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How do people select plants for use? Matching the Ecological Apparency Hypothesis with Optimal Foraging Theory

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Abstract The present study aimed to understand human plant resource usage strategies in the context of the Ecological Apparency Hypothesis and Optimal Foraging Theory. The relationship between plant resource knowledge and availability was tested in a rural community (Palmital) in a dry Atlantic Forest fragment in the state of Minas Gerais, Southeastern Brazil, using data from phytosociological studies and interviews. We considered both total use and separate use categories. Use Value (UV) was significantly associated with all of the analyzed ecological variables, but there was an association with relative dominance and a weak relationship with relative density. When the UVs were separately analyzed for each category, we found that some, i.e., fuel and construction, corroborate the Ecological Apparency Hypothesis, while others do not, particularly the

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medicinal and food categories. In addition, we found large differences with respect to the ecological variables that best correlated with UV. The data suggest that the cost/benefit relationship predicted by Optimal Foraging Theory can explain the Ecological Apparency Hypothesis when the following factors are considered: (a) resource acquisition optimization and security; (b) a higher probability of acquiring more abundant species during random collection events; and (c) differential utilization patterns (distinct requirements for a specific use) for each use category. Some implications for conservation are also discussed.

Keywords Ecological apparency theory · Human adaptive strategies · Plant resource use · Optimization theories · Human ecology · Evolutionary ethnobiology

1 Introduction

One of the central themes of ethnobotany is the need to understand the criteria used by people in the selection of plant resources and their use dynamics (Ankli et al. 1999; Albuquerque 2005; Alencar et al. 2009; Alencar et al. 2010). A key question in ethnobotany is why certain species are selected for a particular use instead of others (Ladio and Lozada 2000; Ramos et al. 2008a, b). Understanding the factors that influence the construction of local knowledge about natural resources is essential for studies that investigate the local context of biodiversity management and conservation (Albuquerque 2005).

Studies that have investigated how people select and use plants have evaluated a number of different aspects of this issue, including the following: (1) the quality of the resource in terms of the presence of certain medicinal compounds (Araújo et al. 2008; Alencar et al. 2009), the nutritional quality of food plants (Jin et al. 1999), and the fuel value of plants used as firewood and charcoal (Chettri and Sharma 2007); (2) the ease of management and collection, i.e., some plants are avoided because they are difficult to collect or handle, even in cases in which they are of higher quality and availability (Ladio and Lozada 2000); (3) the presence of undesirable substances or properties in some plants, even those that are adequate for a given use or contain beneficial compounds, in addition to morphological features that prevent or discourage their use (Minnis 2000); (4) choices based on cultural taboos, i.e., certain species can be selected because they are culturally accepted, whereas others must be avoided because their use is taboo in the community (Tabuti et al. 2003); and (5) availability and accessibility (Phillips and Gentry 1993b; Ladio and Lozada 2000; Lucena et al. 2007).

Phillips and Gentry (1993a, b) investigated the last two factors to determine whether the Use Value (UV) of a species is correlated with ecological variables. The relationship between the importance/extent of use and the availability of local resources was introduced to ethnobotany as an adaptation of the Ecological Apparency Hypothesis (Albuquerque and Lucena 2005), which hypothesizes that the most apparent plants will be the most well known by the local population. Beyond this initial line of inquiry, which only considers the supply of resources, some researchers have investigated this relationship from the perspective of the chemical components of plants (Stepp and Moerman 2001; Almeida et al. 2005; Alencar et al. 2010), which is simply known as the “Apparency Hypothesis” (see Gonçalves et al. 2016).

Although the Ecological Apparency Hypothesis is relatively well represented in the ethnobotanical literature (e.g., Phillips and Gentry 1993a, b; Galeano 2000; Stepp and Moerman 2001; Torre-Cuadros and Islebe 2003; Silva and Albuquerque 2005; Albuquerque and Lucena 2005; Almeida et al. 2005; Lawrence et al. 2005; Cunha and Albuquerque 2006; Ferraz et al. 2006; Lucena et al. 2007), few studies have attempted to understand this hypothesis through the ecological processes associated with the relationship between people and plants. To that end, this paper aims to test the Ecological Apparency Hypothesis in an area of Atlantic rainforest considering all contexts of "use." This paper also discusses the Ecological Apparency Hypothesis in light of Optimal Foraging Theory, which suggests that behaviors are determined by cost/benefit relations (see Pyke 1984; Begossi 1993). We use this theory to investigate (a) why some categories of use support the Ecological Apparency Hypothesis, whereas others do not; (b) why different ecological parameters are more explanatory than others for each category of use; and (c) in which situations the relationship between the availability and local importance of resources is favored.

