proxied by the travel time to those sites (Thomas et al. 2009b). In all these studies the visibility of a species tends to be positively associated to its number of uses, thus giving support to the ecological apparency hypothesis.

Focusing on medicinal uses and based on the frequency with which a species had been collected by botanists, Berlin (2003) found that among Highland Mayas in Mexico, common species are more often used as medicines than rare species. Stepp and Moerman (2001) have stressed that weeds, i.e., common species, are the most frequently found life form in the pharmacopoeia of the Mayas, probably because people seek highly bioactive compounds, which are commonly found in weeds. Voeks (2004) also reports the importance of secondary vegetation in traditional medicine. Findings from these studies are important in ethnopharmacological research because they challenge the traditional understanding that people obtain medicinal species from "unique and inaccessible habitats" (Berlin 2003, p. 2). However, a major setback in this body of research is that none of these studies has been based on ecological inventories.

Results from studies measuring ecological apparency based on forest inventories have yielded equivocal results. For example, a study among rural people in areas dominated by *caatinga* vegetation (Brazil) found a negative association between medicinal importance (an index related to UV) and the density and frequency of woody species (Silva and Albuquerque 2005), whereas another study in the same environment revealed a positive association between the medicinal UV and woody species frequency (Lucena et al. 2007). Similarly, a study among indigenous groups of Bolivia found a positive correlation between the medicinal UV and the IVI of woody species (Thomas et al. 2009a), whereas a study among *mestizos* in the Peruvian Amazon reported no association between the medicinal UV and the density, dominance, or frequency of woody species (Phillips and Gentry 1993b).

Within this context, the overall objective of this study is to analyze the relation between tree species' usefulness and their ecological importance in the territory of the Tsimane', a lowland Bolivian indigenous group. Specifically, our goals are to 1) test whether there is an association between the usefulness of a tree species, proxied by its UV, and its IVI, and 2) analyze different patterns of association between IVI and UV across different categories of use. If the ecological importance of a species drives its number of uses because people have more opportunities to learn about salient species, as predicted by the ecological apparency hypothesis, then we should find that the higher the IVI of a species, the larger its number of uses known (and therefore the larger its UV).

The Tsimane': Lands and Knowledge

The Tsimane' are one of the largest ethnic groups in the lowlands of Bolivia. Their territory lies between the foothills of the Andes and part of the Moxos savannas (Fig. 1). Annual mean temperature is 25.8°C (Navarro and Maldonado 2002) and annual mean precipitation is 1,743 mm (Godoy et al. 2008), with important inter-annual climatic variation. The climate is markedly seasonal, with four months with less than 100 mm of rainfall and episodic southern cold winds. Soils are quaternary alluvial sediments of fluvial origin, mostly acrisols and ferralsols (Navarro and Maldonado 2002).

The territory of the Tsimane' is situated at the interface between three biogeographic regions: Amazonia, the Andes, and Brazilian-Paraná. Most of the territory is covered with well-drained upland *terra firme* rainforest (Guèze et al. 2013). In some areas, different types of flooded forests occur according to the history of inundation. The northeastern part of the territory coincides with the edge of the Moxos savannas, where gallery forests and forest islands that seem to have an anthropogenic origin are found (Lombardo et al. 2011). In the southwestern part of the territory the hills form a transition with the Andean submontane forests.

Traditionally, the Tsimane' have been semi-nomadic hunters-gatherers and small-scale horticulturalists. They used to live in nuclear families scattered along rivers and streams. Nowadays they live clustered in permanent villages close to communication axes (main rivers and forest roads). The Tsimane' hold a deep knowledge of wild plants; Reyes-García et al. (2006) reported uses of 410 plant species. Traditional knowledge of wild plants is strongly shared by the whole ethnic group (Reyes-García et al. 2003), and has important consequences for Tsimane' life, as higher levels of knowledge have been found to be associated with less deforestation and more diversity in agricultural fields (Reyes-García et al. 2007a, 2008) and better health (McDade et al. 2007). Nowadays, although the Tsimane' still strongly rely on mostly unfragmented forests for their livelihood, they experience different levels of encroachment upon their territory, integration into the market economy, and cultural changes, which in turn affect their knowledge and use of the forest (Reyes-García et al. 2007b). For example, some Tsimane' still practice subsistence slash-and-burn agriculture while others produce cash crops. It has also been shown that activities that drive the Tsimane' to leave their villages are associated with lower levels of traditional knowledge, whereas activities that keep them in their homelands contribute to the maintenance of this form of knowledge (Reyes-García et al. 2007b).

Materials and Methods

Data Collection

Since our study focuses on the relation between ecological importance and species usefulness, our data collection strategy includes methods from ecology and methods from sociocultural anthropology. Our analysis focuses on trees because they are well known by most Tsimane', and some species are known by a single local name (see below, personal observation). Palms were also included in the analyses because they are among the most useful plant species (Macía et al. 2011), and because—ecologically—palms resemble trees.

