



# Social-Ecological Theory of Maximization: Basic Concepts and Two Initial Models

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## Abstract

Efforts have been dedicated to the understanding of social-ecological systems, an important focus in ethnobiological studies. In particular, ethnobiological investigations have found evidence and tested hypotheses over the last 30 years on the interactions between human groups and their environments, generating the need to formulate a theory for such systems. In this article, we propose the social-ecological theory of maximization to explain the construction and functioning of these systems over time, encompassing hypotheses and evidence from previous ethnobiological studies. In proposing the theory, we present definitions and two conceptual models, an environmental maximization model and a redundancy generation model. The first model seeks to address biota selection and its use by human populations. The second emphasizes how the system organizes itself from the elements that were incorporated into it. Furthermore, we provide the theoretical scenario of plant selection and use from an evolutionary perspective, which explicitly integrates the phylogenetic relationships of plants (or other living resources) and human beings.

**Keywords** Evolutionary ethnobiology · Human ecology · Optimization theories · Social-ecological systems

## Introduction

How has our species, throughout its evolution, structured, enriched, and maintained its knowledge systems about natural resources? This question seems trivial. However, human resource use represents one of the most expressive chapters

of humans' journey on earth. In fact, strategies used to survive in different environmental conditions are under selection, and thus, human groups change the construction and functioning of this system over time. Many scientists from different disciplines have wondered about resource use by humans based on different theoretical and methodological tools (see Levine et al. 2015; Winterhalder and Smith 2000; Orlove 2005), which have influenced one of the central questions of modern ethnobiology: what are the factors affecting people's use and selection of natural resources?

In this article, we cover a set of recent hypotheses that have guided studies in ethnobiology towards the construction of a new theory that explains the organization and functioning of the relationships between people and biota. This theory essentially postulates that *over time, human beings construct social-ecological systems to favor their survival in different environments*. To this end, human cognitive and behavioral mechanisms interact with the environment to prioritize strategies for survival.

Our theory is influenced by several theoretical approaches, such as studies involving folk biological classification (Berlin 1992; Atran et al. 2002, 2004; Atran and Medin 2008), the scenarios of cultural evolution (Claidière

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et al. 2014; Mesoudi 2015; Kendal et al. 2018) and the resilience of social-ecological systems (Folke 2006; Faulkner et al. 2018). Many of these studies assume that humans have developed strategies to favor their survival in different environments. For example, studies by Atran et al. (2002, 2004) show how cognitive biases benefit human understanding about natural resources, which enhances their survival. In addition, studies involving cultural evolution theory have advanced the understanding of human learning strategies (see Kendal et al. 2018), and other researchers have studied human strategies that allow for adaptive capacity in the face of disturbances in social-ecological systems (Folke 2006; Delgado-Serrano et al. 2017; Faulkner et al. 2018).

Several ethnobiological studies have dialogued with these approaches in recent decades, accumulating an interesting body of empirical evidence (see Gaoue et al. 2017). However, there is still a growing need to develop advances in theoretical approaches that integrate ethnobiological investigations and help propose new hypotheses that will guide future efforts in the field. Thus, in this article, we propose a new theory in the context of evolutionary ethnobiology (Albuquerque and Ferreira Júnior 2017; Santoro et al. 2017, 2018; Ferreira Júnior et al. 2019), which encompasses different hypotheses that have been tested by ethnobiologists, especially in the last 30 years. Initially, we review the ideas that precede our proposal, and then we present the theory and the main models it encompasses.

We do not assume here that other scenarios cannot explain people's interactions with their environments, considering the multifactorial nature of such interactions. For example, our proposal seeks to address very specific aspects of the relationship between humans and biota. (1) How humans choose elements of biota that will be part of their socioecological systems from a perspective of evolution and ecology of foraging strategies. Therefore, we do not address at this moment human cognitive structure (given that other fields theorize on this subject—e.g., evolutionary psychology) or how cultural information is transmitted and how it evolves (which is the object, for example, of cultural evolution theory) (see Rendell et al. 2011; Mesoudi 2015). However, we appropriate concepts from these related fields, given that such subjects can provide further developments of the theory that we propose. (2) Another approach is the understanding of how elements of biota, once incorporated into social-ecological systems, internally organize to give structure and function to these systems. Here, we seek to understand by what mechanisms these systems are organized and structured to attend to human demands and how they evolve to maintain their functionality and resilience. We largely appropriate ecological concepts to structure our proposal and improve knowledge, from an ethnobiological perspective, on how social-ecological systems evolve.

Studies on social-ecological systems have described a great diversity of these systems, as well as their adaptive value and resilience capacity (see Delgado-Serrano et al. 2017; Falkner et al. 2018). To the best of our knowledge, our proposal is the first formal theory that arises from ethnobiological studies and from the accumulation of different sources of evidence.

Finally, our proposal is strongly enriched by studies of human behavioral ecology, especially studies on optimal foraging theory (OFT) (MacArthur and Pianka 1966; Pyke et al. 1977). Although our proposal is strongly influenced by OFT, this theory analyzes foraging behavior from an energetic point of view. By contrast, we assume costs and benefits beyond the energetic logic, as we consider variables that are not easily translated into energetic terms.

