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Theories and Major Hypotheses in Ethnobotany

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Ethnobotany has evolved from a discipline that largely documented the diversity of plant use by local people to one focused on understanding how and why people select plants for a wide range of uses. This progress has been in response to a repeated call for theory-inspired and hypothesis-driven research to improve the rigor of the discipline. Despite improvements, recent ethnobotanical research has overemphasized the use of quantitative ethnobotany indices and statistical methods borrowed from ecology, yet underemphasized the development and integration of a strong theoretical foundation. To advance the field of ethnobotany as a hypothesis-driven, theoretically inspired discipline, it is important to first synthesize the existing theoretical lines of research. We review and discuss 17 major theories and hypotheses in ethnobotany that can be used as a starting point for developing research questions that advance our understanding of people–plant interactions. For each theory or major hypothesis, we identify its primary predictions and testable hypotheses and then discuss how these predictions have been tested. Developing research to test these predictions will make significant contributions to the field of ethnobotany and create the critical mass of primary literature necessary to develop meta-analyses and to advance new theories in ethnobotany.

Key Words: Hypothesis-driven research, medicinal plant selection, optimal defense theory, utilitarian redundancy model, taboo as luxury, theory in ethnobotany..

Introduction

Ethnobotany, the science of survival (Prance et al. 2007), has long been concerned with its relationship to theory. In its early stages, ethnobotanical research largely consisted of acontextual lists of plants with their associated preparations and uses in remote areas (Balick 1996; Etkin 1988). This work, and by extension the discipline, has been criticized as “weak” or “pseudoscience” (Albuquerque and Hanazaki 2009; Alexiades

1996). Exceptions include the theoretically grounded, extensive body of research in cognitive ethnobotany (e.g., Atran 1998; Alexiades 1996: xii; Brown 1977; Conklin 1954; Hunn 1975; Medin and Atran 2004; Turner 2000) which led to general principles of folk biological classification (Berlin et al. 1973; Berlin 1973; Brown 2000). Of particular interest are the principles of *ranked taxonomy* and *biological essentialism*. Fundamentally, people tend to think/rank/classify plants and animals in the same way across culture (folk biology), and this contrasts with the way they think/rank/classify other elements of the world. Furthermore, there is a cross-cultural convergence in the way people realize that species appearance, behavior, and ecological niche are not randomly established but guided by

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lawful underlying internal processes (Medin and Atran 2004). In contrast to cognitive ethnobotany, research in ecological ethnobotany has lacked clear theoretical frameworks. Notable exceptions include biocultural research which focuses on an in-depth analysis of the biochemical basis and pharmacologic implications of food, psychoactive, and medicinal plant uses by local people (Etkin 1988; Johns 1986). As the discipline has continued to evolve, there has been a repeated call for a paradigm shift and more theory-inspired research mainly in ecological ethnobotany.

Nearly 40 years ago, Ford (1978) questioned whether or not ethnobotany had a unifying theory, while Phillips and Gentry (1993a) criticized the predominant use of descriptive studies in ethnobotany as well as the lack of theoretical frameworks and/or methodological rigor. This self-criticism successfully prompted more recent ethnobotanical studies to follow the lead of Begossi (1996) by incorporating ecological methods in ethnobotany but without a clear theoretical framework. As a result, an increasing number of studies, in an effort to include quantitative rigor, utilized species-area curves to estimate the diversity of species used by cultural groups, and ethnobotanical indices (see Hoffman and Gallaher 2007). International and locally meaningful protocols and procedures for conducting ethical research are now considered essential components of the research process. Recent efforts have focused on advancing ethnobotanical education based on interdisciplinary training, core concepts, and competencies that bridge the natural and social sciences (McClatchey et al. 2013). Though important, these approaches have not addressed Phillips and Gentry's (1993a,b) call for formulating a theoretical framework, emphasizing instead methodological rigor (Albuquerque 2009) and a generalized use of ethnobotanical indices (Hoffman and Gallaher 2007).

Acknowledging the persistent lack of theory-inspired research in ethnobotany, Martin (2007, pp. 23–25) detailed precisely how this progress could be achieved using a hypothetico-deductive approach. This approach includes developing testable hypotheses (from theory or general principles) on the drivers of the patterns in people's knowledge and use of their environment, collecting data collected using ethnographic methods, and using statistical analyses to test if these data lend support (or not) to these hypotheses. Recently, Bennett (2005) and Albuquerque and Hanazaki (2009) repeated the call for "less quantification" and more theory-inspired and hypothesis-driven research in ethnobotany. In

addition, Bennett (2005) noted that ethnobotanical education also needs a major shift to meet the needs of the discipline's evolution. The challenges faced by ethnobotany are similar to those of other sister disciplines. For example, in the 1990s, several prominent ecologists questioned if the discipline of ecology had general laws or a unifying theory (Aarssen 1997; Lawton 1999; Marquet et al. 2014; Weiner 1995). As a result of this self-reflection, ecology progressed as a discipline, moving from simply documenting patterns to understanding the underpinning processes that generate ecological patterns across time and spatial scales. Ethnobotany, drawing inspiration from sister disciplines (ecology, evolution, anthropology, archeology, etc.), can do the same (Salick and Alcorn 2003).

The most promising hypothesis-driven approaches to date have come from testing whether patterns of human use of medicinal plants align with the predictions of the theoretical frameworks from ecology (e.g., Albuquerque 2006; Albuquerque and de Oliveira 2007; Alencar et al. 2010; Bennett 2007; Bennett and Husby 2008; Vandebroek and Balick 2012; Reyes-García et al. 2013b; Quiroz and van Andel 2015; Voeks and Leony 2004; Voeks 2007). However, for such efforts to expand beyond individual research groups and sites, it is important for ethnobotanists to recognize the breadth of current ethnobotanical theories and understand how these theories can be used to develop testable hypotheses. Further, it is critical for emerging ethnobotanists to be exposed to these theories in a systematic way. We postulate that *providing a synthesis that clearly identifies theories and major hypotheses about people–plant interactions will focus future ethnobotanical research toward delineating the theoretical bases for plant selection and use by people*. These theoretical frameworks are resources for designing research questions and developing testable hypotheses to advance our understanding of the dynamic relationships between plants and people.

