THEORIES AND MAJOR HYPOTHESES IN ETHNOBOTANY:
CULTURAL KEYSTONE SPECIES, UTILITARIAN REDUNDANCY, ETHNOBOTANY OF
THE SHIPIBO-KONIBO, AND EFFECTS OF HARVEST ON AYAHUASCA

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For my mother and father, Anna and Michael; my daughters, Lianna and Kaya Luna; my son, Brenden; our ancestors; *la medicina*; the plant teachers; and my mentors.

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Abstract

Understanding the patterns and processes surrounding plant use has been at the forefront of ethnobotanical research since its inception. Several theories and hypotheses in ethnobotany have been proposed recently to facilitate a greater understanding of the roles culturally important plants play among human societies in addition to the factors that influence plant selection, harvest and use-pressure. Cultural keystone species are plant and animal species considered irreplaceable to cultural communities and expected to play fundamental roles in maintaining cultural community structure and cultural stability. Although this theoretical framework in ethnobotany has been proposed to help inform biological and cultural conservation strategies, it is unclear if quantitative methodologies often employed to measure or infer cultural keystone designation are adequate. Further, culturally important plant species that fulfil unique or non-redundant therapeutic functions, that are preferred and used for multiple purposes in ethnomedicinal contexts are expected to experience greater use-pressure while plant species that fulfill redundant therapeutic functions are expected to experience reduced impact or harvest pressure. Though, the major predictions surrounding species use-pressure and species functional redundancy in ethnomedicine are expected to aid defining conservation priority, our understanding of the factors that predict species use-pressure and of the effect of harvest on culturally important plants are still limited. This dissertation tested if the fundamental components of species cultural keystone designation were predicted by cultural importance indices, which factors are strong predictors of medicinal plant species use-pressure, and if the current rate of harvest of ayahuasca (*Banisteriopsis caapi)* is sustainable in a localized area of the Peruvian Amazon Rainforest. The dissertation is divided into four chapters including (1) an in-depth literature review of the cultural keystone species theory to assess how the theory has been tested over time and geographic ranges, (2) a critical assessment of the use of cultural importance indices to predict species cultural keystone designation of medicinal plant species used by the Shipibo-Konibo community of Paoyhan, (3) a test of the utilitarian redundancy model to evaluate which factors predict medicinal species use-pressure while controlling for evolutionary relatedness among plant species used by the Shipibo-Konibo community of Paoyhan, and (4) an assessment of the effect of harvest on ayahuasca *(Banisteriopsis caapi)* in a

localized area of the Peruvian Amazon region. Results have indicated most studies on cultural keystone species have occurred in North America and applied cultural keystone designation to species without a direct measure of cultural keystone status, most cultural importance indices are correlated are limited in terms of a direct measure of species cultural keystone status, and the elasticity patters of the population growth rate to perturbation of vital rates of ayahuasca (*B. caapi*) population are driven by survival of long-lived individuals in both the short- and long-term. These findings help to further our understanding of the use of cultural keystone species theory and the most common methods employed to predict species cultural status, patterns surrounding medicinal plant use with respect to the utilitarian redundancy model and the factors that predict species use-pressure, and the population dynamics of *ayahuasca*, a culturally and economically important plant species.

TABLE OF CONTENTS

List of Tables

Chapter 1: Introduction

  Investigating the patterns and processes surrounding plant species use for ethnomedicine in cultural societies offer unique insights on the interrelationships humans have developed with the natural world (Etkin, 1988a). Often, *emic* or local perceptions of plants and their roles in cultural traditions differ from the *etic* or observer's perspective and worldview (Etkin, 1988b). As such, the unique interrelationships human societies have developed with plant species highlights the biocultural diversity of the human experience. While numerous threats to biological and cultural diversity have been highlighted, such as, cultural assimilation and language loss (Davis, 2007; Maffi, 2002), globalization and erosion of knowledge (Vandebroek and Balick, 2012), habitat loss and global change (Davis, 2007; Meine et al., 2006; Pilgrim et al., 2009), there is a growing consensus that coupled adaptive management and conservation efforts seem critical for facilitating social and ecological resilience (Berkes et al., 2000; Higgs, 2005; Maffi, 2005).

  Over the last couple decades, the links between biological and cultural diversity have been investigated to develop methodologies for determining conservation priority of culturally important plant species (Albuquerque and Oliveira, 2007; Cristancho and Vining, 2004; Garibaldi and Turner, 2004). As a result, several theories and hypotheses have been developed to further our understanding of local ethnomedicinal use patterns and processes (Gaoue et al., 2017) and their potential to help facilitate biocultural conservation (Albuquerque and Oliveira, 2007; Cuerrier et al., 2015; Garibaldi and Turner, 2004). Though these theoretical frameworks have long been proposed, few studies thoroughly examine and test their major predictions. Thus, the second chapter of this study consists of a literature review on the cultural keystone species theory, a theoretical framework in ethnobotany aimed at identifying plant species that are integral to the identity of cultural groups. Further, the second chapter focuses on how this theoretical framework has been tested over time and geographic ranges as well as methodologies often employed for cultural keystone species designation. The third chapter tests if quantitative techniques such as, cultural importance indices are strong predictors of cultural keystone species designation. The fourth chapter investigates the utilitarian redundancy model, a theoretical framework in ethnobotany proposed to aid in defining conservation priority, and tests which factors are strong predictors of medicinal species use-pressure. The fifth chapter seeks to identify the effect of harvest on ayahuasca (*Banisteriopsis caapi)*, a culturally and economically

important plant species employed for ethnomedicine, in a localized area of the Peruvian Amazon Rainforest.

Preliminary fieldwork for this study began in 2014 in Iquitos, Peru. Interviews were conducted with local experts and harvesters to assess the wide-spread use of medicinal plants in the Peruvian Amazon region and harvesting practices linked to ayahuasca harvest. Follow-up fieldwork was conducted between in May 2017 and July 2018 with several Shipibo-Konibo communities that live along the Ucayali river of Peru. The majority of the data collection for Chapter 3 and Chapter 4 was done in the Shipibo-Konibo community of Paoyhan which primarily consisted of semi-structured interviews, focus group discussions and other ethnobotanical methods discussed in sections below. In Chapter 5, I assessed the effect of harvest on ayahuasca (*B. caapi)* where I conducted several demographic censuses with Shipibo colleagues, and independent researchers and volunteers from a local non-profit organization *Alianza Arkana*. Demography on ayahuasca was conducted in a Shipibo-Konibo community territory that will remain nameless due to the cultural and economic importance and use-pressure linked ayahuasca harvests. These interviews, discussions, and demographic assessments revealed a growing concern and interest in determining the sustainable harvest limit of ayahuasca due to locally perceived scarcity of the vine used in preparation of ayahuasca, a psychoactive decoction used in healing contexts and ethnomedicinal practices throughout the Amazonian region (Coe & McKenna, 2017; Luna & White, 2000). Additionally, due the globalization and wide-spread use of ayahuasca, this work sought to provide data to local stakeholders in efforts to aid in the development of a community-driven forest management plan. Interview and focus group data revealed the wide-spread use of many plant species in Shipibo-Konibo ethnomedicine in healing contexts, the use-pressure linked to these species, and their therapeutic roles and functions from a local perspective. Additionally, numerous medicinal plant species used in Shipibo-Konibo ethnomedicine were identified that are thought to be culturally important and becoming rare at local level.

The Shipibo-Konibo consist of approximately 50,000 indigenous peoples living along the Ucayali river and its tributaries. They are often recognized for their textile and artesian (*artesania*) works, vast knowledge of medical plant species, and use of ayahuasca in ethnomedicinal contexts (Brabec de Mori, 2013). The community of Paoyhan consists of approximately 2000 Shipibo-Konibo whom rely primarily on harvesting non-timber forest

products, artesian works, and logging secondary forests in community territory for local livelihoods. While the widespread harvest of medicinal plants and logging of community territory has positively impacted some Shipibo-Konibo communities including Paoyhan, the potential for overharvesting and depletion of natural resources in the Ucayali region remains persistent. Many Shipibo-Konibo who live in Paoyhan also have family in neighboring cities such as Yarinacocha and Pucallpa whom they rely on for aiding in supplemental income by marketing and selling of NTFPs and locally hand crafted textiles from the community. Further, the globalization and widespread use of ayahuasca is impacting the local livelihoods of the Shipibo-Konibo in the area with plant specialists locally known as *maestros* or *maestras* becoming well-known and respected for providing both short and long-term ethnomedicinal treatments with ayhahuasca and other medicinal plants to local and non-indigenous participants. This phenomenon is providing income to some Shipibo-Konibo and their communities. Thus, it is expected that there is an increase in harvest of *B. caapi* with the large-scale production of ayahausca, yet a clear understanding of the socio-ecological impacts that result due to increased use and harvest of plants employed for traditional ethnomedicine is currently lacking. Further, although these livelihood strategies have allowed for many Shipibo-Konibo in Paoyhan to provide for their families, many people in the community are concerned for the future of their people due to challenges faced in the contemporary world.

This study was inspired by a community driven-workshop on local perceptions of global climate change where fellow volunteers and colleagues from *Alianza Arkana* and I worked with Shipibo-Konibo in Paoyhan to identify concerns and challenges linked to global change and potential approaches to aid in community resilience. As such, fieldwork for this study was specifically aimed to be less extractive in that research objectives were aimed to coincide with needs and future goals identified by community members of Paoyhan during the workshop. Several objectives defined by the Shipibo-Konibo community were documenting the local medicinal plant use and harvest patterns as well as ways to help provide medicinal plant knowledge for youth and other members of the community. Thus, medicinal plant data from this work was also used to help aid in the development of a Shipibo-Konibo managed botanical garden, the living indigenous pharmacy *(La Farmacia Viva Indigena),* aimed at facilitating cultural resilience, transfer of local ecological knowledge, and subsistence strategies.

Chapter 2: Cultural Keystone Species revisited: Are we asking the right questions?

2.1. Introduction

Two decades ago, ethnobotanists proposed the cultural keystone species concept, an ethnobotanical theoretical framework (Gaoue et al., 2017) as complementary approach for conservation of social and ecological systems (Cristancho and Vining, 2004; Davic, 2004; Garibaldi and Turner, 2004; Platten and Henfrey, 2009). Cultural keystone species are "*culturally salient species that shape in a major way the cultural identity of a people, as reflected in the fundamental roles these species have in medicine, materials, diet, and/or spiritual practices*" (Garibaldi and Turner, 2004) or "*species whose existence and symbolic value are essential to the stability of a cultural group over time*" (Cristancho and Vining, 2004). Cultural keystones are often embedded within social and ecological systems where they are thought to play critical roles in maintaining cultural or ecological stability at a local level (Garibaldi and Turner, 2004). Cultural keystones are expected to affect culture, language, and to be irreplaceable therefore, the loss of these species is predicted to have a significant effect on cultural integrity and equilibrium compared to other species that are likely to have little or no effect. In this context, the loss or removal of cultural keystones from their sphere of influence or *ethnosphere* is expected to result in significant cultural community disruptions (Cristancho and Vining, 2004; Garibaldi and Turner, 2004; Winter and McClatchey, 2009).

Several parallels between cultural and ecological systems have been highlighted in efforts to help define conservation priority and provide a platform for an in-depth understanding of the significant roles cultural keystones can play among cultural societies and ecological systems. Garibaldi and Turner (2004) proposed a synthesis of the cultural keystone species theory within an ecological context by suggesting "*a decline in biological diversity often means a loss of cultural diversity*." The premise of this argument is rooted in the *ecological keystone species* concept which suggests that '*all species are not created equal*' and the loss of these species will significantly affect ecosystem function and stability (Walker, 1992). Further, the ecological keystone species theory was founded on the idea that effective conservation efforts likely depend on understanding the underlying mechanisms by which keystone species play critical roles maintaining stability of their respective ecosystems (Power et al., 1996; Simberloff, 1998). While conservation approaches historically focused primarily on ecosystem processes,

4

fundamental components often overlooked are the cultural implications of keystones— which the cultural keystone species concept aims to address. In highlighting relationships between cultural and ecological domains, Garibaldi and Turner (2004) posed the idea that certain keystone species are likely to occupy similar functions in both cultural and ecological systems. Thus, suggesting an explicit interconnection between socio-cultural-ecological systems where the functional role cultural keystones are expected to play within the community structure and stability of human societies is analogous to that of the ecological role of keystone species (Garibaldi and Turner, 2004).

It is important to mention noted limitations of the ecological keystone theory have long been discussed. There have been persistent calls to action for a functional consensus definition (Garibaldi and Turner, 2004; Mills et al., 1993; Power, et al., 1996; Simberloff, 1998) as well as standardized approaches to identify ecological keystones and to quantify the extent to which a given species has an effect on a particular community or ecosystem trait (Berlow et al., 1999; Power et al., 1996), However, the notion that there is a link between identifying ecological keystones and conservation has become popular in the literature (see for example Kotliar, 2000; Power et al., 1996; Simberloff, 1998). Developing successful conservation and restoration plans likely depends upon understanding the socio-ecological components such as cultural knowledge (Higgs, 2005) and an in-depth understanding keystone species function (Garibaldi & Turner, 2004). However, the parallels between critical roles keystone species are predicted to play concomitantly in social and ecological systems have been criticized (Nuñez and Simberloff, 2005; Platten and Henfrey, 2009) and a robust test of these predictions has yet to occur. Our understanding of socio-ecological dynamics of keystone species function and their potential to facilitate biocultural conservation remains limited.

While the overall objective of the cultural keystone species theory is to provide a complementary framework that highlights the mechanisms underlying interrelationships between biological and cultural diversity, discussions surrounding the functional roles of keystones among human societies has been the primary focus in ethnobiological and anthropological research. Researchers have long highlighted the *importance* of keystones in cultural societies yet a global synthesis on the effect of keystone species function in terms of the stability of both cultural and ecological domains is lacking as is a standardized and objective approach in identifying keystones.

To identify cultural keystone species Cristancho and Vining (2004) as well as Garibaldi and Turner (2004) proposed several criteria to determine whether a given species qualifies for keystone designation including: (1) intensity, type, and multiplicity of use, (2) species abundance, (3) naming and terminology associated with a given species, (4) species irreplaceability, (5) species use in trade or resource acquisition, (6) species psycho-socio-cultural function (e. g., symbolism, knowledge transmission, etc.) and (7) a high level of importance. Although these criteria aim to provide a framework for researchers to clearly identify cultural keystone species, accurately measuring and defining species cultural keystone status has proven challenging. Aside from highlighting criteria for cultural keystone designation, Cristancho and Vining (2004) have yet to provide a clear methodology (qualitative or quantitative) to measure cultural keystone status. In contrast, Garibaldi and Turner (2004) proposed the use of the index of cultural significance (ICI) to determine whether a given species qualifies for keystone designation. Subsequently, the use of cultural important indices which are expected to measure the *importance of the role a given plant and or animal species plays within a particular culture* (Hunn, 1982), have often been used by ethnobiologists to predict cultural keystone status. These approaches have been criticized (Platten and Henfrey, 2009) as they have yet to provide reliable and reproducible results in identifying cultural keystone species. Consequently, it is unclear whether there is support for the theory or how much progress has been made over the last several decades in terms of testing the theory as well as its use by researchers to determine the keystone status of a given species.

Here I explore the way in which researchers have been studying cultural keystone species. This review provides a retrospective examination of the cultural keystone species theory while posing a call to action for the development of novel approaches for keystone designation. I ask if most studies, rather than testing the link between species cultural keystone status and the functional role cultural keystone species are expected to play in maintaining cultural community strtucture, directly identified cultural keystone species without a robust measure of species cultural keystone status. I explore how the utilization of the cultural keystone species theory has changed over time and across continents to identify any gaps of knowledge that warrant further considerations. I highlight how far researchers have come in providing a direct test of the cultural keystone species theory, prior methods used for keystone designation, and encourage a critical examination of how the theory may be used in examining the links between human

environmental impacts effecting biological diversity. This review aims to address the following questions including (1) How has the cultural keystone species theory been tested over time and space? (2) How has cultural keystone designation been predicted? and (3) What have been the limitations of prior studies that have tested the cultural keystone species theory?

2.2. Methods

I conducted a systematic literature review using 473 peer-reviewed publications on cultural keystone species theory from 2003 to 2016. Publication search was conducted in January 2016 using the key words *"Cultural Keystone Species"* in PoP (Publish or Perish) software which aims to retrieve and analyze academic citations (Harzing, 2007). This search was refined to 409 publications through critical systematic review and exclusion processes discussed below. The literature review as well as the approach used to extract data is described in Table 2.1.

Table 2.1. Methodology for data collection/exclusion.

Steps	Procedure	Results
Data Search	Peer-reviewed article database search on PoP - Publish or Perish (Harzing, 2007) using key words "Cultural Keystone Species."	Title, abstract, and keyword information for 473 articles correlated with initial search.
Data Review	Screening the title, abstract, keywords, methods, and publication format to exclude those not relevant to study.	409 articles aligned with study/search criteria following screening procedure
Data Collection	Downloaded and gained full text access to all that were relevant.	409 downloaded full text with 18 with no access
Data Refinement	Key word search articles for cultural keystone species using finder option. Additionally, read publications that specifically focus on / test cultural keystone species criteria defined by Turner & Garibaldi (2004) and Cristancho & Vining (2004).	409 articles were relevant to study criteria.
Data Classification	Systematic classification of the 409 relevant articles using 5 defined criteria (randomly cited, test of theory, mention concept, mention species as cultural keystone, review of the theory / concept) integral to gaining insight on the use/application of cultural keystone species theory.	Dataset of 5 defined criteria for each relevant article
Data Analysis	Summarize and analyze data.	Citation of theory over time

The categories for data collection were chosen and defined by the authors to extract data pertaining to this study. These criteria include (1) the *authors mention a species or several species as cultural keystones* in lieu of measuring cultural keystone status, (2) the *authors solely mention the concept of cultural keystone species* rather than discussing a given cultural keystone or measuring keystone status, (3) the authors *review the cultural keystone species concept*, (4) the *authors cite a paper* on or discussing cultural keystones rather than the criteria mentioned above, and (5) the *authors explicitly measure cultural keystone status* and thereby test the theory. Additionally, cited methods employed for a direct test of the cultural keystone species theory were classified into seven categories including (1) *index of cultural significance* (ICI) adapted from Garibaldi and Turner (Garibaldi & Turner, 2004), (2) *use-value index* (UV) adapted from Philips and Gentry (1993), (3) *word counts* (WC), (4) *cultural value index* (CV) adapted from Reyes-García et al. (2006), (5) *multivariate frequency analysis* (MFA), (6) *cultural significance index* (CSI) following Silva et al. (2006), and (7) *participant consensus* (PC). All relevant publications were classified based on data.