Ecological Data

To obtain the IVI of tree species we established 48 0.1-ha plots in the territory of six Tsimane' villages (eight plots per village, hereafter called "villages with plots") (Fig. 1). We selected villages on the basis of homogeneity in 1) forest types and topography, through the analysis of Landsat satellite images (Paneque-Gálvez et al. 2013), and 2) village characteristics, such as the number of households, based on a previous census (Reyes-García et al. 2012). Within each village we established plots in old-growth *terra firme* forest with no apparent sign of recent human activity (at a minimum distance of 500 m from any agricultural field or fallow, and without large canopy gaps). In each plot we inventoried all trees with a diameter at breast height (dbh) ≥ 2.5 cm. We counted all stems rooting within the plot limits. Multiple stems were considered as one individual. We measured the dbh of each individual at 1.3 m from the ground. We collected voucher specimens for all individuals that could not be identified in the field. Duplicates of the vouchers are deposited in LPB (Herbario Nacional de Bolivia, La Paz, Bolivia) and MA (Real Jardín Botánico, Madrid, Spain), and unicates are kept in LPB.

We selected 58 useful species, among all the tree species inventoried, following these criteria: 1) usefulness of the plant reported by at least three

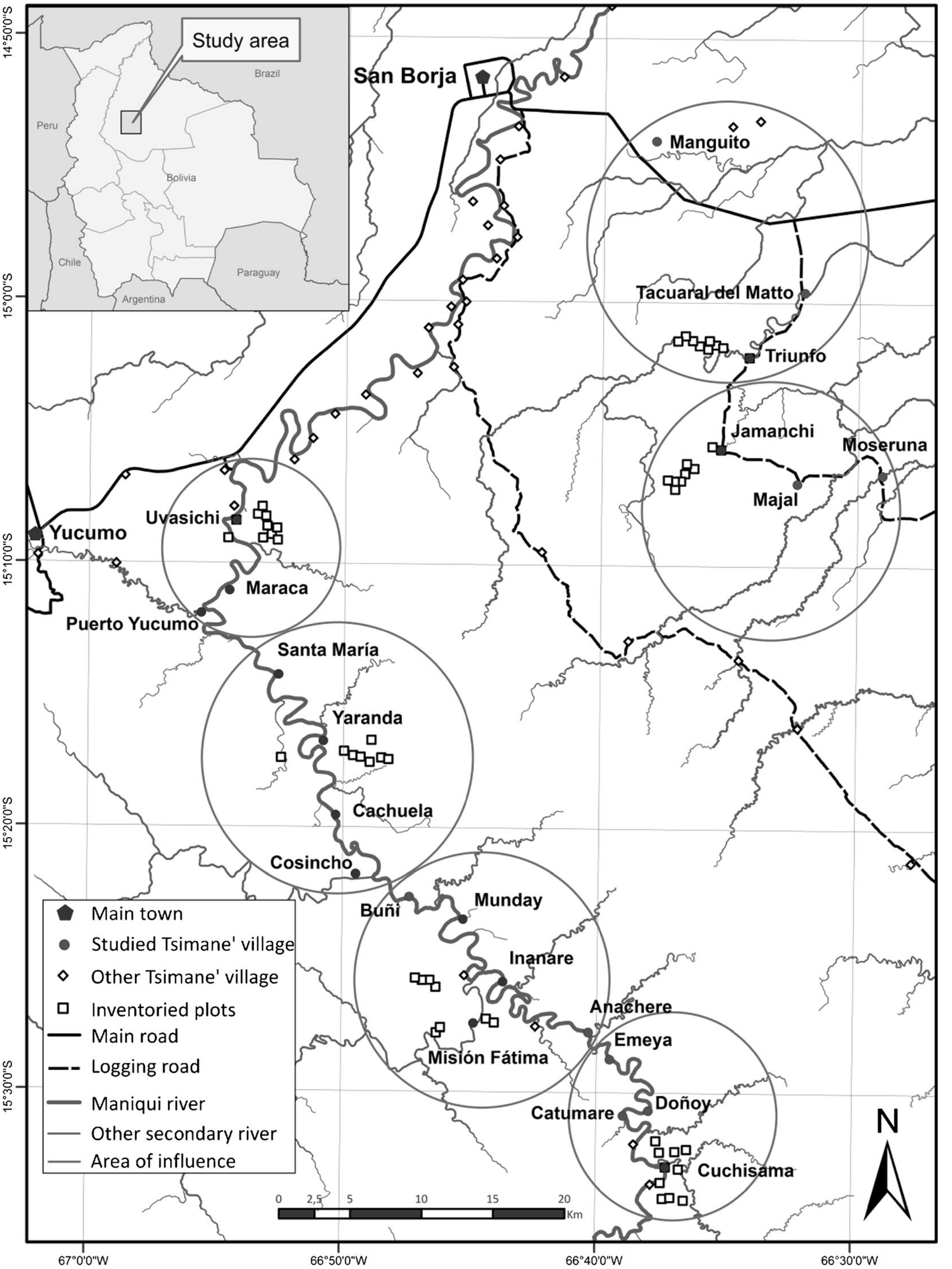

Fig. 1. Map of the sampling area showing the distribution of 48 0.1-plots inventoried in the territory of six Tsimane' villages, Bolivian Amazon, along with areas of influence including 22 villages where data of plant uses were collected.

local guides while measuring them in plots; and 2) unique correspondence between the vernacular name and the scientific name of the species, based both on the names reported by local guides and on two databases on Tsimane' ethnobotany (Huanca 1999; Reyes-García 2001).