2 Ecological Apparency Hypothesis

The Ecological Apparency Hypothesis was proposed in studies of herbivory and postulates that more visible plants are more susceptible to insect attack (Feeny 1976; Rhoades and Cates 1976). The adaptation of this hypothesis to ethnobotany has both chemical and ecological applications. The chemical view asserts that more obvious plants (with long life cycles, typically trees) tend to invest in defensive compounds with a high molecular weight, representing a quantitative strategy, whereas more obscure plants (typically herbs) invest in compounds with a low molecular weight, constituting a qualitative strategy (Albuquerque and Lucena 2005). Compounds of medicinal interest are produced via the qualitative strategy, which favors herbaceous species as sources of bioactive compounds (Stepp and Moerman 2001; Albuquerque and Lucena 2005). The ecological perspective, which is discussed further, postulates that more available and accessible plants are also of great local importance (Phillips and Gentry 1993b; Albuquerque and Lucena 2005). It is notable that although the chemical perspective highlights the quality of a resource as a key factor in the selection of species, the ecological perspective focuses on the "quantity" of the resource as a determinant of its selection.

The explanation proposed by Phillips and Gentry (1993b) for the relationship between resource availability and its local importance considers that the most available plants are more likely to be culturally encountered, which, in turn, means that these plants would be subjected to greater experimental and, consequently, broader use. We propose an alternative view in which the logic of use based on availability can be explained in light of Optimal Foraging Theory and is not exclusively based on the probability of finding a resource, as proposed by Phillips and Gentry (1993b).

3 Optimal Foraging Theory

Optimal Foraging Theory is one of the most widely applied ideas in studies of human populations, especially human ecology (Begossi 1993). In brief, Optimal Foraging Theory assumes that there is a cost/benefit relationship involved in obtaining any necessary resource and that natural selection favors foraging behavior that invests the least energy to obtain the greatest return (Pyke 1984). The theory suggests that in addition to their structural or physiological attributes, the behaviors of all foragers are naturally selected to increase the net intake rate of the resource to be maximized (Begossi 1993; Pierre and Ollason 1987; Begon et al. 2006).

Because studies based on this theory initially analyzed the securing of food/nutrition by non-human animals, the variable analyzed was always "energy." Thus, the theory predicts that there is an energy expenditure and an energy gain involved in obtaining a given resource. However, it is known that strategies not only maximize net energy intake (Begon et al. 2006) but are also influenced by the quality of a resource, such as the presence of proteins, nutrients, toxins, or bioactive compounds (Begossi and Richerson 1992; Estomba et al. 2006). Predation risk is another factor considered in Optimal Foraging Theory (Begon et al. 2006). However, this factor has not been considered in studies in which the foragers are humans.

From the perspective of Optimal Foraging Theory, the conflicting relationship between costs and benefits can expand or constrain collection strategies, resulting in two extreme solutions that can each maximize the net energy intake: a "generalist strategy" and a "specialist strategy" (Begon et al. 2006). "Generalist" animals maximize their energy intake by reducing the time spent collecting, essentially consuming a wide variety of readily available resources, regardless of how nutritionally profitable they are. Such animals are favored in less productive environments where the availability of beneficial resources is low (Setz 1989). "Specialist" animals focus on the selection of a few resources that require greater time for searching but that maximize their energy intake.

4 Materials and methods

4.1 Regional context and study area

Ethnobotanical interviews were conducted in the city of Viçosa (20°45′14″S; 42°52′54″W) in the state of Minas Gerais in Southeastern Brazil (for a map, see Soldati et al. 2011). There are approximately 75,000 inhabitants in Viçosa, most of whom reside in its urban center (IBGE 2010), and the city is located in a region known as the "Zona da Mata Mineira," which is part of the Atlantic Forest ecosystem (Ab'Saber 2003). The region has a hilly topography covered with montane semideciduous seasonal forest (Veloso et al. 1991) and is characterized by a seasonal climate and a mix of deciduous and evergreen species. Agriculture in this area is concentrated in its valleys (because 85 % of the area is mountainous) and is the most important economic activity in the city (Prefeitura de Viçosa 2010). Historically, coffee, corn, and beans have been the most important crops in the region. Although the area is not characterized by the use of intensive agricultural technology, the "Zona da Mata Mineira" has been subjected to widespread deforestation (Valverde 1958).

Ecological inventories were conducted in one of the remnant forest fragments of the "Zona da Mata Mineira," which is located at the Station for Environmental Research, Training, and Education (SERTE), also known as the "Mata do Paraíso." This forest fragment, with an area of 194.36 ha, is the largest remaining in the region, and it is located approximately 6 km from the urban center of Viçosa. The fragment was exploited for the sale of timber and then used as a pasture and plantations as well as for gravel extraction.

Subsequently, management was transferred to the municipality of Viçosa, and the area was used to supply the city's water and as a source of timber. In 1966, the Department of Forestry of the Federal University of Viçosa (UFV) took over administration of the area.

The activities performed in the reserve have not historically supported the sustainability of the ecosystem. Currently, the vegetation is composed of residual secondary forest in various seral stages, forming a mosaic forest (Silva 2003). Because control of the reserve was assumed by the UFV, pressure from forestry has been reduced. However, the fact that this area is protected by law does not prevent the collection of natural resources. The "Mata do Paraíso" is extremely important regionally because it is one of the few remaining areas of native (secondary) forest and is considered to be of "high biological importance and requires scientific research" (Drummond et al. 2005).

