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Addressing Social-Ecological Systems across Temporal and Spatial Scales: a Conceptual Synthesis for Ethnobiology

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Abstract

We develop an integrative conceptual framework for addressing social-ecological systems across different spatial and temporal scales. Ethnobiologists study social-ecological systems through the lens of heterogeneous disciplines from the natural sciences, social sciences, and humanities. Despite the integrative ambitions of the field, ethnobiology often remains fragmented through research programs that emphasize different methods and scales. We propose a conceptual synthesis of three processes: (1) cognitive processing, (2) cultural transmission, and (3) biocultural evolution. We also discuss how social negotiation is embedded in them. By showing how these different processes interact across different spatial and temporal scales, we develop a framework for ethnobiological scholarship that can address complex dynamics in social-ecological systems.

Keywords Ethnobiology · Natural sciences · Social science · Humanities · Cognitive processing · Cultural transmission · Biocultural evolution · Knowledge integration · Social-ecological systems

Introduction

Human interactions with biota in social-ecological systems are inherently complex and develop along different spatial and temporal scales. Ethnobiology has emerged as a multidisciplinary field that studies complex dynamics in social-ecological systems through heterogeneous disciplines from ecology and evolution to cognitive psychology and linguistics to cultural and environmental anthropology to Indigenous studies and political ecology. A more classic definition would be the study of the direct interrelations between people and biota, including the fields such as ethnobotany, ethnozoology, ethnoecology, and ethnomycology.

Ethnobiologists widely embrace an integrative identity of their field and ethnobiology has been hailed "as the interdiscipline with the greatest explanatory power in helping society understand biocultural complexity" (Nabhan 2016: 11). Along similar lines, Wolverton (2013) argued that "ethnobiology is well-suited to serve as an interdisciplinary umbrella for environmental scientists, conservation biologists,

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restoration ecologists, environmental philosophers, and others who engage in applied research related to human-environment interactions." "Ethnobiology 5" (Wyndham *et al.* 2011; Wolverton 2013) has emerged as a label for these ambitions to provide an integrative framework for the study of social-ecological systems. Reflecting on Hunn's (2007) periodization of the field into four phases, ethnobiology 5 brings together the intellectual resources of earlier phases with applied concerns about social-ecological change at local and global scales. The prior four phases concern the advances of ethnobiological approaches, since its formal beginning with the concept of ethnobotany in 1895, before reaching cognitive ethnobiology (phase 2), characterized by studies documenting indigenous knowledge from an emic perspective. It also achieved a higher ecological focus - ethnoecology (phase 3:) before reaching a focus on understanding the intellectual property rights of indigenous peoples and local communities (phase 4) (Hunn 2007).

However, as Ludwig (2018) argued, these inter- and trans-disciplinary promises of programmatic articles do not match the often-fragmented multidisciplinary reality of the field. Indeed, ethnobiology provides space for researchers with heterogeneous training in the natural sciences, social sciences, and humanities. At the same time, these researchers often employ concepts and methods that remain disconnected. Therefore, the diversity of academic formations and approaches, which should undoubtedly become an advantage of the field, sometimes leads to the establishment of clusters in terms of interests and world views, which often compromises the dialogue among ethnobiologists or between ethnobiologists and scientists in other disciplines. Therefore, ethnobiology does not currently provide an integrative framework that guides scholars in other fields. In fact, ethnobiological scholarship often remains underrepresented or even invisible in wider interdisciplinary debates about issues such as inclusive development, human ecology, sustainability, resilience, and the utility of trans-disciplinary approaches.

Another issue that permeates ethnobiology is that basic and applied studies are often seen as competing or unassociated. As most theory-driven and hypothesis-testing studies are developed under the "basic" label, applied studies are often viewed as contributing little to scientific development. On the other hand, the basic approach is often criticized for not matching the needs of local communities. Therefore, we believe that a more integrative practice in ethnobiology could help to approximate basic and applied research.

Here we aim to contribute to this more integrative practice in ethnobiology through a conceptual synthesis of research in different areas of the field. We depart from the recognition that ethnobiological scholarship engages with different spatial scales from the individual to the macrosystem level and with different temporal scales along intra- and intergenerational dimensions. As a second step, we identify three general processes (cognitive processing, cultural transmission, and biocultural evolution) and address their interaction across scales. Finally, we discuss how social negotiation is embedded in these general processes. Social negotiation should not be seen here as a discipline or academic approach, but rather as a dialoguing strategy among different social actors.

Towards a Synthesis in Ethnobiology

We propose a synthesis for relating different domains of ethnobiological research that address fundamental processes along different temporal and spatial scales. We take inspiration from integrative frameworks in other fields, such as population genetics and community ecology. In population genetics, the four fundamental processes are mutation, gene flow (migration), genetic drift, and natural selection. Likewise, the conceptual synthesis in community ecology recognizes four processes: speciation, dispersal, ecological drift, and selection (Vellend 2010, 2020). In general terms, the fundamental processes of these two disciplines represent (i) the origin of new types (genes or species), (ii) the movement (of individuals) across space, (iii) a stochastic component adding or removing individuals from one time to another, and (iv) selection (Vellend 2020). In ethnobiology, we suggest three general processes: cognitive processing, cultural transmission, and biocultural evolution.

Cognitive processing refers to resources of individuals and communities to store and recover information about the environment through classification, memory, perception, and decision making. *Cultural transmission* is a process that entails copying and sharing information among individuals. *Biocultural evolution* is a process where changes caused by humans to the environment have an influence on the evolution of other organisms, but this effect also has a feedback loop determining the evolution of humans.

