Ulysses Paulino Albuquerque
Patrícia Muniz de Medeiros
Alejandro Casas *Editors*

Evolutionary Ethnobiology

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Editors
Ulysses Paulino Albuquerque
Departamento de Biologia
Universidade Federal Rural de Pernambuco
Recife, Brazil

Alejandro Casas
Instituto de Investigaciones en
Ecosistemas y Sustentabilidad
Universidad Nacional Autónoma de México
Morelia, Michoacán, Mexico

Patrícia Muniz de Medeiros
Institute of Environmental Sciences
and Sustainable Development
Universidade Federal do Oeste da Bahia
Barreiras, Pernambuco, Brazil

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Contributors

Ulysses Paulino Albuquerque Laboratory of Applied and Theoretical Ethnobiology, Department of Biology, Federal Rural University of Pernambuco, Recife, Pernambuco, Brazil

Wendy Marisol Torres-Avilez Laboratory of Applied and Theoretical Ethnobiology, Department of Biology, Federal Rural University of Pernambuco, Recife, Pernambuco, Brazil

José Blancas Centro de Investigación en Biodiversidad y Conservación, Universidad Autónoma del Estado de Morelos, Cuernavaca, Morelos, Mexico

Letícia Zenóbia de Oliveira Campos Laboratory of Applied and Theoretical Ethnobiology, Department of Biology, Federal Rural University of Pernambuco, Recife, Pernambuco, Brazil

Alejandro Casas Instituto de Investigaciones en Ecosistemas y Sustentabilidad, Universidad Nacional Autónoma de México, Morelia, Michoacán, Mexico

Andrew C. Clarke McDonald Institute for Archaeological Research, University of Cambridge, Cambridge, UK

Margarita Paloma Cruz Colombian Society of Ethnobiology, Bogotá, Colombia

Carmen J. Figueredo Instituto de Investigaciones en Ecosistemas y Sustentabilidad, Universidad Nacional Autónoma de México, Morelia, Michoacán, Mexico

Susana Guillén Estación Científica La Malinche, Universidad Autónoma de Tlaxcala, La Loma Xicohtencatl, Tlaxcala de Xicohténcatl, Tlaxcala, Mexico

Julie A. Hawkins School of Biological Sciences, University of Reading, Reading, Berkshire, UK

Washington Soares Ferreira Júnior Laboratory of Applied and Theoretical Ethnobiology, Department of Biology, Federal Rural University of Pernambuco, Recife, Pernambuco, Brazil

Ana Haydée Ladio Laboratorio Ecotono (Ecotono Laboratory), INIBIOMA—Instituto de Investigaciones en Biodiversidad y Medio Ambiente (Biodiversity and Environmental Research Institute), CONICET-Universidad Nacional del Comahue (National University of Comahue), Centro Regional Universitario Bariloche, Quintral, San Carlos de Bariloche-Río Negro, Argentina

Patrícia Muniz de Medeiros Ethnobiology and Human Ecology Group, Center of Biological and Health Sciences, Universidade Federal do Oeste da Bahia, Barreiras, Bahia, Brazil

Joabe Gomes de Melo Federal Institute of Alagoas - Matriz, Campus Maragogi, Maragogi, Alagoas CEP, Brazil

André Luiz Borba Nascimento Laboratory of Applied and Theoretical Ethnobiology, Department of Biology, Federal Rural University of Pernambuco, Recife, Pernambuco, Brazil

Fabiola Parra Centro de Investigaciones de Zonas Áridas, Universidad Nacional Agraria la Molina, Lima, Peru

Andrea Pieroni University of Gastronomic Sciences, Pollenzo, Cuneo, Italy

Marcelo Alves Ramos Department of Biological Sciences, University of Pernambuco, Nazaré da Mata, Pernambuco, Brazil

Selene Rangel Instituto de Investigaciones en Ecosistemas y Sustentabilidad, Universidad Nacional Autónoma de México, Morelia, Michoacán, Mexico

Victoria Reyes-García Institució Catalana de Recerca i Estudis Avançats (ICREA), Barcelona, Spain

Institut de Ciència i Tecnologia Ambientals, Universitat Autònoma de Barcelona, Bellaterra, Barcelona, Spain

Nina Rønsted Natural History Museum of Denmark, University of Copenhagen, Copehagen, Denmark

Flávia Rosa Santoro Laboratory of Applied and Theoretical Ethnobiology, Department of Biology, Federal Rural University of Pernambuco, Recife, Pernambuco, Brazil

C. Haris Saslis-Lagoudakis Natural History Museum of Denmark, University of Copenhagen, Copehagen, Denmark

Gustavo Taboada Soldati Department of Botony, Institute of Biological Sciences, Federal University of Juiz de Fora, Juiz de Fora, Minas Gerais, Brazil

José Ribamar Sousa Júnior Laboratory of Applied and Theoretical Ethnobiology, Department of Biology, Federal Rural University of Pernambuco, Recife, Pernambuco, Brazil

Fábio José Vieira Department of Biology, State University of Piauí, Picos, Piauí, Brazil

Chapter 1
Evolutionary Ethnobiology

Ulysses Paulino Albuquerque, Patrícia Muniz de Medeiros, and Alejandro Casas

A number of concepts and views about ethnobiology can be found in a vast literature produced during the last decades. A newcomer scholar in the field often feels trapped in a maze of concepts and assumptions that generate more questions than explanations. This is commonplace for a discipline that is growing, defining its nature, and assessing its interests, research methods, and connections with other scientific areas overlapping questions and fields of interest. No science constructs and matures without continually questioning its own bases and premises looking for its own identity. In addition, some research fields have more than one identity, and this is the case of Ethnobiology. This field convenes and joins researchers with various theoretical and epistemological backgrounds. The complexity of ethnobiological problems require the working together of a high diversity of perspectives, methods and viewpoints for approaching theoretical questions and applied perspectives in common.

This text is a modified version of Albuquerque and Medeiros (2013).

U.P. Albuquerque (✉)
Laboratory of Applied and Theoretical Ethnobiology, Biology Department,
Universidade Federal Rural de Pernambuco, Rua Dom Manoel de Medeiros, s/n,
Dois Irmãos, Recife, Pernambuco 52171-900, Brazil
e-mail: upa@db.ufrpe.br

P.M. de Medeiros
Ethnobiology and Human Ecology Group, Center of Biological and Health Sciences,
Universidade Federal do Oeste da Bahia, Estrada para o Barrocão, s/n,
Morada Nobre, Barreiras, Bahia 47805-100, Brazil

A. Casas
Instituto de Investigaciones en Ecosistemas y Sustentabilidad (IIES),
Universidad Nacional Autónoma de México, Campus Morelia,
Antigua Carretera a Pátzcuaro 8711, Col. San José de la Huerta,
Morelia, Michoacán 58190, Mexico
e-mail: acasas@cieco.unam.mx

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Anderson (2011:1) defines ethnobiology as "the study of the biological knowledge about certain groups of plants and animals and their interrelationships." In order to approaching the interrelationships, it is necessary an ecological perspective. Hurrell and Albuquerque (2012) stated that ethnobotany can also be understood as a part of ecology.[1] The same can be said to ethnobiology; and also it is possible to say that ecology may be part of ethnobiology. At the end of the day both definitions visualize that ecosystems and ecological problems cannot be understood without influence of humans, and similarly, human cultural and social problems cannot be understood without considering ecosystems and ecological interactions. In fact, nowadays making reference to social-ecological problems is an explicit recognition of this intimate interaction (Berkes and Folke 1998; Folke 2004; Walker et al. 2004). Ethnobiology is eminently a social-ecological science, concerned with interrelationships between people and their biological resources (plants, animals, and other organisms). It deals with interaction between the different biotic components and frequently also with abiotic components of ecosystems and their dynamic relationships occurring in time and space.

It is not unusual for us to consider the relationships between people and biological resources from an ecological perspective. The conventional ecological science (the modern ecological research) insufficiently considers human aspects as topics of theoretical interest. The classic notion of ecology, dissociated from human beings, may constitute a source of bias, given that humans interfere directly in ecological and evolutionary processes. Similarly, sociological or anthropological approaches decontextualized of ecological systems and interactions do not allow a holistic comprehension of the real problems. According to Fritjof Capra (2004), the contemporary environmental crisis is the crisis of a conception of environment dissociating nature from society. Therefore, the synthetic approach of social and ecological issues is not only a theoretical challenge, but also an applied necessity. As social-ecological science, ethnobiology may make important contributions in this direction.

Ethnobiology has been predominantly focused on the utilitarian role of plants and animals (Toledo and Alarcón-Cháires 2012). The most common approach in ethnobiology today is to focus on lists of useful plants and animals, which leaves out attempts to understand the complex relationships between people and biological resources but fails to identify patterns in the use of such resources. This approach belongs to the history of ethnobiology (strongly influenced by an economic and perhaps taxonomic perspective because of the preoccupation with the listing of organisms). It is an important step of Ethnobiological research because it records knowledge that may otherwise soon be lost by communities and because it aids in the search for "new products". This approach on the other hand is insufficient to for the theoretical foundations of ethnobiology, that are indispensable for any scientific field. Although concerns and descriptions of utilitarian aspects are undoubtedly part of ethnobiology, these topics and approaches do not define the body of a science. Constructing a social-ecological science like ethnobiology requires much more theory and methods.

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[1] More specifically, the authors discuss a biocultural ecology to account for the human dimension in the traditional ecological approach.

The broad concept of ethnobiology presented above does not fully meet the current need for including concepts of ecology and evolution in ethnobiology. Although some researchers advocate that it is redundant to address ecology and evolution in ethnobiology, we doubt whether these researchers are using these perspectives in their work at all. On the one hand, these concepts are used extensively as theoretical scenarios for interpreting and guiding research (as in the case of plant management and domestication studies; see, for instance, Casas et al. (2007). On the other hand, they appear to be completely forgotten in many studies. Johns (1990) presents interesting ideas and approaches, from an ecological and evolutionary perspective, for understanding the use of medicinal plants and food by humans. Unfortunately, very few researchers consider this perspective in their investigations. Even so, Johns (1990) strongly influenced the construction of a theoretical scenario accounting for an evolutionary view on health and disease (see Fabrega Jr 1997).

What may then justify this lack of ecology and evolution in ethnobiology studies, especially in countries where the science is practically performed by professionals from the natural sciences? We are not arguing for the exclusion of the humanities and social sciences, given that humans are a cultural species. Belonging to a cultural species does not eliminate our biological-evolutionary trajectory. Our social behavior is also a product of biological evolution, and our cognitive, social and cultural components were primarily responsible for our dominance over most other species. What we are and how we act are influenced by a biological-cultural complex. Ecological and human cultural processes influence to each other and delineate crucial aspects of nature of humans and humanized nature. It is not our intention to rekindle here the debate about human behavior, i.e., whether our choices and tendencies are biologically determined or whether they are the result of the culture in which we find ourselves. We have already outgrown this debate by accepting that, in the case of our species, ecological and human cultural processes are strongly linked in an evolutionary trajectory. We will not advance in our understanding of the relationships between people and nature by ignoring either the animal (biological-ecological) nature of humans or the natural context of human culture. We consider it is possible to substantially advance in constructing ethnobiological science by drinking at the fountains of different areas that have been busy understanding human beings from an ecological and evolutionary perspective.

The ecological approach seeks to account for the current aspects that explain the relationship between people and nature, considering the interrelationships that people establish with different natural resources and ecosystems in space and time. This approach asks how people behave in different environments and how they deal with diversity, in addition to asking what determines the properties of social-ecological systems. The evolutionary approach also studies current behaviors, but with the intent of trying to unravel which pressures have shaped us, i.e., how and why certain traits or characteristics emerged.

Thus, we have a challenge ahead of us: to define the field of ethnobiology that seeks to combine ecology and evolution in understanding how people from different cultures cope with (influencing and being influenced by) the natural resources in different environments given the ecological, evolutionary, and cultural pressures to which our species is subject. It is important to point out that the evolutionary branch of ethnobiology may consider two aspects of evolution: the biological evolution and the cultural evolution. Although they may follow similar trajectories, the first one requires genetic and/or epigenetic changes while the second can be performed in a single generation, by means of environment-influenced behavioral changes. Thus, we call evolutionary ethnobiology the branch of ethnobiology that studies the evolutionary histories of human behavioral patterns and human understanding about biological resources (about both cognition and behavior), considering the historical and contemporary aspects that influence these behaviors at both the individual and societal levels.[2] An ethnobiology that adopts this perspective will routinely address concepts such as adaptation, adaptability, evolutionary trends of traits, and phylogeny.

The first two basic premises are clear[3]: (a) that human behavior, variable between pairs of the same group and related to the use of natural resources, evolves by means of the selection of traits that confer adaptive advantages; and (b) that large behavioral variability should be inherited, not necessarily on a genetic basis, but primarily by cultural transmission. In a single human population, distinct individuals may have different strategies for dealing with natural resources and different ways of interacting with other members of the same population that influence their decisions and their behavior. Our understanding of the relationship between people and natural resources can very much benefit from the incorporation of all concepts built over the years in other areas and from methodological approaches that assess the role of an individual and the influence of different social-environmental contexts in structuring our ecological understanding.

Ecological and evolutionary perspectives are undoubtedly important theoretical issues for making ethnobiology a holistic science. Evolutionary ethnobiology accounts for social, cultural, ecological, and evolutionary issues derived from the interactions between humans and biotic components of ecosystems. An evolutionary ethnoecological perspective allows including the modelling of ground, water, and other abiotic elements. With this perspective, throughout this book we review the ecological and evolutionary consequences of interactions between humans and nature. As discussed in Chap. 4 by Casas et al. (2015), evolutionary ethnobotany is a research approach that combines different perspectives from a broad spectrum of disciplines. Its general purpose is analyzing the evolutionary processes derived from interactions between humans and plants, animals, fungi and a broad spectrum of microorganisms, which may have consequences on: (1) organisms

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[2] This perspective makes sense in light of Niche Construction Theory, which is still neglected and not well known. All living beings (including humans), through their activities and decisions, modify their own niches and those of other organisms. In altering niches, organisms would also be altering natural selective pressures (see Odling-Smee et al. 2003).

[3] These premises are inspired by the fundamental ideas of behavioral ecology (see Jeanne 1998). However, in behavioral ecology, a behavior is considered adaptive when it generates a positive impact on the fitness of its descendants. It is difficult, but not impossible, to measure such an impact when we work through the issues of interest in ethnobiology.

interacting with humans, (2) humans themselves, their culture and societies, and (3) ecosystems and landscapes. This perspective indicates that evolutionary ethnobiological questions are eminently social-ecological complex problems and their understanding therefore requires interdisciplinary research approaches.

Examining the interrelationships between people and nature and considering the forces that helped shape this complex relationship will help us undoubtedly to moving forward in building theories in ethnobiology.

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Chapter 2
Ecological-Evolutionary Approaches to the Human–Environment Relationship: History and Concepts

Patrícia Muniz de Medeiros, Marcelo Alves Ramos, Gustavo Taboada Soldati, and Ulysses Paulino Albuquerque

2.1 Introduction

Ethnobiology is characterized by a substantial diversity of theoretical frameworks and fields of knowledge. Insofar as this diversity makes ethnobiology a complex research area, it also expresses an important concern how can other fields of knowledge contribute to the strengthening of ethnobiology? In this chapter, we discuss how different theories concerning ecological and evolutionary understanding of social-ecological systems can be useful in studying or interpreting ethnobiological questions. The history and the concepts that we present are understood as part of the historical construction of disciplines such as ecological anthropology and human ecology. We do not present this history and these concepts as if they were part of a trajectory followed by ethnobiology but as a set of factors that influenced different researchers at various points in time.

P.M. de Medeiros (✉)
Ethnobiology and Human Ecology Group, Center of Biological and Health Sciences,
Universidade Federal do Oeste da Bahia, Estrada para o Barrocão, s/n, Morada Nobre,
Barreiras, Bahia 47805-100, Brazil
e-mail: patricia.muniz@gmail.com

M.A. Ramos
Universidade de Pernambuco, Campus Mata Norte, Rua Amaro Maltez, 201, Centro,
Nazaré da Mata, Pernambuco 55800-000, Brazil

G.T. Soldati
Department of Botany, Institute of Biological Sciences, Federal University of Juiz de Fora,
Av. José Lourenço Kelmer, s/n, São Pedro, Juiz de Fora, Minas Gerais 36036-900, Brazil

U.P. Albuquerque
Laboratory of Applied and Theoretical Ethnobiology, Biology Department,
Universidade Federal Rural de Pernambuco, Rua Dom Manoel de Medeiros, s/n,
Dois Irmãos, Recife, Pernambuco 52171-900, Brazil

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In the chapter's first part, we rehabilitate several historical concepts related to the contribution of ecological and evolutionary approaches to the understanding of the human–environment relationship, particularly those concepts that originate in ecological anthropology and human ecology. To better understand this relationship, we present examples of ethnobiological investigations and the respective philosophical currents adopted (even implicitly) by their authors. In the second part, we address the interactions of ethnobiology with other disciplines, particularly environmental psychology and evolutionary ecology.

We understand that an evaluation of the human–environment relationship in this manner implies the adoption of a materialistic outlook. However, in adopting this perspective, we remain unwilling to reduce the complexity of that relationship to explanations of a biological nature while neglecting the influence of cultural factors. In truth, this discussion has a long history and has been controversial. However, we believe that this materialistic outlook can improve our understanding of part of the phenomenon and contribute to the evolution of a theory of the human–environment relationship.

2.2 The Human–Environment Relationship and the Evolution of Ecological Anthropology

2.2.1 Determinism and Environmental Possibilism

Among the main discourses that attempt to explain the person–environment relationship, one finds environmental determinism (see Kormondy and Brown 1998; Hawley 1986). According to the determinist discourse, the environment is the primary force that defines human behavior[1] and possesses substantial power to modulate our cultural traits. This view discomfits the scientific community because, for example, it diminishes the importance of human choices. Therefore, over time, the determinist discourse has lost credibility and adherence in scientific circles.

Historically, within the humanities, social sciences, and ethnosciences, the term "determinism" has been distorted. It is not uncommon that studies that consider the environmental influence in any aspect of human life are labeled deterministic. When not provided with a scientific basis, this label can be dangerous because it typically marginalizes investigations that seek to understand the extent to which the environment can influence certain aspects of human behavior. Such marginalization can result in a lack of interest in the question of environmental influence, and consequently, reduce the çevel of knowledge generated regarding this topic.

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[1] As Mesoudi (2011) emphasized, human behavior is the performance of information that is genetic or acquired through individual or social learning. Thus, strictly speaking, behavior is not necessarily related to cultural information, that is, learned socially. However, to facilitate the presentation of positions, in this paper, the term "behavior" is only linked to information of cultural origin.

For instance, in ethnobiology, it is customary to investigate the factors that influence the selection of useful plants. For example, a determinist discourse would consider environmental questions to be key modulators of such selection. However, although current research seeks explanatory environmental factors (e.g., the availability of species, as discussed in other chapters of this book), it also considers that other factors influence the selection of natural resources, such as historical, symbolic, and religious factors. Thus, to investigate the role of the environment as another variable of importance cannot be labeled a deterministic approach. On the contrary, the failure to consider this variable can make the understanding of reality, at some point, reductionist.

Accordingly, we agree with Carvalho-Júnior (2011) when he considers it "incorrect, imprecise and semantically invalid to label a theory as deterministic when in fact it only emphasizes the influence of environmental factors without negating the role of other factors or human activity."

In fact, several non-deterministic ethnobotanical studies have demonstrated that an environment can exert a powerful affect on human behavior (see Ladio et al. 2007; Albuquerque et al. 2008), which prevents us from disregarding such influence. Thus, what lesson for an ethnobiological investigation can we learn from this theoretical approach, without accepting the theory in all of its ramifications? The environment can be one of the factors that influence human behavior with respect to the foraging of natural resources. Although the environment plays a highly important role in human behavior, we cannot deny that human choices as well as cultural and genetic factors also influence behavior.

Environmental possibilism emerged as an attempt to overthrow deterministic thinking as the only explanation for human behavior. In this view, the environment appears as a factor that limits the options of human populations but without determining behavior (Kormondy and Brown 1998). For instance, with respect to the employment of useful plants, the environment acts such that only the plants to which a given population has access could be used. However, from this accessible set, cultural choices could be made during the selection process.

Therefore, environmental possibilism helps us better understand the relationship between human beings and natural resources by revealing that environmental factors cannot be viewed as the only explanation of human behavior. That is, the environment offers human population opportunities to choose. However, other factors should also be considered, such as the history of natural resource exploration, human migration events, and the mechanisms of cultural transmission.

2.2.2 The Insertion of Evolutionary Thought in the Understanding of Cultures

Despite the conflicts between determinism and environmental possibilism, both discourses share an understanding of a one-way relationship between humans and the environment based on their common view of the environment as a primordial element in the construction of human behavior. Nevertheless, a number of schools of thought criticize this position and seek to understand culture as an active (not merely passive) element in the construction of social-ecological systems. Two exponents of this new approach were the Americans Leslie White (1900–1975) and Julian Steward (1902–1972), who were forerunners in the area of ecological anthropology. It is important to clarify that anthropologists had previously developed evolutionary explanations of culture. However, these explanations are based on an understanding of evolution as a continuous, unique, and linear progress (see Mesoudi 2011).

White was a student of Franz Boas (American, 1858–1942), one of the most important thinkers, who initially structured anthropology by developing historical particularism. According to Boas, cultures evolve in specific manners that are related to their history and environmental context. The same evolution does not occur in each society. Therefore, Boas proposed to understand each cultural system individually without the pretension of explaining general patterns. White rejected this proposal and sought to understand evolution as universal. White's ideas were essentially materialistic as a result of his exposure to the social theory of Karl Marx. Thus, he proposed a structured concept of culture according to which culture consists of three spheres: ideological, social, and technological. These spheres are not equally important: the third sphere is the driving force behind the creation of cultural patterns. As noted by Neves (2002), "life can be boiled down to the struggle for the capture of free energy. For him [White], culture is nothing more than a tool used by Homo sapiens to capture and to control energy available in systems and place it at the service of human societies." The universal law of cultural evolution can be reduced to the ability of cultural systems to transform energy into labor.

2.2.3 Cultural Ecology

Like White, Julian Steward was trained in historical particularism and was a materialist par excellence. However, he was influenced by physical geography. Steward's ideas contributed to the field of cultural ecology in which (as in White's view) certain cultural elements are considered to be the most important and most worthy of scientific attention. However, according to Steward, the cultural characteristics that require investigation are associated with production and thus reflect adjustments of a culture to the environment more than the culture's ability to transform energy. According to Neves (2002), "he [Steward] establishes a research focus, a "*cultural core*," cultural aspects more related to subsistence activities and to economic arrangements. The core is formed by all the religious, social, and political aspects that are more directly related to the support material bases of these societies." This component directly affects the environment, and the environment would be affected by it, whereas the other elements that constitute the culture of a social group, such as social elements, organization, beliefs, and ideologies, would be only indirectly influenced by the environment and vice versa. In this perspective, the idea of mutual influence (i.e., a "two-way street") between the environment and the culture is introduced into scientific circles. Additionally, Steward selected other, relatively more important environmental characteristics for investigation, for example, the quantity, quality, and spatial distribution of food supplies.

In addition to this "cultural core," and perhaps more clearly, cultural ecology is differentiated by its use of a method in which (a) above all the forms of local production and the environment should be analyzed and (b) it is necessary to understand how the strategies of environmental production and exploitation influence other cultural aspects. Accordingly, Stewart introduces an important cultural reading from the evolutionary perspective: an adaptive understanding of cultures with respect to the environment.

To illustrate the contribution to ethnobiological approaches of the mutual influence between environment and culture that emerges from cultural ecology, we can think about a hypothetical situation in which a given community has a set of plants or animals that are considered sacred and thus excluded from use. What are the ecological implications of this scenario? Possibly, the distribution of these species will change because their persistence is favored at the expense of other species. Primate hunting exemplifies this situation, in which, for example, chimpanzees are not hunted by certain human populations because of the physical resemblance of the animals with human beings or because of folk beliefs regarding the ancestry of human beings (Silva et al. 2005; Putra et al. 2008; Alves 2012).

The use and preference for specific biological resources can also result in the depreciation and subsequent decrease in the availability of these species over time. A number of studies conducted in the semiarid region of Brazil on the use of firewood as a household fuel source demonstrate that the collection behavior of this resource is selective to the extent that it prioritizes the species perceived as locally preferred (Ramos et al. 2008; Ramos and Albuquerque 2012). Thus, as cultural ecology advocates, the forms of exploitation of the resource, i.e., the specificities in the local practices of production and lifestyle maintenance, reflect cultural adjustments and should be targeted for investigation. This type of relationship can result in structural modifications in the populations and plant communities.

Thus, the primary lesson that cultural ecology can teach ethnobiologists (without requiring the acceptance of all of its ramifications) is that the environment must be understood as the result of its historic relationship with human populations that over the course of their evolution have used natural resources to supplement their cultural and substantive needs. This relationship is capable of shaping natural landscapes inasmuch as certain species are tolerated and others are overexploited.

In addition to introducing cultural ecology, Steward theorized regarding cultural evolution, arguing that cultures evolve along several different lines. That is, they are multilinear. Thus, cultural changes do not progress on a single evolutionary path, and cultural similarities between distant populations may be the result of convergence[2] (Netting 1986) or information diffusion.

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[2] In biological evolution, it is held that convergence occurs when natural selection favors the development of similar characteristics in certain organisms as solutions to problems created by similar environments (Freeman and Herron 2009).

An example of convergence applied to ethnobiological research relates to the botanical families that are primarily used as medicines in different parts of the world. The studies that perform this type of analysis seek to decrease the importance of family size because it is to be expected that large botanical families include more species of medicinal value than small families. Therefore, based on this idea of proportionality (and regardless of method) (see Bennett and Husby 2008; Weckerle et al. 2012), the fact that certain families, such as Asteraceae, Rosaceae, and Lamiaceae, are prominent in different parts of the world, whereas others, such as Poaceae, Cyperaceae, and Orchidaceae, are strongly underutilized (i.e., with apparently little medicinal use) becomes interesting (see Moerman 1979; Weckerle et al. 2012; Medeiros et al. 2013). These patterns converge in remote populations and can be related to the greater pharmacological efficiency of certain families compared with others. That is, this factor can influence human behavior and choices.

Thus, for ethnobiologists, multilinear evolution supports the understanding that certain human behaviors (which are often similar in distinct social groups that are isolated from one another) reflect general patterns and therefore can be predicted. However, in accepting this thesis, we must remember that the relationship between human beings and the environment involves highly complex processes that differ from culture to culture.

2.2.4 Systems Ecology and Neofunctionalism

The development of systems ecology has made new contributions to ecological anthropology (Kormondy and Brown 1998) by altering its focus from the study of culture to the study of populations. Systems ecology uses *cybernetics* to understand culture (i.e., traits, knowledge, behaviors, and social institutions) as self-regulatory and *homeostatic systems*, thus revealing a clear influence of the ecology of ecosystems. Cybernetics is a branch of systems theory that seeks to understand a series of systems with differing characteristics (i.e., mechanical, biological, and social systems). Cybernetic studies can examine the design and function of any system as well as analyze its forms of receiving, storing and processing stimuli or information. Homeostatic systems are systems that can maintain their state of equilibrium through self-regulation mechanisms. In this cybernetic context, the ideas of positive *feedback* (i.e., forces that catalyze changes in a culture) and negative *feedback* (i.e., forces that resist changes to domains of stability)[3] emerge (Marten 2001).

To illustrate several of these ideas, let us examine a hypothetical situation involving the medical system of Community X. Suppose that this community recognizes

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[3] Stability exists when a system is found in (or near to) a state of equilibrium (Holling 1973). A strong variation can transform a system from one state of equilibrium to another. Accordingly, negative *feedback* refers to forces that operate for the self-correction and maintenance of a system's equilibrium, whereas positive *feedback* refers to the forces that cause disequilibrium and change in the domains of stability (Keesing 1974).

a wide repertoire of animals and plants for medicinal purposes. This community maintains its curative practices and is isolated. Therefore, external information is not introduced into its reality. In our view, these circumstances characterize a closed system (see Garro 1986). Then, a migrant community (Community Y) establishes itself near Community X. The migrant community brings with it a new set of medical knowledge and practices. The two communities have sporadic contact. However, although Community X receives the novel information, it does not adopt any aspect of Community Y's medical system. In this case, Community Y's information arrives at Community X, which is now an open system by virtue of its contact with another system. However, because of the strong effect of negative *feedback*, this information cannot be incorporated by Community X and therefore does not alter its dynamic.

Later, increasing contact between Communities Y and X introduces a disease to the latter group. The disease was previously unknown and is introduced by the migrants. Community X is unprepared to cure this unknown, or at least untested, disease. However, Community Y, which has a history of living with the disease, possesses a list of medicinal plants that can cure it. Community X incorporates this knowledge. However, it does not fully incorporate Community Y's medical system. Over time, a hybrid of the medical systems of the two communities may form, which would represent an example of intermedicality (Soldati and Albuquerque 2012a). In a study on Fulni-ô Indians, Soldati and Albuquerque found that the local pharmacopoeia represented the merging of different medical traditions.

In this case, there is a partial input of information into the system, which is catalyzed by the impairment of negative *feedback*. However, if we consider that this information did not replace the previous medical system but only added to it, theoretically, the social system's stability domain would remain unchanged. We illustrated these ideas using a simple hypothetical situation. However, we should remember that the exchanges that occur between communities depend on the individuals who are part of these communities and the nature of the relationship between individuals. The exchanges do not depend only on the efficiency and usefulness of the information that is transferred, which makes this process even more complex.

We imagine now another situation. At another time, an area near the two communities is the target of a large urbanization project. Soon, the communities begin to have access to external resources, such as television, cooking gas, and health centers. The presence of this last element can cause individuals to relinquish their traditional healing practices and replace medicinal plants with allopathic medicines. In this case, positive *feedback* acts substantially more forcefully than negative *feedback*, and all of the new information is assimilated by the system. Because the incorporated content can be competitive by nature and not complementary, a social system substitution could occur, which would encourage a transition toward another stability domain, in this case, from a traditional to a Western medical system. In this hypothetical example, the domain change can be irreversible because after a certain time the knowledge of the practices related to the first domain may be lost. However, according to the anthropological and ethnomedical literature, there are actual cases in which the two systems can coexist, creating a dynamic in which the medical system is not necessarily transferred to another stability domain (Soldati and Albuquerque 2012a).

What determines whether the external information will be accepted is the resistance ability of the negative *feedback*. Not all more "efficient" or "higher quality" information will replace the old system. What is replaced depends on circumstances. For instance, even if in a given location the allopathic remedies have can cure more effectively than the medicinal plants and animals, the population may not accept, for example, Western medicine because of a belief that the failure to use sacred plants from the region can result in bad luck. In these cases, the role of myth, beliefs, and tradition is clearly an important buttress for negative *feedback*.

The neofunctionalists emerge as a response to the structural functionalism of Radcliffe-Brown (Kormondy and Brown 1998), who notes that the social level is a level of reality that differs from the biological level, and thus, social phenomena must be explained only within the social domain. This view is shared by many ethnobiologists, who explain culture through culture. That is, they believe that the use of natural resources can only be explained by cultural phenomena. In turn, neofunctionalism seeks rational explanations for apparently irrational behaviors and asserts that beliefs, ritual acts, and symbols can be explained by environmental factors.

Let us consider another example: in a given community, small-sized fish are considered to be sacred and may not be consumed until they grow. This prohibition may suggest an adaptive trait that facilitates the sustainable maintenance of the fish population by safeguarding young individuals and ensuring that they reach the reproductive stage and can procreate. Often, after the passing of generations, the practical reason for maintaining a certain behavior becomes lost. Thus, what remains in the culture to be transmitted is the myth regarding a behavior, for example, that "eating young fish brings bad luck." Although in practice it is difficult to demonstrate that a given taboo had an ecological rather than a purely religious or social origin, it is clear that restrictions on the use of resources exist in various cultures around the world that can promote the conservation and sustainable use of plants and animals (see Colding and Folke 2001).

Despite their substantial contributions, the neofunctionalists are a target of criticism with respect to their subject matter. One criticism is based on the neofunctionalist view that all human behaviors and practices are adaptive. To a degree, this view is shared by many ethnobiologists who advocate for the complexity of the relationships between human beings and natural resources, which often involve adaptive responses to ecological and evolutionary forces (Hurrell and Albuquerque 2012). Concerning the adaptability of human behavior according to environmental influences, we can cite the hypothesis of climatic seasonality, which predicts that individuals in environments that undergo a marked seasonality tend to use native and perennial resources locally considered to possess equal efficiency (whether they are herbs or woody plants) that during certain periods of the year are more abundant and more easily accessible (Albuquerque et al. 2005). If this hypothesis is true, it has important implications for seasonal environments. That is, from the biological viewpoint (i.e., therapeutic activity), it is more important to guarantee that individuals have access to the resources than more efficient resources.

Still more researchers accept the possibility of maladaptive behaviors, as can be perceived, for example, in studies that analyze the ancient practices and beliefs of certain social groups as elements that have no evolutionary rationale. In ethnobiology, direct empirical evidence that supports this affirmation seems not to exist. However, several studies reflect this opinion. For example, Tanaka et al. (2009) discussed the controversy regarding the use of complementary and traditional medicines, which are often practiced and shared between human populations without assurance of efficacy and safety in the treatment of disease. These authors noted examples of maladjusted and superstitious treatments that are curiously disseminated among human populations, such the use of drinks concocted from decomposing cobras to treat leprosy, the eating of vultures to treat syphilis, and the drinking of teas brewed from dog tails to heal victims bitten by these animals. Are these beliefs examples of maladaptive behaviors or does the use of resources without therapeutic proof hide evidence of adaptive traits that have not been identified by the research?

Another criticism of the neofunctionalists is that they consider the population rather than the individual to be the basic unit of study and disregard internal important variations in their analyses. The population was considered by the neofunctionalists to be an analytical unit because in their view the population, not the individual, adapts to the environment. This idea was criticized by other schools of thought, which believed that for adaptation to occur, changes must operate primarily individually. Applying this discussion to ethnobiology, we know that even the populations that share among themselves their practices and beliefs cannot be regarded as homogenous with respect to the adaptive behavior of their members. Individuals commonly exist who exhibit knowledge and practices not socialized with the social group in which they live.

In ethnobotany, the study of medicinal plants provides excellent evidence that the knowledge of a community cannot be viewed as homogeneous, particularly when we refer to the role of gender in the construction of this knowledge. Several studies have demonstrated the difference in knowledge between women and men by noting the exclusive use of certain plants by each of these groups. Typically, women rely on the richness of the noted plants, a practice that has been explained by the fact that women are more involved with the treatment of the illnesses of family members (Silva et al. 2011; Voeks and Leony 2004). Similarly, differences in knowledge between the genders do not occur only in terms of the diversity of recognized species. Often, these differences are expressed in terms of the specialization in the treatment systems used. For example, in Brunei Darussalam, in southeast Asia, women specialize in the treatment of spiritual diseases, whereas men specialize in diseases related to organic disorders (Voeks and Nyawa 2001).

2.2.5 Neo-Darwinism

The neo-Darwinist approaches reinforced the criticism of neofunctionalism regarding the unit of study. Neo-Darwinism is based on the theory of natural selection (see Dunbar 2012), according to which changes primarily act at the level of the individual or the gene, not directly on the population. Such an approach strongly resembles that of ethnobiological investigations in the sense that the individual is considered to be the analytical unit. (Thus, most of ethnobiological studies perform individual interviews.) Subsequently, population patterns are assessed through the collective analysis of individual results.

The primary data analysis techniques of ethnobotany provide an idea of how individual responses can be combined to create a population profile. These techniques include use value, relative importance, and the informant consensus factor and consider that a plant is locally important when it is recognized (or used) by a considerable number of individuals in a population but not necessarily by all individuals (Silva et al. 2010). These techniques aim to establish the most important species based on the informant consensus, whereby it is acknowledged that not all local individuals consider a given species to be important.

2.2.6 The Processual Approach

With the advancing development of ecological anthropology, the processual approach emerged. Processual anthropology avoids the conventional approaches that are primarily linked to negative *feedback*, i.e., the population characteristics that are maintained. This approach (i.e., the processual approach) is interested in the changes (see Orlove 1980). Its focus is the understanding of the processes of transformation as a population responds to environmental changes or increasing urbanization, such that now more than ever populations are considered to be open systems.

Ethnobotanical studies tend to follow this approach when seeking to observe if factors such as urbanization, access to allopathic medicines, and access to the media interfere with the knowledge of plants and the use of plant resources. Previous investigations studied relatively isolated communities to identify peculiar traits of knowledge regarding plants, which characterizes the classic stage of ecological anthropology. In our view, the preoccupation with transformations (e.g., insertions, deletions, and additions of information and practices) in ecological anthropology and ethnobotany is not only a new trend but also a perceived need in recent decades because the process of urbanization has affected even the most isolated communities.

From this perspective, the processual approach addresses the need to reconstruct certain concepts used in ethnobiological studies, such as those that identify communities as isolated, untouchable, and pure systems. We understand that recent studies on the dynamics of social-ecological systems in the contexts of urbanization (Hurrell and Pochettino 2014) or migration (Medeiros et al. 2012) can supply information relevant to understanding certain processes because such contexts display substantially more rapid and thus more easily captured changes than more stable social-ecological systems.

2.2.7 The Contribution of Other Disciplines to Understanding the Human–Environment Relationship

Other disciplines have made important contributions to ecological anthropology and human ecology that can similarly enrich ethnobiological research. Environmental psychology primarily addresses the perceptions of individuals of their environment (Kormondy and Brown 1998). This focus is important because perception precedes the use of resources and can influence the relationship of individuals with resources. Such studies can facilitate understanding human behavior with respect to the use of natural resources. Here, perception's psychological component is only one of the aspects to be investigated because perception also includes physical, psychological, and cultural elements (Bell 2001; Silva et al. 2010).

An example of the interface between environmental psychology and ethnobiology can be found in Almeida et al. (2008). Examining the use of traditional bonfires in the June celebrations of a rural community, for which the collection of timber resources is prohibited, these researchers determined that the population is willing to sustain this custom because it believes that such a tradition cannot be broken. Thus, despite the recognition of the difficulties of obtaining wood to make the bonfires, which was noted by 90 % of the studied respondents, the behavior has been adjusted over time, and currently the species of disturbed and anthropogenic areas are prime targets for collection, although the native forest resources continue to be preferred.

Similarly, evolutionary ecology had a strong influence on human ecology and several current ethnobiological approaches. According to this proposal, to understand the interactions between organisms and the environment, it is necessary to analyze the reproductive success of species, which is governed by natural selection. Evolutionary ecology influenced a large number of ecological anthropological and ethnobiological that sought to understand the person–environment relationship through the evolutionary perspective. Evolutionary ecology also encompassed studies on models of the optimal use of resources, which were later adapted by human ecology. Among these models, optimal foraging is emphasized. This model's fundamental principle is that organisms are selected over generations to achieve an optimal level of resource acquisition and use (Kormondy and Brown 1998). This model includes cost-benefit relationships, in which the costs are the loss of energy through foraging and the exposure to predators and the benefits are the acquisition of food or other resources, such as wood or medicinal animals (see Soldati and Albuquerque 2012b).

2.3 Final Considerations

In this chapter, we have sought to demonstrate that the relationship between human beings and biological resources can be interpreted in light of different ecological and evolutionary approaches. Therefore, in the development of ethnobiological investigations, it is important to know which theoretical bases are involved in the explanation of phenomena that ethnobiologists have registered. A single theory or discipline, evoked in isolation, cannot always afford the best explanation of a given phenomenon. Similarly, to adopt a theory in its entirety may not be useful in practical terms and may involve outdated scenarios.

Thus, what paths is one to follow if in developing an investigation one perceives that human behavior cannot be explained by environmental factors? The understanding of the role and the historical relationships within a group under study, of the mechanisms of cultural transmission and diffusion, and of the influence of issues of a genetic and cultural nature can be useful. There are multiple paths, and given ethnobiology's interdisciplinary character, one would not expect otherwise. Independent of the position that one adopts, one can drink at the fountain of all these theories, so to speak, and make conclusions that may be useful in developing an ethnobiological theory of ecological and evolutionary foundations (Hurrell and Albuquerque 2012):

1. "The relationship between human beings and nature is complex and often involves adaptive responses to ecological and evolutionary forces.
2. The behaviors and practices of human populations can be adaptive.
3. The environment can be assumed as a limiting factor but not as determinant of human behavior.
4. The perception of nature is a process with structural (i.e., biological/sensorial) and cognitive characteristics.
5. Traditional ecological knowledge emerges from the relationship between human beings and their surroundings and is manifested in acts and practices. This knowledge guides actions, which provide feedback regarding knowledge, which evolves".

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Chapter 3
Evolution of Humans and by Humans

Alejandro Casas, Fabiola Parra, and José Blancas

3.1 Introduction

Humans are the result of evolutionary processes operating through principles similar to those that originated all species populating the Earth. This is an extraordinary conclusion derived from scientific research during the last one and a half century, and that has had one of the greatest influences on human thinking (Bowler 1986; Jacob 1993). *Homo sapiens* is a unique species, as all species are, but it arose through mechanisms that operate on all species; these features confer to humans their uniqueness and at the same time, their generality, resulted from material processes occurring in all living things. But the interactions of humans with other living beings of their surrounding world have also determined evolutionary processes in both humans and the interacting species. Some of the evolutionary processes influenced by humans are incidental, derived unintentionally from cultural actions (for instance, evolution of weeds, arising of new varieties of pests and pathogens

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A. Casas (✉)
Instituto de Investigaciones en Ecosistemas y Sustentabilidad (IIES), Universidad Nacional Autónoma de México, Campus Morelia, Antigua Carretera a Pátzcuaro 8711, Col. San José de la Huerta, Morelia, Michoacán 58190, Mexico
e-mail: acasas@cieco.unam.mx

F. Parra
Centro de Investigaciones en Zonas Áridas (CIZA), Universidad Nacional Agraria La Molina, Camilo Carrillo 300-A, Lima 11, Peru
e-mail: fparra2@gmail.com

J. Blancas
Centro de Investigación en Biodiversidad y Conservación (CIByC), Universidad Autónoma del Estado de Morelos, Av. Universidad No. 1001, Col. Chamilpa, Cuernavaca, Morelos 62209, Mexico
e-mail: jblancas@gmail.com

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resistant to herbicides, insecticides or antibiotics; see Baker 1974; Rindos 1984; Ridley 2003; Futuyma 2013). Nevertheless, consciousness, symbolism, and intentionality of their actions (Ehrlich 2000) are crucial aspects of human natures, and humans have also guided intentional evolutionary processes through deliberate management and transformation of ecosystems and organisms these ecosystems contain. These are the processes of evolution associated to domestication of ecosystems and landscapes, as well as plants and animals used by humans from ancient times with a wide variety of purposes (Schwanitz 1966; Harlan 1975; Hawkes 1983; Casas et al. 1997). But the processes have also included fungi and microorganisms that have been less frequently analysed, however their high biological and economic importance. These are also evolutionary processes occurring at landscape level, resulting from modelling the physiognomy, the components and functions of ecosystems according to human needs and values. And all these processes are the main study matter of evolutionary ethnobotany, when directed to study plant evolution, evolutionary ethnobiology when including plants and animals, fungi and microorganisms, and evolutionary ethnoecology when including also deliberate modelling of landscapes including biotic and abiotic elements.

3.2 Evolution of Humans

The modelling of the modern scientific idea about human origins and evolution has among its earliest formal expressions in the “Systema Naturae” published by Carolus Linnaeus in 1758 (Linnaeus 1758). In that work, Linnaeus names humans as *Homo sapiens*, considering them animals, which are classified into the group of Primates together with monkeys and apes. Such crucial idea was published in an epoch in which, according with the Judeo-Christian and several religions, humans should be considered apart from the rest of “creatures” since them resemble the image of god and vice versa (Smith 2009).

Nearly one century later, in “The Origins of Species”, Charles Darwin (Darwin 1859) concluded that his theory about the origin, diversification and evolution of living beings might help to clarify the origins and history of humans themselves. With this reasoning, Darwin confirmed the consideration of the non-exclusivity of humans as living things and went beyond Linnaeus, looking for an explanation about their origins and transformations throughout time. Later on, in “The Descent of Man”, Darwin (1871) published a more explicit and greater treatment of his conception about human evolution, which was the basis of the present scientific theory for explaining the origins of humans from other ancestral organisms, in the context of natural history.

A series of discoveries progressively supported with material evidence the fact that the present humans evolved from previous relatives, all of them grouped together within the Primates. One of the first meaningful discoveries was that of 1856, during the time Darwin wrote “The Origins of Species”, and that was carried out by Johann Carl Fuhlrot and Hermann Schaaffhausen, who found the remains of an interesting ancient human-like organism in the Neander Valley, Germany. Those remains belonged to organisms that are currently named *Homo neanderthalensis*. Later on, fossils similar to those from Neander were discovered in La Chapelle aux Saints, France, by Bardon et al. (1908), and during the twentieth century numerous remains of these humans were uncovered in Europe, Middle East, China and Siberia (Hublin; 2009; Tattersall and Schwartz 2006).

By the end of the nineteenth Century, Eugene Dubois (Dubois 1894) reported the finding of a human-like fossil apparently older than the Neanderthal Man. The discovery occurred in Trinil, Java, and the remains were named *Pithecanthropus erectus*. Later on, during the 1930s G. H. von Koenigswald in Java and Davidson Black in Beijing found fossils similar to those found by Dubois and the latter was considered by Black (1931) to belong to *Zynjanthropus pekinensis* (Black 1931; Antón 2003). During the 1950s Louis and Mary Leakey and their research team found the oldest remains of relatives of this human-like fossil in Tanzania, concluding that both *P. erectus* and *Z. pekinensis* were related and similar to the fossils they found in Africa, naming all of them *Homo erectus* (Leakey et al. 1964; Leakey 1996) a binomial that is currently used.

During the 1920s and 1930s palaeoanthropologists were particularly prolific in discoveries, reporting a great variety of fossils of several species of African human relatives that were grouped into the genus *Australopithecus* and later on, some of them into the genus *Kenyanthropus*. Particularly relevant were the discoveries of the "Taung boy" by Raymond Dart in 1924 (Dart 1925), which was named *Australopithecus africanus*, as well as the larger crested skull of *Australopithecus robustus* reported by Robert Broom (originally with the name *Paranthropus robustus*; Broom 1938, 1950; Broom and Robinson 1949).

During the 1960s the most outstanding discovery was the finding of *Homo habilis* by Louis and Mary Leakey team in 1964 (Leakey et al. 1964). At this point of the history of palaeoanthropology, the analysis of trends of skull volume, the degree of perfection of the erect position and the use of tools became the most relevant signs for identifying the evolutionary trends or organisms towards current humans. For this reason, the discoveries of *Homo habilis* and tools fabricated by this humans' relative are particularly important. *Homo habilis* had more perfect erect posture than any species of *Australopithecus*, and the manufacture of stone tools evidences complex processes involving designing of actions. Use of tools is not a feature exclusive of humans, but manufacturing tools it is. The design of actions according to a purpose is what philosophers have defined as *praxis* (Sánchez-Vázquez 2003), which is widely considered a feature dramatically more dimensioned in humans than in any other animal species. Following this thinking, the concept of "human" goes beyond the species *Homo sapiens*. Organisms defined as "humans" are properly those designing actions (Harari 2014). The most ancient evidence of such process is hitherto associated to manufacturing of tools. It is generally accepted that *Homo habilis* definitely fabricated tools (the Oldowan tools) nearly 1.7 millions of years ago, but in addition it has been discussed evidence of bones apparently scratched by tools associated to *Australopithecus grahi* at Bouri, Ethiopia some 2.5

millions of years ago (de Heinzelin et al. 1999). The latter would be the oldest evidence of human way of making and using tools.