For simplicity, we have adopted a less-rigid use of the terms "theory" and "hypothesis" in this paper. However, readers should be aware of existing discussions on theory and how it differs from a hypothesis, a prediction, a model, or a universal law (Krebs 2000; Quinn and Dunham 1983). Hypotheses are proposed explanations of observed natural phenomena or patterns, whereas a theory is an "integrated and hierarchical set of empirical hypotheses that together explain a significant fraction of a scientific observation" (Krebs 2000). As such, theories are hypotheses which have been rigorously tested and

for which we found support for the generalization. Most of the theories or hypotheses we present are adapted from ecology or related disciplines and serve as possible explanations of ethnobotanical patterns. Some of these theories have not yet been formally presented as major theoretical frameworks among ethnobotanists. For this reason, we refer mostly to “hypotheses” with the understanding that they represent part of the nascent theoretical body of ethnobotany. In cases where a given hypothesis has been widely tested and accepted in ethnobotany, or where the name is carried directly from a theory in ecology, we use the term “theory.”

In this paper, we review 17 theories and major hypotheses used in ethnobotany with a strong focus on economic ethnobotany. This review is selective and representative, but not exhaustive. Scholarly works were selected to cover the diversity of question-oriented research in ethnobotany based on the lead author’s teaching and research experience. We group the theories/hypotheses into two main categories that relate to the overarching questions that each set seeks to address (Table 1). The first set of hypotheses addresses how and why people select plants for ethnobotanical use. The second set addresses the implications of plant selection by people and addresses how people mitigate the potential negative effects of plant use. For these theories and hypotheses, we clearly identify their central prediction(s). In addition, we discuss refinements to these theories and hypotheses based on how they have been tested in the literature. For related hypotheses, we provide a discussion on how they interrelate and why some of them should be tested separately, despite similarity. In cases where we do not identify rigorous tests of a given theory or hypothesis from the literature, we suggest methodological approaches and statistical analyses to test their predictions. Finally, we call for a shift in ethnobotanical educational approaches to increase the awareness and application of these theories/hypotheses, and train ethnobotanists to develop and implement theory-inspired, hypothesis-driven research.

How and Why Do People Select Plants for Ethnobotanical Uses?

THE VERSATILITY, AVAILABILITY, AND DIVERSIFICATION HYPOTHESES

The versatility, availability, and diversification hypotheses attempt to explain the increasing or

disproportionately large number of exotic plants utilized in traditional medicine. They acknowledge traditional medicine as dynamic systems and suggest possible drivers of this phenomenon.

The *versatility hypothesis* suggests that introduced plants are incorporated as medicine by way of experimentation with introduced food and ornamental plants (Alencar et al. 2010; Bennett and Prance 2000). This hypothesis has been supported by several studies that found a high proportion of non-native medicinal plants were first introduced as food and ornamental plants (Bennett and Prance 2000) or for other non-medical uses (Ceuterick et al. 2008; Jernigan 2012). Documenting the chronology of the incorporation of different plant uses would be important for future tests of this hypothesis. The versatility hypothesis has also been expanded to suggest versatility is a positive selection factor for plant use in general (Alencar et al. 2010). Thus, this hypothesis predicts that people are more likely to retain knowledge, use, and access to a plant that has a greater number of applications for humans. It also predicts that the most cosmopolitan plants (those used in the largest number of regions) are the most versatile since versatile plants would be more likely to be shared or carried by emigrants to new areas. This has been tested by comparing the number of uses reported for introduced and native medicinal plants, but it has found mixed support (Alencar et al. 2010). The versatility hypothesis, in this broader sense, overlaps with the plant use value hypothesis (see below), as use value indices are largely versatility indices, and therefore, these two theories could benefit from further integration.

The *availability hypothesis* states that plants are used for medicine because they are more accessible or locally abundant (Albuquerque 2006; Voeks 2004). This hypothesis was born, in part, out of studies revealing the importance of anthropogenic habitats or disturbed areas in provisioning weedy and introduced species for medicine (Gavin 2009; Stepp and Moerman 2001; Voeks 2004). Availability is often conceptualized as a physical distance from a home or community to the location where a plant grows in the wild, but could also be considered in terms of seasonality, abundance, price, as well as access to markets, gardens, or natural areas where plants are found (Albuquerque 2006; Estomba et al. 2006). The availability hypothesis has been tested by examining the location where people indicate they collect medicinal plants and, more broadly, by correlating the local abundance or dominance of plants with use-values. The

TABLE 1. OVERARCHING QUESTIONS IN ETHNOBOTANY AND THE ASSOCIATED THEORIES OR HYPOTHESES. REFERENCES REPRESENT AUTHORS WHO PROPOSED OR FORMALIZED THE THEORY/HYPOTHESIS, OR KNOWN TO HAVE TESTED IT THE FIRST TIME.

Questions, theories, or major hypotheses
1. How and why do local people select plants for use?
1.1. Is plant selection directly related to the demographic traits of the plant?
A. Versatility hypothesis (Alencar et al. 2010; Bennett and Prance 2000)
B. Availability hypothesis (Albuquerque 2006; Voeks 2004)
C. Plant use value hypothesis (Phillips and Gentry 1993a, b)
D. Theory of non-random plant selection (Moerman 1979, 1991)
E. Optimal foraging theory (Sih and Christensen 2001)
F. Doctrine of signatures (Bennett 2007; Etkin 1988)
1.2. Is plant selection directly linked to its phytochemistry?
A. Diversification hypothesis (Albuquerque 2006; Alencar et al. 2010)
B. Optimal defense theory (Mckey 1974; Zangerl and Rutledge 1996)
C. Ecological apparency hypothesis (Albuquerque and Lucena 2005; Feeny 1976)
D. Resource availability hypothesis (Coley et al. 1985; Stepp 2004)
1.3. How social dynamics and human traits affect plant selection?
A. Age, gender, and dynamics of knowledge (Voeks 2004, 2007)
B. Urbanization and knowledge loss (Voeks and Leony 2004)
C. Social network and knowledge dynamics (Hopkins 2011)
2. What are the conservation and livelihood implications of plant use?
2.1. What are the implications of plant selection to the people and the plant?
A. Cultural keystone species (Garibaldi and Turner 2004)
B. Utilitarian redundancy model (Albuquerque and de Oliveira 2007)
2.2. How do local people mitigate the negative effect of plant use?
A. Taboo as luxury (Rea 1981; Quiroz and van Andel 2015)
B. Taboo as conservation strategy (Colding and Folke 1997, 2001)

hypothesis has received mixed support (Albuquerque 2006; Gonçalves et al. 2016; de Oliveira Trindade et al. 2015), with native species sometimes preferred, despite their lower abundance or accessibility. Further investigations should focus on defining what availability means in different

contexts. A multi-dimensional index incorporating ecological, socio-cultural, economic, and political aspects and drivers of availability could be used to test the availability hypothesis in different contexts.