2.3. Results

2.3.1 Cultural Keystone Species Theory Over Time and Space

A total of 4.4% of the studies that have mentioned the words *"Cultural Keystone Species"* have tested the theory, 1.7% reviewed the theory, 29.6% cited a paper on cultural keystones, 16.8% mentioned the cultural keystone concept and 47.4% mentioned a given cultural keystone without explicitly measuring keystone status (Figure 2.1).
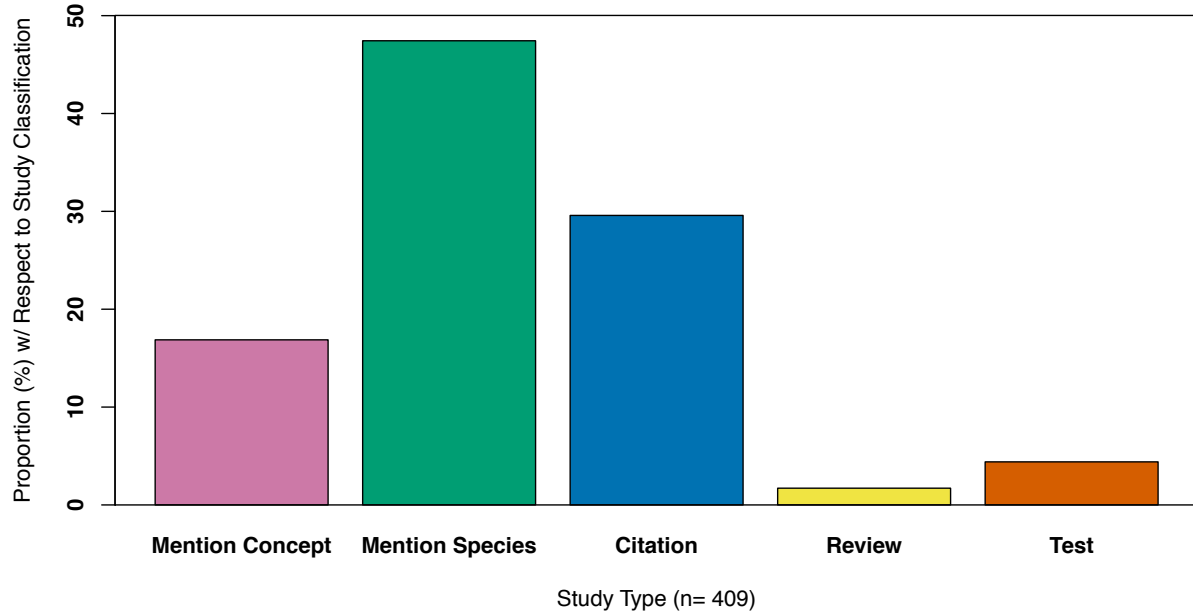
Figure 2.1. Proportion of Studies linked to study type classification (n = 409). Study type classifications include (1) studies that solely mention the cultural keystone species concept, (2) studies that mention a given species as a cultural keystone species without a direct test or measure of species cultural keystone status, (3) studies that cite a paper on or that discusses the cultural keystone concept, (4) studies that review the cultural keystone species concept and (5) studies that provide a direct test or measure of species cultural keystone status.

Over time the cultural keystone theory has gained momentum with respect to the study type. Publications that have solely *mentioned a given species* as a cultural keystone, publications that *cited* a given paper on cultural keystones, and publications that *mentioned the cultural keystone concept* have gradually increased over ten years (2003-2013) (Figure 2.2). However, these study types have been declining since 2013. Publications that *reviewed or tested* the cultural keystone species theory have remained low throughout the study period (Figure 2.2) suggesting most studies have mentioned a given species as a cultural keystone, cited papers on cultural keystone species, or mentioned a cultural keystone species while few studies have provided a direct measure of species cultural keystone status or have reviewed the cultural keystone species theory (Figure 2.2).
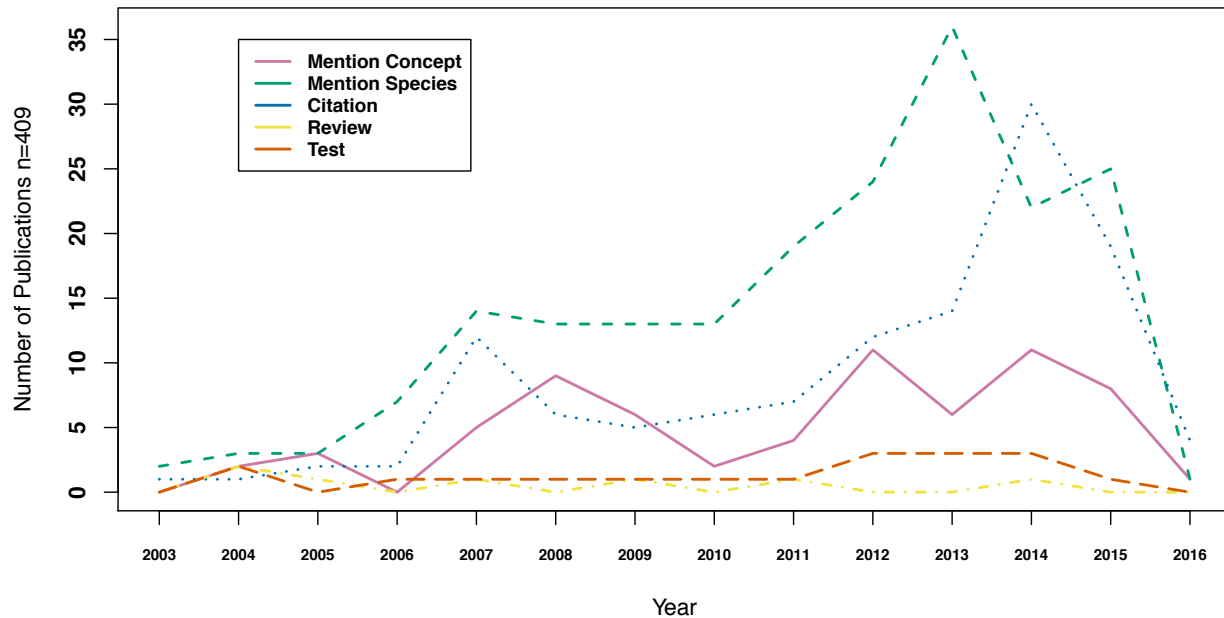
Figure 2.2. Number of publications on Cultural Keystone Species over time (2003-2016) available from Publish or Perish software (n = 409). Publication types include (1) studies that solely mention the cultural keystone species concept, (2) studies that mention a given species as a cultural keystone species without a direct test or measure of species cultural keystone status, (3) studies that cite a paper on or that discusses the cultural keystone concept, (4) studies that review the cultural keystone species concept and (5) studies that provide a direct test or measure of species cultural keystone status.

The regional differentiation analyses included 238 articles (59%) out of the total number of studies (N=409). Data for region was not available for 171 articles (41%) and subsequent analyses. However, these data were available for all direct tests of the cultural keystone species theory. Globally, most studies to date have mentioned cultural keystone designation (86%, 203 articles total) for a given species without testing the theory (Figure 2.3). For example, most studies conducted in Australia listed a given species as a cultural keystone species (12.3%, 25 articles) whereas few studies in this area have tested the cultural keystone species theory (11%, 2 articles). Most studies that tested the cultural keystone species theory occurred in North America (33%, 6 articles). North America also had the greatest number of studies in total (126 articles) with 56% (114 articles) solely mentioning a species as a cultural keystone species, 33% (4 articles) solely mentioning the cultural keystone species concept, 66% (2 articles) solely citing a paper on cultural keystone species and no review papers on the cultural keystone species theory (Figure 3). This suggests, regardless of classification criteria for study type, most studies on

cultural keystone species have been conducted in North America —which is not surprising considering North America was where the cultural keystone species theory originated. In contrast, the fewest number of studies on cultural keystone species in total (13 articles) occurred in Africa with 5.4% (11 articles) solely mentioning a species as a cultural keystone species, 16.7% (2 articles) that solely mention the cultural keystones species concept, and no studies that cited, reviewed or tested the cultural keystone species theory suggesting the diversity of studies investigating cultural keystone species on certain continents such as Africa, Australia, and Europe is limited (Figure 2.3).

Figure 2.3. Regional distribution of Study Classifications linked to cultural keystone species theory (n = 238). Study classifications include (1) studies that solely mention the cultural keystone species concept, (2) studies that mention a given species as a cultural keystone species without a direct test or measure of species cultural keystone status, (3) studies thatcite a paper on or that discusses the cultural keystone concept, (4) studies that review the cultural keystone species concept and (5) studies that provide a direct test or measure of species cultural keystone status.

Studies that provided a direct test (n=18) of the cultural keystone species theory used a variety of methodologies to identify cultural keystone species (Figure 2.4). Several methodologies have been used concurrently including the use-value index (UV) adapted from Philips and Gentry (1993) and the index of cultural significance (ICI) adapted from Garibaldi and Turner (2004) or

the index of cultural significance (ICI) combined with participant consensus (PC). This was always the case with respect participant consensus (PC), which was often used (5 articles, 28%) in conjunction with cultural importance indices or was a component of a given index (Butler et al., 2012; Garibaldi and Straker, 2009; Jackson and Jain, 2007; Quave and Pieroni, 2015; Shrestha, 2013). Most authors (61%, 11 articles) cited the use of the index of cultural significance (ICI) to infer cultural keystone status. The use-value index (UV) was used for keystone designation in 22% (4 articles) of studies that tested the cultural keystone theory. Word counts (11%, 2 articles) were either used by themselves (Garine, 2007) or in addition to the proportion of participants that mentioned a given species for keystone designation (McCarthy et al., 2014; Figure 2.4). Several authors cited other indices of cultural importance including the cultural value index (CV) (5.5%, 1 article) and the cultural significance index (CSI) (5.5%, 1 article) to infer cultural keystone status. Finally, one author cited multivariate frequency analysis (5.5%, 1 article) for keystone designation (Figure 2.4)
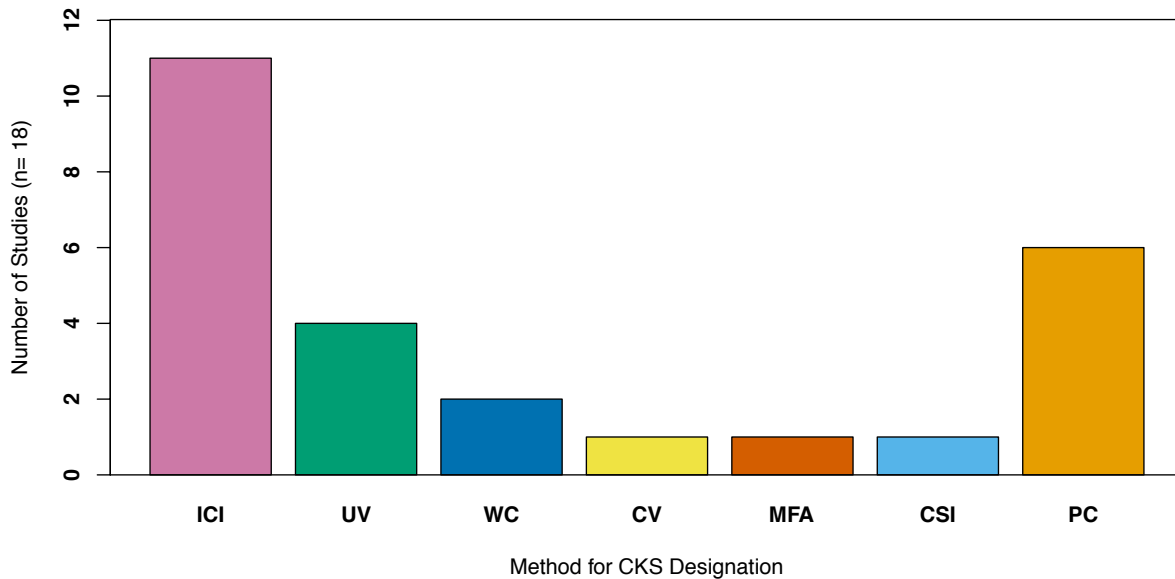
Figure 2.4. Methods commonly employed for a direct test of CKS theory (n = 18). Methods include the index of cultural significance (ICI), the use-value index (UV), word counts (WC), the cultural value index (CV), multivariate frequency analysis (MFA), the cultural significance index (CSI), participant consensus (PC).

2.4. Discussion

I showed how the cultural keystone species theory has been tested and applied on both a temporal and spatial scale. Since Cristancho and Vining's (2004) and Garibaldi and Turner's (2004) elaboration on cultural keystone species concept as well as its proposed application, the theoretical framework has clearly gained momentum over time and been tested across geographic ranges.   Although it is expected most studies that tested the cultural keystone species theory occurred in North America where the idea of proposing a direct measure of keystone designation originated (Garibaldi and Turner, 2004), it is surprising to note the lack thereof or a limited direct test of the theory in continents such as Africa, South America, and Europe — especially given that certain culturally important plant species in regions such as these have been shown to be deeply rooted in cultural community structure and local livelihoods (Gaoue and Ticktin, 2009; Schmidt et al., 2015). This suggests over time these areas and moreover the cultures linked to them are largely understudied with respect to cultural keystones. Further, the total number of studies that have provided a test of the cultural keystone theory are rather limited (less than 5%) as supported by Figure 2.1 while most studies to date have either mentioned the cultural keystone species concept or species related to it (~ 50%) (Figure 2.3). This supports my initial prediction and brings into question, *"why a direct test of the cultural keystone species is rare?"*

2.4.1. Testing the Theory

Although it may be expected the index of cultural significance proposed by Garibaldi and Turner (2004) would serve as an exclusive approach to designate keystone status based on the reproducibility, results indicate the lack of consistent approaches employed for measuring keystone status (Figure 4). For example, numerous studies did not explicitly identify cultural keystones based measuring all the proposed indicators of cultural keystone status. Instead, researchers often focused on measuring one to several keystone criteria (see for example Barnes, 2008; Garnie, 2007; McCarthy et al., 2014) to infer keystone designation. Further, most designated keystones were defined as such primarily based on researcher judgement or inference without a direct test of the theory (see for example Downing and Cuerrier, 2011; Farina, 2008; Gelcich et al., 2006; Hill et al., 2010; Lefler 2014; Loring and Gerlach, 2009; see also Figure

2.1). This brings into question, *"What methods are most used and appropriate for cultural keystone species designation?"*

2.4.2. Qualitative approaches

There is no doubt that qualitative approaches provided in-depth understanding of complex systems on a local scale (Drury et al., 2011). Although several researchers that tested the cultural keystone species theory primarily focused on qualitative data alone to infer keystone status (see for example Cristancho and Vining, 2004; Garine, 2007; McCarthy et al., 2014), it is unclear what these approaches may yield in the long-term with respect to reproducibility and global syntheses and application in conservation biology. Given the broad application of methods employed to investigate the cultural keystone species theory, it is important to consider the overarching goals of a given study as they may not be focused on the application of the cultural keystone species theory for conservation approaches or global inferences. Perhaps arguments could be made for whether cultural keystone status is best observed at a local level through qualitative methodologies often employed by anthropologists or for whether the theoretical framework could be adequately applied on a broader scale through standardized quantification often employed by interdisciplinary and natural scientists. Regardless of these approaches it is important for researchers to acknowledge potential biases of the methods employed. This highlights fundamental challenges in terms of testing the cultural keystone species theory, determining keystone status and its application in conservation. While discussions surrounding the appropriate use of qualitative and quantitative methods in conservation biology has become widespread, it has often been suggested that interdisciplinary approaches involving complementary frameworks from both social and natural sciences may yield sound results (Drury et al., 2011; Fox et al., 2006).

2.4.3. Quantitative Indices

The use of quantitative indices to measure the cultural importance of a given species is widespread in ethnobotany (Albuquerque et al., 2014; Medeiros et al., 2011). Although the primary aim of these indices is to estimate species *cultural importance* (see for example Lajones & Lemas, 2001; Reyes-García et al., 2006; Silva et al., 2006; Stoffle et al.,, 1990; Thomas et al., 2009; Turner, 1988), several of them were used to predict cultural keystone status (Butler et al.,

2012; Quave & Pieroni, 2015; Shrestha, 2013; see also Figure 4), For example, Garibaldi and Turner (2004) were the first to propose a standardized methodology for predicting keystone status through the use of the index of cultural significance. This index including subsequent versions were the most widely used approach to test if a given species qualifies for keystone designation (see Assis et al., 2010, Brandt et al., 2012; Garibaldi and Straker, 2009; Franco et al., 2014a, b; Jackson and Jain, 2006; Salazar et al. 2012; Uprety, 2013; Uprety et al., 2013; Wello, 2008; see also Figure 4). Although this index may yield interesting results, a significant limitation of its suggested use is the potential for incorporating researcher biases in terms of directly assigning value or scores to the predictors of keystone designation (see Tardío and Pardo-De-Santayana, 2008; Thomas et al., 2009). Directly assigning value or weight to the indicators of cultural keystone designation may not accurately account for the emic (view from an individual within a given culture) perspective in terms of cultural keystone species designation. Again, this highlights the importance of considering the reliability of the data collected given the methods employed.

Several authors have acknowledged the limitations of Garibaldi and Turner's index and modified it to account for participant consensus (Garibaldi and Straker, 2009; Jackson and Jain, 2006) or used it in conjunction with the use value index adapted from Philips and Gentry (1993) in attempts to maximize objectivity (Franco et al., 2014a, b). Whereas other authors have employed preferential ranking as well as the cultural value index (Shrestha, 2013) adapted from Reyes-García et al. (2006), the clutural significance index (Butler et al., 2012) folowing Silva et al., (2006), or the use value index by itself (Castellanos Camacho, 2011; Quave and Peroni, 2015) to predict species cultural keystone status. These approaches yielded mixed results (Jackson and Jain, 2006) in identifying cultural keystone species. Therefore, the use of cultural importance indices alone may not be sufficient to measure species cultural keystone status (Garibaldi & Straker, 2009). Further, there is no consensus among researchers on robust approaches to predict cultural keystone status. Given the conservation implications of the cultural keystone species theory, the development of novel approaches for keystone designation as well as an engaging dialogue among researchers in terms of reproducible results stemming from robust methods seems critical.