Homo erectus was discovered previously to *Homo habilis*, and although both species coexisted at some time, *Homo erectus* continued on Earth for much longer time than *Homo habilis*. Two aspects are relevant characteristics of *Homo erectus*. One of them is their more perfect erect posture compared with *Homo habilis*, the perfection of processes for manufacturing tools, the deliberate use and management of fire, and the larger volume of their skull size relative to their whole body size. The second relevant aspects is their great migratory activity, apparently favoured by the use of tools and fire, which allowed what is known as the first colonisation of Eurasia by *Homo*, or the First Out of Africa. According to Leakey (1996) and Fleagle et al. (2010), the ancient *Homo erectus* originated in Africa, and the fossil records found in Java and Beijing are signs of such extraordinary migration capacity.

The most spectacular finding of palaeoanthropology and possibly one of the most important discoveries of the twentieth century was "Lucy" the fossils of *Australopithecus affarensis* reported by Donald Johanson (Johanson and Maitland 1981). Lucy was not the oldest nor the closest relative of modern humans, but the most relevant aspect of this finding was that nearly 40 % of the skeleton of Lucy was recovered. This fact allowed corroborating and developing hypothetical allometric relations deduced from previous studies, which were of great value during the later decades for more precise interpretation and reconstruction of palaeoanthropological remains.

During the 1990s and the beginning of the twenty-first century the palaeoanthropology increased the finding of a great amount of fossils and information about the high diversification of human relatives such as *Kenyanthropus*. The discovery of *Orrorin tugenesis* by Brigitte Senut and Martin Pickford in the year 2000 (Senut et al. 2001), is also significant, since this fossil appears to be the oldest relative of humans (6 millions of years old approximately) hitherto.

The discovery of fossils and the development of dating techniques based on radioactivity and molecular clocks have significantly influenced our knowledge about human evolution and its relation to Primates (Fig. 3.1). Radioactive dating generally allowed identifying the oldest relatives of humans documented until the present (*Orrorin tugenensis*), lived on Earth approximately 6 millions of years ago. In addition, that several species of the genus *Australopithecus* diversified in Africa within a broad period, from approximately 4.2 to nearly 1.4 millions of years ago. *Homo habilis* populated the current territory of Tanzania from 2.3–1.6 millions of years ago, coexisting with several species of *Australopithecus*. Then, *Homo erectus* arose in Africa from 1.8 millions of years to 300,000 years ago having coexisted with several species of *Australopithecus* and *Homo habilis*. The First Out of Africa started very early after *Homo erectus* appeared on Earth. *Homo erectus* has been recognised at the basis of divergent lineages of the genus *Homo*, including *Homo neanderthalensis*, which lived in Asia and Europe from approximately 250,000 to 30,000 years ago. And *Homo sapiens*, our species, originated in Africa nearly 200,000 years ago and populated practically all corners on the Earth (the Second Out of Africa by *Homo*) throughout this relatively short period.

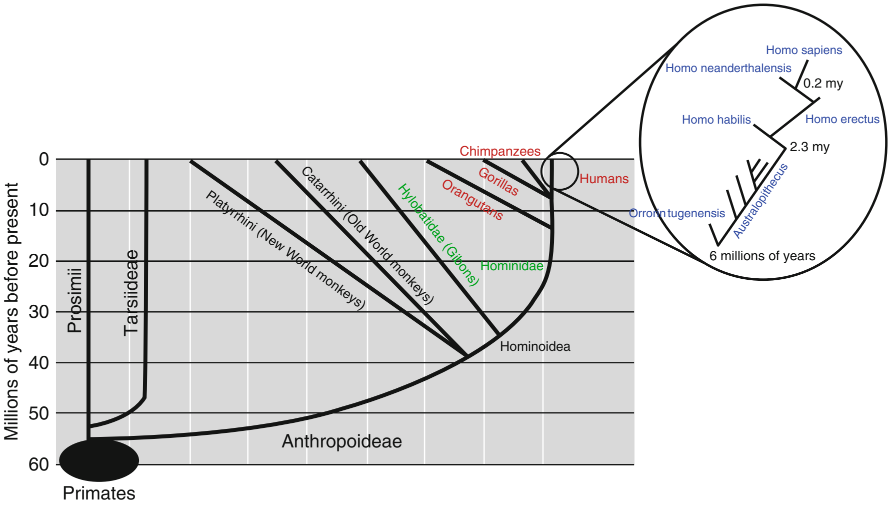

Fig. 3.1 Panorama of human evolution within the context of the general phylogeny of Primates. At the basis of the Figure, the *black ellipse* represents the ancestral organisms preceding Primates, which are out of the analysis of this study. Within the Anthropoideae, the Hominidae diverged from the Hylobatidae some 35 millions of years (my) ago. Within the lineage of Hominidae, Orangutans diverged some 12 my ago, Gorillas some 9 my ago, and Chimpanzees nearly 8 my ago. Humans lineage includes the most ancient fossil of *Orrorin tungenensis* (6 my old), several species of Australopithecus, and several species of Homo, a genus originated 2.3 my before the present. *Homo sapiens*, the species of current humans, appeared on the planet approximately 200,000 years ago somewhere in central Africa, and all human races and variants recognised at present have common ancestors in the earliest African populations of *Homo sapiens*

Homo sapiens and *Homo neanderthalensis* coexisted and apparently interbred from 200,000 and 30,000 years ago (Harvati and Harrison 2006). Actually, for long time both taxa were motive of discussion about their belonging to one single or two species. However, after a series of studies starting by Svante Pääbo of the Max Planck Institute and then other numerous scholars reconstructing mtDNA from remains of Neanderthal bones, it is now clearer that the two species hypothesis is the correct (Caramelli et al. 2003).

It is also clear that all humans that currently populate the planet derived from the earliest *Homo sapiens* populations originated in Africa. Several research groups, but outstandingly that of Luigi Luca Cavalli-Sforza (Cavalli-Sforza et al. 1994; Li et al. 2008; Creanza et al. 2015), have investigated through different biochemical and molecular markers the relation of genetic similarity, cultures and spatial distribution of humans. These scholars have documented with an increasing precision the fascinating relation of genes, populations and languages (phonems, see Creanza et al. 2015), and this approach has been particularly powerful for answering the question about time of genetic and cultural differentiation and occupation of different areas of the planet. Together with archaeological records, molecular biology has allowed a more precise panorama about the Second "Out of Africa".

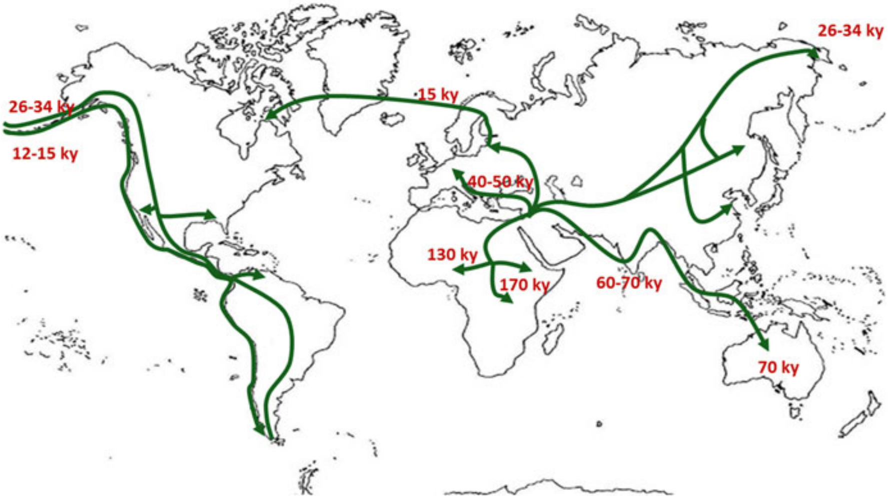

Fig. 3.2 Several routes of dispersal of *Homo sapiens* throughout the World, and their antiquity in thousands of years (ky) before present, according to archaeological radioactive and mtDNA dating (based on Endicott et al. 2009; Pringle 2011). It can be appreciated the relatively rapid diffusion of current humans throughout Africa and tropical Asia, whereas colonisation of Europe and notoriously Beringia took longer time, most probably due to technology needed to survive in such extreme climate conditions. The colonisation of the Americas was the most recent process of colonisation, and the study of this process helps understanding the rapidness of developing of human culture diversification

Based on mtDNA and archaeological remains Endicott et al. (2009), estimate that the earliest populations of *Homo sapiens* started to diverge in Africa 170,000 years ago (Fig. 3.2). Lineages populating southern Asia and Australia diverged from humans at the Middle East some 60,000–70,000 years ago, whereas the lineages that populated Europe diverged from humans that populated the Middle East between 40,000 and 50,000 years ago. Two lineages diverged from human populations of Central Asia, one of them occurred 26,000–34,000 years ago and leaded humans to Beringia and then to populate the Americas. McEvoy et al. (2011), Pickrell and Pritchard (2012), and other authors, using single nuclear polymorphism (SNPs), published finer UPGMA and Bayesian classifications of human genetic groups. This are great pieces of work confirming and making more precise the relation between cultural and linguistic groups of the World.

Recent information (Pringle 2011) confirms that the New World was populated from at least two main waves of human migrants from Beringia. One of them some 18,000 years ago and the others later on. This information also provides evidence that the occupation and diversification of cultures and languages of the Americas occurred in a relatively short time. According to Ethnologue (http://www.ethnologue.com/), at present, nearly 1250 languages are spoken in the Americas (207 in the US and Canada, 547 in Mexico and Central America, and about 400 in South America). This is a still amazing number of languages, but it was even higher some Centuries ago. It has been estimated that after the European Conquest, the indigenous populations dramatically decreased and the native cultures of the Americas felt down at least to one-half of those originally existing when Europeans arrived. These figures suggest that in about 20,000 years, in this area of the World became developed nearly 2500 languages, which in some way are representative of a similar number of cultures. Migration, isolation and eventual reencounters are all processes considered for explaining such a profuse linguistic and cultural diversification.

Such context of human diffusion throughout the New World, the historical waves of entrance from Beringia and later migrations from other regions of Asia and Europe configured a complex setting of cultural effervescence. This human cultural diversification included progressive innovation of management techniques to domesticate ecosystems and biotic resources contained on them. Evolutionary ethnobotany and ethnobiology deals with understanding such important processes.

3.3 Evolution of Management and Control of Ecosystems and Natural Resources

Homo sapiens and other human species were hunter and gatherers, or foraging organisms during most of their time on Earth (Leakey 1996). They designed and used tools maybe nearly 2.5 millions of years ago, apparently for cutting and scratching carrion of animals consumed as food. Humans used and managed fire nearly 1.8 millions of years ago. These technological features meant revolutionary forms of interacting with nature, significantly controlling the high uncertainty of ecosystems and resources of environments where humans lived. Such technologies changed notoriously throughout time, every step presumably improving the human abilities for controlling that uncertainty.

It has been recognised, that after fabricating tools and domestication of fire, one of the most significant technological changes developed by humans was agriculture (Diamond 1997, 2002). Agriculture should be defined as the combination of two main forms of control of the surrounding world by humans: that involving ecosystems and that involving biotic resources (Casas et al. 1997). On one hand, agriculture involves management of ecosystems, for instance through clearing forests, tilling land, providing irrigation, and protection to the organisms of the managed system that are interesting to human purposes. On the other hand, agriculture involves the management of variation of the organisms they consider good resources. At one level, humans select species desirable and undesirable within the system and act in consequence let standing or removing them, respectively (Casas et al. 1996, 2007; Blancas et al. 2010, 2013). At a more specific level, humans have identified intra-specific variation and have decided to promote or remove the beneficial and the undesirable variants (Darwin 1859). This are the general principles of artificial selection as we discuss below, and the evolutionary process resulting from this and other evolutionary forces guided by humans has been called domestication.

Agriculture is therefore the expression of management of domesticated organisms in managed ecosystems (Casas et al. 1997). Use of tools and fire allowed managing and controlling in some way ecosystems for long time before practising domestication. Once people started combining ecosystem management for propagating domesticated organisms, agriculture arose.

Ecosystem management is older than domestication of organisms. How old it is? According to Rose-Innes (1972), peoples of Africa fired the savannahs deliberately some 50,000 years ago in order to increase abundance of some grasses particularly valued as cereals. The different responses of grass species to fire were of course result of natural selection. Anyway, this human action, favoured those species preferred by humans and this is the principle explaining the recurrent use of such technique. Similar forms of management exist at present in Africa and in other parts of the world, and these allow understanding the principles moving people to this kind of practices that are not agriculture nor simple gathering. At the end of the day, it is a way of transforming ecosystems to improve the conditions for gathering resources. In several parts of Mexico, people use to fire recurrently forest areas in order to favour the abundance of grasses for livestock. In addition, in the Mixtec region of Oaxaca and Guerrero people fire different types of forest to promote the abundance of the palm *Brahea dulcis*, which is used as an important resource for weaving handcrafts (Casas et al. 1994, 1997). Groube (1989) documented that in Papua, New Guinea there are archaeological remains indicating intensive felling of trees in the rainforest in order to favour abundance of plants that attracted herbivores for hunting, as well as species like yams (*Dioscorea* spp.) and taro (*Colocasia esculenta*), which were (and currently are) important edible resources for humans.

Another management principle for a similar purpose was documented by Julian Steward (Steward 1938) among the Paiute in California. Until the early twentieth century, this people constructed systems of channels, in order to irrigate grasslands areas, artificially increasing the abundance of *Cyperus* sp., a species used for its edible rhizome.

Numerous forms of management that are more than simple gathering but that are not *sensu stricto* agriculture, have been documented in several parts of the world. These management forms are called “incipient management” or “silvicultural management”, since these represent form of modifying populations and communities of wild plants. In Mexico, our research team has studied the spectrum of these forms of plant resources management that currently are carried out by indigenous peoples in several regions, but we have conducted deep studies particularly in the Balsar River Basin (Casas et al. 1996), and the Tehuacán Valley (Blancas et al. 2010, 2013). In the Tehuacán Valley we have documented that nearly 300 native plant species are silviculturally managed. And we have distinguished silvicultural management occurring in the forests in situ (in natural forests or in patches of forests associated to agroforestry systems), as well as management involving moving plants from their natural distribution areas to other transformed systems (ex situ management) (Fig. 3.3).

In situ management involves gathering, which may be simple gathering or simple harvesting of products from the wild. However, gathering commonly involves strategies, specialised techniques, social organisation and construction of agreements. All these practices indicate that gathering may be a real complex management strategy. In addition, these practices indicate that different forms of gathering may be identified within a gradient of complexity according to: (1) The energy invested

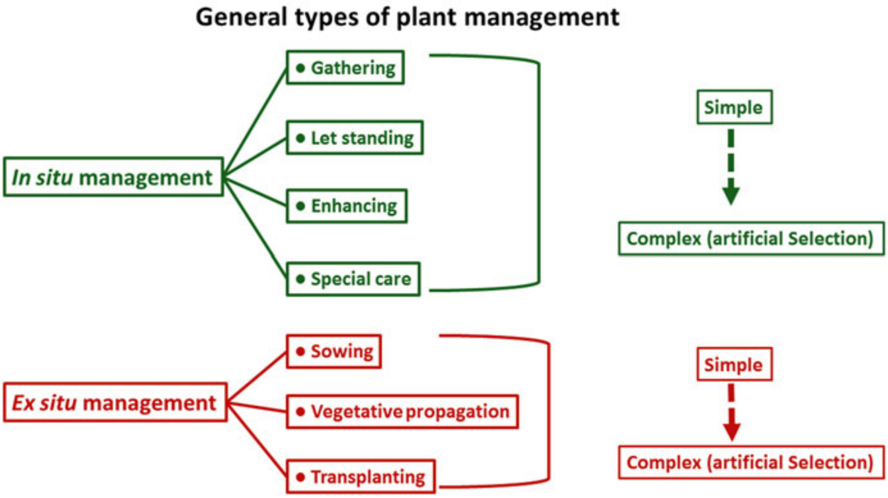

Fig. 3.3 General types of plant management documented in the Tehuacán Valley, Mexico, according to Blancas et al. (2010). The in situ management types occur in natural forests or patches of forest associated to agroforestry systems, whereas ex situ management types occur in artificial environments close to human settlements. Explanation of each management type in the text. All management types have been found to be in gradients from simple to complex forms depending on investment of energy, tool types, amounts of products and productivity (production per area managed). The most complex forms involve artificial selection

in the system (e.g. number of persons involved in the activity, hours of work invested per person, use of fossil energy); (2) the complexity of tools involved (from rocks or sticks to sawing machines or tractors); (3) the strategies followed (organised, planned, landscape ordinated, among others), (4) the areas under gathering, and the amount of products extracted in relation to those areas (Blancas et al. 2010, 2013). Similarly, other in situ managed practices may involve gradients of complexity. These is the case of tolerance, through which people let standing individuals of particular species or particular phenotypes of a given species (Casas et al. 1996, 2007; Parra et al. 2010, 2012). Another management form is the in situ promotion of abundance of those plant resources appreciated by people. The examples of intentional firing and irrigation referred to above are examples of this management form (Casas et al. 1996, 1997). Indigenous people also use to practice special caring actions for protecting species or phenotypes of wild plants interesting to them. They, for instance, protect particular plants against herbivores or pest attacks, frosts, excessive solar radiation or excessive shade (Blancas et al. 2010, 2013). All these forms of in situ management may have consequences on fitness of plants that are favoured or not; in other words, these practices may involve artificial selection and domestication processes occurring in management systems different to agriculture (Casas et al. 2007). We have documented effects of artificial selection in these in situ management systems on morphology, physiology, reproduction and population genetics, in herbaceous, shrubby and arboreal species. More details of these studies will be discussed in the Chap. 4 of this book.

We have documented other forms of managing wild plants: the ex situ management. Through these management forms people propagate in human-made environments, closer to sites of human settlements those plants that find in the forest and that are interesting for them. These are the cases mainly of edible, medicinal, crafting used and ornamental plants (Casas et al. 2007; Blancas et al. 2010, 2013). People move sexual and asexual propagules and cultivate them in the desirable environments, but they also move complete individuals (transplantation), more commonly of young plants, but in some cases also adult plants (Blancas et al. 2010, 2013). These are also forms of silvicultural management, since it is wild plants those that are managed (Casas et al. 1996, 2007).

What is more relevant for the moment to mention is that domestication may operate not only associated to agriculture, but also in other forms of ecosystem management. This fact, tested based on current ongoing processes of management (Casas et al. 2007; Parra et al. 2010, 2012), makes possible suggesting that not only ecosystem management preceded agriculture, but even domestication could have been associated to those pre-agricultural (or silvicultural) forms of management. Agriculture is, therefore, an advanced stage of the convergence of these two forms of managing ecosystems and organisms comprised within those ecosystems (Fig. 3.4). It is an (in reality there is a high diversity) advanced form of controlling environmental variables and organisms particularly adapted to those variables, as well as to human needs and values, as we will review in the following section.

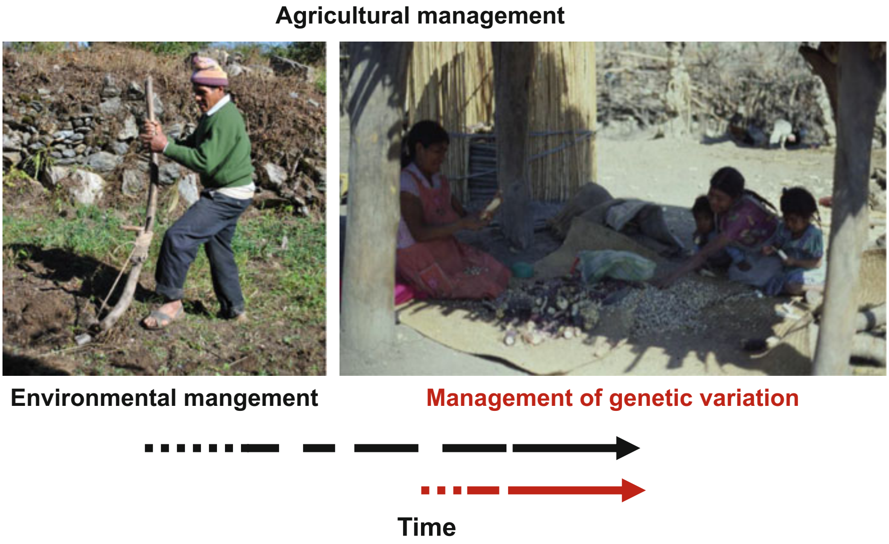

Fig. 3.4 Agricultural management is the convergence of environmental or ecosystem management and management of genetic variation or domestication. Ecosystem management has been documented to be significantly more ancient than domestication. However, the occurrence of artificial selection in non-agricultural management forms suggests that both ecosystem management and domestication may have occurred before agriculture, which became agricultural management when ecosystem management and domestication reached a significant integration

3.4 Evolution by Humans

Domestication is an evolutionary process guided by humans in order to adequate variation of organisms that are domesticated according to human purposes. The first theoretical treatment of domestication was the Chap. 1 of “The Origins of Species” (Darwin 1859), whose main premises were later on developed in the two volumes treatise “The variation of animals and plants under domestication” (Darwin (1868). In these works, Darwin developed four main ideas that were crucial for his thinking on the origins of biological diversity. The first one is the recognition that variations in plants and animals are frequent and measurable, which was an important conclusion based on extensive observations, in a world dominated by fixist ideas. It is widely known the detailed Darwin’s work measuring and analysing numerous morphological and physiological variations among individuals of particular species. This important approach contributed to develop empirical evidence of evolutionary processes.

The second main idea is that artificial selection practised by humans (including Darwin himself) favours some variants and disfavours others, and that such a simple mechanism is a principal cause of differentiation of varieties and races of domestic plants and animals. The third main idea is that the high diversity of varieties and races that have been generated by artificial selection have one or few common ancestors, and that it is possible to reconstruct the history of the divergence and common ancestry of the varieties and races. Based on his own experience as breeder of pigeons Darwin reconstructed the phylogeny of some main European races of these animals, and similarly speculated about the ancestors of some of the most important domestic plants and animals. The fourth main idea is that the three principles enunciated above occur similarly in both human and natural contexts moved by artificial and natural selection, respectively (Darwin 1859, 1868).

This is certainly the route of thinking that made possible arising the concept of natural selection, a crucial idea in the modern evolutionary theories. In addition, this thinking allowed the analysis of artificial processes that may be used as models for explaining what may occur in nature. In other words, the analysis and praxis of domestication allowed Darwin developing a theory about the origin of biological diversity and empirical bases to support his thinking.

The mechanisms of artificial selection described by Darwin were simple. In the case of animals, the breeders commonly select the male and female organisms with desirable attributes (general body or particular parts size, colour, quality of hair or feathers, among others), and the exacerbation of some features determine that the lineages diverge, with time becoming different races. In the case of plants, in Darwin times the breeders were able to drive crosses of particular lineages and practised systematic artificial selection on the descendent phenotypes. These simple processes were what the breeders practised with strong directionality and Darwin called them to practice “conscious selection”. Darwin contrasted this type of artificial selection from that practised progressively and more slowly in peasant rural contexts. Darwin called that kind of artificial selection “unconscious selection”, to distinguish it from the relatively more intensive and systematic artificial selection described before. Nevertheless, it is not exact that this selection is "unconscious", as it has been widely demonstrated during the twentieth and the early twenty-first centuries by ethnobotanical researches studying traditional agriculture (Hernández-Xolocotzi 1959; Zizumbo and Colunga 1982; Casas et al. 1994, 1996).

Whatever the type of artificial selection, its common purpose is favouring those variants of a population of organisms that are desirable to humans, while disfavouring in the extreme case eliminating those variants that are not desirable to humans (Darwin 1859). Nevertheless, what is "desirable" or "undesirable" is a complex issue since human cultures may consider something desirable in a context and undesirable in other context, and both natural and cultural factors may influence in those considerations (Casas et al. 1996). This is one of the reasons why domesticated organisms have as particular characteristic a high morphological and physiological variation compared with the variation that can be recognised among wild populations of a species (Schwanitz 1966; Hawkes 1983; Brush 2004). Nevertheless, humans have in common some physiological and cultural aspects in common which have determined similar artificial selection pressures in different social-ecological contexts. Such similarities have determined numerous evolutionary convergences in features of plants and animals that have been domesticated. Such convergences have been called the domestication syndrome. The domestication syndrome has been polemic, but in fact, it is a hypothetical premise particularly helpful to analyse the result and progress of ongoing processes of domestication through comparative biology, as it will be discussed in Chap. 4.

In plants, among the main features of domestication syndrome (Schwanitz 1966; Hawkes 1983) we can mention: (1) Gigantism, which is the enlargement of parts or increasing of content of fluids (sap, latex, oils) or elements (nutriments, aromatic compounds) that are used or beneficial to humans. Of course, not only the useful parts increase their size, other highly correlated parts and the general architecture of the plant have changed as consequence of selection in favour of gigantic desirable parts. (2) Suppression of natural mechanisms of dispersion, particularly for those species whose fruits or seeds are the useful part. For instance, in plants like cereals that disperse their caryopsides by fracturing their rachis, people have selected those variants with strong rachis; in the case of legumes, commonly dispersing their seeds by explosive dehiscence of their pods, humans have selected those variants with indehiscent pods. Some fruits with natural attractive colours to attract seed dispersers have been selected favouring colours cryptic for the dispersers in order to decrease damage of the useful part. (3) Suppression of mechanisms of protection against herbivores. Plants generally have mechanical (spines, thick peel or cortex, flaxy surface, among others) or chemical (toxic, unpalatable, or repellent compounds) that defend the plant or some of its parts of herbivores. Humans are herbivores and have selected in favour of those variants lacking defence mechanisms. (4) Loss of dormancy mechanisms and increasing synchronic germination of seeds. Natural mechanisms adapting seed germination to the appropriate environmental conditions in order to increase the probability of establishment, are generally undesirable for human management of plant stands. Therefore, this is a character commonly found in domesticated plants.

Comparing features of domesticated plants like those described above, with those showed by wild plants is a common methodological strategy to document when domestication started, how advanced is the domestication process, and how it has operated and it is currently operating (Casas et al. 2007; Parra et al. 2010). Domesticated plants become completely dependent on humans for surviving and reproducing. This is the most advanced stage of domestication. But not all domesticated species have achieved this stage, and some are partially independent of humans in their most advanced stages of domestication. Even more, in the regions where the crops originated, it is possible to observe populations or subpopulations of organisms in a continuum of stages of independence and dependence from humans.

Domestication is an evolutionary process and, therefore, it is continually operating. Even on those species that are completely dependent of humans for their survival and reproduction, artificial selection is continually changing intensity and direction. This is because human culture is highly dynamic, much more than natural factors guiding natural selection; and also because humans move relatively rapidly plants and animals in the space. The diffusion of crops has been extraordinarily rapid throughout human history and it is progressively more and more accelerated. This context confers a highly dynamic change of environmental conditions where the crops grow. In addition, the management technology of agriculture has dramatically changed, particularly during the last Century. These three factors confer to domestication highly dynamic conditions to operate. Therefore, in a time lapse relatively brief, domestication has determined the appearance of a high agrobiodiversity, which constitutes the basic process that has generated the valuable genetic resources for current and future needs.

Artificial selection is the most documented evolutionary process influencing domestication, but it is not the only one. Other general evolutionary processes influence domestication: The random changes generated through genetic drift, which are favoured by the relatively small populations predominantly managed by the human domesticators throughout the world. The gene flow among wild relatives and crops that frequently occur in their centres of origin are main sources of agrobiodiversity. In addition, gene flow occurring between varieties originated in distant geographic areas are progressively more common as human cultures rapidly increase their contact. Some of these processes are incidental, not guided, unintentional, but some others are deliberately managed. These evolutionary processes when guided by humans, like artificial selection, should be considered part of the process of domestication. But even when they are not intentional, as it is natural selection, they also influence the evolution of domesticated organisms. A holistic comprehension of domestication requires understanding these evolutionary processes that have been increasingly studied in natural evolution, but scarcely in evolution determined by humans.

3.5 Conclusions

Evolution by humans has therefore two main expressions: changes in ecosystems that configure evolution of landscapes adapted to human purposes, based on needs, customs, values, technology and other elements of human culture. The other is the transformation of organisms guiding their fitness according with the human cultural contexts. But both processes are connected: what happens at landscape level influences the criteria for selecting and modelling the organisms in process of domestication. In counterpart, the result of domestication of organisms influences the characteristics of the production system and, in turn, on the configuration of the landscape.

Documenting these processes is the general purpose of evolutionary ethnobotany. How human cultures determine changes in landscapes and in organisms composing those landscapes is crucial for understanding the human culture itself and the shaping the configuration of most of the surface of our planet. At the same part, evolutionary ethnobotany and ethnobiology may help to understand how changes in landscapes and in organisms influence the configuration of human cultures throughout the time and space.

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Chapter 4
Evolutionary Ecology and Ethnobiology

Alejandro Casas, Fabiola Parra, Selene Rangel, Susana Guillén, José Blancas, and Carmen J. Figueredo

4.1 Introduction

Evolutionary ethnobiology is a social-ecological science whose research approach requires making use of perspectives from biological-ecological sciences, as well as social-economic and anthropological disciplines. Its general purpose is to analyse the evolutionary processes derived from interactions that have occurred for hundreds or thousands of years between humans and plants, animals, fungi, and micro-organisms, and the ecosystems they form part and that are also managed by humans. These humans–nature interactions had in the past and currently have evolutionary consequences on: (1) the organisms interacting with humans, (2) the humans themselves, their culture and societies, and (3) the ecosystems and landscapes of the

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A. Casas (✉) • S. Rangel • C.J. Figueredo
Instituto de Investigaciones en Ecosistemas y Sustentabilidad (IIES), Universidad
Nacional Autónoma de México, Campus Morelia, Antigua Carretera a Pátzcuaro 8711,
Col. San José de la Huerta, Morelia, Michoacán 58190, Mexico
e-mail: acasas@cieco.unam.mx; srangel@cieco.unam.mx; figueredocj@gmail.com

F. Parra
Centro de Investigaciones en Zonas Áridas (CIZA), Universidad Nacional
Agraria La Molina, Camilo Carrillo 300-A, Lima 11, Peru
e-mail: fparra2@gmail.com

S. Guillén
Estación Científica La Malinche, Universidad Autónoma de Tlaxcala,
La Loma Xicohtencatl, Tlaxcala de Xicohténcatl, Tlaxcala 90070, Mexico
e-mail: sguillenro@conacyt.mx

J. Blancas
Centro de Investigación en Biodiversidad y Conservación (CIByC), Universidad
Autónoma del Estado de Morelos, Av. Universidad No. 1001, Col. Chamilpa,
Cuernavaca, Morelos 62209, Mexico
e-mail: jblancas@gmail.com

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territories occupied by humans, which currently constitute already most of the surface of the planet.

Such a perspective indicates that questions of evolutionary ethnobiology are eminently social-ecological complex problems, and their understanding therefore requires interdisciplinary research approaches. The purpose of this Chapter is to show a panorama of conceptual and methodological approaches adopted and constructed by our own research group for analysing problems in relation to the main aspects of evolutionary ethnobiology analysed from an integrated perspective of ethnobiology and evolutionary ecology.

4.2 Evolution of Organisms Under Domestication

Evolution of organisms interacting with humans is guided by purposes and projects in humans mind, and the process is called domestication. The fundamental mechanisms allowing evolution of organisms are the processes generating variation (primarily mutations and different types of changes in genomes, as well as recombination at molecular and chromosomal levels), as well as evolutionary forces modifying such variation in populations (natural or artificial selection, genetic drift, gene flow, and breeding systems). It is certainly not the intention of this chapter to summarise a panorama about the operation of these mechanisms, which are reviewed in textbooks on evolutionary biology (outstandingly, Futuyma 2013 and Ridley 2003). Rather, we synthesise information about how these processes operate on domestication, and about general strategies for studying and understanding them. In addition, we identify some of the main challenges of research on this topic.

4.2.1 Recognition of Variation

Differential fitness (fitness in Darwinian terms, meaning the capacity of organisms for survival and reproductive success) of individuals composing populations is a basic concept associated to natural selection and adaptation (Darwin 1859; Mayr 1983; Lynch and Walsh 1998; Ridley 2003). The principle is simple; there is nothing to select and no options for adaptation if there is no variation in fitness; similarly, this concept is crucial in artificial selection. But in studies of domestication, it is in addition relevant not only documenting the existence of variation but also how people practising artificial selection recognise that variation, differentially using, valuing, and managing it. Adaptation under domestication relates with the success of organisms for living and reproducing in the human ecological, technological, and cultural contexts. Domestication involves a continual transformation of organisms according to changing culture, social organisation, and technology, as well as landscape and ecosystems transformation, all of them extraordinarily dynamic processes. Domesticated organisms are generally adapted to these contexts and artificial selection guided by humans, as well as to those associated to natural selection not guided but still acting on domesticates influence modelling such adaptations.

In order to document all these aspects, ethnobiology and evolutionary ecology are valuable research tools. The integration of these disciplines is what we should call evolutionary ethnobiology. Ethnobiological approaches are particularly relevant for: (1) Documenting nomenclature and classification of variation of organisms that humans interact with; (2) understanding the differential cultural meaning of resources, including their use, value, and management of variants of those organisms; (3) the characteristics that are deliberately favoured or disfavoured, in other words, the targets of domestication; and (4) the morpho-physiological, reproductive, and genetic consequences of human actions on the phenotypic and genotypic composition of populations.

Ethnobiology helps to exploring how people visualise, value, and manage variation of plants, animals, fungi, and micro-organisms (mainly bacteria and yeasts) utilised by humans. Nomenclature and classification of groups of biotic species or variation contained within one single species is particularly important. Names of variants are normally associated not only with the recognition of variation but also with the identification of their differential properties. For instance, our studies in plants of *Leucaena esculenta* allowed identifying sweet, bitter, and vomiting varieties (Casas and Caballero 1996; Casas et al. 1996, 2007)—the sweet ones being appropriate for consumption and the vomiting ones being toxic. The bitter varieties cause digestive disorders but such problem can be solved through cooking their seeds. People prefer to practise selection in favour of the sweet varieties since they are better for consumption, although the bitter ones are more resistant to bruchid pests (Table 4.1). Similarly, Casas et al. (2007), Parra et al. (2012), Blancas et al. (2013), and Aguirre-Dugua et al. (2012), documented several plant species in which people recognise varieties and even name them, recognising different attributes and selecting them differentially (see some examples in Table 4.1).

Another aspect that it is possible to document through ethnobotanical approaches is how people value the resources according to their particular features and properties. At a first level, within a universe of commonly several dozens of useful plant resources, the rural communities have preference on a smaller number of species with particularly good attributes as food, medicine, material for construction, for making handcrafts or for fodder, among other uses (Camou et al. 2008; Blancas et al. 2010; see Table 4.2). Quantitative ethnobotany has developed a broad spectrum of techniques for evaluating the meaning of different resources for a human culture (Phillips and Gentry 1993; Ladio and Lozada 2000, 2001; Pieroni 2001; Lucena et al. 2007; Camou et al. 2008). These techniques may include the use frequency, amounts used, prices, explicit preferences, among other indicators (Arellanes et al. 2013; Blancas et al. 2013). These approaches allow identifying the most meaningful species. But, in addition, these techniques allow identifying the variants of particular species that are more valued by humans in a given human cultural and ecological context. In turn, this information may be compared with other variables related to availability (for instance, their temporal and spatial availability, the amounts of products demanded in markets), and their natural or human-caused vulnerability.

Table 4.1 Examples of species and their varieties recognised by peoples in different regions of Mexico

Species	Varieties	Attributes	Selection	Reference
Leucaena esculenta	Sweet	Large pods and seeds, good flavour but vulnerability to bruchid attack	In favour	Casas and Caballero (1996); Casas et al. (1996a, b; 2007)
	Bitter	Intermediate size of pods and seeds. Bitter flavour that can be eliminated by cooking. Intermediate resistant to bruchid attack	In favour	
	Vomiting	Small seeds and pods, toxic. Resistant to bruchid attack	Against	
Anoda cristata	Male	Leaves pubescent, narrow, cartaceous, bitter flavour	Against	Casas et al. (1996a, b, 1997a, b, 2007)
	Female	Leaves tender, wide, glabrous, not bitter flavour	In favour	
Crotalaria pumila	Male	Leaves narrow, pubescent, cartaceous texture	Against	Casas et al. (1996, 1997a, b, 2007)
	Female	Leaves wide, glabrous, tender, good flavour	In favour	
Amaranthus hybridus	White	Light green inflorescences and leaves, tender leaves	In favour	Blancas et al. (2013)
	Purple	Red inflorescences and purple leaf edges	Against	
	Spotted	Red inflorescences, purple spots in leaves	Against	
Brassica campestriis	*Colesh*	Tender, glabrous stems and leaves, nice flavour	In favour	Blancas et al. 2013
	Colesh teneztli	Tomentous stems and leaves, asperous, bitter flavour	Against	
Cestrum nocturnum	Buena	Tender leaves, abundant flowers, nice flavour	In favour	Blancas et al. 2013
	Cimarrona	Cartaceous leaves, scarcer flowers, bitter flavour	Against	
Chamaedorea tepejilote	*Tepejilote metlapilli*	Large and thick inflorescences, good flavour	In favour	Blancas et al. 2013
	Tepejilote tronquitos	Small and thick inflorescences, good flavour	In favour	
	Tepejilote de Cafetal	Intermediate size and thickness of inflorescences, high production, good flavour	In favour	
	Tepejilote de monte o de Chorpus	Small and thin inflorescences, bad flavour	Against	

Artificial selection is directed to favour the desirable varieties, thus increasing their numbers in managed populations. This is the elementary principle of domestication

Table 4.2 Examples of data about total amounts, frequency of consumption and preference of some species of edible greens (quelites) and fruit species used by households of the community of Quiotepec, Oaxaca in the Tehuacán-Cuicatlán Vlley, Central (based on Pérez-Negrón and Casas 2007)

Species	Annual consumption per household (kg)	Use frequency (times/season)	Preference (%)
Quelites			
Quintonil *Amaranthus hybridus*	3.0	8.1	92.9
Verdolaga *Portulaca oleracea*	3.0	5.3	89.3
Quelite *Chenopodium berlandieri*	2.3	3.2	78.4
Chipile *Crotalaria pumila*	1.0	2.4	63.4
Yerba mora *Solanum nigrum*	1.0	2.3	46.3
Edible fruits			
Chonosle *Escontria chiotilla*	2.1	12.3	93.5
Pitaya *Stenocereus pruinosus*	2.0	13.1	90.5
Cardón *Pachycereus weberi*	2.0	11.7	90.1

The comparison of these sources of information may be helpful to document the factors causing management decisions.

Motives of management and domestication is a topic highly speculated because of its meaning for explaining the origins of agriculture. However, these have been relatively scarcely studied and that requires higher research efforts, in order to understand factors that led humans in the past to initiate management practices and how these are still ongoing processes determining routes of technological innovation. Understanding the use of technologies available and the processes of innovation are nowadays not only important for understanding the starting of processes of domestication but also keystones for developing strategies of sustainable management (Blancas et al. 2010; Torres et al. 2015).

Another aspect that ethnobiology helps to document, is the spectrum of mechanisms through which artificial selection operates. In the Origin of Species, Darwin (1859) describes simple mechanisms favouring and disfavouring individuals of a stock of organisms, according to their characteristics. Darwin distinguished the conscious and unconscious selection (Darwin 1859, 1868), practised by breeders making use of specialised techniques of crosses and systematic selection, and the techniques practised by rural peasant societies, which generally make use of variation naturally emerged for then selecting the desirable variants. Unconscious selection is not really unconscious, but relatively slower compared with the systematic programmes managing reproduction and artificial selection.

However, this is a simplified view of artificial selection. When ethnobotanists have studied how artificial selection occurs in different ecological and human cultural contexts, a broad spectrum of criteria and mechanisms has been documented (Casas et al. 1997a, b). Among animals, the mechanisms for selecting reproductive males and females vary according to the biology of the animals involved, and the criteria for favouring particular features (Darwin 1859). Among plants, the mechanisms may be more variable, as the variation of life cycle, pollination and breeding systems are widely variable. Selection of seeds for producing a new generation of plants is one of the most common mechanism, which is effective to determine new stocks with the desirable character as long as heritability of the characters is high and segregation of characters is more certain (Fig. 4.1), all aspects depending on the nature of the breeding system. The second more common mechanism is propagation of vegetative propagules of desirable organisms. Based on this process, the resulting populations may have high frequency of individuals with the desirable characters. The latter mechanism may determine rapidly stocks or populations of desirable phenotypes; and for this reason some authors have called it "immediate domestication" (Harlan 1975; Hawkes 1983). However, in nature, numerous plant species managed by humans are perennial and out-breeders. These organisms require several steps of selection. One of them is selection of mother individuals with good phenotypes. The second step is normally associated to the quality of seedlings and saplings whose vigour is commonly a criterion. The third step may occur during juvenile steps, when people recognise vegetative characters associated to the quality of desirable phenotypic features. A fourth step may occurs after the first or subsequent reproduction seasons, when the quality of flowers, fruits or seeds can be visualised (Fig. 4.1). Documenting such different mechanisms may be determinant for analysing the evolution through artificial selection (Casas et al. 1997a).

Nevertheless, not only artificial selection is involved in domestication. According to Alcorn (1984) the Teenek frequently determine conditions of genetic drift in order to obtain interesting variation that is subsequently subject to other processes of domestication. Genetic drift is particularly relevant in small populations, which are the common way the traditional rural human cultures manage their plant resources. Parra et al. (2010) and Aguirre-Dugua et al. (2012, 2013) illustrate cases of the columnar cactus and gourd trees, respectively, in which people move propagules (seeds and vegetative propagules) from the wild to homegardens, this directed gene flow determining the advantages of variation differently used and valued (Fig. 4.2). All these processes allow visualising domestication beyond artificial selection, but requires more investigation to document the role of other evolutionary forces and their interactions for a better explanation of the origin and evolution of crops.

Documenting management forms is, therefore, a main task of ethnobotany. Our research group has identified and characterised two main groups of management forms: in situ management and ex situ management. The first group involves gathering, tolerance or let standing of particular species or phenotypes of a species, enhancing of these favourable phenotypes and special care of them. The second group or ex situ management forms involve seed sowing, vegetative propagation and transplanting of entire plants. All these activities may be selective and are also expressions of different types of artificial selection. In addition to management types we should include the analysis of management intensity. Agroecologists have used as indicators of intensive agricultural systems the amount of energy invested on the system and the productivity obtained from it. The use of specialised tools, machinery and management of inputs are also indicators. Similarly, we have

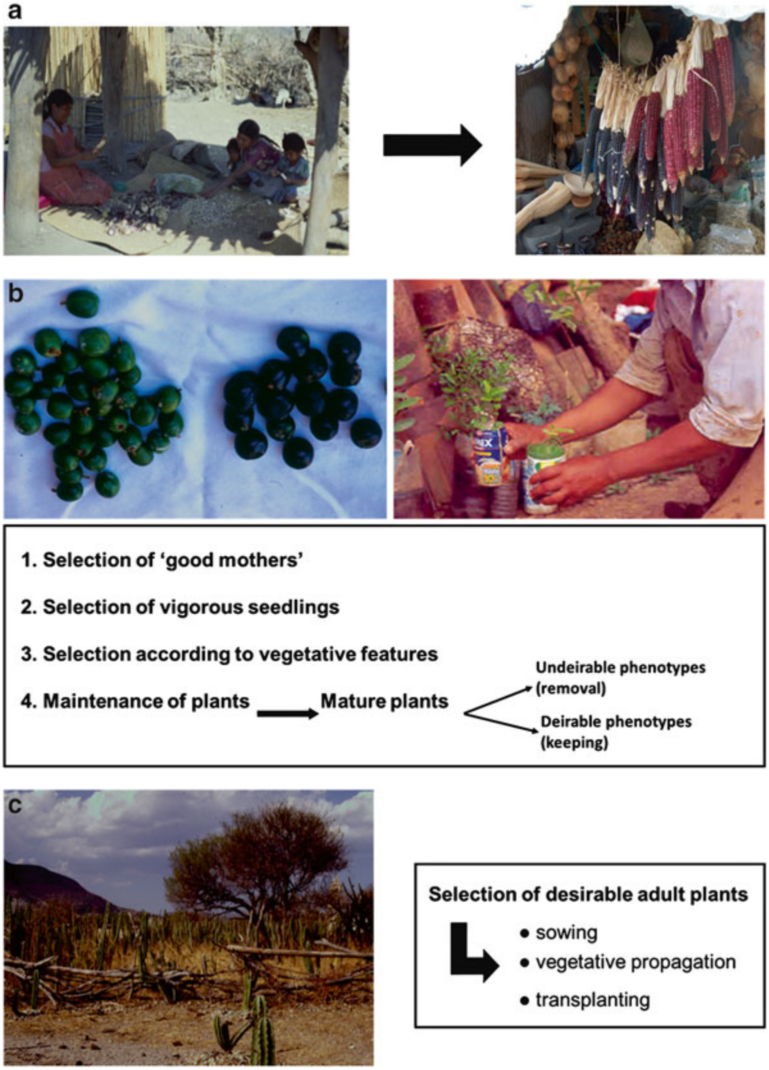

Fig. 4.1 Mechanisms of artificial selection. (**a**) Selection of maize seeds based on the quality of cobs and grain. When de-kernelling people decide which are the best cobs to be separated as seeds for the following generation. (**b**) Selection of "tepesquistle" (*Sideroxylon palmeri*). Seeds are collected from mother trees recognised to have better attributes in their fruit (larger and round, with higher proportion of mesocarp). The most vigorous seedlings are selected for transplanting in homegardens. Young plants may be let standing or removed according to vegetative characters that some persons recognise to be related with fruit quality. The mature plants are removed or let standing according to the proved quality of their fruits (González-Soberais and Casas 2004). (**c**) Plants with both sexual and vegetative propagation (the cases illustrated in the photograph are *Stenocereus stellatus* and *S. pruinosus*, according to Casas et al. 1999a, b; Parra et al. 2012) are selected according to the phenotype of mother plants (producing larger sweeter fruits, with peel thinner and fewer spines); saplings are managed similarly as indicated in the case (**b**). According to Casas et al. (1999b), people know that from time to time plants originated from seeds are surprisingly good; some of them being hybrids between *S. stellatus* and *S. pruinosus*, which have two periods of fruit production. Vegetative propagules, in the cases illustrated the branches, are collected from the considered good phenotypes from wild and cultivated populations and then planted in homegardens or agroforestry systems. In addition, people use to transplant entire young plants from one site to other, particularly in agroforestry systems

Fig. 4.2 Mechanisms of gene flow between wild and cultivated populations of *Stenoceres pruinosus*. Photographs at the top illustrate the main vectors of natural gene flow through pollen (at the *left* bats *Leptonycteris yerbabuenae* and *L. nivalis*), and seeds (at the *right*) including several species of seed dispersers, mainly birds and bats. Photographs at the *bottom* illustrate branches (at the *left*) cut from wild populations that will be planted in homegardens similar to that illustrated at the *right*. The latter is the main mechanism of gene flow determined by humans among wild and cultivated populations

discussed the use of such type of indicators for characterising the level of intensity of gathering, silvicultural and other non-agricultural practices (Fig. 4.3). Again, ethnobotany allows characterising this type of systems and management intensity. These variable intensities of management may determine different velocities to achieve divergence between wild and managed populations (Fig. 4.4).