Ethnobotanical Data

After plots were inventoried, we collected ethnobotanical data on tree species uses through interviews based on vernacular names. Specifically, we gathered ethnobotanical information of the 58 selected tree species in 22 Tsimane' villages (hereafter called "villages with ethnobotanical prospection"), among which we included the 6 villages with plots. In each village, we asked participants to identify the most knowledgeable people about plant uses to interview them. Our initial target was to interview two men and two women per village, but the gender and the actual number of people interviewed in a village finally varied depending on the number of experts available and willingness to participate. We interviewed a total of 93 people.

To keep the interviews within a reasonable duration, we randomly split the list of 58 species into two lists of the same length. In each village we used one list to interview half of the informants (one man and one woman whenever possible) and the other list to interview the other informants. Interviews were conducted in the Tsimane' language with the help of translators. We asked each informant "Do you know species X (vernacular name of the species)? Can you tell me all its possible uses?" We wrote down verbatim all the uses reported by the informants.

Data Analysis

To analyze the relation between usefulness and apparency we used a multivariate model designed to explain the UV of a species as a function of its IVI. To do so, our first step was to match the ethnobotanical data collected in 22 villages and the ecological data collected in 6 villages. For most of their daily subsistence activities (hunting, fishing, and non-timber forest products collection), the Tsimane' use neighboring forest areas as well as a large common territory, often overlapping the territory of neighboring villages (Cruz-Burga et al. 2013). Therefore, we assumed that respondents' information on a species would be drawn from observations at the landscape level, not just from observations of areas around their own village. Consequently, a species' ecological importance in each of the six villages with plots would be associated with the uses reported by people from nearby villages with ethnobotanical prospection. We then defined "areas of influence" around the six villages with plots. These areas of influence comprised the closest villages with ethnobotanical prospection to the villages with plots (3–5 villages per area of influence; Fig. 1), and represented the area where people would normally carry out their subsistence and foraging activities. The distance between the center of any village (its school) and any plot in its area of influence ranged between 4.9 (±3.4) and 8.0 (±3.4) km. We calculated the IVI of a species in the inventoried plots per area of influence as the sum of its relative density, relative dominance, and relative frequency (Curtis and McIntosh 1951).

We calculated: 1) the total UV of the species as the average number of use-reports per species (Phillips and Gentry 1993a); and 2) the categorical UV of the species as the average number of use-reports per species within each of six categories. We followed Thomas et al. (2009a) to define five categories (food, firewood, construction, materials, and medicines). However, we grouped "environmental uses," "social uses," and "poison" in the category "other uses" since each of these categories had few use-reports for a small number of species. The category *construction* included house and canoe building and timber, and the category *materials* included tools, handicrafts, and toys. To calculate the categorical UV we counted each single use-report, even if there were several use-reports in the same category. For example, we counted all medicinal use-reports of a species mentioned, because the fact that a species has more medicinal use-reports is an indicator of its usefulness and could be related to its density or frequency.

Our units of analysis are tree species per area of influence; therefore, our analysis relates the average UV of one tree species in one area of influence to the ecological importance of the species in the same area. We selected this approach because for each tree species the relation between usefulness and apparency might be specific for the area of influence (Macía 2008). Moreover, the approach also increases the number of observations for multivariate analysis (6 observations for each of the 58 species). We studied the relation between both the total and the categorical UV and the IVI of the species per area of influence using scatter plots and Pearson's correlations, as well as ordinary least-square regressions. All regression models were run with robust standard errors and clustered by area of influence (Woolridge 2003). We included two controls in the models: one set of dummy variables for areas of influence and another set of dummy variables that capture the life form of the species (large tree, small tree, or palm). The dummies used for buffer areas (not shown in the tables) are binary variables that capture fixed effects of the areas of influence not measured in this study (Suits 1957). Such fixed effects include proximity to towns, ecological characteristics, and the like. We attributed the life form of each species on the basis of the dbh in the plots, verifying reported life forms in Killeen et al. (1993). Small trees, such as understory species, were defined as all the species that failed to reach 10 cm dbh (Guèze et al. 2013).

Results

We surveyed an average of 3.2 people per village. Overall, 1.6 informants in each village, or 35.2 informants in all the dataset, provided ethnobotanical information for each of the 58 species studied.

Out of the 58 useful species studied, 33 were ecologically important with an IVI > 1 (Table 1). The four most ecologically important species, *Iriartea deltoidea* Ruiz & Pav., *Hura crepitans* L., *Poulsenia armata* (Miq.) Standl., and *Socratea exorrhiza* (C. Martius) H.A. Wendl. showed a high UV. The three species with the highest UV were *Attalea phalerata* Mart. ex Spreng, *Swietenia macrophylla* King, and *Clarisia biflora* Ruiz & Pav., but only *C. biflora* showed a high IVI. *A. phalerata* and *S. macrophylla* were among the less ecologically important species.