2.4.4. Call to Action

As demonstrated above, cultural importance indices were most often used to predict species cultural keystone status. It is important to consider the appropriate use of a given index based on the questions addressed and or hypotheses being tested (Hoffman and Gallaher, 2007). Given cultural importance indices were originally defined to quantify species cultural values it is critical to consider their intended use rather than a panacea used to infer cultural keystone status. Although Cristancho and Vining (2004) included a high level of cultural importance in their proposed keystone designation criteria, a critical examination of cultural importance indices seems warranted as it is unclear if these indices are explicitly measuring all the criteria for cultural keystone designation. Further, alike noted criticisms of the ecological keystone species theory, a robust standardized methodology for predicting cultural keystone status is clearly lacking. Developing robust methodologies is a critical step toward a paradigm shift in terms of how this theoretical framework is applied. Therefore, I pose the question, *"Are word counts, use values, participant consensus, or cultural importance indices alone sufficient to predict keystone status?"*

Some authors concluded that the inherent value in the cultural keystone species concept is merely a *'process of exploration'* rather than the quantification of cultural significance (Jackson and Jain, 2006), whereas others have continued to support the idea that it is useful tool for conservation and restoration (Uprety et al., 2013). Whether researchers employ qualitative, quantitative, or both methodologies for keystone designation it is clear there are limitations, potential biases, as well as advantages in these approaches. In light of these results and in efforts to contribute to the ongoing debate, I ask, *"if researchers are solely using the cultural keystone designation to suggest the conservation of plants,* (Garibaldi and Turner, 2004) *animals,* (McCarthy et al., 2014)*), insects* (Salazar et al., 2012), *or places* (Cuerrier et al., 2015)*?"* I argue if progress is to be made in identifying cultural keystone species, then it is critical for researchers to approach the cultural keystone species theory in a serious systematic way—to think critically about how to accurately define and measure cultural keystone designation.

Chapter 3: Most cultural importance indices do not predict species cultural keystone status

3.1. Introduction

Understanding the risks posed by the increasing rate of species extinction on the cultural integrity of coupled human-natural systems is critical for facilitating bio-cultural adaption in a context of a changing world. Medicinal plant substitution is one strategy widely used by cultural groups to cope with ever changing environments or colonization events. Ideally, such botanical substitutions must be made without disrupting the efficacy or cultural significance of traditional ethnomedicine. Our understanding of the importance, moreover of the cultural keystone status, of most medicinal plant species is limited. It is expected that identifying Cultural Keystone Species (CKS) will aid in prioritizing conservation approaches and in the development of culturally sound and ecologically appropriate conservation programs. cultural keystone species, "culturally salient species that shape in a major way the cultural identity of a people," (Garibaldi and Turner, 2004) are plant species considered absolutely paramount to the structure and survivability of community or cultural identity. The theory of cultural keystone species implies that the loss of cultural keystones would have a significant effect on cultural integrity and equilibrium compared to other species that are likely to have little or no effect (Cristancho and Vining, 2004; Gaoue et al., 2017; Garibaldi & Turner, 2004) and that these species are likely to be irreplaceable. Cultural keystone species are predicted to have *high use values*, species use in trade or *resource acquisition*, species *function* within the *psycho-socio-cultural* structure of a particular group, species *cultural irreplaceability*, *ethnotaxonomic diversity,* and a *high level of importance* (Berlin, 1992; Cristancho and Vining, 2004; Garibaldi and Turner, 2004). Identifying cultural keystones has proven challenging. The use of cultural importance indices, which are expected to quantify the cultural salience or importance of a particular species in a given culture (Hunn, 1982), have become widespread in in the field ethnobotany (Albuquerque and Oliveira, 2007; Bennett and Prance, 2000; Garibaldi and Turner, 2004; Lajones and Lemas, 2001; Pardo-de-Santayana, 2003; Phillips and Gentry, 1993; Reyes-García, et al., 2006; Silva, et al., 2006; Stoffle et al., 1990; Tardío and Pardo-De-Santayana, 2008; Thomas et al., 2009; Tudela-Talavera et al., 2016; Turner, 1988). These indices are commonly employed to infer cultural keystone species status (Garibaldi and Turner, 2004; Lajones and Lemas, 2001; Platten

& Henfrey, 2009; Quave and Peroni, 2015; Silva et al., 2006; Stoffle et al., 1990). However, these approaches have been criticized for their limited predictive power and failure to yield reliable and reproducible findings (Tardío & Pardo-De-Santayana, 2008; Platten & Henfrey, 2009; Thomas et al, 2009) and it is unclear how these indices are related and if they are robust measures of species cultural keystone status.

To date, a total of 87 quantitative indices primarily based on *informant consensus*, *subjective allocation*, and *uses totaled* have been employed to assess the overall importance of a given plant species to human societies world-wide (Medeiros et al., 2011). Although researchers may employ one to several indices in attempt to quantify species cultural importance or to infer cultural keystone species designation (Franco et al. 2014a, b), it is critical to thoroughly understand the assumptions made when employing quantitative indices to analyze data linked to local knowledge as cultural systems are often multi-dimensional in their complexity. Given these indices are estimated using similar parameters, it is expected that most of them will be correlated among each other. Further, whether these indices are strong predictors of species cultural keystone status remains unclear. Understanding the predictive power and limitations of cultural importance indices may aid the appropriate use of quantification for hypothesis testing in ethnobotany and facilitate sound decisions on community driven conservation efforts.
In this study, I investigated twelve indices proposed to measure cultural importance (Albuquerque et al., 2006; 2014; Garibaldi and Turner, 2004; Hoffman and Gallaher, 2007; Freidman et al., 1986; Lajones and Lemas, 2001; Pardo-de-Santayana, 2003; Phillips and Gentry, 1993; Reyes-García, et al., 2006; Silva et al., 2006; Stoffle et al., 1990; Tardío and Pardo-De-Santayana, 2008; Thomas et al., 2009; Tudela-Talavera et al., 2016; Turner, 1998). I test whether or not these indices are strong predictors of species cultural keystone status as defined by (Cristancho and Vining, 2004; Garibaldi and Turner, 2004). In addition, I examine similarity between indices, and discuss possible shortcomings with respect to the use of these quantitative indices alone as a measure of species cultural keystone status, and propose a means to provide a direct measure of species cultural keystone status.

3.2. Study Area

The present study was undertaken in a Shipibo-Konibo native community of Paoyhan located in the Peruvian Amazon along the Ucayali River (07° 50.941'S, 075°00.800'W). The

Shipibo-Konibo community (Comunidad Nativa de Paoyhan) is located along the banks of the Ucayali River, Province of Ucayali, department of Loreto, Peru. The climate is tropical with a mean annual temperature of 26.4°C (Kottek et al., 2006), an annual rainfall of 1600mm and the community is approximately 132.3m above sea level (Casimiro et al., 2013). This Shipibo-Konibo community consists of approximately 2000 inhabitants belonging to the Pano-linguistic family stemming from several ethnic backgrounds that have long inhabited the Ucayali River. Livelihood strategies employed by the community are primarily focused on logging secondary forests and harvesting of non-timber forest products in community territory that are sold around the city of Pucallpa.

3.3. Methods

The goal of the data collection was to estimate the 12 indices of cultural importance to compare them and to estimate a cultural keystone status score for each species cited by participants. Ethnobotanical data were collected using free-listing to measure the frequency of plant use and to collect the data to estimate each index of cultural importance. To do so, participants were first asked to first mention the names of the medicinal plants that they use for healing. In a complementary approach to free-listing, open and semi-structured interviews (Albuquerque et al., 2014) were also held between June and September 2017 to gather data to quantify the cultural keystone status for each plant species mentioned and to estimate their local importance. Participants consisted of experts as well as those with generalized knowledge. Interviews were either conducted in Shipibo, Castellano, or both depending on the preferred dialect of the participant. When necessary, terms or questions were translated into English, Castellano or Shipibo with the help of both native and non-native field assistants to facilitate communication (see Appendix A-2). A total of 30 participants (13 men and 17 women) were interviewed. I adopted the following protocol to respect intellectual property rights: prior to each interview, introduced myself, explained the objectives of my research, and asked each participant for permission to record the interview (Ferreira et al., 2012). Participation was voluntary, in accordance with University of Hawaii at Manoa IRB (CHS#23611), and all participants were at least 18 years old. Prior to each interview, I obtained free and prior informed consent. Participant

observation was employed to allow for a more enriching data collection (Albuquerque et al., 2014).

As part of the interview process, a *walk in the woods* approach (Albuquerque et al., 2014) with one or more participants was employed to observe medicinal plants *in situ* and to collect botanical specimens cited by participants during free-listing or interviews. Medicinal plants cited by participants were identified and deposited in the UNAP (Universidad Nacional de la Amazonia Peruana) Herbarium. During the interview process and the *walk in the woods*, medicinal plant data on the following categories were collected including: species naming and terminology or ethnotaxonomic diversity (Berlin, 1992) in Castellano and Shipibo, species uses, species irreplaceability (probability of a species can be substituted to fulfill the same function), quality and frequency of uses, species management, species use preference, species availability, plant part used, extent to which the species provides resource acquisition (species sold or traded), species psycho-socio-cultural function (species spiritual role, use in ritual and rites of passage, role in transmission of knowledge, species stories or myths, and whether species has an spirit or anthropomorphic form), species life-form, species origin, and species collection locality. These data were used to calculate the twelve cultural importance indices and cultural keystone status score for each species mentioned below. To do so, for each plant species cited during free-listing participants were asked questions on the following topics including (1) local name for a given plant, (2) species uses, (3) species substitution to fulfil the same therapeutic function (4) frequency of use, (5) species management, (6) species preference, (7) harvest availability, (8) harvest location, (9) plant parts used, (10) species use in traded (or sold), (11) species psycho-socio-cultural function, (12) quality of species use.

Using data collected from interviews, free-listing, and the *walk in the woods*, the local importance of each species cited was calculated using the following 12 indices of cultural importance: Index of Cultural Significance (Turner, 1988), Fidelity Level index (Friedman et al., 1986), Ethnic Index of Cultural Significance (Stoffle et al., 1990), Use-Value index (Albuquerque et al., 2006) modified from (Phillips and Gentry, 1993), Relative Frequency Citation index (Bennett and Prance, 2000; Tardío and Pardo-De-Santayana, 2008), Ethnobotanical Importance Value Index, (Lajones & Lemas, 2001), Relative Importance index (Pardo-de-Santayana, 2003; Tardío & Pardo-De-Santayana, 2008), Cultural Value index (Reyes-García et al., 2006), Cultural Significance index (Silva et al., 2006), Cultural Importance index

(Tardío and Pardo-De-Santayana, 2008), Quality Use Value Agreement index (Thomas et al., 2009), and the Cultural Significance and Conservation index (Tudela-Talavera et al., 2016). Formulas and variables for the above mentioned indices are summarized in Appendix A-1.

To estimate a cultural keystone species score for each plant cited by participants I employed the following protocol:

3.3.1. Measuring intensity, type and multiplicity of use

I suggest measuring species use values (**UV$_s$**) modified from (Phillips and Gentry, 1993) and following (Albuquerque et al., 2014) as follows: **UV$_s$ = ($\sum$UV$_{is}$)/n$_{is}$,** where $\sum$**UV$_{is}$** is the sum of the participants use values for a given species and **n$_{is}$** the total number of participants interviewed. I have employed this approach to maximize objectivity as Turner's ICS index along with several modifications have been found to be overly subjective (Platten and Henfrey, 2009; Silva et al., 2006; Tardío & Pardo-De-Santayana, 2008; Thomas et al., 2009)

3.3.2. Measuring whether a given species provides opportunity for resource acquisition

To estimate whether a given species provides opportunity for resource acquisition, I modified Turner's (1988) approach. Turner (1988) and both Garibaldi and Turner (2004) employed subjective scoring with respect to estimating this criterion of cultural keystone status. I adopted an alternative approach for this measure of cultural keystone status in that I asked each participant for each species if it was traded or sold for other resources. All responses were recorded as binary (0, 1) data to reduce potential for researcher biases.

3.3.3. Measuring psycho-socio-cultural value

I estimated the psycho-socio-cultural function of a given species by asking each participant the following questions adapted from Cristancho and Vining (2004) and Garibaldi and Turner (2004)

Does this plant have a story associated with the ancestors?

Does this plant have a song?

Is this plant involved in a ritual (*dieta or sama*)?

Does this plant have a spirit (*anthropomorphic form*)?

21

Is this plant frequently discussed or known within the community?

To ensure objectivity, all responses were recorded as binary data (i.e. 0 or 1). The totals for each species were summed across categories to estimate a given specie's psycho-socio-cultural function score.

3.3.4. Measuring Species Ethnotaxonomic Diversity or Naming and terminology in a native language

I estimated species ethnotaxonomic diversity using the following formula adapted from Shannon Wiener species diversity index $\mathbf{EH = -\sum(p_i*log(p_i))}$ where $\mathbf{p_i}$ is the proportion of the number of participants that list a given specie's vernacular name and the total number of participants that mention vernacular names for a species.

3.3.5. Measuring Species irreplaceability or level of unique position

I estimated species irreplaceability as the proportion of the total number of species that can substitute a given use or function of a given species (across all uses for a given species) and the total number of species cited across participants in the sample divided by the total number of uses for a given species. For example, consider species *x* cited as having 2 uses while 15 species can be substituted to fulfill the same functional role. If there are a total of 30 species cited across participants, then species irreplaceability (SI) is equal to (15/30)/2 or 0.25.

3.3.6. Calculating Cultural Keystone Status

I estimated species cultural keystone status by conducting principal component (PCA) analysis for the predictors of cultural keystone status in *R* using the LABDSV package. The developed keystone status score for each species was estimated by selecting the principal components with the highest significant correlation coefficient and multiplying them (see data analysis).

3.3.7. *Data analysis*

I conducted pairwise correlations using the LABDSV package in *R* 3.4.3 (R Development Core Team, 2019) to test if the 12 indices of cultural importance were correlated among each other. Following the correlation test or from the pairwise correlations, I selected the cultural value index (CV) (Reyes-García et al. 2006) as a representative index for significantly correlated indices to test if they predict species cultural keystone status. The fidelity level (FL) (Friedman et al., 1986) was also selected from correlated indices and the quality use-value agreement (QUAV) (Thomas et al., 2009), which was not correlated with other indices, was selected for subsequent analysis. To calculate the cultural keystone status score for each species I conducted principal component analysis (PCA) using cultural keystone species criteria estimated for each species. The cultural keystone species predictors included *use values*, *ethnotaxonomic diversity*, *cultural irreplaceability*, *psycho-socio-cultural function*, *high level of importance*, and *extent to which a species provides opportunity for resource acquisition* (Cristancho & Vining, 2004; Garibaldi & Turner, 2004). Species *use-values* for the developed cultural keystone status score were estimated indirectly via the Use-Value (UVs) index adapted from Philips and Gentry (1993) to ensure objectivity. I calculated a cultural keystone species score for each species cited by participants by multiplying principal component scores for PC1 (34%) and PC2 (26.4%) which explained a significant proportion (60.4%) of variance (Figure1B). To do so, I first normalized PC1 by multiplying the scores obtained via PCA for each species by -1 to ensure that the cultural keystone species scores were positive. Then, for each species I multiplied the normalized PC1 scores with those scores obtained for PC2 to calculate the cultural keystone status score for each species (Figure 3.1B). Generalized linear models (GLMS) as well as phylogenetic generalized least squares (PGLS) in *R* (R Development Core Team, 2019) were used to test if cultural importance indices predict cultural keystone species status (developed CKS status score). Given plant species share evolutionary history (Heinrich and Verpoorte, 2012), I controlled for phylogeny in the PGLS model by using the S. PhyloMaker function in *R* (Jin & Qian, 2019; Qian & Jin, 2016). To do so, I first developed a phylogeny of plant species cited by participants (Figure 3.1). I then, utilized the phylogeny to test the effect of evolutionary relatedness between species in the PGLS models.
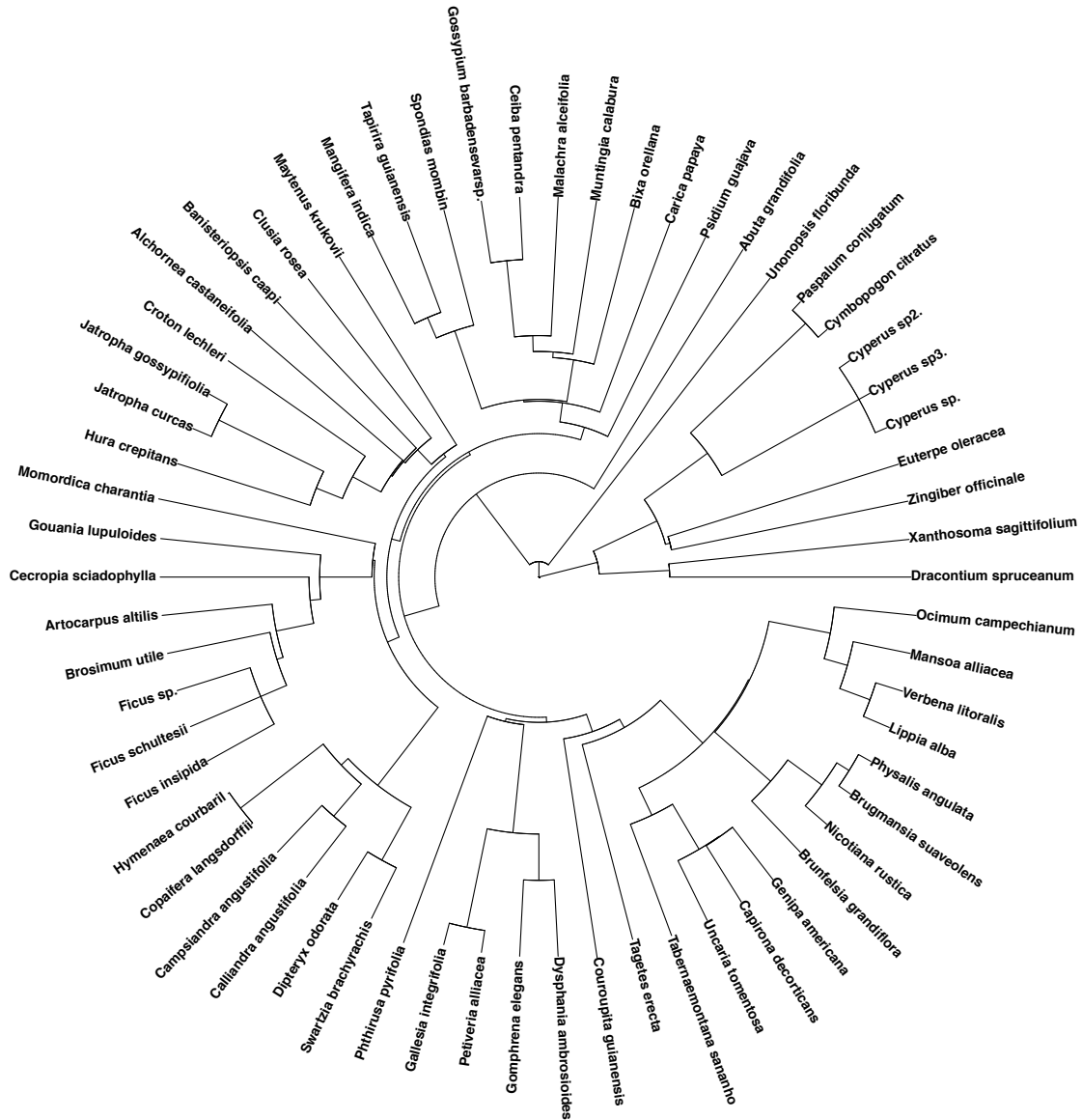
Figure 3. Phylogenetic tree developed using the S. PhyloMaker function in *R* (Qian & Jin, 2016). The phylogenetic tree was constructed from a comprehensive phylogeny for vascular plants (Jin & Qian, 2019). The phylogenetic tree obtained from the comprehensive phylogeny has 31389 tip labels and 31387 internal nodes.