4.2.2 Documenting Phenotypic Variation

Evolutionary change involves inherited changes; otherwise, the memory of a change is lost in the following generation. Therefore, one of the main challenges of evolutionary biologists, including those studying domestication, is analysing the nature (genetic or environmentally influenced) of variation that is under artificial selection and other evolutionary mechanisms. In other words, it is of primary importance to evaluate the heritability of the characters that are perceived, valued, and managed

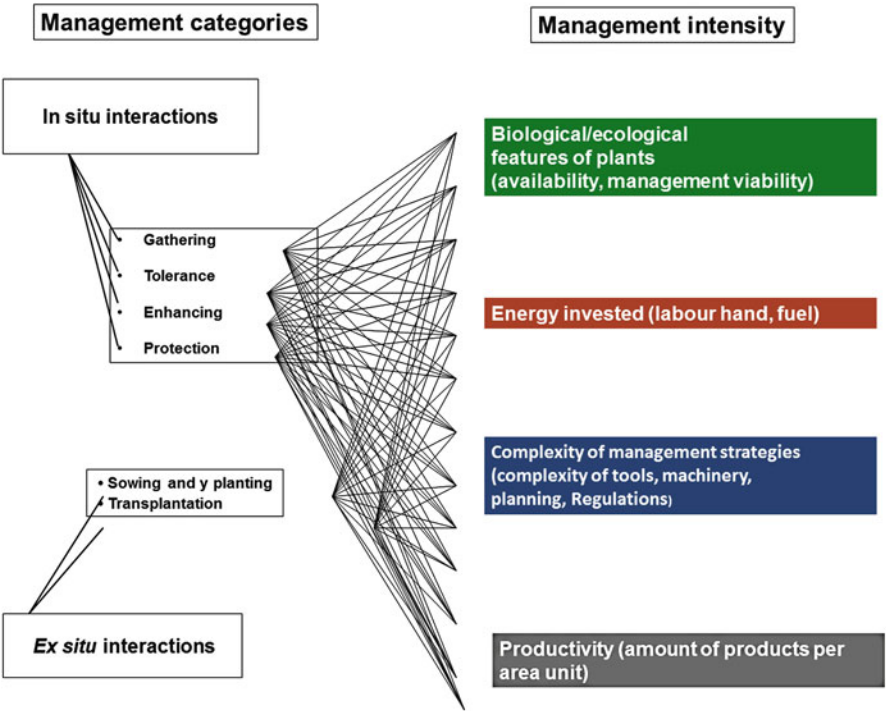

Fig. 4.3 A general typology of the forms of management that our team has documented in different communities and regions of Mexico. In situ management are carried out in the areas where the plant species naturally occur (forests and silvicultural patches in agroforestry systems). Gathering is the general harvest of products from wild and weedy plants, tolerance is the deliberate lets standing of species and phenotypes that are particularly desirable by people; enhancing and special care are activities to promote and protect those desirable species. All these activities may be conducted at different levels of intensity, according to how viable are for management (nature of reproduction and propagation and length of life cycle are particularly important), and how much are already available in natural environments (abundant species or phenotypes are generally considered unnecessary to be managed). The amount of energy invested in the system is another indicator of management intensity. Number of persons involved in an activity, hours of work invested in such activity, use of fuel and other inputs derived from fossil energy are specific indicators of energy invested. The complexity of tools (from sticks and stones to machines) are definitely indicators of the intensity of a management activity. Finally, the amounts of products obtained per area unit

by people. Several research strategies may be used from the theoretical approaches of quantitative genetics. Heritability of phenotypical characters can be estimated, for instance by evaluating the phenotypes of parents and offspring. In this type of controlled experiments the linear regression (COV_{xy}/VAR_x), the value of the slope is a measure of the heritability (Lynch and Walsh 1998; Ridley 2003; Futuyma 2013). Another approach is the estimation of the selection differential (S) which is the deviation of the mean value of a phenotypic feature of the selected parents compared with the mean value of the offspring population. This parameter in addition to

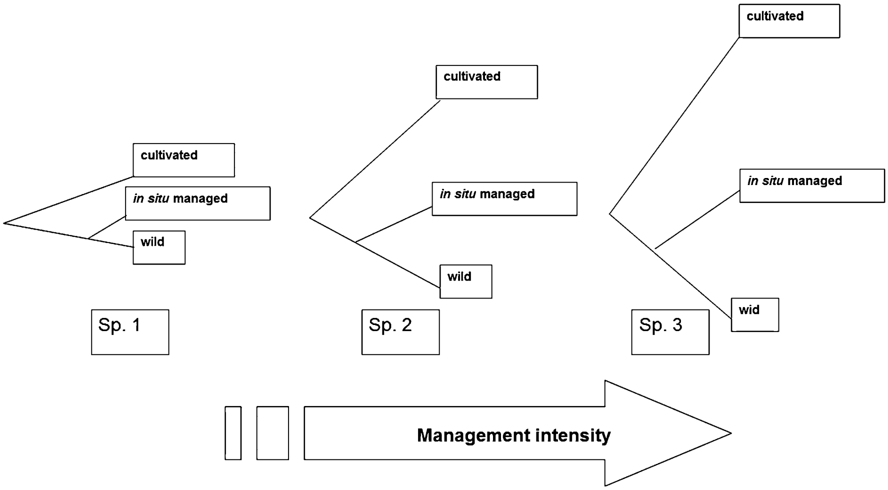

Fig. 4.4 Phenotypic and genetic divergence resulting from management is the result of the processes of domestication. Within a single species, it is possible to document divergence between wild, silvicultural in situ managed and cultivated populations. However, when comparing among species under different management intensity, it is possible to see that the divergence among wild and managed populations is more pronounced as long as the management intensity is also higher

the response of selection (R), which is the mean value of the offspring population compared with the parental population mean. Heritability (h) can be calculated as the relation $h^2=R/S$ (Fig. 4.5).

Other methods may be used based on the estimation of the fraction of the phenotypic variance that is genetic and environmental. Common garden and reciprocal transplanting experiments are particularly useful to evaluate how constant or not are the phenotypic features in similar and different environments, respectively. An additional method, useful in long-lived perennial plants is conducting experiments as referred to above for testing germination and seedling performance (Guillén et al. 2011, 2013, 2015; Rangel-Landa et al. 2015) (Fig. 4.5). The phenotypes of those perennial species with vegetative propagation such as cacti species can be monitored in the field (Casas et al. 1999a). Molecular markers are helpful to identify clones and monitoring their characteristics in different environments (Fig. 4.5).

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Fig. 4.5 (continued) *Stenocereus stellatus*. With time, this clonal propagation determine forests whose genotype and relation is uncertain. However, through molecular markers it is possible to identify which ones of a sample of individual plants are clones. In the *middle*, at *right*, we have a view of the alluvial valley just in front of the Coxcatlán cave studied by MacNeish and his archaeologists' team. In this area it is possible to identify areas of alluvial deposits with different ages and a gradient from humid to drier micro-environments. A condition like this allows monitoring the phenotypic expressions of clones in different environments. The photograph at the *bottom* indicates the starting of a long term common garden experiment in a green house where stems of *Stenocereus stellatus* from different populations and whose morphology was characterised in field, were put together for growing

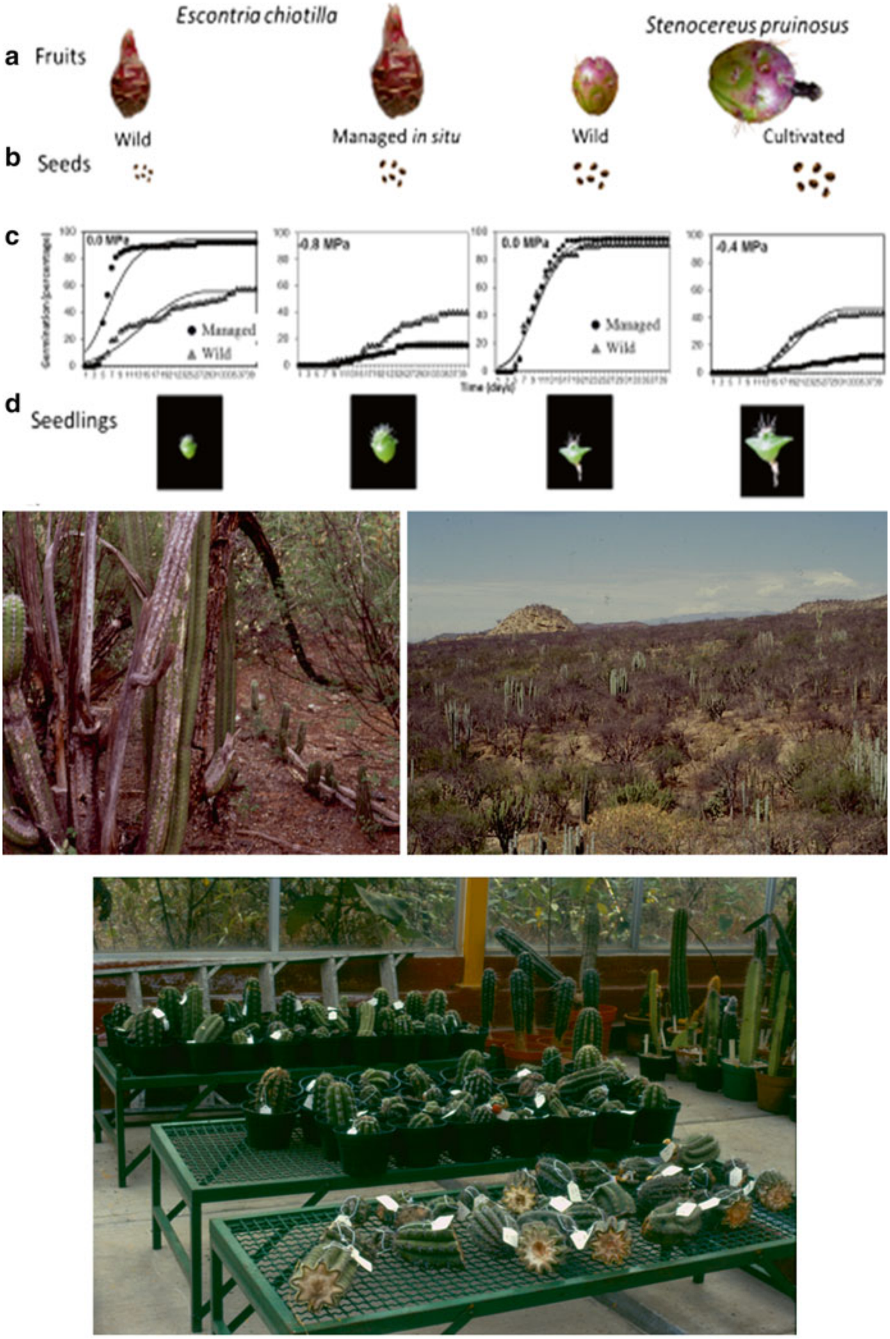

Fig. 4.5 Different strategies to evaluate the heritability of morphological characters. In the *upper* photographs, results of common garden experiments of germination of seeds from wild and managed populations. In the middle, we show a common mechanism of vegetative propagation in

Mechanisms of artificial selection. Artificial selection is the main evolutionary mechanism of domestication. The general principle is simple: favouring some varieties (in principle those preferred, desired, valued by a human culture involved in management) while disfavouring others. These mechanisms directly intervene with determining differential fitness of organisms: those preferred by humans survive and achieve reproducing. The intensity of selection modulates how strong this mechanism is. The extreme situation is the direct removal of undesirable varieties and their extinction as consequence. Other situations determine a slow and progressive process, but the result is the same: extinction of undesirable varieties and increase of frequency of the desirable ones. The rapidness of this process therefore depends on the strength of artificial selection. But other aspects such as life cycle length (annual or long-lived perennial), type of reproduction (vegetative propagation, inbreeding, facultative or obligate outbreeding), the strength of natural selection and gene flow from wild populations, which counterbalance the results of artificial selection, are all processes influencing on how rapid the domestication process may be.

Artificial selection and other evolutionary forces act guiding the frequency of phenotypes that are favourable to a human culture. Therefore, documenting the results of both artificial and natural processes influencing domestication can be achieved through comparative evaluation of morphological, physiological, reproductive, and genetic aspects between wild and domesticated populations. Therefore, after the first step of information provided by ethnobotanical investigation about targets and mechanisms of artificial selection and other evolutionary forces, measuring the results of such forces helps to evaluate the degree of advance of domestication. Occurrence of divergences and the degree of such divergences are basic information to evaluate how much the domestication has guided evolution of crops.

Morphological variation generally involves size, flavour, and texture of useful plant parts (e.g. leaves, fruits, seeds, stems, roots, tubers). In addition, it involves the general architecture of plants since useful plant parts are in turn part of integrated modules which may in turn maintain correlation with other structural and functional modules. In principle, for evaluating divergence between wild and domesticated organisms, the studies of domestication should focus on quantitative and qualitative characters meaningful, and favoured and disfavoured by people; but also, with other likely related characters. For comparing populations average values of structure composing individual plants and then average values per population should be estimated. Univariate comparisons may provide information of particular characters, their state divergence and trends in wild and managed populations. Multivariate analyses (Cluster Analysis, Principal Component Analysis, and Discriminant Analysis) are helpful for exploring patterns of similarity and differences in phenotypes of individuals and populations. Also, these analyses allow identifying how relevant are certain characters in explaining the dissimilarities between wild and managed populations.

Testing divergence of populations may be conducted through discriminant function and multivariate analysis of variance (MANOVA). In an attempt to characterise and compare multivariate estimations of morphological diversity, we adapted the

Table 4.3 Morphological diversity (*MD*) and genetic diversity (expected heterozygosity *He*) in different species of columnar cacti under different management intensity

	E. chiotilla	*P. chende*		*P. chichipe*		*M. schenckii*	*S. stellatus*	
Management	*He*	*He*	*MD*	*He*	*MD*	*MD*	*He*	*MD*
Wild	0.134	0.539	0.343	0.431	0.546	0.652	0.253	0.408
Silvicultural	0.110	0.516	0.353	0.368	0.630	0.768	0.270	0.461
Cultivation				0.369	0.592	0.670	0.289	0.479

Notice that in general wild populations have higher genetic variation and lower morphological diversity. The exception being *Stenocereus stellatus*, species in which we documented higher morphological and genetic variation in cultivated populations

Table 4.4 Morphological (upper table A) and genetic (lower table B) differentiation among populations of columnar cacti under different levels of management intensity (from lower to higher from top to bottom rows and from left to right columns)

Species	Differentiation among wild and silvicultural populations	Differentiation among wild and cultivated populations
(A)		
Polaskia chende	0.009	–
Escontria chiotilla	0.011	–
Myrtillocactus schenckii	0.069	0.110
Polaskia chichipe	0.193	0.363
Stenocereus stellatus	0.251	0.379
Stenocereus pruinosus	?	?
(B)		
Polaskia chende	0.023	–
Escontria chiotilla	0.031	–
Myrtillocactus schenckii	?	?
Polaskia chichipe	0.041	0.045
Stenocereus stellatus	0.050	0.059
Stenocereus pruinosus	0.069	0.075

In both cases, we used the algorithm of the genetic distance developed by Nei

Simpson's index to analyse frequencies of character states (Table 4.3). Multivariate morphological divergence between wild and managed populations may similarly be estimated through Nei's Genetic Distance or other similar algorithms (Casas et al. 2006) (see Table 4.4 for some examples estimated in columnar cacti studied by our research team).

4.2.3 Variation of Reproductive Systems

Reproduction is commonly a main target of artificial selection. Particularly in those plants whose reproductive structures (fruits, seeds, flowers) are the main plant parts used by humans. But also, because they may determine bridges or barriers to reproductive contact between wild and managed populations and, therefore, the nature of reproductive systems may influence how fast the fixation of a desirable characteristic is achieved in the domesticated stands. Changes in reproductive biology as consequence of domestication may involve: (1) increasing frequency of in-breeders and self-pollination systems, (2) increasing frequency of successful vegetative propagated individuals, (3) more generalist pollination systems, (4) changes in phenology, more commonly longer periods of producing flowers and fruit, (5) loss of dormancy and increasing germination velocity, (6) higher adaptation to human-managed environments and higher vulnerability to wild environmental conditions for seed germination, seedling survival and sapling growth.

The increasing frequency of in-breeders and self-pollination systems, as well as the increasing frequency of more generalist pollination systems, are strategies directed to decrease dependence of fruit-seeds production from availability of pollinators. In our experience, traditional management of breeding system is not practised and therefore, a conscious selection in this direction is unlikely. However, people select in favour of those more productive individuals with higher certainty, and these are individual plants with higher capacity of self-pollination or those that maintain open their flowers for longer time in order to favour the visits of both nocturnal and diurnal visitors (Casas et al. 1999b; Otero-Arnaiz et al. 2003; Arias-Cóyotl et al. 2006; Ortiz et al. 2010; Fig. 4.6).

Success of vegetative propagation is differential among individual plants. Especially in long-lived perennials, vegetative propagation is a management strategy with great advantages. It is therefore possible finding a higher frequency of vegetative propagated individual plants within managed stands than in the wild. Casas et al. (1997b) and Parra et al. (2012) documented that peoples of the Tehuacán Valley frequently collect branches of *Stenocereus stellatus* and *S. pruinosus* for planting them in homegardens. Casas et al. (2007) documented that in the case of *Polakia chichipe* and *P. chende* vegetative propagation is more difficult to find in natural populations, but more common in agroforestry systems and homegardens.

Changes in phenology are commonly associated to the intention of making longer the period of production of useful parts (leaves, flowers, or fruits). And sometimes such changes in addition contribute to reproductive isolation of wild and managed populations. In the cases that we have studied (mainly columnar cacti), changes in phenology do not have drastic consequences in reproductive isolation, but we have identified changes in flowering peaks whose consequences in reproductive isolation are yet to be studied.

Changes in seed germination and seedling survival patterns have been scarcely studied from a comparative perspective between wild and managed populations. We have documented in several species of columnar cacti that vulnerability to wild environmental conditions increases with the degree of domestication measured as a degree of general phenotypic and genetic divergence (Guillén et al. 2011, 2013, 2015). In the cases studied, seed germination is not a character directly submitted to artificial selection. Rather, it appears that the result is a combination of artificial selection in favour of larger fruits (which indirectly results in larger seeds), and natural selection associated to human-made and wild environments.

Fig. 4.6 Examples of landscape domestication. In the *upper part*, terraces in the Tehuacán Valley Mexico and in Morai, Perú. Both photographs illustrate the intention of modifying the geomorphology of natural slopes in order to maintain for long time the permanence of soil and humidity according to human interests. In the *lower part* the photographs illustrate agroforestry systems designed to maintain wild patches and elements of vegetation with different purposes, among them providing useful products of the forest, shade, soil and water protection, and other benefits (Moreno-Calles et al. 2012, 2013)

4.2.4 Genetic Variation and Domestication

Neutral genetic markers have been used by evolutionary biologists for several decades. Isozymes and a wide variety of nuclear, chloroplast, and mitochondrial DNA polymorphism (RAPD, RFLP, AFLP, ISSR, microsatellites, among others) have been useful tools for evaluating amounts of genetic variation in wild and managed populations of plants and animals, gene flow, and genetic structure among these populations. Such indicators are powerful indicators about evolutionary divergence between populations, as well as for inferring historical and recent interactions between populations. In addition, neutral markers have been valuable tools or reconstructing phylogenies of crop species and their wild relatives. And more recently, the analyses of phylogenies and lineages of genes in geographic spaces have helped to identify areas or origin and routes of diffusion of crops, agriculture, and, consequently, civilisation.

The most common pattern found when comparing wild and domesticated populations is high diversity in the wild (reservoirs of genetic variation modelled by millions of years) and low diversity in managed populations, even lower in those more intensively managed. Such a pattern can be explained since domesticated populations involve a fraction of the wild genetic variation, and the intensive regimes of production have privileged some particular highly productive genotypes for specialised environmental conditions. However, in traditional rural contexts, some important exceptions can be found. For instance, in the cases of *Stenocereus stellatus* and *S. pruinosus*, Casas et al. (2006, 2007) and Parra et al. (2010), respectively, found that some silvicultural and almost all cultivated populations had on average higher genetic diversity than wild populations. This pattern can be explained because the species studied coexist with their wild relatives, and gene flow is naturally and artificially procured and favoured, including the continual replacement of plants and the introduction of variants from other villages and regions. Probably the most important aspect of this pattern is the illustration of the high potential of wild relatives in increasing the genetic diversity of crops, as well as the important role of cultivated stands as reservoirs of genetic diversity.

Monitoring lineages of genes in the geographic space is currently known as phylogeography (Avise 2000), a science that has had relevant contributions to evolutionary biology, and that has started to better explain aspects about origin and diffusion of domestication. Nowadays, the integration of archaeological and phylogeographical information allows higher precision in relation to the main sources of genes and regions of the world providing them for a number of plant and animal species. The information has generally confirmed the Vavilov's centres of origin but have refined information about multiple areas of origins for some species. Our research group has studied the cases of *Stenocereus* (Parra et al. 2012, 2015) and *Crescentia* (Aguirre-Dugua 2015), which add information to previous studies on *Spondias* (Miller and Schaal 2005) and maize (Matsuoka et al , Matsuoka 2005). These studies and other in progress will allow soon a better understanding of the meaning of the Mesoamerican Centre of Origin, which now appears to be a net, rather than a centre, and its connection with other historical nets providing genetic resources in the Americas through history.

4.3 Human Culture and Domestication

Domestication has had consequences on human evolution. For instance, domestication of animals greatly determined the appearance of new illnesses horizontally transmitted from domestic animals to humans. The history of devastating illnesses influencing catastrophic decline of human populations and their recovery from resistant genotypes illustrate that human evolution is an ongoing process and that domestication has influenced several important chapters of the history of human societies. However, particularly dynamic has been the influence of domestication on human culture and social organisation. The most representative of such influence is undoubtedly the origins of agriculture and settled life, which changed the prevailing pattern of hunter gatherer bands to progressively permanent villages and the arising of cities (the *civita*, a term rooting the word civilisation). Social organisation changed dramatically during the last 12,000 years in different parts of the world, apparently starting in the Middle East, and then in other regions including the Vavilov's centres and those identified later on.

The most recent influence of the process of domestication on human societies is the Green Revolution. The premises of this worldwide project was to attend the needs of food production in order to guarantee food security. Its achievement have been polemic and motive of extensive discussion. The programme included the intensification of systematic breeding and artificial selection in order to make faster the processes of domestication, producing and patenting germplasm for modern systems of production. Productivity increased dramatically, producing much more food than needed by humans, but hunger was not solved. Nearly two billion people of the world have nutrition problems and nearly one third of total production is wasted. Numerous social phenomena developed in association to the adoption of Green Revolution, including migration to agro-industrial zones, increasing dependence of communities to agrochemical inputs, genetic erosion and eutrophication of extended fresh water reservoirs and oceans, causing tremendous impact and high risk on the ecosystems of the Earth. The perspective of this model of production is unsustainable, since the conditions of irrigation and agrochemicals needed for attending the projected human population growth have overpassed what it is possible. Nevertheless, companies and governments throughout the world insist in the promotion of the model, now with genetically modified organisms (GMO), which increase the requirements of water and agrochemicals, the dependence of producers, without achieving their dreams of productivity. This is a failed route for designing future and it is time for a deep criticism to the model and turning our eyes to sustainable agriculture and agroecology.

4.4 Evolution of Landscapes

Landscapes are biophysical spaces that may include wilderness but that are eminently human constructions, resulting from transformation of key aspects of the systems that conform them. The latter may include geomorphology, hydrological systems, vegetation cover, flora and fauna composing the ecosystems, among the most important aspects. Changes of landscapes may be result of incidental, non-intentioned or undesirable human impacts on ecosystems (for instance, contamination of atmosphere and water, destruction of the ozone layer), but others are deliberately guided with a purpose (for instance, the construction of terraces, dams and channels, living fences, forest gardens, among others, Fig. 4.6). Transformations of ecosystems by humans is very ancient, having influenced in these processes the invention of tools and fire management and, more recently, machines. Pre-agricultural transformations of landscapes have been identified through firing, vegetation taming, and management of natural hydrological systems, in order to hydrate or inundate ones or desiccate others (see Chap. 3). However, undoubtedly the transformation of ecosystems started to intensify with the arising of agriculture and the intensive raising of livestock. Then, with the industrial revolution, this process became dramatic, and since the 1950s has seriously affected nearly one-half of the continental surface of the Earth. Different indicators of global change (MEA 2005; Barnosky et al. 2012; IPCC 2013) identify clearly that the industrial processes have been the main causes of the severe impact on the ecosystems of the planet. Nearly 50 % of the forest cover of the Earth has been transformed during the last 8000 years, but there is no doubt that the impacts increased since the eighteenth Century and these have been accelerated from the second half of the twentieth Century (Barnosky et al. 2012).

Landscape domestication involves biophysical transformations in order to adequate environments to human needs and values. Some deliberate transformations are particularly destructive such as open pit mining, deforestation of rainforest and expansion of urban areas. Other domesticated landscapes are more friendly and resilient. Different studies strongly suggest that the domesticated landscapes are more resilient as long as they simulate or substitute original functions of the ecological systems that were transformed (Holling 1973; Maass and Martínez-Yrízar 1990; Gunderson 2000; Peterson 2002). Some aspects are particularly important, those related with the maintenance of biodiversity are crucial, as well as those preventing soil erosion and retention of water. However, the rural areas of the world, particularly where the small-scale agriculture is practised, have been able to maintain for longer time their basic features of their physiognomy.

Agroforestry systems are among the earliest domesticated landscapes and they are functioning throughout the world. These systems have the particularity that combine wild and domesticated elements, favouring the maintenance of high biodiversity and ecosystem functions favourable for resilience. Numerous types of agroforestry systems have been described in different parts of the world (Moreno-Calles et al. 2013) and they are considered by agroecologists as important systems alternative to the agro-industrial systems referred to above.

The main causes of the catastrophic modelling of landscapes of the Earth have been identified and it is still time to reverse such a destructive process with global consequences. But there are primary production systems constructed based on thousands of years of human experience. These are domesticated landscapes that deserve higher efforts of research for building a more sustainable future.

4.5 Conclusions

Evolutionary ethnobiology is a social ecological science that looks for understanding the principles of change involved in the interactions of humans and biotic components of ecosystems and landscapes. It is a scientific approach gaining high advantage from evolutionary ecology and ethnobiology. The main topics that should be understood by this research field are: evolution of organisms, social organisation and landscapes determined by human guidance. Evolutionary processes determined by humans have been crucial throughout history and may be keystones for designing a sustainable future.

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Chapter 5
Evolutionary Approaches to Ethnobiology

C. Haris Saslis-Lagoudakis, Nina Rønsted, Andrew C. Clarke,
and Julie A. Hawkins

5.1 Introduction

Phylogenetic trees depict species' relationships and evolutionary histories. In recent years, phylogenetic research has revolutionised our understanding of species relationships (Driskell et al. 2004; Soltis et al. 1999; Bininda-Emonds et al. 1999; Kjer 2004), building on decades of taxonomic and comparative biology research. Though reconstruction of the Tree of Life is far from complete, progress towards the representation of organismal relatedness as a vast evolutionary tree has enabled fundamental biological questions to be addressed in innovative and robust ways, creating opportunities to benefit society through applied research. Alongside the phylogenetic tools for building trees, phylogenetic methods have been developed to test ecological and biogeographical hypotheses about the distribution of biodiversity (Donoghue 2008; Crisp et al. 2009; Barker et al. 2004; Buckley et al. 2010), and the interrogation of phylogenies is an established part of conservation science (Forest et al. 2007; Faith 1992), epidemiology (Gaunt et al. 2001; Smith et al. 1988), and developmental biology (Arthur 2002), providing a comparative framework incorporating evolutionary history. In many cases, traits are not randomly distributed among species, but closely related species are more likely to share traits [e.g. Martiny et al. 2013; Prinzing 2001; Willson et al. 2008]. The power of phylogenetic tools is based

C.H. Saslis-Lagoudakis (✉) • N. Rønsted
Natural History Museum of Denmark, University of Copenhagen,
Sølvgade 83, Entrance S, Copenhagen 1307, Denmark
e-mail: C.H.SaslisLagoudakis@gmail.com

A.C. Clarke
McDonald Institute for Archaeological Research, University of Cambridge,
Downing Street, Cambridge CB2 3ER, UK

J.A. Hawkins
School of Biological Sciences, University of Reading, Reading, Berkshire RG6 6BX, UK

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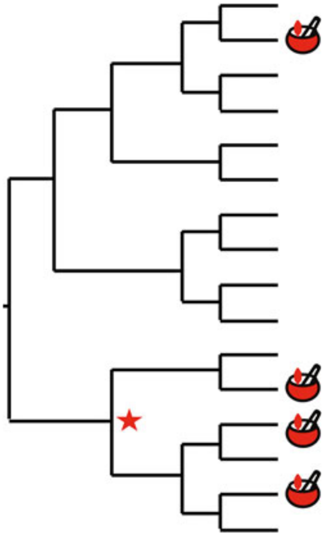

Fig. 5.1 Phylogenetic exploration of medicinal plant diversity. The figure shows a hypothetical phylogeny, representing the relationships among several species, some of which are used in traditional medicine (marked with a *mortar* and *pestle*). The distribution of traditionally used species is not random with regard to phylogeny. Therefore, phylogenies can help focus the search for new medicinal plants, by focussing searches within nodes that are overabundant in traditionally used species (marked with a *star*)

on their ability to assign information to nodes of a phylogenetic tree instead of one species at a time and, therefore, explore the distribution of traits across organisms, mining and linking multiple biological databases (Cracraft 2002).

That related organisms share properties also has explanatory power in ethnobiology. Ethnobiologists are concerned with how people from different cultures make use of natural resources in different environments, and phylogenies can contribute to understanding the uses of biodiversity (Albuquerque and Medeiros 2013; Saslis-Lagoudakis and Clarke 2013; Saslis-Lagoudakis et al. 2011a, 2012, 2014). For example, phylogenetic approaches can help test the view in ethnopharmacology—the study of indigenous drugs and their uses—that traditional medicine is characterised by underlying patterns of species' phylogenetic relatedness (e.g. Moerman 1991) and that similar traditional uses are clustered among closely related species (e.g. Unander et al. 1995) (Fig. 5.1). Phylogeny can also provide a comparative framework that can enhance cross-cultural ethnobiological studies (Fig. 5.2), complementing studies of cognitive criteria used by humans to select useful biodiversity resources. Here we discuss the role of phylogenetic tools in exploring the uses of biodiversity. We summarise the studies that have been carried out to date and discuss future applications and interactions with other disciplines. Although these approaches can be applied to a wide range of biodiversity resources, such as microbes and animals (Leal et al. 2012; Zhu et al. 2011; Pacharawongsakda et al. 2009; Smith and Wheeler 2006; Thaker et al. 2013), we emphasise the work on medicinal plants, where most research has focused so far. We show how new approaches to the phylogenetic characterisation of life can interpret traditional uses of the natural world. We conclude that these approaches can help identify branches of the Tree of Life, which harbour useful products, and help us understand how ethnobiological knowledge is shaped and transmitted.

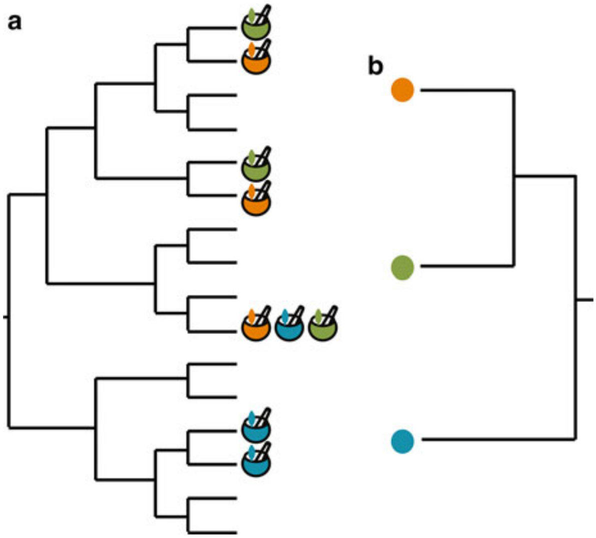

Fig. 5.2 Comparative phylogenetic methods in cross-cultural ethnobiology. The figure shows a hypothetical phylogeny, representing the relationships among several species (**a**). Species used in traditional medicine by three different cultural groups ("*blue*", "*green*" and "*orange*") are marked with a *mortar* and *pestle* of the respective colour (**a**). In (**b**), the hypothetical relationships of the three cultural groups are shown. Each cultural group uses three species, and one species is shared among all three groups. By calculating similarities between the ethnofloras of these groups based on species used in common, all ethnofloras are equally similar. However, when underlying phylogenetic relationships are taken into consideration, "*green*" and "*orange*" use closely related species, while "*blue*" use species from different lineages. This reflects the relationships among these cultural groups

5.2 Phylogenetic Exploration of Medicinal Plant Diversity

The integration of evolutionary theory in ethnopharmacology provides the opportunity to reveal patterns in peoples' selection of plants in traditional medicine (Fig. 5.1). In particular, phylogenetic tools can test the hypothesis that species' evolutionary relationships underlie their usage in ethnopharmacology. Systematics has been incorporated in ethnobiological research for a long time, as systematic principles have been known to underlie traditional knowledge (Berlin et al. 1966). Ethnopharmacologists have demonstrated systematic patterns in medicinal properties across different plant groups. A study of traditionally used species of *Phyllanthus* (Phyllanthaceae) showed that some subgenera of the genus have more medicinal species than others, even correcting for the sizes of subgenera (Unander et al. 1995). Numerous studies have investigated systematic patterns across whole medicinal floras, from a series of human cultures and geographic regions, including Africa (Douwes et al. 2008; Saslis-Lagoudakis et al. 2011b), Asia (Saslis-Lagoudakis et al. 2011b; Moerman et al. 1999), Central America

(Leonti et al. 2013, 2003; Amiguet et al. 2006), North America (Moerman 1991), South America (Bennett and Husby 2008; Gottlieb 1982; Gottlieb and Borin 2002), and Europe (Weckerle et al. 2011). These studies have employed different statistical methods to show that species usage in traditional medicine is not randomly distributed across species groups, demonstrating underlying phylogenetic patterns in traditional medicine.

All these studies have used classic, Linnaean taxonomic ranks to provide estimates of relatedness amongst organisms. Using phylogenetic trees brings significant advantages over estimating relatedness by membership to taxonomic ranks, which have been shown to be non-equivalent across divergent lineages and often non-monophyletic (do not reflect evolutionary relationships). Although molecular systematics has led to taxonomic revision (e.g. A.P.G. 2009), and has therefore reduced previous sources of error, analyses at fixed higher taxonomic ranks will be more arbitrary than direct phylogenetic measures of relatedness, which allow rank-free tests to be performed across all sampled taxa.

To the best of our knowledge, the first study that mapped ethnobotanical data on a phylogenetic tree was a review of the traditional uses of *Plectranthus* (Lamiaceae). The authors used a phylogenetic tree of the genus to show that species used medicinally in *Plectranthus* are close relatives and most come from the same clade (Lukhoba et al. 2006). However, as no explicit measure of phylogenetic relatedness was applied, this was simply a visual interpretation of putative evolutionary patterns. Beyond visualising these patterns on phylogenetic trees, explicit tests of phylogenetic signal have been developed and used in evolutionary biology. For example, a variety of methods exist that can formally test for the degree of phylogenetic clustering of ethnopharmacologically used species. Mean phylogenetic distance (MPD) and net relatedness index (NRI) can be measured among medicinal species, and then compared to a random distribution of these values to test whether medicinal species are more closely related that expected by chance, either within a region's flora, or within a higher taxon (Webb et al. 2008). Similarly, the *D* statistic of Fritz and Purvis (2010) can compare phylogenetic distribution of medicinal species to distributions generated by random or by Brownian motion. Additionally, methods determining the position of phylogenetic clustering of ethnopharmacological use can identify lineages that are prominent in traditional medicine. These methods test all nodes of a phylogenetic tree for overabundance in ethnopharmacologically used terminal taxa distal to it [e.g. "nodesig" command (Webb et al. 2008)], and can identify nodes that have given rise to taxa that are more likely to be used traditionally.

A handful of studies have recently demonstrated the potential of these methods for ethnopharmacology and ethnobotany in general. For example, a recent study constructed a phylogenetic tree of the legume genus *Pterocarpus* (Fabaceae), which is distributed pantropically and used in traditional medicine across its range. The uses of all species were collated from published sources and were mapped on the phylogenetic tree. The findings of that study demonstrated that species used to treat similar conditions are closely related and highlighted lineages within *Pterocarpus* that are overrepresented in species used to treat certain conditions, such as malaria, inflammations, gastrointestinal and musculoskeletal conditions (Saslis-Lagoudakis et al. 2011a). The identification of those groups of species allows the prioritisation of species with high potential to treat these conditions. Similar patterns have been found at a higher taxonomic level. For instance, a study that generated a phylogenetic tree for the flora of the Cape of South Africa demonstrated that traditionally used plants are not randomly phylogenetically distributed. Instead, traditionally used plants are concentrated in some parts of the tree, and taxa used for different purposes (e.g. medicine and food) are found in different parts of the tree (Forest et al. 2007). A similar study on the floras of Nepal, New Zealand and the Cape of South Africa showed that in all three floras phylogenetic clustering is demonstrated when medicinal usage is broken down into categories of medical conditions that species are used for (Saslis-Lagoudakis et al. 2012). This demonstrates that, within a flora, closely related plant taxa are used to treat similar medical conditions. However, another study demonstrated that, depending on the statistical approach used to test for phylogenetic pattern, there might not always be phylogenetic clustering in medicinal use. Using data on plant species used to treat 33 categories of medical conditions in South Africa, it was shown that, depending on the null models considered, phylogenetic clustering was shown for up to 45 % of use categories (Yessoufou et al. 2014).

Phylogenetic studies of ethnofloras to date have not considered cultural importance and have scored plants as used or not (for specific therapeutic applications, or in traditional medicine generally). There are several measures of cultural importance (Prance et al. 1987; Moerman 1991) and consensus on use of taxa in traditional medicine (Trotter and Logan 1986), which aim to identify prominent taxa in local ethnopharmaocopoeias. Methods handling continuous traits in phylogenetic trees, such as Blomberg et al.'s K and K^* (2003), Pagel's lambda (1999), can be applied to investigate the phylogenetic distribution of values for these measures across taxa. This approach can reveal whether medicinal use is phylogenetically clustered, when the cultural importance of taxa is taken into consideration. The number of uses per taxon, which is a simple measure of cultural importance, has been considered from an evolutionary distinctness perspective (Yessoufou et al. 2014)—that is, the degree to which species are located on phylogenetic branches without many close relatives (Isaac et al. 2007). By incorporating number of uses per taxon, the authors demonstrated that evolutionarily distinct taxa have significantly fewer uses than those that are not, suggesting that people tend to use species with many close relatives in a more diverse way (Yessoufou et al. 2014).

At a broader level, evolutionary tools can be applied to shed light on the relationship of humans with the natural environment (Albuquerque and Medeiros 2013; Saslis-Lagoudakis and Clarke 2013), such as the utilisation of other biodiversity resources broader aspects of ethnobiological research, such as food (Valussi and Scirè 2012), or the elucidation the human cognitive and behavioural underpinnings of biodiversity use. Organoleptic properties (sense perceptions, including sight, smell, and touch) appear to be particularly important in the selection of medicinal species (Etkin 1988; Bennett 2007; Leonti et al. 2002). Also, widespread species are more likely to be utilised, as they are more apparent to humans (Leonti et al. 2013;

Lucena et al. 2012). Using phylogenetic trees, ethnobiologists can test for the correlation between the usage of a group of organisms and organoleptic or ecological traits, shedding light on the criteria humans use to explore and utilise their natural environment. These methods can be used at different hierarchical levels and across organismal groups.

5.3 Comparative Phylogenetic Methods in Cross-Cultural Ethnobiology

Beyond identifying lineages that stand out in terms of their uses in traditional medicine, phylogenetic tools can also enhance the way we perform cross-cultural ethnobiological comparisons. In cross-cultural ethnobiology, researchers compare the use of biological resources across different regions and/or cultures, in order to investigate the extent to which ethnobiological knowledge is shared among cultures, the factors underlying this shared knowledge, as well as the applications of shared patterns, such as identifying lineages with the potential to yield new natural products. Comparative phylogenetic methods can explicitly test whether the phylogenetic patterns observed in ethnomedicine are similar in different parts of the world, across cultural groups and natural environments (Fig. 5.2).

Several studies have demonstrated that there is agreement in the plant groups used across different cultures (Moerman et al. 1999; Saslis-Lagoudakis et al. 2011b; Leonti et al. 2003). However, due to differences in plant availability among regions, comparability of plant use is reduced. To circumvent this issue, medicinal species are placed into higher taxa that are more easily comparable among localities. Nevertheless, the use of high Linnean taxa in comparative studies has certain limitations. Some information will be discarded when a higher taxon is present only in one locality and not the rest. Phylogenetic tools enable datasets from different localities to be combined, because all plant species used in different localities can be included in the same phylogenetic tree, and phylogenetic distance between species used in different regions can be calculated. In addition, the phylogenetic approach also recognises that, within higher taxa, species may be more or less closely related. This information about relatedness within higher taxa is lost where Linnaean higher taxa are used; conversely, the inclusion of phylogenetic trees in comparative studies allows medicinal species to be placed on a continuum of phylogenetic relatedness. The cross-cultural phylogenetic study of three complete floras (Nepal, New Zealand, and the Cape of South Africa) demonstrated not only that species used to treat specific medical conditions are clustered in a few plant lineages, but also that the same lineages are used to treat similar conditions in disparate regions, suggesting that their bioactivity has been independently discovered (Saslis-Lagoudakis et al. 2012). These patterns might be attributed to shared properties of the closely related plants selected by different people. Indeed, lineages used in common in these three regions are the ones that have already produced several pharmaceutical drugs (Saslis-Lagoudakis et al. 2012), suggesting that bioactivity underlies traditional medicinal knowledge.

Although the fact that people have selected the same lineages in disparate regions suggests that similar cognitive criteria across human cultures underlie plant utilisation (Moerman et al. 1999; Saslis-Lagoudakis et al. 2012), cross-cultural ethnobotanical studies using comparative phylogenetic methods can also generate hypotheses about how plant use is transmitted among ethnic groups. For example, a comparative study of dye plants used by 11 indigenous tribes in Southwestern USA analysed the ethnobotanical data using cladistic analysis (Hart and Cox 2000). This analysis estimated relationships of the tribes based on which dye plants they used. Although these relationships cannot necessarily be used to reflect cultural relationships, the authors note that they can be used to generate hypotheses of cultural diffusion: by identifying how tribes are grouped from the cladistics analysis, one can observe patterns underlying those groupings (e.g. similarity of environments, close geographic distance). In turn, these can help uncover the processes that affect how discoveries and uses of plant species spread among groups (Hart and Cox 2000). Bringing phylogeny to bear directly on this question, a recent study collated information on medicinal plant use for 12 ethnic groups in Nepal, in order to test how shared ancestry, geographical proximity, and interaction with the natural environment shape cross-cultural similarities in plant use (Saslis-Lagoudakis et al. 2014). First, pairwise similarities of the medicinal floras of ethnic groups were calculated. To do that, a phylogenetic tree of the flora on Nepal was used, and the medicinal floras were plotted on that tree so phylogenetic distances between pairs of medicinal floras could be calculated. The phylogeny was used to minimise the effects of taxonomic biases as described earlier, i.e. assigning species to high taxonomic ranks in order to make medicinal floras comparable and excluding taxa that are not present across localities due to differences in plant availability in the country. Three more pairwise distances were calculated: (1) shared ancestry based on linguistic affinities of the ethnic groups, (2) geographic proximity based on the distributions of the ethnic groups in the country, and (3) similarities of the floristic environments to which ethnic groups are exposed, again using phylogenetic distances from the phylogenetic tree of the flora on Nepal. Using Mantel tests, the authors tested for the correlation between the similarities between medicinal floras and the three other pairwise distances, and found that cultures found in similar floristic environments have significantly similar medicinal floras. On the contrary, the effects of shared ancestry and geographical proximity were not significant. The findings of that study demonstrate that medicinal floras converge in similar floristic environments, showing that medicinal floras adapt to local environments (Saslis-Lagoudakis et al. 2014).

Another question explored by ethnobotanists is how migrant people adapt their ethnopharmacopoeias to new environments (Pieroni and Quave 2005; Ceuterick et al. 2008, 2011), and phylogenies can also be useful in this exploration. Several studies have found evidence that migrant communities tend to use some species in common between their new and old floristic environments. For example, a comparative study of the ethnomedicine of the Akha people in Thailand and China found that 16 out of 95 species were used in common (Inta et al. 2008), while a study of three Afro-Surinamese populations and their African ancestor groups found 15 out of a total of 324 traditionally used species were used in common (Vossen et al. 2014).

However, both studies found that similarities were higher at the family level, and that concepts of ethnomedicine were preserved in migrant groups (Inta et al. 2008; Vossen et al. 2014). This suggests that, due to differences in floristic compositions, migrant communities might select species that are closely related to the ones used in the environment of origin, as has been discussed in other studies (Albuquerque and Andrade 1998; Medeiros et al. 2011; Voeks 1990). Phylogenetic tools, particularly measures of phylogenetic distance (Faith 1992; Webb et al. 2008), can test if this "phylogenetic replacement" occurs in ethnomedicine of migrant communities, by calculating phylogenetic proximity among species used in the environment of origin and the new environment.

5.4 Challenges and Opportunities for Interdisciplinary Research

Major caveats for the analysis of ethnobiological data using phylogenetic methods lie in the comparability, relevance and limitations of existing data. Traditional knowledge is largely limited to local species and diseases. Unmet medical needs related to welfare and ageing diseases are less likely to be met by traditional medicine, and organisms that are rare or difficult to access are more likely to have been overlooked (Lucena et al. 2012; Leonti et al. 2013). Additionally, local ethnopharmacological datasets are likely to be partial, particularly from regions where ethnobiological fieldwork has been scarce. Hence, there is great need for more fieldwork, particularly with poorly known cultural groups. Another limitation is that phylogenetic relationships are not clear for all branches of the Tree of Life (http://www.phylo.org/atol/), and phylogeny cannot be explored for all groups of organisms.

Despite these limitations, a phylogenetic view of ethnobiology can help address a major challenge in ethnopharmacology: the investigation of overlap between the "traditional healer vs. the modern physician" (Gottlieb et al. 2002). The time and resource costs of ethnobiological fieldwork and assays or trials have limited the systematic review of the relationship between ethnopharmacological use and bioactivity. Phylogeny can provide a unifying framework for these fields. In the same way that ethnobiological data can be analysed using phylogenetic methods, pharmacological data can also be placed in a phylogenetic context. The observation that related organisms could be chemically similar gave rise in the 1970s to chemosystematics, the use of chemical data to explore species relationships (Gibbs 1974; Harborne and Turner 1984; Bisby et al. 1980). Since, phylogenetic studies have investigated evolutionary patterns in the production of chemical constituents (Wink 2003; Wink and Mohamed 2003; Agrawal et al. 2009; Ekenäs et al. 2009) and it has been suggested that phylogenetic insights into organismal chemistry have potential for exploring medicinal plant diversity (Cox and Balick 1994; Gottlieb and Borin 2002). This has been explored in recent studies, which have shown that bioactivity is constrained by phylogeny (Rønsted et al. 2008; Harris et al. 2012; Bay-Smidt et al. 2011; Larsen et al. 2010; Rønsted et al. 2012).