The *diversification hypothesis* explains the incorporation of exotic plants in traditional medicine as enriching culture, rather than being a response to cultural erosion or environmental degradation (Albuquerque 2006). The diversification hypothesis suggests that exotic plant species are selected to fill therapeutic vacancies in an ethnopharmacopoeia, perhaps due to novel bioactivity, thereby diversifying the set of treatment options (Albuquerque 2006; Alencar et al. 2010, 2014). This hypothesis has been supported by studies which found that exotic medicinal plants provide medicinal treatment not available from native plants (Albuquerque 2006; Alencar et al. 2014; Santos et al. 2014) and that exotic medicinal plants provide different bioactive compounds than native medicinal plants (Alencar et al. 2010).

PLANT USE VALUE HYPOTHESIS

The plant use value hypothesis proposes that the usefulness of a plant (e.g., for medicine, food, construction, technology, or trade) in a given community is directly related to its botanical family, life form, local abundance (density), and/or maximum size (Phillips and Gentry 1993a,b). This work was highly influential in providing a pathway to apply statistical analyses to ethnobotanical data through a use value index. The statistical approach could be improved further by testing the additive effects of plant traits in the same statistical model, rather than testing the individual effects of these traits in separate models. This would help account for the fact that people often select plants for use based on multiple traits at the same time. The multiple predictors approach (additive model of family, life form, abundance, and maximum size) is what separates the *plant use value hypothesis* from the *availability hypothesis* (Albuquerque 2006) or the *theory of non-random plant selection* (Moerman 1979) and the *apparency hypothesis* (Gonçalves et al. 2016), each of which propose single predictors (e.g., number of species per family or species abundance).

Although the *plant use value hypothesis* suggests that the utilitarian value local people associate with a given plant species is solely a function of the traits of the plant species, several other factors related to the individual collector can also influence estimates of use value. For example, Lawrence et al. (2005)

found that gender, ethnicity, age, and proximity to markets all had an influence on the perceived importance of wild harvested plants for local people. In that study, women tended to place more importance on fruits, whereas men placed more importance on timber. Studies that have entirely or primarily focused on male participants (Galeano 2000; Phillips and Gentry 1993a) may bias conclusions toward plants considered important by men. The socio-cultural and demographic backgrounds of the researchers themselves can also influence the outcome. Pfeiffer and Butz (2005) described how gender-imbalanced field research has biased ethnobiological data collection, hypothesis testing, and application of theory. Contrary to Phillips and Gentry (1993a), who calculated plant use value indices from interviews, Lawrence et al. (2005) asked participants to list and rank the ten most important plants they had harvested from the forest over the last 10 years. They also interviewed participants to contextualize their findings and allowed use categories to emerge from interviews. This emic approach may provide more reliable data, as results could be cross-checked with interviews, and factors such as efficacy, frequency, palatability, and availability could be integrated by the participant themselves in determining which plants are important.

THEORY OF NON-RANDOM PLANT SELECTION

The *theory of non-random plant selection* was developed by Daniel Moerman (Moerman 1979, 1991, 1996). It was intended, in part, to counter the belief at the time that Native American medicine was only placebo (Moerman 1979). If traditional medicines were only placebo, he contends, plants would be selected at random with respect to plant family. The theory of non-random selection predicts that medicinal plant selection is not random. The number of medicinal species in a given plant family in a given region would be a linear (on a log scale) function of the total number of plant species in that family. However, particular plant families tend to be over- or under-represented in a given pharmacopeia (Moerman 1979, 1991; Moerman and Estabrook 2003) and as food (Moerman 1996).

This theory is one of the most widely tested in ethnobotany. For example, non-random plant selection by family has been confirmed with the ethnopharmacopoeia in Amazonian Ecuador (Bennett and Husby 2008), in Belize (Amiguet et al. 2006), in Kashmir (Kapur et al. 1992), and in Hawai'i (Ford and Gaoue 2017). Additionally,

Phillips and Gentry (1993b) found family to be a strong determinant of plant use value. Moerman (1991) explains that species in the same family, due to their evolutionary relatedness, share some characteristics of plant defense, inherited from common ancestors, which influence their physiology and effectiveness as medicines. Certain plant families have chemical compounds more useful or effective as medicines (e.g., Asteraceae), while other families are much less useful as medicines (e.g., Poaceae because they often depend on resprouting and physical defenses rather than chemical defenses). Support for this hypothesis requires linking chemical activity with plant selection and disentangling the impacts of other factors as drivers of this over- and under-representation of particular families. Further, if non-random plant selection is driven primarily by bioactivity, we would expect that species within a family used for a particular illness would have the highest bioactivity relevant to that illness (under the over-simplifying assumption of single plant recipes). This could be tested by comparing the medicinal uses of a set of related species with their respective concentrations of bioactive compounds. Finally, the theory predicts that plant families which are closely related are more likely to have similar medicinal uses than those that are phylogenetically distant (Saslis-Lagoudakis et al. 2014; Yessoufou et al. 2015).

THE DOCTRINE OF SIGNATURES

The *doctrine of signatures* has been used as a framework to understand the medicinal plant selection process in traditional cultures. As early as 40–90 AD, Dioscorides wrote of a plant species that resembled a scorpion's tail, which coincidentally was used to treat scorpion attack (Bennett 2007). The *Doctrine of Signatures* suggests a plant's form recapitulates its function—where physical or sensory characteristics of plants (shape, color, taste, and smell) reveal their potential therapeutic value and use (Bennett 2007; Leonti et al. 2002). In this context, specific plant characteristics are used in the identification of species' potential medicinal qualities. For example, the presence of antimicrobial and hemostatic red quinones found in some species of red plants potentially reflect their common use and ethnomedical application for healing a variety of epidermal disorders (Etkin 1988). Although the doctrine of signatures is primarily concerned with plant's form, in a wider sense, it can include organoleptic properties. For example, pungent odors or bitter tastes may reflect the presence of

monoterpenes or alkaloids corresponding not only to a given plant's physiological properties but also its potential medicinal/therapeutic application (Bennett 2007; Leonti et al. 2002).