Certainly, it is possible to link some of the fundamental processes of ecology and genetics (dispersal or migration, speciation or mutation, and selection) with the proposed processes of ethnobiology. For example, cognitive processing might steady a cultural innovation in one population if this innovation is beneficial, which is analogous to speciation (ecology) or mutation (genetics). In addition, this innovation could spread to other populations (cultural transmission) when some individuals disperse or migrate to new areas, which is similar to the dispersal processes of ecology and genetics, increasing the amount of information in the systems (e.g., novel medicinal species). Finally, certain resources can offer people greater adaptive advantages. These resources may increase in popularity (and cultural importance) over time, decreasing the popularity or excluding resources that offer fewer advantages. This can negatively affect the richness of known species over time in a human group. Such processes, which are included in the scope of biocultural evolution, may correspond to the selection processes in ecology and population genetics.

Here, we propose a conceptual synthesis for ethnobiology that explicitly considers the three general processes mentioned that can underlie the relationships between humans and nature at multiple spatial and temporal scales in social-ecological systems. The proposed synthesis was motivated by previous syntheses in ecology and evolution (Johnson and Stinchcombe 2007; Vellend 2010), but also by provocative studies in ethnobiology (Wyndham *et al.* 2011; Wolverton 2013; Ludwig 2018). We first present the scale problem in ethnobiology to demonstrate the need for more studies at different spatial and temporal scales and how our proposal for conceptual synthesis considers the fundamental processes in ethnobiology at these scales. Then, we represent the theoretical aspects of each general process and provide some practical examples of studies in each of them. We also provide some follow-up questions that illustrate our approach, which might also stimulate future studies in ethnobiology. Finally, we discuss how these processes are related to the topic of social negotiation.

The Issue of Scale in Ethnobiology

To understand social-ecological systems, a key entity in ethnobiology, it is necessary to consider different spatial and temporal scales. For that, it is necessary to carry out interdisciplinary research that brings together different fields, from ecology and evolution to psychology and linguistics to anthropology and sociology, that have produced investigations at different scales (for ecology and evolution studies, see Roy *et al.* 1996; Haloin and Strauss 2008). Particularly for ethnobiology, most studies have been carried out at the local (community) scale (Albuquerque and Alves 2016) and relatively few have investigated different communities in a region (local metacommunities) (for example, Reyes-García *et al.* 2013; Silva *et al.* 2016) or groups living in different regions of the planet (macrosystems) (see Saslis-Lagoudakis *et al.* 2012; Gonçalves *et al.* 2016; Santoro *et al.* 2017) (Table 1, Fig. 1).

Table 1 Explanations of some important terms for a conceptual synthesis in ethnobiology

Important terms		Definition
Processes	*General processes*	Processes that affect patterns linked to the structure, dynamics, and evolution of social-ecological systems; cognitive processing, cultural transmission and biocultural evolution
	Specific processes	Contingent factors that contribute to changes in general processes.
Spatial scale	*Individual*	Smaller spatial scale for investigating processes in ethnobiology, representing each of those who are part of a social-ecological system. At this scale, it is possible to investigate how cognitive processing contributes to the retention of information about the environment, in addition to verifying the individual biases that affect the transmission of this information.
	Local community	Scale involving a human group and interactions with its environment. Studies at this scale, for example, can verify how general processes affect the cultural importance of certain resources to the detriment of others in the group.
	Local metacommunities	A set of distinct human groups living in a region where they can interact with each other. Studies that consider this spatial scale, for example, can investigate the similarity of knowledge about useful species between these groups and how general processes (e.g., cognitive processing) determine this resemblance.
	Macrosystem	A larger spatial scale covering systems living in different regions with limited or prevented contact between groups. Studies with these larger scales can inform patterns of social-ecological systems at a global level, for example.
Temporal scale	*Intragenerational*	Scale involving studies that investigate processes in a punctual manner or that follow the communities studied in the short term, in a generation.
	Intergenerational	Research on processes in social-ecological systems over two or more generations that uses large temporal investigations or use analytical tools to evaluate evolutionary patterns of human populations.
Fitness	*Biological*	Relative to biological (reproductive) success.
	Cultural	Relative to cultural success of information and/or behavior at an individual or societal scale.

Despite the great importance of local studies, going beyond the focus on small spatial scales (local community) is a necessary investment of ethnobiological investigations, which might look at broader spatial or temporal scales to better understand processes shaping social-ecological systems. For example, there is evidence indicating that actions at the individual (small spatial scale) level can affect general processes at a broader spatial scale. The individual processes linked to gaining different types of knowledge (such as traditional and non-traditional) can contribute to a decrease of traditional knowledge at the level of the local community over time when individuals acquire more information external to the system (non-traditional knowledge) in response to socioeconomic and environmental changes (Reyes-García *et al.* 2013). In addition, human-driven environmental changes can affect even broad spatial scales (regional and global), as in the case of the ongoing global climate crisis where humans are promoting the rearrangement of social-ecological systems across the planet (Pincetl 2017; Fedele *et al.* 2019). Recent research has also shown that interactions between different communities in a region at a broad spatial scale can interfere with individuals' decisions related to cooperation and competition in resource collection within local communities (small spatial scale) (Berkes 2010; Waring *et al.* 2015). Therefore, a general process acting on a certain scale can cascade up or down across different spatial or temporal scales.

Ethnobiological studies that consider the time scale are even rarer (for example, Reyes-García *et al.* 2013; Nascimento *et al.* 2018). One of the characteristics present in social-ecological systems that can be investigated over time involves feedback loops. Human actions in the environment, such as landscape management, can modify functions and processes in the ecological system, which, in turn, can affect human knowledge and behavior (Chen *et al.* 2017). For example, some studies have shown that high pressure on preferred species (for food, medicine, etc.) by past generations might force later generations to change resource use by selecting less preferred but more available species (see Spainer and Lavalli 2007; Rao *et al.* 2010). This example reinforces theoretical expectations that sociocultural and ecological systems influence each other over time, so that actions taken in the environment by earlier generations affect the environmental decisions of later generations.