By incorporating species' evolutionary relationships, data from ethnobiology and pharmacology can be compared, even if they are not derived from the same species. These approaches have been attempted, however rarely in an explicitly phylogenetic context. For example, a study showed a correlation between the presence of different classes of chemical compounds and traditional medicinal use: there was a strong positive correlation between presence of caffeates (caffeic acids) and traditional medicinal use in a dataset of plants used by various Amazonian communities (Gottlieb et al. 2002). An investigation of the Popoluca ethnopharmacopoeia (Mexico) showed that medicinal use was largely centred around plant families that have been demonstrated to produce pharmaceutical drugs, and that clades with particular traditional uses are characterised by the presence of pharmacologically active chemical compounds (Leonti et al. 2013). These two studies used classification as a proxy for phylogeny, however the finding that the lineages rich in traditional medicines include significantly more pharmaceutical drugs than expected (Saslis-Lagoudakis et al. 2012) testifies to the potential of combining traditional knowledge with pharmacology. Of course, plant groups that are intensively used are more likely to have been investigated pharmacologically. Therefore, the overlap between pharmacologically active plant groups and those used traditionally can be attributed to bioactivity in traditionally used species, or to bias in selection of species for development of pharmaceutical drugs, leading to problems of circularity. Future efforts can plot biochemical and pharmacological data, along with traditional uses and organoleptic and ecological properties of species on phylogenetic trees, in order to test for similar trends in their phylogenetic distribution. This can ultimately allow the influences of perception and inherent pharmacological properties to be teased apart, and provide the strongest test of whether species selected for inclusion in "the healer's pouch" should also be those targeted in biodiversity exploration for research and development (Cox 2000). Interdisciplinary research and network or correlation-based bioinformatic tools may improve drug discovery efforts by providing more accurate and realistic interpretations of complex data and connections, and are receiving increasing attention in the drug industry (Csermely et al. 2013).

These interdisciplinary approaches will require interaction between evolutionary biologists, ethnobiologists and biochemists, who can collaborate to explore data and methods (Saslis-Lagoudakis and Clarke 2013). Recent actions testify to the future of these interactions. For example, the MedPlant Marie Curie International Training Network (www.medplant.eu), places a group of 15 early-career researchers from these scientific fields within a network involving several partners from academia and the industry, in order to explore medicinal plant diversity within a phylogenetic framework. In the interactions among scientists from these fields, ethnobiologists can contribute ethnobiological data. Possibly more importantly, however, they can lead and supervise the ethical aspects of this research, as well as ensure that the outcomes of this type of research meet the needs of local communities.

5.5 Conclusions

Phylogenetic methods have enabled the interpretation of biodiversity utilisation through an evolutionary lens, allowing the exploration of traditional use of biodiversity in a phylogenetic context. Interdisciplinary collaborations between evolutionary biologists and ethnobiologists are poised to use data accumulated over decades of research to answer long-standing questions in ethnobiology. Further interaction with biochemists can give rise to opportunities, while broadening the applications and scope of these approaches through further exploration of data and methods. In turn, these collaborations can inform and promote the sustainable and efficient use of biodiversity.

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Chapter 6
Niche Construction Theory and Ethnobiology

**Ulysses Paulino Albuquerque, Washington Soares Ferreira Júnior,
Flávia Rosa Santoro, Wendy Marisol Torres-Avilez,
and José Ribamar Sousa Júnior**

6.1 Introduction

Evolutionary ethnobiology focuses on studying the dynamic relationships between humans and biota and uses evolutionary assumptions to construct models and hypotheses for understanding these relationships. Evolutionary assumptions are used by disciplines other than biology to understand a broad range of natural and social phenomena. Cultural phenomena are also of interest to ethnobiologists, and different researchers have proposed scenarios for the study of cultural evolution based on Darwinian reasoning (e.g., Cavalli-Sforza and Feldman 1981; Richerson and Boyd 1985).

Humans materially and symbolically appropriate nature in a manner unlike any other living organism. In addition to being the dominant species, humans have transformed the planet on a scale that continues to expand. Humans are one of the largest agents of ecological change, and the effects of these changes are still poorly understood. For example, the domestication of plants and animals has produced dramatic global transformations and affected the evolution of domesticated species as well as human populations (Larson and Fuller 2014).

Garrido-Pérez and Glasnovic (2014) argued that human actions can alter the patterns and dynamics of such diversity. When humans collect seeds, they behave as seed predators; and when they hunt animals, they promote top-down changes in the trophic structure (see Garrido-Pérez and Glasnovic 2014). These relationships can be modeled in terms of ecology, culture, and genetics.

U.P. Albuquerque (✉) • W.S. Ferreira Júnior • F.R. Santoro
W.M. Torres-Avilez • J.R. Sousa Júnior
Laboratory of Applied and Theoretical Ethnobiology, Biology Department, Universidade Federal Rural de Pernambuco, Rua Dom Manoel de Medeiros s/n, Dois Irmãos, Recife, Pernambuco 52171-900, Brazil
e-mail: upa@db.ufrpe.br; upa677@hotmail.com

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Thus, by altering the environment, humans act as a powerful niche constructor. Niche construction (NC) is a process by which living beings, including humans, modify their own niches or those of other organisms through their activities and decisions. By altering their niches, organisms can also alter the natural selective pressures. The notion of NC is intuitive and there is significant evidence detailing the consequences of organismal activity on the environment (see review in Odling-Smee et al. 2003).

In general, ethnobiological researchers automatically assume that NC occurs. For example, when an ethnobiologist studies the effect of stem bark extraction on the population structure of a plant species, he or she assumes that the extraction action may alter a plant population in one or more aspects. Such assumptions are more explicit when ethnobiologists study the management of species and processes of plant and animal domestication. In the previous examples, the ecological and evolutionary impact of humans on other living beings is clear because it contributes to the creation of selective environments; however, the inference that these same practices may generate selective pressures is not usually made.

NCT is considered an interesting concept for understanding the consequences of changes that organisms produce in environments and how these modifications may have evolutionary implications. The different implications and ramifications of NC are still underestimated and poorly investigated, both theoretically and experimentally (see Laland and Sterelny 2006; Scott-Phillips et al. 2014; Matthews et al. 2014), which may be a result of standard evolutionists not recognizing NC as an essential evolutionary process with the same explanatory power as natural selection (for a discussion of the different viewpoints on the role of NC, see Scott-Phillips et al. 2014).

In this chapter, we explain how NCT can provide scenarios to test the ability of evolutionary and ecological hypotheses to describe the relationships between humans and nature (the interest of ethnobiology) and detail opportunities for further research. We also briefly argue why we believe NCT offers insights that can be useful for approaches in evolutionary ethnobiology. To illustrate how NCT can be an integrating concept in ethnobiology, we focus on classical examples available in the literature on NCT and gene–culture coevolution.

6.2 What Is Niche Construction Theory?

The idea that humans are niche constructors is not recent, and over time, it has been addressed in different ways. Certain organisms have such pronounced NC abilities that they are known as ecosystem engineers. Numerous empirical studies have emphasized the ability of these engineers to create or modify characteristics of ecosystems and generate positive impacts on biodiversity (see the meta-analysis in Romero et al. 2014). One classic example found in many studies on NCT is the ability of beavers to build a dam. Dam building not only creates a lake and affects river flow but also dramatically alters entire local dynamics. Additionally, it affects the propagation of dam-building genes, which can influence the evolution of beavers (Wright et al. 2002). Once a dam is built, future generations of beavers can still benefit from it as a legacy from previous generations. Thus, this example demonstrates an important concept in NCT: *ecological inheritance*. Therefore, niche construction occurs if at least two criteria are present: (1) "an organism (i.e., a candidate niche constructor) must significantly modify environmental conditions; (2) the organism-mediated environmental modifications must influence selection pressures on a recipient of niche construction" (Matthews et al. 2014: 247). This implies that NC can occur without influencing the evolution of an organism, but if it occurs, we have a third criterion pointed out by Matthews et al. (2014: 247): "there must be a detectable evolutionary response in a recipient of niche construction that is caused by the environmental modification of the niche constructor." Note that the niche constructor and the recipient of niche construction can be the same organism (see the above example of a dam built by beavers). Thus, NC differs from ecosystem engineering because the latter meets only the criterion 1 mentioned above.

Thus, in a broad sense, "niche construction occurs when an organism modifies the feature-factor relationship between itself and its environment by actively changing one or more of the factors in its environment, either by physically perturbing factors at its current location in space and time, or by relocating to a different space-time address, thereby exposing itself to different factors" (Odling-Smee et al. 2003: 41). Therefore, changes in time and space and the responses of organisms to these changes are included in the NC concept. The modifications performed by organisms that affect themselves and other species are not always adaptive and do not necessarily have evolutionary consequences.

The effects of NC can be positive or negative. NC effects are positive when they increase the fitness of the niche-constructing organisms, and they are negative when they reduce fitness (Odling-Smee et al. 2003; Barker and Odling-Smme 2014). However, NC does not always increase the fitness of organisms, and the effect is often better characterized by increases in the intrinsic growth and survival rates than reproductive success (see Odling-Smee et al. 2003).

Applying the abovementioned notions to humans, their legacy is observed in changes through space and time and ecological inheritance but also inherited cultural knowledge that is transmitted to future generations, which reinforces culture-mediated NC. Thus, cultural NC can operate by generating genetic changes as well as ecological and cultural changes. For example, the aggregation of people in large communities can lead to the emergence and rapid dissemination of many diseases. Humans can respond to this new selective pressure by building hospitals or developing vaccines (Odling-Smee et al. 2003). Thus, when we build a hospital, we are responding to the effect of a previous NC, and this response may damp out selection on human genetics; such a response is referred to as a counteractive cultural NC. The cultural NC usually responds more rapidly through an adaptive cultural response. However, when a cultural response does not occur, an important genetic response with evolutionary implications may occur if natural selective pressures were modified.

Table 6.1 Examples of the four categories of niche construction

	Perturbation	Relocation
Inceptive	Organisms initiate a change in their selective environment by physically modifying their surroundings e.g., emission of detritus	Organisms expose themselves to a novel selective environment by moving to or growing into a new places e.g., invasion of a new habitat
Counteractive	Organisms counteract a prior change in the environment by physically modifying their surroundings e.g., thermoregulation of nests	Organisms respond to a change in the environment by moving to our growing into a more suitable place e.g., seasonal migration

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Odling-Smee et al. (2003) proposed two basic types of NC: *counteractive* and *inceptive*. The *counteractive* (responses to externally produced changes) form involves all of the activities of niche-constructing organisms that reduce existing selective pressures or oppose changes in environmental conditions, whereas the *inceptive* (produce novel changes) purpose involves activities of the niche-constructing organisms that initiate a specific change, such as dam building by beavers (Odling-Smee et al. 2003; Barker and Odling-Smme 2014). Two other classes of niche construction also require consideration: perturbation and relocation. Perturbation occurs when a niche-constructing organism modifies the environment by either construction or destruction, whereas relocation occurs when a niche-constructing organism moves to a new location (Odling-Smee et al. 2003; Barker and Odling-Smme 2014) (Table 6.1).

Laland and Brown (2011) addressed the question of whether recent human NC is typically adaptive and argued that population growth from the Holocene to the present is strong evidence that many human characteristics remain adaptive. From an ethnobiological perspective, the manner in which humans intellectually and materially appropriate nature could be considered adaptive. Traditional ecological knowledge (TEK) is understood by certain researchers as adaptive knowledge (Berkes et al. 2000). However, despite the claim “that adaptive human behavior will be the norm and maladaptation the exception,” there is evidence that some cultural phenomena are maladaptive cultural traits (Laland and Brown 2011: 126).

Based on the transmission of TEK, many cultures have transferred information (cultural inheritance) to subsequent generations that ultimately modified their local ecosystems (Smith 2011a). However, despite the ethnobiological focus on describing the methods by which cultures have modified their environments, the term NC has not been conceptually employed to describe phenomena or theoretically employed as a framework for understanding these phenomena. There are various terms used by ethnobiologists that essentially describe human NC, including domesticated landscape, anthropogenic landscape, forest management, human-modified environments, indigenous management, traditional resource management, etc. (for additional terms employed in the literature, refer Smith (2011a, b)). According to Smith (2009), all of these terms could comfortably be included under the “general reading of niche construction.”

The adoption of NCT could offer a unifying perspective for ethnobiologists to address the relationship between people and nature. Because many ethnobiologists are interested in the management and conservation of biodiversity, Laland and Boogert (2010: 732) argued that "the properties and dynamics of ecosystems will never be satisfactorily comprehended until it is recognized that organisms do considerably more than compete with each other, eat and be eaten (i.e., engage in trophic interactions) (…). As human are enormously potent niche constructors, understanding how niche construction regulates ecosystem dynamics and affects selection pressures on other species is central to understanding our impact on the environment."

6.3 Key Concepts of NCT

According to evolutionary biology, adaptation is a process through which natural selection molds an organism to a specific environment (Scott-Phillips et al. 2014). NCT does not focus on the evolution of organisms as an isolated process but rather as a coevolutionary process between organisms and the environment. Thus, NCT views adaptation as a complex, dynamic and reciprocal interaction between the processes of natural selection and NC through which niche-constructing organisms modify the environment (Table 6.2) (Odling-Smee et al. 2003). Therefore, organisms inherit environments through the process of ecological inheritance as well as genes. Compared with the process of genetic inheritance, ecological inheritance is transmitted by organisms through modifications to their environments; in addition, it is not necessarily transmitted by genetically related organisms but rather continuously transmitted by multiple organisms to other organisms within and between various generations (see Odling-Smee and Laland 2011). From a human perspective, the changes made by our species to the environment are not only inherited by parents of the niche constructors but also by an entire unrelated population. However, cultural inheritance must be considered along with the process of ecological inheritance in relation to human populations.

Humans inherit environments as well as information on how to alter (manage or create) and live in these environments. Cultural inheritance differs from genetic inheritance because it is continually transmitted from many people to many people and involves different strategies of information transmission and social learning (see Odling-Smee and Laland 2011). Thus, we can understand cultural NC as a "subset of NC that is the expression of culturally learned and transmitted knowledge (as opposed to individually learned or genetic information)" (Odling-Smee and Laland 2011: 226). According to Laland et al. (2014: 77) "much of human niche construction is guided by socially learned knowledge and cultural inheritance, but the transmission and acquisition of this knowledge is itself dependent on pre-existing information acquired through genetic evolution, complex ontogenetic processes, or prior (a)social learning."

Table 6.2 Comparing standard evolutionary theory and niche construction theory

Standard evolutionary theory	Niche construction theory
Focus: Organismic evolution in response to environments	*Focus*: The coevolution of organisms and environments
Causation: Primarily unidirectional, with autonomous selective environments shaping organisms. Reciprocal causation is recognized in some "special cases" where the source of selection is biotic (e.g., sexual selection, predator–prey (coevolution)	*Causation*: Primarily reciprocal, with selective environments shaping organisms, and organisms shaping selective environments, either relative to themselves or other organisms
Niche construction: Organisms acknowledged to change environmental states, but this is treated as the product of natural selection and rarely as an evolutionary process in its own right. Focus is restricted to adaptations expressed outside the bodies of the organisms (e.g., extended phenotypes)	*Niche construction*: Treated as an evolutionary process in its own right. Focus is not exclusively on adaptations, but includes changes in environments caused by the byproducts of organisms (e.g., detritus), acquired characters (e.g., learned), or the collective metabolism or behaviors of multiple individuals/species
Inheritance: Primarily genetic, although maternal, epigenetic, cytoplasmic, and cultural inheritances recognized as "special cases"	*Inheritance*: Genetic and ecological inheritance (i.e., legacies of selection pressures previously modified by niche construction). Genetic and ecological inheritance interact to form "niche inheritance." Maternal, epigenetic, cytoplasmic, and cultural inheritances can be examples
Organism–environment complementarity (adaptation): The product of natural selection	*Organism–environment complementarity (adaptation)*: The match between organism and environment results from dynamic interactions between niche construction and natural selection

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Laland and O'Brien (2011: 193–194) list phenomena that when considered from an NCT viewpoint, provide insight into topics of ethnobiological interest:

- "There is selective feedback from niche construction to genes in the constructor other than those expressed in niche construction.
- Niche-constructed effects can persist and act as modified sources of selection for longer than the lifetime of their constructors (ecological inheritance).
- By-products can play an evolutionary role by modifying selection pressures through niche construction.
- Acquired characters can play an evolutionary role by modifying selection pressures through niche construction.
- Evolutionary causality does not always start in the environment.
- Niche construction can drive (diffuse and direct) coevolutionary events.
- Niche construction can modify developmental environments.
- Adaptation (adaptive complementarity) results from two processes (selection and construction), not one."

We are convinced that NCT can be an integrating and unifying concept in ethnobiology because it can accommodate scientists that may or may not feel comfortable with concepts derived from evolutionary biology. Laland and O'Brien (2011: 195) argued that "recognition of the significance of niche construction to developmental and cultural processes does not require any commitment to evolutionary epistemology, and the niche-construction perspective is broad enough to encompass those who regard learning and cultural change as only weakly analogous to biological evolution."

6.4 Interpretations Based on NCT and Its Ethnobiological Implications

6.4.1 Plant Domestication and the Case of Amylase

Plant domestication is a subject that is of interest to ethnobotanical researchers seeking to assess the influence of human management on plant populations either directly (Smith 2007; Parra et al. 2010; Lins Neto et al. 2013) or indirectly by altering the environment. The entire set of archaeological, genetic, and ecological evidence indicates that humans profoundly altered the evolutionary history of many plant and animal species (Larson et al. 2014). By focusing attention on a specific species by artificially selecting phenotypes that are desirable or by altering the environment in which these species live, its frequency may be increased and specific alleles may be propagated. Additionally, the descendants of these original populations can inherit an environment that was generated and/or modified by these actions. However, limited studies have examined the possible effects that domestication, among other cultural practices, can have on the domesticators themselves. In all scenarios, the focus is placed on how humans alter other species, whereas limited studies have examined how these decisions also affect human populations. Human actions can involve different changes depending on the plant or plant part that is the target of interest to the domesticator. For example, many species were selected to increase the size of their tubers or concentration of starch (Smith 2007). In promoting these alterations, however, the domesticators also generated consequences for themselves.

Starch is one of the primary components of foods cultivated throughout the world, and because of its importance, the ability of human groups to digest starch may be associated with the history of agriculture (Perry et al. 2007). Human agricultural populations have a higher proportion of individuals that have a large number of copies of the gene that promotes the expression of the enzyme amylase (*AMY1*) compared with hunter-gatherer, fishing or pastoral populations, whose diets are primarily based on proteins, fats and simple sugars. Additionally, a strong correlation has been found between the number of copies of this gene and expression level of amylase. Because a greater number of *AMY1* copies and the concomitant increase in salivary amylase improve the efficiency of starchy food digestion, the cultural practice of cultivating starch-rich foods increased the frequency of genes responsible for starch assimilation.

High amylase levels enable the rapid absorption of sugars in the mouth. In addition, the activity of salivary amylase continues during digestion in the stomach and intestines (Fried et al. 1987), thus providing a rapid method of obtaining energy that may be crucial to the survival of individuals when they are stricken with diseases of the digestive system, such as inflammation and diarrhea (Perry et al. 2007). Human populations with a poor ability to digest starches encountered various associated problems, such as diseases of the digestive system. From an ethnobiological perspective, these populations most likely had to develop a traditional pharmacopoeia to address these problems. If this hypothesis is correct, differences should be observed in the incidence of specific diseases associated with starch consumption and in strategies for curing these diseases between populations with high or low amylase production.

6.4.2 The Case of Lactase

In the context of this discussion, perhaps the most well-known and discussed case is the dispersal of the lactase persistence allele in the global population. This case is one of the few well-documented cases (genetically as well as ethnographically) of gene–culture coevolution. The ability to digest milk in adults occurs because of the expression of a gene that is responsible for lactase persistence and produces an enzyme involved in the digestion of lactose. The strong correlation between the phenotype of lactase persistence with the history of the cultural practice of cattle domestication and milk consumption suggests that cultural evolution led to the increased frequency of the lactase persistence allele in adults (Fig. 6.1). The distribution of this allele is concentrated in northern Europe and Africa, which are regions where milking practices have historically been performed by human groups (Ingram et al. 2009). According to these authors, this cultural practice acted as a source of selection in humans and produced a higher frequency of specific lactose absorption alleles in people from these regions. However, exceptions to this pattern that are driven by "cultural pressure" have produced a hypothesis wherein other processes could be modulating this phenomenon in certain cultures (for a more detailed explanation, see Ingram et al. 2009).

Feldman and Cavalli-Sforza (1989) suggest that the probability of spreading the allele responsible for lactose absorption in a group depends on the probability that the descendants of a population that consume milk copy this behavior (cultural inheritance) and become milk consumers. If milk consumption is present in the entire generation, there will be an adaptive advantage for the gene that confers tolerance to lactose, and it will become fixed in the population in a few generations. Considering the high incidence of lactose tolerance in the global population, the authors attribute the permanence of this gene to the cultural practice of consuming

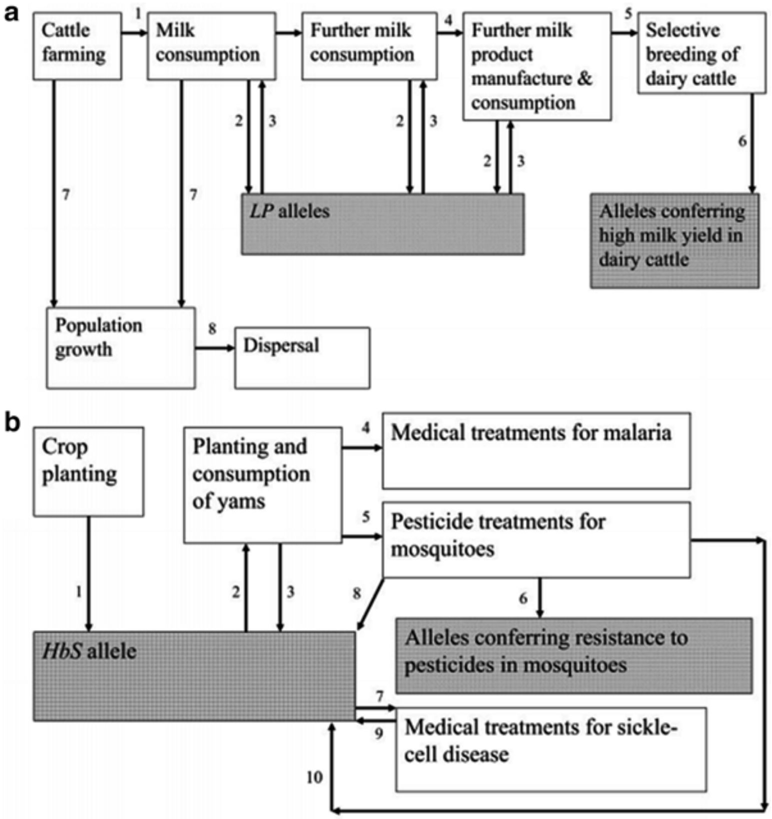

Fig. 6.1 Construction chains, depicting the chain of causal influences following a cultural niche-constructing practice for (**a**) dairy farming and (**b**) crop planting. Cultural processes are shown in *white boxes*, and genetic change is shown in *shaded boxes*. In *panel* (**a**), the domestication of cattle triggers (*1*) milk consumption, which (*2*) favors the spread of lactase persistence (LP), (*3*) promoting further milk consumption, which (*4*) elicits further milk-product manufacture and consumption, which (*5*) leads to selective breeding of cattle, which (*6*) selects for alleles conferring high milk yield in dairy cattle. In addition, cattle farming and dairy-product consumption (*7*) lead to population growth, which (*8*) triggers dispersal into new environments. In *panel* (**b**), crop planting (*1*) inadvertently promotes the spread of malaria, leading to selection for (HbS), and the resulting incidence of sickle-cell disease (*2*) favors the planting of yams and other crops with medicinal benefits, which (*3*) further promotes the spread of (HbS) and (*4*) scaffolds the development and/or application of medical treatments for malaria, as well as (*5*) pesticide treatments for mosquitoes, which (*6*) generates selection for alleles conferring resistance to pesticides in mosquitoes. The spread of sickle cell (*7*) scaffolds the development and/or application of medical treatments for sickle-cell disease. Pesticide treatment of mosquitoes (*8*), medical treatment for sufferers of sickle-cell disease (*9*), and malaria victims (*10*) affect the intensity of selection on the HbS allele. Taken from O'Brien and Laland (2012) with permission of the publisher (Grant number: 108546—University of Chicago Press)

milk for various generations. From the perspective of NCT, lactose tolerance in our evolutionary history was caused by the adoption of the practice of consuming milk, which preceded any genetic modifications (refer to Scott-Phillips et al. 2014). Stated more clearly: "(…) evolution proceeds not because genes that cause dairy farming have higher fitness than those that do not (no such gene exist), but because dairy farming causes a change in the selective environment to favor the lactose absorption alleles, even in societies dominated by lactose intolerants" (Scott-Phillips et al. 2014: 4).

The previous example raises important questions to be addressed in evolutionary ethnobiology studies that adopt an NC perspective. Hypothetically, populations that currently exhibit low frequency of the allele responsible for lactose absorption may use a repertoire of medicinal plants to treat digestive disorders of varying severity caused by the ingestion of milk. However, an extensive medicinal repertoire for these disorders may be not observed in lactose-tolerant human populations, almost certainly because they would not need to develop these medicines. We sought to show that historical decisions made by human populations (adopting the cultural practice involved in the ingestion of milk) affected our resistance to milk products and may have influenced the medical systems studied today. This is a hypothesis that should be investigated in future ethnobiological studies.

6.4.3 The Case of Malaria

Another example of genetic modification caused by cultural practices of a human group is found in the high rates of malaria in agricultural communities in eastern Africa (O'Brien and Laland 2012), which is a robustly documented example of coevolution that has implications for evolutionary ethnobiology. For thousands of years, human groups cultivated edible plants, primarily yams (*Dioscorea* sp.), in eastern Africa (Posnansky 1969). The opening of clearings for the cultivation of yams resulted in the accumulation of water in the soil after rainfall, which formed flooded regions because the removal of trees reduced the soil's capacity to percolate water. This environment favored the reproduction of the mosquito that is the vector for the protozoan *Plasmodium falciparum*, the malaria pathogen (Livingstone 1958), thus generating high rates of malaria in the region. Figure 6.1 illustrates the cascade effect of this cultural practice, which influenced decisions on the use of other natural resources.

Driven by a cultural practice, malaria acted as an evolutionary pressure that increased the frequency of the hemoglobin allele (HbS) and led to a condition known as sickle cell anemia. Individuals that are homozygous for this allele can present with severe anemia, whereas individuals that are heterozygous have sickle-shaped red blood cells, which inhibits the ability of the malaria protozoan to cause infection because the sickle-shaped cells are constantly destroyed by the spleen, which also destroys the parasite. Thus, several years of yam cultivation intensified the selection of the allele responsible for the deformation of red blood cells.

Further evidence that the cultivation of yams acted as an evolutionary pressure is that adjacent communities with distinct agricultural practices did not exhibit an increase in the frequency of this allele (Durham 1991).

However, the practice of deforestation to produce clearings may have generated consequences that have not been investigated. Using traditional medical systems as a reference, we can assume that populations that adopted deforestation as an agricultural practice and show higher resistance to malaria would have developed a much smaller repertoire of plants to treat this disease or its symptoms compared with populations that did not adopt deforestation as an agricultural practice.

Assuming that a specific cultural practice, such as the act of medicating a person for a specific disease, was a result of past decisions that led to a coevolutionary process, then certain cultural differences observed in ethnobiological studies may reflect a cascade of events wherein genes, culture and environment interact (Fig. 6.1). Well-documented examples, such as that of malaria and lactose tolerance, are unavailable to demonstrate how the niche construction theoretical framework can be applied to ethnobiological research. Thus, the interactions between humans and nature may have an even more complex character when considered from an evolutionary perspective.

6.5 Medical Regimens and Local Adaptations

In the previous examples, the consumption of starch and milk were dietary regimes derived from cultural practices that resulted in a coevolutionary process. When our species consumes different plant foods, compounds contained in these plants that can have undesirable effects must be processed. For starch, this process led to an increase in the frequency of the allele that improves digestion of starch. Based on local adaptations, other cultures can reduce these undesirable characteristics by using appropriate food preparation or cooking techniques (see Wollstonecroft 2011). In addition, "medical regimens" of natural products (plants or animals, for example) were developed by humans and added to their cultural systems to treat or prevent diseases.

Pharmacogenetic studies can provide examples of how cultural practices can explain the presence of polymorphisms of specific genes in humans and their implications on evolutionary ethnobiology from the perspective of NCT. Pharmacogenetics studies the genetic variations related to differences in the therapeutic responses of drugs of clinical interest (Ingelman-Sundberg 2001). For example, a dose of a specific drug may have a therapeutic effect on one group of individuals, have no effect on other groups, and be toxic in certain individuals. Thus, pharmacogenetics seeks to investigate genetic explanations of these inter-individual differences (Evans and Relling 2004; Ortega and Meyers 2014).

For example, polymorphisms of the cytochrome *P450* 2D6, also known as CYP2D6, represents a set of enzymes responsible for the metabolism of exogenous substances that protect organisms against toxins (Seripa et al. 2010). Certain individuals have multiple copies of the *CYP2D6* gene, which is responsible for encoding the enzymes of cytochrome P450, and this leads to the high production of CYP2D6 enzymes and high metabolism of exogenous substances, thus compromising the therapeutic response to drugs of clinical interest. In contrast, people that have fewer copies of this gene show lower metabolism of these substances, which can cause adverse effects when administering a small dose of drugs of clinical interest (Ingelman-Sundberg 2005). The distribution of individuals with many and fewer copies of the active gene *CYP2D6* varies in different human populations. Populations in Saudi Arabia and Ethiopia have a low number of inactive copies of the gene *CYP2D6* because of mutations (Ingelman-Sundberg 1997). Variations in the distribution of active copies of the gene in different human populations can be explained through an evolutionary scenario.

The CYP2D6 enzymes have a high affinity for plant alkaloids. Thus, it can be hypothesized that the selection of individuals with many copies of the *CYP2D6* gene in certain human groups is associated with selective pressure caused by previous diet patterns containing large quantities of plant alkaloids, which would be toxic in individuals that have few copies of the gene (Ingelman-Sundberg 2005). Native Ethiopians and a group of migrant Ethiopians living in Sweden were compared to determine their rate of debrisoquine metabolism, a substrate selective for the CYP2D6 enzymes (Aklillu et al. 2002). Individuals with the same genotype were selected from the two groups, and the group living in Ethiopia showed a lower rate of debrisoquine metabolism compared with the group living in Sweden (Aklillu et al. 2002). This result may have been caused by dietary differences between the two groups because the native Ethiopians consume a larger variety of plants, which has resulted in greater ingestion of alkaloids, increased expression of the enzymes and decreased rates of debrisoquine metabolism (Aklillu et al. 2002; Ingelman-Sundberg 2005). Thus, a diet composed of a larger variety of plants requires a greater production of enzymes for the detoxification of alkaloids, which occurs when individuals have multiple copies of the *CYP2D6* gene. Thus, it can be hypothesized that food scarcity suffered by the Ethiopian population 10,000–20,000 years ago generated positive selection in certain individuals that had multiple copies of the *CYP2D6* gene because they could expand their consumption of a wider diversity of plants during periods of food scarcity (Ingelman-Sundberg 2005). Thus, the distribution of individuals with multiple copies of the *CYP2D6* gene in different human groups may reflect a history of food scarcity in each group.

The CYP2D6 enzyme example illustrates how past dietary patterns in human evolution, particularly in relation to cultural decisions in periods of food scarcity, may have influenced the selection of individuals with more copies of the *CYP2D6* gene. Changes in historical dietary patterns in different human populations may also have influenced the presence of polymorphisms of other genes involved in the production of metabolic enzymes (Nebert and Dieter 2000). Moreover, because alkaloids have a broad range of biological activities, it is reasonable to suppose that the presence of individuals with multiple copies of this gene may have affected the therapeutic response of these substances in human populations. If this is true, human groups may have developed their traditional pharmacopoeias according to the severity of their reactions to plant chemicals. The above example of the Ethiopian population suggests a “local food adaptation”; therefore, it is likely that a “local medical adaptation” also occurred in this specific case.

The subject addressed here may have an impact on ethnobiological studies and provide a better understanding of how food resources were used and diseases were treated in different human groups. Let us hypothetically consider the following situation. In a specific group consisting of individuals with many copies of the *CYP2D6* gene, we should expect that a high diversity of plants will be used as food because these people would be less affected by the toxic alkaloids in edible plants. However, the medicinal use of such plants might also be affected because even if a medicinal plant has alkaloids with biological activity, these alkaloids will most likely be degraded by metabolic enzymes. Thus, certain plants may be perceived by a human group as ineffective for medicinal use not necessarily because it does not contain pharmacologically relevant compounds but because a higher dosage, which might be lethal in sections of the population, would be required to exert the desired effect on individuals that exhibit high expression of CYP2D6 enzymes and enzymes responsible for the degradation of exogenous substances. Most likely, adaptive issues caused different cultures to avoid performing adjustments in dosages because of the harm that could be caused at the population level.

Thus, a pharmacopoeia is developed that is adjusted to cultural decisions, genetic variations in the population, and the environment. By adopting a specific “food regimen” or “medical regimen,” genetic and cultural changes begin to mutually reinforce each other. Although limited studies have examined this specific scenario, specific alleles could be selected that would lead to increased or decreased therapeutic responses to specific plant chemicals present in remedies from different peoples. During our group’s field study with the Fulni-ô Indians, which is an ethnic group of northeastern Brazil that has shown a remarkable preservation of their language Yathee (Soldati and Albuquerque 2012), we collected ethnographic evidence that supports our hypothesis. This group frequently stated that allopathic medications did not have the desired effects for certain conditions compared with traditional preparations based on plant resources available in the region.

6.6 Final Considerations

We are still in the early stages of understanding how interactions between human populations and their environments may have been molded by historical decisions; thus, such interactions are open for exploration by ethnobiologists. If the arguments and interpretations from the examples above are accepted, then it becomes clear that NCT can offer a useful conceptual framework for ethnobiology that may strengthen the relationships and dialogue between ethnobiologists with training in the social sciences and ethnobiologists with training in the biological sciences and/or with those scientists who feel comfortable adopting ecological and/or evolutionary concepts in their studies.

NCT can provide ethnobiological insights that may improve our understanding of the relationships between humans and nature, particularly in relation to human actions on the biota, including important information generated from such interactions, and help illustrate the biological and cultural impacts that our actions have had and still have on the environment and our own species.

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Chapter 7
Knowledge Transmission: The Social Origin of Information and Cultural Evolution

Gustavo Taboada Soldati

7.1 Introduction

It is certainly possible to affirm, even in general, that all living beings are essentially structures capable of storing and processing information. It does not mean that this property defines life itself, as other physical systems are capable of storing and processing information as well. What distinguishes living systems from physical systems? The difference is based on their origin and nature. Living systems, besides acquiring information ontologically, i.e., as an inherent part of their nature, have the special ability to constantly incorporate the available data on their environment through learning (cognition). The classical learning concept considers any change in animal behavior that comes from the processing of new information, acquired through experience at a given moment in time (T_1) and which can be detected at a later moment (T_2) (Heyes 1994). Therefore, cognition is one of the basic properties that characterize living beings, since even lesser organisms display some kind of learning process (Maturana and Varela 2007).

But if acquired information distinguishes living systems from physical systems, what distinguishes humans from other living beings? This chapter shares the opinion of Mesoudi (2011), who stated categorically that "humans are a cultural species," because much of human behavior is determined by an information system acquired via social transmission, through specific processes such as imitation, teaching and language. In this sense, the concept of social transmission equals the concept of culture (Richerson and Boyd 2005; Mesoudi 2007; Mesoudi 2011). In summary, it is assumed that humans are characterized by the display of behaviors derived from information processing of three distinct natures: ontological, those acquired by individual experience, and those acquired by social transmission.

G.T. Soldati, Ph.D. (✉)
Department of Botany, Institute of Biological Sciences, Federal University of Juiz de Fora,
Av. José Lourenço Kelmer, s/n, São Pedro, 36036-900 Juiz de Fora, Minas Gerais, Brazil
e-mail: gtsoldati@gmail.com

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To investigate knowledge through social transmission is essentially to analyze the peculiar nature of human beings, i.e., their culture. Furthermore, it is recognized that culture can evolve following Darwinian assumptions, and that knowledge transmission is one of the elementary processes in cultural evolution and in the relation between people and their understanding of nature. This chapter now turns to the three bases description of human information, and then it turns its attention to social knowledge transfer from an evolutionary perspective. Finally, we discuss how information transmission has been analyzed by ethnobiological studies and how it can be used to understand the evolutionary dynamics of social-ecological systems, drawing upon standard ethnobiological works.

7.2 Genetic Basis Information

Some kinds of human behavior are the result of information processing stored in genetic material. These behaviors are characterized by not being influenced by peers during the acquisition process (Mesoudi and Whiten 2008). Genetic inheritance is not related to a trait of specific knowledge, such as knowing a plant is used for a particular purpose, but by determining individual characteristics that favor or not this knowledge construction, such as the capacity and speed of learning (Reyes-Garcia et al. 2009). However, there are few studies within ethnobiology that explicitly discuss inherited or genetically predisposed behaviors. Thus, little is known about the cultural aspects that are influenced a priori by an individual biological basis, i.e., inherent to an individual.

7.3 Individual Knowledge Production

Individual knowledge production is the process by which the individual builds, mostly through trial and without any social influence (Rendell et al. 2009), new information that may spread and settle in wider culture or not. This cognitive process is also named “individual learning” (Heyes 1994) or “asocial production” (Laland 2004). However, the use of the term “individual learning production” rather than the term “asocial learning” is defended, as it is believed that no knowledge is, in its entirety, “asocial”. Even when knowledge is produced by a single individual, its necessity and the reality in which it is produced are the result of a context and of social relations.

From an evolutionary point of view, individual learning is important for the following reasons: (a) it demands time and energy to access information; (b) in special situations it may cause risk to the individual, for example, when developing knowledge about medicinal plants; (c) although costly, new information will always adapt to the context in which it was conceived, even in unstable environments; and (d) being analogous to the mutation process in biological evolution, it diversifies traits and behaviors to be selected in a culture. Based on the considerations above, considering *trade off,*[1] energy expenditure and adaptability, individual knowledge production is favored under environmental instability conditions, because although costly, innovations will always be adapted to the new context (Cavali-Sforza and Feldman 1981; Hewlett and Cavali-Sforza 1986; McElreath and Strimling 2008).

It is important to know in ethnobiological studies that the evolutionary assumptions outlined above are not always true, because depending on how it occurs, individual learning will have different evolutionary implications. As stated, the theoretical accumulation of individual learning through evolutionary implications assumes that the production of new information, or innovations, will always be costly and in some situations will present risks to the individual, such as trying new plants for the treatment of a serious illness. However, it is possible to discover an innovation without energy expenditure and without risk to the individual, a point that is generally disregarded by evolutionary approaches. Considering that planting is an action determined by rain stimulus, for example, a farmer needs to know the ideal time to perform it. Thus, through his/her perception, but without any landscape management or planning experience, he/she realizes that a given plant, such as a "ipê rosa[2]," for example, flourishes days before the rain. The farmer then determines the "plant" action to the "flourish" stimulus offered by the plant. In this case, the new knowledge (behavior), "it is good to plant when the 'ipê rosa' flourishes", is the result of an event that did not require additional time or energy for its production. If this hypothesis is true, it is necessary to relativize discussions on cultural evolution guided by the premise that, although highly adaptive, individual knowledge production demands surplus energy expenditure.

7.4 Information Transmission or Social Learning

Social learning is the process by which information is transmitted in a social group through the interaction between peers, or of those with interaction products (Boyd and Richerson 2005; Mesoudi and Whiten 2008). For many authors, culture is nothing but shared knowledge, i.e., the information set acquired by social transmission through mechanisms such as imitation, teaching and language (Rogers 1988; Boyd and Richerson 2005; Mesoudi 2011).

One of the most fruitful discussions, especially in comparative psychology, is the one that seeks to understand the social learning process, i.e., whether this culture is exclusive to human beings or if it also exists in nonhuman animals. On the one hand,

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[1] *Trade off*, in an evolutionary context, refers to dilemma situations, and a beneficial alternative entails inherent losses. For example, it is important that a feline has the strength to hunt its food. But strength requires body mass. The bigger its body mass is, the greater the animal's weight and, of course, the lower its ability to run fast. In this case, there is a *trade off* between strength and speed.

[2] *Tabebuia roseoalba* (Ridl.) Sandwith.

some studies suggest that certain animals, especially chimpanzees, are able to develop their own language mechanisms and behavioral traditions, which are transmitted through many generations (Boesh and Tomasello 1998). Such evidence suggests that human cultural systems have evolutionary roots prior to *Homo sapiens*. So, what are the unique features of human cultural systems that distinguish them from other cultural animals? Boesh and Tomasello (1998) suggested two: (a) the use of a complex language (b) the accumulation of cultural changes. Concerning the first feature, the authors stated that developed language allows further dissemination of cultural traits both in time and space and, possibly, the transmission of different types of information. Concerning the second, it is considered that humans have a considerable capacity to accumulate information and its modifications, making the human cultural system unique because it is progressively more complex (Boesh and Tomasello 1998; Mesoudi 2011). It is improbable that a single child or a group of isolated children would create a cultural system as complex as human society, because human cultures are historical products built over many generations.

7.5 Social Transmission and Cultural Evolution

From an evolutionary perspective, it is believed that the cognitive structure of the human mind was selected to permit cultural groups, thus making culture a human adaptation (Rogers 1988; Boyd and Richerson 2005; Mesoudi and Whiten 2008). Many arguments support this belief, such as humankind's ecological success in different environments (Cavali-Sforza and Feldman 1981; Boyd and Richerson 1995; Richerson and Boyd 2005) and the capacity to accumulate adaptive information without individual production costs, increasing the fitness of the population (Rogers 1988; Boyd and Richerson 1995).

Historically, one of the most important studies on the role of social transmission in cultural evolution, which determined the future of this scientific field of investigation, was the work of Rogers (1988). His first major contribution was to evaluate the adaptability of information transmission and, therefore, its role in cultural evolution. Rogers (1988) assumed that natural selection tends to increase the average population *fitness*, otherwise there is no reason to believe that selection results in adaptation. In this way, if culture is adaptive, a population that transmits its information among its peers (recalling that the concept of culture equals the concept of social knowledge transmission) should have a better average *fitness* than a population with poor social transmission. In a variable environment, Rogers mathematically modeled a population in which individuals take two behavior types: (a) produce their own information (producers) or (b) copy it from their peers (social learners). In both situations, individuals will take *trade off* implications: energy consumption during knowledge production versus produced knowledge adaptability. Producers expend a lot of energy but the knowledge produced is highly adaptable to environmental changes, while social learners get their information at no additional cost but are susceptible to acquiring outdated or inappropriate information for a changing environment (Rendell et al. 2009).

Rogers' (1988) model states that: (a) individuals who rely on their own knowledge *fitness* depend only on its production cost and benefits. They have no relation to their peers' behavior which is, therefore, continuous; (b) when individuals who copy information are rare in a population, most pairs will behave as producers, which will offer low-cost, constantly adapted knowledge to social learners. In this situation, the average *fitness* of learners is greater than that of producers. When learners are the majority, little of the information available for copying will take into account recent environmental changes (i.e., adaptive changes). In this population configuration, the average *fitness* of producers will be higher. However, the most important point is that, regardless of the two strategies' population frequency, the existing *trade off* between learners and producers creates a stable balance between their frequencies when the average *fitness* of these behaviors is the same. The first striking conclusion of Rogers (1988) is that a population with social learning does not have a higher average *fitness* than that of a population without social learning. Therefore, from an evolutionary point of view, cultural systems should not be expected if culture is understood only as social knowledge transmission. These notes do not say that culture is inherently adaptive; they only suggests that, in cases where it is, it must be because of properties not considered in the evaluated model. Due to the impact of Rogers' work on the academic community, the author's notes are known in scientific literature as "Rogers' Paradox".

Boyd and Richerson (1995) questioned whether the paradox was an artifact, due to the simplicity of Rogers' (1988) basic model design. After all, the modeling considers only two behaviors (strategies): individual production (producers) and social knowledge transmission (learners), trying to adapt them closer to reality. The first model alteration, made by Boyd and Richerson (1995) was to model a population of individuals inserted into an environment that varies spatially. The second alteration allowed the modeled population of individuals to assume more than two behaviors. Finally, Boyd and Richerson (1995) adapted the model to include the possibility of individual producers that devised false or ill-adapted information. Despite these modifications, which made the model more realistic, Boyd and Richerson's (1995) results corroborated Rogers' model. Thus, inserting (a) an environmental variation and (b) other learning strategies, or (c) the existence of unprofitable information from an evolutionary point of view did not explain the existence of cultural systems, because, as had been seen in Rogers (1988), there was no increase in the average *fitness* of individuals who copy information from their peers.

In an attempt to find evolutionary explanations for culture, Boyd and Richerson (1995) constructed a mathematical model in which information transfer does not occur randomly, but selectively, and where individuals from the modeled group assess the behavior of peers and choose the one that appears to be the best. This type of transmission was named "biased transmission" and it happens when knowledge transfer follows certain trends, i.e., depending on some variable. This modification to the model, proposed by Boyd and Richerson (1995), assumes that if individuals are able to copy those peers recognized as the "best", with the most advantageous information, the biased transmission would justify the existence of cultural systems because it would favor adaptive knowledge. However, this model analysis confirmed that this assumption is false, and therefore does not explain, from an evolutionary point of view, the advent of culture. Based on the above, Boyd and Richerson (1995) concluded that the ideas proposed by Rogers (1988) are mathematically robust.

How to resolve Rogers' paradox then? How can information transfer, i.e., culture, be adaptive? It can be stated that culture increases the average *fitness* of a population and has an evolutionary justification if it increases the aptitude of learners and producers. As already revealed, when modeled by Rogers (1988), the presence of social transmission only optimized the average *fitness* of the individuals copying behavior, but not of the producers, whose *fitness* remained constant. When Richerson and Boyd (1995) modeled a situation in which the average *fitness* of individuals who produce their own knowledge increased as the population frequency of individuals who copy their peers increased, Roger's paradox disappeared. In this sense, culture is adaptive only if (a) it makes individual learning less costly and (b) that learning becomes more accurate.

And how does culture perform these two elemental functions? First, the existence of social learning as a behavioral alternative to individual production allows producers to be selective. In this case, individuals can learn opportunistically, i.e., producing their own information when this strategy is more accurate and less costly, or in situations less favorable to production, choose to learn socially. The central question of this weighting is behavioral versatility, to what extent individuals are able to condition their behavior towards the reality in which they live. Second, culture allows information to be accumulated from generation to generation. Learning in small steps is less costly and more accurate than learning in large steps because, during complex knowledge construction, each required a small investment of energy . In every innovation event, new information is selected, creating adapted knowledge. Given the above, it is recognized that culture can play an adaptive role in the occurrence of additional processes, which are able to make social transmission more accurate and less costly.

However, from an evolutionary point of view an important question deserves an explanation: is knowledge transmission always accurate and does it favor useful traits? Certain authors believe the answer is "no," stating that culture can set maladaptive traits (e.g., Boyd and Richerson 2005). Tanaka et al. (2009), mathematically modeled medicinal plants transmission and showed that a maladaptive character, in this case the absence of effective therapeutic resources, can remain in the population, because people may use it many times even though it is inefficient, allowing peers to copy and disseminate this behavior.

In summary, one can say that culture itself is not adaptive; in some situations it may even produce maladaptation. However, as stated earlier, there are procedures that make knowledge transmission an effective process from an evolutionary point of view. Enquist et al. (2007) stated that culture, to be adaptive, needs (a) information transfer to be faithful enough and (b) biases that favor adaptive traits and inhibit the perpetuation of maladaptive traits.

Given these observations, a better understanding of how to achieve advantages by copying information is necessary, assuming the possible risks of this learning strategy. Many studies have sought this understanding, and, according to Rendell et al. (2010), advances in this research area are due mainly to the union of theoretical and empirical studies. These advances have attempted to answer four basic questions: (a) “what is copied?” i.e., whether or not some information is favored during transmission; (b) “when is it copied?” i.e., what are the situations where individuals must choose to copy information; (c) “how is it copied?” which questions the copy, observation, education, and language mechanisms; and (d) “who to copy?” i.e., whether there is any trait that makes an individual a model to be copied (Laland 2004; Mesoudi and Whiten 2008). These questions are now discussed.