The response variables were measurement data (cultural keystone status score developed from PCA; Figure 3.2B). Therefore, I used GLMS with normal error structures (Crawley, 2013). To select the best fitting models that had greater explanatory power, I used an information-theoretic approach following Gaoue et al. (2011) where for each response variable I estimated the Akaike information criterion (AIC) (Crawley, 2013) for each model, the difference in the AIC between

each model, and the model with the lowest delta AIC. I then, selected the models with the lowest delta AIC< 2 (Gaoue et al., 2011).

3.4. Results

Pairwise correlation analyses indicate that 11 of the 12 indices of cultural importance were all significantly correlated amongst themselves (Figure 3.2A). There was no significant correlation between the Quality Use Value Agreement index (QUAV) and other indices indicating that this index of cultural importance was novel (eg. 18.5 % correlation between the cultural value index and QUAV, p = 0.1173); Figure 3.2A). The Fidelity level (FL) index was negatively correlated with 10 cultural importance indices that were positively correlated with each other (Figure 3.2A). In developing the species cultural keystone score for each species, PC1 was dominated by use-values explaining 34% of the variance whereas PC2 was dominated by species irreplaceability explaining 26% of the variance.
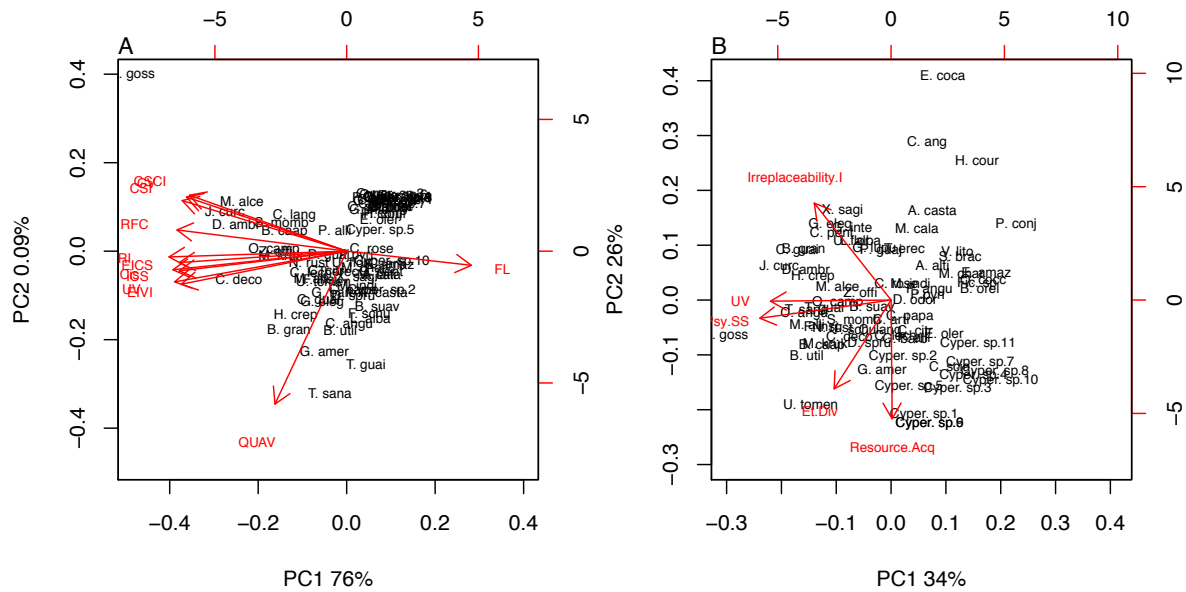
Figure 3.2. Pairwise Correlation biplots for thirteen Ethnobotanical Indices of Cultural importance and of cultural keystone designation predictors used for developed CKS score. **A)** PC1 explains 76% of the variance and PC2 explains 9% of the variance. Abbreviated Latin binomials indicate plant species cited. Loadings for PC1 were dominated by use-values whereas, loadings for PC2 were dominated by species irreplaceability. Correlated indices include index of cultural significance (ICS), ethnic index of cultural significance (EICS), use-value index (UV), relative frequency citation index (RFC), ethnobotanical importance value index (EIVI), relative importance index (RI), cultural value index (CV), cultural significance index (CSI), cultural importance index (CI), and the cultural significance and conservation index (CSCI). Uncorrelated indices include the quality use-value agreement index (QUAV) and fidelity level (FL) indices. **B)** Predictors for the cultural keystone score including

species cultural irreplaceability (Irreplaceability. I), species use value (UV), species pycho-socio-cultural function (PSY.SS), species ethnotaxonomic diversity (Et.Div), and species opportunity to provide resource acquisition (Resource.Acq). The developed score was obtained by multiplying PCA scores for each species for PC 1 and PC2 explaining 60% of the variance.

Controlling for evolutionary relatedness did improve the model by 4.96 units of AIC. (AIC_{PGLS} = 382.80 vs. AIC_{GLMS} = 387.49: Table 3.1 and Table 3.2) indicating that a significant part of the predictive power of cultural importance indices is related to species shared evolutionary history. I found no significant association between the species cultural value index (CV) and the cultural keystone status score for each species (β = -2.482408 +/- 34.38893, t = - 0.072186, p= 0.9427; Table 3.1) indicating most correlated cultural importance indices do not significantly predict species cultural keystone status. Similarly, the fidelity level (FL) index did not significantly predict species cultural keystone status (β = 0.004671 +/- 0.01676, t = 0.278755, p= 0.7813; Table 3.1; Table 3.2). The quality use value agreement index (QUAV) significantly predicted cultural keystone species status (Table 3.1; Table 3.2). Further, the species cultural keystone score was moderately but positively correlated (r = 0.45, p<0.001) with the quality use-value agreement (QUAV) index (Figure 3.3).

Table 3.1. Results of phylogenetic generalized least squared models (model selection) to test the effects of cultural importance indices Cultural Use Value (CV) index, Fidelity Level (FL) index, and Quality Use Value Agreement (QUAV) index on the Cultural Keystone Species Score of medicinal plants used by the Shipibo community of Paoyhan. This (pgls) model controls for evolutionary relatedness of medicinal plants cited by participants. Significant predictors are in bold.

	Estimate	Std. Error	t value	Pr(>ltl)	AIC
(Intercept)	5.189253	2.89039	1.795349	0.0770	382.801
CV	-2.482408	34.38893	-0.072186	0.9427	
FL	0.004671	0.01676	0.278755	0.7813	
QUAV	3.660636	0.85985	4.257306	**0.0001**	

Table 3.2. Results of generalized linear models (model selection) to test the effects of cultural importance indices Cultural Use Value (CV) index, Fidelity Level (FL) index, and Quality Use Value Agreement (QUAV) index on the Cultural Keystone Species Score of medicinal plants used by the Shipibo community of Paoyhan. This (glm) model does not control for evolutionary relatedness of medicinal plants cited by participants. Significant predictors are in bold. Significance codes: '***' <0.001, '**' <0.01, '*' <0.05, '.' <0.1, n.s. >0.1

	Estimate	Std. Error	t value	Pr(>|t|)	AIC
(Intercept)	5.49219	1.69598	3.238	**0.001850 **	387.49
CV	65.81083	35.58032	1.850	0.068648 .	
FL	-0.02769	0.01878	-1.475	0.144886	
QUAV	4.97747	1.28286	3.880	**0.000236 ***	
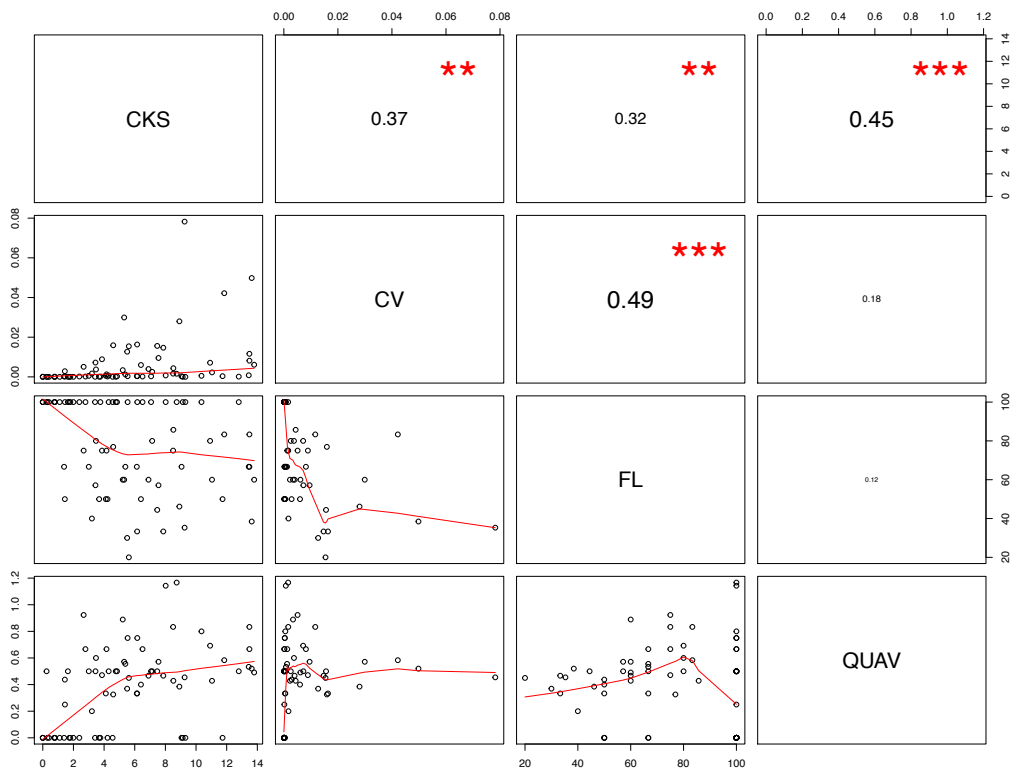
**Figure 3.3.** Pairwise Spearman Correlation (two by two) for the developed cultural keystone status score with the representative cultural value (CV) index and uncorrelated indices including the fidelity level (FL) index and the quality use value agreement index (QUAV). Significant correlation coefficients are indicated by red stars. Significance levels: "***" = p<0.001, "**" = p<0.01, "*" = p<0.05, and "ns" = not significant.

3.5. Discussion

3.5.1. Most cultural importance indices are correlated — a call for robust development of ethnobotanical indices

These results articulate the complexity involved in assessing cultural keystone species designation for medicinal plants that are used by the Shipibo-Konibo community of Paoyhan. I found that out of 12 indices of cultural significance commonly used by ethnobotanists, 11 of them were strongly correlated amongst themselves. This indicates that most cultural importance indices are not unique in terms of what they attempt to quantify.

I developed a species cultural keystone status score integrating all of the components of cultural keystone species status including high *use values, species irreplaceability, species ethnotaxonomic diversity, species psycho-socio-cultural function*, and *extent to which a given species provides opportunity for resource acquisition* (Cristancho and Vining, 2004; Garibaldi and Turner, 2004; Figure 3.1B). The fidelity level index (Friedman et al, 1986) and the cultural value index (Reyes-García et al., 2006), were not significantly associated with species cultural keystone species status of medicinal plants used by the Shipibo-Konibo. In contrast, the quality use-value agreement (QUAV) index was a significant predictor of species cultural keystone status. However, given the quality use-value agrrement (QUAV) index was moderately correlated with the cultural keystone status score, I caution the use of this index may fall short of capturing 50% of the variance of species cultural keystone status (Figure 3.3).

It has been two decades since the Cultural Keystone Species concept was first proposed (Cristancho and Vining, 2004; Garibaldi and Turner, 2004). Although this theory in ethnobotany (Gaoue et al., 2017) may show great promise with respect to the conservation potential of cultural and ecologically important plant species that are integral to both cultural and ecological systems, results indicate that prior methods involving the use of cultural importance indices to infer or predict cultural keystone species status are limited and in most cases have fallen short of implicitly capturing the proposed indicators of cultural influence highlighted by Garibaldi and Turner (2004) as well as Cristancho and Vining (2004). To help encourage the use of appropriate methods to produce reliable data interpretation, I suggest the cautious use of cultural importance indices to predict species cultural values or cultural keystone species status. A similar

conclusion was reported by Hoffman and Gallaher (2007) who suggested that it is important for researchers to clearly understand the assumptions of a given index with respect to appropriate methods employed for hypotheses being tested. This sentiment was later echoed by Medeiros et al., (2011) who suggested inappropriate use of quantitative approaches may lead to unreliable and ungeneralizable data interpretation. Finally, in reviewing the cultural keystone species theory (Coe and Gaoue, 2018, unpublished data), I am not aware of a single study that has developed a cultural keystone status score for a given species objectively using principal component analysis (PCA) or that has used the quality use-value agreement (QUAV) index following Thomas et al. (2009) to predict cultural keystone status (Coe and Gaoue, 2018 *In Review)* suggesting these approaches are likely underutilized.

3.5.2. "Why do most cultural importance indices seem to fall short of measuring species cultural keystone status?"

It's not surprising most cultural importance indices commonly used in ethnobotany were correlated amongst themselves. Most of these indices contain similar parameters such as species use-values and the number of participants in a given study. A critical and logical step toward an objective examination of how cultural importance indices are employed in ethnobotany is a thorough reevaluation of the indices themselves, specifically, the formulas employed to quantify cultural importance and infer keystone status. For example, the first index proposed to measure keystone status was the Index of Cultural Significance (ICS) (Garibaldi and Turner, 2004; Turner, 1988). This index may be limited by researcher subjectivity (Platten and Henfrey, 2009; Tardío and Pardo-De-Santayana, 2008; Thomas et al., 2009) and although subsequent adaptations of this index were employed by Lajones and Lemas (2001) and Stroffle et al, (1990) it has been noted these variations of the ICS also incorporate researcher biases (Silva et al., 2006). Subsequently, the cultural significance index developed by Silva et al., (2006) was adapted and modified from the ICS (Turner, 1988) and proposed as a more objective index that measures cultural significance while limiting subjectivity. Although the aim of the cultural significance index is to reduce subjectivity with respect to the weighted value of the importance of a given species and to consider participant consensus (Silva et al., 2006), reevaluation of the variables in the formula indicate it is clear they do not account for all the predictors or indicators of cultural keystone species status. This index includes species management *(i)*, species use

preference *(e)*, and species use frequency *(c)* and a correction factor (CF) to account for cultural consensus and to determine cultural importance of a given species (Appendix A-1; Silva et al., 2006). However, this index lacks several criteria that define species cultural keystone status such as species irreplaceability and species ethnotaxonomic diversity (Garibaldi and Turner, 2004; Turner, 1988). Similarly, the cultural importance (CI) index (Tardío and Pardo-De-Santayana, 2008) includes the sum of the proportion of informants who mention each species use *(ΣUR_{u})* and total number of participants (N). Further, the relative frequency citation (RFC) (Bennett & Prance, 2000; Tardío & Pardo-De-Santayana, 2008) index includes the total number of participants who mention a use for a given species without considering a use category (F_{cs}) and the total number of participants (N) (Appendix A-1). Given the original parameters of these indices, it is reasonable to suggest that most cultural importance indices have failed to predict species cultural keystone status due to the lack of variables to explicitly account for species cultural keystone criteria (Cristancho & Vining, 2004; Garibaldi & Turner, 2004). I suggest similar conclusions may be drawn when reexamining most cultural importance indices as supported by the findings (also see Appendix A-1).

3.5.3. Some cultural importance indices are challenging to replicate

Several notable limitations have arisen with respect to lack clarity in terms of methodologies used to calculate cultural importance indices, which has led to challenges in replicating results. For simplicity, I highlight several indices below:

The CSCI index proposed by Tudela-Talavera et al. (2016) is as follows where: **CSCI = SI [∑(m*pr*f) + ∑(QMU+pp+d)]**. In this formula, the authors rank *resource availability (d)* on scale from 1-5 from the view of the respondents yet did not clearly identify incremental criteria for numerical scoring. Tudela-Talavera et al. (2016) also note higher scores imply greater cultural importance of given plant species considered less available under the caveat that these species require greater conservation efforts. In this context, Tudela-Talavera et al. (2016) provide no support as to why a less available species are considered more important from an emic perspective. Further, the authors do not clearly define whether conservation efforts considered are from the view of the Shipibo community with whom they worked. It is likely cultural groups

have differing perspectives of conservation strategies compared to management plans often employed by resource managers. Therefore, utilizing these same approaches to estimate a score for plant resource availability may incorporate researcher biases. To remedy the lack of clarity on estimating this variable and for replication purposes I employed a ranking of $1, 3, 5$ where species that were available to harvest in the community territory received a score of (1), species that were available but difficult to find received a score of (3), species that were not available for harvest in community territory received a score of (5).