## Background in Ethnobiological Literature

### The Influence of the Environment on the Human and Biota Interrelationship

The first empirical evidence, in ethnobiology, on the role of the environment in the selection of resources by human populations appeared in the 1990s with the work of Phillips and Gentry (1993a, b). These authors proposed the *apparency hypothesis*, which emerged from classical herbivory studies, as an extrapolation to understand human behavior. The main idea is that the apparency of a plant resource, measured by population parameters of a plant community (e.g., relative density, relative frequency), explains the relative importance of plants in a given cultural system. Although not explicitly stated by these authors, the hypothesis is premised on an optimization strategy driven by species abundance (i.e., availability) because it reduces the costs associated with time and energy in the search of resources and favors experimentation, which, in turn, can optimize resource use. Therefore, the apparency hypothesis is based on the availability of a resource for foraging by humans. Predictions from this hypothesis have been tested several times from various perspectives (see synthesis in Gonçalves et al. 2016).

Thus, this relationship between availability and local importance of resources, especially plants, has also been tested in several studies as the *hypothesis of availability*. The idea of availability is quite generic and may refer to several factors, such as the distance from the collection site, seasonality, price, and access to markets, gardens, or natural areas where plants are available. Regardless, the idea behind availability is that of optimization, be it energy, time, or efficiency (see Gaoue et al. 2017). Although Gaoue et al. (2017) consider the apparency hypothesis and the hypothesis of availability distinct hypotheses, both suggest very similar predictions and therefore, in our view, are indistinguishable.

In general, robust evidence has been obtained favoring the idea of apparency. However, the robustness depends on the utility domain considered (Gonçalves et al. 2016). Availability, in this case measured by phytosociological variables, may have an explanatory power that is expressed only in conjunction with other parameters, such as the specific type of use. This phenomenon was observed in a study developed in the northeast of Brazil (Santos et al. 2018), which tested the explanatory power of availability, in this case measured by local perception, flavor, and efficiency on the differential use for influenza and constipation. When tested in isolation, the availability variable did not explain the differential use. However, when tested in conjunction with the other variables, the variable remained in the final model for constipation.

Furthermore, it should be emphasized that the predictive power of the availability hypothesis varies according to the category of use (Gonçalves et al. 2016). For fuel use, for example, availability tends to be a preponderant factor in species selection. In other categories, such as medicinal, efficiency tends to present a greater weight in the process of species selection, even in a context of low availability. This finding suggests that plant selection by human groups is not random but is influenced by several factors, which may vary depending on the utility domain.

### The Human Strategies of Resource Selection are Nonrandom

Different evidence supports the *hypothesis of nonrandom selection of plants* proposed by Moerman (1979), which is likely one of the most tested in ethnobotany. This hypothesis originally proposes that the number of medicinal species in a botanical family and in a given region would be a linear function (on a log scale) of the total number of plant species in that family (see Gaoue et al. 2017). However, certain plant families tend to be over- or underrepresented in a certain pharmacopeia (Moerman 1979, 1991). Furthermore, the hypothesis entails that families of phylogenetically close plants are more likely to have similar medicinal uses than those that are phylogenetically distant. In this sense, Saslis-Lagoudakis et al. (2015) discussed the power of phylogenetic tools in providing useful information to ethnobiological studies and presented a set of evidence that amounts to the idea of nonrandom selection. These studies indicate that species used to treat the same diseases are closely related to the phylogenetic point of view at different taxonomic levels.

If the entry and use of plants are not random, as suggested by previous hypotheses, then we could assume that they would follow cost-benefit logic, as predicted in many optimization models, such as *optimal foraging theory (OFT)*. We highlight that OFT is one of the most commonly used models in the scope of research in ethnobiology and human

ecology (see MacArthur and Pianka 1966; Pyke et al. 1977; Ladio and Lozada 2003; Oliveira and Begossi 2011). However, recent OFT tests in ethnobiological research suggest that classical predictions do not explain foraging behavior in various human groups (see Alves et al. 2017; Lopes et al. 2011; Feitosa et al. 2018), suggesting no optimization or suboptimal behavior and challenging the cost-benefit logic of OFT and that human behavior always tends toward optimization. Perhaps this limitation of predicting behavior emanates from the fact that important variables (e.g., cooperation or competition between individuals, social norms, commercial demands, contexts of resource use prohibitions—see Rode et al. 1999; Fehr and Fischbacher 2004) that shape human behavior are not considered in the classic OFT models. In addition, certain variables that may be highly important in terms of plant selection (e.g., the taste of plants for medicinal and edible purposes) may not be easily translated to an energetic logic, as predicted by OFT. Such cases may be adequately studied within the framework we propose with our maximization theory.

### People Maximize the Entry of Resources in Social-Ecological Systems

Researchers have long interpreted the inclusion of exotic species in different social-ecological systems as a process of acculturation that displaces the use and loss of knowledge about native resources. However, the interpretation may be quite different within the logic of maximization, as we propose later in our theory.

In this context, Albuquerque (2006) proposed the hypothesis of diversification, whose predictions have often been confirmed over time (Alencar et al. 2010; Hart et al. 2017). The hypothesis predicts that the incorporation of plants into a social-ecological system is an active process based on the need to fill gaps in the system or enrich it in various respects. If exotic plants enter traditional pharmacopeias to fill gaps, one could expect that they treat diseases differently from those treated with native species. In a meta-analysis of Brazilian ethnobotanical studies, Medeiros et al. (2017) indeed found gaps in local pharmacopeias. However, most diseases have a strong overlap of native and exotic species. The authors inferred that such overlap can be due to two scenarios: (1) exotic species enter to fill gaps and then spread to other components of the system (which would be in consonance with the diversification hypotheses), or (2) exotic species enter pharmacopeias directly competing with native species, and the gaps are a subsequent case of competitive exclusion of native species. Regardless of the most suitable scenario, a recent study has shown that exotic species are only highlighted in local medical systems when they present competitive advantages over native plants (Gama et al. 2018).