Most of the 58 species had at least one use-report in the categories firewood and construction (54 and 53 species with more than 1 use-report in those categories, respectively). However, in the other categories the number of species with more than one use-report was much lower. Some patterns arise when examining the association between IVI and UV by categories. The most useful species in the categories construction and materials tended to have a high IVI (e.g., *I. deltoidea*, *S. exorrhiza*). The species with higher UV in the medicine category had low IVI, suggesting that medicinal species in our list were rare species (e.g., *Aniba canelilla*, (H.B.K.) Mez, *Galipea longiflora* K. Krause). This tendency was also observed, although to a lesser extent, for food uses. For firewood and other uses, no tendency was found.

We found a positive but weak correlation between the total UV of the species and their IVI (Pearson's r = 0.18, P = 0.002). However, a close visual analysis of this relation suggests that two species (*H. crepitans* and *I. deltoidea*) with high IVI values (> 27) in two areas of influence averaged upward the regression line (Fig. 2).

Three findings from the regression analyses between the total UV of a species and its IVI deserve comment (Table 2). First, a bivariate regression without controls (model [1]) indicates a positive and statistically significant (although weak) association between total UV and IVI. The coefficient in model [1] implies that an increase of 1 unit in the IVI of a species would be associated with an increase of 0.027 units in its total UV (P = 0.000). Since the IVI ranges from 0.04 to 17.05 and the UV ranges from 0.73 to 3.52, this corresponds approximately to a 1% increase in UV for each 6% increase in IVI. Second, when we control for life form and for village fixed-effects (model [2]), the association between UV and IVI found in model [1] remained significant, but weakened. Third, the analysis segregating between "rare" species (IVI ≤ 1, model [3]) and "common" species (IVI > 1, model [4]) yielded a significant positive association (P = 0.004) between UV and IVI only for common species. The number of observations was only 293 because some species were not found in the plots of two areas of influence.

The association between the categorical UV of a species and its IVI showed particularities (Fig. 3). A species UV showed a positive linear relation with its IVI within the categories construction (Pearson's r = 0.36, P < 0.001) and materials (Pearson's r = 0.22, P < 0.001), indicating that most species used for construction and materials were common species. However, a species UV showed a negative, although weak, linear relation with its IVI within the category medicine (Pearson's r = -0.19, P < 0.001) and an also negative tendency with its IVI within the category food, indicating that rare tree species had more use-reports as foods and medicines. Last, we did not find a linear relation between IVI and UV in the categories firewood or other uses.

In Table 3 we present the results of the bivariate and multivariate regressions using only

Table 1. IMPORTANCE VALUE INDEX (IVI) AND USE VALUE (UV) OF 58 TREE SPECIES USED IN TSIMANE' VILLAGES, BOLIVIAN AMAZON, RANKED BY DECREASING AVERAGE IVI. THE UV OF THE FIVE SPECIES WITH HIGHEST UV IN EACH OF THE USE CATEGORIES ARE IN BOLDFACE.

				Mean UV						
Scientific name	Family	Tsimane' name	Mean IVI	Food	Firewood	Construction	Materials	Medicine	Others	Total
Number of species				33	54	53	46	43	29	58
All species			2.44	0.43	0.39	0.36	0.34	0.28	0.09	1.94
Iriartea deltoidea Ruiz & Pav.	Arecaceae	ojdo'	17.05	0.46	0.04	**1.29**	1.03	0	0	2.84
Hura crepitans L.	Euphorbiaceae	conojfoto	13.80	0	0.28	0.90	0.08	0.27	**1.10**	2.65
Poulsenia armata (Miq.) Standl.	Moraceae	asha'ba	10.65	0.73	0.46	0.07	0.99	0.01	0.01	2.30
Socratea exorrhiza (C. Martius) H.A. Wendl.	Arecaceae	vijri	9.78	0	0.07	0.81	**1.43**	0.01	0.03	2.39
Leonia crassa L.B. Sm. & A. Fernández	Violaceae	rojro	6.51	0.07	0.61	0.04	0	0.13	0.17	1.13
Otoba parvifolia (Markgraf) A. Gentry	Myristicaceae	cam	5.35	0	0.53	0.86	0.04	0.16	**0.50**	2.09
Astrocaryum murumuru Mart.	Arecaceae	shibo'	4.90	0.49	0.09	**1.09**	0.61	0	0	2.51
Unonopsis floribunda Diels	Annonaceae	veya	4.84	0	0.65	0.67	0.43	0.05	0	1.85
Celtis schippii Standl.	Ulmaceae	ñove	4.72	0	**0.89**	0.23	0.04	0	0	1.31
Clarisia racemosa Ruiz & Pav.	Moraceae	väväij	4.66	0	0.34	0.93	**1.40**	0.06	0.03	2.83
Iryanthera juruensis Warburg	Myristicaceae	po'cocos	4.33	0	0.34	0.45	0.52	0.15	0	1.46
Rinorea viridifolia Rusby	Violaceae	shayimo	4.32	0	0.30	0.24	0.50	0.17	0	1.20
Clarisia biflora Ruiz & Pav.	Moraceae	mu'suru	2.91	0.88	0.67	0.17	**1.16**	0	0.04	2.95
Duguetia spixiana Mart.	Annonaceae	pi'serej	2.74	0.98	0.45	0.20	0.12	0.74	0	2.53
Rheedia acuminata Miers	Clusiaceae	tsocon	2.73	1.00	0.61	0.04	0	0	0	1.66
Rheedia gardneriana Miers	Clusiaceae	ibijqui	2.68	0	0.53	0.58	0.09	0.08	0	1.34
Symphonia globulifera L. f.	Clusiaceae	puñipuson	2.68	0.96	0.34	0.14	0	0.14	0	1.63
Dipteryx odorata (Aublet) Willd.	Fabaceae	cojma	2.65	1.00	0.42	0.34	0.38	0.05	0.20	2.44
Spondias mombin L.	Anacardiaceae	moco'	2.59	**1.13**	0.41	0.21	0.02	0.13	0.05	2.06
Tetragastris altissima (Aublet) Swart	Burseraceae	na'fa	2.42	0.98	0.47	0.23	0.78	0.30	0.10	2.93
Stylogyne cauliflora (C. Martius & Miq.) Mez	Myrsinaceae	viñaj	2.37	1.04	0.33	0.08	0	0.10	0	1.65
Siparuna bifida (Poeppig & Endl.) A. DC.	Siparunaceae	vatason	2.12	0.03	0.19	0.05	0.06	0.41	0	0.73
Guarea gomma Pulle	Meliaceae	roson	2.02	0	0.53	0.60	0.15	0	0.04	1.32
Terminalia oblonga (Ruiz & Pav.) Steudel	Combretaceae	cotison	1.84	0	**0.97**	0.19	0.10	0	0	1.30
Pourouma cecropiifolia Mart.	Moraceae	moväij	1.79	1.00	0.71	0	0	0	0	1.75
Cordia nodosa Lam.	Boraginaceae	tayei	1.72	1.00	0.15	0	0	0.24	0	1.48
Terminalia amazonia (Gmelin) Exell	Combretaceae	cavaquis	1.68	0	0.57	0.67	0.13	0.04	0.08	1.54
Sloanea obtusifolia (Moric.) Schumann	Elaeocarpaceae	shesherena	1.64	0	0.81	0.29	0.65	0	0.15	1.94
Abuta grandifolia (C. Martius) Sandw.	Menispermaceae	odo' odo'	1.39	0.98	0.34	0.09	0	0.03	0	1.59
Pourouma minor Benoist	Moraceae	ajmo	1.23	0.78	0.38	0.24	0.04	0.03	0	1.54