4.2 The focal community

Palmital is one of the six communities found within the "Mata do Paraíso" (SERTE). This forest fragment was selected for this study because it was determined to be the largest and best preserved in the region based on a series of papers representing the available ecological information, and it is also one of the few for which a community has historically made use of its resources. Community residents have used the plant resources in this forest fragment for medical, technological, food, and fuel purposes, and as a result, they have developed a rich knowledge of the tree species in the landscape (for more details, see Soldati et al. 2011). Because agricultural mechanization is not possible in this area due to its slope, agricultural practices are confined to subsistence farming and supplying the local market. The most common production is associated with crops of corn, beans, and vegetables in addition to dairy cattle breeding. The inhabitants of the region maintain a number of traditional practices, such as the use of ox carts and stone mills, and they depend on natural ecological cycles and have a family-based production system. The sizes of their properties are small, and the reduction in private property due to inheritance is substantial. When a parent dies, his or her land is subdivided among all of his or her children. In addition to these attributes, the Palmital community was selected for this research due to its existing relationship with researchers from the Federal University of Viçosa, including one of the authors of this study.

The community is connected to the Viçosa town center, and municipal transportation to/from the city passes through the community four times a day. Most children and adolescents in Viçosa study in schools. Some supermarkets and pharmacies in the town center deliver orders to the Palmital community. A few properties are used for leisure and/or agricultural production. The owners of these properties either were not born here or live in Palmital year-round or they are professors at the university. Additionally, there are no garbage collection services or water sanitation in the community.

4.3 Ecological parameters of apparency

The botanical data used to test the Ecological Apparency Hypothesis were obtained from a compilation of three studies conducted in the region of the "Mata do Paraíso" performed by Marangon (1999), Silva (2003), and Ribas et al. (2003), all of whom sampled fixed-area plots that were randomly distributed (Mueller-Dombois and Ellenberg 1974); as the locations of the plots were selected randomly, the distances between them vary. Although they were performed in the same forest fragment, each of these works sampled different plots, expanding and diversifying the botanical characterization of the area. The first two studies were conducted inside the station, whereas the third was performed on a private property located at the boundary between the "Mata do Paraíso" and Palmital. Marangon (1999) and Silva (2003) both sampled a total of 1 ha distributed among 10 plots of 0.1 ha each. Ribas et al. (2013) sampled a total of 0.6 ha distributed among three 0.2-ha plots. These studies provided information for an area of 2.6 ha, with several seral stages represented (primary, initial secondary, or late secondary) as well as differing topographies (hilltop, upper and lower thirds of the slopes, and lowlands) and canopy openings. We compiled and reanalyzed the ecological data from these studies.

In building the three databases, the criterion for inclusion was a diameter at breast height (dbh) greater than or equal to five cm, so all of the sampled individuals were arboreal. The relative density (RD), relative dominance (RDo), and relative frequency (RF) were calculated according to Mueller-Dombois and Ellenberg (1974), and according to the ecological context of this manuscript, these parameters represent the number of individuals, the volume of individuals, and their spatial distribution, respectively. The sum of these three parameters was used to calculate the Importance Value Index (IVI) (Mueller-Dombois and Ellenberg (1974), which reflects the "apparency" of a species, considers different ecological parameters, and is used as an "ecological importance" parameter. All four of these variables are used as ecological appearance parameters.

4.4 Ethnobotanical survey

This study was part of a larger study conducted in Palmital with the aim of understanding the environmental, political, and economic factors that influence local botanical knowledge. The data were collected using free lists (Albuquerque et al. 2014) in which the subjects were asked to indicate the plants that they knew in the "Mata do Paraíso," the way the plants were used, and what part was collected. When necessary, we re-interviewed residents to clarify issues and ambiguities. We used the free list because it is the most versatile methodological tool to access information about the distribution of local knowledge and versatility of known and exploited plants (Albuquerque et al. 2014), data which are essential for hypothesis testing. The interviews were conducted between August 2005 and February 2006 and included a total of 27 households out of a total of 41, covering 63.41 % of the residences. Some residents refused to participate in the study or were not found in their homes during the interviews. We interviewed a total of 21 men, ranging from 27 to 78 years of age, and 6 women, from 28 to 78 years of age. All of the homes in Palmital were visited, and those individuals who consented to participate in the study were interviewed. Thus, the informant selection criteria were not guided by the knowledge of the individuals about plants but by their social distribution with respect to housing.

In addition to the interviews, seven guided tours of the forest communities were conducted to precisely identify and validate the plants listed (Albuquerque et al. 2014). Seven residents were chosen as guides either because of the support they received from the community or because they demonstrated considerable knowledge. The collected plants were subjected to the usual herborization process (Santos et al. 2014) and deposited in the VIC Herbarium, Federal University of Viçosa. The botanical identifications were made by experts from the VIC.