Another limitation of calculating the CSCI is replicating methods to estimate *(pp) part of the plant used*. Again, Tudela-Talavera et al. (2016) are unclear in their methodologies to estimate this variable. It is noted that a score between 3-0.5 were assigned to plant parts whose impact means a greater impact on the resource. This said, it is unclear exactly which plant parts and how many are considered other than roots (noted as an example by the authors) and how scores were allocated among plant parts. I caution that employing these approaches, which are expected to indicate the degree of harvest impact of a given plant species are likely misleading. Specifically, the authors have provided no support from in the literature on the effect of harvest for specific plant parts on a given species. Demographic studies have long demonstrated that not all plant parts are created equal and the effect of harvest on a given species often not only depends on the type of organ harvested but also on the life history of the species, harvesting intensity, harvesting method, and other anthropogenic and environmental factors (Sampaio and Santos, 2015; Schmidt et al., 2015; Ticktin, 2004). In addition, the effect of harvest has been shown to vary among life-forms (tree, shrub, herb) (Schmidt, et al., 2011) and multiple organs are often harvested simultaneously suggesting a compound effect. Thus, a thorough understanding of the effect of organ harvest on a given species likely requires long-term demographic studies to make significant projections. In this study, regardless of life-history and life-form and for replication purposes I employed ranking *pp* as follows: Root (3), bark (2.5), stem (2), foliage (1.5), fruit (1), flower (0.5). It is important to note I estimated the effect of multiple organ harvest as this was commonly cited by participants. Thus, if bark and foliage were harvested then I added corresponding values (2.5+1.5= 4).

A final limitation of the CSCI was inspired by the estimation of (*QMU*) = *quality of medicinal use*. Tudela-Talavera et al. (2016) indicate in their methods employed the most common diseases registered through free-listings and were calculated via an adaptation of

Smith's index to account for most frequent diseases taking higher values for those *uses* that treat more frequent conditions according to participant's emic perspective. The suggested scoring for *QMU* is a range between 3–0.5 (Tudela-Talavera et al., 2016). Again, the authors were not explicit on the incremental values assigned to each *quality of medicinal use* therefore; clarity is needed to replicate these methods. Another challenge with utilizing these approaches in terms of estimating *QMU* is that a given plant species may solely treat a more common disease whereas, another species may treat numerous uncommon diseases. Therefore, ranking species uses or therapeutic functions under these circumstances may prove challenging in that one may over or underestimate the *QMU* unless critical and systematic approaches are employed. In this study, participants defined the most common diseases and uses. These were ranked as follows: Infection (parasites), Gastrointestinal (diarrhea), and Fever (3); Respiratory and Staff infection (2); Aids, Diabetes, Cancers (1.0); Other Disease (0.5).

The relativized ethnobotanical index (EIVI) was proposed by Lajones & Lemas (2001) as a means to estimate species cultural importance, to provide a standardized approach for comparisons of species cultural values between cultural communities, and to account for the effect of harvest on a given species (Lajones and Lemas, 2001). In this formula, **EIVI =** U_q+ C_l+ P_{ha}+ P_u + P_o, the authors rank *use quality* (U_q) on a scale from 1-6, *collection locality* (C_l) from 1-4, plant habit from (P_{ha}) 1-4, *plant part utilized* (P_u) from 1-4, and *plant origin* (P_o) was ranked where a score of (2) was assigned for native species or (1) for introduced species). Although the authors mention the aim of this index was to reflect the emic perspective, it is unclear if and how all variables of this index were weighted according to the view of the communities studied. For example, the authors mention the values assigned to *use-quality* reflects the local values linked to subsistence strategies employed by the communities studied however, it has been suggested all values assigned for variables of this index were done so directly by the authors (Silva et al., 2006). For example, the authors state *plant part utilized* (P_u) was directly ranked and scored as follows where (6) was assigned for the use of a stem, (5) for the root, (4) for the leaves, (3) for the fruits, (2) for the flowers and (1) the latex. For instances where multiple plant parts were used, plant part scores were summed and in the case where the whole plant was used, the authors summed all the values for plant parts for a total score of 21. Given Lajones and Lemas (2001) mention the scores for plant part used were assigned directly, this approach is likely limited by researcher subjectivity. Further, as mentioned above, it has been shown that not all plant parts

are created equally where the effect of harvest on a given species will vary between life forms depending on numerous abiotic, biotic, and anthropogenic factors (Sampaio & Santos, 2015; Schmidt et al., 2015, 2011; Ticktin, 2004). In this study, regardless of life-history and life-form and for replication purposes I employed ranking for (P_u) following Lajones and Lemas (2001). Additionally, I ranked *use-quality* following the numerical scoring proposed by Lajones and Lemas (2001). Similar limitations of the EIVI index are linked to the scores directly assigned to the variables *plant habit* (P_{ha}), *plant origin* (P_o), and *collection locality* (C_l). For example, *plant habit* (P_{ha}) was ranked were a score of (4) was assigned for Trees, (3) for Palms, (2) for shrubs or grasses, and (1) for lianas. *Plant origin* (P_o) was ranked where a score of (2) was given to native species and a score of (1) was given to non-native species. *Collection locality* (C_l) was ranked where a score of (4) was given to species located in primary forest, (3) for secondary forest, (2) for agroforestry plot, and (1) for orchard or garden. It remains unclear how the numerical values for these variables were assigned or weighted. Further, the authors do not provide cultural or ecological support for methodologies linked to values assigned to variables of this index which may limit reliable and reproducible findings. Again, given the values assigned to these variables were done directly, this approach to estimate species cultural keystone status is likely limited by researcher subjectivity. Regardless of these limitations, I estimated these variables following Lajones and Lemas (2001).

3.6. Conclusions

Given the findings and limitations articulated above, I encourage researchers to cautiously consider the assumptions along with potential short-comings of the use a given index for quantification. This call to action is anything but new. While the use of cultural importance indices in ethnobotany have become widespread, careful consideration of what theses indices attempt to measure and critical evaluation of the variables comprising a given index are highly recommended to help ensure reliable data interpretation and thus, accurate predictions on the underlying patterns linked to plant-human interactions. Finally, ethnobiologists should consider if cultural importance indices are accurate measures of cultural importance as what defines cultural importance (Hunn, 1982) is unclear and perhaps, may be overlooked in terms of quantitative indices.

How species cultural keystone status is measured warrants further discussion among ethnobiologists. Rather than utilize cultural importance indices that may only capture a limited proportion of species cultural keystone status, a direct measure of species cultural keystone status that includes all the criteria is recommended. In efforts to help address this concern, this study offers an alternative quantitative approach to account for the predictors of species cultural keystone status.

I acknowledge that cultural keystone status of plant species tied to a particular cultural group is undoubtedly complex while likely involving numerous factors including but not limited to cultural cosmologies, beliefs, local knowledge and socio-cultural values tied to community identity. Further, these cultural domains are likely rooted in socio-cultural underpinnings that are both challenging for observers (etic perspective) to thoroughly understand qualitatively, let alone quantify. There is no doubt that prior approaches to measuring cultural keystone status of a given species have often failed to objectively account these factors. Although I offer alternative methods to help remedy where most quantitative indices may have fallen short of implicitly measuring keystone status, an in-depth understanding of cultural keystone status likely requires critical engagement in the socio-cultural practices of a given culture during long-term periods of fieldwork. Finally, I caution it is important to consider the motives behind and contexts in which researchers measure species cultural keystone status. Regardless if robust indices are developed and employed by ethnobiologists to help inform management plans, I suggest it is important to consider how these approaches should mutually benefit the cultural communities studied. This brings into question, *"if we really need an objective index to tell us which species are cultural keystones and therefore important to focus on for conservation?"*

Chapter 4: Phylogeny explains why therapeutically redundant plant species are not necessarily facing greater use pressure

4.1. Introduction

Understanding medicinal plant selection by cultural groups from a psycho-social-cultural perspective is a central goal of ethnobotanical research. Intrepid explorers such as Richard Evans Schultes (1915-2001) brought ethnobotany as a discipline into international focus as published reports of long-lived ethnomedicinal traditions practiced by peoples of the Upper Amazon River Basin became widespread among cognoscente academics and general public alike (see for example Schultes, 1954, 1957). Subsequent research conducted by Schultes' graduate students notably, Wade Davis and Timothy Plowman (1944-1989), has undoubtedly continued to inspire up-and-coming researchers in the fields of ethnobotany and ethnopharmacology to investigate the profound impact specific species of plants have had on not only the social organization of various cultural groups but also their applications in traditional ethnomedicine as well as their potential psychotherapeutic effects (Davis, 1996; Plowman, 1981; Schultes and Plowman, 1979). As a result, ethnobotanical research focused on the cultural use of medicinal plants to treat various forms of illness has become widespread (see for example Luna, 1984; McKenna, Luna, and Towers, 1995; Rivier and Lindgren, 1972).

More recently, ethnobotanical studies have become focused on theory-inspired, hypothesis-driven research aimed to facilitate a paradigm shift within the discipline of ethnobotany (Gaoue et al., 2017). As such, ethnobotanical studies driven by research questions aimed to help gain an in-depth understanding of the underlying patterns and processes surrounding plant use and local resource management—have gained momentum and yielded informative results. Several examples include investigations of the loss of medicinal plant knowledge linked to urbanization, globalization, and access to public health facilities (Vandebroek et al., 2004; Vandebroek and Balick, 2012), investigations of non-random selection of medicinal plants for ethnomedicinal uses (Bennett and Husby, 2008; Ford and Gaoue, 2017; Moerman, 1979), and investigations of community based conservation approaches driven by locally enforced taboos (Colding and Folke, 1997). While these studies highlight plant use-patterns and help to identify numerous threats to biological and cultural diversity, we lack a clear mechanistic understanding of the drivers of such unique and coupled anthropogenic threats.

The utilitarian redundancy model has emerged as a complementary framework that highlights how species cultural values can be used in defining conservation priority (Albuquerque and Oliveira, 2007; Gaoue et al., 2017). The utilitarian redundancy model predicts plant species that are culturally important, used for the multiple purposes, and fulfill a unique or non-redundant therapeutic function within local ethnomedicine, are more likely to be under greater use-pressure (Albuquerque and Oliveira, 2007; Nascimento et al., 2015). Further, species that are therapeutically redundant are predicted to experience reduced use impact because use-pressure is expected to be diffused across a greater number of species. Therefore, local ethnomedicinal practices employed by a given culture are expected to experience little to no overall effect as a result of the loss of redundant species and the contrary for non-redundant species (Gaoue et al., 2017; Nascimento et al., 2015). To date, the utilitarian redundancy model has been used in measuring species redundancy (Albuquerque & Oliveira, 2007; Alencar, et al., 2014; Ferreira et al., 2012) to help identify focus species for conservation and in understanding the effects of species *use-values* and *preference* on the use-pressure (Albuquerque & Oliveira, 2007; Ferreira et al., 2012) of medicinal plants in a local ethnomedicine. Though these studies have shown that local preference and redundancy can have a significant effect on medicinal species use-pressure, our understanding of main and interactive effect of therapeutic redundancy, preference, and use-value on the use-pressure of medicinal plant species is limited. Further, little is known about the effect of species evolutionary relatedness on the use-pressure of medicinal plants.

Given plant species are related evolutionarily, several plant families have been over- or under-utilized for medicinal purposes due to shared evolutionary traits such as the presence or lack thereof high concentrations of secondary plant compounds often employed for ethnomedicine (Ford and Gaoue, 2017; Heinrich and Verpoorte, 2012; Moerman, 1979; Souza, et al., 2018). In addition, plant family has been shown to be strong predictor species use-values (Phillips and Gentry, 1993). Yet we lack an in-depth mechanistic understanding of the relationship between species shared evolutionary history and medicinal species use-pressure. The objectives of the current study were to (1) understand the effect of species shared evolutionary history on medicinal species use-pressure and (2) to understand the effect of species use-preference, therapeutic redundancy and species use-values on species use-pressure of medicinal plant species used for ethnomedicine in the Ucayali Region of the Peruvian Amazon rainforest.

4.3. Materials and Methods

4.3.1. Study Area

The present study was undertaken in Paoyhan, a Shipibo-Konibo community, located in the Peruvian Amazon along the Ucayali River (07° 50.941'S, 075°00.800'W). In this area, the climate is tropical with a mean annual temperature of 26.4°C (Kottek et al., 2006). Annually, the rainfall is approximately1600mm. The community is approximately 132.3m above sea level (Casimiro et al., 2013). Approximately two-thousand inhabitants in the community rely on harvesting of economically important trees as well as Non-Timber Forest Products for livelihood strategies and medicinal use.

4.3.2. Objectives

The goal of the data collection was to estimate species therapeutic redundancy, use-values and preference and to test their effects on species use-pressure of medicinal plants used by the Shipibo-Konibo for healing. Ethnobotanical data were obtained from semi-structured interviews to estimate therapeutic redundancy and species use-values. Focus group discussions (Albuquerque et al., 2014) were employed to estimate species use preference and species use-pressure. Fieldwork was conducted between June and September 2017 and between May and July 2018. A total of 30 participants (13 men and 17 women) at least 18 years old were interviewed. Interviewees were composed of local experts and those with generalized knowledge. Interviews were either conducted in Shipibo, Castellano, or both depending on the preferred dialects of the participant. When necessary, terms or questions were translated into Shipibo, Castellano or English with the help of both native and non-native field assistants to facilitate communication. Interviews were based on medicinal plants that exist in the community or the surrounding area (community territory of Paoyhan). A complementary approach employed during the interview process was a *walk in the woods* or *guided tour* (Albuquerque et al., 2014) to observe medicinal plants *in situ* with one or more participants considered local experts, to collect botanical specimens cited by participants during interviews, and to observe harvested species biomass. Medicinal plants cited by participants were identified and deposited in the UNAP (Universidad Nacional de la Amazonia Peruana) Herbarium.

To gather data for estimating species use-value and therapeutic redundancy, I used a standardized format in that participants were asked questions on the participant's knowledge, use, and use preference of medicinal plants in the region. Based on responses, follow up questions were asked on the plant part used, location of harvest, therapeutic use, frequency of use, species management, species use in ritual (when applicable), and species local name in Shipibo and Castellano (see Appendix A-2). Prior to each interview, I obtained free and prior informed consent. Participation was voluntary and in accordance with UH-Manoa IRB (CHS#23611). To gain a deeper understanding of medicinal plant use among the Shipibo-Konibo, participant observation was employed to observe medicinal plant harvest, preparation, and use in ritual (Albuquerque et al., 2014) which allowed for a more enriching data collection.

4.3.3. Estimating species use-value

To estimate species use-values, I used the use-value (UV) index *(UV= Σ U_i/n)* adapted from Phillips and Gentry, (1993b) to determine the relative importance or species use-value of each plant species cited form a local perspective following (Albuquerque et al., 2014; Lucena et al., 2007). In this formula, U_i = the number uses cited for a given species and *n* = the total number of participants

4.3.4. Estimating species use-pressure and preference

Following initial interviews among the general community, local experts were selected for a focus group discussion regarding species use-pressure and use-preference (Albuquerque et al., 2014). During the focus group discussion, medicinal species use-pressure and use-preference for 62 medicinal plants fulfilling 31 therapeutic categories were discussed among local experts or harvesters. Local experts were selected based on their in-depth knowledge of plant use and their direct involvement or knowledge of harvest practices employed by the community. Given it has been demonstrated harvest estimates based on local knowledge can be reliable (Jones et al., 2008), estimates on use-pressure were done based on the participant's emic perspective. Thus, all participants of the focus group were asked to estimate the how much of a given species was harvested per month by community harvesters. As such, all use-pressure for a given species was

estimated as kilograms of biomass (the local unit of measurement) harvested per month by the community.

4.3.5. Measuring therapeutic redundancy

For each medicinal plant species cited by participants during interviews, local therapeutic categories and disease classifications were also recorded. It is important to mention local classifications or nosology from the participant emic perspective were retained, without transformations to therapeutic or disease profiles known by western medical systems (Alencar et al., 2014). Further, plants cited to treat a given illness were recorded as such for the treatment of adult participants. Although prior estimates of species therapeutic redundancy have been employed (Albuquerque and Oliveira, 2007), these approaches may be limited by subjectivity due to authors directly assigning weight to levels of redundancy (eg. where *highly redundant* represented greater than 15% species used to treat a disease within the therapeutic category, *redundant* represented between 15% and 5% of the total number of species, and *non-redundant* represented less than 5% of the total number of medicinal plant species cited). To remedy the need to assign levels of redundancy directly, I propose the following approach to classify species therapeutic redundancy as follows: $R = (\Sigma\, S_i / n) * W$. In this formula S_i = the total number of plant species that can be used to treat a given illness or fulfill a given therapeutic function, n = the total number of species cited and W = the total number of therapeutic functions fulfilled by a given species. For example, if species x is cited to treat cataracts and nausea, fulfills 2 therapeutic functions and there are 2 species that were cited to treat cataracts and 3 species cited to treat nausea out of 62 total cited species, then redundancy equals: $((2+3)/62)*2 = 0.161$. In this study, redundancy estimates for medicinal species cited by participants ranged between a low of 0.032 units and a high of 5.8 units.