Another interesting aspect involves human responses to markedly seasonal climates. For example, in the Brazilian semiarid region, people tend to concentrate the use of medicinal plants spatially and temporally on perennial resources instead of ephemerals, even if the latter are more efficient (in terms of biological activity, for example) (Albuquerque 2006). A study showed that for an important medicinal species in the Brazilian semiarid region, the bark is the most indicated part for use in two human groups, although the leaves presented a greater amount of therapeutically interesting compounds in the rainy season compared with the bark (Monteiro et al. 2006). In this case, the focus on the bark during the rainy season, when leaves are also available, can be considered a suboptimal strategy, and we must question the motives that lead this behavior to remain in the system. The abovementioned case may reflect a human strategy adopted in response to climatic seasonality. Albuquerque (2006) suggested that human populations would select strategies promoting the security of resource use (maximizing the resource always available) rather than using a more efficient resource that presents limited access to only one season. This hypothesis is known as the climatic seasonal hypothesis, which is particularly true in highly seasonal environments (Albuquerque 2006).

Thus, the concept of maximization considers the relative balance between different variables that are used to explain a phenomenon, i.e., the resulting payoff. In this context, although the climatic seasonality hypothesis is constructed to explain the selection of medicinal plants in semiarid environments, it leads us to deduce that in environments where these environmental limitations do not exist, the balance between availability and efficiency, for instance, would be modeled in another direction, and the resulting payoff could range across a combination of efficiency and availability.

If social-ecological systems behave as previously mentioned, then one can expect that redundancy, a very common phenomenon in such systems, will follow a similar logic. The idea of redundancy in social-ecological systems was initially proposed by Albuquerque and Oliveira (2007) and systematized as a utility redundancy model (URM). For these authors, redundancy would be configured as an intrinsic strategy in any and all systems to confer resilience in space and time. Nascimento et al. (2015, p. 124) indicate that

the model is based on the following assumptions: (a) species have different functions within social-ecological systems, but a level of overlap in function occurs, the so called redundancy; (b) increased redundancy promotes resilience in social-ecological systems, and (c) redundancy depends on the knowl-

edge characteristics and practices of a given human community. Therefore, the URM is an operational concept used to determine the (i) role of redundant species in the structure and dynamics of a cultural system; (ii) contribution of redundant species to the resilience of knowledge and local practices; and (iii) effects of human activities on biodiversity.

Based on the initial hypotheses proposed, several predictions were tested in different cultural systems and at different scales (Ferreira Júnior et al. 2011; Santoro et al. 2015; Nascimento et al. 2016). The studies reveal that this redundancy depends on the social structuring of a human group, such as differences in gender (Díaz-Reviriego et al. 2016) and the characteristics of the use of a resource (Santoro et al. 2015).

Finally, the role of the environment in shaping plant use behaviors may be identified based on two different situations: (1) convergent use of plants by distinct populations in similar environments and (2) divergent use of plants by related populations in distinct environments. In the first case, the literature has shown that people from different ethnic groups that inhabit nearby regions tend to use very similar medicinal plant repertoires (Coe and Anderson 1999; Albuquerque et al. 2008). Coe and Anderson (1999), for example, compared two indigenous communities from different ethnic groups in Nicaragua who shared 80% of their medicinal plant repertoires. Although cultural exchanges may have had an important influence on this similar behavior, environmental possibilities may have also played a significant role. Similarly, Albuquerque et al. (2008) compared an indigenous community with a rural nonindigenous group in the Brazilian semiarid region and found a high similarity in their medicinal plant repertoire. Such similarity increases when only native species are considered.

The second case typically occurs in human migration studies. For example, Ladio et al. (2007) studied medicinal plant knowledge held by Mapuche groups inhabiting the steppe and forest areas of Argentinean Patagonia. The authors found that although they were addressing the same ethnic group, only 40% of medicinal plant species were shared between them. This low value is due to difficulties in finding the same species in different ecosystems. Another interesting example is derived from the study developed by Inta et al. (2008) with Akha groups that spread more than 100 years ago and inhabit China, Thailand, and other eastern Asian countries. Although Chinese and Thai Akha share many practices and traditions, migration forced them to use distinct medicinal plants.

Such patterns may indicate the importance of acquisition difficulties in shaping medicinal plant repertoires, which converges with the above-cited apparen- cy/availability hypothesis.

## The Social-Ecological Theory of Maximization: Concepts and Models

The new theory that we propose arises from the “apparency hypothesis,” “hypothesis of nonrandom selection of plants,” “hypothesis of diversification,” and “climatic seasonality hypothesis,” which have provided important insights into the relationship between humans and biota. Furthermore, we provide a theoretical *corpus* of biota selection and use from an evolutionary perspective, which explicitly integrates the phylogenetic relationships of plants (or other living resources) and human beings.