The doctrine of signatures is a valuable mnemonic aid for traditional cultures that facilitates the transmission of knowledge about its uses (Bennett 2007; Leonti et al. 2002). However, most scholars dismiss the doctrine of signatures as "primitive" or "prescientific" (Bennett 2007) even though its major predictions have been rarely tested. Most existing work on the doctrine of signatures lists different signatures that correspond with a given plant and the therapeutic functions the plant provides (Dafni and Lev 2002). In one of the rare direct tests of the doctrine of signatures, Bennett (2007) tested if plants with heart-shaped leaves were used in cardiac medicine. Out of the 80 species randomly selected from a literature review, 21 were used as medicine and only 3 were used in cardiac medicine, indicating no support for the doctrine of signatures. However, people in the selected studies may not associate the human heart with the form resembling a "Valentine's heart," so failure to find a significant proportion of species with cordate leaves being used to treat cardiac disease does not provide a rigorous test of the doctrine of signatures. Further work through participant observation and semi-structured interviews could explore the types of clues (potentially signatures) that healers use to identify plant species to test for medicinal uses. Another approach would be to use a binomial regression with the presence or absence of a given signature as the predictor and the indicated therapeutic function as the response variable. For example, one could test if a given plant is more likely to be a galactagogue, based on the presence or absence of white sap.

It is important to note that the meanings of medicines are subjective but not trivial. These meanings affect their efficacy in all cultures. For example, the color of a pill can be a "signature" or signal of its therapeutic value to its consumer. Moerman (2002) reported how the same pharmaceutical had different effects based on its color. Pills colored blue were reported to promote sleep among populations that associate blue with tranquility, but in Italy, where blue is the color of a popular football team, the pills colored red had more of a soporific effect than the blue ones.

OPTIMAL DEFENSE THEORY

Several plant defense theories, borrowed from ecology, have been adapted to ethnobotany to explain why local people select medicinal plants from a given life form, habitat, or plant part (Albuquerque et al. 2012; Almeida et al. 2005; Coley et al. 2003; de Lucena et al. 2012). These plant defense theories are based on the premise that plants produce chemicals to protect themselves from herbivory and that this defense comes at a cost to the fitness of the plant, which is proportional to the risk of herbivore attack, and the abiotic resource available for the plant's growth (Endara and Coley 2011; Feeny 1976; Mckey 1974; Rhoades and Cates 1976).

Plant chemical defense is classified into two broad categories: quantitative and qualitative defense. Quantitative defense obligately uses digestibility reducers such as lignins that are immobile, are difficult for herbivores to adapt to, and have low rates of turnover but require a large energy investment to produce. Qualitative defense uses highly active molecules such as alkaloids that are toxic to herbivores at low concentrations, have high turnover rates, are often facultative and mobile, and require low energy investments, but can be adapted to by specialist herbivores (Feeny 1976; Rhoades and Cates 1976).

The *optimal defense theory* predicts that plant tissues that are unlikely to be attacked by herbivores or which have low fitness value have low amounts of quantitative defense but high inducibility of qualitative defense compounds, while tissues that are likely to be attacked or have high fitness value should have high levels of quantitative defense and low inducibility of qualitative compounds (Mckey 1974; Zangerl and Rutledge 1996). Therefore, from an ethnobotanical perspective, if humans select medicinal plants to optimize secondary chemistry, they would more likely select plant organs that are subject to less frequent herbivory because these organs would have more qualitative than quantitative defenses which are more useful for medicinal purposes. Furthermore, young leaves/plants are more likely to have qualitative defenses such as alkaloids (with more medicinal use) than quantitative defenses that take time to develop, so they will be selected more often for medicinal purposes than old leaves/plants (Coley et al. 2003).

THE ECOLOGICAL APPARENCY AND RESOURCE AVAILABILITY HYPOTHESES

The *ecological apparency hypothesis* is directly related to the optimal defense theory. The primary prediction of this hypothesis is that species with short lifespans (non-apparent) face lower herbivore pressure and are more likely to use “inexpensive” qualitative defenses whereas species with long lifespans (apparent) face higher herbivore pressure and invest in more “expensive” quantitative defenses (Feeny 1976). Qualitative defense compounds (e.g., alkaloids) have more medicinal bioactivity than quantitative defense compounds (e.g., lignins). Thus, from an ethnobotanical perspective, “non-apparent” plants (short lived, herbaceous, early successional) are more likely to be used for medicine than “apparent” plants (perennial, woody, dominant plants) (Albuquerque and Lucena 2005).

The *resource availability hypothesis* shares the predictions of the ecological apparency hypothesis. However, it suggests that plant defense investment is not primarily related to the risk of herbivory but to the resource level of the habitat to which the plant is adapted (Endara and Coley 2011). The *resource availability hypothesis* predicts that species adapted to high resource environments (e.g., high-light, nutrient-rich habitats) are more likely to grow quickly and use qualitative defense, while species adapted to low resource environments (e.g., low-light, nutrient-poor habitats) are more likely to grow slowly and have high levels of defense—primarily quantitative but also qualitative (Coley et al. 1985; Endara and Coley 2011; Stamp 2003). Fast-growing/short-lived species that can tolerate higher rates of herbivory and invest more in qualitative defense (e.g., alkaloids) will have more medicinal uses and will be more sought after than long-lived/slow-growing species which invest more in quantitative defenses. This might explain why some weeds and plants in disturbed areas or secondary vegetation are sometimes more highly sought after locally for medicinal purposes than non-weedy plants and those in primary forests (Stapp and Moerman 2001; Voeks 2004).

Few studies have tested the above theories in ethnobotany. Of those that have, most found no support for the ecological apparency hypothesis, but they did provide support for the resource availability hypothesis (Alencar et al. 2009; Almeida et al. 2005, 2012). Almeida et al. (2012) found that plants from a low resource environment (especially trees) tended to have high levels of quantitative and qualitative defense compounds and have higher

antimicrobial activity than plants from a high resource environment (especially herbs), which often had qualitative defense compounds but with lower antimicrobial activity.

Testing many of these ethnobotanical hypotheses is challenging because of difficulties in quantitatively assessing the chemistry of plants and accounting for how compounds may interact. For example, using dried plant material can potentially reduce actual bioactivity (Kursar and Capson 1999), and failing to compare the plant part used medicinally with other plant parts not used medicinally can bias results (but see McCune and Johns 2007). The synergistic effects of combining multiple species in one medicine is also difficult to understand (see Coe and McKenna 2017). Future studies could explore the widespread practice of using certain plant parts, harvest times, and harvest places in relation to the genetic and phenotypic chemical variation of plants as predicted by these two theories and if the disproportionate use of exotic plants as medicine in some contexts is primarily due to their high intrinsic growth rate rather than for diversification purposes.