Previous studies have argued that human actions in the environment can produce environmental legacies that are maintained over the long term. Human management of species in the past might favor changes that are maintained in the landscape. In the Amazon, past management practices modified current forest landscapes, so that species domesticated in the past currently have high abundance compared to non-domesticated species (Levis *et al.* 2017).

A theoretical example of how different scales can be incorporated in ethnobiology is the Social-Ecological Theory of Maximization proposed by Albuquerque *et al.* (2019b), which explains that social-ecological systems are built to favor the survival of human beings in their interactions with different environments over different spatial and temporal scales. In this case, a set of human cognitive and behavioral mechanisms influence the construction of these systems to maximize benefits and minimize costs in interactions with the environment (ibid.). In one model, the Model of Maximum Environmental Performance, they postulate that the incorporation and differential use of resources in social-ecological systems are directed toward resources that offer the maximum return within the various parameters that influence the selection process (ibid.). The model can be evaluated at different spatial scales. For example, at the small spatial scale (a local community), an investigation of how cognitive processing (e.g., organoleptic properties, local availability, and efficiency) can determine resource selection (e.g., incorporation and differential use). Additionally, at a broad spatial scale, it is possible to consider other determinants dictating the selection of resources that are affected by three general process, such as climate. For example, in macrosystems a preference for perennial resources in human groups living in markedly seasonal environments has been observed in different semi-arid regions of the planet (in northeastern Brazil, see Albuquerque 2006; in Morocco, see Linstädter *et al.* 2013). This means that general processes affecting the selection of resources work at different spatial scales. Therefore, the climate of a region (broad spatial scale) influences local preferences for certain resources of a local community (small spatial scale).

Given the importance of spatial and temporal scales for the study of social-ecological systems, to the best of our knowledge, there are no syntheses organizing ethnobiological studies at different scales. We present a synthesis based on three general processes in social-ecological systems (cognitive processing, cultural transmission, and biocultural evolution) based on interdisciplinary dialogue with ecological and evolutionary scenarios (see Albuquerque and Ferreira Júnior 2017). We organized the relative importance of these general processes across different spatial and temporal scales. We argue that our proposal allows different approaches in ethnobiology to be related so that their contributions at different levels and scales within the field become clear.

The three general processes can be evaluated at different spatial and temporal scales, but their relative importance varies with scale (Fig. 1). The basic process linked to cognitive processing can range from the individual to macrosystems on the spatial scale, but it can generally operate over a short time period of just one generation (Fig. 1 first rounded circle: left). However, although processes of cultural transmission and biocultural evolution can be observed at different spatial scales, they are mainly composed of evolutionary processes that need different generations to be observed. Furthermore, the three processes do not occur in isolation and can influence each other over time and space (Fig. 1; see also Fig. 2). For instance, although cognition and memory are dominant at the intragenerational scale but spatially widespread, these processes can be accumulated in different metacommunities and macrosystems, which, in turn, may impact a new generation and affect cultural transmission and biocultural evolution processes. Note that social negotiation is not a process but rather a way of communicating with different actors. We further elaborate on this below.

General Processes

Cognitive processing includes gaining and understanding both the innate and cultural aspects of knowledge (information). Ludwig (2018) argued that it often remains unclear how ethnobiological scholarship relates to earlier phases of ethnobiological research that have approached local knowledge through fields such as cognitive psychology and linguistic anthropology. This general process includes the specific processes of (i) classification, (ii) perception, (iii) memory, (iv) decision making, (v) knowledge and use, and (vi) knowledge construction in new environments (Table 2, Fig. 2).

By classifying the environment, human groups can develop strategies that favor their survival, such as recognizing potential fishing areas and identifying patterns of fish migration (see Braga *et al.* 2019). Human classification of the natural world emerges from general cognitive and specific folk biological forms of reasoning that are shaped by cultural learning and utilitarian factors (Berlin 1992; López *et al.* 1997). It has become widely recognized that local classificatory systems do not only reflect local forms of cognitive processing but also the expertise of communities regarding biota and environments (Nabhan 2016).

Perception is a vital portion of cognitive processing, since the way people perceive nature has a direct impact on their behaviors and decisions (Rangel-Landa *et al.* 2016). For example, responsibility diffusion is common in local communities when people do not feel that their actions lead to environmental changes but rather perceive changes as a product of other people's behaviors (Gonçalves *et al.* 2019). In such cases, engagement in co-management strategies may be more challenging than in situations where people perceive their actions as directly connected to environmental changes. The way people perceive specific resources may also influence their current knowledge and use. For example, a group of plants known as famine foods is often consumed in situations of scarcity when other edible products are not available. Because they are associated with poverty and moments of difficulty, people often feel ashamed to reveal their knowledge of such plants, which compromises their actual use and blocks cultural transmission (Guinand and Lemessa 2001; Nascimento *et al.* 2012).

Memory is often neglected in ethnobiological studies, but it plays a significant role in how people interact with nature. Studies in the scope of evolutionary psychology have suggested that people preferentially store adaptive information related to their survival and reproduction (Nairne *et al.* 2007; Nairne and Pandeirada 2008). Such a pattern may shape, for example, the composition of local pharmacopeias and a society's most valued plants.