The theory states that the construction and functionality of social-ecological systems are driven by the selection of strategies mediated by cognitive and behavioral mechanisms that favor the survival of human groups in their interactions in various environmental contexts. The social-ecological systems are constructed such that they maximize benefits (e.g., a plant with a strong medicinal activity) and reduce costs (e.g., plant acquisition or bad taste of an edible plant) of human actions (satiating hunger, treating illnesses, building homes) in their interactions with the environment. With respect to this topic, we detail the models covered by the social-ecological theory of maximization with a set of working hypotheses and the definitions and important concepts of the theory (see Table 1 for definitions and concepts).

## Model of Maximum Environmental Performance

### Enunciation

This model implies that the entry and differential use of natural resources by human populations follows a logic of cost reduction and benefit maximization. Thus, the resources most likely to be incorporated and used in social-ecological systems are those that give the **maximum return** between the parameters that influence the entrance and the differential use. Thus, the model is based on complex and multivariate relationships. These parameters do not eliminate the possibility of ethnobiological studies performing univocal tests (e.g., studying only the effect of availability in plant resource use). However, the absence of a direct relationship between the variables tested does not necessarily mean that there is no explanatory power when in association with other variables. For example, hypothetically, the most commonly used medicinal plants may not be the most available. Instead, they would be the most efficient. However, considering species with the same efficiency, one with higher availability would be used more often than one with lower availability.

### Postulates

1. *The entry of resources into social-ecological systems via experimentation is not random. Experimentation is biased such that the probability of a resource being chosen for experimentation is high depending on its already known attributes.*

**Table 1** Definitions and concepts of the social-ecological theory of maximization

*Cultural domain:* The entire social-ecological system is structured around knowledge domains. The system is an operational concept for heuristic purposes. We may consider, for example, knowledge about how to grow plants associated with practices, beliefs, and perceptions as a cultural domain

*Utility domain:* When a cultural domain is contemplated from a utilitarian perspective. For example, plants useful for firewood in a given social-ecological system

*Experimentation:* A process involving trial and error conducted by an individual or group of individuals in the search for innovations in terms of natural resource use

*N-dimensional hypervolume:* A vector space that presents  $n$  independent axes. The concept of an  $n$ -dimensional hypervolume is useful when addressing multivariate functions (see Blonder 2017; Blonder et al. 2017). A resource (e.g., a medicinal plant) can be characterized in terms of  $n$  variables (e.g., availability, taste, efficiency). Each variable is represented by an axis of this  $n$ -dimensional hypervolume

*Potential redundancy:* The theoretical capacity of redundancy storage in a utility domain. Considering a system with 10 species in the environment, the potential redundancy for a given use would be 10. Therefore, the potential redundancy represents the maximum amount of redundancy a given use could store

*Accession:* This concept concerns the entry of an information or biological entity into a social-ecological system

*Maximum return:* Best possible result from the combination of different explanatory variables that influence certain phenomena in social-ecological systems

*Decision rules:* All behaviors involve decisions about the value of a given choice by weighing all available choices. When people know the costs and risks of a given decision, we will necessarily have behavioral optimization. When this situation does not occur, the result is a nonoptimal or suboptimal behavior

*Biocultural traits:* Information units that are present in a human group and that are produced from the interaction between people and their environments, for example, a given medicinal plant that is used for analgesic purposes by a traditional community

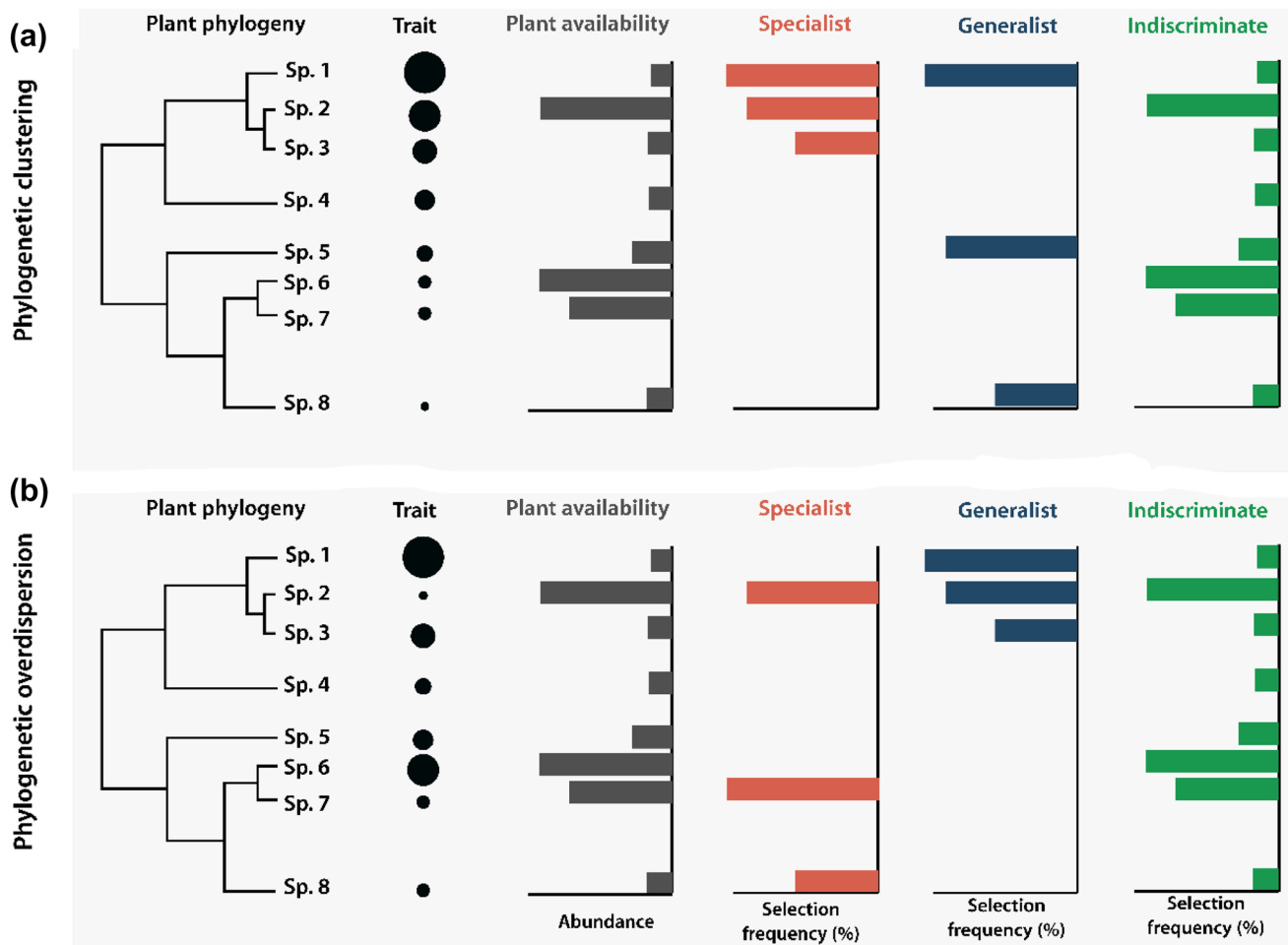
*Differential use:* More effective use of certain species over others, although they are all part of the same utilitarian domain