7.5.1 “Who to Copy?” Questions

When copying, individuals must choose some of their peers as models and sources of knowledge. Strategies that identify the “who” show the characteristics of the selection process. Cavali-Sforza and Feldman (1981) initiated “who to copy” investigations, establishing a classification that became classic in cultural evolution studies, based on the degree of relatedness between model and learner. According to this classification, knowledge can be transferred culturally: (a) from parents to children (vertical type); (b) between same generation (horizontal type); (c) between generations, but only when young people copy adults who are not their parents (oblique type) (Fig. 7.1).

Hewlett and Cavali-Sforza (1986) re-structured the original Cavali-Sforza and Feldman (1981) classification, subdividing the “oblique” category into two types: (a) that of a teacher, leader or medium, such as radio or television directed towards many individuals in a group (*one-to-many*), which are generally pupils or learners; or (b) from older to new members in a social group (*many-to-one* or *concerted*) (Fig. 7.1). Although not explicit in Hewlett and Cavali-Sforza’s (1986) text, fission seems to be justified because these two new categories have distinct evolutionary implications that, when united in the “oblique” category, were indistinguishable.

Vertical transmission promotes a high knowledge variation between individuals in a group and between different groups. Parents-to-child transmission is highly conservative because it hinders the diffusion of innovation. As a result, the cultural evolution of a group that supports this type of strategy is rather slow (Fig. 7.2). On the other hand, systems that present knowledge transmission horizontally find that innovations are easily diffused and well developed. In these groups, knowledge variation between individuals and groups can be high and cultural evolution is very fast. “One-to-many” and “many-to-one” strategies have distinct evolutionary implications. In the first case, innovation diffusion occurs very easily. As a result of the knowledge homogenization process, knowledge between individuals in the group is very similar, although variation between groups is occasionally high. As in horizontal transmission, cultural evolution in groups using the “one-to-many” strategy is pretty quick. The second case, “many-to-one” type, is rather conservative, as elders’ values, traits and skills are transmitted on a large scale to other group members. This transmission form creates a situation that inhibits innovation diffusion and knowledge diversification within the group, as well as cultural evolution (Fig. 7.2).

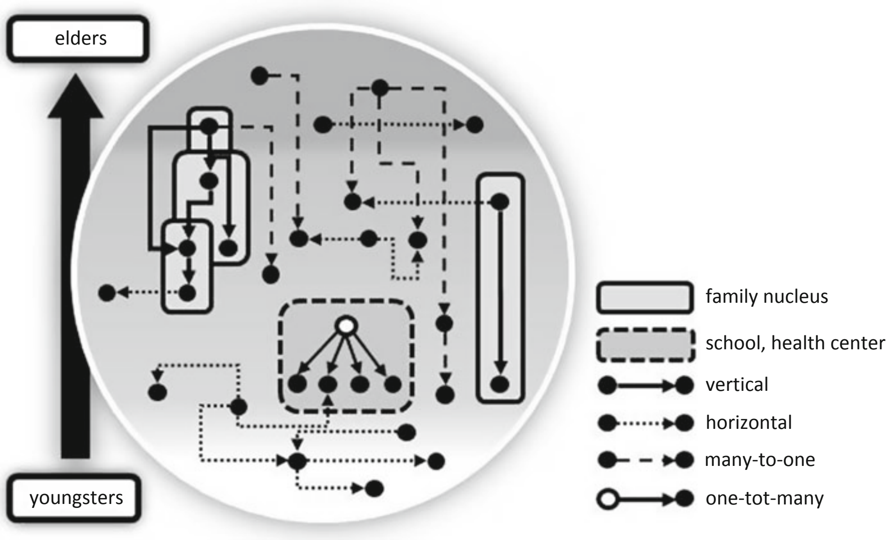
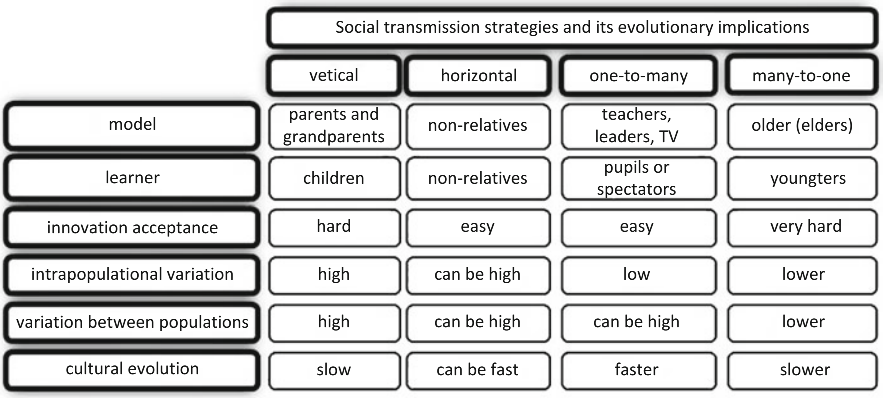


Fig. 7.1 Social information transmission types. The large sphere represents a cultural system, such as a traditional community composed of different individuals (*small spheres*). Some of them are special because they are recognized as containing great knowledge and/or social prestige (*centered white spheres*). These are usually elders, healers, teachers, doctors and nurses. The tone distinction in the largest sphere seeks to represent age differences in individuals, i.e., distributing them in generations. Vertical transmission occurs within a family unit, while horizontal transmission occurs between unrelated pairs belonging to the same age group. When elders are the model to be copied, the transmission is called a "many-to-one". In this case, the information always passes over a generation or more. The "one-to-many" transmission is modeled on a teacher, doctor or other agent with enough social prestige to influence many people



	Social transmission strategies and its evolutionary implications			
	vetical	horizontal	one-to-many	many-to-one
model	parents and grandparents	non-relatives	teachers, leaders, TV	older (elders)
learner	children	non-relatives	pupils or spectators	youngters
innovation acceptance	hard	easy	easy	very hard
intrapopulational variation	high	can be high	low	lower
variation between populations	high	can be high	can be high	lower
cultural evolution	slow	can be fast	faster	slower

Fig. 7.2 The evolutionary implications of different social transmission strategies, adapted from Hewlett and Cavali-Sforza (1986)

The frequencies of each transfer pathway in a cultural system are not random and depend on many factors, especially the environmental and social background (McElreath and Strimling 2008; Reyes-Garcia et al 2009.). McElreath and Strimling (2008) concluded that copying parents is the most favorable situation for vertical type transmission. Using mathematical models, the authors stated that this social learning type should be more common in situations where the behavior is associated with fertility and care of their children and grandchildren than survival itself. Vertical transmission is favored in stable environments, as discussed earlier, and in situations where evolutionary pressures are very strong (McElreath and Strimling 2008). In contrast, horizontal transmission pathways and "one-to-many" strategies, which result in less conservative and more diffusive processes, are stimulated in varying environments (McElreath and Strimling 2008; Reyes-Garcia et al 2009).

Remember that information provided by the parental route has exactly the same nature of genetic transmission, because it shares the same common ancestor. Therefore, would it be possible to use the most modern tool of evolutionary biology, i.e., phylogeny, to investigate cultural evolution? Undoubtedly, yes, as argued by Boyd et al. (1997) and Mace (2005). Phylogeny, in short, seeks to understand evolutionary history and to establish historical relations between species, families and subfamilies. To do so it uses homologous characters, analyzing a set of shared characteristics among the organisms. Each of these has the same embryological origin and is present in all descendants of the same ancestral line. All phylogeny and evolutionary hypotheses on knowledge construction, often represented by phylogenetic trees or cladograms, are based solely on homologous characters. To have the same kind of genetic transmission, i.e., to share a common ancestor, the information transmitted by the parental route is recognized as homologous. In this sense, cultural systems where vertical transmission predominates should, therefore, adapt and be fully explained by phylogenetic models. In such cases, it is believed that cultural system evolution is determined by phylogeny events, i.e., conservative transmission (Fig. 7.3).

However, as stated by Mesoudi (2011), transmission types that diffuse horizontally, using "many-to-one" and "one-to-many" information do not present correspondents in biological evolution. These transmissions diffuse information beyond

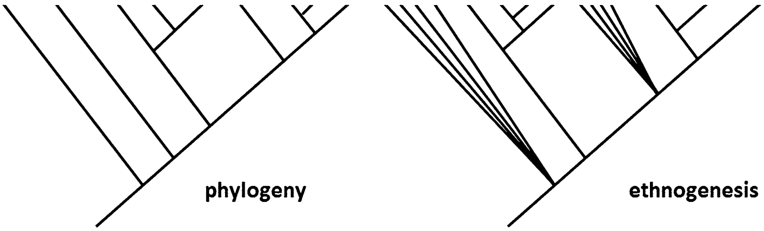


Fig. 7.3 Schematic representation of two hypothetical social groups and their cladistics knowledge analyzes. In the first case, vertical transfer dominates (phylogeny events), and in the second case horizontal transfer, "many-to-one" and "one-to-many" are prominent (ethnogenesis events)

parental logic and in this way produce homoplastic similarities, i.e., shared characteristics. Unlike homologues they do not have a common ancestry. As phylogenic order is based on ancestry, homoplasy, by reflecting similarities of a non-homologous nature, should invalidate phylogenetic tools used for cultural systems (Mesoudi et al 2006; Greenhill et al. 2009). However, despite this contrast, some studies show that horizontal transmission does not invalidate this evolutionary approach and its tools. For example, Greenhill et al. (2009) constructed a mathematical model to determine different diffusion level effects on the accuracy of phylogenetic estimates. The authors concluded that phylogenetic inferences are quite robust, even in situations influenced by high horizontal transmission levels. Collard et al. (2006) compared phylogenetic trees produced from biological and cultural information with trees models and concluded that these two databases produce similar patterns.

However, systems dominated by processes that spread information horizontally do not fit into phylogenetic models and, as a result, trees originating from these cultural systems do not exhibit the typical bifurcation structure (Fig. 7.3). Similarities between people and cultural groups that do not share a common ancestor are called, in the context of cultural evolution, ethnogenesis, which blurs phylogenetic analyzes (Fig. 7.3). Therefore, it is possible to evaluate the processes that underlie cultural evolution by assessing cultural information adequacy in a phylogenetic tree.

7.5.2 "When to Copy?" Questions

Laland (2004) made an ecological reading of social learning strategies and concluded that there are three ways for an individual to behave in a cultural system: (a) to ignore information (cultural traits); (b) to imitate their peers and copy the desired information; and finally, (c) to produce their own knowledge. In the first case, for example, the author considered the feeding behaviors of an animal that had no knowledge of the ways to obtain food. In this case, the animal was unaware of the necessary information to obtain the desired resource, but met his demands by depending on or looting his peers. In a second strategy, the animal acquired knowledge by observing or copying others from his group (cultural transmission). In the third and last option, self-production, where animals are seen as information producers, they construct new knowledge individually through their own methods, such as "trial and error".

Laland (2004) constructed a hierarchical model of these strategies (Fig. 7.4) and argued that human and nonhuman animals preferably opt for the less costly strategy, following this order: not knowing, copy and produce. Therefore, behavior selection is determined by the strategy cost-benefit ratio, which in turn is determined by the particular environment in which the group is inserted (greatly or little productive) and the frequency of each strategy in the group (Laland 2004). The author assumes that individuals benefit by copying information, because by doing so, they will acquire valid information in a quick manner, freeing up knowledge and individual

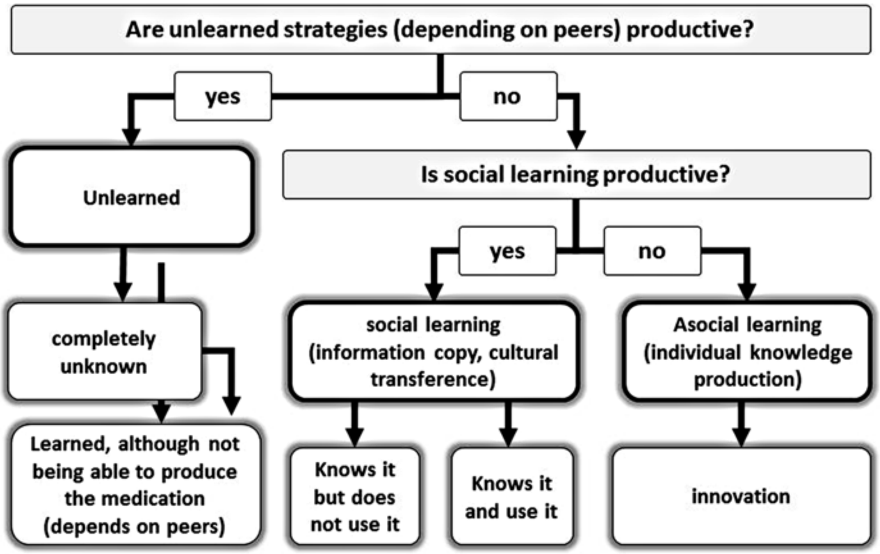


Fig. 7.4 Hierarchical control of social learning strategies. Adapted from Laland (2004)

production costs. However, simply copying information is not the key to success, since this strategy requires that individuals feed the group with new information. In a group where nobody produces knowledge, copying information cannot be a profitable strategy (Laland 2004).

Using the ecological cost-benefit ratio, Laland (2004) tried to understand "when to copy" social strategies, seeking to specify circumstances that favor information diffusion. The author considered that individuals must first absorb knowledge from their peers when the lack of such information is unproductive, i.e., does not provide the necessary benefits. Otherwise, when the environment or social context is productive, individuals will preferentially adopt the most convenient strategy, unlearn information and rely on their peers for their basic needs. Seen in these terms, keeping in mind the context of traditional medicine, individuals will likely invest in knowledge production when there are no less costly alternatives to curing a disease available, for example, using traditional medicines prepared by others. According to Laland (2004), individuals from a social group will preferentially copy the information from their peers when the production of new knowledge is highly costly or dangerous. Producing knowledge that aims to solve problematic new situations demands a high investment of energy and thus individuals have a lower risk and little to lose when guided by others (Laland 2004).

Another situation where knowledge production can be highly costly occurs in unstable environments or when new situations are presented to the group (Laland 2004). In these situations, individuals may display conservative or indifferent behavior, depending on their peers' action and knowledge, or they may rely on their own knowledge. For the latter alternative, there is the example of emergency foods (*famine foods*) where an information set about food plants is put into practice in adverse situations, such as when the environment presents some limiting situation (Nascimento et al. 2012).

Another context in which environmental change can play a key role in knowledge structuring is in instances of migration. With each new event the social group has new experiences, especially environmental knowledge. Individuals, therefore, will preferably ignore information or rely on their past knowledge of medicinal plants. But how does this second option take place, bearing in mind that, when migrating a new set of sources is available? The alternative would be to invest in knowledge of widely distributed cosmopolitan plants. Thus, migration events can influence the richness of known species in relation to their biogeographic origin (see Medeiros et al. 2012).

7.5.3 "What to Copy?" Questions

What kind or set of information must be copied into a cultural system? Possibly the most parsimonious strategy is to copy the majority, i.e., the most widespread behavior and knowledge in the social group (Laland 2004). This strategy is dependent on information distribution because the probability of an individual acquiring knowledge depends on his frequency within the cultural system (Henrich and Boyd 1998; Laland 2004). However, information copying may not only depend on the frequency but also on the content of the information. Nairne et al. (2008), for example, found that information related to survival is favored during memorization and, therefore, in information reproduction, what is known as adaptive bias. The human mind is predisposed to recall information related to subsistence because it confers greater adaptive advantage. Such predisposition is one of the best storage and decoding procedures identified in the human mind (Nairne et al. 2008).

7.5.4 "How to Copy?" Questions

According to Mesoudi and Whiten (2008), few studies have been concerned with understanding "how" information is transmitted within a group, especially when comparing different social learning processes. Available data suggests that botanical knowledge in a rural community is acquired through practice, as individuals perform daily activities (Zarger and Stepp 2004; Lozada *et al* 2006; Mesoudi and Whiten 2008; Reyes-Garcia *et al* 2009). Many authors claim that popular knowledge is transmitted mainly orally. However, it is necessary to investigate other transfer forms. Cordel literature, for example, is a widely known and widespread literary style in northeastern Brazil. Poems are presented in small booklets sold at fairs and streets, always fixed by strings (hence the "cordel" name). The booklets contain popular poems that record knowledge, practices, values, myths and legends of the popular universe. They are a prime example of knowledge transfer in writing. It is worth quoting verses from João Martins de Athayde, from in the booklet "Gypsy Esmeralda's Testament": "dream of peppermint, is a vain dream, it means that there are women, with voluminous hair, to arrest men, in a perfumed tie".

7.6 Knowledge Transmission in Ethnobiology Studies

Most of the papers previously discussed address knowledge transmission from mathematical models or from empirical data of different types. However, social learning has also been the target of ethnobiological investigations (Frazão-Moreira 1997; Ladio and Lozada 2004; Garcia 2006; Lozada et al. 2006; Reyes-Garcia et al. 2009; Tehrani and Collard 2009). What are these studies' contributions to our understanding of cultural evolution? Some studies simply focus on the description of a process, usually answering questions like "when," "how" and from "whom" do you learn? Lozada et al. (2006), for example, described the transmission of knowledge about medicinal and food plants, focusing on the following aspects: when and where the informant-initiated plant resources were used, who taught him this knowledge, and where and how knowledge was taught. Other research, as well as describing knowledge transmission, tested hypotheses about transmission mechanisms. In two communities, one in Thailand and another in Argentina, Ladio and Lozada (2004) and Srithi et al. (2009) respectively tested whether knowledge erosion was due to information transmission failures. In principle, there are two approaches in transmission studies: process descriptions or process descriptions with hypothesis testing.

However, there are few examples of ethnobiological investigations that discuss their positions cultural evolution using the existing theoretical approach. A prime example is Garcia's (2006) investigation of knowledge transmission and the use of wild foods among the Paniya. The author concluded that there is both positive and negative feedback in the transfer of this knowledge. Mothers teach why they think wild plants are "good" and "healthy foods," but at the same time they attach a pejorative value to the value of these resources because, locally, they are associated with poverty. This is a *trade off* example, showing the conflict between biology and cultural spheres, which can be the cornerstone of a great evolutionary debate. What are the evolutionary dynamics of this knowledge that is both biologically basic (plants for food) and culturally disposable? Is there a tendency for this information to be perpetuated or will it be lost over time? Which sphere is most crucial in the transmission process, the biological demand or cultural values? However, despite the importance of feedback in knowledge transmission, no discussions were made from an evolutionary perspective.

Reyes-Garcia et al. (2009) moved in this direction, as they used existing theoretical approach to predict the cultural evolution of the group they studied. In that text, the authors showed that oblique transmission is very important among the Tsimane of the Bolivian Amazon. They commented: "… research suggests that oblique transmission, involving many demonstrators for a learner, tend to generate a high uniformity within a social group, while allowing cultural changes across generations.

If, as data suggested, Tsimane favor oblique ways for cultural knowledge transmission, then a uniform change in Tsimane society is expected. Moreover, this growing oblique transmission dependence produces faster innovation diffusion in ethnobotanical knowledge [than]if vertical transmission was favored". It is possible to do an exercise to recognize Reyes-Garcia et al.'s (2009) findings in Fig. 7.2. Another example is the Tanaka et al. (2009) study that, despite being merely mathematical, used transmission dynamics to discover why maladaptive traits remain in cultural systems. In summary, Tanaka et al. (2009) used prediction and transmission models to answer a real question with strong evolutionary implications.

It is not intended to disparage or discredit currently existing studies here. The intention is to point out that a big discussion about cultural evolution has not yet been incorporated into ethnobiological investigations. A theoretical approach, which goes beyond the knowledge transmission routes description, is necessary. An approach that includes, for example, the evolutionary implications of different learning strategies is needed.

7.7 Final Considerations

This chapter's main objective was to characterize humans as beings who handle information from three different sources: genetic, individual learning and social transmission. Social transmission allows the establishment of a cultural system that, in humans, is established only through cognitive processes and achieves a greater degree of complexity. Therefore information transfer is a fundamental process to understanding human nature and cultural evolution, because this process allows traits diffusion and fixation through cultural selection.

By focusing on local knowledge as one a main area of study, ethnobiology can greatly help to clarify the dynamics of socialization and information, and consequently, of cultural evolution. However, as was noted above, this theoretical approach is still in its infancy. Today the existing research, despite describing the process, lacks a strong approximation of theories that explain the spatial and temporal variation of cultural traits. A program that guides investigative efforts in ethnobiology, building generalizations and theories about local knowledge transmission and its evolution is now necessary.

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Chapter 8
Resilience and Adaptation in Social-Ecological Systems

Washington Soares Ferreira Júnior, André Luiz Borba Nascimento, Marcelo Alves Ramos, Patrícia Muniz de Medeiros, Gustavo Taboada Soldati, Flávia Rosa Santoro, Victoria Reyes-García, and Ulysses Paulino Albuquerque

8.1 Introduction

In most animals, behaviors are mainly encoded in the genes, but in humans, the behavioral characteristics that confer greater fitness can have a cultural nature in addition to the genetic component (Henrich and McElreath 2003; Boyd and Richerson 2006). Furthermore, the human species is the only one having developed cultural systems able to accumulate information: while many species have culture, only humans have cumulative culture. Cultural knowledge, with genetic variability, has played a major role in the adaptive strategy of human populations (Cheverud and Cavalli-Sforza 1986; Rendell et al. 2009).

W.S. Ferreira Júnior (✉) • A.L.B. Nascimento • F.R. Santoro • U.P. Albuquerque
Laboratory of Applied and Theoretical Ethnobiology (LEA), Department of Biology,
Federal Rural University of Pernambuco, Av. Dom Manoel de Medeiros, s/n, Dois Irmãos,
52171-900 Recife, Pernambuco, Brazil
e-mail: kba.bio@hotmail.com

M.A. Ramos
Department of Biological Sciences, University of Pernambuco, Av. Amaro Maltez,
201, Centro, 55800-000 Nazaré da Mata, Pernambuco, Brazil

P.M. de Medeiros
Center of Biological Sciences and Health, Federal University of Western Bahia,
Estrada para o Barrocão, s/n, Morada Nobre, 47800-000 Barreiras, Bahia, Brazil

G.T. Soldati
Institute of Biological Sciences, Department of Botany, Federal University of Juiz de Fora,
Av. José Lourenço Kelmer, s/n, São Pedro, 36036-900 Juiz de Fora, Minas Gerais, Brazil

V. Reyes-García
Institució Catalana de Recerca i Estudis Avançats (ICREA), Barcelona, Spain

Institut de Ciència i Tecnologia Ambientals, Universitat Autònoma de Barcelona,
08193 Bellaterra, Barcelona, Spain

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People appropriate the environment to obtain the resources that provide their livelihood. In such appropriation, human groups develop a set of knowledge and practices on the local resources that enable them to live under different conditions and environmental adversities (Berkes et al. 2000). Far from being a research topic only for scholars interested in the evolutionary process, the discussion of human adaptation to the environment is also critical in ethnobiological studies aiming to understand which characteristics favor the maintenance of practices, knowledge, values and beliefs that ensure people's livelihood in adverse contexts (see Ladio and Lozada 2008; Berkes and Ross 2013). Furthermore, the topic is even more relevant in the current context of global change, as human populations are exposed to disturbances that affect their known environmental (e.g., deforestation) and cultural orders (e.g., the presence of health centers near populations that historically have kept traditional medical systems). Such an context confronts us with the challenge of understanding how humans behave when faced with changes, either environmental or cultural. We argue that ethnobiologists can draw on a set of concepts developed in other disciplines (i.e., systems, stability, resilience, disturbance, and adaptation) to understand current human adaptive strategies.

8.2 The Concept of Systems and Its Application to Ethnobiology

The concept of system refers to a set of individual components with mutual and complementary relations capable of being analyzed by science. The components, or elements, would be the basic individual units to build a system (Odum and Barrett 2004). To facilitate the understanding of the concept of systems, we will use as an example a forest and some environmental components in it, such as nutrients and water. In the proposed example, the environmental components are plant and animal species, but also bacteria, nitrogen, phosphorus and water. These elements are connected to each other and have specific functions in the system. Functions are the activities necessary for the establishment and maintenance of a system, which can be performed by one or more components, provided that they have the basic characteristics required to perform such activities. Pollination, decomposition and dispersal would be good examples of functions performed in a forest. The decomposition of organic matter is performed by several species of fungi or bacteria because they have characteristics that enable them to perform the function "decomposition." Thus, a process can be performed by one or more components of a system.

The interaction between the components of a system ends up building additional characteristics not detectable in their individual components; these characteristics are known as emergent properties (Odum and Barrett 2004; Maturana and Varela 2007). A system combines the individual properties of its components and the additional features arising from the interaction between them. In our example, the relation between plants, animals, and nutrients, pervaded by the functions performed by each one, lead to higher-hierarchy properties that are typical of and unique to the systems as a whole, such as diversity, richness, productivity, and nutrient cycling. Such properties are different to the relation between components, as they emerge from the systemic organization.

Thus, one can consider that the system establishes functional dynamics supported by its primary functions and emergent properties. We make a distinction between structure and organization of a system. The first concept combines the processes of the system and the nominal components that perform its functions. The second concept considers only the relation of the functions performed in the systemic organization, regardless of whether they are performed by component A, B or C.

In summary, a system is recognized as a set of components that are distinguishable but interconnected by the functions they perform, so that the connections between the parts build, on a hierarchically higher and broader level, a cohesive and dynamic unit (see Odum and Barrett 2004).

All that is external to a system is called environment.[1] The type of relations between a system and its environment characterize the system as closed or open. Closed systems are completely isolated from the environment, whereas open systems influence and are influenced by the environment. Such distinction is important because the concepts of resilience and adaptation can only be applied to open systems (Trzesniak et al. 2012).

Regardless of whether a system is open or closed, all systems exhibit mechanisms that manage their functioning, or rather their stability. Such mechanisms are known as feedback loops and can be positive or negative (Odum and Barrett 2004). Negative feedbacks act to keep the system in the same regime, i.e., to ensure its order, organization, and structure. Positive feedbacks, also known as disturbances, tend to disrupt the system's equilibrium, triggering a new organization. Throughout their history, systems are affected by different disturbances, i.e., events that threaten its functioning and hence its identity. These disturbances can be physical events related to environmental disasters or climate fluctuations. Negative feedbacks deny the change of state by strengthening the system stability; in contrast, positive feedbacks promote new organizations by destabilizing the system.

Considering that ethnobiological studies seek to study the relations between human groups and their environments, one could argue that there are two systems involved: the ecological and the cultural. The ecological system consists of the natural living organisms and the relations established both among such organisms and with the external environment. The cultural system consists of human beings and the interactions between them, including the set of knowledge, practices, and beliefs developed by different human groups. Because both systems have an open nature, they strongly interact. For example, as a result of this close connection,

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[1] We use the concept of environment, as understood in physics, representing all that is beyond the limits of a system and, thus, is not part of it. If the system studied is a person, then the family and social context be considered the environment. If the system is a plant fragment, all factors external to the fragment, including the people living around the fragment and that depend on it for their subsistence, are considered the environment.

there is a mutual dependency between the two systems that produces an ongoing change and, in particular, an adjustment between their structures and their organization, thus indicating a coevolutionary relation between them. This interaction is so strong that, according to some researchers, is more appropriated to refer to a social-ecological system, rather than to two separate systems (Berkes and Folke 1998).

We argue that the concept of social-ecological systems could be useful in ethnobiology. To explore the argument, we use the example of a local medical system. A local medicinal system is a system composed by people of a given social group and plants with therapeutic potential. Both components have their intrinsic, and thus individual properties, however, these components interact through different functions. For example, people manage the landscape, building backyards and vegetable gardens, which are important places for the cultivation of medicinal plants. This management should be understood as a function performed by people that connect them with the plant resources. In turn, plants have potentially therapeutic properties, such as a "curing diseases of the gastrointestinal tract" or "curing worm infestations." Let us consider the need to cure the flu as the function "curing the flu." Plants such as "spearmint," "peppermint," "lemongrass," and "lemon balm" can potentially perform this function, either individually or together in a single preparation. The function will only be performed if there is an element with the basic characteristics necessary to do so. In any time interval, the local medical system, of which both people and plants are components, will have a specific equilibrium state, organization and structure. Negative feedbacks, such as beliefs that will reiterate local practices, and positive feedbacks, such as the emergence of new diseases, can affect the structure of the local medical system.

To understand what local medical systems represent, we assume that -throughout human history—diseases have influenced the structure and evolution of cultures, acting as important forces in natural selection in the sense that many cultural characteristics are adaptive responses to disease prevention and treatment (Dunn 1976; Brown 1987). Accordingly, human groups have built medical systems formed by a set of concepts and practices regarding health and disease in which the perception of diseases and customs are connected to the chosen treatment strategies (Jain and Agrawal 2005). These systems bring together local perceptions of disease causes, the recognition of the symptoms of different diseases by the human group, and the strategies and alternatives for their treatment, including the set of elements used in the healing process (i.e., plants, animals, etc.), in addition to the evaluation of the results of each of the treatment strategies available (see Kleinman 1978; Bhasin 2007).

While not having a strictly physical nature, the social-ecological systems are considered as open because they are strongly influenced by the environment. For example, in a situation of resource shortage, a certain local community can suffer pressures due to the absence of basic elements for survival. However, people being affected by resource shortage may use different management strategies to adjust the environmental context to their demands, i.e., they may use different strategies to deal with pressures (see Berkes et al. 2000; Walker and Salt 2006; see also on this book, the chapter on the niche construction theory).

8.3 Understanding the Classic Concepts of Resilience

The term resilience is used in many different areas of knowledge with, mainly, two different understandings. The first understanding of the concept of resilience considers that there is an overall stability that the system must achieve to remain resilient. The second understanding considers that there are multiple stability states, or regimes, and the system can achieve different configurations within the same regime. When we refer to regimes, we are addressing a range of states in which a system can exist, reaching or failing to reach an equilibrium state. This range is defined by the variables and processes that control the system (Gunderson 2000). For example, a semiarid forest region can be deforested and used for agricultural activities. At first, it is possible that, once agricultural uses are abandoned, the forest regenerates and the area returns to its regime. However, if the agricultural activity leads to soil exhaustion, the region may suffer a process of desertification and never return to the forest state. In this situation, the area would be reorganized into a new regime, in this case formed by few species tolerant to this desert condition (see Gunderson 2000, for more examples).

Thus, the basic difference between the two understandings of resilience is that the first assumes the need for stability, while the second assumes the existence of multiple regimes with different stable states. Within the framework of the first understanding, Pimm defined resilience as “How fast the variables return towards their equilibrium following a perturbation” (Pimm 1984:322). The advantage of this definition is that resilience can be measured as the time required for the system to return to equilibrium, and this measure can be scaled in time units.

The second definition assumes that a system can constantly change and may rarely achieve an equilibrium state. According to these assumptions, a system may exist in several regimes, not necessarily reaching a permanent equilibrium state. Resilience is defined as “the capacity of a system to absorb disturbance and reorganize while undergoing change so as to still retain essentially the same function, structure, identity, and feedbacks” (Walker et al. 2004:2). In other words, a system is more resilient the greater its capacity to absorb disturbances, and the system vulnerabilities would be related with its transition to another state.

Notice that the concepts of stability and resilience are different. A system can be considered stable when it is either in equilibrium or near an equilibrium state. In other words, the less fluctuations occur in a system, the greater its stability is (Holling 1973). According to the second understanding, a system can be resilient, even if it is not stable.

Which of the two definitions of resilience best applies to the study of social-ecological systems? Given that ecological systems are essential constituents of social-ecological systems, it seems reasonable to assume that the ecological definition would fit the purpose better. Thus, we will use the notion of resilience linked to the existence of multiple stable estates.

Although the most popular concepts of resilience previously discussed bring to light its conservative character (i.e., of absorbing disturbances while maintaining its original function), the study of social-ecological systems has suggested a new way of viewing resilience that is related to the capacity of renewal, reorganization and the development of these systems (Folke 2006). According to this logic, in a resilient system, disturbances have the potential for creating opportunities and innovations (Folke 2006). Therefore, depending on the perspective adopted, resilience can indicate either a system that maintains its characteristics and properties upon facing a disturbance, or the capacity of that system to transform itself, thus completely changing its characteristics (Walker and Salt 2012). This latter system strategy is known as transformability. Both strategies can lead to an adaptation of the system to the disturbance conditions.

When addressing the concept of resilience in the sense that the system absorbs disturbances, we are not claiming that the system does not undergo any changes: there are changes, but they occur within the limits that allow the maintenance of the system in a given state. In this case, in addition to transformability, there are other system properties that can favor resilience because they represent the responses of the system to disturbance, such as flexibility and adjustment. Flexibility and adjustment are related to the number of possibilities that a system has to respond to a disturbance, thereby increasing the range of choices and potential solutions which prevent the system from losing its functional identity, thus favoring resilience (see Walker and Salt 2012). The following study exemplifies how resilience and flexibility can be applied in social-ecological systems. Over time, farmers of the Iberian Peninsula have incorporated commercial varieties of cultivated plants at the same time that they continue to grow local varieties that are part of their tradition. In this case, people who hold a high knowledge of the commercial varieties also have greater knowledge of local varieties (see Reyes-García et al. 2014). This example illustrates that information on both commercial and local varieties is not mutually exclusive and suggests that the knowledge systems of these farmers has been resilient by incorporating changes (i.e., commercial varieties) while simultaneously keeping the knowledge associated with local varieties (Reyes-García et al. 2014). Furthermore, this situation may also promote the resilience of the social-ecological system by increasing the flexibility of responses to future disturbances as farmers hold knowledge of both commercial and local varieties to which they can resort to in times of crisis.

8.4 The Interpretations of Resilience in Ethnobiological Studies

Ethnobiological studies have the potential to contribute to the understanding of the characteristics that could lead to resilience of social-ecological systems. However, the notion of resilience can be interpreted in different ways in ethnobiological studies. We separated these interpretations into three basic sets. To illustrate them, we will use again the example of a local medical system.

8.4.1 Structuralist Interpretation of Resilience

According to this interpretation, disturbances that cause major structural changes would entail the loss of resilience and the system's transition to a new regime. Such an interpretation does not take into account the assumption that, for the system to change its identity, it needs to suffer functional changes. However, despite its apparent disagreement with the classical concepts of resilience, this interpretation can be implicit in ethnobiological studies, as in studies that attribute the loss of resilience of a local medical system to the introduction of exotic species or allopathic medicines.

8.4.2 Functionalist Interpretation of Resilience

According to this interpretation, for the system to continue under a regime, its functions need to be maintained, even if there are strong structural changes, i.e., in the system components. To illustrate this idea, consider that our hypothetical local medical system has ten species that are used by the community for the treatment of headache and, consequently, that these species share the same function in the system: "to treat headaches." If any disturbance, such as deforestation, leads to the disappearance of a species in that category, people can use the other species to accomplish the function of the lost species (see the chapter of this book about utilitarian redundancy). This characteristic demonstrates its flexibility, which favors its resilience (Ladio and Lozada 2008). In this case, the system could absorb disturbance without changing its functions, i.e., its identity, although the system also suffered changes in the number and composition of the species. With this hypothetical example, and according to the functionalist interpretation, we can say that the local medical system based on the use of plants was shown to be resilient upon the disturbance. However, for the functionalist perspective (which mainly focus on the maintenance of the system's functions), discontinuing the use of plants while incorporating the use of allopathic medicines would not lead to another stable estate, because the main function of the system (i.e., the treatment) would still be guaranteed.

8.4.3 Processual Interpretation of Resilience

This interpretation represents a compromise between the two interpretations above. On the one hand, structural changes would not be sufficient for the loss of resilience and to the entry of the system into a new regime. On the other hand, maintaining the system functions would also not be sufficient to ensure its resilience. To avoid changes in the system's regime, in addition to its functions, the system must retain the processes governing them. In the previous examples, the loss of one species to treat "headache" would not lead to loss of resilience because the function of the system was maintained and it would still be governed by the same processes based on the traditional concepts of health and disease in its methods of diagnosis, the selection of products (such as plants) for treatment, etc. Even the introduction of allopathic medicines in the system would not necessarily lead to the transition to a new regime. The coexistence of traditional and western medicine could also keep the system in the abovementioned regime, provided that the functions of the system were not changed and that the processes that govern it would remain the same. According to this assumption, a complete replacement of the plants by allopathic medicines could even occur if the processes were maintained. However, the introduction of western medicine in a local medical system might eventually change the processes governing the system. The predominant factors that once included the transmission of knowledge, experimentation, and, occasionally, rituals and beliefs related to the cure might be replaced by the search for a doctor who prescribes medicines based on biomedical concepts typically external to the society. According to the processual perspective, the introduction of allopathic medicines would not necessarily lead the system to a new regime.

8.5 Factors that Can Interfere with Resilience: Analysis Based on Ethnobiology

The ethnobiological literature still tends to address the topic of resilience only superficially, theorizing about its concepts and its importance, without actually mentioning the factors that increase resilience and the factors that can led a social-ecological system to shift regimes. Below, we suggest some factors that can interfere with the resilience of these systems and that—therefore—deserve special attention.

8.5.1 Utilitarian Redundancy

The concept of utilitarian redundancy is based on the assumptions of functional redundancy in ecology, which establishes that several species can perform the same function in an ecosystem (Walker 1992; see also the chapter on redundancy on this book). Thus, when a disturbance occurs, each species may respond in different ways, being more or less vulnerable. This diversity of responses contributes to the resiliency of the ecosystem. Thus, the utilitarian redundancy of a system relates to the number of species that share a particular utilitarian function in a social-ecological system, i.e., that are used for the same purpose (Albuquerque and Oliveira 2007). Thus, the higher the utilitarian redundancy in a social-ecological system, the greater the flexibility of a system, and the greater its resilience, given that the loss of a species would not bring great damage to the system as others could replace it.

8.5.2 *Transmission of Knowledge*

One of the major pillars of the maintenance and diversification of social-ecological systems is the transfer of information. Thus, the exchange of information among members of a community is expected to affect the system's resilience. This consideration suggests that a high utilitarian redundancy does not necessarily favor the resilience of a social-ecological system if this redundancy is not shared among the social actors (Ferreira Júnior et al. 2013). We can illustrate this idea based on a hypothetical community in which the knowledge of certain practices involving natural resources, at a given point of time, is restricted to only one person. Thus, if such a person dies before having transmitted such information, this loss will affect the resilience of a system, as it will not be available when needed.

8.5.3 *Symbolic and Cultural Aspects*

Frequently, the capacity of a system to resist disturbances (e.g., changes resulting from urbanization processes) also depends on cultural and symbolic factors related to the elements, processes, and functions of the system. Certain communities do not accept different cultural practices simply because they do not believe in the assumptions that support other cultures. For example, Medeiros et al. (2012) found that, despite establishing an intimate contact with a new environmental context, some migrants maintain their traditional medical system, which forms part of their cultural identity. In contrast, the influence of the media and increasing urbanization leads other communities to adhere to new medical systems due to the often-disseminated notion that plants "do not cure" or are less effective than biomedical treatments. Thus, the same disturbance may have different effects in different systems, depending also on the social representations and symbols.

Recently, some ethnobotanical studies have applied resilience concepts to understand some aspects of the relation between people and plants. For example, the strategies adopted for the use of medicinal plants in the communities of Patagonia, Argentina, involve the use of medicinal plants from diverse environments. Such practice relate to the migration of these communities when families travel with cattle to different grazing areas. These travels can promote the resilience of local systems by increasing the system's flexibility in the use of medicinal plants from different environments (Ladio and Lozada 2008).

8.6 Adaptive Processes of Social-Ecological Systems

Adaptation is related to characteristics that provide advantages for a population, leading to increases in what is known as adaptive fitness. In biology, this increase in fitness is understood as an increase in the number of fertile descendants over time (see Jeanne 1998). However, this concept does not imply that adaptation is a modification or response perfectly suitable to the environment, but that is an appropriate modification to circumvent environmental problems, weighing costs and benefits in an environment undergoing rapid and continuous changes (Dunn 1976; Wiley 1992). However, from a cultural viewpoint, not every change leads to increased fitness, as they can instead promote some other advantages.

One of the key biological phenomena to help us understand the evolution of the cultural component in humans is phenotypic plasticity. The phenotype is the expression of a genotype as a result of the environment in which it develops. A phenotype may be rigid in its expression (e.g., two eyes, one nose) or flexible (blue eyes), depending on the environment in which it develops. In this case, cultural choices can be understood as flexible features since the practices of a human group can be adjusted to meet environmental demands, such as climate changes. This flexibility was a step in human evolution that allowed the development of multiple behavioral possibilities in several circumstances of our lives. Culture, therefore, which is a result of evolution, is essential to the human condition.

An important characteristic of social-ecological systems which can be understood in light of these adaptive processes, is Traditional Ecological Knowledge (TEK). According to Berkes et al. (2000), TEK can be defined as a set of knowledge, practices, and beliefs about the environment that is cumulative over generations and dynamic and flexible in face of the fluctuations of that environment. The cumulative and adaptive character of this knowledge system allows people to adapt to the environments where they live (see Berkes et al. 2000).

The adaptive characteristic of cultural systems is based on the statement that beneficial environmental information passes from generation to generation, creating what is known as cumulative reservoirs of adaptive information, where human populations store the best efforts of the minds of previous generations (Boyd and Richerson 2006; Henrich and McElreath 2003). In addition, information that assures greater fitness is preferably transmitted through a cognitive process known as adaptive memory (Nairne et al. 2008; Nairne and Pandeirada 2008; Nairne 2010). An example of this TEK property can be found in the difference between "knowledge" and "actual use," as people do not necessarily use all resources stored in memory. According to this distinction, the group of species referred as known, but not used by a community, is designated as "stock knowledge." The species that are actually used are recognized as "mass knowledge" (Albuquerque 2006). From an evolutionary viewpoint, the stock knowledge may be a strategy of local populations to ensure the existence of alternatives that can help them meet their needs if some resource is extinguished locally. In the event of a disturbance that threatens the availability of "mass" species, the "stock" species would assume the function of the firsts, thus entering the domain of the currently used species. The use of such species would therefore allow to maintain the local system, in this case the use of medicinal plants, functioning. In sum, stock knowledge increases the resilience of the local system because it enriches the utilitarian redundancy.

Another example that can indicate the adaptive nature of cumulative knowledge relates to the process of choosing species for medicinal use. Through experimentation, often by trial and error over generations, people select species for the treatment of diseases (Dunn 1976). The knowledge that a plant is useful in the treatment of some disease is not encoded in the genes; new generations will learn this information through cultural transmission mechanisms (Henrich and McElreath 2003). Thus, in local medical systems, species are selected for medical use based on criteria that are passed down through generations. Moreover, some of such criteria can be found in several places across the world. Thus, many human groups select plants based, for example, on their organoleptic properties (Brett and Heinrich 1998; Ankli et al. 1999). The medicinal plant selection criteria may have been subjected to natural selection so that different cultures could recognize and select medicinal plants for the treatment of diseases over different generations (see Johns 1990). For example, people from different societies seem to identify medicinal plants based on their effectiveness. One study showed that different communities of Nepal, New Zealand, and the Cape region in South Africa treat the same therapeutic conditions with phylogenetically related species. Although the species used in each region are different, people select evolutionarily related species for the treatment of the same diseases in the three regions studied. More importantly, the groups of related plants are those that exhibit higher numbers of species with biologically proven active principles (see Saslis-Lagoudakis et al. 2012). Another example is found in the inclusion of exotic species in traditional pharmacopoeia. The diversification hypothesis attempts to explain this phenomenon by affirming that, over time, people included exotic species in medical systems to fill therapeutic gaps (Albuquerque 2006; Alencar et al. 2010). This behavior would ensure that the exotic species enter the pharmacopoeias to diversify the treatment repertoire, thus gaining important adaptive value for these populations because they can increase the possible options for disease treatment.

Even when the exotic species are included in local medical systems to replace the uses of native plants (rather than to diversify the system), their entry may represent an adaptive character of these systems. What is often seen as erosion of traditional knowledge systems can indeed indicate a choice based on the adaptive advantages of some exotic species (such as greater efficiency, increased palatability, smaller distances for collection, etc.). Under this perspective, if—in a given medical system—replacement of native species by exotic ones occurred, such replacement could be due to the fact that the exotic plants had higher benefits for that local population than the native ones. This, however sets a future threat: What if, in the future, people need native plants, but the knowledge about them is already lost? Although we should acknowledge that this loss can happen, we need to avoid assigning positive or negative values to adaptive choices, as such losses are inherent in the evolutionary process (see Gómez-Baggethun and Reyes-García 2013 for an example with knowledge systems). Thinking from the perspective of biological evolution, a population can evolve to exhibit features that are advantageous for a particular environmental situation, however, if new drastic changes in environmental conditions occur, the characteristics obtained through evolution may no longer be useful or desirable, thus generating new evolutionary pressures.

Moreover, local practices can also change the environmental selective forces, acting on human groups and, consequently, in cultural systems (Wiley 1992). In a way,

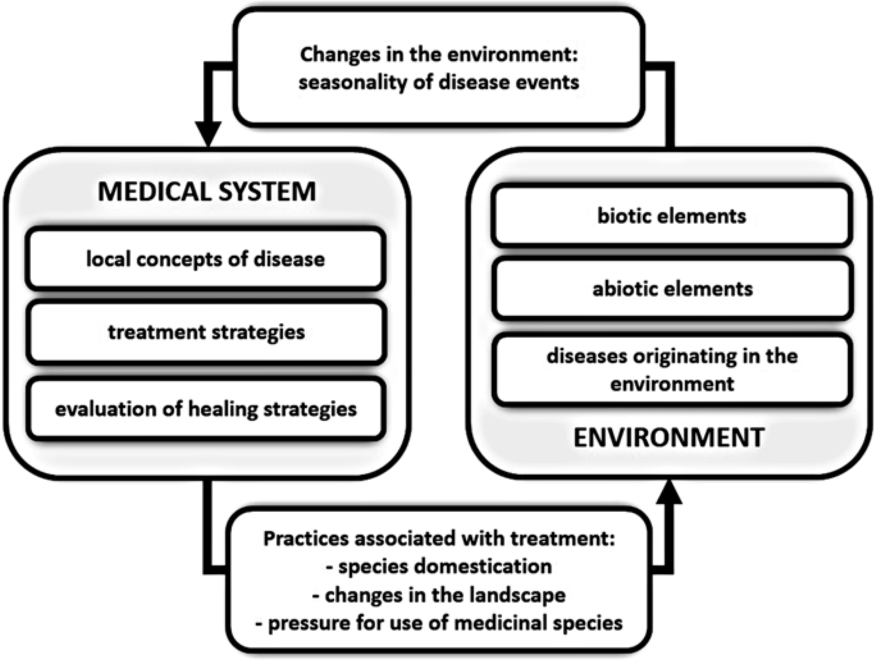

Fig. 8.1 Diagram showing the interrelation between a medical system and the environment in which it is placed. The diagram shows how medical systems, formed by a set of local concepts of diseases associated with treatment strategies and evaluations of therapeutic practices, may change environmental landscapes through the selection and use of medicinal species over time. The environment is represented by biotic and abiotic elements, which can be interpreted as disturbances of the medical system. Over time, certain changes in this environment, such as climate change and the very local practices that alter the landscape, may favor the emergence of diseases (i.e., disturbances) and, thus, influence the behavior of medical systems

as in the overharvest of local medicinal plants or in the plant domestication (Monteiro et al. 2006; Albuquerque and Oliveira 2007), local practices may change environmental landscapes and the selective forces acting on either the resources used or even the people themselves. Figure 8.1 shows this interrelation using the example of a medical system and the environment with which it interacts. We can use the niche construction theory as an example of a theoretical framework that evaluates the modification of environments by organisms from an evolutionary viewpoint. This theory takes into account the organisms' capacity to modify the environment on which they depend to the point of changing the evolutionary pressures, favoring the selection of advantageous traits for the propagation of their own species (Laland and Boogert 2010). For example, in the process of species domestication, human groups have selected, over time, characteristics of species to meet their needs to the point that current plant species show morphological changes to suit human dietary preferences (Parra et al. 2012).