4.3.6. Data Analysis

I tested the effects of species use-preference, species therapeutic redundancy, and species use-values on species use-pressure using generalized linear models (GLMS) and phylogenetic generalized least squares (PGLS) in *R* 3.4.3 (R Development Core Team, 2019). I used both models to understand role of species shared evolutionary history (Heinrich and Verpoorte, 2012) on the prediction of species use-pressure. For both models I used a Gaussian error structure

(Crawley, 2013). I built a phylogeny of medicinal species cited by participants using the S. PhyloMaker function in *R* (Jin & Qian, 2019; Qian & Jin, 2016; Figure 4.1). To select the best fitting models that had greater explanatory power, I used an information-theoretic approach following Gaoue et al. (2011) where for each response variable I estimated the Akaike information criterion (AIC) (Crawley, 2013) for each model, the difference in the AIC between each model, and the model with the lowest Δ AIC. I then, selected the models with the lowest Δ AIC< 2 (Gaoue et al., 2011).
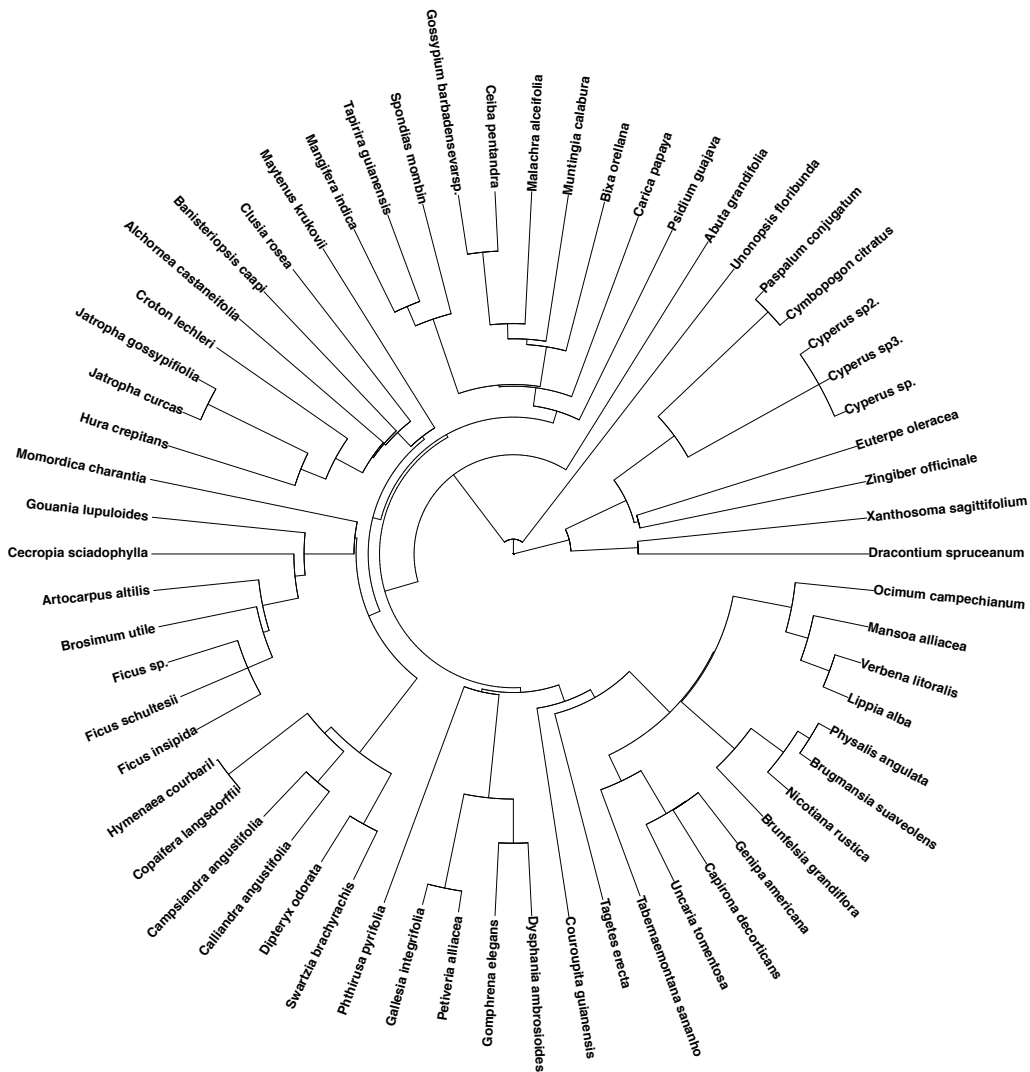
Figure 4.1. Phylogenetic tree developed using the S. PhyloMaker function in *R* (Qian & Jin, 2016). The phylogenetic tree was constructed from a comprehensive phylogeny for vascular plants (Jin & Qian, 2019). The phylogenetic tree obtained from the comprehensive phylogeny has 31389 tip labels and 31387 internal nodes.

4.4. Results

4.4.1. Medicinal plant species and illnesses

Sixty-two medicinal plant species belonging to 33 families and 57 genera were identified. The medicinal plant families most represented were Fabaceae (6 species), Euphorbiaceae (5 species), Moraceae (5 species), and Solanaceae (4 species). The plant families with the highest number of medicinal uses reported were Euphorbiace followed by Rubiaceae, Solanaceae, Fabaceae, Amaranthaceae and Malvaceae. Of these 62 medicinal plant species, 27 species were cited as preferred for treating a given medicinal therapeutic function. Thirty-one local therapeutic categories were cited by participants. Most plant species were often used to treat the following illnesses: diarrhea (n=17 species), rheumatism (n=17), clean wounds and cuts (n=15) and body pain (n=13) (Figure 1). In contrast, fewer plant species were used to treat AIDS (n=2 species), heal or remove scars (n=2), as anti-purgative (n=2), and cataracts (n=2)(Figure 4.2).
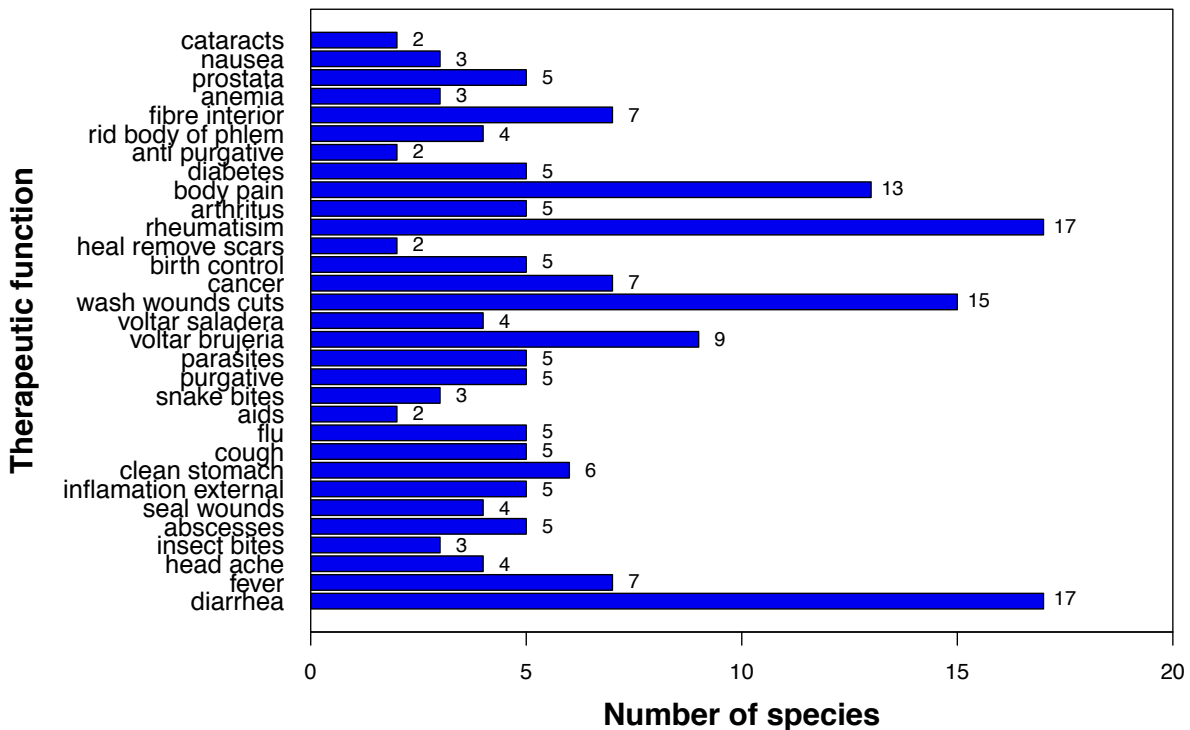
Figure 4.2. Species therapeutic redundancy according to the Shipibo community of Paoyhan. Numbers at the end of the bars represent the total number of medicinal plant species cited by participants to fulfill the therapeutic functions.

4.4.2. Do species therapeutic redundancy and use preference affect species use-pressure?

The main effect of species use-preference on use-pressure was marginally significant (β_{PGLS} = 9.862988 $\pm$ 5.319230, t_{PGLS} = 1.854214, p_{PGLS} 0.0688; Table 4.1) indicating that preferred species were under greater use-pressure (Figure 3). Species use-preference and therapeutic redundancy interactively had a significant effect on species use pressure (β_{PGLS}=-9.267 $\pm$, t_{PGLS} = 3.565, p_{PGLS} = 0.0018, Table 4.1). This suggests although there is a positive relationship between therapeutic redundancy and medicinal species use-pressure, as the use-preference of a given species increases the relationship between redundancy and use-pressure becomes less positive. Thus, less therapeutically redundant species may experience a high level of use-pressure if they are preferred (Figure 3). The main effect of species therapeutic redundancy on use-pressure was significant (β_{PGLS} = 13.254 $\pm$3.29, t_{PGLS} = 4.03, p_{PGLS} = 0.0002) suggesting species therapeutic redundancy may drive species use-pressure.
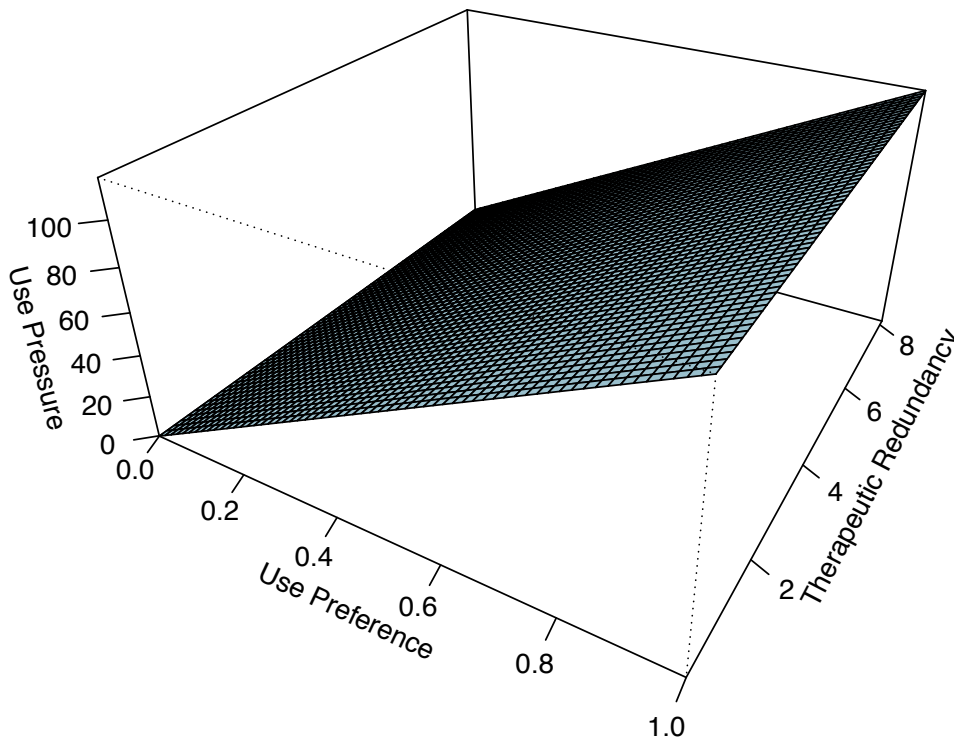
Figure 4.3. Correlation between species use-pressure *(z)* therapeutic redundancy *(y)* and use-preference *(x)*. The *line* is the linear fit of the log relationship and represents the line where the use-pressure *(z)* for each species is predicted by species therapeutic redundancy *(y)* and use-preference *(x)* via the phylogenetic generalized least squares model *y=a +blog x*.

Table 4. 1. Results of phylogenetic generalized least squared models to test the effects of cultural importance, species use-preference and species functional redundancy on the use-pressure of medicinal plants used by the Shipibo community of Paoyhan. This model controls for evolutionary relatedness of medicinal plants cited by participants. Significant predictors are in bold.

	Estimate	*Std. Error*	*t value*	*P*	*AIC*
Intercept	-0.569358	16.414317	-0.034687	0.9724	558.446
Preference	9.862988	5.319230	1.854214	**0.0688**	
Redundancy	13.253970	3.287464	4.031670	**0.0002**	
Preference:Redundancy	-9.267225	3.565200	-2.599356	**0.0118**	

4.4.3. *Phylogeny affects the predictive power of the drivers of species use-pressure?*

Controlling for evolutionary relatedness between species resulted in a difference in the models by 8 units of AIC (AIC_{PGLS} = 558.45 versus AIC_{GLM} = 550.84; Table 4.1, 4.2). The phylogeny-controlled model included all the two-way interactions. This demonstrates that beyond the main effect of redundancy, species use-preference, and species use-value, there is an interactive effect between therapeutic redundancy and species use-preference on species use-pressure. Not controlling for phylogeny masked the interactive effects between species use-preference and therapeutic redundancy (Table 4.2).

Table 4.2. Results of generalized linear models to test the effects of cultural importance, species use-preference and species functional redundancy on the use-pressure of medicinal plants used by the Shipibo community of Paoyhan. This model does not control for evolutionary relatedness of medicinal plants cited by participants. Significant predictors are in bold. Significance codes: '***' <0.001, '**' <0.01, '*' <0.05, '.' <0.1, n.s. >0.1

	Estimate	*Std. Error*	*t value*	*P*	*AIC*
Intercept	9.569	3.415	2.802	0.006824	550.84
Preference	9.761	5.785	3.620	**0.000606**	

4.5. Discussion

I have shown species therapeutic redundancy can predict species use-pressure thus, there is support for the utilitarian redundancy model (Albuquerque & Oliveira, 2007). These results demonstrate also the complexity involved in understanding medicinal plant use and species use-pressure. Several plant species were cited by the Shipibo-Konibo as preferred to treat more than one illness while other species were cited as preferred to simultaneously treat an illness. Thus, I expected some medicinal plants may experience greater use-pressure if they are preferred for more than one therapeutic function and the same plants used to treat a given illness are equally available despite seasonality, life-form, and effect of harvest. This was supported by the results indicating significant interactive effect of species use-preference and therapeutic redundancy on species use-pressure (Table 1). Some medicinal plants that were preferred to treated more than one illness experienced higher levels of use-pressure. For example, Pionis (Jatropha gossypifiolia L. and Jatropha curcas L.) had a high level of redundancy and were cited as preferred to treat headaches (dolor de cabeza) and abscesses experienced moderate use-pressure despite local preference. Further, Uña de gato (Uncaria tomentosa Willd. ex Schult. DC.) and Chuchuwasa (Maytenus krukovii A.C. Sm.) had a high level of redundancy and were cited as preferred to treat body pain (dolor de cuerpo) and experienced a high level of use-pressure (Coe & Gaoue 2019, unpublished data).

I have demonstrated the importance of considering shared species evolutionary history in understanding the patterns and processed surrounding medicinal plant species use-pressure. If I had not controlled for phylogenetic relatedness between the medicinal plant species used by the Shipibo-Konibo, I would have wrongly suggested that the main effect of species use-preference solely driving species use-pressure. In contrast to other studies that have solely shown support for preference as a driver of medicinal species use-pressure (Ferreira al., 2012), findings suggest that the effect of species-use preference on use-pressure, when one controls for phylogeny, depends on species therapeutic redundancy. This suggests the relationship between medicinal species use-pressure and redundancy is not solely driven by local preference. Finally, given controlling for phylogeny is an important consideration in medicinal plant use patterns, it is likely that a significant part of the predictive power of species therapeutic redundancy and its interactive effect with use-preference on medicinal plant species use-pressure is related to species shared evolutionary history. As such, species within a given phylogenetic clade may be

more likely to be harvested because they share evolutionary traits with other medicinally important species rather than a shared level of redundancy or preference. Therefore, I suggest it is critical to control for shared evolutionary history between species in defining species prioritization and in developing conservation and management strategies.

Among the Shipibo-Konibo community of Paoyhan species therapeutic redundancy and species use-preference were significant predictors of species use-pressure. Medicinal plant species experienced greatest use-pressure if they were preferred over other plants to treat a given illness. Further as preference increased, the relationship between redundancy and use-pressure decreased. This is consistent with the central prediction of the utilitarian redundancy model that species fulfilling non-redundant therapeutic functions experienced greater use-pressure (Albuquerque and Oliveira, 2007). Additionally, in contrast to previous studies (Ferreira et al., 2012) and what is expected according to the utilitarian redundancy model, I found when controlling for phylogeny, species use-preference alone does not significantly affect species use-pressure (Table 1). Furthermore, although it is expected medicinal plant species that are locally important or have greater use-value would drive species use-pressure, species use-value was strongly correlated with redundancy (r= 0.80, p<0.001). Thus, I excluded use-value as a predictor of species-use pressure in my models. It is noteworthy to mention, the data indicated species with low-to moderate use-value experienced greater use-pressure. For example, Rome (Nicotiana rustica L.) and Ayahuasca (Banisteriopsis caapi Spruce ex. Griseb.) which had low to moderate use-values and therapeutic redundancy are often used in ritual for ethnomedicinal purposes (Coe and McKenna, 2017; Luna, 1986) and as a result were cited by participants to experience moderate to high levels of use-pressure. Therefore, it may be expected that species with high use-value are more likely to be used for purposes beyond medicinal qualities thus are more likely to be redundant. However, I also acknowledge high use-pressure of medicinal plant species such as *rome* (*Nicotiana rustica L.*) and *ayahuasca* (*Banisteriopsis caapi Spruce ex. Griseb.*) may be driven also by a compounding effect such as local use and the globalization and use of these species beyond traditional ethnomedicine (see for example Tupper, 2009).