4.5 Data analysis

The plant resources were divided into six categories of use: food, fuel, construction, medical, technological, and other. The parameter used to express the local importance of the plants was the total UV of a species proposed by Phillips and Gentry (1993a, b) and modified according to Galeano (2000) and Lucena et al. (2007). The UV for each species was calculated by dividing the sum of all reports of its use by the total number of people interviewed (i.e., 26). The UV by category of use for each species was calculated by dividing the total citations of the species in a particular category by the total number of people interviewed (i.e., 26).

We used simple linear regressions to test the existence of a relationship between the total UV and the UV by category, considering the four ecological parameters. The data were square-root-transformed to normalize the residuals. All statistical analyses were performed using the BioEstat 5.0 (Ayres et al. 2007) and Statgraphics Plus 5 (Manugistics Inc., Rockville, MD) programs.

5 Results

5.1 Vegetation survey and local knowledge

Together, the three ecological studies surveyed 273 species from 49 families, with 43 taxa being identified only to the genus level and 5 only to the family level. A total of 69 species in the "Mata do Paraíso" were reported as being useful in the interviews (for more details, see Soldati et al. 2011).

Siparuna guianensis Aubl. is the species presenting the highest IVI (8.7), followed by *Piptadenia gonoacantha* (Mart.) JF Macbr. (5.88), *Apuleia leiocarpa* (Vogel) JF Macbr. (3.69), *Vernonia diffusa* Less. (8.44), *Cecropia glaziovii* Snethl. (2.00), *Dalbergia nigra* (Vell.) allemao ex Benth. (1.70), *Anadenanthera peregrina* (L.) Speg. (1.37), and *Sparattosperma leucanthum* (Vell.) K. Schum. (1.33). The total value of the RD of species was dominated (1195.06 individuals) by *S. guianensis* Aubl. (475 individuals), which also showed the highest RF, an ecological parameter that indicates spatial distribution. *Piptadenia gonoacantha* exhibited the highest RDo in the compilation.

When we separated (a) the sampled species that could not be identified by the informants and (b) the sampled species that were known by the residents into IVI classes, we found that the vast majority were concentrated in the first class (0–0.5), which is characterized by low values of ecological importance. The data suggest that the number of species decreases with an increase in the IVI; i.e., few species of value are of high ecological importance (estimated by the IVI). The same pattern was found when we considered the species richness by UV classes because many species (high diversity) had a low UV.

The species with the highest UVs were *A. leiocarpa* (2.23), *Xilopia sericea* (1.92), *Myrcia fallax* (1.84), *Ocotea odorifera* (1.76), *Piptadenia gonoacantha* (1.69), *Anadenanthera peregrina* (1.61), *Nectandra oppositifolia* (1.26), *Dalbergia nigra* (1.07), *Myroxylon peruiferum* (1.03), and *Cedrela fissilis* (0.88). Four of these were also among the 10 species exhibiting the highest IVIs: *A. leiocarpa*, *P. gonoacantha*, *A. peregrina,* and *D. nigra*. Among these species, only *Pseudobombax longiflorum* (Cav.) A. Robyns and *Anadenanthera macrocarpa* (Benth.) Brenan were not cited by residents during the interviews.

The species with the highest UV in the food category were Myrciaria sp., *Inga cylindrica*, *Inga striata*, *Passiflora speciosa,* and *Annona cacans*. *Annona cacans* had the 25th highest IVI value. *Piptadenia gonoacantha* had the highest UV in the fuel category, followed by *Aegiphila sellowiana*, *Cecropia hololeuca*, and *Cecropia glaziovii*. In this group of species, only *A. sellowiana* was not among the ten species with the highest ecological importance (IVI). *Apuleia leiocarpa* was cited 56 times as a resource for construction, highlighting its importance in this category, in addition to *Xilopia sericea*, *M. fallax,* and *Anadenanthera peregrina*. Of these species, *A. leiocarpa* and *A. peregrina* were among the species with the highest IVIs.

A few species were noted in the medicinal category, mainly *Ficus* sp. 1, *Ficus* sp. 2, *Joannesia princeps*, *Eupatorium* sp., and *Lecythis pisonis*. All of these species exhibited low values of ecological importance (IVI). Finally, the most frequently noted species in the technology category were *Olyra micrantha*, *Tabebuia chrysotricha*, *Brosimum sellowii*, *Aspidosperma subincanum*, and *Zanthoxylum riedelianum*. Of these species, only *Z. riedelianum* was among the species with a high IVI.

5.2 Ecological Apparency

UV was significantly correlated with all of the analyzed ecological variables, but the strongest correlation was with RDo (Table 1). However, the relationship between UV and RD was weak ($R^2 = 0.07$; $p < 0.05$), i.e., this parameter explained only a small amount of the variation in the knowledge of the species.

When the UVs were analyzed for each category separately, we found low support for the Ecological Apparency Hypothesis because there were large differences with respect to the ecological variables that were best correlated with UV. The fuel category was related to all parameters, with similar values being observed for RF, RDo, and importance value (Table 1) and a low value being determined for RD ($R^2 = 0.06$; $p < 0.05$). Dominance and the importance value explained a great amount of the variation in knowledge regarding the plants used for construction ($R^2 = 0.18$; $p < 0.001$ for UV of building × RD, and $R^2 = 0.12$; $p < 0.001$ for UV construction × importance value), whereas the RF explained a small portion of the knowledge ($R^2 = 0.07$; $p < 0.05$); the RD was not significant ($R^2 = 0.003$; $p < 0.05$).