How memory influences local ecological knowledge at the individual level is also of relevance to ethnobiology as it may impact biological and cultural fitness. Several studies that

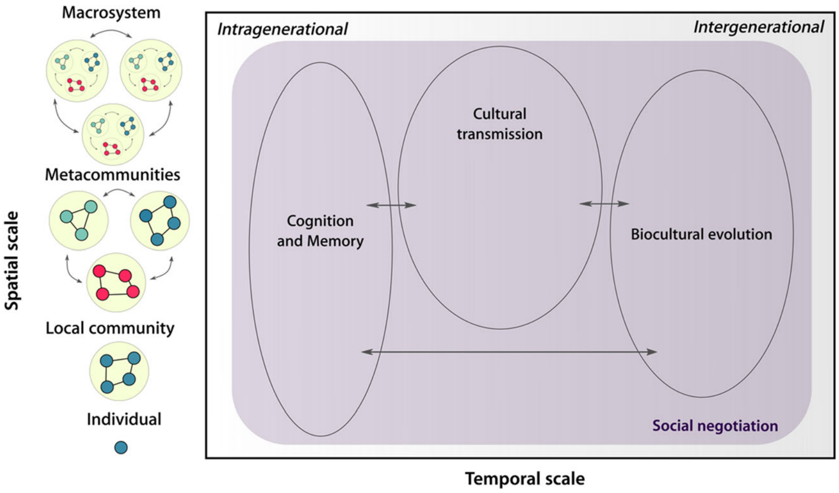

Fig. 1 Proposed conceptual synthesis of ethnobiology. We consider three general processes and their relationships that operate in social-ecological systems (cognitive processing, cultural transmission, and biocultural evolution) at different spatial and temporal scales. The gradient in light gray represents an increase in the temporal scale from intragenerational to intergenerational (x-axis). Conversely, the dark-shaded area demonstrates the social negotiation that is embedded in the three general processes. The arrows connecting the three general processes describe the reciprocal influence between them that occur over different temporal and spatial scales. The long, rounded circles correspond to the spatial or temporal scale for which each process is prominent

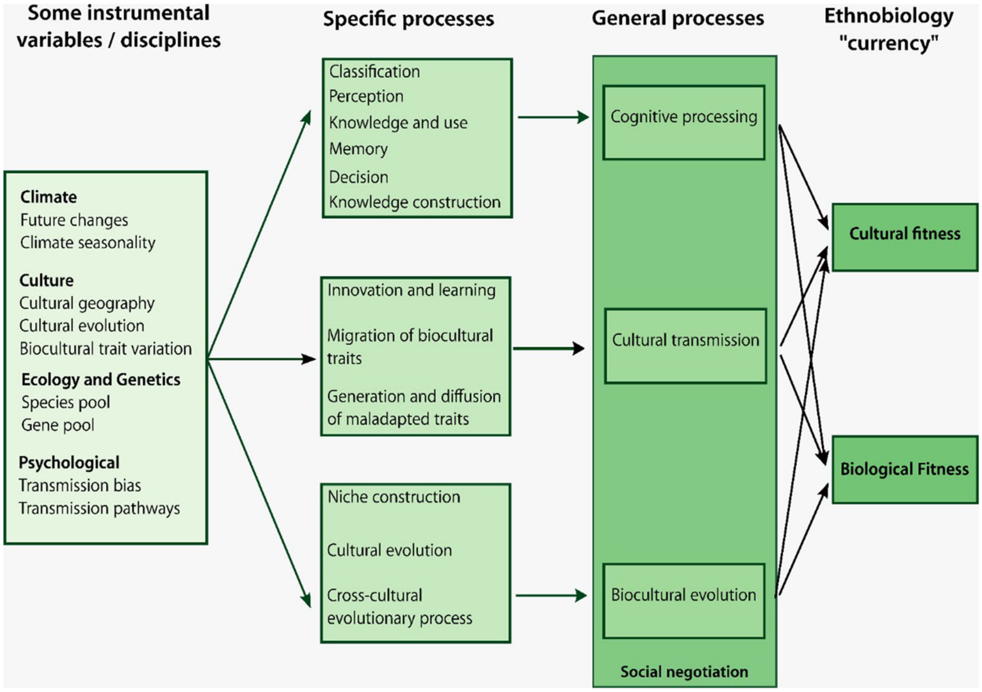

Fig. 2 Schematic diagram showing the nested structure of specific processes that are typically contingent but useful when aggregated in general processes. General processes represent the drivers of the variation in cultural and biological fitness

associate age and local ecological knowledge have found a common pattern in which knowledge reaches its peak among middle-aged adults and is maintained or decreases for as they age (Reyes-García *et al.* 2005; Ayantunde *et al.* 2008; Koster *et al.* 2016; Brito *et al.* 2017). This may be related to greater difficulty in storing new information after a certain age and may directly influence, for example, the ways elders incorporate recently introduced plants into their routines.

Decision making is directly linked to landscape changes and management strategies, usually addressed in agroecosystems (Bellon 2014) and plant management studies (Rangel-Landa *et al.* 2016). Decision making may take place at the individual level (e.g., an individual's decisions when searching for the best or most abundant resources available in the environment) (Medeiros *et al.* 2011), community level (e.g., when communal decisions are made concerning land use for agricultural purposes) (Bellon 2014), or outside the community, such as at the metacommunity level, when decisions may involve social negotiations among different stakeholders (Table 3) (Spalding 2020).

Ethnobiological research focuses in particular on the study of knowledge and resource use. Many of these studies report that knowledge is not evenly distributed among individuals (Hanazaki *et al.* 2000; Miranda and Hanazaki 2008; Reyes-Garcia *et al.* 2010; Paniagua-Zambrana *et al.* 2014; N'Danikou *et al.* 2015; Díaz-Reviriego *et al.* 2016; Poderoso *et al.* 2017; Maua *et al.* 2018) (see below). For example, women often have more knowledge about cultivated medicinal plants as they tend to be responsible for preparing these resources (see Hanazaki *et al.* 2000), while men often know more about wild medicinal plants (Ruddle 2000; Kujawska and Łuczaj 2015). However, there currently is mixed evidence regarding the generalities of this association of knowledge with degree of engagement with a resource (Torres-Avilez *et al.* 2016). In fact, we argue that as a general process, cognitive processing has a prominent role in influencing knowledge that is independent of scale. Conversely, specific attributes, such as sex, might be less or more important depending on location or scale, highlighting how contingent some specific processes are despite being central to understanding biological and cultural fitness variation.