Table 1. (Continued).

Scientific name	Family	Tsimane' name	Mean IVI	Mean UV						
				Food	Firewood	Construction	Materials	Medicine	Others	Total
Euterpe precatoria Mart.	Arecaceae	ma'ñerej	1.21	0.54	0	0.81	0.08	0.30	0.07	1.90
Calyptranthes lanceolata O. Berg	Myrtaceae	bunau'	1.11	0.95	0.34	0.12	0.05	0.07	0	1.55
Triplaris poeppigiana Wedd.	Polygonaceae	ji'tyi	1.03	0	**0.86**	0.35	0.07	0.03	0.04	1.35
Sloanea fragrans Rusby	Elaeocarpaceae	copo'tare	0.99	0.03	**0.81**	0.27	0	0	0	1.19
Attalea butyracea (Mutis ex L. f.) Wess. Boer	Arecaceae	bitire'	0.94	**1.09**	0.01	0.58	0.86	0.14	0	2.82
Alibertia pilosa E.H. Krause	Rubiaceae	shishibutuj	0.71	1.00	0.54	0.04	0	0	0	1.58
Aspidosperma rigidum Rusby	Apocynaceae	vambason	0.61	0	0.53	0.03	0.97	0.89	0	2.41
Gallesia integrifolia (Sprengel) Harms	Phytolaccaceae	shepi'	0.60	0.02	0.29	0.03	0.39	**1.48**	0.05	2.26
Pseudolmedia macrophylla Trécul	Moraceae	pomo	0.59	1.03	0.37	0.19	0	0.16	0	1.79
Bactris maraja Mart.	Arecaceae	cocope'	0.47	0.83	0	0	**1.04**	0	0	1.91
Copaifera reticulata Ducke	Fabaceae	copaiva	0.40	0	0.23	0.32	0.02	**1.62**	0.16	2.36
Myroxylon balsamum (L.) Harms	Fabaceae	chuna	0.37	0	0.24	0.77	0.57	0.29	0.08	1.94
Triplaris americana L.	Polygonaceae	chij	0.33	0.05	0.81	0.05	0	**1.09**	0	1.99
Bactris major Jacq.	Arecaceae	chijchiva'	0.29	0.91	0	0	0.54	0	0.04	1.53
Galipea longiflora K. Krause	Rutaceae	tam'tac	0.24	0	0.16	0.01	0.05	**2.07**	0	2.30
Borojoa claviflora (K. Schum.) Cuatrec.	Rubiaceae	vuvujri	0.22	**1.05**	0.32	0.06	0.05	0	0	1.57
Cedrela odorata L.	Meliaceae	siyamo	0.20	0	0.34	**1.19**	0.11	0.04	**0.44**	2.17
Calophyllum brasiliense Cambess.	Clusiaceae	yäjdyä'dyä	0.20	0	0.40	**0.99**	0.24	0.37	**0.52**	2.51
Calycophyllum spruceanum (Benth.) Hook f. ex Schumann	Rubiaceae	tunenes	0.19	0	**0.82**	0.20	0.10	0.11	0	1.23
Swietenia macrophylla King	Meliaceae	chura'	0.17	0	0.23	**0.96**	0.53	1.06	0.34	3.12
Attalea phalerata Mart. ex Spreng	Arecaceae	mana'i	0.13	**1.19**	0.01	0.85	0.93	0.45	0.03	3.52
Chrysophyllum venezuelanense (Pierre) Penn.	Sapotaceae	ejtere'	0.12	0.36	0.20	0.12	0.06	0.03	0.02	0.97
Heliocarpus americanus L.	Tiliaceae	mu'	0.11	0	0.38	0.26	**1.07**	0.17	0	1.87
Cariniana estrellensis (Raddi) Kuntze	Lecythidaceae	cocoma	0.08	0	0.37	0.35	0.16	0.08	0.08	1.04
Protium aracouchini (Aublet) Marchand	Burseraceae	vi'si	0.08	0	0.31	0.20	0.89	0.70	0.07	2.25
Aniba canelilla (H.B.K.) Mez	Lauraceae	chorecho	0.06	0.54	0.27	0.24	0	**1.30**	0.07	2.43
Aiphanes aculeata Willd.	Arecaceae	cajna	0.04	**1.05**	0	0	0.11	0	0.05	1.26
Genipa americana L.	Rubiaceae	tyi'	0.04	1.00	0.46	0.05	0.05	0.58	**0.64**	2.87