Different results were obtained regarding knowledge of medicinal resources compared to the previous categories, and only the RD showed a significant relationship with UV ($R^2 = 0.06$; $p > 0.05$). The food and technology categories alone did not support the Ecological Apparency Hypothesis, with R^2 values close to zero being found for all parameters studied. Therefore, the positive relationships between UV and the ecological parameters are explained by the other categories of use: construction and fuel.

6 Discussion

6.1 Ecological Apparency

The majority of the studies that have tested the Ecological Apparency Hypothesis have found weak but significant correlations between UV and ecological parameters (Phillips and Gentry 1993a, b; Galeano 2000; Torre-Cuadros and Islebe 2003; Lawrence et al. 2005; Cunha and Albuquerque 2006; Lucena et al. 2007; Lucena et al. 2012) (Table 2). In studies that have used regression analysis and considered general uses, the significant ($p < 0.05$) R^2 values detected ranged from 0.11 (Galeano 2000) to 0.19 (Lucena et al. 2007), indicating that, although availability is important, it is not the only factor that explains the

Table 1 Relationship between the total Use Value by use category and the analyzed ecological parameters in Palmital, Minas Gerais

	S	RF	RD	RDo	IVI
Total UV	69	0.13**	0.07*	0.21***	0.16***
Fuel UV	49	0.14**	0.06*	0.14**	0.14**
Construction UV	51	0.07*	0.03	0.18***	0.12**
Medicinal UV	15	0.05	0.06*	0	0.04
Food UV	19	−0.01	−0.01	−0.01	−0.01
Technology UV	52	0	0.03	0.17	0

R^2 values and significance are shown

S, number of species in each category; *RF* relative frequency, *RD* relative density, *RDo* relative dominance, *IVI* Importance Value Index

* $p < 0.05$

** $p < 0.01$

*** $p < 0.001$

selection and use of plant resources. The data obtained in this study support this statement because the frequency, dominance, and RD did not fully explain local knowledge regarding plant resources considering all categories of use.

When the categories of use were considered separately, it became clear that some categories are more likely to support the Apparency Hypothesis than others. For example, the construction category, which was found to present the highest R^2 values among the ecological parameters examined in this study, was also found to support the hypothesis in other studies (Phillips and Gentry 1993a, b; Lawrence et al. 2005; Lucena et al. 2007). This indicates that the selection of species for this use is strongly influenced by their availability in the environment. However, it was also observed that the ecological parameters that support the hypothesis vary between the categories of use.

However, we did not find a clear pattern in some categories because certain categories showed significant results in some studies and negative results in others. For example, the medicinal category was highly positively related to ecological parameters in Lucena et al. (2007), whereas recent investigations have found a negative relationship between this category and ecological parameters (Guèze et al. 2014). The most common behavior for the medicinal category, however, is non-significance, as recorded in this study and certain others (Phillips and Gentry 1993a, b). We attribute these conflicting results to the inclusion criteria used in studies testing the Ecological Apparency Hypothesis that have only focused on woody plants, excluding grasses. Almeida et al. (2005) demonstrate that native trees are the most important medicinal resources in the Brazilian semiarid region, which is also the environment investigated by Lucena et al. (2007). Thus, the most preferred medicinal plants are likely to be sampled and to have their availability in the environment evaluated. By contrast, other studies have been performed in humid environments, where exotic herbs are the most cited plants (Stepp and Moerman 2001), and these species were not included in the present study. Thus, the fact that herbs are the main medicinal product in various pharmacopoeias of the world and that this plant type is not considered in studies that test the Ecological Apparency Hypothesis may explain why the evaluated resources do not match those associated with the greater use and preferences of local people in many studies, disrupting the relationship between UV and ecological parameters. However,

Table 2 Studies that have tested the Ecological Apparency Hypothesis and their relationship between the total Use Value by category of use and ecological parameters

	Parameters of Use	Parameters of availability	Statistical analysis	Main category of use	Main parameter	Main relationship
Phillips and Gentry (1993a, b)	Total UV, Construction UV, Food UV, Commercial UV, Medicinal UV, and Technology UV	Density, frequency, mean diameter, maximum diameter, mean growth rate, and maximum growth rate	Multiple linear regression	Food UV	–	Food UV × ecological parameters (multiple regression) ($R^2 = 0.58$)
Torre-Cuadros and Islebe (2003)	Total UV	Importance Value Index	Simple linear regression	–	Importance Value Index	Total UV × Importance Value Index ($R^2 = 0.17$; $p < 0.01$)
Cunha and Albuquerque (2006)	Total UV	Relative dominance, relative density, relative frequency, and Importance Value Index	Pearson's correlation coefficient	–	Relative frequency	Total UV × relative frequency ($R^2 = 0.22$; $p < 0.001$)
Galeano (2000)	Total UV	Abundance	Simple linear regression	–	Abundance	Total UV × Abundance ($R^2 = 0.11$; $p < 0.0001$)
Albuquerque et al. (2005)	Total UV	Relative density and relative frequency	Simple linear regression	–	–	No significant correlation ($p > 0.05$)
Lawrence et al. (2005)	Total UV, Wood species UV (related to market), House Cover UV, Construction UV, Food UV, Medicinal UV, and Technology UV	Basal area	Pearson's correlation coefficient	Wood species UV (related to market)	Basal area	Wood species VU × basal area (without outliers) ($R^2 = 0.37$; $p < 0.01$)
Ferraz et al. (2006)	Total UV	Importance Value Index	Pearson's correlation coefficient	–	–	No significant correlation ($p > 0.05$)