Factors such as age (Koster *et al.* 2016; Brito *et al.* 2017), education level (Giovannini *et al.* 2011), urbanization (Ávila *et al.* 2017), distance from urban areas (Vandebroek *et al.* 2004; Tangjitman *et al.* 2013), and migration (Miranda and Hanazaki 2008; Medeiros *et al.* 2012) can also generate differences in knowledge. For example, Giovannini *et al.*'s (2011) study of the influence of the variables gender, age, and education on local knowledge of medicinal plants among indigenous communities in Mexico found that schooling and age showed positive correlations with extent of knowledge of the properties and uses of these plants.

That human knowledge constantly adapts to changing circumstances is fundamental to the resilience of social-ecological systems (Díaz-Reviriego *et al.* 2016). There are two basic processes to form individual or group knowledge repertoires: the production of knowledge and the transmission of this information (Cavalli-Sforza and Feldman 1981; Mesoudi *et al.* 2006). These processes are not random as they vary in response to environmental and social factors (Boyd and Richerson 2005). The adaptive capacity of systems allows individuals and groups to adjust to changes in their

Table 2 A proposed synthesis of general and specific processes in ethnobiology

General process	Specific process	Spatial scale	Main temporal scale	Instrumental variables and/or support disciplines
Cognitive Processing	Classification: Linguistic and cognitive structuring of the world through classification and categorization	Individual to local community	Intragenerational	Taxonomy, linguistics, psychology, anthropology
	Perception: how people perceive the world and how different factors affect their perception.	Individual to local community	Intragenerational	Socioeconomic, psychological, ecological
	Knowledge and use: factors affecting people's knowledge and use of the biota	Individual to local community	Intragenerational	Socioeconomic, psychological, ecological, urbanization, education level, gender, ethnicity
	Memory: an influential factor neglected in ethnobiological studies. The role of memory on the retention and recovery of social-ecological information	Individual to local community	Intragenerational	Retention rate, psychological, biological
	Decision: factors affecting people's decisions regarding the use and management of biota	Individual to local metacommunity	Intragenerational	Psychology, economy, anthropology
	Knowledge construction in new environments	Local community to macrosystem	Intragenerational	Migration, climatic change effects, natural fluctuations in environments
Cultural trans-mission	Innovation and learning of biocultural traits	Individual to local community	Intragenerational	Biocultural trait variation, transmission bias and pathways, environmental effects
	Migration of biocultural traits: systems hybridization and cultural diffusion	Local community to macrosystem	Intra- and intergenerational	Cultural geography, ecology
	Generation and diffusion of maladapted biocultural traits	Individual to macrosystem	Intra- and intergenerational	Cultural evolution, psychology, genetics
Biocultural evolution	Niche construction: human decisions and their effects on the environment	Local community to macrosystem	Intergenerational	Ecology, genetics, psychology
	Niche construction: effects of niche construction on social-ecological systems	Local community to macrosystem	Intergenerational	Extractivism of natural populations and landscape management
	Cultural evolution: shifts of variation and innovation of biocultural traits	Local metacommunity to macrosystem	Intra and intergenerational	Cultural evolution, genetics, ecology
	Cross-cultural evolutionary processes: demic and cultural diffusion	Local metacommunity to macrosystem	Intergenerational	Cultural geography, cultural evolution, genetics, ecology

Table 3 Social negotiation as "transversal strategy" in our proposal

	Approach	Spatial scale	Main temporal scale	Support disciplines
Social Negotiation	Management practices: negotiation of agricultural, conservation, hunting, medical, etc. practices	Local community to macrosystem	Intragenerational	Agriculture and agroecology, conservation biology, human ecology, sustainability studies
	Policy: negotiation of framework for addressing management practices	Local community to macrosystem	Intragenerational	Research and innovation policy, conservation governance, transdisciplinary design
	Political contestation: identifying and challenging inequity and marginalization in management practices and policy frameworks	Local community to macrosystem	Intragenerational	Political ecology, political epistemology, Indigenous studies, decolonial theory

environment, including human-driven disturbances that lead to a decrease in available resources or the introduction of previously unknown diseases (Ladio and Lozada 2008; Díaz-Reviriego *et al.* 2016) .

Cultural transmission is the process of production, copying, and sharing of information among individuals (Reyes-García *et al.* 2009; Mesoudi 2015; Salpeteur *et al.* 2015), including specific processes that have been widely studied in ethnobiology; (i) innovation and learning of biocultural traits, (ii) migration of biocultural traits, and (iii) generation and diffusion of maladapted cultural traits (see Dantas *et al.* 2020) (Table 2, Fig. 2).

Previous studies have indicated that biases occur during the process of cultural transmission (see Heath *et al.* 2001; Barrett and Broesch 2012; Eriksson and Coultas 2014) that can affect contingent patterns for local populations facing different environmental pressures or diseases outbreaks. In addition, the specific processes might exhibit distinct effects depending on the spatial or temporal scales studied (see Santoro *et al.* 2020).