8.7 Final Considerations

The previous explanations make clear the complexity of studying resilience and adaptation in social-ecological systems. To date, one of the main setbacks in the study of resilience is that it cannot be directly measured. The resilience of a social-ecological system can, however, be inferred indirectly by the evaluation of the system characteristics. With such premise, we suggest some questions that can guide future research:

1. What are the main strategies present in social-ecological systems that allow them to deal with disturbances? From the ethnobiological studies analyzed, we can identify two main types of disturbances. The first disturbance refers to processes that affect people and their cultural systems, such as diseases that threaten the health and well-being of people. The second disturbance refers to processes that affect the environment, including human-induced change, leading to the decrease of available functional species in a system. In face of these disturbances, which strategies are selected by different groups of people to increase the flexibility of their social-ecological systems? Redundancy can be one of the methods in a situation in which a certain community introduces exotic species into their pharmacopoeia as a strategy to increase the flexibility of functions with few functional analogues.
2. In addition to disturbances affecting the cultural systems mentioned above, there could be a wide variety of disturbances that affect a community to which the researchers do not have direct access by observation. It is therefore important to assess what do the local people identify as the main disturbance that affects the resilience of their social-ecological system? Focusing on local strategies formulated to address what people themselves consider as disturbances may help to elucidate important characteristics about their resilience and may assist in the design of governmental strategies for biocultural conservation.
3. Considering the work already performed, to the best of our knowledge, there are no studies that evaluate the effect of a disturbance on the different functions of a knowledge system. If we know that uses of natural resources can have different characteristics, can functions be maintained in the system by distinct mechanisms upon facing the same disturbance? To observe this phenomenon, it is necessary to understand that disturbances may affect different functions, as for example would occur if few species were inserted in different utilitarian categories.

In this chapter, we discuss the roles that some concepts developed in biology can play in understanding dynamics in social-ecological systems. In addition to redundancy, environmentalists have used the concept of functional diversity as one of the characteristics for the stabilization of ecological systems in their environments. Thus, when comparing local communities in different systems, which environments would favor the appearance of greater diversity of function and utilitarian redundancy? To answer some of the above questions, long-term investigations are needed.

Ad-hoc studies, with very small time scales, make it difficult to infer results about resilience mechanisms in social-ecological systems. Although this limitation does not impede the studies, it hampers the interpretation of the phenomena.

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Chapter 9
Utilitarian Redundancy: Conceptualization and Potential Applications in Ethnobiological Research

André Luiz Borba Nascimento, Washington Soares Ferreira Júnior, Marcelo Alves Ramos, Patrícia Muniz de Medeiros, Gustavo Taboada Soldati, Flávia Rosa Santoro, and Ulysses Paulino Albuquerque

9.1 Introduction

Human populations develop bodies of knowledge, beliefs, and practices from their relationships with other human populations and living beings as well as the environments in which they live. These relationships are modulated by adaptive processes (Berkes et al. 2000), and knowledge is passed down to future generations through social learning, which forms complexes known as social-ecological systems. Social-ecological systems have many functions that are performed by structural components, e.g., plants, animals, and fungi can be used to treat different diseases.

Ethnobiological research focusing on the use of medicinal plants by human populations has shown that different species are used to treat the same diseases (Gazzaneo et al. 2005; Almeida et al. 2006; Ceuterick et al. 2011; Molares and Ladio 2012; Kunwar et al. 2015). This statement prompts the following question: could this therapeutic overlap of medicinal plants promote adaptive advantages for the

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A.L.B. Nascimento (✉) • W.S. Ferreira Júnior • F.R. Santoro • U.P. Albuquerque
Laboratory of Applied and Theoretical Ethnobiology (LEA), Department of Biology,
Federal Rural University of Pernambuco, Av. Dom Manoel de Medeiros, s/n, Dois Irmãos,
Recife 52171-900, Pernambuco, Brazil
e-mail: andreborba_3@hotmail.com

M.A. Ramos
Department of Biological Sciences, University of Pernambuco,
Av. Amaro Maltez, 201, Centro, 55800-000 Nazaré da Mata, Pernambuco, Brazil

P.M. de Medeiros
Center of Biological Sciences and Health, Federal University of Western Bahia,
Estrada para o Barrocão, s/n, Morada Nobre, 47800-000 Barreiras, Bahia, Brazil

G.T. Soldati
Institute of Biological Sciences, Department of Botany, Federal University of Juiz de Fora,
Av. José Lourenço Kelmer, s/n, São Pedro, 36036-900 Juiz de Fora, Minas Gerais, Brazil

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human populations that use these resources? To answer this question, Albuquerque and Oliveira (2007) proposed an investigative ethnobiological model analogous to functional ecological redundancy: the utilitarian redundancy model (URM).

In summary, the URM considers the different conditions that are treated with the natural medicines as functions to be fulfilled by the local medical system, and it further considers the multiple species used to treat the same illness as a functional redundancy within the system. Based on these premises, the model aims to answer the following questions: What are the ecological and evolutionary implications of potential redundancies of use? Are certain species preferable to others under redundancy conditions? If so, does this preference somehow change the use patterns of the species with redundant functions?

The goal of this chapter is to show how the URM could answer these questions and the interesting theoretical and practical framework for ethnobiological research that it offers. We will initially explain the original ecological redundancy model and its concepts and definitions before presenting the applications of the URM. We will show how the model can illustrate the ways in which people relate to the resources available in their local environments.

We assume that the ways in which species are functionally organized determine the dynamics of a system. Therefore, this chapter focuses on species within a functional context to determine how the knowledge and use of resources by local populations influence how traditional medical systems change or evolve.

9.2 The Ecological Redundancy Model

Understanding the role of species in ecosystem regulation is a growing concern in conservation that has led ecologists to examine several processes and systemic relationships, such as the relationship between ecological function and species richness (Bengtsson 1998; Peterson et al. 1998; Cadotte et al. 2011). Numerous explanations have been formulated to help clarify this relationship, including the ecological redundancy (ER) model proposed by Walker (1992), which is based on several assumptions. First, the species in an ecosystem perform ecological functions, such as pollination, dispersal, photosynthesis, and decomposition. Second, when different species fulfill the same ecological role, there is an overlap in function, so functionally analogous species can occur. Third, certain ecological functions are redundant because they are performed by multiple species (Walker 1992; Wellnitz and Poff 2001). The ER model shifts our understanding of ecosystems away from the conventional taxonomic approach to one focused on function (Walker 1992). Wellnitz and Poff (2001) argue that “complete functional redundancy would occur if, following the removal of one species, the remaining species increase their densities to compensate for the lost functional contribution of the removed species.” In this hypothetical state, a biological entity may become locally extinct without compromising the entire system because its function will be performed by the redundant species. In other words, the focus would shift from the individual species to the functions of those species at the ecosystem level.

Despite the potential of ER to guide biological conservation initiatives, many problems may occur when researchers attempt to quantify the relationship between species richness and ecosystem function (Bengtsson 1998) or identify the functions of each species inspired by the complex dynamics among species. ER offers a practical approach to developing strategies for ecosystem management despite the aforementioned difficulties. Thus, the ER approach could be used to assess the composition of the pollinator guild in an area where conservation studies will be conducted on native vegetation. Plant species evolved along with their pollinators and include adaptations that allow greater reproductive success when both plant and pollinator species co-occur (Machado and Lopes 2004). Therefore, knowing the organisms that perform this ecological function in the region and determining the species that are in population decline are necessary for the development of more appropriate conservation strategies.

Political decisions related to biodiversity management and conservation must consider both functional diversity and ER (Walker 1992; Low et al. 2003). Functional diversity and ER are based on the principle that species richness generates stability, although there is evidence showing that this is not always true (see Reynolds 2002). According to the ER model, a given area may have a great number of species with certain ecological functions performed by a limited number of species (low redundancy). Thus, a local pollination guild can consist of many species and still have only one hummingbird species, which would compromise ornithophilic functions (bird-mediated pollination) despite the occurrence of several other pollinator species in the area. Therefore, biodiversity management and conservation initiatives should focus on ecosystem functions with little or no redundancy.

Considering that redundancy is present in many systems (e.g., genetic, ecological etc.), we can assume that it is a characteristic or attribute of a system (Low et al. 2003) and not necessarily costly. According to Low et al. (2003:86), “Costs are always associated with redundancy because building more than one unit involves the use of energy, materials, and time that could be used for other purposes. System performance can, in turn, be measured along multiple dimensions, e.g., capacity to cope with risk and uncertainty; adaptation to exogenous change; error reduction through repetitive learning or learning from others; matching system responses to local conditions; and ability to reduce the probability of system failure. Whether the benefits (of improved system performance) are worth the costs (of added time, effort, and resources used to build multiple units) of redundancy depends on: (1) the type of problems faced in governing a system, (2) how the particular kind of redundancy copes with these problems, and (3) the cost of the particular type of redundancy”.

The concepts presented above can be transposed and used to study the ecological/evolutionary relationship between people and natural resources. The established bridge between the discussed ecological concepts and ethnobiology framework provides insight into the functioning of local knowledge systems, and it can be used to determine if a wide diversity of species with functions that meet the same demand reflects a more resilient body of knowledge, i.e., one that is capable of sustaining its structure and dynamics even if the use of one or more species is locally abandoned.

9.3 The Utilitarian Redundancy Model

The URM emerges from the ER by adopting a functional perspective in the analysis of natural resource use by human populations, and it evaluates the role of functional overlap in knowledge systems and local management (see Albuquerque and Oliveira 2007). This analytical perspective arose from the observation that several species are traditionally used for similar functions, i.e., they are culturally redundant regarding local use indications. Therefore, the redundancy concept applied to ethnobiology can be a useful tool for evaluating local natural resources management and conservation strategies under an adaptive perspective.

The URM model is based on the following assumptions: (a) species have different functions within social-ecological systems, but a level of overlap in function (i.e., redundancy) occurs; (b) increased redundancy promotes resilience in social-ecological systems, and (c) redundancy depends on the knowledge characteristics and practices of a given human community. Therefore, the URM is an operational concept used to determine the (a) role of redundant species in the structure and dynamics of a cultural system; (b) contribution of redundant species to the resilience of knowledge and local practices; and (c) effects of human activities on biodiversity.

We attempt to explain the conceptual connection between ecological and utilitarian redundancy before proceeding to the analysis of different topics. Consider any social-ecological system, such as that of plants and animals used as food or raw materials used in construction. Redundant species share the same **function** and fulfill the same local demand, i.e., they have the same **use**. In a local medical system, the term function is used as the **therapeutic target** to which the species is associated. Therapeutic targets are the indications to which medicinal plants and animals are employed, according to local classifications. Therefore, therapeutic targets may designate only one symptom (e.g., pain or cough) or several symptoms of a more serious condition (e.g., flu or tuberculosis) that may be recognized as a “disease” by biomedicine. Our decision to use the term therapeutic targets instead of diseases reflects the local concepts of health and illness (or the local nosology) because these concepts may be important in selecting a treatment (see Beiersmann et al. 2007). The URM model is advantageous because it enables the quantification of the relationship between species richness and function within a system, despite the complex dynamics of traditional ecological knowledge.

As previously stated, the URM may be used to assess whether a medical knowledge system is resilient, in other words, if a local medical system is able to absorb disturbances, reorganize and maintain its functions and structure (see Holling 1973). The dynamics of a system depend on the integrity of its functions. In addition, the same ecological assumption of the dynamics in an unchanged system regardless of species loss occurs when other entities performing the same function fill the void of the initial loss. Therefore, if a local medical system experiences a loss of knowledge (e.g., the death of a person holding the knowledge) or the loss of use of a species (e.g., by local extinction) that is a treatment for a redundant therapeutic target, such losses do not affect the overall functioning of the medical system despite the reduction in the diversity of the useful species in the system.

We further analyze the contribution of the URM to the understanding of the effective use of a species and, consequently, human pressures on natural resources. Initially, we might logically assume that the occurrence of a number of species with the same function will minimize the use pressure on specific species if the exploitation of those species is evenly distributed. Therefore, higher redundancy is implied by the existence of more species that may be subject to collection, thus reducing the impacts on individual species. However, we must consider an additional factor, which is that certain resources are locally preferred and receive increased attention with rising demand. The species known as "best" or most important will be preferred despite a larger set of species being available to fulfill the function. Here, preference is related to the conscious selection of a species instead of another that is equally available (Albuquerque et al. 2005), so mutual reinforcement ends when there is preference for a specific species in a given category. Thus, utilitarian redundancy would not lead to single species protection but only to the maintenance of local function.

Finally, we highlight the potential application of the URM model to other areas of ethnobiological research despite being initially conceived from the perspective of medicinal plants. For example, the use of fish species by coastal communities may be studied through the URM with different fish categorized as functions: alimentary, medicinal, commercial, mystical-religious, and companion. The same assumptions of the URM could be applied to such a situation, leading to the following predictions: (a) fish species belonging to less redundant use categories could be subject to greater pressure; (b) in the case of greater preference for a specific fish species, the most preferred use category would be subject to greater use pressure; and (c) greater redundancy within fish use categories makes the fish knowledge system more resilient. However, it is noteworthy that different knowledge systems have peculiar use dynamics, and these peculiarities must be considered to reach a more accurate conclusion about which adaptive mechanisms explain the observed patterns. We must also consider the importance of social dynamics in shaping the access, use and knowledge of natural resources (e.g., intracultural dynamics) and the functioning of social-ecological systems.

9.4 Applications of the Utilitarian Redundancy Model

Most of the therapeutic targets treated with medicinal plants in a local medical system may have low redundancy, which could indicate high specialization in the local medical system (Albuquerque and Oliveira 2007). According to the assumptions of the URM, greater specialization in the local medical system would result in the system being more susceptible to disturbances and less resilient with the loss of a species having the potential to lead to a loss of function.

However, the definition of "function" must be standardized to avoid incorrect interpretations of the URM. In a medical system, for example, we may consider uterine inflammation as a function and obtain a certain number of plants capable of treating it (redundancy), or we may consider it as overall inflammation and obtain a different number of plants. Although inflammation is redundant, when the URM was applied for the inflammatory subcategories recorded in a rural community in northeastern Brazil, certain inflammation subcategories were not redundant (e.g., throat, ear, vaginal, and wound inflammation) (see Ferreira Júnior et al. 2011). Thus, it is important analytically define a system's functions, because the results may differ depending on how the functions are classified (e.g., an overall category for inflammation or a specific classification for a type of inflammation). It is important to include the local classification of an illness (considering the local nosology) to make the scientific data relevant to the local people.

Because the distribution of intracultural knowledge is not homogeneous among the individuals of a population, certain people within a community will know more than others on specific topics (see Araújo et al. 2012), and this unequal distribution of knowledge may affect the interpretations of the URM (see Ferreira Júnior et al. 2013). If a single person within the community retains much of the local knowledge and withholds it from the rest of the population, his or her death or migration may lead to the loss of a function from the system (e.g., shamans or specialists). A study conducted in the Brazilian Caatinga, for example, reported that the redundant knowledge of therapeutic conditions was restricted to a small portion of the population (Ferreira Júnior et al. 2011). This situation is a major impediment to resilience because the disappearance of one of the informed people may cause a shift in the system (Albuquerque and Oliveira 2007). It also may have important cultural implications in terms of sacred knowledge and access to knowledge that might not be available to everyone in a group.

The URM may also be used to identify species that are under greater pressure from local use due to preferences for the treatment of slightly redundant or unique therapeutic targets. For example, the preferred tree species in a rural community of the Brazilian Caatinga (seasonal dry forest) were subject to bark extraction over larger areas, and a greater number of individuals were exploited, which confirms the hypothesis that preferred species experience greater use pressure (Ferreira Júnior et al. 2012).

However, precautions are required when evaluating the use pressure on slightly redundant therapeutic targets because such species may be uncommon in the community (Ferreira Júnior et al. 2011). In this case, the pressure of use on the species involved in treating therapeutic targets would be reduced despite the low redundancy (rare occurrence) of these species, which would lead to the decrease in resource collection frequency.

We can distinguish two situations for the URM assuming specificities in resource usage by local communities. The first situation would be an ideal condition in which only functional redundancy and its preference status interfered in the pressure of use for a species. In this situation (a) a greater functional redundancy is implied when there is a lower pressure of use in the absence of preferred resources and (b) the preferred resource will always suffer greater pressure when available, regardless of other alternatives. The second situation acknowledges that the local requirements for a certain use motivate people to try new species (see Ladio and Lozada 2008).

Other precautions are required when applying the URM, such as when an ideal functional overlap does not occur and there is no complete redundancy. Two species may be redundant for some functions and not others. Redundancy, therefore, is not specific to a group of species but to the interaction among species (see Peterson et al. 1998). The function headache treatment, for example, may consist of species V, W, X, Y and Z. However, species X is exclusive and has no redundancy for the function "wound treatment." This example shows that misinterpretations may occur when we disregard the knowledge system to understand redundancy. To analyze the therapeutic target "headache" separately, we could imagine that species X is protected from overuse once multiple species are available with the same function. However, such an assumption ignores that species X is the only alternative treatment for wounds; thus, the species could be compromised from an ecological perspective because of a greater pressure of use.

An analogy to the ecological functional redundancy was also used in a study on the utility potential of forest fragments in Madagascar (Brown et al. 2011), although the URM as described here was not applied. Brown et al. (2011) studied tree species used in six categories of use (fuel, construction, food, medicine, and material for tools and furniture) in a forest fragment near rural communities. A null model was used to simulate the functional diversity expected for each fragment, and the number of species with overlapping functions in these fragments (redundancy) was estimated from the expected functional diversity. According to the researchers, a greater utilitarian redundancy within the fragment lowered the risk of losing local utilitarian functions when faced with a disturbance that had the potential to cause the disappearance of a species; thus, lower redundancy led to higher risk.

Assessing the availability of resources used by rural communities (Brown et al. 2011) is an interesting strategy for evaluating redundancy. Analyses of forest fragmentation can assess if species subject to higher use pressure under the URM are actually threatened. However, the system may extend beyond forest fragments, and applying the URM-limited areas reduces the access to information on the redundancy and resilience of the system that constitutes the uses of plants in a human population. Certain exotic plant species, for example, may only be found in backyards or overall anthropogenic areas and are absent in forest fragments. However, these species may provide significant contributions to the redundancy of categories and resilience of the local medical system.

The characteristics of the local medical system and use of medicinal species that are detected by the URM may also be applied to research on medicinal animals. Ethnozoological research has reported the use of several animals to treat the same diseases and suggests that usage overlaps may be important in the adaptation of human populations that utilize such resources because certain functions can be maintained in the absence or limited availability of resources. Absence or limited availability could occur due to seasonality or a species' migration cycle. For example, Ferreira et al. (2012) applied the URM to zootherapy research. Their study was conducted in the public markets of five large cities in northeast Brazil, and the results show that most therapeutic indications could be treated by a large number of animal resources (i.e., the animal species were redundant). These results show that the medical system in the public markets (represented by a hybridization of different medical systems, see Ladio and Albuquerque 2014), leads to greater resilience in the local medical system according to the URM. Resilient environments have many alternatives for use and are more likely to absorb various disturbances that have the potential to compromise system functionality. Public markets are spaces where cultural information and influences from other regions are exchanged (Albuquerque et al. 2007). Therefore, it is understandable that a large number of redundant therapeutic targets would be found in these markets because the sellers must include species from other regions to their stores to diversify their treatments of therapeutic targets. This strategy may be highly functional in these systems because it ensures the provision of a wide range of products to buyers from different origins, which contributes to system functionality by providing species that may compensate for the local absence of others due to seasonal variations.

The URM must be evaluated in specific contexts, and it is important to understand the characteristics and dynamics of the knowledge system under study before making inferences regarding the system's behavior under the URM (see Alencar et al. 2014). For example, Santoro et al. (2015) observed that species richness was associated with the frequency of therapeutic targets (popularity) in a local medical system and negatively correlated with severe or lethal illnesses.

9.5 Perspectives

The URM is a valuable tool for evaluating redundancy in uses or functions in a knowledge system and the environmental impacts resulting from human activities that may enhance or decrease the resilience of a specific social-ecological system. We refer to such impacts in terms of the local knowledge system instead of the local medical system. The model is not restricted to medical use despite its original application, and the model may be easily used to test hypotheses in other areas of ethnobiology.

Social-ecological systems are complex, and inferences based on the URM must consider the dynamic characteristics and adaptive components of the system that could explain the observed behaviors. The level of overlap may result from different variables, such as the history of experimentation of the local populations with the resources available in the environment or locally perceived resource quality, which ultimately determine the redundancy of a resource (see Alencar et al. 2014). Thus, studies should be conducted to determine why human populations prioritize certain uses and species to understand if the frequency of occurrence of a therapeutic target increases the level of experimentation with a species used as a treatment.

In addition, the model is not intended to provide a complete explanation of the characteristics of a social-ecological system because other factors, such as historical events within the community and contact with other human groups, may be influential. There are also limitations to the understanding of the dynamics and complexities of social-ecological systems, specifically the social and cultural meanings of some species as therapies and their interrelationships with belief systems. Therefore, new studies are required to test the model in real situations and contribute to a better understanding of different social-ecological systems.

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Chapter 10
The Influence of the Environment on Natural Resource Use: Evidence of Apparency

Ulysses Paulino Albuquerque, Gustavo Taboada Soldati, Marcelo Alves Ramos, Joabe Gomes de Melo, Patrícia Muniz de Medeiros, André Luiz Borba Nascimento, and Washington Soares Ferreira Júnior

10.1 Introduction

Little is known regarding the factors underlying the selection process and the consequent incorporation of a plant into a culture, that is, "how" and "why" a given resource, previously unknown, becomes an integral part of the practices of a certain group. If one accepts that traditional botanical knowledge results from evolutionary processes, then the assumption that variables in addition to culture can explain the dynamics of social-ecological systems is reasonable. There are many more questions than concrete answers regarding these processes, despite the advances made by ethnobiological studies worldwide.

Some of these questions, which can be grouped based on an ecological and evolutionary framework, include the following: what factors influence people's

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U.P. Albuquerque (✉) • A.L.B. Nascimento • W.S. Ferreira Júnior
Laboratory of Applied and Theoretical Ethnobiology (LEA), Department of Biology, Federal Rural University of Pernambuco, Av. Dom Manoel de Medeiros, s/n, Dois Irmãos, Recife 52171-900, Pernambuco, Brazil
e-mail: upa677@hotmail.com

G.T. Soldati
Institute of Biological Sciences, Department of Botany, Federal University of Juiz de Fora, Av. José Lourenço Kelmer, s/n, São Pedro, 36036-900 Juiz de Fora, Minas Gerais, Brazil

M.A. Ramos
Department of Biological Sciences, University of Pernambuco, Av. Amaro Maltez, 201, Centro, 55800-000 Nazaré da Mata, Pernambuco, Brazil

J.G. de Melo
Federal Institute of Alagoas - Matriz, Campus Maragogi, Maragogi, Alagoas CEP 57955000, Brazil

P.M. de Medeiros
Center of Biological Sciences and Health, Federal University of Western Bahia, Estrada para o Barrocão, s/n, Morada Nobre, 47800-000 Barreiras, Bahia, Brazil

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decision to select a natural resource for sampling and possibly to incorporate it in their social-ecological systems[1]? Which variables influence the choice of a resource for use among the many others that are also known? Why and how are alternative strategies developed for the exploitation of these resources?

This chapter poses a theoretical reflection based on a simple question: can a certain intrinsic characteristic of a species, such as its environmental availability or chemical composition, affect its local use and the local knowledge regarding the species? In short, can ecological variables influence local ecological knowledge? We have chosen certain theoretical scenarios to answer such questions, in particular, the ecological apparency hypothesis (EAH), the optimal foraging theory (OFT) and the resource availability hypothesis (RAH). The examples used herein, as seen below, are largely derived from ethnobotanical studies because we lack empirical data that test this hypothesis in ethnozoological studies, for example.

10.2 What Is the EAH?

The EAH, conceived by Feeny (1976), revolutionized the field of ecology by proposing a means to understand the distribution among plant communities of the different strategies of plant defense against herbivores (Endara and Coley 2011). For Feeny (1976), the nature of these strategies basically depends on the ease with which a plant can be found by foragers, in that case, by herbivores. In this sense, the author categorizes the plant resources into two groups: (a) "apparent" resources, large trees and shrubs with a wide and aggregate distribution, and (b) "unapparent" resources, usually small herbs with a restricted and scattered distribution. As a result of their distributions, the apparent plants would be more highly consumed, and their defensive strategies would be a reflection of the higher rate at which these plants are grazed.

Applying this hypothesis to ethnobiology, people can be considered as foragers, similar to nonhuman herbivores, who constantly seek useful resources or plants that can be selected and incorporated into social-ecological systems. Following the EAH, the plants that are most used by a human population correspond precisely to the most "apparent" ones, the easiest ones to find. Consequently, because they are more frequently demanded, these resources and their properties become more familiar to people and thus have a greater cultural importance and greater richness of uses.

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[1] We hereby adopt the concept of Berkes and Folke (1998:4). Thus, "the term ecological system (ecosystem) is used in the conventional ecological sense to refer to the natural environment. We hold the view that social and ecological systems are in fact linked, and that the delineation between social and natural systems is artificial and arbitrary. Such views, however, are not yet accepted in conventional ecology and social science. When we wish to emphasize the integrated concept of humans-in-nature, we use the terms social-ecological system and social-ecological linkages."

10.3 Relationship Between the Apparency of a Resource and Its Local Importance

The first explicit test of the EAH applied to ethnobotanical questions was conducted by Phillips and Gentry (1993a, b) and based on the simple prediction, previously mentioned, that relates the availability of a resource with its local importance to human population. Thus, easily detected plants offer a greater chance for experimentation and inclusion in a cultural system, considering, of course, the validation process. Such apparent plants would be more in demand, and the many need/experimentation events would stimulate their uses, making them more culturally important (Fig. 10.1). These authors proposed a measure of relative importance to assess the status of a plant in a given culture. This measure, the use value[2] (UV), is based on the number of uses attributed to a plant by a set of people (Phillips 1996). Since this pioneering work, many studies have been conducted to test the EAH in different environmental contexts.

The first important insight from this body of research regarding the selection process of plants to be included in a culture is that, when considering all categories of use in the same analysis, the apparency of a resource, although significant, weakly influences the local importance of the resource (see Phillips and Gentry 1993a, b; Galeano 2000; Torre-Cuadros and Isbele 2003; Lawrence et al. 2005; Cunha and Albuquerque 2006; Lucena et al. 2007). This scenario leads to a number of questions: (a) Are the ecological factors analyzed in those studies, such as the importance value index (IVI), good availability indicators? The availability perceived by the people may not correspond to the availability measured through ecological parameters because certain abundant plants occur far from the community, which could affect the perception of availability for certain species; (b) Could the cultural importance of plants be influenced by the past availability of a resource? If so, current native vegetation areas may represent a scenario influenced by past management, which may have caused a decrease in the population of dominant species, considering that these species are the most heavily used. Thus, the phytosociological parameters currently collected to understand this phenomenon are incapable of establishing a significant relationship; (c) Are these data indicating that environmental availability, although important, is not the only variable that can explain the phenomenon?

One can advance the search for answers to these questions by considering the studies that have evaluated the EAH by separately analyzing the use categories. Although Maldonado et al. (2013) found positive relationships between the environmental availability of a resource and its importance in several categories, most of the available studies indicate that the EAH is supported only in certain plant groups

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[2] The use value (UV) for a given plant is the simple ratio of the number of uses cited divided by that reported by people. We recommend Medeiros M et al. (2011) to access the different measures of the relative importance of a resource that have been designed by ethnobotanists over the last 20 years, as well as the variations that have been proposed for calculating the UV.

with similar use dynamics but not in all of them (see Phillips and Gentry 1993a, b; Lawrence et al. 2005; Lucena et al. 2007, 2012) (Table 10.1). For example, in several situations, the EAH is supported only (or more expressively) by the category "construction" (see Lawrence et al. 2005; Lucena et al. 2007, 2012), indicating that the selection of species for this category is under the strong influence of their environmental availability. However, certain categories behave in an unpredictable fashion, exhibiting positive relationships between the availability and the importance of the plants in some studies and negative ones in others. For example, the medicinal category is strongly explained by environmental availability in certain studies (Lucena et al. 2007) but not in others (Phillips and Gentry 1993a, b; Lucena et al. 2012). Moreover, there are also differences in the phytosociological parameters that better explain the studied relationships. Dominance, and not other apparency estimates, is usually the variable that best explains the relative importance of a plant in the construction category; that is, the volume of a species is more important than its spatial distribution (relative frequency) or abundance (relative density).

Therefore, when the different use categories are separately analyzed, three main conclusions are reached that help to answer the previously presented questions: (a) the different categories can prove or disprove the EAH; (b) when a category supports the hypothesis, it does so to a greater or lesser degree, depending on the environmental context; and finally, (c) when the categories prove the hypothesis, the phytosociological parameters of greater expression (more explanatory) vary among the use categories (Table 10.1).

Therefore, the evidence suggests that different use categories have different dynamics and that diverse factors can influence the knowledge regarding the resources in these categories. Thus, analyzing an entire group of plants using the same test may skew a complex reality. In addition, the importance value index can be a valuable availability parameter for use categories such as the construction category that demand bulky plants but may not be an interesting parameter for the medicinal category since it has different requirements. Additionally, differential use has implications from the viewpoint of conservation, especially for the construction category, which has historically been identified as one of the categories that exerts the most pressure on native vegetation areas (Dahdouh-Guebas et al. 2000). Therefore, for this category, the fact that environmental availability significantly influences the selection of species can indicate the use of target species with a greater wood yield, regardless of whether this yield is expressed as relative density or as dominance.

In addition, one must consider that the relationship of resource use to resource availability is a dynamic one and can lead to the decreased use of certain species as the environmental supply decreases. When resource management does not environmentally favor the useful species but only seeks to exploit them, a relationship between the availability and the importance of a species can weaken. This weakening occurs because the use of the most available and therefore the most managed plants tends to decrease the plant population. Thus, the local importance of species, measured by the UV, may vary over time in response to different environmental (Lawrence et al. 2005) or cultural pressures.

Table 10.1 Main results of studies on the ecological apparency hypothesis (EAH) from an ethnobotanical perspective

Use category	Abundance	Apparency parameters				
		Basal area	RDo	RD	RF	IVI
Food				x		
Timber		x				
Medicinal					x	x
All uses	x		x		x	x

RDo represents relative dominance, *RD* is relative density, *RF* is relative frequency, and *IVI* is the importance value index

10.4 The EAH in the Light of the OFT: A New Perspective

Although the EAH has been relatively well studied, few studies have attempted to explain the ecological processes that build the relationship between the environmental availability of a species and its local knowledge base and use. Phillips and Gentry (1993b) argued, as previously mentioned, that the importance of a resource is related to its availability in the environment because people are more likely to test and validate their knowledge using the most available species. The explanation provided by these authors is supported by probabilistic and not ecological arguments. Other studies related to this hypothesis use this same logic to explain their findings.

Thus, it is proposed herein to theoretically reflect on and contextualize the EAH based on predictions from the OFT. According to this theory, human behaviors reflect attempts to optimize the return during plant collection and extraction events. Foraging events involve basically two variables that counteract each other and determine plant collection behavior: (a) the energy spent in the pursuit of the resource and (b) the return, energetic or of another nature, offered by the collection event itself. Foraging behaviors must optimize this relationship by increasing the volume collected or reducing the energy spent. By assuming that there is a relationship between the availability and the relative importance of a resource, the EAH remains rooted in the optimization rationale advocated by the OFT because the most important resources are precisely those with the highest availability, that is, the ones that ensure continuous exploitation with relatively high recoveries (greater benefit) and low energy expenditures during the search (lower cost).

Observing the collection/extraction phenomenon in detail, we can establish a direct relationship with evolutionary dynamics, given that the phenomenon is influenced by the mechanisms of variation, selection, competition and heredity. For instance, why are plants chosen for inclusion in the practices and the knowledge base of a population? The following are several plausible reasons: (a) variation in the characteristics of the resources, particularly regarding their supply (availability), that provides a concrete scenario in which different collection behaviors are possible, according to the diversity of those characteristics; (b) under an evolutionary perspective, these different behaviors compete with each other because the behaviors have the same cultural function (selecting plants to be used) and produce different results; (c) with this competition, selection evidently favors the more adaptive behaviors; (d) the adaptability of a selected behavior may be the result of biases in the act of choosing, such as cognitive tendencies that favor certain characteristics intrinsic to the plant resource, making it, for instance, more memorable; and (e) these mechanisms, which are in principle more adaptive, become fixed in the population through social learning, thus allowing the system to accumulate information and evolve over time.

Considering all these evolutionary processes, let us imagine again the incorporation of a plant into a culture and add to this scenario the OFT assumptions. To be known and used, a resource is sifted through the knowledge-building process and should therefore be socially (a) understood, (b) recognized, (c) tested and (d) validated. The first cost-benefit ratio that determines the set of known and used plant resources is established early in the construction of this knowledge. Producing new information about any natural resource demands time and energy, and according to the OFT assumptions, the current behaviors are the result of natural selection favoring optimal behaviors. Therefore, the construction of knowledge only has adaptive value when this knowledge is associated with a set of resources that allows its implementation, that is, that ensures a return, also optimal, clearly supported by the greater availability of the resource.

Our position is based on the supply of a resource. However, unlike Phillips and Gentry (1993a, b), who highlight the richness of uses reported by the people, we argue that availability influences the knowledge base by reflecting an optimal structure that follows two basic purposes: (a) the optimization and security of obtaining resources so that the more abundant species provide greater availability for extraction, and (b) a higher probability of finding the most abundant species, therefore those already known and considered useful, in random collections. Security in the use of resources finds echoes in the argument presented initially by Albuquerque (2010) for explaining the use of perennial products for medicinal purposes by populations in the Brazilian semiarid region, even when nonperennial resources have better quality or therapeutic efficiency. The same principle can then be used to explain why local populations tend to predominantly use the most available plants.

This first relationship, which favors the most available plants during the building of a knowledge base, supports the second one, which ensures access to plant resources in desired amounts (Albuquerque 2010). The latter relationship is quite explicit in the use category ‘construction’, previously mentioned, which has exhibited significant relationships in many studies with the relative dominance or basal area of the useful species. Thus, the use dynamics specific to this category, that is, the demand for species with large sizes and amounts, yielded higher use values for species with greater environmental availability.

We have already demonstrated the way in which the optimal assumptions theoretically support the resource use behavior predicted by the EAH, in this case, the relationship between environmental availability and relative importance. However, we have yet to understand the mechanism by which the differential utilization in use categories can be explained from a cost-benefit ratio. The OFT predicts that the return can be understood by not only the quantity exploited (volume) but also the quality of the resource that is collected, such as a higher wood density, better flavor, or higher nutritional value or the specific requirements for a particular use (Soldati and Albququerque 2012). This assumption explains the differences in the EAH related to the different use categories and raises two questions: (a) Why is there a weak relationship in the categories that support the hypothesis? (b) Why do some categories not support this hypothesis?

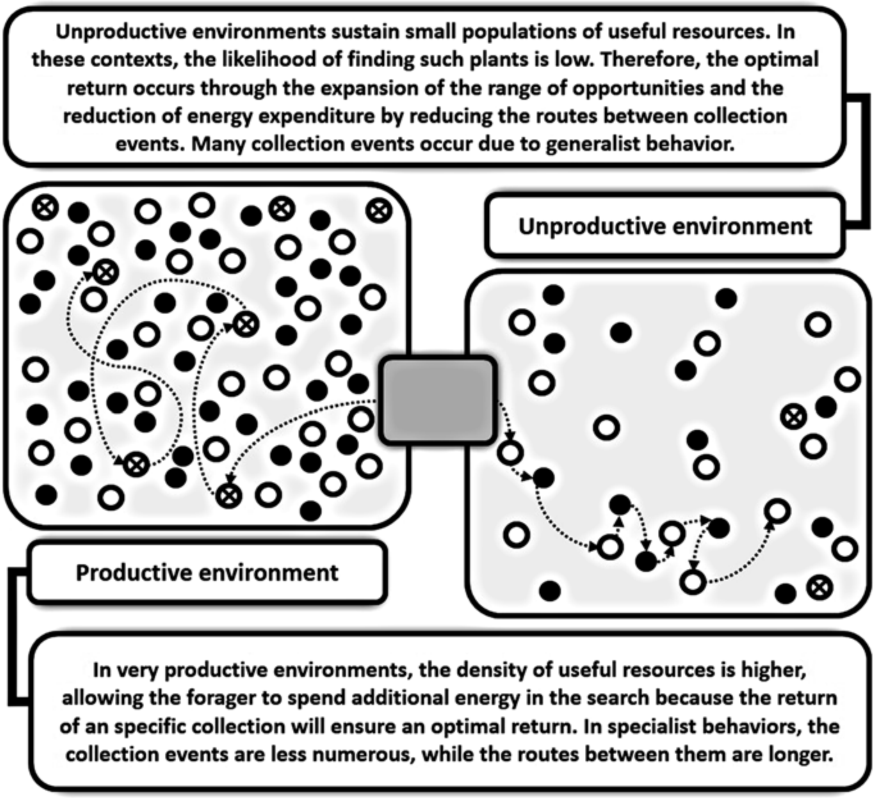
Both questions can be answered by the differences in the requirements of the different categories. Let us consider, for example, the construction category and its different uses, as well as the medicinal category. Construction imposes a wide variety of demands; for example, compare the building of a house with that of an animal shelter. Our studies indicate that the preferred resources for the production of a dwelling are relatively more abundant to ensure a higher extraction volume and greater quality so that the building does not collapse over time (Medeiros P et al. 2011; Medeiros et al. 2012). The requirements for building a chicken coop, for example, are comparatively less, and the resources are not selected because of their quality. Therefore, there are uses that require availability and quality, whereas other uses only require availability. As a result, the construction category tends to corroborate the EAH. The optimal use of medicinal species does not follow the same rationale as that adopted for the species used in construction, which is a mixture of quality and quantity (volume), but is instead based mainly on the quality of the resource, expressed by the type of bioactive compound (responsible for the therapeutic effect) present in the plant. Studies conducted in the Brazilian semiarid region, for example, have found strong relationships between the presence of certain bioactive compounds and the use of certain species for therapeutic purposes (Almeida et al. 2005; Araújo et al. 2008; Alencar et al. 2009, 2010).

Given the above, we believe that because use categories have specific requirements, they must also have different optimal situations, which explain the presence or absence of the relationship between availability and local importance predicted by the EAH. For example, environmental availability is crucial to the collection behaviors in categories that have a lower need for high-quality resources or for categories such as construction that demand abundant, better quality plants. By contrast, medicinal uses require less quantity than quality, and because the EAH tests do not include qualitative variables, this use category showed little relationship between apparency and UV. In short, the following conclusion can be drawn: (a) categories governed only by availability respond very well to the model, (b) categories governed by availability and quality (such as construction) respond well to the model (but part of the unexplained variation is due to quality) and (c) categories without interference from availability show no results for the EAH.

10.5 Generalist and Specialist Behaviors in the EAH Context

The two aforementioned dimensions present in plant resources, i.e., quality and quantity, stimulate additional questions regarding collection patterns and, therefore, patterns of plant use that have as a background the optimal relationships that should be herein discussed. One question that arises is whether the relationships predicted by the EAH are sensitive to the environmental contexts experienced by human populations. If so, a second question concerns the situations and contexts in which such relationships are favored.

Like nonhuman foragers, people can behave in a specialist or generalist manner; thus, the plant resource selection patterns by local communities can follow the same principle. On one hand, an optimal return can be achieved by the exploitation of the most available species, without discrimination between resources or quality levels (Fig. 10.1). This generalist pattern results in the extraction of a large amount of



Unproductive environments sustain small populations of useful resources. In these contexts, the likelihood of finding such plants is low. Therefore, the optimal return occurs through the expansion of the range of opportunities and the reduction of energy expenditure by reducing the routes between collection events. Many collection events occur due to generalist behavior.

In very productive environments, the density of useful resources is higher, allowing the forager to spend additional energy in the search because the return of an specific collection will ensure an optimal return. In specialist behaviors, the collection events are less numerous, while the routes between them are longer.

Fig. 10.1 Relationship between environmental productivity and foraging behavior. The *black, white* and *crossed circles* correspond to slightly useful, useful and very useful plant resources, respectively. Note that the density and frequency of the most useful resources are lower in the unproductive environments, thus promoting a generalist collection pattern resources with the expenditure of little energy and reduced distances between the collections. On the other hand, in certain contexts, the optimization of foraging is centered on the selection of better quality species, even if the species demand more time and energy for their collection (specialist pattern) (Fig. 10.1). In this case, despite much energy invested in the search, the high-quality resources ensure a large return, thus resulting in an optimal relationship.

The available evidence generally suggests that regions with scarce resources stimulate generalist collection patterns, whereas areas with a high availability of resources favor specialized patterns (see Marufu et al. 1997; Top 2004). This difference occurs because the search for better quality resources would be too costly in less productive regions with lower resource availability; therefore, implementing this strategy would not be useful (Fig. 10.1). A study that tested the assumption of the EAH for forage species provides an interesting example for an arid region with high environmental variability in Morocco (Linstädter et al. 2013). The study results showed that the local importance of a forage plant is not explained by local criteria related to the quality of the species for forage use, such as its "nutritional value" or "palatability", but by the lifetime (visibility) abundance and frequency of the species in the environment, that is, its availability. However, in environments with a high availability of resources, foragers (humans or nonhumans) can invest time and energy in finding species of better quality for specific purposes.

In resource-poor contexts, the generalist collection pattern increases the likelihood that the most available species are the most frequently collected and thus the ones most conspicuously included in the repertoire of useful species and most important in a given culture. In parallel with this idea, the importance of apparent plants can increase in arid environments with high variability because these plants also offer greater security in use, given that the unapparent species are only available in these environments during certain periods (Linstädter et al. 2013). This security reflects an optimal return for the communities living in environments with high variability and scarce resources.

The resources with a high environmental availability do not always exhibit specialist collection patterns. In a situation of high resource availability, a legal prohibition on resource extraction produces mixed patterns in the selection of utilized species (Medeiros et al. 2011; Medeiros et al. 2012). In the same community, generalist and specialist patterns may be equally present. Certain studies have attributed this mixed behavior to the inspection of forest areas, a factor that can be considered analogous to the presence of predators in a classic foraging system (nonhuman animals). The OFT proposes that the selection of collection sites and the collection behaviors adopted are also determined by the presence of potential predators, that is, by the danger of foraging.

In the case of timber products, one can opt to spend less time exposed to the "predator" (inspection) and collect, without many criteria, the plants that are in the most accessible locations, which are likely to be the most available. These plants are not necessarily of the best quality, and their use therefore forces the collector to return more often to the vegetation. Otherwise, one can spend more time exposed to inspection during a collection event while selecting the best quality plants that will have higher durability, thus lengthening the replacement time and decreasing the number of collections. In certain cases, both strategies can ultimately result in the same cost-benefit ratio, explaining the presence of both in certain contexts.

Thus, people can critically adjust their foraging strategies according to the context in which they operate. Note that flexibility in the choice of different or antagonistic behaviors in relation to the environmental and social context is presented in knowledge transmission studies and called an evolutionarily stable strategy (Cowden 2012). Moreover, the elucidation of the mechanism by which people make these adjustments in their behavior is an interesting research topic that arises from these statements. Game theory is an analytical tool that can be applied to help understand these different strategies because this tool seeks to "understanding the outcomes of interactions between two or more individuals when benefits and costs of the interactions depend on the strategies of each individual" (Cowden 2012).

10.6 Applying the EAH and Other Hypotheses to Understand the Selection and Use of Natural Resources: The Case of Medicinal Plants[3]

One can also use the scenario proposed by the EAH, as well as other ecological theories, to explain the pharmacopoeia structure of local communities, making an effort to predict the characteristic traits of these pharmacopoeias (Table 10.2). Stepp (2004) proposed that the EAH could explain the large representativity of herbs in pharmacopoeias of traditional communities worldwide. To understand this statement, it is necessary to introduce the chemical ramifications of the EAH.

Table 10.2 Predicted characteristics of the pharmacopoeias of local communities based on the plant apparency hypothesis (PAH) and the resource availability hypothesis (RAH)

Pharmacopoeia characteristic	Apparent plants (PAH)/slow-growing species (RAH)	Unapparent plants (PAH)/fast-growing species (RAH)
Cultural importance for local communities	Low	High
Bioactivity of plants	Low	High
Occurrence of secondary metabolites of high molecular weight, e.g., tannins	High	Low
Occurrence of secondary metabolites of low molecular weight, e.g., alkaloids	Low	High
Variety of chemical defenses	High	Low

Taken from Albuquerque et al. (2012) with the publisher's permission

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[3] A few excerpts here are reproductions, with adaptations, taken with the publisher's permission from the article published by Albuquerque et al. (2012).

According to Feeny (1976), the apparent plants, which are usually large-volume trees, tend to produce large quantities of high-molecular-weight chemicals that are effective at high concentrations. The author named this approach a quantitative strategy. By contrast, the unapparent plants, ephemeral in their life cycle, produce small amounts of low-molecular-weight defensive compounds that are effective at low concentrations. This approach was called a qualitative strategy. Because most herbs have a short life cycle and are ephemeral (unapparent), they accumulate compounds that are strongly bioactive and consequently very useful for treating human diseases. Thus, it can be assumed that the herbaceous plants used by traditional communities would form groups of plants potentially more likely to be incorporated into a culture. Thus, one could concentrate bioprospecting efforts on these resources.

Another hypothesis that attempts to explain the distribution of plant defenses and can contribute to the understanding of medicinal plant use is the resource availability hypothesis (RAH). The difference between the EAH and RAH is that the latter uses a cost-benefit rationale to explain the plant response to herbivory (Endara and Coley 2011). In other words, this hypothesis proposes that the growth rate of the species, which is influenced by the availability of resources in the environment, contributes to the differences among plants in the mechanisms by which the plants invest in antiherbivory defenses. In simple terms, according to this hypothesis, the investment in defense depends on whether the plant has rapid or slow growth and on the richness or scarcity of resources in the environment. Thus, plants found in environments with high resource availability tend to grow rapidly because the competition for space is greater in these environments; thus, it is more beneficial to invest in growth rather than defense. For plants found in poor or limited environments, that is, exposed to a low availability of resources, the competition for space is relatively less; thus, these plants invest relatively more in antiherbivory defense and less in growth.

Given the above, there are certain possible predictions for the RAH: “(1) species adapted to resource-rich environments have intrinsically faster growth rates than species adapted to resource-poor environments; (2) fast-growing species have shorter lifetimes than slow-growing species; (3) fast-growing species have lower amounts of constitutive defenses than slow-growing species; and (4) fast-growing species support higher herbivory rates than slow-growing species” (Endara and Coley 2011:4).

Stepp and Moerman (2001) suggested that both hypotheses, the RAH and EAH, can explain the use and selection of medicinal plants by local communities. The suggestion proposed by these authors is based on simple evidence; namely, that in many parts of the world, the medicinal plants compiled in different human groups are dominated by herbs. If the pattern is, in fact, worldwide, it is possible to predict the types of environments in which there is a greater likelihood of finding plants with medicinal potential, according to their floristic composition. Figure 10.2 illustrates the possible gradient in the richness of medicinal plants, which is supported by many studies and suggests that anthropic environments and secondary forests are the richest in plants with therapeutic potential (see Voeks 1996).