Table 2 continued

	Parameters of Use	Parameters of availability	Statistical analysis	Main category of use	Main parameter	Main relationship
Lucena et al. (2007)	Total UV, Medicinal UV, Food UV, Construction UV, and Technology UV	Relative frequency, density, relative dominance, and Importance Value Index	Simple linear regression	Medicinal	Importance Value Index	Medicinal UV × Importance Value Index ($R^2 = 0.30$; $p < 0.01$)
Ramos et al. (2008a, b)	Frequency of Mention of Fuel Category	Absolute density	Spearman's correlation coefficient	–	–	No significant correlation ($p > 0.05$)
Lucena et al. (2012)	Total UV, Medicinal UV, Fuel UV, Construction UV, Technology UV, Foraging UV, Food UV, and Veterinary UV	Basal area, relative frequency, relative density, relative dominance, and Importance Value Index	Spearman's correlation coefficient	Construction	Relative dominance	Total UV × relative dominance ($r_s = 0.75$; $p < 0.001$)
Present study	Total UV, Medicinal UV, Fuel UV, Construction UV, Food UV, and Technology UV	Relative frequency, relative density, relative dominance, and Importance Value Index	Simple linear regression	Construction	Relative dominance	Total UV × relative dominance ($R^2 = 0.21$; $p < 0.001$)

The main category and the main appearance parameter that corroborate the hypothesis are presented. R^2 values and significance are shown

Ayantunde et al. (2009) found perennial plants to be more important than herbs, and in a semiarid environment, Blanco and Carrière (2016) found evidence to support the Apparency Hypothesis.

A differential dynamic of use is also found for the food category, which yielded no significant results in either our study or that by Lucena et al. (2012) but showed high values in a study by Phillips and Gentry (1993a, b). The technology category has received little attention in most studies with only a weak correlation (Phillips and Gentry 1993a, b; Lucena et al. 2007) or no correlation with ecological variables (Lucena et al. 2012). Some studies have shown that many uses in this category are specific, although heterogeneous, such that only one or a few species are suitable for the manufacture of certain products. This pattern may explain the lack of a relationship between the availability and importance of resources for technological purposes, but the conceptual circumscription of the technology category is difficult. As stated above, the uses associated with this category are heterogeneous, and some reports may include them in the construction or food categories, underestimating use in the technology category.

We observed that the RD was the ecological parameter with the highest R^2 values and that this parameter was highly explanatory in some studies (Galeano 2000; Lucena et al. 2007, 2012), including the present study. Furthermore, it is worth noting that the RD was the most explanatory ecological parameter for the construction category, i.e., the volume of a species has a greater effect on its extraction than its spatial distribution (RF) or density (abundance estimation).

Therefore, the evidence presented above suggests that use categories have a distinctive use dynamic and that different factors may affect the knowledge of resources in these categories. Although the analyses employed in studies of the Ecological Apparency Hypothesis do not consider environmental factors, the phenomenon of differential use is evident in other studies (see Walters 2005; Medeiros et al. 2010). This fact has strong implications for future investigations because it emphasizes that the selection of a species for a given use may be determined by a set of factors that act in another category, i.e., the categories of use cannot be analyzed indiscriminately.

These results show that this differential use among categories can influence biodiversity conservation, especially when we consider the construction category, which has historically been identified as having a great impact on native vegetation (Dahdouh-Guebas et al. 2000). As evidenced, the selection of species for wood depends on environmental variables, especially the dominance of the species (Albuquerque et al. 2015). Therefore, it is reasonable to assume that if use pressure was directed to less common species, then the local extinction and scarcity of resources could be aggravated.