Cultural transmission interacts with cognitive processing (see Nairne *et al.* 2007; Eyssartier *et al.* 2008; Santoro *et al.* 2018; Brito *et al.* 2019). For example, people both easily remember and readily share their experience of contaminated foods (Eriksson and Coultas 2014), or a disease outbreak could trigger social learning about medicinal plants which, in turn, increases the likelihood of local populations' survival (Soldati *et al.* 2015). However, we need to understand how factors occurring at individual levels can scale up shaping cultural transmission.

Some biases of the content of information are cultural traits most likely to be transmitted (Mesoudi 2016). For example, Henrich and Henrich (2010) found that information regarding food taboos for toxic marine species tended to be faster learned and transmitted by pregnant and lactating women than information about other species. As a result, content bias may act on knowledge learning and transmission (ibid.).

As human memory tends to privilege information that contributes to survival chances (see Nairne *et al.* 2007; Nairne and Pandeirada 2008), it has the greatest likelihood of being copied and shared. Therefore, memory biases that favor adaptive information may be intrinsically linked to the process of cultural transmission as it affects both biological and cultural fitness.

People's environmental circumstances can also determine how information is copied and differentially shared (context bias) (Soldati *et al.* 2015; Santoro *et al.* 2018). For example, when there are no public policies for controlling malaria the incidence of the disease in areas of Africa interferes with the use of antimalarial medicinal plants (Santoro *et al.* 2017). The recurrence of such a risk event is likely to be an important factor altering the information surrounding medicinal plants that will be preferentially copied and transmitted by people, which, in turn, is relevant information that can have an adaptive role in dealing with the environmental challenge.

Another bias active in the process of cultural transmission in social-ecological systems that can occur from the individual to community level is related to the "temporal lags" in transmission. Previous studies suggest there are differences between the knowledge of older and younger people due to intergenerational baselines (Hanazaki *et al.* 2013; Bender *et al.* 2014; Fernández-Llamazares *et al.* 2015). This dynamic reference syndrome can occur in a human group when the following conditions are met: (1) relevant environmental changes due to disturbances that affect, for example, the availability of resources; (2) lack of communication between generations, which limits the transmission of information regarding previous environmental states to younger generations; (3) differences between generations regarding perceptions of environmental changes (Fernández-Llamazares *et al.* 2015).

The process of cultural transmission can also be biased by a complete lack of intragenerational communication, although this has been little studied and evidenced in ethnobiology. Environmental changes associated with a lack of intergenerational communication can affect the capacity of individuals and populations to deal with rapid changes and, consequently, influence the resilience of the social-ecological system. This change occurs because with each new generation, previous environmental changes and their causes are less and less apparent. In this case, younger generations can assume that certain species are naturally scarce or abundant in their environment, possibly leading to, for example, the unsustainable use of some species. Therefore, an awareness of the basic processes that occur at the individual level is extremely important for understanding the complexity of social-ecological systems and provides a broad perspective of the interactions among different levels of the system, identifying, for example, points of convergence between them.

Biocultural evolution involves a process of reciprocal causation between human groups and their environments, so that cultural practices can affect properties of the environment and, in turn, human-driven or natural changes can lead to the selection of certain biocultural traits over time. This general process comprises different specific processes; (i) niche construction, (ii) cultural evolution, and (iii) cross-cultural evolutionary processes (Table 2, Fig. 2).

Human agricultural practices that emerged some 12,000 years ago entailed new selective pressures that impacted the evolutionary history of our species and others (Altman and Mesoudi 2019). Human beings, like other organisms, can modify their environment to suit their needs, influencing their own evolution or that of other organisms, a process referred to as niche construction (Laland and Brown 2006; Albuquerque *et al.* 2015, 2018; Albuquerque *et al.* 2019a, 2019b). Among humans, the processes of niche construction are distinct since they are influenced by learning processes and are culturally transmitted (Albuquerque *et al.* 2019a, 2019b).

Ethnobotanical studies at the local community (Monteiro *et al.* 2011) and metacommunity levels (Bufford and Gaoue 2015; Feitosa *et al.* 2017; Amahowe *et al.* 2018; Gaoue *et al.* 2019) (Fig. 1) show how human management and extraction practices can alter the strategies of certain plant species. Gaoue *et al.* (2019) analyzed how human harvesting and environmental stressors (e.g., drought) can influence the responses of the plant species *Khaya senegalensis* in two regions of West Africa with contrasting climates (dry vs. wet). They argue that frequent harvesting of biomass acts as a selective pressure on plants mediated by climate. Harvesting in the dry region favored a rapid transition of plant reproductive stages, which, in turn, buffered the negative effect of drought decreasing plant mortality. Their results illustrate the relevance of integrating spatially heterogeneous data, because locally focused information may fail to detect different strategies of the same species.

Another recent study demonstrated that pre-Columbian societies determined present-day patterns of plant species composition by domesticating preferred plant species (Levis *et al.* 2017). Their resource use may have altered vegetation structure on a large scale over time, and the study notes that about 1.5% of tree species in the Amazon forest represent half of all individual trees found in different areas of the forest (ibid.). Some of these trees are at different stages of domestication; incipient, semi-domesticated, or domesticated, as a result of pre-Columbian management practices (ibid.).

In the Araripe National Forest in northeastern Brazil, Silva *et al.* (2017) studied the effects of human actions on landscape domestication based on biological evidence and the perceptions of local populations. In this case, landscape management in the past favored the development of heliophile species useful for contemporary communities. However, with the creation of a conservation area in the region, communities were removed from the interior of the forest and the process of natural regeneration increased the forest cover to favor abundant ombrophilous species over the species used by people (ibid.) (for a more complete treatment of the niche construction process, see Albuquerque *et al.* 2019a, 2019b).