Experimenting (innovating) generates energy expenditure. This expenditure is amplified with the increase in the number of failures in the experiments. Therefore, human populations have developed strategies to reduce the chances of error when trying new resources. Such strategies include organoleptic and morphological cues of the efficacy of a resource. For example, some studies have shown that different diseases are treated with plants that present different tastes (Ankli et al. 1999; Heinrich 2003; Medeiros et al. 2015), and some studies indicate that migrant human populations may incorporate into their systems the resources present in new environments that have morphological or organoleptic similarity to the species of the environment of origin (see Medeiros et al. 2012). Food plants that are eaten by other animals and species with obvious signs of herbivory would tend to be more experienced for human feeding purposes because such attributes would be indicative to humans of no toxicity. Thus, considering the biases that guide the experimentation of plants over time, there are tendencies towards utilitarian accumulation among certain groups of resources. For example, some botanical families tend to be proportionally used more often as medicine or as food than others (Moerman 1979; Gottlieb et al. 1995; Saslis-Lagoudakis et al. 2012, 2014).

To better understand the mechanisms by which humans select plant or animal resources, we must articulate ecological and evolutionary factors dictating the nonrandom nature of this selection. First, human forage will be affected by resource quantity and quality. Whereas resource quantity varies in space and time, resource quality depends on several aspects (e.g., nutrient concentration, digestibility), and thus, a combination of availability and return will determine consumer-resource relationships. Second, because the evolutionary history of living resources (e.g., plants) defines their similarities (e.g., morphology, behavior), human foraging behavior can be modulated by phylogenetic relatedness (see Toney et al. 2018). However, to advance the understanding of how this behavior generates specialization, we must establish a better framework. A recent study improved this limitation by incorporating such phylogenetic information into the specialization concept (Jorge et al. 2014). The authors proposed an approach to explain how herbivores use plants and how ecological and evolutionary processes dictate these interactions. In addition, the authors argue that the following approach can be applicable to any system involving resource use:

- (1) Construct a phylogeny of the available living resources in a defined region.
  - (2) Investigate whether a specific trait (e.g., wood density, firewood) is clustered or overdispersed in the phylogeny.
  - (3) Measure plant (or animal) availability in the region.
  - (4) It is thus possible to define whether the behavior of humans is (a) specialized, (b) generalized, or (c) indiscriminate. Specialists are those human populations that select a nonrandom subset of closely related species (Fig. 1a, Specialist column), as defined by Jorge et al. (2014). However, in plant communities with a divergent evolution of a specific trait, specialists can select distantly related species sharing similar traits (Fig. 1b, Specialist column). Generalists are those populations selecting the most different traits of phylogenetically distant species (Jorge et al. 2014, Fig. 1a, Generalist column). In contrast, an alternative generalist scenario may be observed when human populations select closely related species with divergent traits (Fig. 1b, Generalist column). However, such a scenario has not been investigated. Finally, a necessary improvement of the specialization concept is to recognize that generalist species are not necessarily those species consuming a variety of items. Instead, those species that consume resources according to their availability have been considered indiscriminate feeders (Jorge et al. 2014, Fig. 1a, b, Indiscriminate column).
2. *The best-known and most-used resources for a given purpose are those that give **maximum return**, considering a balance between the explanatory variables in an **n-dimensional space**.*

Considering that multiple variables interfere with the use and knowledge of natural resources, the resources that are best known and/or used at any given time are not necessarily the ones that are most successful, according to specific parameters (e.g., availability, efficiency). Conversely, those resources that present the maximum return considering the trade-offs or positive correlation of all parameters related to the **utility domain** in question could be preferred by local people. Considering that there are multiple parameters, the maximum return is identified in an n-dimensional hypervolume. Figure 2 simplifies this hypervolume in two dimensions (availability and efficiency) to demonstrate three resources that can have the same return from a trade-off between availability and efficiency (first scenario) or that cannot have similar returns because people should maximize the selection of the best resource (second scenario).