OPTIMAL FORAGING THEORY

The *optimal foraging theory* is also borrowed from ecology. The theory predicts that foraging organisms will balance the benefit received from a food with the effort it took to search for and eat that food. “Generalists” will consume a wide variety of available resources, regardless of their energy content, because they are readily available, while “specialists” will use energy to seek out only a few kinds of resources that provide high energy content (Perry and Pianka 1997). This theory stems from the optimality model—a mathematical model from ecology applied to animals foraging for food (Charnov 1976).

When applied to ethnobotany, the optimal foraging theory predicts that (1) individuals will place higher value on plants that yield more benefit per unit of foraging/processing time; (2) as the abundance of plants with higher value increases, plants with lower value will no longer be used; and (3) individuals should have a quantitative threshold to decide when specific plants should be included or excluded (Sih and Christensen 2001). These hypotheses have been adapted in ethnobotany to understand how people select plants for use for food, medicine, or construction and are related to the diversification or availability hypotheses and the taboo as luxury hypothesis.

Tests of the optimal foraging theory that quantify the distance or time spent acquiring the resource and the benefit of the resource are rare, but they suggest that generalist and specialist strategies for harvesting food plants exist simultaneously. For food, most harvesting takes place around dwellings, but people will travel long distances to collect large amounts of highly nutritious resources (Ladio 2001). Energy use is also optimized by collecting larger amounts of resources that require longer preparation time (Nascimento et al. 2013). Although individuals have high knowledge of the use of plants around their dwellings with low nutritional value, foraging is more selective in farther ecosystems where there are plants with higher nutritional value (Ladio 2001). In the only current test of this hypothesis for the collection of medicinal plants, Soldati and Albuquerque (2012) show that people preferred to collect plants from closer sites regardless of the quantity or quality of products they can collect from these sites.

Although limited in number, these ethnobotanical tests support the predictions of the optimal foraging theory, which are also generally well supported within ecological research (Perry and Pianka 1997; Sih and Christensen 2001). Limitations to ethnobotanical tests of the optimal foraging theory include lack of geographic diversity, difficulty quantifying nutritional value, lack of consideration for cultural value, and lack of accounting for the potential confounding effects of age and gender.

AGE, GENDER, AND DYNAMICS OF KNOWLEDGE HYPOTHESIS

This hypothesis suggests that various individual socio-cultural and demographic traits such as gender, age, and literacy/formal educational level are all correlated with an individual's level of plant knowledge (Albuquerque et al. 2011; Hanazaki et al. 2013; McCarter and Gavin 2015; Souto and Ticktin 2012; Voeks and Leony 2004; Voeks 2007). Age and gender are the most commonly examined variables (Albuquerque et al. 2011), with women and older people tending to have greater knowledge of the local medicinal flora (Albuquerque et al. 2011; Torres-Aviles et al. 2016; Voeks and Leony 2004). Higher literacy and greater access to formal education are often negatively correlated with medicinal plant knowledge (Voeks and Leony 2004; Voeks 2007). Although most studies rarely provide mechanistic explanation for why age or gender and literacy can drive knowledge dynamics,

there are various arguments put forward to explain these patterns. For example, accumulating medicinal plant knowledge is a life-long process, so elderly people have simply had more time to acquire it (Brandt et al. 2013; Hanazaki et al. 2013), while, in many traditional cultures, women serve as the primary healthcare providers in their families, so it is understandable their medicinal plant knowledge is greater than that of men (Albuquerque et al. 2011). However, the context in which knowledge transmission occurs can influence results. For example, in a medicinal plant market context, patterns found in other studies on the effects of level of formal education, age, and years of experience did not hold true (McMillen 2012).

Difficulties in testing this hypothesis relate to how the variables are defined and measured. For example, men and women may possess different kinds of knowledge due to their different culturally defined gender roles (e.g., agroforestry versus medicinal plant knowledge), so the type of knowledge investigated matters (Albuquerque et al. 2011; Brandt et al. 2013; Souto and Ticktin 2012). Similarly, which plants are chosen to test ethnobotanical knowledge can be a proxy for knowledge type. Clearly, selection of plants primarily used by one gender would bias the study if gender roles are not properly taken into account (Brandt et al. 2013; Hanazaki et al. 2013; Souto and Ticktin 2012). Comparing different studies based on age can also be difficult since the intervals for age classes used are arbitrary (Hanazaki et al. 2013), and the length of residency in a community can be a stronger predictor of local plant knowledge than age (Gandolfo and Hanazaki 2014). Finally, socio-cultural variables interact with each other, in that the effect of one variable depends on the level of another (Souto and Ticktin 2012). Thus, to test this hypothesis, studies should be designed carefully to measure each variable in the local context and account for the interactive effect of these predictors of local knowledge dynamics. In addition, while most studies simply tested if there was any significant difference in knowledge between gender or age group, it is important to directly test hypotheses related to the mechanisms/processes that generate such age- or gender-based knowledge patterns.

URBANIZATION AND KNOWLEDGE LOSS HYPOTHESIS

This hypothesis explores the effect that urbanization has on traditional knowledge. The general

prediction is that urbanization (and commercialization of plant products) decreases traditional and/or local ecological knowledge. Drawing from the fields of anthropology and economics, multiple authors report a negative impact of various measures of urbanization on the preservation/retention of local ecological knowledge (Brandt et al. 2013; Gandolfo and Hanazaki 2014; Reyes-García et al. 2013a; Sogbohossou et al. 2015; Voeks and Leony 2004). In many regions of the world with rapid economic development, pressures for rural communities and minority ethnicities to assimilate, abandon traditional practices in favor of modern conveniences, and economic necessities have significantly contributed to acculturation and the increased endangerment of traditional knowledge systems. However, scholarship has yielded conflicting results, with some authors finding that the link between urbanization and knowledge loss is not straightforward (Furusawa 2009), that knowledge is not lost but rather transformed (Mathez-Stiefel et al. 2012; Poot-Pool et al. 2015), that knowledge survives (selectively) or remains constant (McMillen 2012; Müller-Schwarze 2006; Zarger and Stepp 2004), or that knowledge actually increases with urbanization (Vandebroek and Balick 2012).