The ways cultural practices cause environmental changes and influence the relationship between humans and nature can also be analyzed from a macrosystem perspective (Figs. 1 and 2). Santoro *et al.* (2017), for example, analyzed whether local medical systems respond to environmental changes mediated by humans in their role as niche builders. They suggested that in highly deforested places with a higher incidence of malaria, there would be an adaptive response from local populations that would reflect a greater wealth of medicinal plants used to treat malaria. Moreover, populations that historically dealt with malaria but that currently have a low incidence of the disease may have a richer pharmacopeia for the treatment of malaria compared to populations that currently have a high incidence but no previous experience of treatments or transmission of malaria (ibid.). Therefore, the complexity of people-environment interactions can be understood more broadly if the experimental designs of ethnobiological studies aim to incorporate both inherent genetic and cultural aspects of this relationship (Moura *et al.* 2020).

In general, a macrosystem comprises larger spatial and temporal scales (Fig. 1). Although each local community has its own cultural system that affects its relationship with its environment, there are some emergent properties of these interactions that tend to occur in regional patterns (Albuquerque and de Medeiros 2012; Gutiérrez-Santillán *et al.* 2019). Hypotheses and theories regarding the organization patterns of social-ecological systems need to be generated to identify these patterns. In fact, whereas specific processes may be contingent in different local communities, general processes encapsulate those emergent properties. A new approach termed macroethnobiology (ibid.) may be useful in generating large scale strategies for conservation and bioprospecting (Albuquerque and de Medeiros 2012).

Most ethnobiological studies focus on use patterns of medicinal plants on regional and global scales. Macroethnobiology addresses spatial patterns in taxonomic and phylogenetic structures of traditional pharmacopoeias. By using statistical approaches comparing traditional pharmacopeias with the regional flora, species from the families Rosaceae, Asteraceae, and Lamiaceae were found to be over-represented in traditional pharmacopoeias, while the families Poaceae, Orchidaceae, and Bromeliaceae were under-represented (Moerman 1991; Moerman 1979; Weckerle *et al.* 2011; Medeiros *et al.* 2013). A global test has also demonstrated that the selection of medicinal or crop plant species and livestock animals is not random and can be guided by phylogenetic relationships (Milla *et al.* 2018).

Other studies have focused on a broader geographical scale to test whether these patterns persist in pharmacopoeias of very different cultures (comparing the medicinal flora of Nepal, New Zealand, and the Cape of South Africa) (Saslis-Lagoudakis *et al.* Saslis-Lagoudakis *et al.* 2011, Saslis-Lagoudakis *et al.* 2012). Despite the considerable cultural differences, there are some phylogenetic lineages that are highly valued in all these traditional pharmacopoeias, including the botanical families of Lamiaceae, Malvaceae, Rubiaceae, and Solanaceae (ibid.). Therefore, there is a cross-cultural phylogenetic conservatism in the selection of medicinal plants guided by a phylogenetic conservatism in phytochemistry. Moreover, this convergent medicinal use of the same species is a strong indication of their biochemical efficacy. These and similar ethnobotanical findings are beginning to be used in bioprospecting. For example, most of the plant species of the Fabaceae family cited with records of medicinal use in the ethnobiological literature have been subjected to ethnopharmacological screening (Souza *et al.* 2018).

Another approach is the study of phenomena affecting the inclusion of introduced plant species in traditional pharmacopoeias. Hart *et al.* (2017) compared the indigenous use of medicinal plants before Spanish colonization and current data in several local communities in Ecuador and found that introduced plants were over-represented in the traditional pharmacopoeias, although they are not as frequently used to treat diseases that appeared after Spanish colonization. Hart *et al.* proposed three different explanations for this finding; a) the ingress of these plants in the Ecuadorian pharmacopeia happened well after the Spanish conquest, thus, they could not be used to treat endemic diseases, at least initially; b) because of social disruption and epidemics during and after the Spanish conquest, Indigenous communities were unable to experiment with introduced plants; and c) post-contact diseases may be perceived as more severe, thus, Indigenous communities would prefer to use native species that they knew and trusted (ibid.).

The eco-evolutionary dynamics arising from the relationship between human beings and their environment can be studied at a large temporal scale. For example, McGraw (2001) tested the effect of high extractive pressure on the morphological traits of the medicinal plant *Panax quinquefolius*, examining specimens from 17 herbariums from four regions of Canada collected from areas of high vs. low extractive pressure. He observed a decline in the size of morphometric traits in areas of high extraction. It is likely that human harvesting of larger plants (probably due to their high economic return) has driven natural selection and, consequently, microevolution for these species (ibid.). On a larger temporal scale, comparisons among archeological sites and the occurrence of useful species in current plant communities in forests indicates that ancient human populations managed the landscapes to increase the abundance or geographical range of useful species (Levis *et al.* 2017; Lauterjung *et al.* 2018; see also Albuquerque *et al.* 2019a). Since some evolutionary phenomena cannot be accessed from the perspective of populations, the macroethnobiology approach may prove useful in identifying how humans have affected species evolution and biogeographical patterns.

Taken together, the three general processes incorporate several specific processes that are contingent and scale dependent. Instrumental variables (e.g., climate) are used to compare how specific processes vary under certain conditions (e.g., dry and wet seasons). However, general processes (not contingent or scale dependent) represent the drivers of variation in cultural and biological fitness (Fig. 2).

How Social Negotiation Is Embedded in the Three General Processes

Ethnobiological scholarship is increasingly concerned with the applied and societal dimensions of negotiating knowledge in complex social-ecological systems (Wyndham *et al.* 2011; Wolverton 2013). Rather than documenting knowledge surrounding biota and environments, ethnobiologists have turned their attention to how this knowledge becomes negotiation in practice. For the purposes of our discussion, we propose distinguishing among (1) management practices, (2) policy, and (3) political contestation as three core processes of social negotiation of ethnobiological knowledge.