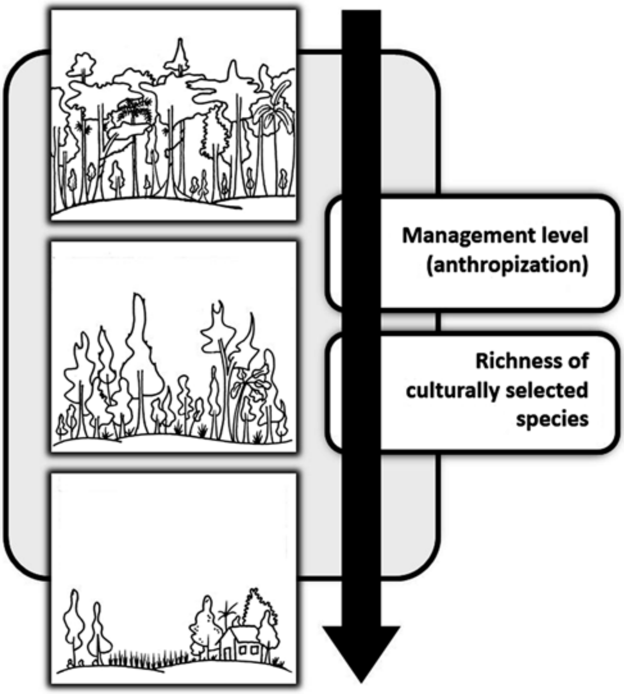

Fig. 10.2 Diagram illustrating a likely consequence of the ecological apparency hypothesis (EAH) applied to the use and selection of medicinal plants by local populations (adapted from Albuquerque and Lucena 2005). If the worldwide pharmacopoeias are in fact dominated by herbs that are selected by different cultures according to their bioactivity, then there is a gradient of environments in which it would be possible to find greater richness of medicinal plants according to the predominance of plants with a herbaceous habit or short life cycle

Assuming differences in the cultural importance of plants from a certain pharmacopoeia according to their habit, we would expect that herbaceous plants have predominated in local medical systems because of their tendency to produce highly bioactive compounds (usually, very toxic), especially alkaloids and terpenes, which have a wide range of biological activities of medical and pharmaceutical interest. In turn, the quantity of defensive chemicals (or investment) would be less in such groups for the following reasons: the plants would make a qualitative investment to act on specific targets, being effective against generalist herbivores and bearing a low cost to defend against the negative effect of herbivory (Endara and Coley 2011).

However, are these assumptions supported by empirical data? The currently available information to assess such predictions was produced in the context of ethnobotanical studies in rural communities of northeastern Brazil, especially in semiarid environments marked by strong climate seasonality. Let us analyze the consistency of such predictions in light of the available studies.

10.6.1 Cultural Importance of Apparent and Unapparent Plants

Comparative studies conducted with native species used as medicinal by local human populations in the caatinga (dry tropical forest) environment of northeastern Brazil do not support the prediction that unapparent plants have greater cultural importance (Almeida et al. 2005; 2011), as predicted by the EAH ramification discussed by Stepp (2004) and previously considered here. In general, appearing unapparent is not a predictor of the relative importance of a plant used medicinally, neither in the caatinga vegetation nor the Atlantic Forest (Almeida et al. 2011). Moreover, trees tend to be relatively important to the populations located in seasonal environments (Alencar et al. 2010; Almeida et al. 2011). Many studies conducted in the Brazilian semiarid region reinforced the evidence supporting the importance of woody plants to local communities (Albuquerque et al. 2007).

We have already suggested for the previous topic that the foraging behavior of local communities, focused on the use of perennial resources, may have been selected as an adaptive strategy to ensure continued access to the resource, thus providing security to the system. In environments such as the northeastern Brazilian caatinga (seasonal dry forest), the herbs and leaves of deciduous woody plants are available for a short duration (usually 2–4 months), and this supply is often not predictable because of variation throughout the years (hypothesis of climate seasonality) (see Albuquerque 2006; 2010).

People in the caatinga often use the stem bark of woody plants (perennial structure) (Ferreira Júnior et al. 2011) for different therapeutic indications and targets, even when other structures are available for the same purposes (leaves or herbaceous plants). Monteiro et al. (2006a, b) found evidence that people tend to use the stem bark of a medicinal plant to the detriment of the leaves, even when the latter apparently have a higher concentration of the desired bioactive compounds. These findings have important implications for bioprospecting studies because in markedly seasonal environments with abundant deciduous plants, people may not have selected the resources with the best biological activity. This possibility would contradict a basic assumption that guides bioprospecting studies based on local knowledge.

10.6.2 Investment by Apparent and Unapparent Plants in Qualitative Defenses

Again, the studies available for seasonal environments do not entirely support the prediction that unapparent compared with apparent plants invest more in qualitative defenses. There are two reasons for this discrepancy: (a) the unapparent (herbs, for instance) compared with the apparent plants (trees, for example) do not significantly invest in qualitative defense strategies and (b) the apparent plants show greater investment in qualitative strategies (Almeida et al. 2005, 2011; Alencar et al. 2009). The most important conclusion that we can draw from these studies is that apparency does not predict the occurrence of certain classes of chemical compounds. However, studies by Almeida et al. (2011) generated new perspectives. These authors tested whether the EAH explains the selection of medicinal plants by populations in Caatinga and Atlantic Forest environments. Although the authors clearly rejected the hypothesis, a curious pattern emerged from the data: the plants from the semiarid regions tended to significantly invest in defenses classified as quantitative strategies (based on phenolic compounds, such as tannins), when compared with the rainforest-derived plants which exhibited a high occurrence of defenses classified as qualitative strategies (alkaloids, for example), especially in the unapparent plants. Only flavonoids were significantly very common in plants from both regions. This pattern is curious because even certain species occurring in the same environment tended to show differences in their secondary metabolism. Although we may think that way, Herms and Mattson (1992) suggested that this variation in secondary metabolism results from "regulated changes in biosynthetic pathways in response to environmental cues rather than an incidental response to environmental variation". In this sense, we can assume that this regulation in the biosynthetic pathways occurs because of ecogeographic variation (between different ecosystems, for example) in light intensity, water availability and the balance between carbon and nitrogen.

To date, the tested hypotheses show a weak predictive power in explaining the selection of medicinal plants in traditional pharmacopoeias of seasonal environments, and the findings suggest the existence of other factors that can act together to explain this phenomenon. In herbivory studies, the EAH has gained much acceptability, being supported by many empirical studies (Endara and Coley 2011). However, considering the available evidence rejecting its predictions when applied to the ethnobotanical studies performed to date, further tests are necessary with plants and communities living in other environments.

10.6.3 The Investment of Fast-Growing and Slow-Growing Plants in Chemical Defenses

The RAH predicts that fast-growing plants do not strongly invest in defenses. Endara and Coley (2011), for example, stated in their review that fast-growing compared with slow-growing plants actually invest less in chemical defenses. However, this prediction is apparently not fulfilled when the medicinal compound is isolated from a local flora.

Coley et al. (2003), in an ecologically based bioprospecting study, found that the growth pattern of a plant is weakly related to its biological activity (in bioassays against three lines of cancer cells, leishmaniasis, malaria and Chagas disease), despite detecting the highest activity in extracts of bushes and trees. The results obtained by Donaldson and Cates (2004) reinforced this trend in that they recorded a higher cytotoxicity against epithelial carcinoma cell lines in extracts of leaves from perennial plants than in leaves from perennial deciduous plants, perennial herbs and annual species, which exhibited the lowest activity. To the best of our knowledge, there are no studies evaluating this prediction in an ethnobiological context.

Although the evidence presented herein is limited because of its production by basically one research group in one environment (Brazilian semiarid Caatinga), certain inferences can be formulated. Although the EAH and the RAH offer a plausible scenario for testing the predictions in ethnobotanical research, neither seems to fully explain the behavior of local communities in building their pharmacopoeias. This situation does not suggest that the predictions should be discarded but that new studies that incorporate different predictions and involve different environments must be conducted. Finally, evaluating the presented scenario, we suggest the need to test certain assumptions of the EAH and the RAH according to the plant use by human populations. The available evidence, although scarce and geographically restricted, suggests that human populations may have adapted the use of plant resources in their medicinal practices to the growth and defense strategies of the plants.

10.7 Final Considerations

In this chapter, we present information that supports the claim that people's behavior can be influenced by the ecological context of the behavior. In this sense, local practices exhibit mechanisms and properties adapted to the environmental contexts in which these practices developed.

The application of the EAH and RAH along with the OFT suggest that human populations optimize their foraging behavior. However, these theories do not explain all facets of the selection and use of these resources, possibly because of their weak predictive power or because the currently available evidence derives from a few geographically restricted studies whose sometimes diverse methodological approaches make comparisons between studies extremely difficult.

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Chapter 11
Local Criteria for Medicinal Plant Selection

Patrícia Muniz de Medeiros, Ana Haydée Ladio,
and Ulysses Paulino Albuquerque

11.1 Introduction

People living in any region have a wide range of plants at their disposal. However, only a subset of those plants are selected for medicinal purposes, and an even smaller subset may be considered of great cultural importance (Heinrich 2003). Therefore, one of the great challenges in ethnobiological research is to identify the factors that lead to plants being chosen for inclusion in local medical systems[1] and to assess the variables that affect the cultural importance of the plants once they are included in the system.

Therefore, this chapter aims to discuss general aspects of the selection and of use of medicinal plants by local populations, focusing on the following aspects:

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[1] We refer to a local medical system in the same way as Kleinman (1978), who considers it to be a *health care system* that "articulates illness as a cultural idiom, linking beliefs about disease causation, the experience of symptoms, specific patterns of illness behaviour, decisions concerning treatment alternatives, actual therapeutic practices, and evaluations of therapeutic outcomes."

P.M. de Medeiros (✉)
Ethnobiology and Human Ecology Group, Center of Biological and Health Sciences,
Universidade Federal do Oeste da Bahia, Estrada para o Barrocão, s/n, Morada Nobre,
Barreiras, Bahia 47805-100, Brazil
e-mail: patricia.muniz@gmail.com

A.H. Ladio
Laboratorio Ecotono (Ecotono Laboratory), INIBIOMA—Instituto de Investigaciones
en Biodiversidad y Medio Ambiente (Biodiversity and Environmental Research Institute),
CONICET-Universidad Nacional del Comahue (National University of Comahue), Centro
Regional Universitario Bariloche, Quintral, San Carlos de Bariloche-Río Negro 1250-8400,
Argentina

U.P. Albuquerque
Laboratory of Applied and Theoretical Ethnobiology, Biology Department, Universidade
Federal Rural de Pernambuco, Rua Dom Manoel de Medeiros, s/n, Dois Irmãos, Recife,
Pernambuco 52171-900, Brazil

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(a) the inclusion of species as components of local pharmacopoeias, and (b) the differential use of species that are actually employed within a set of available medicinal plants.[2]

11.2 Terminological and Conceptual Aspects

The local criteria for species selection correspond to the bases that are consciously or unconsciously used by the people to select one or more plants for medical use.

We will employ the terms *determinant*, *cue* and *mnemonic resource* throughout the text. A factor that by itself explains the inclusion of a species in a pharmacopoeia, i.e., the factor responsible for the choice of a species to cure an illness, is a determinant factor of medicinal plant selection. The term cue will be used when the factor being analyzed is not specifically the determinant factor for the selection of the plant to treat an illness but instead indicates that the plant might be useful for a given purpose. Finally, the expression mnemonic resource will be used when a trait of a plant reminds people of its medicinal use.

It is also important to distinguish between two items discussed here: (a) the number of species that make up a local pharmacopoeia and (b) the species in the pharmacopoeia that are actually used by the population. Some authors have demonstrated the difference between knowing the properties of a plant and effectively using it, in regard to either medicinal plants or types of use (Reyes-Garcia et al. 2005; Albuquerque 2006; Ramos et al. 2008a). We will discuss both the inclusion of plants in a pharmacopoeia and the differential use[3] of said plants.

The conflicting manner in which the literature addresses such selection criteria is another important issue. What some authors consider to be determinants of species selection may be considered by others as cues or indicators that a plant has a given property. Taste and smell, for example, may be considered determinants of selection when considering that people may select medicinal plants based on such parameters. However, taste and smell may also be considered to be cues for finding efficient plants, and in this case, efficiency would in fact be the determinant factor. These aspects will be thoroughly discussed under the topic "Criteria for the introduction of species to a local pharmacopoeia."

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[2] We consider selection as a more general process that includes both inclusion and differential use.

[3] The expression "differential use" is employed in this text to refer to the more frequent use of some plants over others, although all are included in the pharmacopoeia. However, the expression "differential use" can also be employed when different species are used for different therapeutic purposes.

11.3 Evolutionary Aspects of the Inclusion of Medicinal Plants in Traditional Pharmacopoeias

The use of plants in health care systems is not exclusive to the human species (Clayton and Wolfe 1993; Halberstein 2005; Hart 2005; Krief et al. 2005). Some items consumed by chimpanzees, for example, have low nutritional value, and evidence shows that the behavior of ingesting such resources may be related to self-medication (Krief et al. 2005). Many of the plants that are apparently consumed by nonhuman primates for medicinal purposes are also part of the pharmacopoeia of the human population (see Clayton and Wolfe 1993; Halberstein 2005; Krief et al. 2005).

Hart (2005) believes that humans use medicinal plants mainly for therapeutic purposes (treating established diseases), while other animals use such plants mainly prophylactically (to avoid diseases, such as parasitic diseases). Therefore, it can be inferred that evolution has played an important role in the development of human health care strategies and in resource selection. However, the role of natural selection in building local pharmacopoeias is not entirely clear, nor has it been fully investigated. Hart (2005) points to two alternatives for the origin and the foundation of medicinal plant use: learning and natural selection. Before presenting the hypotheses regarding such alternatives, it is important to clarify two issues. First, there is no solid empirical evidence to support the two proposed hypotheses, which are therefore hypotheses put forth by researchers that are still in the realm of possibilities and that have not been empirically tested. Second, the two hypotheses do not intend to clarify the dissemination of knowledge about the medicinal attributes of plants but to explain the origin of this behavior, referring to the first time when the properties of a plant (X) were discovered by a person (Y). Therefore, both hypotheses consider the dissemination of information about the use of a given plant to occur through knowledge transmission and social learning.

The learning hypothesis postulates that individuals learn by trial and error when choosing the most effective plant among a wide range of plants that prevent or combat a certain disease. Thus, the individual establishes the association between the use of a plant and its effect on health and starts using it when necessary. The natural selection hypothesis, in turn, defends the evolution of a predisposition of individuals to seek and consume plant products characterized by one or more sensory markers that are correlated with the effectiveness of the species in preventing, mitigating or curing certain diseases (Hart 2005). Hence, from an evolutionary point of view, the predisposition to consume certain plants would first have been an “unlearned” response but would later have been selected due to increasing the fitness of individuals, thus reducing the likelihood of acquiring diseases. The difference between the two hypotheses (learning and natural selection) is that the first posits that the plant searching process occurs through constant experimentation until plants with medicinal properties are identified, while the second assumes that men already inherently have some of the information necessary to infer whether a plant has medicinal properties.

Some human behaviors, however, may be explained in light of gene-culture coevolution. Lumsden and Wilson (1980) suggest that culture may be acquired through one of three routes: (a) purely genetic transmission, in which all individuals learn only a "culturgene" (cultural homologues of genes) among several possibilities within a given category; (b) purely cultural transmission, where there is no innate predisposition for acquiring particular "culturgenes"; and (c) gene-culture transmission, in which a "culturgene" is favored due to innate information, although other "culturgenes" may also be adopted. If gene-culture transmission is applied to the selection of medicinal plants, we would expect that the role of natural selection in this process would be to provide pathways to learning, also known as prepared learning.[4] Therefore, learning would not be genetically determined or predetermined, but the learning processes would be genetically influenced. In this case, people could decide among many possibilities, where one possibility would be genetically favored but not determined, such that environmental changes or cultural artifacts could disfavor it. The consumption of bitter food and beverages by human populations is a supporting example. A genetic predisposition to avoid bitter food is believed to exist among mammals because most toxic compounds found in nature taste bitter (Glendinning 1994; Kurihara et al. 1994). However, humans learned over time that not everything that tastes bitter is necessarily toxic (Kurihara et al. 1994), leading to the incorporation of such foods into the human diet.

The manner in which traditional pharmacopoeias are built may help elucidate how humans and their genetic evolution influence culture as well as how culture may co-influence processes at the population level. Thus, the criteria for introducing plants to a local pharmacopoeia may arise from the interaction of two transmission routes: our chemoreceptor system, which presumably includes an apparatus that associates flavors/smells with beneficial properties, and cultural information regarding what is good or bad, useful or not useful, and concerning values, symbolism and so on. This complex scenario, arising from multiple possibilities related to genetic, cultural, and even environmental (as seen in other chapters of this book) influences, is far from being elucidated, and greater scientific attention therefore needs to be focused on this issue.

11.4 Criteria for the Inclusion and Differential Use of Species in a Local Pharmacopoeia

In this section, we will discuss some of the factors that may affect the inclusion and differential use of medicinal species, specifically chemical efficiency, cultural factors, and organoleptic properties (the latter of which includes the form–function relationship known as the *Doctrine of Signatures*). We will discuss how each of these factors can be associated with the inclusion of species in local

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[4] The expression "prepared learning" has been used in evolutionary psychology in reference to an innate predisposition to learn and thereby reinforce one opinion over another (Wilson 2012).

pharmacopoeias, whether via determining the choice of a species, acting as cues for people to discover plant properties, or acting as artifacts for people to remember how a plant must be used.

Other factors may influence the selection or differential use of medicinal plants, such as (spatial and temporal) availability, accessibility, and other morphological attributes that are not mentioned here but that are addressed in another chapter of this book. Moreover, factors that are still unknown may also influence the processes of inclusion and differential use, and studies broadly addressing those criteria are therefore extremely desirable.

11.4.1 The Role of Chemical Efficiency

The chemical efficiency of a plant has a strong influence on the choice of species for medicinal purposes. Efficiency is therefore one of the main determinants of plant selection.

Plants used in traditional medicine by local people have been shown to exhibit interesting chemical properties, including properties that are of interest for the pharmaceutical industry (Heinrich 2008). The increasing number of traditionally used species with proven medicinal activity has caused current ethno-directed research strategies to become one of the main approaches for finding medicinal products (Araújo et al. 2008; Albuquerque et al. 2014), and in some cases, this strategy is more efficient than the random approaches used to search for new drugs. For example, Khafagi and Dewedar (2000) studied plants with antimicrobial activity that spontaneously grow in Sinai, Egypt, and reported that the ethnobotanical approach revealed a greater number of plants with antimicrobial activity than the random approach. Similarly, Slish et al. (1999) reported that four out of 31 Belizean plant species examined using the ethnobotanical approach showed a relaxing effect on vascular smooth muscle, while none of 32 randomly collected species exhibited such effect.

Efficiency is a key factor in the selection of species that will become part of a pharmacopoeia and may also play an important role in determining differential usage, i.e., in the popularity of the species belonging to the pharmacopoeia. Species that are more efficient are expected to be more valued and more commonly used by people.

However, few studies have tested the relationship between the local importance of plants and pharmacological efficiency. We have indirect evidence of this relationship, such as the high correlation found between the local importance of plants cited as showing anti-inflammatory properties and significant contents of tannin, which is a compound that may be responsible for the anti-inflammatory activity of the species (see Araújo et al. 2008).

A similar relationship was tested in regard to the antimicrobial activity of plants used by North American indigenous people and the frequency of their use (Omar et al. 2000), with the results presenting a significant correlation. These relationships show that plants with greater biological activity are used by more people, thus indicating the ability of people to recognize the most efficient plant species. Similar relationships are being reported in contexts beyond use as medicinal plants, such as local preferences for species employed as firewood and their combustible properties (Ramos et al. 2008b; Sá e Silva et al. 2009).

Efficiency is an important determinant of the selection and differential use of plants. However, the following question remains: which other factors play a role in addition to efficiency in the construction of local pharmacopoeias?

11.4.2 Cultural Aspects

It is common for plants in local pharmacopoeias to not exhibit proven efficiency against the diseases for which they are used for several reasons, such as errors in the methods applied in phytochemical and pharmacological studies. These studies may sometimes disregard popular knowledge, such as information on the parts that are used, dosage, location, season and plant collection methods, some of which may be closely linked to the behavior of certain compounds (see Gobbo-Neto and Lopes 2007).

However, plants may become part of local pharmacopoeias for reasons other than their pharmacological efficiency, or they may be removed from the medicinal plant repertoire despite showing a high pharmacological efficiency. For example, some studies have shown the importance of dreams in selecting medicinal plants (Ankli et al. 1999; Mollik et al. 2010). The healers in some traditional societies may start using certain plants after "spiritual revelations" regarding their efficiency, obtained through dreams or rituals, which usually involve the use of hallucinogenic plants (Ferreira Júnior et al. 2010).

Interestingly, each *wajaca* (expert on medicinal plants) of the Kraô Indians of the Brazilian Cerrado (Brazilian savanna) uses a repertoire of medicinal plants that is different from those employed by other *wajacas* (Rodrigues and Carlini 2006). Such high idiosyncrasy in plant use among members of the same population may be explained by the influence of other ethnic groups and by the differential inheritance of knowledge from parents and grandparents. However, the authors state that the *wajacas* attribute these differences to the differential spiritual learning because each healer has a different *pahi* (a spiritual mentor usually represented by the spirit of an animal, a plant, a mineral, an object or a dead person), and each *pahi* teaches different applications for plants. This is a strong example of how cultural factors may affect the selection of plant species for medicinal purposes.

In some cases, plants may exhibit high cultural efficiency (success in the treatment of certain diseases for a given human population group) without presenting chemical properties that could explain the treatment of the diseases. The official medicine usually refers to this phenomenon as a placebo effect (Moerman and Jonas 2002). However, Moerman and Jonas (2002) disagree with the application of the placebo concept to justify such processes, instead using the expression "meaning response." This expression may be employed when an element (e.g., a plant or amulet) has a physiological or psychological effect that favors the treatment of a disease and may be explained by the cultural meaning of that element. Plant traits such as color, smell or cultural meaning may help treat diseases because their meaning to a community is a key factor in the healing or recovery process, regardless of any pharmacological effect.

Importantly, according to Moerman and Jonas (2002), the meaning response influences not only the psychological domain but also physiological processes. When applying this approach to the universe of plants in local medical systems, we can expect the cultural meaning of some plants to produce psychological responses that encourage the individual to respond physiologically, thus helping to cure their disease. This process can be even more effective when the plant is administered along with healing rituals because the ritual itself has a significant symbolic value in treating diseases (Dow 1986).

The symbolic value and cultural efficiency may also be applied to explain the use of plants to treat diseases that are scientifically known as cultural diseases, i.e., phenomena that are interpreted as diseases without a cause recognized by biomedicine (Pinto et al. 2006). Many societies do not distinguish the natural from the supernatural, a dichotomy that is also absent in their medical systems (Winkelman 2008). Therefore, the meaning effect could operate independently from the origin of the disease (natural or supernatural). However, scientists must further investigate these cultural diseases and identify the foundations of the selection of medicinal plants for their treatment.

Culture is one of the main determinants of the differential selection of medicinal plants because the knowledge passed from generation to generation is a key factor determining whether a plant is considered to be medicinal (Ankli et al. 1999) as well as the cultural importance and use intensity of the plant. The differential selection process is mostly a *continuum* that originated in past generations through choices based on criteria such as efficiency, accessibility and taste. Therefore, the transmission of knowledge to disseminate and maintain cultural practices regarding health care is important.

Cultural taboos are another important aspect of the influence of culture on the differential use of medicinal plants. Some species, despite being efficient, may show limited use due to social beliefs and norms, as observed in the seasonal gathering of the roots and rhizomes of some African species (Cunningham 1993). In such cases, collection is restricted to winter months because local beliefs dictate that summer gathering of these species may generate storms and lightning (Cunningham 1993). Often, as in the case just described, the cultural taboo does not directly influence the consumption of a species, only its gathering. Nevertheless, the impossibility of gathering the plants during a season may affect their consumption throughout the year. Restrictions on the use of plant resources, including medicinal plants, were also found in Gabon and Benin (Quiroz and van Andel 2015) and those restrictions were related to resource scarcity and protection.

11.4.3 Organoleptic Properties

Some plant traits are important in the species selection process, such as flavor, smell and texture. These traits aid in the identification and characterization of certain species because some taxonomic groups have a particular taste, smell and texture (Shephard Jr 2004). It is believed that human beings are able to identify phytochemical attributes of plants using chemosensory organs, especially taste and smell (Ankli et al. 1999; Leonti et al. 2002; Molares and Ladio 2009).

The true role of chemosensory properties has not been explicitly addressed by scientists, despite the existence of a significant number of studies on the effect of such markers in the selection of medicinal plants (Brett and Heinrich 1998; Ankli et al. 1999; Casagrande 2000; Leonti et al. 2002; Heinrich 2003; Shephard Jr 2004; Halberstein 2005; Molares and Ladio 2008; Molares and Ladio 2009; Mutheeswaran et al. 2011; Medeiros et al. 2015). Based on what is implicitly or explicitly mentioned in the above-cited studies, we synthetized three hypotheses to explain the role of organoleptic properties in the selection of medicinal plants: (a) organoleptic properties as chemical efficiency cues; b) organoleptic properties as selection determinants; and (c) organoleptic properties as mnemonic resources. These hypotheses are developed below.

Organoleptic properties as chemical efficiency cues: let us consider the hypothesis that the association of organoleptic properties and medicinal properties is not genetically fixed. Instead, people would learn from observation and association that certain organoleptic characteristics are related to a given therapeutic indication. In this case, the efficiency of the plant would determine its selection as a medicinal plant, while the organoleptic properties would serve as cues for people to identify the most efficient plants. These cues would be the result of historical learning regarding the association between a medicinal property and an organoleptic attribute. It is reasonable to imagine that people would use organoleptic properties as indicators of plant efficiency if these properties are thought of as cues and not as determinants per se. However, people would cease to use such plants in the event of a false attribute-efficiency association that does not lead to a cure or mitigation of the disease.

Organoleptic properties as determinants of selection: It is reasonable to assume that the chemosensory markers that characterize a product would in fact be the determinants of species selection if people had a genetic predisposition to use such products. In this case, the association of organoleptic properties with the chemical properties of the plants would be genetically fixed at some point in the evolutionary history of humans, without efficiency serving as a mediator recognized by people. Therefore, organoleptic properties would not act as efficiency cues but as the determinant. Many researchers (even if implicitly) assume that organoleptic properties are determinants when stating that smell and taste determine the selection of plants as medicinal species. For example, Brett and Heinrich (1998) reported that the association between taste and plant properties appears to be innate (present from birth).

Organoleptic properties as mnemonic resources the first two hypotheses postulate that organoleptic properties influence species selection somehow, differing only in the evolutionary explanation and in the presence of efficiency as a mediator recognized by people. However, some researchers have shown a correlation between chemosensory properties and medical attributes, which does not mean that people select plants based on such organoleptic properties. Heinrich (2003), for example, addresses this issue by stating that traits such as smell, taste, and texture may be used as selection criteria for new medicinal plants and may also be used to qualify (identify) the species that have become part of the pharmacopoeia. Thus, organoleptic properties can be seen as mnemonic resources, and the association of an organoleptic attribute with a therapeutic indication would therefore help people to remember the therapeutic application of the plant or simply to characterize it. Thus, the plants would be selected based on other criteria, and their organoleptic properties would become a memory and association artifact. If, for example, plants X and Y have sweet leaves and are useful in treating stomach problems, people could use such information to remember that these plants are useful for treating gastric disorders due to being sweet. In this example, the sweet taste would not be employed to find plants to treat stomach problems but to characterize plants with uses that were discovered by other means. This hypothesis does not invalidate the others because organoleptic properties may influence selection in some cases and be used as memory artifacts in others.

Findings from the literature: the efforts of scientists to identify the role of organoleptic properties have brought about intriguing results. Ankli et al. (1999) analyzed the local criteria for distinguishing medicinal from non-medicinal plants and found that one informant used the cause–effect relationship as a criterion (e.g., the plant is good for stomachache because it smells good), while most people made associations such as the plant being good for stomachache *and* smelling good. In this case, it is inconclusive whether the organoleptic properties actually lead to selection (cues or determinants) because plant use information is passed from generation to generation (Ankli et al. 1999), and the original cause–consequence association may therefore have been lost. Ankli et al. (1999) also reported that plants were not randomly chosen for medical purposes because, for example, plants that were sweet and exhibited a strong smell were preferred for treating breathing problems, while plants used for treating animal bites were often bitter. Moreover, plants that were not used to treat illnesses usually did not have a particular smell or taste according to the population's perception, while medicinal plants were aromatic and tasted sweet or astringent (Ankli et al. 1999). Similarly, Heinrich (2003) stated that astringent plants are usually used for treating diarrhea, bitter plants for gastrointestinal pains, and sweet plants for cough and respiratory problems. Molares and Ladio (2015) also suggest an association between taste/smell and therapeutic uses. In this case, for example, species with mild tastes and smells are often used to culturally based syndromes.

Medeiros et al. (2015) tested the associations of taste × use and smell × use for the entire local pharmacopoeia in a study developed in northeastern Brazil. The authors observed these associations to be true only for the diseases and organoleptic attributes that were most cited by the community. This finding indicates a higher likelihood of people associating certain smells or tastes with the treatment of illnesses when dealing with popular diseases and when using plants with more common flavors as a foundation.

In some cases, communities adopt a *hot/cold* system to choose the plants to be used in the treatment of diseases. In these cases, the disease is perceived as being caused by a hot or cold agent, and plants with properties opposite to those of the disease agent are therefore applied in the healing process (Ankli et al. 1999; Leonti et al. 2002). Leonti et al. (2002) reported that the use of plants with the attributes of being bitter and red, which are considered hot characteristics, is common in Popoluca, Mexico, to cure diseases such as stomachache, cramps, menstrual problems and pains in general because the population believes that such diseases are caused by cold agents. In contrast, according to local beliefs, cold properties are present in green leaves (especially big and watery leaves) and in sour products and are used to cure fever, a condition caused by hot agents (Leonti et al. 2002).

Organoleptic attributes and differential use: taste, smell and texture not only affect the inclusion of species in a pharmacopoeia but may also serve as determinants for the choice of plants to be used within a larger set of species known as medicinal. Species with more remarkable organoleptic attributes (easily recognizable smell and taste) may show a greater consensus regarding their use than plants with more discrete attributes (mild or less recognizable smell and taste) (Molares and Ladio 2008, 2009).

However, the role of organoleptic properties may also be analyzed from another point of view. Species with a pleasant smell and taste and a conventional texture tend to stand out when a medicinal plant is orally administered because people naturally favor more pleasant flavors, textures and aromas. Nevertheless, few studies have addressed the preference for pleasant plant flavors, smells and textures, though examples of the association between flavor and local preferences can be found in studies carried out by Estomba et al. (2006) and Albuquerque (2006).

Exotic plants are more frequently cited for use in treating certain conditions, such as gastrointestinal disorders, despite native medicinal plants being preferred for treating most illnesses (Estomba et al. 2006). Many substances may be employed to treat digestive disorders due to their low specificity (Estomba et al. 2006). A low specificity would facilitate the replacement of native species by exotic species with a pleasant taste. Albuquerque (2006) also uses the palatability argument to justify the replacement of some native plants of the caatinga (seasonal dry forest) by exotic equivalents.

11.4.4 Doctrine of Signatures

The true role of the association between the "signatures" of a plant and its medicinal use is another controversial issue. In many cultures, from pre-Columbian America to those of ancient China (Halberstein 2005), people have used plants that resemble the organs to be cured in some way, for example, in the shape of their leaves or roots or the color of some part of the plant that resembles a body part. The use of yellow plants to treat jaundice and urinary problems and of plants with heart-shaped leaves or red flowers for heart disorders are examples of this phenomenon, known as the Doctrine of Signatures (DOS) (Halberstein 2005).

Historically, scientists interpreted the DOS as a cue or a determinant in species selection. Thus, the DOS was considered a primitive superstition and was ridiculed in the medical and scientific community (Bennett 2007) because, according to the DOS, people would choose plants for medical use without a solid empirical basis. However, this conception of the role of the DOS has recently been questioned. Bennett (2007) argues that if researchers were not present when plants were chosen for medicinal purposes, it is not possible for them to categorically state that the signatures were used as the criteria for a species inclusion in a pharmacopoeia.

Therefore, the DOS is a symbolical artifact used to transfer information on plant use, especially in pre-literate societies (Bennett 2007). In other words, the association between the shape of the plant and the organ that it treats would be defined a posteriori, i.e., after people had empirically discovered the medicinal use of the plant. Hence, the DOS is a mnemonic resource and not actually a cue or determinant of selection. The transmission of this knowledge over time may have concealed the true cause–effect relationship, leading people to justify the use of the plant due to its signature. Finally, Bennett (2007) notes that if the DOS were a determinant of selection, a high percentage of the plants in a pharmacopoeia would be expected to show an association between their shape/color and the medicinal use, which does not occur.

When considering the DOS as a mnemonic resource, plants that coincidentally exhibit an association between their shape/color and medicinal use would have a competitive advantage over other plants because the symbolic association would facilitate knowledge transmission between generations (Bennett 2007). This reasoning could explain the popularity of such plants in local pharmacopoeias and their significant intercultural dissemination, despite the fact that these plants are not always the most efficient in treating diseases.

11.5 Final Considerations

In this chapter, we discuss the notion that the use of medicinal plants by local populations is not random. The processes of inclusion and differential use are guided by determinants (e.g., chemical efficiency, cultural aspects) and assisted by cues (e.g., indicators of chemical efficiency). In addition, mnemonic resources aid in perpetuating information on plant-therapeutic indications.

The inconclusive nature of the factors underlying the selection of medicinal plants is also noteworthy. Is there a genetic influence? Cultural influence? Environmental influence? Or are all these aspects part of the same complex? We believe that selection behaviors are difficult to explain and may not be reduced to simplistic conclusions, precisely due to such gene–culture–environment complexes.

Thus, we stress the need for an integrated examination of the process of inclusion and differential use of medicinal plants because isolated variables will not answer the main questions on this topic satisfactorily.

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Chapter 12
Use Patterns of Medicinal Plants by Local Populations

Patrícia Muniz de Medeiros and Ulysses Paulino Albuquerque

12.1 Introduction

The growing number of ethnobotanical studies has revealed an important finding: behaviors related to the use of plant resources are recurrent in different human populations. These repeated behavioral tendencies in plant use are also known as use patterns. A pattern may be expressed in the general characteristics of the pharmacopoeia[1] (habits of dominant plants, main therapeutic indications of the plants, etc.), and it may also be observed in the ways by which different human populations use the same plant species.

In this chapter, we use medicinal plants as a model to discuss the factors leading to the formation of these patterns. However, it is important to note that such patterns may be observed in studies focusing on any natural resource. Many of the questions approached here may potentially be applied to other research areas, including ethnozoological research because little is known of the behavioral patterns related to animal use.

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[1] Local pharmacopoeia or traditional pharmacopoeia are defined here as the repertoire of products used for health care by a given population, and they may include animals, plants, and/or minerals.

P.M. de Medeiros (✉)
Ethnobiology and Human Ecology Group, Center of Biological and Health Sciences,
Universidade Federal do Oeste da Bahia, Estrada para o Barrocão, s/n,
Morada Nobre, Barreiras, Bahia 47805-100, Brazil
e-mail: patricia.muniz@gmail.com

U.P. Albuquerque
Laboratory of Applied and Theoretical Ethnobiology, Biology Department,
Universidade Federal Rural de Pernambuco, Rua Dom Manoel de Medeiros, s/n,
Dois Irmãos, Recife, Pernambuco 52171-900, Brazil

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12.2 Factors Leading to the Formation of Use Patterns

In general, patterns may be generated in two ways: (a) diffusion and (b) convergence (Bletter 2007). Diffusion is the process of information transmission between individuals belonging to the same or different human groups. Patterns generated through diffusion may occur because of contact between individuals and exchanges of information between close or distant populations, which occurs for members of a local population who migrate[2] to a distant location and transmit their knowledge to the inhabitants of this new location.

When information on plant use crosses community borders and reaches new locations, the resulting plant-use patterns do not result from independent discoveries by the communities. Instead, the information shared between different populations has a common origin. This process characterizes the diffusion of knowledge. Different communities may also acquire the same plant-use behavior independently in a process known as convergence.

It might appear as if independent discoveries related to plant use are coincidental, chance events; however, these discoveries are influenced by certain key factors that eliminate the effect of chance and provide valuable information. Thus, the environment plays a key role in stimulating exploration for similar resource appropriation solutions according to different populations in similar environmental contexts. In addition, because chemical efficiency is an important factor for species selection and the same species can be found in geographically distant regions, processes of trial and error[3] may lead different human populations to the same conclusions on the therapeutic indications of a species.

In practice, it is difficult to conclude whether the formation of a pattern resulted from diffusion or convergence because it is not possible to map all of the pathways of information entry into a social-ecological system. However, theories of the origins of such patterns may be developed. Bletter (2007), for example, studied the plants used to treat diseases such as malaria, Chagas disease, Leishmaniasis, and diabetes by two human populations in Mali and Peru and observed that the two populations used related plant species as treatment for the same therapeutic indications.

This example is useful because of its discoveries as well as its interpretations. Bletter selected communities in those two countries precisely because they are distant from each other and have little historical relation to one another, which implied a lower probability of information exchange between the two populations and higher probability that the discoveries are independent. To assure this independence, Bletter (2007) excluded exotic plants from the analysis because their use was more likely to be associated with cultural diffusion.

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[2] The importance and strategies of medicinal plant use by migrant peoples may be found in Medeiros et al. (2012).

[3] The expression “trial and error” is frequently used in ethnobotany to describe the learning process in medicinal plant use; in this process, subjects use plants for a given end until one (or more) plant shows positive results and is effective in treatment.

Thus, cases occur in which patterns are likely to have originated from convergence, although unequivocal conclusions of convergence cannot be made. Diffusion is not always direct because several communities may constitute a knowledge distribution network and two communities may share information from the same origin, even if they are not directly linked.

12.3 Taxonomic Patterns

Because chemical compounds with medicinal value are not equally distributed among different botanical families (Gottlieb et al. 2002), at least two behaviors can be expected: (a) certain families have higher medicinal value and are therefore more frequently used than others and (b) different families are used to treat different afflictions. If the same botanical families are more frequently used for medicine in different settings, this trend would be strong evidence that plant use by local populations does not occur randomly (Moerman 1979) and is inconsistent with the placebo effect hypothesis[4] of popular medicine.

Thus, studies have been performed to determine whether certain families are used in a greater proportion than others and whether these families are the same in different locations. Daniel Moerman was a pioneer in this line of research. In his first work on the topic, which was published in 1979, he compared a list of native medicinal plants of North America with a list of plants used by native North American populations. These lists of North American species were used for an important reason: the analysis of the families with a greater number of medicinal species could not be performed in absolute terms but had to be performed relative to the size of the family.

According to this reasoning, if family A has ten species and all (100 %) are medicinal, this family has greater proportion of medicinal plants than family B, for which 30 of its 60 species (50 %) are medicinal. If this information was analyzed in absolute terms (ten medicinal species from A against 30 species from B), family B would be incorrectly considered to have a greater proportion of medicinal plants.

Using relatively simple statistics, Moerman (1979) identified families that did not have the expected proportion between the total number of species and the number of medicinal species, with some of these families having more medicinal species than predicted and others having less. The families of the first group were referred to as overused, and the families of the second group were referred to as underused.

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[4] The myth of the placebo effect refers to the belief that medicinal plants used by local populations do not, in fact, have healing pharmacologic properties and are kept in these pharmacopoeias because of their symbolic value and psychological effect, which may help reduce the effects of the disease (placebo effect). This myth has been advocated by several medical doctors, especially before the performance of scientific studies with plants used in popular medicine.

The method proposed by Moerman (1979) was developed further in several additional studies. More robust statistical methods were used to identify the overused and underused families (see Bennett and Husby 2008; Weckerle et al. 2011, 2012). A consistent finding among these studies was overused and underused families by the human populations studied are always found.

In addition, certain families have strong overuse and underuse patterns, which was observed in several studies performed in different regions. Families such as Asteraceae, Piperaceae, and Rosaceae have been reported in several studies as overused, and Poaceae, Orchidaceae, and Cyperaceae have been reported as underused. The high use of families frequently observed as overused is explained by their production of bioactive compounds, which has been supported by chemistry studies (Gottlieb et al. 2002). Families such as Poaceae and Cyperaceae have low biological activity (Amiguet et al. 2006), which would explain their lower medicinal use.

However, overused or underused families are not always the same in different studies. Families such as Fabaceae, for example, have been classified as overused in certain studies and underused in others. If evident patterns occur, why do certain families appear to behave so discrepantly? Additional information must be gathered by scientists to explain whether these discrepancies are caused by cultural or other factors or whether certain botanical families (especially those with wide distributions) include species that are strongly divergent in terms of chemical composition. Such discrepancies, however, do not invalidate the evident and universal patterns observed for the taxonomy of medicinal species.

The second case in which different families could be used to treat different afflictions has not received much attention by the scientific community; therefore, patterns related to this definition have yet to be discovered. However, studies have already shown that different diseases tend to be treated with different botanical families (Weckerle et al. 2011; Medeiros et al. 2013). For example, there is little similarity between different systems of the body in terms of the families used to treat them, which means that there is a tendency to use different plant families to treat different anatomical systems (Medeiros et al. 2013). In our previously cited study, we observed that a greater number of similar body systems (disorders, infections and parasitic diseases of the respiratory system) have greater similarities in their cure requirements (in this case, plants with antimicrobial properties, which can be used for conventional infectious diseases and certain respiratory problems related to colds, bronchitis, etc.).

12.4 Patterns Related to Plant Habit

Reports have suggested that plant selection for medicinal purposes is also related to plant habit. One of the premises advocated by scientists is that herbaceous habits are the most important from a medicinal perspective (Stepp and Moerman 2001), and it is derived from observations of the predominance of herbs, especially ruderals, in pharmacopoeias worldwide, and intimately associated with the application of the ecological apparency hypothesis (EAH) to plant chemistry. According to the EAH, apparent plants (more visible or abundant in the environment and generally woody) invest in high-molecular weight compounds (quantitative defense), whereas non-apparent plants (herbaceous) invest in low-molecular weight compounds (qualitative defense) (Albuquerque and Lucena 2005). Qualitative compounds are more bioactive, explaining the success of herbs as medicinal products.

Despite the wide acceptance of herbs as the main components of local pharmacopoeias, exceptions have been found, especially in semiarid regions. In a study conducted in a semiarid region of Ethiopia, a higher number of trees used for medicinal purposes was observed than any other plant habit (Zone et al. 2007). In addition, studies conducted in the Brazilian Caatinga (seasonal dry forest) showed that although more herbaceous plant species were present in the pharmacopoeias, which included a great number of exotic herbs, trees had higher versatility of use or greater importance for the local populations (Albuquerque et al. 2007; Almeida et al. 2010). Caatinga pharmacopoeias are not consistent with the expected chemistry because the trees that are considered medicinal include quantitative compounds and have qualitative metabolites associated with herbaceous species (see Almeida et al. 2005; Alencar et al. 2009).

There are still gaps in the ethnobotanical knowledge of the main habits of medicinal plants. First, if the presence of herbs in pharmacopoeias is so high, then it is unclear why exceptions occur. Can these exceptions be explained by environmental (e.g., semiarid environments) or cultural factors? Do environments with different characteristics lead to different patterns related to plant habits? Increased scientific research on this topic, especially in regions where these studies are scarce, will certainly lead to conclusive answers.

12.5 Patterns Related to Species' Origin and Biogeographical Distribution

Scientists have speculated whether the function of native and exotic species in traditional pharmacopoeias may follow the same logic in different local communities. For example, although it is believed that the inclusion of exotic species in traditional medicine is necessarily connected to acculturation processes,[5] it may be part of the pharmacopoeias' evolution to adapt to cultural and ecological changes (Palmer 2004; Medeiros 2013).

Assuming that traditional knowledge is dynamic and the inclusion of exotic species may enrich pharmacopoeias, hypotheses have been developed to explain why these species are included in the local repertoire of medicinal plants. According to Bennett and Prance (2000), exotic species enter the daily life of local populations for non-medicinal uses, such as for food and ornamental uses, and medicinal uses

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[5] The term "acculturation" has been used in the literature to describe cultural change processes experienced by local communities (see Eyssartier et al. 2008).

are developed a posteriori; thus, these species are usually introduced to communities for non-medicinal reasons. Therefore, exotic species that have more versatile uses have a higher probability of entering a new location and being subsequently used for medicinal purposes. This hypothesis was termed the versatility hypothesis, and it was tested by Alencar et al. (2010).

Another attempt at explaining the inclusion of exotic plants in traditional pharmacopoeias is the diversification hypothesis, which was originally proposed by Albuquerque (2006) and later tested by his research group (see Alencar et al. 2010). This hypothesis was one of the first formal attempts to defy the acculturation hypothesis (discussed above). According to the diversification hypothesis, exotic plants are included in traditional pharmacopoeias to fill gaps left by native species. The hypothesis was tested in the Caatinga and supported by chemical and ethnobotany evidence in which exotic species were exclusively cited for certain therapeutic indications and certain compounds were only present in these plants (Alencar et al. 2010; Almeida et al. 2010).

Gaps may occur in a pharmacopoeia if a disease is recent to a location or difficult to diagnose (such as cancer, high blood pressure, and diabetes); thus, they may not be related to the inefficiency of native species in treating certain diseases. In these cases, the challenge of diagnosing the disease prevents experimenting with and applying native species for its treatment. Often, the diagnosis of such diseases is determined from outside of the community, such as through biomedicine, which may also introduce exotic species that are widely used for the treatment of maladies with difficult diagnoses. Therefore, these types of disease are expected to be treated predominantly by exotic plants. A study conducted in southeast Morocco with plants used for the treatment of diabetes and hypertension showed that most of these plants were exotic, although they may have been wild, cultivated, or brought from other locations in Morocco (Tahraoui et al. 2007).

If the diversification hypothesis is true, then the entry of exotic plants into pharmacopoeias does not occur randomly but follows a general pattern of gap filling. However, further studies are required to test this hypothesis in multiple settings.

12.6 Patterns Related to Therapeutic Indications

One of the most evident patterns observed by scientists and researchers is the emphasis on the digestive system among the body systems treated with plants; thus, there is a higher number of plants used as treatments for digestive disorders as well as a higher number of citations for such disorders (for examples, see Ankli et al. 1999; Molares and Ladio 2009). Respiratory and skin diseases are also among the most represented in local medical systems (see Heinrich et al. 1998; Rehecho et al. 2011).

Therapeutic indications with a higher number of plants used as treatment tend to have one (or both) of the following characteristics: (a) among the most recurrent in the community, with individuals having developed more thorough repertoires for the treatment of diseases that are a part of their daily lives, and (b) include a variety of different possible treatment paths using several (and different) bioactive compounds, which would explain the higher number of plants that can be used for their treatment.

Let us consider the example of digestive disorders and their predominance in ethnobotany studies. These disorders are frequent in several local communities because of a lack of adequate sanitary conditions and bad water quality, and the high incidence of species and use citations for digestive problems may be related to the greater effort dedicated to establishing plant repertoires to cure these frequent diseases. However, digestive diseases may be treated with a wide range of bioactive compounds, which might also explain the large number of plants associated with their cure. If this reasoning is valid, then complex diseases whose treatment is associated with only one or a limited number of bioactive compounds will tend to have a small number of species used for their treatment, which is the case for cancer, certain diseases of the nervous system, and many others.

However, the study of therapeutic indication patterns may be impaired by theoretical and methodological problems. Ethnobotanical studies generally do not focus on therapeutic indications, which are usually only used to compose lists of plants or calculate indexes of species importance. Studies that only record the medicinal properties of each plant without considering local disease concepts, which may be very different from western models, are common. A condition that is considered a disease by western society may be considered a different type of condition by a local community; thus, the definition of what constitutes a disease varies. In communities of northern Argentina studied by Hurell (1991), disease is not considered a transitory state from a normal condition; instead, health and disease are considered two states of an individual's life.