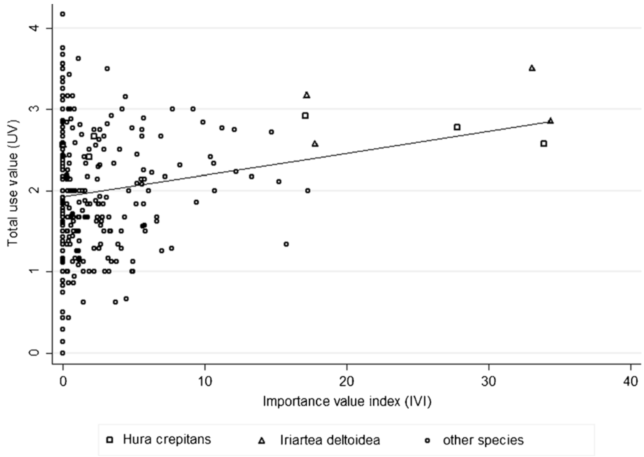

Fig. 2. Scatter plot of the average use value (UV) against importance value index (IVI) of 58 useful species in six Tsimane' areas, Bolivian Amazon. Each point represents the combination of UV and IVI of each species in one of the six surveyed areas (n = 293).

the average number of uses in a given category. We highlight three main findings from this table. First, after controlling for village fixed-effects and life form of the species, we found a positive but weak association between IVI and UV in the categories construction (model [6]) and materials (model [8]). Second, when including the controls, we found a negative association between IVI and UV in the categories food (model [2]) and medicine (model [10]). Third, the UV for the categories firewood and other uses showed no association with the IVI in bivariate models (models [3] and [11]). Thus, the significant association observed for the category firewood in multivariate analysis (model [4]) is probably an interaction effect between explanatory and control variables.

Discussion

Use Value and Ecological Importance of Tree Species

The main finding of this work is that, when considering its overall UV, the more ecologically important a tree species is, the more uses it has, although the correlation is weak. Our finding is consistent with other studies that have related species usefulness and IVI (Lucena et al. 2007; Thomas et al. 2009a; Torre-Cuadros and Islebe 2003) and with studies that have related species usefulness and apparency estimated with indica-

Table 2. Results of ordinary least-square bivariate and multiple regressions of overall use value (UV) of 58 tree species against importance value index (IVI) with robust standard errors and clustering by area of influence.

	All species		Species with IVI ≤ 1	Species with IVI > 1
	Model [1] Bivariate	Model [2] Multivariate	Model [3] Bivariate	Model [4] Bivariate
IVI	0.027***	0.019***	-0.328	0.040**
Dummy for life form (palms: omitted category)				
Small trees	^	-0.825***	^	^
Trees	^	-0.367*	^	^
Constant	1.92***	2.395***	2.056***	1.765***
N	293	293	161	132
R^2	0.032***	0.170	0.014	0.137**

Notes: N = 293. Cells are coefficients followed by a sign for statistical significance (* P ≤ 0.05; ** P ≤ 0.01; *** P ≤ 0.001). In model [2] six dummy variables were included to control for village fixed-effects. ^ = variable intentionally omitted.