Firstly, there has been increased recognition of Indigenous and local knowledge in the management of local environments. This recognition has co-evolved with wider sustainability discourse, as the influential Brundtland Report *Our Common Future* stated: [tribal and Indigenous] 'lifestyles can offer modern societies many lessons in the management of resources in complex forest, mountain, and dryland ecosystems' (WCED 1987: 12). Debates surrounding traditional ecological knowledge stand out as especially influential in emphasizing the knowledge of local communities in managing local ecosystems and highlighting the importance of this expertise in collaborative co-management practices (see Berkes 2010). Accordingly, the last reports of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) have emphasized integrating social knowledge and concerns as a prerequisite for improving public policy initiatives (IPBES 2018).

Secondly, recognition of local expertise in the management of social-ecological systems has become increasingly reflected in policy discourses. As expert-driven policy frameworks often depart from the sole recognition of Western academic expertise, ethnobiology challenges policy discourse to reflect on a variety of concerns and knowledge in constructing frameworks for management practices. Some frameworks are developed at local community or national scales (Castro and Nielsen 2001; Nursey-Bray and Rist 2009), while others aim to increase recognition of Indigenous and local knowledge at global policy scales, such as IPBES (Borie and Hulme 2015; Tengö *et al.* 2017).

While recognition of Indigenous and local knowledge in management practices and policy points towards more optimistic agendas of knowledge integration, ethnobiology has also become concerned with the limitations of such integration projects and the political contestation of different knowledge systems. Well-intentioned projects of knowledge integration often collide with conflicting epistemologies and ontologies as well as political realities of marginalization and oppression (Ludwig and El-Hani 2020). Rather than simply emphasizing the relevance of Indigenous and local knowledge, ethnobiology has also become increasingly concerned with environmental injustices and the political ecology of knowledge production more broadly (Wolverton *et al.* 2016; Fowler and Herron 2018).

Social negotiations of management practices and policies are affected by cognitive processing on different scales. Social stratification along dimensions such as gender, education level, and urbanization modulate cognitive processing, which, in turn, affects social negotiation processes (Table 3). First, differences in cognitive processing are crucial for understanding management practices that often reflect division of labor in communities that interact with different practices in areas such as conservation, education, farming, hunting, and medicine (Atran *et al.* 2002; Villagómez Reséndiz 2017). Second, differences in cognitive processing are crucial for the design of adequate policies and transdisciplinary collaborations that are responsive to the distribution of expertise across different stakeholders (Burger *et al.* 2003). Third, cognitive processing also relates to political contestation as the de facto exclusion of stakeholders often contrasts with expertise that is embedded in local classifications, perceptions, and decision making. Environmental and social injustices are commonly entangled with the marginalization of Indigenous and local knowledge in the negotiation of management practices and policies (Ludwig and Macnaghten 2020).

When social negotiation is taking place, the specific process of decision making may not be evaluated only at the local level. It includes the integration of knowledge and world views among different actors to reach common purposes (e.g., natural resource conservation). Therefore, such an approach undoubtedly moves ethnobiological research from the local level to broader spatial scales. Furthermore, when local and scientific knowledge interacts, the resulting knowledge coproduction may, for example, have a vital role in adaptation to environmental change (Armitage *et al.* 2011).

Social negotiation is also connected to cultural transmission since it involves collective learning. Information sharing among different actors has the potential to insert novel management strategies and knowledge in a social-ecological system. In the context of environmental management, for example, there is evidence that such learning may improve governance, as it can help actors learn about each other and resolve conflicts (Biggs *et al.* 2012).

Finally, social negotiations may cross the generational barriers and shape, in many ways, the dynamic relationships between people and nature. For example, the province of Himachal Pradesh in the western Himalayas (India) has experienced for more than 150 years an institutional engagement between the people and the state for the control of forests in the region, which led to a series of inter-related changes in management practices and forests (Chhatre 2000). Therefore, despite the lack of information on this matter, the influence of stakeholder interactions in the dynamic inter-relations between people and nature may be a matter of interest for ethnobiology in future.

Conclusion

Social-ecological systems are inherently complex and require inter- and transdisciplinary approaches that bring together methods from heterogenous stakeholders. Ethnobiology is well-positioned to meet this challenge of complexity by combining resources from diverse disciplines, such as evolutionary biology, comparative linguistics, cognitive psychology, cultural anthropology, and political ecology. Despite this interdisciplinary potential, we argue that ethnobiology often remains fragmented through research programs that emphasize different methods and scales.

Our review addresses this problem of fragmentation by proposing a conceptual synthesis for ethnobiological studies of social-ecological systems. First, we argue that ethnobiology studies of social-ecological dynamics occur across different spatial (individual, local community, metacommunity, and macrosystem) and temporal (intra- and intergenerational) scales. Second, we distinguish between three general processes (cognitive processing, cultural transmission, and biocultural evolution) that are studied in ethnobiology and emphasized by researchers from different disciplinary backgrounds. Moreover, social negotiation is a transversal strategy affecting how the general processes determine biological and cultural fitness at different scales.

By addressing heterogeneous processes across spatial and temporal scales, the proposed framework relates factors that are entangled in social-ecological systems but are often studied in isolation. The integrative potential of the proposed framework is especially relevant in the context of ethnobiology 5 (Wyndham *et al.* 2011; Wolverton 2013) by bringing together applied questions about the negotiation of practices with basic research regarding cognitive processing, cultural transmission, and biocultural evolution. Rather than regarding applied and basic research in ethnobiology as competing for attention, our proposed framework shows how they can complement each other by increasing reflexivity about the structure of local knowledge in negotiations of issues, such as biodiversity conservation or food security.

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Compliance with Ethical Standards

Conflict of Interest The authors declare they have no conflict of interest.

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