As stated above, the high use of a resource depends on its high availability but leads to a decline in its population. Therefore, an important species whose availability is reduced may subsequently have low local importance. As a result, the relative importance of species in a given location may be dynamic (Albuquerque et al. 2015). When management efforts are not performed to sustain useful species but rather to exploit them, the correlation between the importance and availability of a species may be weakened (Phillips and Gentry 1993b). Because more common plants are the most used and therefore are subjected to greater management efforts, their populations tend to decline as a result of a dynamic process that may favor different species in different periods of time (Albuquerque et al. 2015). Thus, the importance of local species, represented by their UV, may vary over time in response to their availability (Lawrence et al. 2005). What is then captured at any given moment is only a snapshot of the entire process, which may dictate a decrease in correlations between the importance and availability of local resources and ultimately constrain the testing of the Ecological Apparency Hypothesis. The issue of temporal dynamics may also explain some of the discrepancies between the results of different studies that have tested the Ecological Apparency Hypothesis because they may have captured distinct time periods. Additionally, we consider people to be conscientious agents who manage landscapes, so it is possible that people favor certain useful species, dispersing their propagules and thus changing the structure of the plant community. This is particularly true in the Amazon rainforest, where the special distribution of many species is determined by human management (see Clement et al. 2015).

6.2 The Ecological Apparency Hypothesis in light of Optimal Foraging Theory

What are the ecological processes that underlie the relationship between the environmental availability of a resource and its knowledge and local use? Few studies have attempted to answer this question. Phillips and Gentry (1993b) argue that the UVs are related to the supply of a resource because people are more willing to attempt to validate the uses of more common species. This explanation is based on probability rather than on ecological arguments. In explaining their findings, other studies that address this hypothesis have used the arguments advanced by Phillips and Gentry (1993b) and Lucena et al. (2007), who propose an explanation of the Ecological Apparency Hypothesis based on the predictions of Optimal Foraging Theory. As previously shown, it is believed that human behavior reflects an attempt to optimize returns during the collection and extraction of plants. By assuming that a relationship between UV and the availability of a resource exists, the Ecological Apparency Hypothesis also follows the logic of optimization because more available resources allow for ongoing high-volume exploitation (greater returns).

Albuquerque et al. (2015) state that to be incorporated into the list of useful plants, a resource must be perceived, recognized, experienced, managed, and socially validated. These authors analyze this production of knowledge in an optimal logic, in which cost/benefit relations determine which features are selected and incorporated into this process. Producing new information takes time and energy, and optimal knowledge is only guaranteed when it is associated with species with high environmental availability (Albuquerque et al. 2015). Phillips and Gentry (1993b) explain the relationship between use and availability by the mere probability that a person identifies a plant and experiments with it. However, we follow Albuquerque et al. (2015), who explain this relationship using ecological principles. The influence of availability on plant importance occurs because availability not only increases the probability of a resource to be gathered in random collection events but also leads to an optimal behavior (Albuquerque et al. 2015). The cost of knowledge production is suppressed by the high return guaranteed by abundant resources, ensuring that local needs are supplied. The issue of safety in obtaining resources has been proposed by Albuquerque (2010) to explain why the populations of semiarid regions use perennial products for medical purposes, even when non-perennial resources present better qualities or higher therapeutic efficiencies. The same principle may explain why more common plants tend to be the most used by local populations.

Albuquerque (2010) states that that a more available resource is also more reliable because it is most likely to be accessed when demanded. In this sense, the trend of incorporating more available plants into the knowledge production process may be an early stage associated with the acquisition of security based on plant extraction, thereby ensuring that individual and family needs are met (Albuquerque et al. 2015). A great example of this relationship is the construction category, which in many studies supports the Ecological

Apparency Hypothesis by its dominance or basal area, both of which are indirect parameters that indicate the volume available. That is, the demand for larger and higher volume species results in higher UVs for more abundant species (Albuquerque et al. 2015).

Based on this line of reasoning, we raise the following question: how can the differential use observed among categories be explained from a cost/benefit perspective? As noted above, the Optimal Foraging Theory suggests that the net energy intake can be understood not only based on the quantity of the resource but also in terms of its quality, such as presenting an increased wood density or a better taste, being more nutritious, or meeting the specific requirements of a particular use. This premise justifies the differences in the Ecological Apparency Hypothesis related to different categories of use, such as (a) why low R^2 values were found in categories that support the hypothesis and (b) why some categories do not support the hypothesis.

The first question may be explained by the differences in the demand for certain categories. Some categories, such as fuel and construction, demand not only high resource availability (quantity) but also a high quality (Ramos et al. 2008a, b). For these categories, it has been observed that some uses require wood of high quality, as in the case of house building. However, other types of use of the most available species in the environment are often made, as in the case of the construction of animal shelters (Medeiros et al. 2010). Thus, the low R^2 values (<50 %) found for the construction category indicate that other factors influence the selection of species for this category, possibly including the quality of the resource.

Additionally, we believe that these differences in demand between categories of use may be the reason for the greater or lesser response of certain categories to the Ecological Apparency Hypothesis. Therefore, the need for high-quality resources may also explain the lack of a relationship between the availability of a plant and its UV in certain categories. An example is the medicinal category, which, as highlighted above, does not support the Ecological Apparency Hypothesis in the majority of studies, except for that by Lucena et al. (2007). Unlike the construction category, in which plants are more easily substitutable in terms of their physical qualities, medicinal plants can hold exclusive properties of rare chemicals, meaning that quality outweighs availability (Guèze et al. 2014). Studies conducted in semiarid areas have found strong relationships between the presence of certain bioactive compounds and the use of certain species for therapeutic purposes (Almeida et al. 2005; Araújo et al. 2008; Alencar et al. 2009, 2010).