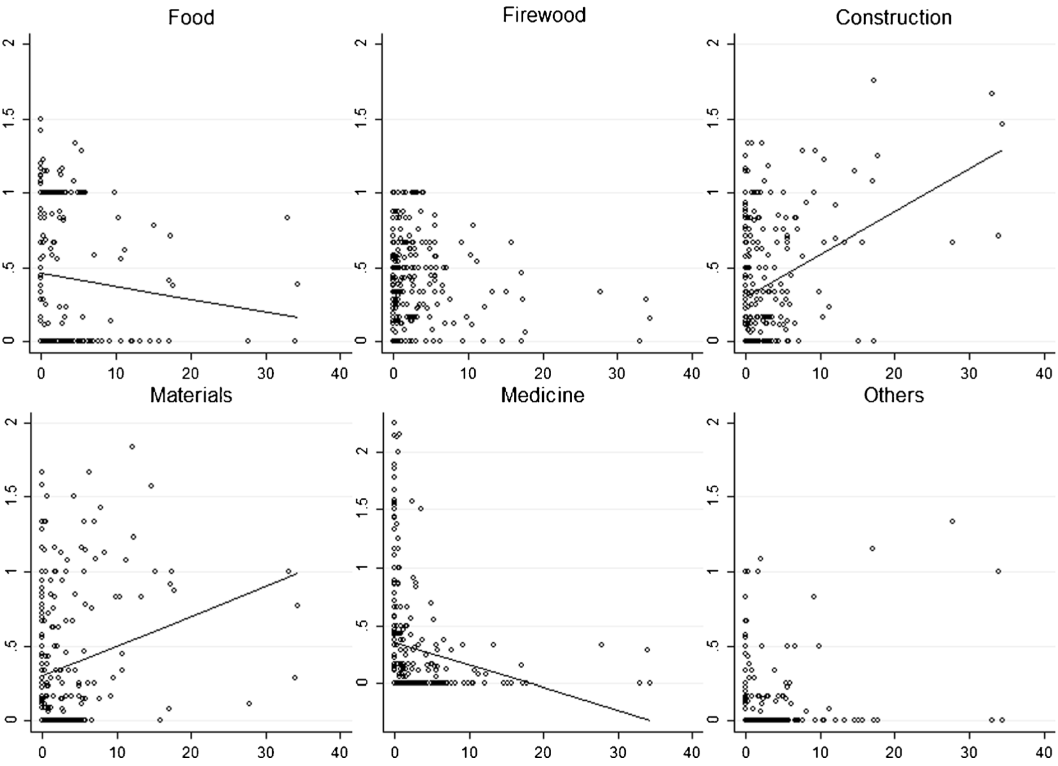

Fig. 3. Scatter plot of the average use value (UV) per ethnobotanical category, against importance value index (IVI) of 58 tree species in six Tsimane' areas, Bolivian Amazon. Each point represents the combination of UV and IVI of each species in one of the six surveyed areas (n = 293).

tors other than IVI (Galeano 2000; Paz-y-Miño et al. 1995). Thus, our finding provides additional support to the hypothesis that people use more of the most apparent species in the forest.

However, our analyses provide insightful nuances to this finding. First, our results suggest that, despite the significance of the association found between IVI and UV, the coefficients of the regressions are small. Second, much of the variation in a species UV is captured by its life form. This is consistent with studies that found that a species' family is more important than its apparency when explaining its uses (Phillips and Gentry 1993b; Thomas et al. 2009a). Here, palms (Arecaceae) are the most useful life form for the Tsimane', as reported widely in other Amazonian studies (Byg et al. 2006; Macía 2004; Macía et al. 2011). A potential explanation for their common use is that palms are among the most easily identifiable species. For instance, although *A. phalerata* is rare in our study area, it has a high UV. Since *A. phalerata* is common (i.e., visible or apparent) around Tsimane' villages settled in pampas (personal observation), and because it is useful and easily identifiable, it is possible that people talk more about this species than about others. Third, the relation between IVI and UV tends to be negative when the species are "rare" (IVI ≤ 1), because some of these rare species are useful. Rare species in our study (e.g., *S. macrophylla*, *Cedrela odorata* L., medicinal tree species such as *Genipa americana* L.) are often planted in home gardens. Thus, the pattern observed for these species could be due to the fact that they are well known among the Tsimane' regardless of their ecological characteristics in old-growth forests. Indeed, we proxied the usefulness of a species with its UV (i.e., knowledge), but other measures, such as actual frequencies of use, might yield different results (Albuquerque 2006; Albuquerque and Hanazaki 2009; Lucena et al. 2012; Reyes-García et al. 2006).

Additionally, results from this study must be taken with caution at least for two reasons. First, part of the variation in the results is probably due to sampling methods. Ecological values are likely biased due to sample size and vary depending on

Table 3. Results of bivariate and multiple ordinary least-square regressions of categorical use value (UV) of 58 tree species against their importance value index (IVI), with robust standard errors and clustering by area of influence.

	Food		Firewood		Construction		Materials		Medicine		Other uses	
	Model [1] Bivariate	Model [2] Multivariate	Model [3] Bivariate	Model [4] Multivariate	Model [5] Bivariate	Model [6] Multivariate	Model [7] Bivariate	Model [8] Multivariate	Model [9] Bivariate	Model [10] Multivariate	Model [11] Bivariate	Model [12] Multivariate
IVI	-0.0085**	-0.0119**	-0.0022	0.0024*	0.0289**	0.0241**	0.0202**	0.0141**	-0.0199***	-0.0184**	0.0086	0.0092
Life form (palms: omitted category)												
Small trees	^	-0.1375*	^	0.2573***	^	-0.5421***	^	-0.6484***	^	0.2827***	^	0.0015
Trees	^	-0.3838***	^	0.4437***	^	-0.2749*	^	-0.4239***	^	0.1956**	^	0.1281***
Constant	0.4596***	0.7602***	0.3817***	-0.0395	0.2987***	0.5700***	0.2982***	0.7091***	0.3665***	0.2744***	0.0752***	0.0198
R^2	0.0076	0.1089	0.0015	0.4381	0.1261	0.2744	0.0498	0.2294	0.0393	0.0831	0.0356	0.1117