**Fig. 1** Proposed framework for differentiating resource use by humans, which depends on trait evolution. Communities with phylogenetic clustering where **a** species traits (e.g., wood density) are more

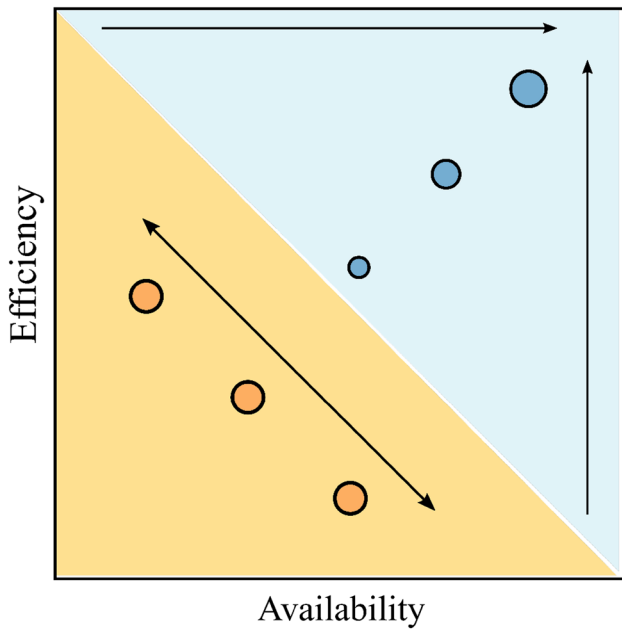
similar within closely related species and **b** species traits are more divergent within closely related species. See main text for definitions

In the case of temporary availability, the model of maximum environmental utilization applied to seasonal environments would privilege the resources available throughout the year compared to resources of equal efficiency that are unavailable at certain times of the year. In these cases, temporal availability translates into reliability in obtaining a resource, considering that resources that are not frequently available do not provide reliability because they are not available whenever people need them. Thus, the climatic seasonality hypothesis (Albuquerque 2006) would only be one among several developments of the maximum utilization model. Another example that fits the model is the growing popularity of cosmopolitan exotic species in local pharmacopeias. It is possible that these species only excel in local pharmacopeias when the cost and benefit balance yield greater returns than the native species. Silva et al. (2018) indicated that the number of exotic species for use of firewood can be favored in situations of envi-

ronmental modifications that lead to scarcity of native vegetation areas.

3. *The explanatory power of the predictors of knowledge and differential use is affected by the utility domain.*

Although maximum response guides knowledge and differential use across all utility domains, the importance of each parameter may vary across domains. For example, the importance of spatial availability is often greater for wood uses than for medicinal uses (Gonçalves et al. 2016). Thus, the smaller the proportional weight of a parameter is, the more variation it will need to present modifications in the return of a resource. In the case illustrated in Fig. 2 (scenario 1), a small decrease in efficiency must be compensated for by a large increase in availability (or vice versa). This negative feedback will vary in intensity (the slope of the regression curve) depending on the selected resource. Conversely, in locations where plant availability and efficiency are posi-



**Fig. 2** The lower part of the figure demonstrates a hypothetical scheme of trade-offs between efficiency and availability. Whereas the highlighted dots there represent species that yield the same return, the double-headed arrow indicates the expected behavior of human populations that should decide to choose plants that are more available but that are less efficient (or more efficient and less available). This selected resource will then affect the slope of this relationship without changing the negative feedback between availability and efficiency. Conversely, there is an alternative scenario (upper portion) in which plant availability correlates positively with plant efficiency. As a result, people should concentrate on the selection of plants with maximized returns (upper right), followed by increasing efficiency and availability (one-headed arrows)

tively correlated (Fig. 2, scenario 2), resource use tends to be maximized.

### Redundancy Generation Model

#### Enunciation

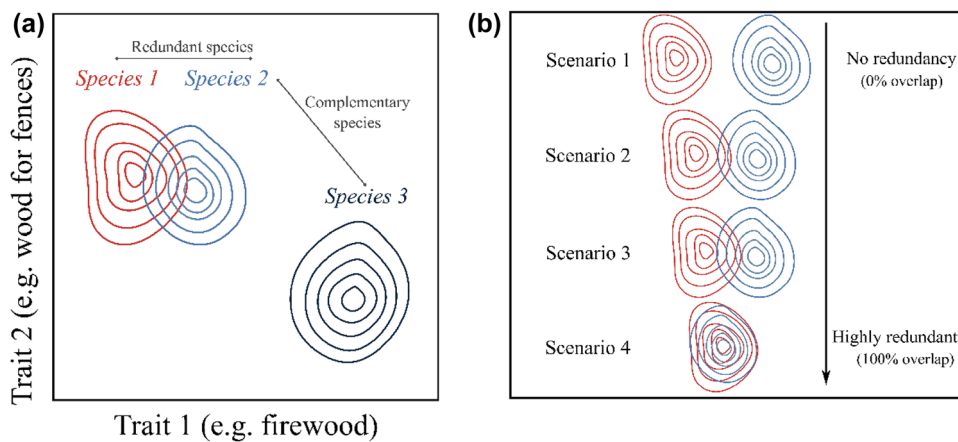
In this model, it is assumed that people develop strategies to generate **flexibility** in their choices of responses in space and time. Regardless of culture or specific type of environment, a set of universal rules guides human beings in their efforts to favor the redundancy of a social-ecological system.