These mixed results in testing the link between urbanization and loss of knowledge may be due to several factors. First, the various studies may be looking at different kinds of knowledge (Müller-Schwarze 2006; Reyes-García et al. 2007; Souto and Ticktin 2012). Some knowledge types may benefit from urbanization to the detriment of other types. Secondly, what may be called “urbanization” is not directly comparable from study to study, due to differing geographic or cultural scales (Müller-Schwarze 2006; Vandebroek and Balick 2012). Additionally, studies do not always clearly define urbanization and use different measures of urbanization, such as population size, e.g., towns/cities in contrast to rural areas and increases in population over time (Zarger and Stepp 2004); rapid development of previously rural areas (Gandolfo and Hanazaki 2014; Mathez-Stiefel et al. 2012; Reyes-García et al. 2013a); isolation versus proximity to roads and market towns (Reyes-García et al. 2007, 2013a); migration from rural to urban areas (Gandolfo and Hanazaki 2014; Mathez-Stiefel et al. 2012; Srithi et al. 2009; Vandebroek and Balick 2012); economic development and introduction of new industries, e.g., tourism, logging, and coffee production and various measures of “modernization,” such as public education,

adoption of *lingua francas*, and Western healthcare services (Furusawa 2009; Gandolfo and Hanazaki 2014; Reyes-García et al. 2007; Voeks and Leony 2004; Zarger and Stepp 2004); or various combinations of these factors (Gandolfo and Hanazaki 2014; Zarger and Stepp 2004). Carefully defining which type of knowledge is being tested and what measure of urbanization is being used will provide more accurate tests of this hypothesis and facilitate future meta-analyses.

SOCIAL NETWORK AS DRIVER OF KNOWLEDGE DYNAMICS

Social network theory is increasingly used in various disciplines to document the interplay between natural systems and human knowledge systems, including the distribution and dissemination/preservation of ethnobotanical knowledge within societies (Crona and Bodin 2006; Hopkins 2011; Wasserman and Faust 1994). This theory states that the nature and structure of relationships shape the flow of information in social networks (Granovetter 1973). In ethnobotany, the derived hypothesis predicts that the knowledge of an individual is influenced/shaped by the individual’s position in their social network and the collective knowledge of that network. The primary predictions of this hypothesis are that individuals who are more connected will have greater knowledge, that more connected networks will have a more uniform distribution of knowledge, and that the uniform distribution is more robust/resilient to being lost.

Boster (1986) was one of the first to show that women’s agricultural knowledge was more influenced by an individual’s number of relationships (analogous to degree centrality) than by kinship. Hopkins (2011) showed a weak positive correlation between in-degree centrality (how many people refer to an individual as a knowledge source) and medicinal plant knowledge. Similarly, Kawa et al. (2013) found that individuals perceived as knowledgeable by their community tend to have higher in-degree centrality, although this result may be confounded by other variables. Reyes-García et al. 2013a found a significant correlation between agroecological knowledge and betweenness centrality (a measure of how one’s position within the social network enables one to influence it). Díaz-Reviriego et al. (2016) also showed a significant correlation between degree centrality (the number of contacts an individual has in a network) and medicinal plant cultivation (as a proxy for medicinal

plant knowledge), suggesting that social interaction increases medicinal plant knowledge.

The characteristics of a social network are only some of many factors that can affect the dynamics of ethnobotanical knowledge. While observed variation of ethnobotanical knowledge in the studies discussed above may be due to the social network, when conducting social network analyses, it is important to simultaneously investigate the confounding influence of individual attributes such as age, gender, religion, education level, and ethnicity.

The Implications of Local People's Plant Selection on Both Plants and Culture

CULTURAL KEYSTONE SPECIES

The cultural keystone species concept stems from the ecological keystone species concept first coined by Paine (1969) when referring to certain species that are essential to the stability of ecological systems. Similarly, the *cultural keystone species theory* suggests that certain species of plants or animals are fundamental to socio-cultural systems and that the loss of these species would result in negative impacts on cultural identity and stability (Cristancho and Vining 2004; Garibaldi and Turner 2004). Cultural keystone species are “culturally salient species that shape in a major way the cultural identity of a particular cultural group” (Garibaldi and Turner 2004). The cultural keystone species theory, as proposed by Garibaldi and Turner (2004), was not meant to be tested but rather as a framework to underscore the importance of particular species that underpin cultural identity and wellbeing. However, this framework provides the opportunity to test hypotheses related to biocultural diversity dynamics. One hypothesis that can be tested from this theory is that a decline in biological diversity will be coupled with a loss of plant knowledge. One way to test this hypothesis would be to select a set of plant species with different degree of rarity (common, rare, extinct). Then one could test if local people have lower knowledge score of extinct or rare species compared to common species.

Similar to the ecological keystone species, identifying cultural keystone species has proven challenging. Cultural keystone species are expected (a) to have high use values, (b) to have functions within the psycho-socio-cultural structure of a particular cultural community, (c) to have ethnotaxonomic diversity, (d) to be culturally irreplaceable, and (e)

to be used in trade and/or resource acquisition (Garibaldi and Turner 2004). Prior studies often infer species' cultural keystone status by using species cultural importance indices (Platten and Henfrey 2009; Franco et al. 2014), which are expected to measure “the importance of the role it plays within a particular culture” (Turner 1988). These approaches have been criticized (Tardío and Pardo-De-Santayana 2008; Thomas et al. 2009) and it is unclear whether indices commonly used to measure cultural importance also capture the fundamental components of the cultural keystone species theory. In addition, measuring cultural irreplaceability is challenging. Because cultures are dynamic and resilient, they can adapt to new conditions by replacing a critically important species with another one once the original becomes scarce.

Beginning in the 1970s, several hypotheses were developed to link species ethnotaxonomic diversity with their cultural importance (Berlin 1973; Turner 1973). Ethnotaxonomic diversity refers to the richness and relative abundance of vernacular names used for a given species of plant included within a folk taxonomy of a particular cultural group. The theory of ethnotaxonomic diversity predicts that species identified by several traditional names within a native language are likely to be culturally important (Berlin 1973; Turner 1973), possibly because the names employed may capture varietal or utilitarian diversity (Berlin 1973; Martin 2007). Further, it has been predicted that plants employed for food, medicine, technology, ritual, and/or religion are likely to have nomenclatural recognition (at a generic level) which reveals their cultural importance (Turner 1973). Direct tests of these predictions are currently lacking, but would further our understanding of cognitive ethnobotany.

UTILITARIAN REDUNDANCY MODEL HYPOTHESIS

The *utilitarian redundancy model* (Albuquerque and de Oliveira 2007; Ferreira et al. 2012) is an ethnobotanical hypothesis analogous to the ecological redundancy hypothesis (Walker 1992). Unlike the ecological redundancy model, which is used in evaluating the functional redundancy of ecosystem components from a biological perspective, the utilitarian redundancy model seeks to evaluate natural resource use by human populations and aid in defining conservation priorities for culturally important species of medicinal plants and animals (Albuquerque and de Oliveira 2007; Nascimento et al. 2015). Here, utilitarian redundancy refers to

the idea that several species can be used for the same purpose and/or share the same therapeutic function.