Notes: N = 293. Cells are coefficients followed by a sign for statistical significance (* $P \le 0.05$; ** $P \le 0.01$; *** $P \le 0.001$). In multivariate models a set of dummy variables controlling for village fixed effect was included. ^ = variable intentionally omitted.

the tree diameter classes (Macía 2008). Although our ecological sampling seems accurate (all trees ≥ 2.5 cm dbh), we inventoried 0.8 hectares of forest per area of influence, which may not fully capture the actual ecological features sought for the trees inventoried (relative density, relative dominance, and relative frequency). Second, the ecological apparency hypothesis implies causality: the resource is the driver of users' behavior. Researchers have often rejected the alternative hypothesis that management and use of the species influence their ecological importance (but see Thomas et al. 2009a). However, reverse causality cannot be discarded in our study area. On the one hand, our study area seems to have been inhabited for a long time (Denevan 1966), so the actual floristic composition could just be the result of anthropogenic perturbation or management on composition and abundances, as previous research suggest that those perturbations might persist for centuries (Macía 2008). On the other hand, some of the most useful tree species in the area have suffered intensive exploitation. For example, mahogany (*S. macrophylla*) and Spanish cedar (*C. odorata*) are some of the most useful species and have been selectively logged in the last decades (Gullison et al. 1996); *A. phalerata* has probably been overexploited to the point of local extinction in forest areas. Thus, it is likely that the IVI of these species have decreased as a consequence of their own usefulness. A plausible scheme, as suggested by Lawrence et al. (2005), is a negative feedback between apparency and uses; that is, the apparency of the species increases its use value, leading to a negative effect on its abundance.

Categorical Use Values and Ecological Importance of Tree Species

We found a positive relation between IVI and UV in the categories construction and materials. This is consistent with the positive association found in other studies between species' relative dominance and usefulness for construction (Lucena et al. 2007; Thomas et al. 2009a) and with the results of Phillips and Gentry (1993b), which stress a positive association between species' relative density and frequency and their UV for construction and technology (including materials).

We also found a negative association between the medicinal and food UV and the IVI of the species, consistent with some earlier studies (Silva and Albuquerque 2005), but not with others

(Lucena et al. 2007; Phillips and Gentry 1993b; Thomas et al. 2009a). These inconsistencies might be in part because researchers do not always include the same uses in the same categories, particularly when comparing studies that have been conducted among indigenous and among non-indigenous populations (Galeano 2000; Lawrence et al. 2005; Schwantes and Felfili 2001). For example, firewood is sometimes included in a "technology" category (Phillips and Gentry 1993a) and sometimes considered as a category on its own (Galeano 2000; Macía et al. 2011; this study). The association between usefulness and ecological importance may be strongly specific to the area and the people studied.

What would explain the differences in the associations between IVI and categorical UV? We hypothesize that the physical properties of the species, particularly meaningful for the use of the species in construction or materials, are more easily substitutable than their chemical properties, which are more meaningful in medicinal and food uses. On the one hand, physical properties (e.g., mechanical resistance or durability) are likely to be shared by many species, such as palms or common construction trees (e.g., Meliaceae, Euphorbiaceae). The Tsimane' have a large choice of species, which might explain the positive relation between IVI and UV in the categories house construction and materials: if many species have adequate physical properties for those uses, they might just tend to use the most apparent of all the available species. On the other hand, specific chemical properties, such as those responsible for edibility, taste, or chemical compounds used for medicinal purpose, are likely to be much harder to substitute. Since in our study site those properties tend to be more often found in "rare" species, this would explain the negative association between IVI and UV in the categories medicine and food. Stepp (2004) argues that common weedy species invest in mobile compounds such as alkaloids, cardiac glycosides, and terpenoids as a defense against herbivory. These compounds are valued as medicines, which might explain the role of weeds (i.e., common plants) as medicinal plants. Although we do not challenge this finding, we argue that the traits associated with the production of such compounds (short-lived leaves and fast-growing capacity) can also be found in old-growth forest tree species as many present in our study area, especially in understory species and deciduous large tree species. For example, deciduous canopy trees such as *Calycophyllum spruceanum* (Benth.) have been reported to have medicinal uses in Brazil (Costa et al. 2011). Moreover, leaves are not always the most useful part of medicinal trees, but rather people use other parts such as bark or roots.

In this study we do not control for cultural and social factors, which also explain preferences regarding the use of plants (Thomas 2012). For example, the palm *Iriartea deltoidea* has no medicinal use among the Tsimane' although it does for a neighboring group, the Yuracaré (Thomas et al. 2009a). Therefore, cultural uses might impose important limitations to the role of inherent physical or chemical properties of the plants, and require further study.

In sum, the overall results of this work suggest that the ecological apparency hypothesis has to be taken with caution when applied to humans. While herbivores use plants only as food, humans maintain a more complex relationship with plant species, which make the association between the ecological importance and the usefulness of vegetal species—in domains as diverse as medicinal uses and tool-making—far more unpredictable.

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