A social-ecological system can be empirically assessed from various perspectives. For example, we may consider a traditional medical system based on the use of natural resources as a type of social-ecological system. This system is composed of structuring elements: natural resources (plants, animals, or minerals), people (who keep cultural information about these resources), and functional elements or **biocultural traits** (for example: trait  $x$  to treat disease  $y$ ).

#### Postulates

1. *All social-ecological systems are designed to be redundant. This redundancy varies in space and time.*

Considering the available empirical evidence, all systems already studied appear to present some degree of redundancy (Fig. 3a), in the sense that there are elements that exhibit functional redundancy (Santoro et al. 2015; Nascimento et al. 2016). Increasing redundancy in a given utility domain may increase resource alternatives for the same function, which favors people’s response in the face of environmental fluctuations. For example,



**Fig. 3** Schematic representation of intraspecific variability of plant traits representing the  $n$ -dimensional hypervolume (represented here by 2D plot, for simplicity). **a** The variability within each species is represented by a contour of a probability density function (as defined by Carmona et al. 2016). **b** Four different scenarios with increasing

overlap (and, thus, redundancy) between two different species. The left-side species represents a species that is no longer available in a given site, whereas the right-side species in each scenario represents an available species with a gradient of trait overlap



considering the disappearance of a given species, people may use the remaining species that present the same function, which means they could select co-occurring species with the maximum overlap in the  $n$ -dimensional hypervolume (see Albuquerque and Oliveira 2007, scenario 4 in Fig. 3b). Santoro et al. (2015) showed that in the absence of certain species, people selected other known species that provided the same utilitarian function as the absent species. For example, Fig. 3b provides four alternative scenarios in which species 1 (left side) is absent in a specific region, whereas species 2 (right side) is available. The probability of selecting a new species is positively associated with the overlap of the  $n$ -dimensional hypervolume available species (i.e., scenario 4). In contrast, two plant species with no overlapping of the  $n$ -dimensional hypervolume may be less preferred as a substitute for new species (Fig. 3a, b, scenario 1).

In different human groups, redundancy may differ in space and time. Spatially, the degree of redundancy may vary in different human groups as a response to changes in the environment. Several studies have shown that factors related to urbanization and modernization can affect the diversity of knowledge about environmental resources in human groups. Human groups with access to biomedical health services may have less knowledge about medicinal plants (Vandebroek et al. 2004), and groups located near urban areas may have less knowledge about plant uses (Reyes-García et al. 2013). These differences in the diversity of resources known by different groups in response to these factors may lead to a difference in the degree of redundancy between groups located in distinct regions, as a direct relationship between diversity and redundancy can be expected.

Temporally, the redundancy of the system may vary as a response to environmental factors. For example, some evidence suggests that redundancy in medical systems may be a response to the frequency of disease occurrence, where the most frequent diseases present an increase in plant use for their treatment (see Nascimento et al. 2016; Santoro et al. 2015). This finding may indicate that there are utilitarian domains that are more likely to generate redundancy than others. A greater redundancy may thus be related to environmental factors, such as the frequency of occurrence of a given disease, as mentioned previously, although the redundancy always derives from an intrinsic characteristic of that domain. The high occurrence of a disease may allow for a greater number of events to copy information about the treatments in a group (Tanaka et al. 2009), favoring an increase in redundancy. In addition, there are diseases that allow for the inclusion of a greater diversity of resources because they can be treated by a broad chemical spectrum, which may be present among a greater

number of resources, such as gastrointestinal diseases (Medeiros and Albuquerque 2015). In such cases, complementary species may represent a better choice for local people. In addition to redundancy, a set of ecological studies has investigated functional complementarity (Loreau 2004; Blüthgen and Klein 2011; Kelly et al. 2016). Complementarity involves a system property in which species with different niches would have a positive impact on ecosystem functioning because of optimal resource use (Blüthgen and Klein 2011). This hypothesis is known as the niche complementarity hypothesis (Hector et al. 1999).

An increase in system redundancy can occur through different paths. One involves the incorporation of species into the social-ecological system in utilitarian domains that already present some degree of redundancy. An interesting example occurs in the process of entry of exotic species into local medical systems. Considering the recent evidence that exotic plants are present in diseases for which native plants are indicated (Medeiros et al. 2017), it is possible that the entry of exotic plants occurs to increase the redundancy in certain diseases.

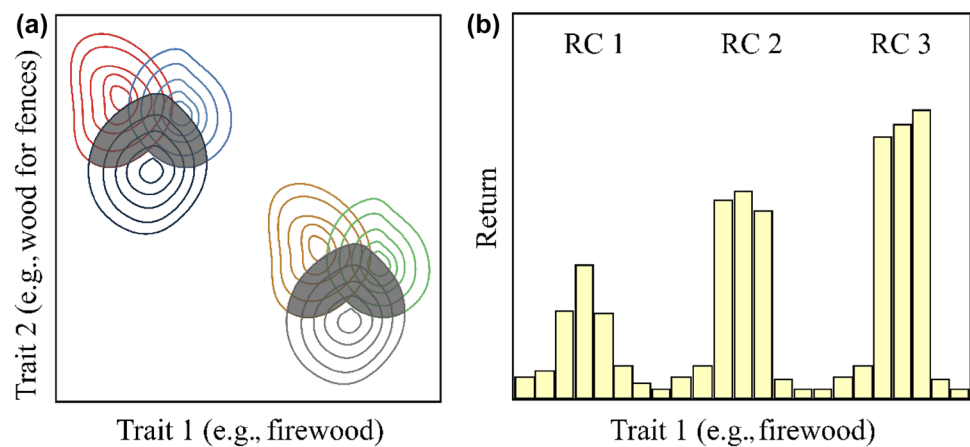
Another way in which redundancy can occur in a system is related to knowledge innovation processes from elements that already constitute the system in other utilitarian domains. For example, a plant indicated as food or ornamental can enter medical use through its experimentation (Bennett and Prance 2000).