While high use-pressure for some species may result in the need for community-driven conservation efforts, it is important to mention that species experiencing greater use-pressure are not necessarily threatened or declining. Demographic studies have shown that the effect of the loss of certain plant parts varies between species (Ticktin, 2004). Thus, the effect of harvest on a

given species often not only depends on the type of organ harvested but also on the life history of the species, harvesting intensity, harvesting method, and other anthropogenic and environmental factors (Sampaio and Santos, 2015; Schmidt et al., 2015; Ticktin, 2004). Furthermore, the effect of harvest has been shown to vary among life-forms (tree, shrub, herb) (Schmidt, et al., 2011). I suggest a greater understanding of the demography of medicinal plant species experiencing higher levels of use-pressure will likely inform sustainable management practices.

Understanding the influence of species therapeutic redundancy, use-values, and species use-preference on the use-pressure of medicinal plants used by the Shipibo-Konibo provided opportunity to better refine the utilitarian redundancy model. Although these findings suggest species that fulfill less redundant therapeutic functions are likely candidates for management and conservation efforts, I caution that these results and conclusions are limited to the Shipibo-Konibo community of Paoyhan. Further, research in other geographic locations should be conducted to provide comparable results and thus inform robust management and conservation efforts.

4.5.1. What are the limitations of this study?

It is important to highlight all treatments were cited as remedies for treatment of adult participants from the emic perspective. According to the Shipibo-Konibo, stronger dosages for treatments and different plant parts (i.e. barks or resins) with potentially higher concentrations of plant secondary compounds are utilized (Coe, & Gaoue 2019, unpublished data) most often for adults. Thus, the estimates of harvest or use-pressure for a given plant are likely conservative as children among the Shipibo-Konibo are often treated with other plant parts or organs such as leaves from several plants which are thought (from the emic perspective) to have less strong of an effect in terms of dosage or bioactivity. For example, the bark of *chuchuwasa* (*Maytenus krukovii A.C. Sm.*) was cited as preferred to treat diarrhea for adults and although not included in this study, children with diarrhea in the Shipibo-Konibo community are often treated with a remedy combining the leaves of several species including *binpish* (*Psidium guajava L.*), *mankoa* (Mangifera indica L.), and *tipo* (Lippia alba (Mill.) N.E.Br. ex Britton & P. Wilson). Therefore, further research on medicinal plant species treating children as well as adults are expected to yield more complete estimates of species use-pressure because they will consider the effect of plant organs harvested, species preference, and therapeutic functions. In addition, further

research on the concentration of secondary compounds in plant parts used in treatments for adults vs. children would likely yield informative results on the patterns and processes surrounding medicinal plant use and selection among the Shipibo-Konibo. Finally, I acknowledge the estimates of medicinal plant species use-pressure solely based on the *emic* perspective are limited. I suggest future estimates of species use-pressure including both the *emic* and *etic* perspective is warranted. Use-pressure estimates based combining local knowledge of harvesters and the demography of medicinal plant species will add to the reliability of these measures.

4.5.2. Acknowledgements

Chapter 5: Demographic and Transient Analysis on Ayahuasca *(Banisteriopsis caapi)*

5.1. Introduction

Harvesting of economically important plant species or non-timber forest products (NTFPs) can contribute to local livelihoods and subsistence strategies (Shackleton, 2015; Ticktin, 2004). Despite the local importance of NTFPs to rural communities worldwide, an increased global interest in these economically important plant species may result in overexploitation, greater rates of harvest, and potentially lead to negative impacts on their demographic and population dynamics thus, result in species decline. NTFP harvests often have a profound impact on the physiology and vital rates of individuals within a given population as well as community and ecosystem dynamics (Ticktin, 2004). Further, reduced yields from NTFP harvested populations may indicate a population decline and therefore warrant conservation efforts.

Tropical South America is home to many economically important NTFPs varying in life form from trees, lianas, shrubs, to herbaceous species (Baldauf et al., 2015; Peres et al., 2003; Sampaio et al., 2015; Schmidt et al., 2015). Understanding their population dynamics and response to harvest is integral to informing management practices. Responses to harvests between populations and life forms are variable. In general, high rates of harvest do not always equate to negative demographic effects as this depends on the life history of the species, harvesting intensity, type of organs harvested, harvesting method, and other anthropogenic and environmental factors (Sampaio et al., 2015; Schmidt et al., 2015; Ticktin, 2004).

To date, the use of matrix projection models is the most common approach to assess the effect of harvest on NTFP population dynamics (Caswell, 2001) where annual measurements from vital rates of individual plants within a given population are used to build a stage-structured matrix model. These data are then used to estimate the population growth rate lambda (λ) that is used to infer whether the population is expected to grow ($\lambda>1$), decline ($\lambda<1$), or remain stable ($\lambda=1$) in the long-term based on current harvesting regimes. However, it has been shown in many cases, the use of stage-structured demographic models to estimate the population growth rate may prove challenging, especially in populations where discrete stage classes of a given life-form are less obvious or cryptic. Thus, the use of Integral Projection Models (IPM) has been

proposed as an alternative approach to remedy the need for the division of life stages among discrete classes without adding any biological assumptions where life stages are defined by a continuous variable such as size (Easterling et al., 2000). Further, it has been suggested that assessing the sustainability of NTFP harvest solely using the asymptotic population growth rate may not be sufficient due to variability in λ, environmental variation, and low sample size, etc. (Schmidt et al., 2011). As a result, complementary frameworks have been proposed including elasticity analysis to account for changes in population vital rates due to the effect of harvest (see Gaoue, 2016; Gaoue, et al., 2011; Pinard, 1993). The use of IPM to infer the population growth rate lambda (λ) and estimate the response to perturbation in changes to vital rates have been shown to be robust (Mandle et al., 2015). These approaches have become widely used to estimate population growth rates and their response to harvest across a range of species however, there is a lack of a clear mechanistic understanding of the response to harvest for certain lifeforms due to a limited number of demographic studies (Schmidt et al., 2011).

Most studies to date, have investigated the effect of harvest on wild plant populations of herbaceous species, trees, and shrubs while few studies have specifically focused on lianas (Salguero-Gómez et al., 2015; Ticktin, 2004). Ecological studies on lianas have primarily examined their role in natural stand dynamics (Phillips et al., 2002; Schnitzer, 2006, 2015; Schnitzer et al., 2005) and identified their important roles in ecosystem level processes (Schnitzer, 2015), yet few studies have provided an in-depth understanding of their population dynamics (see for example Wong & Ticktin, 2015). Lianas have proven challenging to measure (Schnitzer, 2006; Schnitzer et al., 2005) and their population dynamics remain poorly understood. Though it has been demonstrated the use of both short- and long-term population growth rate (λ) along with elasticity analysis for some species of liana can inform conservation and restoration practices (Wong & Ticktin, 2015), more studies on the ecology of liana populations are needed to gain a better understanding of their response to harvest. Given lianas are also economically important NTFP's that play important role in livelihoods of cultural groups worldwide (Guadagnin & Gravato, 2013) and few studies have been done in South America to investigate their response to anthropogenic harvest, research on the effect of liana NTFP harvest on population dynamics are needed.

Ayahuasca or *Banisteriopsis cappi* (Spruce ex. Griseb) C. V. Morton is an economically and culturally important liana throughout the Amazon Region (Luna & White, 2000). *B. caapi* is

harvested for its stems and bark serving as a primary source plant for *ayahuasca* — a psychoactive tea used in traditional Amazonian ethnomedicine that has in recent years become a global phenomenon due wide-spread use in the contemporary world (Tupper, 2009). Though wild populations of *B. caapi* are found in the Amazon, they are thought to be becoming more rare at a local level (Coe and Gaoue, unpublished data). Further, increased use or harvest pressure on ayahuasca populations are expected to force harvest regimes further into the Amazon which may be a result of population decline, overharvesting or deforestation due to the intensity and frequency of logging in the area.

Studies on the effect of harvest on ayahausca are lacking. Additionally, studies assessing how the effect of bark harvest may affect the short-term population dynamics on wild *B. caapi* populations are nonexistent. The impacts of harvest on wild ayahuasca populations are expected to vary due to harvest frequency and intensity. While few studies have assessed the impacts of bark harvest on vital rates (Ticktin, 2004) of lianas, most studies to date have focused on assessing the sustainability of harvest using long-term population growth rates. These approaches which are solely based on long-term projections, may underestimate the short-term effects of harvest (Gaoue, 2016). Results of elasticity analysis of both short- and long-term population dynamics are likely critical for the development of robust management plans (Bialic-Murphy et al., 2017; Gaoue, 2016), especially, for economically important plant species that are harvested under various harvest regimes. Our understanding on how liana populations respond to perturbation of vital rates is limited. This study focuses on assessing the effect of different levels of harvest on *B. caapi* to better understand its population dynamics in the short-term. I investigated the demographic and transient elasticity patterns of *B. cappi* in response to harvest under multiple harvest treatments. As such, I examined the elasticity patterns of the of the short-term population growth rate to perturbation of vital rates for *B. caapi*. In doing so, I also assessed demographic responses to harvest of *B. caapi* through the use of IPM functions.

5.2. **Materials and Methods**

5.2.1. *Study Area*

The present study was undertaken in a Shipibo-Konibo native community territory located in the Peruvian Amazon region. The details on the location of the community and study system are left anonymous due to the globalization and economic interest of *B. caapi* harvest for the production of ayahuasca, a psychoactive tea, often used in ethnomedicinal contexts (Coe and McKenna, 2017; Luna, 1986; Winkelman, 2005). The climate in the area is tropical rainforest with a mean annual temperature of 26.4°C (Kottek et al., 2006). Annual rainfall in the area is 1600mm (Casimiro et al., 2013).

5.2.2. *Study Species*

Banisteriopsis caapi is a jungle liana in the Malpighiaceae family that is economically and culturally important to many groups throughout the Amazon Rainforest. It has been botanically described as a liana with smooth, brown bark and dark green, chartaceous, ovate to lanceolate leaves up to about 7 in. (18 cm) in length, 2-3 in. (5- 8cm) wide; Inflorescence is many-flowered; small flowers, petals 5, pink or rose-colored; Fruit is a samara with wings about 1.38 in. (3.5 cm) long (Schultes et al., 2001). It is speculated that *B. caapi* is native to either Bolivia, the Brazilian or Colombian Amazon, Peru, or Ecuador. Due to its wide range and cultivation among Amerindian groups the origin of the species is unknown (Gates, 1982).

5.2.3. *Population Dynamics and Integral Projection Model*

In this study, I gathered data on vital rates on six *B. caapi* populations using 4-ha plots for each population. Plots varied per bark harvest intensity where three plots experienced high harvest while three plots experienced low harvest regimes. Approximately 300 individuals were tagged and monitored during the *B. caapi* census July 2017-2018. For each individual of *B. cappi* within the plots I tagged and measured diameter at breast height (DBH) or basal diameter for seedlings, ramets or genets following Schintzer et al. (2008) to estimate growth. I measured survivorship for each individual from one year to the next. I measured reproducing individuals in two parts as (1) the number of seedlings produced nearest to a reproducing adult and (2) the number of ramets in genets produced by a given adult. I estimated fertility in two parts as (1) the

proportion of the total number of seedlings produced by a reproducing individual and (2) the proportion of the total number of clones produced by clonally reproducing individuals.

These data were used to develop an integral projection model (Easterling et al., 2000) composed of several size-dependent functions:

$$n(y, t+1) = \int_\Omega K(y, x)n(x, t)dx \qquad\qquad \text{eqn 1}$$

$$n(y, t+1) = \int_\Omega [p(y, x) + f(x,y)]n(x, t)dx \qquad\qquad \text{eqn 2}$$

where the vector $n(y, t+1)$ is comprised of the number of individuals of a given size at time $(t+1)$ is equal to the kernel $(K(y,x))$ times the vector $n(x,t)$ comprised of the number of individuals in a given population at time (t) (eqn 1; eqn 2).

This equation with respect to the kernel can be also defined by the survival-growth and fertility functions below:

$$p(y, x) = s(x)g(y, x) \qquad\qquad \text{eqn 3}$$

$$f(y, x) = s(x)f_f(x)f_n(x)p_g p_e f_d(y) \qquad\qquad \text{eqn 4}$$

Where the probability $p(y,x)$ that an individual will survive and grow to stage (y) if it were size (x) the year prior or $s(x)g(y, x)$ is equal to the probability an individual will survive depending on a given size $s(x)$ and $g(y,x)$ is the probability an individual will grow into a different size (y) if it were a size (x) the year prior. Further, the fertility function $f(y, x)$ or $s(x)f_f(x)f_n(x)p_g p_e f_d(y)$ is equal to the number of seedlings of size (y) that an individual or mother produced given it were size (x) the year prior, the probability that an individual will survive $(s(x))$, $f_n(x)$ how many fruit or seedlings are produced, the probability of fruit or seedling germinating P_g, the probability that given germinated offspring will become established (P_e) and the (f_d) the size distribution of the seedlings in a given population.

Given demographic data collection was gathered for only one census between July 2017-

2018, analyses of vital rates and elasticity patterns of the population growth rate (λ) are conservative representing the short-term projections and are interpreted as a representation of transient population dynamics.

5.2.4. *Analysis of B. caapi individual vital rates and elasticity patterns*

To assess the effects of harvest on vital rates of *B. caapi* I developed an Integral Projection Model (IPM) (Easterling et al., 2000; Ellner and Rees, 2006; Rees and Ellner, 2009) to build functions for growth, survival, and fertility. Vital rates were modeled as a function of size. I then used generalized linear mixed effect models (glmm) in *R* 3-4-3 (R Development Core Team, 2019) using the *lme4* package (Bates et al., 2015) to assess the effect of harvest and other covariates on vital rates (growth, survival, clonal and seedling reproduction). Random effects included plot number. Fixed-effect explanatory variables included the effect of harvest and size of *B. caapi* individuals. I log-transformed *B. cappi* size measurements to meet normality and homogeneity of variance assumptions. I also used generalized linear models (glms) to assess the effects of harvest and size on the number of seedlings and clones produced. The response variables for the glmm models were measurement data for growth, and binary data for survival and the probability of clonal and seedling reproduction. The response variables for the glm models were count data. Therefore, I used glmms or glms with normal, binomial, and poisson error structures (Crawley, 2013). I used an information-theoretic approach following Gaoue et al. (2011) to select the best fitting models that had greater explanatory power, where, for each response variable I estimated the Akaike information criterion (AIC) for each model, the difference in the AIC between each model, and the model with the lowest Δ AIC. I then, selected the models with the lowest Δ AIC < 2 (Gaoue et al., 2011).

Using data gathered on vital rates and the functions described above (see eqn 1; eqn 2), I developed a kernel for B. caapi using the *popbio* package (Stubben and Milligan, 2007) in R (R Development Core Team, 2019). To assess the effect of perturbation on vital rates I conducted elasticity analysis following Easterling et al. (2000):

$$e(Z_1, Z_2) = \frac{k(Z_1, Z_2)}{(\lambda)} \times \frac{v(Z_1)w(Z_2)}{(w,v)} \qquad \text{eqn 5}$$

where (v) and (w) are the left and right eigenvectors of λ and $k(Z_1, Z_2)$ represents the kernel derived from IPM. In this approach elasticity analysis estimates the change in λ resulting in changes in vital rates of individuals of a given size-class distribution (Easterling et al., 2000).

5.3. Results

5.3.1. Transient Elasticity Patterns of B. caapi in response to harvest

The relative contribution of size to λ are dominated by large individuals under both harvesting treatments. Thus, elasticity patterns for *B. caapi* indicate survival of long-lived mature individuals had the greatest proportional changes to the short-term λ and are driving population dynamics by playing a central role to long-term persistence (Figure 5.1a, b). Further, irrespective of harvest intensity, the short-term transient elasticity analysis shows that the best approach to improve the short-term population growth rate is to ensure the high survival of large individuals with size greater than 4.5 mm log scale (Figure 5.1a, b). This contrasts with previous studies suggesting that survival of young individuals contribute most to the short-term population dynamic of long-lived species. Such differences could be explained by low seedling recruitment in the liana populations and subsequent lack change in the number of young individuals over time.
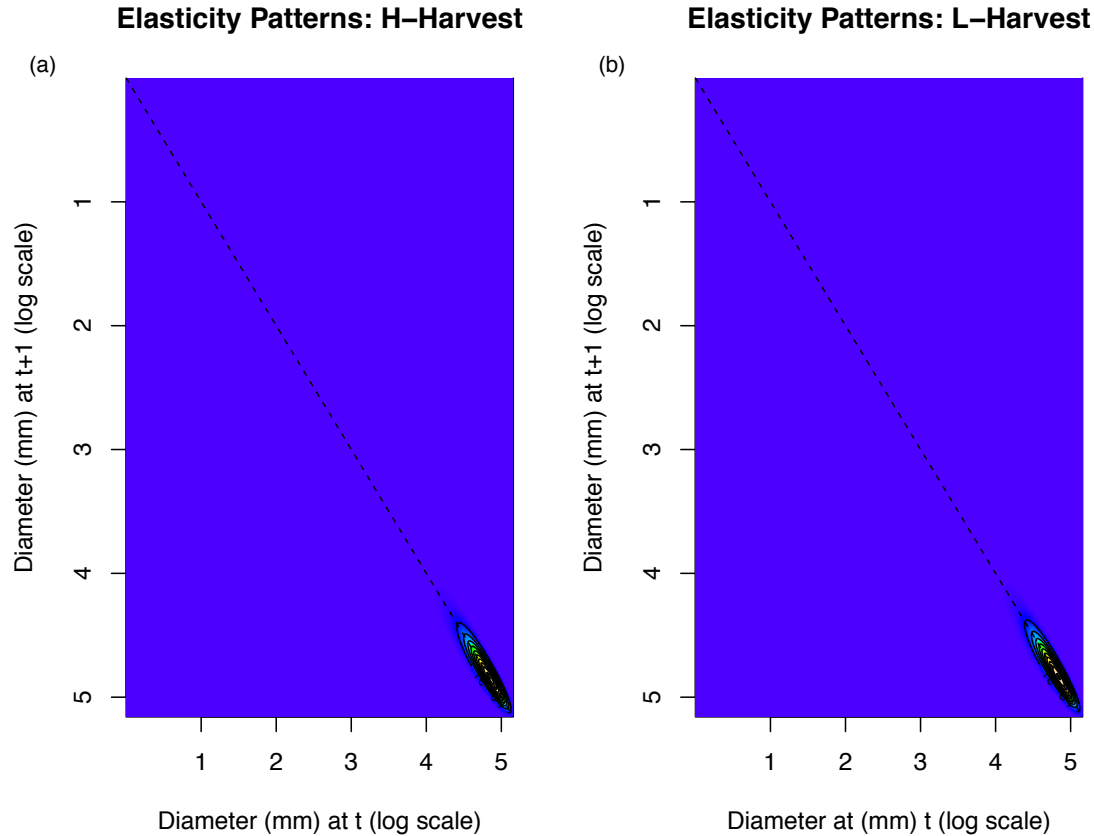
Fig 5.1. Elasticity contour plot for the Ayahuasca (*B. caapi*) kernel. Elasticity patterns of the short-term population growth rate are represented as follows where A = elasticity patterns of *B. cappi* under high harvest conditions and B = elasticity patterns of *B. caapi* under low harvest conditions. The dashed-line represents the survival intercept obtained from survival-growth functions and general linearized mixed effect models.