The notion that the Ecological Apparency Hypothesis can be explained by the greater likelihood of acquiring more available resources in random collection events is no longer considered. We do not intend to make generalizations about the different dynamics associated with different use categories, but we suggest that availability is reinforced in categories that require lower-quality resources, i.e., categories that are associated with more general patterns of selection. For example, when the construction and medical categories are compared, it is noticeable that for the former, the quality of the resource (e.g., expressed as density or elasticity) and its availability are of great importance, whereas for the latter, the literature has shown that the quality of the resource is the only key factor (Moerman 1979; Leonti et al. 2002; Coe and Anderson 1999).

The difference between the quantity and quality to be collected leads to a question that should be noted here: In which situations will the relationship predicted by the Ecological Apparency Hypothesis (knowledge × availability or UV × quantity) be favored? Just as non-human foragers may behave in specialized or general ways, the patterns of selection of plant resources presented by local communities may follow the same principle. Albuquerque et al. (2015) assert that in some situations, the forager chooses a “generalist strategy" in which the optimal return is achieved by a general collection of a wide range of species, whether it is a resource of high or low quality. Otherwise, these same authors state that in certain situations, the optimal behavior is represented by a "specialist foraging strategy," which favors only species of high quality.

Due to the high availability of resources, it is expected that highly productive environments stimulate specialist collection patterns (Marufu et al. 1997; Top 2004; Albuquerque et al. 2015). Furthermore, Albuquerque et al. (2015) suggest that the scarcity of useful resources, which is a typical characteristic of less productive environments, favors a generalist strategy. This occurs because the search for high-quality resources is expected to be too costly in less environmentally favorable regions, and this strategy would therefore be discarded (Albuquerque et al. 2015). In environments where there is a high availability of resources, foragers (human or non-human) can invest time and energy in finding high-quality species for a particular purpose.

Thus, it is plausible that in the context of resource scarcity, the likelihood that the most common species will be the most collected increases and, consequently, they will become part of the repertoire of useful species. Therefore, we suggest that the Ecological Apparency Hypothesis may be better suited to environments with scarce resources, and this prediction may be expanded to account for the relationship between availability and local importance becoming stronger in cases of generalist collecting.

However, other variables, such as geographical constraints and the presence of predators, may influence this prediction, which suggests that a specialized collection will not always be favored in environments with high resource availability (Albuquerque et al. 2015). Medeiros et al. (2010) study the extraction of firewood by a community in a protected area in northeastern Brazil and conclude that both behaviors, generalist and specialist, occur. Despite being a productive environment, generalist behavior is associated with the conscientiousness of people who are subject to local monitoring by police responsible for environmental enforcement, a factor that can be considered analogous to the presence of predators in a classical system (non-human animals) (Albuquerque et al. 2015).

In the case of wood products, a forager can choose to spend less time exposed to the "predator" (surveillance) and make a general collection that will most likely contain high-availability species (Albuquerque et al. 2015). These plants, in turn, may cause the collector to need to return more frequently to the forest because they do not necessarily exhibit the highest quality. Conversely, the forager can choose to expend more time exposed to surveillance and, in return, select the best-quality plants, thus reducing the number of collection events (Albuquerque et al. 2015). In some cases, the two strategies can result in the same cost/benefit relationship, which would explain the presence of both strategies in certain contexts. In these cases, we hypothesize that the relationship between availability and local importance tends to be weak, boosted by the general usage pattern in some cases and weakened by the presence of a specialized pattern in the community in others. However, the hypotheses suggested here should be tested in future studies that address the criteria involved in the selection of local resources.

6.3 Study limitations

It is possible that the results related to the Ecological Apparency Hypothesis for some categories, especially medicinal and food, have been influenced by their low sample sizes. Furthermore, there is a time lag between the collection of the environmental and ethnobotanical information, which may have influenced the results because both plant communities and local knowledge systems are dynamic. Finally, the UV used in this study does not distinguish between "current use" and "potential use" processes, which can also determiner the relationship between environmental availability and traditional knowledge. Although not addressed by this study and its discussion, these factors make it necessary to consider the relativism of the findings.

7 Final remarks

This study shows that the availability of a resource plays a secondary but significant role in the selection of plant species, but the strength of the relationship between environmental and local availability varies in importance depending on the categories of use. In this context, we find great differences in the ecological variables that were best correlated with UV, the variable used to estimate local knowledge. These results can be explained by a cost/benefit relationship predicted by Optimal Foraging Theory when the following factors are considered: (a) optimization and security during resource acquisition; (b) the higher probability of the acquisition of more abundant species during random collection events; and (c) differential utilization patterns (distinct requirements for a specific use) for each use category. However, the differences in behavior observed among the use categories and the variability in the results of studies that address the Ecological Apparency Hypothesis highlights the need for further theoretical discussions about the mechanisms underlying the relationship between availability and local importance as well as the need for case studies to understand the ecological contexts that support the Ecological Apparency Hypothesis.

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