2. *Sharing resource information in a human group favors redundancy and therefore resilience.*

The sharing of information within a system may favor resilience over time (Ferreira Júnior et al. 2013). If a person in the system knows many biocultural traits and does not share this information with others in the group, the person's migration or death may affect the system through impoverishment. For example, considering a medical system, we can expect that sharing will allow individuals in the system to know about more plants for the treatment of diseases, increasing redundancy at the individual level, which may reflect on redundancy at the system level. However, due to memory limitations, it is difficult for individuals to share all the traits present in a system. Thus, the most productive strategy involves sharing only a small set of similar trait spaces (see Barrett 1995; Santoro et al. 2015). For two systems with the same amount of shared information, the one that presents idiosyncrasies in addition to the shared information would be more resilient, considering that the idiosyncratic information has the potential for future sharing.

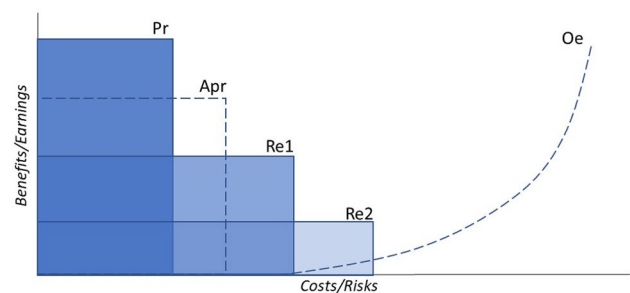
3. *Redundancy is hierarchized from the principle of maximum return.*

**Fig. 4** **a** Hierarchy of redundancy demonstrating groups of species that are more redundant (overlapped gray area) but differ significantly from other redundant groups. **b** These redundant groups (RC) are organized in a lumpy distribution that can be hierarchically prioritized by local people based on maximizing return (RC3). Each bar represents a specific trait class



In a utilitarian domain where redundant species are present, people do not equally prioritize those species. Some plants may be more preferred over others for a given purpose (Albuquerque and Oliveira 2007; Ferreira Júnior et al. 2011), and some may be known but not currently used by people (see Reyes-García et al. 2005). This relationship suggests that redundancy presents a hierarchy (see Scheffer and van Nes 2006), in which certain redundant species for a given use are prioritized over others (Fig. 4a, b). As a result, the lumpy distribution of redundant species groups will create a set of preferred traits yielding maximum return (e.g., RC3 in Fig. 4b). The focus on some species can be explained by a logic of maximizing returns. The trait most prioritized in a redundant category may be the one that provides the greatest return compared to the returns provided by other redundant species.

The knowledge that is not necessarily put into practice comprises an inventory knowledge, which can be retrieved “in situations where it becomes necessary, for example, if a resource that offers the greatest return becomes unavailable in the environment” (Albuquerque 2006). Although human memory has limitations in the storage of information (Nairne et al. 2007), keeping some useful plants and animals in the inventory knowledge may be important under future conditions that may disturb the availability of species in the environment. One example may be the use of emergency food in situations of scarce resources in the environment (Nascimento et al. 2012). In this case, such knowledge would serve as a reservoir of resilience. The probability of an inventory resource replacing a (preferred) resource that was lost is inversely proportional to the difference between the returns obtained from the use of the lost resource and from the use of the inventory resource (Fig. 5). As the return of the inventory resources decreases relative to absent resources, it is possible to increase the probability of insertion of other elements, such as biomedicine resources



**Fig. 5** In the case of the loss of a preferred resource (Pr), an alternative preferred resource (Apr) may take its place in the system. The alternative preferred resource (Apr) will be represented by the inventory resource that presents a smaller difference relative to Pr in terms of return, in this case, Re1. Resources of very low returns in relation to Pr tend to be replaced by other elements (Oe). Pr preferred resource (highest return), Apr alternative preferred resource, Re1 inventory resource with the highest return, Re2 inventory resource with the second highest return, Oe other substitute elements

(for the case of medicinal use) or liquefied petroleum gas replacing firewood (in the case of fuel use), among others.

## Final Considerations

The new theory we propose incorporates hypotheses and models that have been investigated by ethnobiologists over the past 30 years. Several ethnobiological studies have demonstrated the strong influence exerted on the environment when people select plant resources. Therefore, our first model explains this process in an ecological/evolutionary manner by considering the different types of resources that are available to people. The second model, strongly influenced by developments in ecology, accounts for how these types of biocultural information (resources and information) are structured to form complex systems. The models involved are versatile and flexible and thus accommodate new and creative hypotheses that may be further formulated.

Furthermore, we invite the scientific community to test our model and to collaborate with future developments of this new and first theory born into modern ethnobiology.

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