The *utilitarian redundancy model* proposes that species that share the same therapeutic function (i.e., functional redundancy) are *redundant* and are predicted to experience reduced use-impact as the use pressure is diffused across a greater number of species (Albuquerque and de Oliveira 2007). Additionally, the loss of redundant species is predicted to have no overall effect on the ethnomedicinal practices of a particular cultural group regardless of the reduction of the number of species used to treat a given therapeutic function (Nascimento et al. 2015). The main challenge in testing the utilitarian redundancy model is related to the difficulty in accurately measuring realized utilitarian redundancy. Three main factors make such measures complex. First, for medicinal plant species that are versatile and used for multiple purposes, therapeutic redundancy does not necessarily guarantee lower use pressure. Second, it is critical to consider the local preference of particular species within a given therapeutic function. Preferred species employed by a particular group may be under greater use pressure despite therapeutic redundancy with multiple other species (Ferreira et al. 2012). Third, the disease profile of the study region defines which diseases are more common and which ones are rarer. A species that has unique therapeutic function may still be under lower use pressure if the disease it treats is rare in the region.

Accurately measuring therapeutic redundancy requires that one not only estimate the number of other species with similar therapeutic functions but also rank redundant species by preference from an emic perspective, as well as weight redundancy by the frequency of the disease groups considered in the study region. Even with an accurate measure of therapeutic redundancy, high use pressure at a local level does not necessarily suggest that these species are under threat as this depends on the harvesting rate, part harvested, species life form, and the ecological conditions in which harvesting takes place (Ticktin 2004).

How Local People Mitigate the Negative Effects of Plant Use

TABOO AS A CONSERVATION STRATEGY HYPOTHESIS

During the 1970s, attention toward environmental conservation sparked a renewed interest in

the nature–culture nexus (McDonald 1977). In seeking to understand how indigenous peoples might live in harmony or balance with the natural world, the idea of taboo as a conservation strategy was popularized. Cultural taboos are informal institutions that determine human behavior (Colding and Folke 2001). They involve restrictions by certain sectors of society on the use of particular resources and habitats, sometimes only at particular times or in particular places (Colding and Folke 2001). Cultural taboos are an important aspect of medicinal plant selection by traditional societies throughout the world.

The *taboo as a conservation strategy* hypothesis suggests that certain plant and animal species are made taboo to protect them from overexploitation and extinction. This hypothesis has been tested by comparing a list of taboo species for a given region with their International Union for Conservation of Nature (IUCN) red list status (Colding and Folke 1997). This study showed that 30% of the identified taboos prohibited any use of species listed as threatened by IUCN. However, using a global threat status such as the IUCN red list to measure local threat status may be misleading. Such tests could be improved by using an emic approach to estimate the local threat level of species listed as taboo from local people's perception of species vulnerability. One could then use a binomial regression to test if a species is likely to be endangered from an emic perspective, if it is already taboo.

Except for Colding and Folke (1997) who provide a direct test of the theory, most studies have explored taboo as conservation through literature reviews. Evidence includes the correlation of stronger taboos with either habitats or animals that have greater need for conservation (Colding and Folke 1997; McDonald 1977). The similarity of some resource and habitat taboos with Western conservation management approaches has also been used as evidence to support this hypothesis (Colding and Folke 2001). However, there are non-conservation reasons for taboos, such as teaching and enforcing cultural norms, toxicity of particular organisms, the maintenance of certain animals or pets, as a custom following the death of a high-ranking individual, or because of the spiritual meaning or significance of a species or place (Bhagwat and Rutte 2006). Taboos are common in traditional societies across the world and they have been found to sometimes, but not always, align with conservation actions (Bhagwat and Rutte 2006; Colding and Folke 1997). For taboos to qualify as conservation strategies, they

must not only prevent species decline and habitat degradation but also be deliberate (Smith and Wishnie 2000). The authors found weak evidence of such deliberate conservation actions. It would be useful for future tests of this hypothesis to distinguish between the objectives of a given culture or community in enforcing a taboo and the outcomes or consequences of that choice (potentially of conservation value).

TABOO AS LUXURY HYPOTHESIS

The *taboo as luxury* hypothesis predicts that the proportion of taboo plants in a given culture will be greater in communities where natural resources are abundant such that some can be spared from general use (Quiroz and van Andel 2015; Rea 1981). It also predicts that traditional societies in resource-rich areas will be more likely to employ taboos than societies in resource poor areas.

In one of the rare direct tests of the taboo as luxury hypothesis, Quiroz and van Andel (2015) compared the number of ritual plant species between Gabon, a forested country with 4700 plant species, and Benin, a country dominated by savanna with 2800 plant species. The authors showed that ritual plant species in Benin were more likely to be scarce and officially threatened than in Gabon. This provides evidence of less reliance on taboos in the resource-rich region of Gabon than in Benin. However, the scale of analysis may limit the reproducibility of these conclusions. Country-level plant species richness may not accurately account for species availability to a given community where a taboo is actually enforced, species preference by a local community, and/or the total number of *useful species* employed within a given ethnopharmacopeia. In short, this approach may not capture the “luxurious” status of resources at the local community level where species are listed as taboo or not. A more robust test of this theory would compare the proportion of taboo species between villages with different levels of species richness and availability.

Discussion

SYNTHESIS OF THE DIFFERENT THEORIES AND HYPOTHESES

We reviewed 17 major hypotheses and theories which have been used to investigate the relationship between people and plants. These hypotheses and

theories, from ethnobotany and related fields, were grouped into two main categories which correspond to two central questions of interest in ethnobotany (Table 1).