In addition, the way in which plants act on the disease may be approached superficially in different studies. Many studies do not differentiate among plants that can be used to heal a disease, mitigate its symptoms, or prevent it. Thus, clear and detailed presentations and discussions of therapeutic indications in ethnobotanical studies are essential for the study of their patterns.

12.7 The Role of the Environment

In the previous sections, we discuss medicinal plant use behavior patterns and their possible causes. However, these behaviors may differ from one location to another depending on many factors, including the role of the environment in which human groups are included. Thus, we discuss how the environment may bring different communities closer or separate them in terms of similarity in medicinal plant use. We also show how the previously discussed patterns relating to origin, plant habit, and plant therapeutic indications may differ between communities located in different environmental settings.

Different studies have shown that the environment plays an important role in the selection of medicinal plants and reported that individuals from different ethnic groups or origins inhabiting nearby or neighboring regions in similar environments tend to use similar repertoires of medicinal plants. Coe and Anderson (1999) compared two neighboring indigenous groups of different ethnicities in Nicaragua and observed that 80 % of their medicinal plant repertoires was shared between the two groups. Similarly, Albuquerque et al. (2008) compared the plant components of pharmacopoeias from an indigenous group and rural community of the Caatinga of the state of Pernambuco, Brazil, and noted similarities among the plants used, with even greater similarities when the native plants were analyzed separately. More recently, Saslis-Lagoudakis et al. (2014) studied 12 ethnic groups in Nepal and found that local pharmacopoeias are more similar when cultures are placed in similar floristic environments.

The importance of the environment on plant selection can also be observed in studies showing differences in the pharmacopoeias of peoples of the same origin that live in different environments. Ladio et al. (2007) compared the knowledge of medicinal plants of the Mapuche people inhabiting arid steppe and humid forest areas of the Argentinean Patagonia and observed that only 40 % of the plants were used by both groups. The high discrepancy was attributed to the two communities inhabiting different ecosystems, which limits the acquisition of and contact with the same plants by the two groups.

Migrations also provide interesting examples of how the environment can limit species acquisition or decrease similarities between pharmacopoeias (see Medeiros et al. 2012), even between people of the same origin. A particularly enlightening case study was conducted with the Akha people, who were separated between 100 and 120 years ago among China, Thailand, and other Southeast Asian countries (Inta et al. 2008). The study showed that although they maintained similar practices and traditions, the movement towards different areas forced the Akha to use a different group of medicinal plant species.

In addition to variations in the repertoire of medicinal plants reported according to ecosystem, the richness in medicinal plants itself also varies because certain ecosystems can provide a greater number of different plants for use by local peoples. Plants are often selected for medical practices according to bioenvironmental logic, which is guided by the physicochemical properties of the plants (Johnson 2006), and certain ecosystems favor a greater presence of certain bioactive compounds over others (see Voeks 2004; Albuquerque et al. 2012). Thus, certain ecosystems may support a greater use of native medicinal plants; together with historical and cultural factors, these factors may help explain why certain areas have a higher richness of native species in their pharmacopoeias than others.

Another widely discussed but little tested question regarding medicinal plant richness is whether urbanization has decreased the number of plant species in local pharmacopoeias. In general, increasing urbanization is considered to lower the richness of medicinal plants (Amorozo 2002) because urban environments (a) have a lower availability of species, especially native species, which is supported by urban ecology studies (see McKinney 2008), and (b) favor easy access to allopathic drugs (Amorozo 2002), which may decrease the use of plants for therapeutic ends. However, this hypothesis has not been tested, and authors have proposed scenarios that do not support a decrease in richness with increasing urbanization. Amorozo (2002) suggests that when communities are influenced by urban-industrial societies, an initial increase in the knowledge of plants and their uses may occur because of increased opportunities for contact with exotic species, which may be acquired in pharmacies or public markets (see Hilgert et al. 2010).

Therefore, the dynamics of plant knowledge and/or the use of plant species may be consistent with the intermediate disturbance hypothesis,[6] which states that locations with intermediate degrees of urbanization have a higher richness of known and/or used species because they are at an optimal plateau between the ability to obtain native plants (apparently higher in environments with low urbanization environments) and exotic plants. Thus, urban environments can be expected to have a higher proportion of exotic species than rural environments.

The environment and degree of urbanization may also influence plant habits that are more commonly used by the community, which might be caused by the higher or lower availability of a given plant habit (see Thomas et al. 2011) or different biochemical pathways utilized by plants with different habits in different environments (in the specific case of the environment) (Albuquerque et al. 2012). For example, tree species may present a high incidence of qualitative compounds in certain environments, such as in the Caatinga, whereas these compounds may be restricted to herbaceous plants in other environments, which has been observed in many of the studies supporting the EAH. Such a scenario might result in a pattern based on the use of herbs in certain cases and the use of trees in other cases, such as in the Brazilian Caatinga (see Albuquerque et al. 2012).

Although patterns related to therapeutic indications are clear and based on the dominance of digestive and respiratory systems disorders, different environments may at times lead to different dominant diseases and exhibit different patterns of plant usage. These variations may be directly associated with differences in the environments surrounding the communities. Such differences are primarily caused by the (a) occurrence of diseases that are typical to a certain location and do not occur or are less frequent in other locations and (b) environmental influences that favor certain biochemical pathways and alter the predominant compounds and types of diseases that these compounds can treat.

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[6] The intermediate disturbance hypothesis was first proposed within the scope of community ecology to explain why species richness and diversity in environments at the initial stages of anthropization are higher than in completely anthropized or completely natural areas. This hypothesis proposes that areas of intermediate disturbance preserve their original components and gather richness by including pioneer and invasive species.

12.8 Final Considerations

Based on the evidence presented in this chapter, the following conclusions can be drawn:

1. Clear patterns can be observed in medicinal plant use by local populations based on similar forms of resource appropriation by those populations.
2. Although pattern formation is observed, dissonant behaviors will always occur that are inconsistent with the pattern.
3. The environment (among other factors) may play a fundamental role in the observed differences in plant use among different communities and may result in divergent patterns (for example, the higher use of herbs in certain environments and higher use of trees in others.

We believe that future studies will also be presented with the challenge of filling knowledge gaps on this topic. However, studying plant use in humid vs. arid, tropical vs. temperate, or urban vs. rural areas may provide answers to outstanding questions and elucidate subjects that have not been previously investigated.

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Chapter 13
Biological and Cultural Bases of the Use of Medicinal and Food Plants

Washington Soares Ferreira Júnior, Letícia Zenóbia de Oliveira Campos, Andrea Pieroni, and Ulysses Paulino Albuquerque

The ethnobiological literature has usually dealt separately with the use of food and medicinal resources by human populations. There is no doubt that these two types of resources are essential for human survival; they nourish our species and/or prevent or treat illnesses. Some studies show that the use of food plants may impact the maintenance of health in a group or even be used to treat illnesses (Johns 1990; Pieroni and Price 2006; Etkin 2006).

This overlap may suggest much more than the simple fact that individuals use the same resource for both needs. Instead, it may indicate the existence of an evolutionary continuum in the use of food plants and of medicinal plants. This continuum may shed light on the understanding of how humans appropriated nature throughout their evolutionary history and, from this starting point, began to develop the medicinal and nourishment systems.

In this chapter, we attempt to expand on the ideas behind a food–medicine continuum that has enabled humans to deal with plants. From this starting point, we discuss the role of this continuum during human evolution, particularly at the origin of medicinal systems, by presenting some biological and cultural bases that drove human beings to perceive and access the food–medicine continuum.

W.S. Ferreira Júnior (✉) • L.Z. de Oliveira Campos • U.P. Albuquerque
Laboratory of Applied and Theoretical Ethnobiology (LEA), Department of Biology,
Federal Rural University of Pernambuco, Av. Dom Manoel de Medeiros, s/n,
Dois Irmãos, Recife, Pernambuco 52171-900, Brazil
e-mail: kba.bio@hotmail.com

A. Pieroni
University of Gastronomic Sciences, Piazza Vittorio Emanuele 9,
Pollenzo (Cuneo) 12042, Italy

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13.1 The Food–Medicine Continuum

In some situations, it is hard to differentiate between the medicinal and food uses of plants, suggesting the existence of a continuum between these two categories. For example, south-Asian immigrants living in northern England include plants in their cuisine that are also used as medicine (Pieroni et al. 2007). Strong overlap between these two uses has also been observed in communities in Nigeria (Etkin and Ross 1982).

From a pharmacological point of view, there is evidence indicating that certain plants used as food contain substances with important pharmacological activity. The Maasai community in eastern Africa regularly eats certain plants that have been shown to have a large amount of saponins and phenols, which have the potential to minimize the incidence of cardiovascular problems in the community; notably, the diet in this community is rich in cholesterol and fats (Johns et al. 1999). In addition, these food plants have been shown to have in vitro activity against the measles virus, an illness with a high incidence rate in the children of this community (Parker et al. 2007). Thus, given their vast pharmacological potential, the plants added to the diet of the Maasai may have an important role in maintaining local health.

The use of a set of resources as medicine and as food may be classified in the following manner (Pieroni and Quave 2006): (1) There are plants that are indicated for medicinal and food use, but these two uses are unrelated. For example, the fresh shoots may be used as food but are considered medicinal when they are ground and applied topically. In this case, the two uses are unrelated. (2) A plant may be ingested as food, and its use may also be recognized by people as having a positive impact on health without being indicated for one or more specific illnesses. Such plants may act as “folk functional foods” in a human group. (3) Finally, there are plants that are used as food, and this use is also associated with preventing and/or treating one or more specific illnesses. This is the case, for example, when the seeds of a plant are used as food when ingested after cooking, and the same use is indicated to treat illnesses that affect the gastrointestinal tract. These three cases show that a given resource may be used as medicine or as food depending on how it is prepared and/or on the intent and goal with which this resource is used (Jennings et al. 2015). These three examples reflect different levels of a food–medicine continuum, with the third case exemplifying how at times it is difficult to separate between the food and medicinal uses (Jiang and Quave 2013; Jennings et al. 2015).

As diseases have been an important selective force throughout human evolution (Brown 1987), the attribution of food and medicinal use to a set of resources may be due to biocultural adaptations of the human species in response to the occurrence of illnesses (Etkin and Ross 1982). Thus, the selection of nourishing resources that simultaneously aid in the prevention and treatment of diseases may have been advantageous for populations throughout human evolution. For example, hunter-gatherer populations have been considered the most well-nourished populations in human history because they had at their disposal a large variety of species used for food; these food sources contained a wide variety of substances that simultaneously sated hunger and prevented and/or treated illnesses (Etkin 2006).

However, changes in food habits, especially after the development of agriculture, may be connected to the appearance of many illnesses in modern populations, as there was an approximately 50 % decrease in the diversity of plants used in the diet (Etkin 2006; Leonti 2012).

When considering the evidence reinforcing the existence of a food–medicine continuum from an evolutionary perspective, we ask the following question: what does this continuum reveal about the evolution of the relationships between humans and nature? In an attempt to answer this question, we first present the chemical-ecological perspective of Timothy Johns regarding the relationships between human beings and chemical substances in the environment (Johns 1990, 1999). Under this perspective, the use of plants and animals as human food has a long evolutionary history, during which human beings developed a number of strategies to address the chemical substances ingested from the diet to maximize the beneficial substances and minimize the effects of potential toxins. According to Johns (1990), the basis of human medicine is the use of plants for food during our evolutionary past. When experimenting with food plants in the past, it is likely that humans identified some resources that relieved symptoms of illnesses while also providing nutritional benefits (Johns 1990). In this case, the development of the use of medicinal plants may have started when humans observed that certain food plants also treated diseases, thus reflecting the food–medicine continuum. Our first answer to the question above is that the food–medicine continuum was the basis for humans to perceive the medicinal use of plants and is thus the basis of the evolution of medicinal systems.

Daniel Moerman is another scientist who contributed to this discussion. Moerman analyzed a data set on the use of plants by 291 North American tribes, encompassing the use of 3895 different species (Moerman 1996). When assessing the relationships between food and medicinal uses, he found that 19 % of the plants were used exclusively as food, 45 % were used as medicine, and 29 % were used as both as food and medicine, demonstrating an overlap between the two uses. Moerman suggests that these data do not corroborate Timothy Johns' idea that medicinal use derived from food use, as he expected to find a greater number of plants used as both food and medicine. When analyzing the species used as both food and medicine, the uses did not necessarily overlap regarding the parts of the plant used. Therefore, even for species with an overlap between the two uses, the parts used for the different goals were often different. For example, the data show that fruits were indicated mostly for food but were seldom cited for medicinal use. Similarly, lianas and vines were mostly indicated for medicinal use but were seldom used as food (Moerman 1996). Based on these data, Moerman states that medicinal use did not necessarily derive from food use but rather evolved independently from it. Moerman's data are robust, and his argument is valid if we consider that a medicinal or food tradition must remain static. However, the work of Gottlieb et al. (1995) presents interesting evidence that in a certain way supports the findings of Moerman (1996), for which we have a different interpretation.

Gottlieb and collaborators conducted a study with three groups of indigenous peoples of the Amazon to assess the distribution of food and medicinal uses among plant families (Gottlieb et al. 1995). They observed that food plants tend to belong to more basal groups, whereas medicinal plants tend to belong to more derived groups. The subclasses with a large number of food plants had few medicinal plants and vice versa (Gottlieb et al. 1995). These data once again indicate that this low overlap would be expected, corroborating Moerman's findings, but they do not invalidate the idea of a continuum. We thus suggest that the food–medicine continuum had an important role in the origin of the medicinal use of food but that medicinal knowledge and practices evolved independently after originating from the food–medicine continuum. Therefore, the continuum may have played a role in the origin of human medicine but not necessarily in its evolutionary trajectory.

Further confirmation of our ideas comes from recent data collected from a mountainous and remote area of the Southern Balkans (Quave and Pieroni 2015), where pastoralist Albanians have lived together with the Gorani ethnic minority for several centuries. Despite this contiguity and the fact that these groups inhabit the same inhospitable ecological landscape, Gorani and Albanian medicinal plant uses remarkably diverge, while wild food plants and related preparations are similar. The fact that these wild food plants-based dishes are considered important for "maintaining" health, especially during long snowy winters, i.e., they represent "folk nutraceuticals" (Pieroni and Quave 2006), could confirm that this gray area represents the core of an original "medicinal cuisine" from which very divergent plant medicines originated. Moreover, while folk knowledge concerning food and medicinal foods is ubiquitously distributed, specific medicinal plant knowledge is often retained by specific knowledgeable persons/healers.

This could explain also why in the Mediterranean region for example—where medicinal plant healers have surely played a minor role in the last Centuries in the delivery of health care among peasants—the medicinal plant knowledge is still very linked to medicinal foods and it is often considered a common heritage of the whole community.

To understand the role of the continuum in the origin of medicine, it is necessary to answer a second question: how did humans perceive the therapeutic properties of plants based on the food–medicine continuum? To help answer this question, we present two topics on the biological and cultural bases that would have been important during our evolutionary history, as they provided our species with a greater degree of proximity to and experimentation with species that reflected the food–medicine continuum.

13.2 Biological Bases Involved in the Food–Medicine Continuum

Under this topic, we highlight the biological bases that enabled humans to access and perceive the food–medicine continuum. We use as an example the production of detoxifying enzymes by the body and the human chemosensory perception.

13.2.1 Detoxifying Enzymes in Humans

There are a variety of detoxifying enzymes produced by humans that are important for breaking down toxic compounds ingested during feeding (Ingelman-Sundberg 2005), such as UDP-glucuronosyltransferases, glutathione transferases, sulfotransferases, and the cytochrome P450 superfamily (Nebert and Dieter 2000). These enzymes played an important role in human adaptation to the chemical environment to which the first hominids were exposed (Johns 1990), resulting in a high degree of genetic polymorphisms and a large number of copies of some of the genes that code for these enzymes (Wang et al. 2007).

There is evidence that individuals with multiple copies of the genes coding the detoxifying enzyme CYP2D6 are able to metabolize a larger number of toxic compounds than individuals with few copies of this gene (Ingelman-Sundberg 2001; Aklillu et al. 2002). We may therefore infer that a larger number of copies of these genes in a given individual allows for increases in the amount and diversity of food ingested without causing a toxic reaction in the body.

From an evolutionary viewpoint, the presence of these enzymes may have facilitated access to the food–medicine continuum by the first human groups that dealt with nutritional and therapeutic needs (Johns 1990). A diet that included plants with toxic secondary compounds may thus have been favored, as these enzymes can break down a large amount of toxic compounds, decreasing their concentration in the body (Ingelman-Sundberg 2005). The ingestion of these plants may have also aided in maintaining a healthy body, as bioactive secondary compounds have important pharmacological properties (Leonti 2012).

13.2.2 Chemosensory Perception and the Bitter Taste Perception Threshold

Another way in which humans may have perceived the food–medicine continuum is taste perception. For example, communities descending from Albanians, who migrated to Southern Italy in the fourteenth and fifteenth centuries, use plants with a slightly bitter taste only for food and plants with a more intense bitter taste both as food and especially as medicine only; plants with a bitter taste that is perceived as strong are only used as medicine (Pieroni et al. 2002). From this example, we may infer that the use of a plant as food and as medicine may be seen as a continuum that is assessed based on the perception of the bitter taste. A set of studies conducted in several cultural groups suggested a relationship between bitter taste and the indication of a plant as medicinal—in other words, bitter taste is an indicator that the resource has medicinal value (Brett 1998; Brett and Heinrich 1998). In addition, it has been observed that bitter taste is associated with a set of pharmacologically active compounds (Mennella et al. 2013).

Although not all studies found an association between taste and a particular set of illnesses (see Casagrande 2000), some studies have suggested the existence of such an association (Ankli et al. 1999; Leonti et al. 2002). A study by Medeiros et al. (2015), for example, showed an association between perceived taste and the indication of plants for a set of illnesses in a local community in the Brazilian northeast. However, this association was only observed for the most popular therapeutic indications and for the tastes most commonly mentioned by the study group, such as bitter taste. In this case, plants with a perceived bitter taste were indicated mostly for certain illnesses, whereas tasteless plants or plants with a perceived good taste were indicated for other illnesses (Medeiros et al. 2015). This result suggests that taste perception plays an important role in the use of medicinal plants, particularly for the most commonly mentioned illnesses and tastes and that bitter taste is especially important in the recognition of medicinal plants by individuals. When considering that bitter taste is important in the medicinal use of plants, we may infer that the study of human perception of bitter taste may aid in gaining understanding of how humans first perceived the food–medicine continuum.

Bitter taste perception varies among individuals, and this variation is influenced by genes. The *TAS2R38* gene has been associated with taste perception, namely, to a high sensitivity to bitter taste, as individuals with this allele perceive bitter taste even when the concentration of a known bitter compound is low (Mennella et al. 2005). In contrast, another allele of this gene has been associated with low sensitivity to bitter taste, with individuals perceiving bitter taste only when a known bitter tasting compound is present in high concentrations (Mennella et al. 2005). The combination of the alleles of this gene has been associated with the formation of three groups of individuals based on bitter taste perception, namely, (1) supertasters, with high sensitivity to bitter taste, (2) tasters, with intermediate taste perception threshold, and (3) nontasters, with low sensitivity to bitter taste (Bartoshuk 2000). The frequencies of the taster and nontaster alleles in the human population have been estimated to be approximately 50 % (Guo and Reed 2001; Wooding et al. 2004). Analyses of data collected in the USA show the frequencies of the nontaster, taster, and supertaster phenotypes to be 25, 50, and 25 %, respectively, in the American population (Bartoshuk 2000). The identification of these groups of individuals may help elucidate possible variations in the perception of the taste that these individuals attribute to food and medicine plants in different human groups.

Considering that bitter taste perception is important for recognizing plants with medicinal use and that there are people who genetically perceive bitter taste more strongly, it is possible that during the cultural evolution, supertasters encompassed shamans or people with a vast knowledge of medicinal and food plants in human communities. From an evolutionary point of view, individuals with alleles that confer a stronger perception of the bitter taste were able to perceive and approach plants that reflected the food–medicine continuum and to actively participate in the building of medical traditions. Thus, a stronger perception of bitter taste may favor an association of a food's perceived taste with its medicinal properties. We believe that this association may be more difficult for individuals who are genetically less sensitive to bitter taste, as they tend to perceive food as slightly bitter or not bitter. Therefore, the medicinal knowledge acquired by these supertasters through experimentation was transmitted to other individuals by cultural transmission and social learning processes.

13.3 Cultural Bases Involved in the Food–Medicine Continuum

The techniques adopted to process food throughout human cultural evolution also played an important role in the approach to plants reflecting the food–medicine continuum. Thus, food-processing techniques enabled the use of a greater variety of resources for food by reducing plant toxicity and facilitating their ingestion without causing damage to the body.

Culture is an important factor in the interaction between people and the environment because of its role in both altering environmental selective pressures and favoring changes in dietary patterns, which in turn may also affect health and lead to certain types of illnesses (Etkin 2006). From a chemical-ecological perspective, it has been found that the most important cultural stages in the evolution of human diet were the technological leap and the origin of agriculture (Johns 1990). Different practices were developed by hunter-gatherer populations to assess which species were appropriate for consumption, and these techniques are the result of cultural practices developed by these populations.

For example, it was with the use of fire for cooking and with the use of geophagy, fermentation and drying that food considered unpalatable began to be used in the diet. The substances present in some plants that were not consumed by humans include toxic substances, represented by different secondary compounds (Johns 1990). It is also important to note that in some human groups, bitter-tasting foods tend to be considered "bad foods" or "hard foods" and therefore unpalatable (Johns 1990). The use of techniques to reduce the toxicity and the effects of certain flavors may thus have led food previously considered as "hard foods" to become "soft foods", i.e., food appropriate for human consumption (Johns 1990). Although the use of the abovementioned detoxifying techniques has been indicated as important in promoting evolutionary advantages in the human species, we must also consider that this process may affect the amount of nutrients, vitamins and minerals present in a given plant (Etkin 2006).

Geophagy, or detoxification by clay, is an important detoxification method, especially when plants with a high concentration of tannins and alkaloids are consumed. This technique was commonly used in many regions of the globe. For example, geophagy was often used in the Andes to detoxify the body after the consumption of native potatoes. In turn, fermentation is a food detoxification and transformation technique used from ancient to modern times. It is still in use because, depending on the microorganism (bacteria or fungus) used in this process, not only the toxicity but also the flavor and consistency of the food may be altered. This process is commonly used in the production of bread, sauces, and dairy and alcoholic beverages (Etkin 2006). Another important detoxification process is drying, which is used mainly to remove volatile toxins from food. This method is usually used alongside other detoxification methods to remove non-volatile toxic substances (Johns 1990).

Another cultural adaptation factor that significantly influenced the concentration of toxins in plants consumed by human populations throughout the world was domestication (Etkin 2006). Domestication is an essential aspect of agriculture, as it plays an important role in modifying or alleviating the effects caused by the concentration of certain allelochemicals. However, the disadvantages related to domestication must also be considered, as this process may affect the nutritional availability of certain substances in the plant. For example, the origin of agriculture is associated with an increase in the amount of dense carbohydrates present in plants, which considerably reduced the amount of secondary compounds in domesticated plants (Johns 1990). Depending on their concentration, such secondary compounds may be essential for the survival of a species under adverse environmental conditions.

13.4 Final Considerations

The study of the overlap between the use of plants for food and for medicine is an important field of ethnobiological research. Below, we give examples of some topics that may be of interest for future studies:

- In humans, plants used as food can affect certain diseases, such as reducing metabolic diseases and preventing infection. Thus, the addition of these plants to the diet can reduce the use frequency of resources in a local medical system to treat infections. Local systems that utilize plants to treat infectious diseases cannot be appreciated if we neglect to investigate the plants used in the diet.
- Studies related to the food–medicine continuum offer important contributions for bioprospecting, as they may broaden the choice of possible plants with pharmacological potential. For example, plants regularly used as food can be perceived by the members of a group as being effective for the control of specific illnesses and may even contain classes of compounds of pharmacological interest (Johns et al. 1999; Parker et al. 2007). Studies focusing on medicinal plants may often ignore some food resources that may also have medicinal potential.
- Ethnobiological field studies are needed that more seriously consider the “central” part of the continuum between food and medicine, which is often related to domestic practices managed by women within the households. These studies should use appropriate, sophisticated research methods for eliciting data that borders between food and medical anthropology.

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Chapter 14
An Evolutionary Perspective on the Use of Hallucinogens*

Washington Soares Ferreira Júnior, Margarita Paloma Cruz, Fábio José Vieira, and Ulysses Paulino Albuquerque

14.1 Introduction

Hallucinogens have been used by human communities since ancient times. For example, records of the use of the plant *Sophora secundiflora* (Gomez-Ortega) Lag. ex DC. dating from between 8440 and 8129 BC have been found in the state of Texas in the southern USA (Furst 2004). Psychoactive drugs are capable of causing not only visual but also auditory, tactile, and gustatory hallucinations (Schultes and Hofmann 1993). Because of these characteristics, they are often believed to mediate communication with gods or spirits (Schultes and Hofmann 1993; Rodrigues and Carlini 2005; De Feo 2004), earning them the name "entheogens." This term, coined by Gordon Wasson (1992), means "god within me," a reference to the fact that, when such substances are ingested, they establish a closer connection between the person who consumes them and the gods. The term entheogen is arguably more appropriate when we want to refer to the use of psychotropic drugs in the religious, shamanic, or spiritual context. The fact that some hallucinogenic plants induce a certain health condition of well-being may have favored their learning and use by human beings

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W.S. Ferreira Júnior (✉) • U.P. Albuquerque
Laboratory of Applied and Theoretical Ethnobiology (LEA), Department of Biology,
Federal Rural University of Pernambuco, Av. Dom Manoel de Medeiros, s/n,
Dois Irmãos, Recife, Pernambuco 52171-900, Brazil
e-mail: kba.bio@hotmail.com

M.P. Cruz
Colombian Society of Ethnobiology, Bogotá, Colombia

F.J. Vieira
Department of Biology, State University of Piauí, Av. Senador Helvídio Nunes de
Barros, s/n, Junco, Picos, Piauí 64607-760, Brazil

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(Johns 1990). Obviously, as suggested by Johns (1990), the cultural context mediates this use and importance in a culture. A relevant issue for an understanding of the relationship between humans and natural chemicals is how a culture's relationship with these substances originated and developed. In this sense, the following question may be of high importance: is there a hallucinogen–medicine continuum that is similar to the food–medicine continuum discussed elsewhere in this book?

In an article entitled "Mescaline Cactus Used in Folk Healing," Dobkin de Rios (1968) reports the hallucinogenic and medicinal use of *San Pedro* cactus (*Trichocereus pachanoi* Britton & Rose) in a rural community in Peru, suggesting that psychoactive substances are effective in treating diseases. However, the author shows that although the use of hallucinogenic plants in curing disease has been noted by several authors, the use of such plants in medicinal contexts has not been adequately discussed. The fact that there is an overlap between medicinal and hallucinogenic uses may indicate that humans discovered the hallucinogenic uses from the selection of medicinal plants. Rodriguez et al. (1982) suggest that the local people in the Amazon incorporated plants in their rituals that have antiparasitic properties due to the presence of alkaloids. Recent evidence reinforces the interpretation of these authors. Data from Roulette et al. (2014) support the hypothesis that the use of tobacco may protect against parasites.

In this chapter, we present some considerations for developing the hypothesis that hallucinogenic substances are effective in the treatment of diseases, which often does not appear clearly in the literature, and we discuss how the hypothesis can provide insights into human evolution that involve the use of these substances. We then present previous findings on the treatment of diseases using hallucinogens, including the different actions of psychoactive drugs and other elements that may interact in the treatment of diseases. We refer to the use of hallucinogens in the context of traditional or local communities, not as recreational drugs.

14.2 Hallucinogenic and Medicinal Uses

The use of hallucinogenic substances as medicines has been recognized in local medical systems, but little academic study has been undertaken on this relationship. Many studies combine the medicinal and hallucinogenic properties of plants into the same category, recognizing hallucinogens as a secondary feature of some species used in traditional medicine (see Schultes 1938; Rodriguez et al. 1982). For example, Weiner (1971), working in a rural community in Tonga (a country located east of Australia), discussed the strange absence of hallucinogenic plants in traditional medicine, which shows a close relationship between the hallucinogenic and medicinal uses for this author.

We believe that this strong relationship between hallucinogenic and medicinal uses may be due to experimentation with medicinal plants, which led to the development of a culture of traditional hallucinogens. Many authors have shared this idea (Weil 1965; Rodriguez et al. 1982; Etkin 1988; Brussell 2004), proposing that the hallucinogenic effects of plants were discovered subsequent to their medical applications when users of these drugs took higher doses than recommended. This application seems to have been the case with *nutmeg*, according to a report by Weil (1965). Rodriguez et al. (1982) suggest that many hallucinogenic plants were initially used for the treatment of diseases due to their antiparasitic properties. The fact that many cultures around the world have developed entire systems of belief and practice around hallucinogenic plants may suggest the existence of an adaptive component in such practices.

Given the evidence, there seems to be a belief among researchers that these substances may alter the mind, not only in terms of their hallucinogenic effects but also in a medicinal context (Randolph 1905). However, we must separate the two perspectives that seem to emerge from the works of these authors. The cure can be interpreted from the perspective of the researcher (the biomedical model) or from the perspective of the culture studied. For example, when an investigator witnesses a shamanic ritual that includes the ingestion of a psychoactive substance and records testimony that it healed the patient, we must distinguish whether the cure was actually achieved at a physiological level or in the sphere of "cultural diseases," those related to the worldview and beliefs of a particular people.

Determining the moment when medicinal plants were also considered to be hallucinogens is no easy task because the concept of illness for traditional cultures often differs from what "disease" means to Westernized or modern people (Hurrell 1991; Herndon et al. 2009). This subject has been extensively studied (Coelho 1976; Monod 1970; Rodriguez et al. 1982; Fackelmann 1993; Menéndez 1994; Agosta 1997; Shepard Jr. 2002; De Feo 2004; Toledo 2006; Bourbonnais-Spear et al. 2007). Most of these authors indicate that, in addition to recognizing what we might call physiological diseases (diseases that would be accepted by modern medical science), many traditional communities also recognize diseases caused by supernatural agents (for example, see Garro 2000).

Schultes and Hofmann (1993) argue that non-industrialized cultures do not differentiate between physiological and supernatural causes of disease. Rather, disease is the result of "interference with the spiritual world." Therefore, the best medicine to treat diseases would be entheogens, which enable contact with the spiritual world, where an effective cure for the disease can be identified. This complex process is difficult to explain without systematic and specific case studies. A hallucinogenic plant may have medicinal properties that treat some (but not all) physical infirmities. If a particular healing ritual always uses the same plants to treat a complex consisting of several diseases, then it would be reasonable to assume that the cure operates not at a physical level but rather at a "supernatural" level, according to the worldview of the culture. Considering the cause of a disease to be other than physiological or even to be supernatural typically means that the cure is also not "conventional" and that it does not fit the types of treatments recognized by modern medical science.

Agosta (1997), in a review of plant compounds used as medicines, notes that in traditional communities, diseases are often thought to be caused by evil spirits. Therefore, healers should administer psychotropic drugs and use their influence to communicate with the spirit world and achieve the patient's healing. According to

Schultes (1979), healers and shamans take hallucinogens (in this case, entheogens) to make contact with deities through visions or dreams. These visions provide knowledge about the disease afflicting the patient and tell the healers the proper treatment for the condition (see also Rodrigues and Carlini 2005; De Feo 2004). In this case, the entheogen becomes a vehicle that allows the healer to explore aspects of the disease and treat the patient. Thus, the entheogen has an indirect effect because it is ingested by the healer, not by the patient.

In other situations, the treatment is indirect not because the hallucinogens allow contact with the gods to determine the cure for the disease but instead because healers can use hallucinogens to confront and combat a disease through symbolic battles with the cause of the disease (Rivier and Lindgren 1972). In the case presented by Dobkin de Rios (1968), the *San Pedro* cactus is used to cure diseases indirectly through a ritual treatment in which the healer drinks the entheogen and receives information about the cause of the disease. However, Dobkin de Rios explains in his description of the ritual that both the patient and the healer drink the infusion from the *San Pedro* cactus, an act that leads to hallucinations and vomiting in the patient who ingested the substance. Dobkin de Rios (1968) and Rodriguez et al. (1982) suggest that this action may have a curative effect.

This example shows that sometimes the treatment can produce indirect contact between the deities and the healer who ingests the drink, in addition to a direct effect on the patient who also ingests the drink. A similar report on the hallucinogenic cigarette *tira-capeta*, used in healing rituals in Maroon communities in Brazil, can be found in Rodrigues et al. (2008). According to the authors, the cigarette is used by both the healer and the patient and may exert a direct effect on the latter in the treatment of disease. The key issue in these examples is that the act of vomiting or smoking may have more of a symbolic effect than a strictly physiological effect in fighting a specific disease.

However, we regard these actions as a direct treatment because the patient came into direct contact with the hallucinogenic substance, which could have had played a role in curing the disease. Healing through direct treatment is in line with Western biomedical concepts. That is, the patient takes the hallucinogen, which has one or more bioactive compounds with medicinal properties. In addition, the vehicle used (e.g., powder, beverage, or cigarette) and how the substance is consumed contribute to the effect of the active principle in the body.

These examples show that hallucinogens can play both a direct and an indirect role in curing diseases while also facilitating communication with deities, thus allowing healers to decipher the origins of diseases or to symbolically battle diseases. In contrast to the types of treatments already noted, Schultes and Hofmann (1993) have discussed a ritual in which only the patient drinks a hallucinogenic substance while the shaman observes the behaviors and responses to the drink and diagnoses the patient's maladies. This example presents a third type of disease treatment involving hallucinogens but does not suggest any medicinal properties. Thus, there may be a cultural placebo effect in which particular cultural expectations cause a member of the culture to attain the desired effect even without pharmacological elements. For example, Albuquerque and Chiappeta (1994) describe a ritual with the plant *Jurema* (*Mimosa tenuiflora* (L.) Poir.) in which a person consumed the drink offered but did not have the same reactions that the others had (see also Souza et al. 2008).

In addition to the situations presented above, there are other cases, as documented by Dobkin de Rios (1968), Rivier and Lindgren (1972), and Albuquerque and Chiappeta (1994), in which both the healer and the patient (and even other people in the ritual) took the plant to hallucinate. In addition to other factors, the combination of various elements of the ritual (songs and dances, for example) can cause a synergism that leads to the patient's "cure."

Some authors have suggested that healing in rituals is accomplished through a combination of plants with entheogenic properties, songs, and prayers (Monod 1970; Bourbonnais-Spear et al. 2007). This idea is supported by Albuquerque and Andrade's (2005) study on African-Brazilian cults. They argue that, for the remedies to be complete, their administration must be accompanied by an enchantment to facilitate the healing process. Thus, one must consider the complete set of ritual elements that create a contagious atmosphere among participants, leading to emotional states that can produce states of trance (Camargo 1998).

One of the most striking elements in rituals is music, which may consist of whistling or magical songs that accompany the entire ritual. Katz and Dobkin de Rios (1971) provided an important contribution in this area with their analysis of the role of whistling in the *ayahuasca* healing rituals of Peruvian Amazon natives. They concluded that the ingestion of hallucinogenic plants and the whistles produced by healers during the period of intoxication were the method for invoking the forces of nature and the guardian spirits. Dobkin de Rios and Katz (1975) subsequently elaborated on their findings and established a link between musicality, religious rites, and healing. They questioned the importance of music in ceremonies with hallucinogenic plants in Western societies, finding that different types of music can evoke particular moods and may regulate the hallucinogenic effect of the drug administered. Monod (1970), studying the Piaroa Indians in South America, believed that the songs sung during the rituals had curative and preventive effects. Other authors corroborated the assertion that music is essential to ritual divination of diagnoses and healing. Mentally, rhythmic singing with a drumbeat seems to support the flow of visions and minimize fear (see Albuquerque and Chiappeta 1994). Metzner (1998) reported that Western psychotherapy and the healing systems of shamanic indigenous peoples use plants or psychoactive drugs to cure or obtain knowledge and that these objects are invariably essential to the success of healing.

If our goal is to investigate whether hallucinogens are effective in the treatment of diseases, then we must consider the distinct views of disease between human groups and biomedicine as well as the different forms of treatment with hallucinogens (direct or indirect). In this text, however, we adopt an approach based on the biomedical model to evaluate the effectiveness of both medicinal and hallucinogenic applications, focusing on direct treatment.

As weak evidence for direct treatment, some studies have isolated and identified substances with hallucinogenic and medicinal properties in the same plant, which corroborates the idea that plants with hallucinogenic properties also have medicinal properties. However, we must discern whether these substances can actively treat targeted diseases. For example, Mackie et al. (1955) prove the efficacy of the substance *thujone*, a constituent of essential oils from various plants, as an anthelmintic. Albert-Puleo (1978) also reports this substance to be a hallucinogen, demonstrating that a substance may in fact have both hallucinogenic and medicinal properties.

Table 14.1 presents species of plants and fungi with compounds that have proven hallucinogenic and/or medicinal pharmacological properties. As shown in the table, there are substances that have confirmed hallucinogenic properties but where no studies have demonstrated their medicinal properties, for example, muscimol and ibotenic acid in the *Amanita muscaria* species. Other substances, however, have already been proven to have both medicinal and hallucinogenic properties (see Table 14.1). Indeed, this evidence seems to indicate that the initial consumption of a plant for medicinal purposes may lead to the discovery of its use as a hallucinogen.

Table 14.1 List of species with recorded hallucinogenic uses and their substances with hallucinogenic and/or medicinal properties proven in pharmacological studies

Species	Substances	Properties	References
Amanita muscaria (L. Fr.) Lam.	*Muscimol*	Hallucinogenic	Perry and Perry (1995); Satora et al. (2005)
	Ibotenic acid	Hallucinogenic	Satora et al. (2005)
Atropa belladona L.	*Atropine*	Medicinal and hallucinogenic	Rates (2001); Schultes and Hofmann (1993)
	Hyoscyamine; *hyoscine*	Hallucinogenic	van Dongen and Groot (1995); Schultes and Hofmann (1993)
Brugmansia arborea (L.) Lagerh.	*Tropane alkaloids (atropine and scopolamine)*	Hallucinogenic	van der Donck et al. (2004)
Cannabis sativa L.	*Cannabinoids ("arachidonoylethanolamide"; "2-arachidonoyl glycerol"); bioactive fatty acids ("palmitoylethanolamide" and "oleamide")*	Medicinal	Petrocellis et al. (2000)
	Cannabinoids ("4-acetoxy-2-geranyl-5-hydroxy-3-n-pentylphenol"; "8-hydroxycannabinol" and "5-acetyl-4-hydroxycannabigerol")	Medicinal	Radwan et al. (2009)
	Cannabinoids (Cannabicromano)	Medicinal	Ahmed et al. (2008)
	Cannabinoids	Medicinal	Velasco et al. (2004); Beaulieu and Rice (2002)
		Medicinal and hallucinogenic	Ashton (2001); Honório et al. (2006); Bonfá et al. (2008); Ameri (1999)

(continued)

Table 14.1 (continued)

Species	Substances	Properties	References
Claviceps purpurea (Fr.) Tul.	*Ergot alkaloids (ergotamine and ergometrine)*	Medicinal	Komarova and Tolkachev (2001); Lorenz et al. (2009)
	Ergot alkaloids (ergolines)	Medicinal and hallucinogenic	Eadie (2003)
	Ergot alkaloids (ergotamine)	Medicinal and hallucinogenic	van Dongen and Groot (1995)
Datura spp.	*Tropane alkaloids (atropine and scopolamine)*	Hallucinogenic	Perry and Perry (1995)
Datura stramonium L.	*Atropine*	Medicinal	Irambakhsh et al. (2010)
	Atropine	Medicinal and hallucinogenic	Rates (2001)
Digitalis spp.	*Digoxine*	Medicinal	Rates (2001)
Nicotiana sp.	*Harmine*	Hallucinogenic	Davis et al. (1969)
Papaver somniferum L.	*Codeine*	Medicinal	Rates (2001)
Psilocybe spp.	*Psilocybin, psilocin*	Hallucinogenic	Schultes (1998); Huhn et al. (2005)
Salvia divinorum Epling & Játiva	*Salvinorin A*	Medicinal and hallucinogenic	Capasso et al. (2006)
Tabernanthe iboga Baill.	*Ibogaine*	Hallucinogenic	Kubilienė et al. (2008); Sheppard (1994)
	Ibogaine	Medicinal and hallucinogenic	Popik and Wróbel (2001)
Trichocereus pachanoi Britton & Rose	*Mescaline*	Hallucinogenic	La Barre (1979)
Trichocereus williamsii (Lem. Ex Salm-Dyck) Coult.	*Mescaline*	Hallucinogenic	La Barre (1979)

14.3 Adaptive Significance of the Use of Hallucinogens

Based on the evidence we present, it is very likely that the use of hallucinogens, especially in ritual contexts, has arisen from the selection of medicinal or food plants by humans. One possible scenario is that the initial trial plants (for medicine) led humans to encounter the natural chemicals that cause altered states of consciousness, to which different cultures have attributed different meanings. Most likely, the same plant can be taken to act as both a medicine and a hallucinogen (from a biomedical perspective), or the use has focused solely on its hallucinogenic properties. In this sense, we may considerer that the use of hallucinogens is a by-product of the human active search for plant chemicals. Obviously, cultures that assign a meaning to the positive experiences provided by the use of hallucinogens may have started, after the accidental discoveries, an active search for such products.

In many cultures, natural hallucinogens are reported to have a property by which the eyes of the "experimenter" (shamans, in some cultures) are opened to a spiritual world. The hallucinogenic experience allows access to this world because it brings together knowledge and power. Many healers and shamans claim that they have access to different types of knowledge because they were taught by the plants they used. These plants are called by many Amazonian societies "plants with the mother" (see Luna 1984; Jauregui et al. 2011), but they are not necessarily psychotropic. Such plants are used to guide initiation processes and the transmission of traditional knowledge, as noted by Jauregui et al. (2011:747) for *ayahuasca* (a South American psychotropic):

> (…) visions are an expression of the initiates' journey to their inner world and to the spirit world, where different scenes and spiritual entities may appear, depending on the initiate's religious, cultural, and social imprint. In the case of the ethnic Amazonian groups, the entire framework of their cosmovision is expressed. Therefore, it is common among indigenous people to have visions of serpents, jaguars, Amazon river dolphins, and eagles.

Different ethnographic and non-scientific (based on reports of individual experiences) records illustrate the role of hallucinogen consumption as a learning strategy for beginners, not only for the knowledge transmission of traditional rituals and medical practices but also for other aspects of life, including the identification of plants and animals in the local environment (see Lamb 1993). In these reports, the beginner's hallucinogenic experience, guided by a healer or shaman, acts as a key learning strategy (Albuquerque 2001). In such cases, psychoactive plants can play an important role in the adaptation of the human groups in their respective environments. We call this hypothesis the "psychotropic hypothesis of the adaptation" (Albuquerque 2001). If in fact plant hallucinogens play an important role in human adaptation (improving learning and knowledge transmission), then, at the least, we need pharmacological evidence to support this claim. However, experimental studies using rats with psilocin (from hallucinogenic mushrooms) and salvinorin A (from *Salvia divinorum*) have found deleterious effects on learning and memory acquisition (Braida et al. 2011; Rambousek et al. 2014). Other investigations with different animal models and substances (for example, see Molinengo et al. 1986; Koupilova et al. 1989), including humans in a double-blind controlled study (MacLean et al. 2013), reinforce these findings. These findings may suggest that the use of hallucinogens by traditional human groups does not have an adaptive character, particularly affecting learning processes. However, we need more evidence to verify the adaptive role in the use of hallucinogens in human evolutionary history.

Just as evidence of coevolution between humans and plant chemicals used as food and medicine has been presented in other chapters of this book, we can also assume a long coevolutionary process with psychotropics. Sullivan and Hagen (2002) suggest that this coevolutionary history may have been motivated by the scarcity of high-quality food in the ancestral environment, which led hominids to consume these allelochemicals to save energy. Obviously, both the accidental encounter with these plants in search of medicinal substances and the need to save energy in famine situations may have led to this scenario. In particular, we believe that the lack or complete scarcity of high-quality food may have resulted in the consumption of psychotropics either accidentally or intentionally. For example, many modern cultures have a set of foods that are basically consumed only in times of scarcity called famine foods or emergency foods. They are typically highly toxic plants that must undergo detoxification processes to be consumed. We suggest that these scenarios in ancestral environments may have put hominids in contact with these substances as famine foods.

Chemical-ecological evidence, such as the presence of adaptations in mammals to defend themselves against plant chemicals, reinforces this interpretation. Perhaps the most remarkable adaptation is the evolution of liver enzymes (cytochrome P450) that metabolize many plant chemicals, clearly indicating that humans were exposed to plant toxins throughout their evolution (Sullivan and Hagen 2002; Sullivan et al. 2008). There is a large polymorphism in genes coding cytochrome P450 enzymes (named CYP genes), and the frequency varies in different populations, which indicates that the ability of different individuals to metabolize xenobiotics varies across these populations (Sullivan and Hagen 2002; Sullivan et al. 2008). Considering that the deleterious effect on learning and memory acquisition is dependent on the dose of the hallucinogen, as observed for salvinorin A (MacLean et al. 2013) and psilocin (Rambousek et al. 2014), some individuals can ingest a hallucinogen and witness the desired effect without necessarily having a deleterious effect on memory. By presenting multiple copies of the CYP genes, some individuals may have a high metabolic rate for the hallucinogenic compound. Thus, the individual may experience hallucinations because some amount of the compound is not metabolized, but not enough to have a deleterious effect on memory. However, this idea needs empirical verification, as may be the case for other studies on human populations that have undergone positive selection for CYP genes and simultaneously interact with entheogens as part of their culture.

14.4 Final Considerations

According to the discussions raised by this chapter, we can conclude the following points:

1. There is an association between the use of hallucinogenic and medicinal substances. This association is related to the properties of these substances, which may be hallucinogenic or medical, depending on the dosage. However, no systematic study linking ethnographic data with pharmacological uses has been found. For example, have hallucinogenic substances been used pharmacologically in a healing ritual activity for all diseases?

2. To discuss the possible roles of the adaptive use of hallucinogens, we present studies that assess the effect of hallucinogens on learning and memory. We note that many of these studies use isolated substances. An interesting study could assess how traditional hallucinogenic preparations, not simply an isolated hallucinogen, can affect learning and memory.
3. When substances have different properties depending on dosage, researchers tend to assume that the medicinal effects were discovered before the hallucinogenic effects. This idea has been suggested by different studies, but to the best of our knowledge, it has not been studied and tested. Thus, there is a tendency among researchers to consider the hallucinogenic effects to be secondary to the medical effects.
4. The different disease treatments using hallucinogens can be grouped into three types. In the indirect treatment, only the healer takes the hallucinogen and receives contact with deities and insights into the causes of the disease to diagnose and/or obtain treatment for the patient. In the second type, direct treatment, the patient takes the hallucinogen, which may have active ingredients with the desired properties that have a direct effect in curing the disease. In the third type, the patient takes the hallucinogen, but it does not have active compounds for the treatment of the disease in question. Thus, healing can be considered a case of "cultural placebo."
5. In addition to hallucinogens, other elements present in rituals also serve an important function in the healing process. Hallucinogenic substances may have the ability to influence the types of visions experienced. There is evidence of the positive effect of plant hallucinogens on attitude, mood, and behavior in humans. Doblin (1991: 23) discussing the famous "Good Friday Experiment" conduced with psilocybin asserts that "psychedelic drugs can help facilitate mystical experiences when used by religiously inclined people in a religious setting." Recent studies have found similar conclusions (Griffiths et al. 2006, 2011).

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