5.3.2. Ayahuasca demographic responses to harvest

The size of the lianas in the population that were measured at time t +1 (July 2018) were positively correlated with their initial size measured at time (t) (July 2017) (Fig 1a). Individual liana size also had a significant effect on growth suggesting larger individuals within the population experienced greater growth rates. Annual changes in plant size from (t) to t+1 (2017-2018) were independent of harvest and plot as supported by the model (β =0.9389424 +/- 0.03522582, t = 26.654947, p = 0.0000). Survival of the lianas was greatest for individuals of intermediate sizes (Figure 2b).

There was no significant effect of harvest on the growth for ayahuasca *(B. caapi)*. However, harvest had a significant effect on survival (β=-2.3413+/-0.7692, z=-3.044, p= 0.00234). The high harvested population has a lower survival rate than the low harvested populations. There was a significant interactive effect of harvest and plant size on survival of B. caapi (β= 0.8775 +/-0.3542, z=2.477, p = 0.01325) suggesting survival of smaller individuals is greater in the high harvested populations than low harvested populations. Further, size of individual liana's had a significant effect on survival (β= 0.4681, +/- 0.2299, z=2.037, p=0.04170) suggesting the probability of survival was dependent on size. Large individuals 2.5mm log scale were more likely to experience mortality in high harvested populations (Figure 5.1b). For such a long-lived species life history theory suggests that survival of large individuals are most likely to drive the long-term population dynamics. The reduced survival of large individuals in harvested sites suggests that high level of harvest of large individuals may result in reduced in overall population growth rate.

In contrast, there was no significant effect of harvest on clonal reproduction. The size of individuals was shown to have a significant effect on the probability of reproducing clonally (β=2.1176 +/- 0.7941, z= 2.667, p= 0.007660; Figure 5.2d) where intermediate size class of lianas produced the greatest number of clones (Figure 5.2d). Intermediate and larger size class of lianas produced the greatest number of seedlings (Figure 5.2c). There was a significant interactive effect of harvest and plant size on the number of seedling produced of B. caapi (β= -20.283 +/-6.609, z=-3.069, p= 0.00215). Further, irrespective of plant size, harvest had a significant effect on the number of seedlings produced (β= 67.912+/-21.123, z=3.215, p=0.00215).
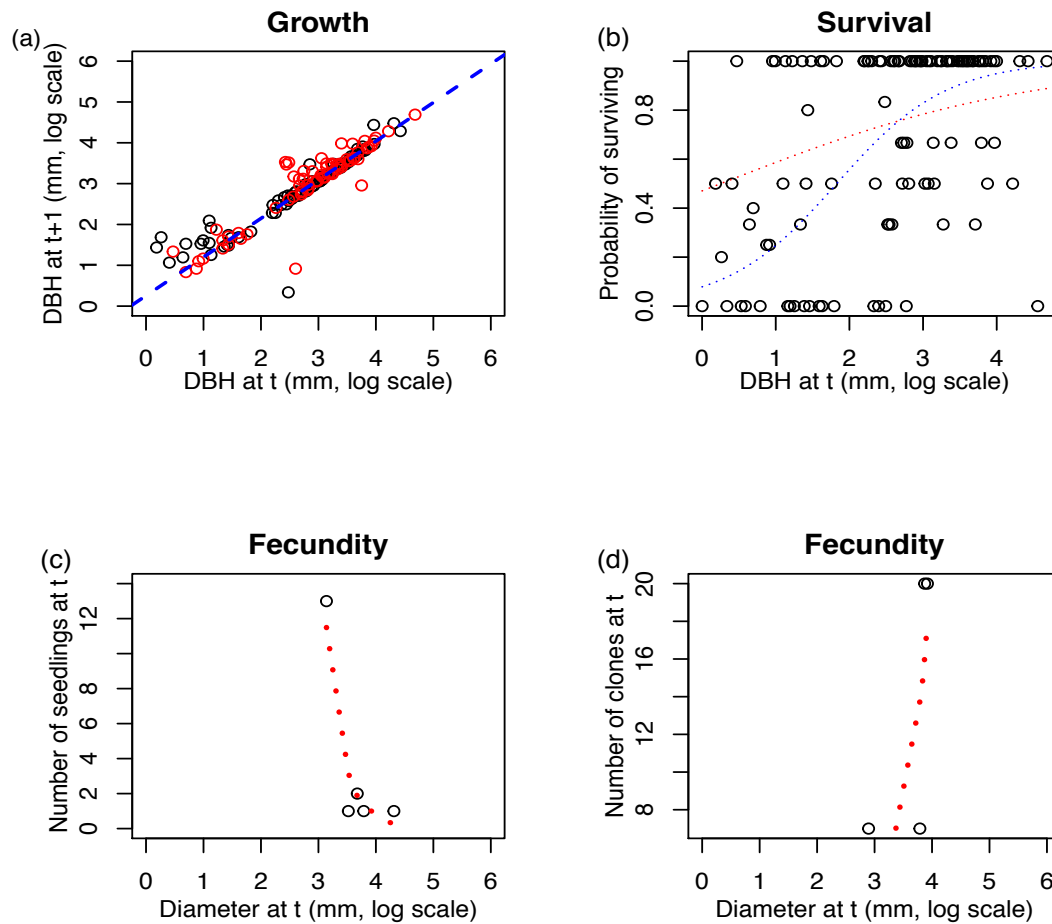
Fig 5.2. Demographic functions (vital rates) for B. caapi. A = growth (log scale) as a function of size (measured in mm) July 2017 – July 2018, B = the probability of survival to July 2018 as a function of size (log scale, previously measured in mm) in July 2017. The red dashed line represents the regression coefficient for high harvest whereas the blue dashed line represents the regression coefficient for low harvest intensity. C = the number of seedlings produced as a function of size (log scale, previously measured in mm) in 2017. D = the number of clones produced as a function of size (log scale, previously measured in mm) in 2017.

5.4. Discussion

I have shown that demographic functions for ayahuasca *(B. caapi)* under the effect of harvest are important to consider in terms of sustainable management approaches (Figure 5.1a; 5.1b; 5.1c; 5.1d). Results indicate that intermediate to larger size lianas had a higher probability of survival (Figure 5.1b) under the effect of harvest. I expect this may be a result of seedling or clonal mortality (Coe, unpublished data) or lack of seedling recruitment due to abiotic, biotic, or

anthropogenic factors. I found intermediate to larger size classes of lianas had a higher probability of reproducing clonally (Figure 5.1d) which may be an indirect effect of harvest as there were fewer seedlings (n= 18) produced than clones (n=54) in response to harvest. This finding warrants further investigation. I found harvest had a significant effect on the number of seedlings produced which I expect could be a life-history strategy in response to anthropogenic harvest as an abiotic stressor. I caution this finding is likely conservative due to sample size and lack of other studies with reproducible findings in similar geographic ranges and climatic conditions. Given there were fewer seedlings produced than clones in this study, future research investigating the life history strategies of ayahuasca (*B. caapi*) and trade-off of favoring clonal reproduction rather than seedling production in response to harvest is critical for understanding not only the population dynamics of ayahuasca in natural habitats but also possible patterns and processes surrounding genetic variability or lack thereof this species in a modern context. I found higher harvest intensity had a significant negative effect on the probability of survival. Given most harvested lianas were of larger size classes (Coe, unpublished data), I expect this effect of harvest is due to the increased harvest pressure and demand linked to the economic value and widespread use of ayahuasca. This said, there was no support for a significant negative effect of harvest of *B. caapi* under low harvest conditions.

I have highlighted the importance of elasticity analysis in determining vital rates that are likely critical for implementing management approaches for *B. caapi*. The elasticity analysis has shown that survival of mature ayahuasca vines are important for the persistence of the liana populations in the short-term (Figure 5.1a, 5.1b). This finding is supported by prior research (Franco and Silvertown, 2004) that has demonstrated survival of long-lived individuals of certain lifeforms such as trees and likely lianas often have a greater relative importance to the contribution of the population growth rate (λ) compared to short-lived species such as perennials. Although it expected that survival of long-lived species are likely to play a more central role in the relative contribution to the long-term population growth rate (λ) (Franco and Silvertown, 2004; Silvertown et al., 1993), I am unaware of any study investigating the transient elasticity patterns of ayahuasca (*B. caapi*) in response to harvest. Interestingly, the contribution of survival of mature ayahuasca vines to the short-term population grow rate (λ) were similar under both high and low harvest treatments (Figure 5.1a, 5.1b). Given it has been cautioned long-term elasticity analysis may not always adequately describe the relative importance of vital rate life

stage contributions to the short-term population growth rate (λ) (Bialic-Murphy et al., 2017; Haridas and Tuljapurkar, 2007), I suggest future research investigating both the short and long-term elasticity patterns of ayahuasca is critical to understanding population dynamics and for the development of sound management plans for this culturally and economically important NTFP plant species.

Chapter 6: Conclusion

In reviewing the literature on cultural keystone species (chapter 2) it was clear that most studies to date have cited or applied keystone designation to a given species without a direct test of the theory. Results also indicate while most studies on cultural keystone species occurred in North America, few studies occurred in Australia, Europe, and Africa suggesting research on cultural keystone species in these areas is limited. Given the potential for the cultural keystone species theory to aid in informing resource management, it is likely further understanding on how we apply cultural keystone designation will lead to the development of consistent methodologies for identifying cultural keystone species, further advance ethnobotanical theory and conservation strategies.

To assess how the cultural keystone species theory has been tested, the second part of this study (chapter 3) tested if twelve commonly used cultural importance indices predict species cultural keystone status. This study was conducted the Shipibo-Konibo community of Paoyhan in the Peruvian Amazon region. Surprisingly, results indicated most indices were redundant or strongly correlated and did not predict species cultural keystone status. Although there was support for the QUAV index, findings suggest its predicative power on species cultural keystone status is limited thus the cautious use of cultural importance indices as a metric to infer species cultural keystone status is suggested. It is noteworthy that results show a significant part of the predictive power of this index is related to species shared evolutionary history suggesting it is important to control for evolutionary relatedness between species.

Considering it is expected that culturally important plants fulfilling non-redundant therapeutic roles in a local ethnomedicine are likely to experience greater use or harvest pressure, the third part if this study (chapter 4) tested the major prediction of the utilitarian redundancy model. Interviews and focus group discussions were conducted in the Shipibo-Konibo community of Paoyhan among local specialists, harvesters, and those with general knowledge. Contrary to expectations, local importance (use-value) was strongly correlated with species therapeutic redundancy therefore, it was removed as a predictor of medicinal species use-pressure. Results indicated therapeutic redundancy predicted medicinal species use-pressure supporting the utilitarian redundancy model. Further, as expected, results indicate the local preference of a given medicinal plant to treat a given illness over other species that can treat the same illness, does affect harvest pressure. However, when controlling for shared species

evolutionary history, preference alone did not significantly predict species use-pressure suggesting it was dependent on the effect of redundancy—where less therapeutically redundant species that were preferred experienced greater levels of use-pressure.

Since ayahuasca (*Bansteriopsis caapi)* is culturally important among the Shipibo-Konibo and its use in ethnomedicinal contexts has become widespread, it is expected to experience the high levels of use-pressure. Thus, it was selected for a demographic study (chapter 5) to test the effect of harvest on vital rates and elasticity patterns of the short-term population growth rate λ. Demographic censuses were conducted in a localized region of the Peruvian Amazon in Shipibo-Konibo community territory between July 2017 – 2018. Results indicated that survival of large individuals are important for the persistence of the ayahuasca populations in the short-term. Given the local importance of ayahuasca, it role as an NTFP, and widespread use globally, this study provides insight for local community driven management plans with implications for sustainable harvest.

APPENDIX A: SUPPLEMENTAL TABLES

Table A-1: [Chapter 2] Cultural Importance indices

Species uses	Species use values	Index	Authors
y	y	$ICS = \Sigma qie$	Turner, 1988; Garibaldi & Turner 2004
y		$Cis = \Sigma\ UR_{ui} / N$	Tardio & Padro-de-Santayana, 2008
y		$CVe = U_{Ce}\ Ic_e\ \Sigma Iu_{ee}$	Reyes-Garica et al. 2006
	y	$CSI = \Sigma(iec) \times CF$	Silva et al., 2006
y		$QUAV_s = QUV_s\ IAR_s$ $QUV_s = \Sigma QU_i / N,$ $IAR_s = N_i - N_i / N_i - 1$	Thomas et al., 2009
y		$CSCI = SI\ [\ \Sigma\ (m\ pr\ f) + \Sigma\ (QMU+pp+d)]$	Tudela-Talavera et al., 2016
y		$RFC = FC_s / N$	Bennet & Prance 2000; Tardio & Padro-de-Santayana, 2008
y	y	$RI_s = (RFC_{(max)} + RNU_{(max)}) / 2$	Pardo-de-Santayana, 2003
y		$UV_s = \Sigma\ UV_{is} / N_i$	Phillips & Gentry 1993a; Albuquerque et al., 2006
y	y	$EICS = \Sigma(p/uiec)$	Stoffle et al., 1990
		$FL = (I_p /I_u)*100\%$	Freidman et al., 1986
y		$EIVI = ((U_q *5) + (C_i *4)+ (P_{fm}*3) + (P_{is}*2)+ (P_o *1)) / 15$	Lajones & Lemas, 2001

Illnesses / health conditions treated for each species	Quality of species use	Plant use frequency	Species preference	Species management	Species irreplaceability	Psycho-socio-cultural function	Species ethnotaxonomic diversity
	y	y	y		y	y	y
		y	y	y			
y	y						
y	y	y	y	y			
y			y				
	y						

Plant origin	Life-form (plant habit)	Collection locality	Number of participants that cited the principal use of the species	Contemporary use	Number of participants citing plant species	Availability (is the plant available to harvest (emic)	Plant part used
				y			
					y		
					y		
					y		
						y	y
					y		
					y		
					y		
				y			
			y		y		y
y	y	y			y	y	y

Indicators

i = intensity (5-1) **q** = quality of use (5-1) **e** = exclusivity of use (5-1)	**Σ UR** = The sum of the proportion of participants who mention each species use. **N**= total number of participants	**UC** = the total number of uses for a given ethnospecies / total possible number of use catagories. **ICe** = Number of participants who listed a species as useful / by total number of participants. **ΣIUce** = Number of participants who mentioned each use-category (therapeutic function) for the ethnospecies divided by the total number of participants.	**i** = species management(managed 2,1) **e** = Use Preference (preferred 2,1) **c** = Use Frequency [frequently (2, 1] **CF** = Correction factor (number of citations for a given species divided by the number of citations for the most-mentioned species).	**QU** = the sum of all the qualites of medicinal uses assigned to a given species (scoring is ranked as follows: (a) good to excellent, (b) fair, or (c) bad, to where values of 1, 0.5 and 0.25) **N** = the number of participants interviewed for a given species **N** = the total number of medicinal responses registered for species **N** = the number of ailments or health conditions that are treated with this species **IAR =** range from 0 to 1, 1 (where the total number of participants agree upon the use of the species for a given illness).	**SI** = Smith's index. **m** = resource management m = [2; 1] **pr** = preference of use. : pr = [2; 1]. **f** = frequency of use. [2; 1]. **QMU** = quality of medicinal use. QMU = [3–0.5]. **pp** = part of the plant used. (e.g., roots): pp = [3–0.5]. **d** = availability of the resource. d = [1–5].	**FC** = The number of Participants who mention the use of the species. **N** = total number of participants .	**RFC** = total number of participants that mention a given species as usefull / total number of participants citing any species (most cited species) **RNU** = number of use catagories (therapeutic functions for (focus) species / the maximum number of use catagories (therapeutic functions) mentioned for a species cited	**Uvs** = the sum of number of uses mentioned by each participant **N** = the total number of participants	**(p/u)** = The sum of the total number of uses and/or plant parts used for a specifc purpose **i** = intensity of use (2,1) **e** = exclusivity of use (2,1) **c** = contemporary usage (2, 1)	**FL**=(*I*p /*Iu*)*100% **Ip**=number of participants that cited the principal use of the species (greatest number of citations for a given therapeutic function) **Iu**=total number of participants that cited the species for any purpose	**U** = use quality **C** = collection locality **P** = plant habit **P** = part utilized **P** = plant origin

Table A-2: [Chapter 2 & 3] Interview questions to estimate cultural importance indices and species use-pressure.

Interview Questions (English and Spanish)

What are the names of the plants you use for healing? Cuales los nombres de las plantas su utiliza para curar enfermidades?

What are the names for this plant? Cuales los nombres de este planta?

What are the uses for this plant? En que sirve?

Are there stories or songs for this plant? Hay cuentas o canciones para este planta?

Does this plant have a spirit? Tiene un espititu?

Is the plant used in rituals? Se utiliza en ceremonia?

Is the plant traded or sold? Se vende este planta?

What plant parts do you harvest or use? Que parte tienes que cosechar?

How much of this plant do you harvest? Cuanto cosechas en un mes?

How often is this plant harvested? Cosechas este planta frequemente? o rara vez?

What plant do you prefer to cure this illness? Cuales la preferencia entre los plantas para curar?

Are there other plants used to cure the same illness? Hay otras plantas para curar este enfermidade?

Where do you harvest this plant? donde encuentras este planta? La selva? La chacra?

Is the plant available to harvest? Esta disponible para cosechar?

Is this plant remedy good, fair, or poor? Este remedio bueno? mas o menos? malo?

How often is the plant used to treat an illness? Se utiliza frequemente? o rara vez?

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