The first set of theories covers three main facets of the central question: what drives medicinal and food plant selection by local people? The first subset of these theories/hypotheses tests if plant selection is directly related to the demographic characteristics of the plants themselves, including abundance and availability (Table 1; 1.1). Each of these theories/hypotheses suggests, directly or indirectly, that the probability a given plant species is selected is a function of how many individuals of the species are available (e.g., abundance, distance to collection sites) for selection, how visible (e.g., height, life form, appearance) these individuals are, and how well the populations are functioning (e.g., growth rate). A second subset of this group asks if plant selection by local people is directly linked to their phytochemistry (Table 1; 1.2). For example, the *diversification hypothesis* (Alencar et al. 2010) asks if local people are introducing some plant species to improve the diversity of botanicals available to treat the range of diseases in their communities. The *optimal defense theory* (Mckey 1974; Stamp 2003), which is also related to both the *ecological apparency* and the *resource availability hypotheses*, suggests that the distribution of secondary chemistry within a given plant drives the selection of plant organs for medicinal purposes. While the optimal defense theory provides the framework to understand why people would select roots instead of leaves from the same plant for medicinal purposes, the *resource availability hypothesis* (Endara and Coley 2011) explains why some plant species in some habitats are used more than others. Together with the theory of non-random medicinal plant selection and its extension from a phylogenetic perspective (Saslis-Lagoudakis et al. 2014; Yessoufou et al. 2015), these theories explain how phylogenetic relatedness (e.g., belonging to the same family, genus, or botanical groups) explain medicinal plant selection.

Previous work interpreted the *apparency hypothesis* in a broader ecological sense (Albuquerque and Lucena 2005; Gonçalves et al. 2016). These authors suggest that because “apparency” can be interpreted as “abundance” (herbivores attack the most apparent/abundant species), it ought to be considered within other hypotheses developed above such as the plant value use hypothesis, the availability hypothesis, and the theory of non-random medicinal plant selection. However, we choose to separate

these hypotheses because this allows for the development of predictions to better understand the *thought process* leading to plant selection by local people rather than the pattern of plant selection. The ecological apparency hypothesis, as proposed by Feeny (1976), was more interested in explaining the differential chemical response to herbivory of groups of plants (apparent versus non-apparent) than apparency itself. From that perspective, we argue that the ecological apparency hypothesis should be tested separately from these other hypotheses.

The third subset of this group of theories/hypotheses explores how social dynamics and people's demographic characteristics (e.g., local people's age or gender) or environment (e.g., urban, rural) drive plant selection (Table 1; 1.3). For example, the *social network as driver of knowledge dynamics* hypothesis (Hopkins 2011; Reyes-García et al. 2013b) provides the framework to investigate why and how *who* an individual knows defines *what* the individual knows and how s/he selects plants for local uses. Such peer influence and how this influences transmission of knowledge will also depend on the age and gender of people within a given network. Additionally, the characteristics of the social network are likely to depend on whether a given community is rural or urban. The *age, gender, and dynamics of knowledge* hypothesis predicts how certain traits of local people, including ethnicity or socio-linguistic diversity, drive their choices.

The second set of theories/hypotheses investigates the conservation and livelihood implications of plant use (Table 1; 2). The first subset of this group of theories/hypotheses focused on the implications of plant selection on a given plant and/or cultural community (Table 1; 2.1). For example, the *utilitarian redundancy model* (Alencar et al. 2014; Nascimento et al. 2015) provides the framework to ask if plants with unique therapeutic functions are under greater harvesting pressure. The *cultural keystone species theory* (Garibaldi and Turner 2004) adds to the uniqueness criteria, with several other criteria (ethnotaxonomic diversity, use value, psycho-sociological functions) providing a novel framework to identify and understand the unique cultural importance of particular species. The second subset of hypotheses provides the framework to investigate the direct or indirect effects of traditional resource management strategies on plant conservation (Table 1; 2.2). The *taboo as luxury* hypothesis (Rea 1981; Quiroz and van Andel 2015) provides the basis to ask if creating taboo is motivated by the need to conserve or an indication

of richness in the options that local people have to use their resources. The *taboo as conservation* hypothesis suggests resource and habitat taboos serve a conservation purpose for communities.

Culture and human behavior are complex. Many of the theories/hypotheses presented here assume humans are rational and efficient in their choices, though we know human behavior is actually more complex and often culturally determined. For example, local explanatory models of health and illness as well as local understandings of kincentric relationships with other non-human organisms critically influence how, when, where, and why people collect one plant over another. Therefore, the theories/hypotheses we presented could be enriched through further integration with relevant anthropological theories related to culture and human behavior and should be tested with a strong awareness of cultural context. Furthermore, the amount of time a researcher spends in a community and the researcher's level of cultural competency can directly influence data reliability, interpretations, and one's ability to account for such cultural context. This is particularly true for studies that rely upon interview data where the level of trust, the characteristics of the person asking the question, and other contextual factors will influence the way a participant responds (Hofisi et al. 2014). Finally, although these theories/hypotheses have been presented separately, they are not always mutually exclusive and, in many cases, are complementary. For example, the availability and versatility and diversification hypotheses are complementary. It is quite possible that some species are selected as medicinal plants not only because they are available but also because they have been used for multiple purposes already. Similarly, there is synergism between selection of plants for their ecological traits and the socio-demographic traits of the local people using these plants. For example, some plant species that are abundant may not be relevant for women's health. As a result, availability will not be a strong predictor of plant selection and use for women in that case. We presented these theories/hypotheses separately for simplicity purpose. However, we encourage ethnobotanists to explore further the synergisms, complementarity, and contradictions between them.

IMPLICATIONS FOR FUTURE RESEARCH AND TEACHING IN ETHNOBOTANY

Ethnobotanical education has rightly focused on training emerging ethnobotanists in key concepts

and methods such as interviews, participant observation, free-listing, livelihood analysis, and emic versus etic approaches (Martin 2007). The potential to learn about herbal medicine, psychoactive plants, or the natural connection to land and organisms can draw students into the discipline of ethnobotany. However, our ability to keep them in this discipline is directly linked to the level of mastery they have in developing research frameworks and methods that are consistent with the scientific methods used in other disciplines. Learning the fundamental theories of a discipline is one of the first steps in understanding that discipline, generating new knowledge, and furthering the discipline's understanding of patterns and processes. We suggest that ethnobotanical education follow this strategy. While ethnobotanical courses should continue introducing concepts and methods while also providing inspirational historical accounts of the discipline, it must also clearly and deliberately expose students to the breadth of theories and major hypotheses in this field. We should further focus on the ability of students to identify the central predictions of these theories, and we should discuss how related hypotheses have been tested, which ones are yet to be tested, and why testing these new hypotheses will advance our knowledge of how and why local people select plants for medicinal, food, and cultural uses. Given that ethnobotanical programs are becoming rarer (McClatchey et al. 1999; Bennett 2005) and most ethnobotanists encounter just a limited number of ethnobotany courses, using such approaches to expose students to the theories will be instrumental for them to choose research topics, develop methodologies, and ultimately add to our collective understanding of these important issues impacting all humans, our environment, and the resources on which we depend.

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