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Phylogeny explains why less therapeutically redundant plant species are not necessarily facing greater use pressure

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Abstract

1. Understanding which factors influence medicinal plant species selection and harvest or use pressure can provide valuable insights for sustainable management of natural resources and conservation efforts. The utilitarian redundancy model, a theoretical framework in ethnobotany, suggests that species that are therapeutically redundant or fulfil similar therapeutic functions within traditional ethnomedicine are less likely to be under greater use pressure. However, species' evolutionary relatedness and the preference of certain species over others to treat a given illness can directly affect how use pressure is diffused across several groups of species. These factors may alter the strength of the therapeutic redundancy–use pressure relationship.
2. Medicinal plant species that fulfil the same therapeutic functions may experience greater use pressure despite their level of therapeutic redundancy because they are preferred, where most people select these species preferably over other species that are equally available for a given treatment. Furthermore, species that are closely related evolutionarily may be more likely to be harvested not because they are therapeutically unique but because they share evolutionary traits such as secondary chemistry with other medicinally important species which may make them more prone to being harvested.
3. We investigate the effects of species therapeutic redundancy, use value, preference and evolutionary relatedness on species use pressure in the Shipibo-Konibo community of Paoyhan in the Peruvian Amazon region. We used phylogenetic generalized least squares models to identify significant predictors of species use pressure for 62 medicinal plant species cited by 30 participants and fulfilling 31 therapeutic functions in Shipibo-Konibo ethnomedicine.
4. Our model controlling for species' shared evolutionary history indicated that therapeutically redundant medicinal plants experienced greater levels of use pressure. However, as preference increased, the effect of therapeutic redundancy on species use pressure became less positive. Contrary to predictions, species preference by local people alone did not predict use pressure. Furthermore, when we

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control for species' shared evolutionary history, the effect of preference on species use pressure was dependent on therapeutic redundancy.

5. Our study illustrates the importance of controlling for evolutionary relatedness between species in studying plant–human interactions and the complexity involved in employing the utilitarian redundancy model to inform management and conservation efforts.

KEYWORDS

biocultural conservation, ethnobotany, phylogenetic generalized least squares, phylogenetic signal, species evolutionary relatedness, theory in ethnobotany, utilitarian redundancy model

1 | INTRODUCTION

Understanding medicinal plant selection by cultural groups from a psycho-social-cultural perspective is a central goal of ethnobotanical research (Schultes & Von Reis, 1995). 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 e.g. 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 & 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 e.g. Balick & Cox, 1996; Luna & White, 2017; McKenna et al., 1995; Rivier & Lindgren, 1972; Schultes & Von Reis, 1995).

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 (Seyler et al., 2019; Vandebroek & Balick, 2012; Vandebroek et al., 2004), non-random selection of medicinal plants for ethnomedicinal uses (Bennett & Husby, 2008; Ford & Gaoue, 2017; Moerman, 1979) and community-based conservation approaches driven by locally enforced taboos (Colding & 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. Such an understanding of underlying drivers can aid in designing more culturally relevant and ecologically sound plant use policies.

The utilitarian redundancy model has emerged as a complementary framework that highlights how species cultural values can be used in defining conservation priority (Albuquerque & Oliveira, 2007; Gaoue et al., 2017). The central prediction of the utilitarian redundancy model is that plant species that are culturally important, used for the multiple purposes, and fulfil a unique or non-redundant therapeutic function within local ethnomedicine, are more likely to be under greater use pressure (Albuquerque & Oliveira, 2007; Nascimento et al., 2015). In contrast, 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 therapeutic redundancy (Albuquerque & Oliveira, 2007; Alencar et al., 2014; Ferreira et al., 2012) to help identify focus species for conservation and to understand the effects of species use values and preference on the use pressure (Albuquerque & Oliveira, 2007; Ferreira Júnior et al., 2012) of medicinal plants in a local ethnomedicine. Although 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. Furthermore, 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 of high concentrations of secondary plant compounds often employed for ethnomedicine (Ford & Gaoue, 2017; Heinrich & Verpoorte, 2012; Moerman, 1979; Souza et al., 2018). In addition, plant family has been shown to be a strong predictor of species use values (Phillips & Gentry, 1993a). 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 (a) understand the effect of species shared evolutionary history on medicinal species use pressure and (b) to understand the effect of species use preference, therapeutic redundancy and species use value on species use pressure of medicinal plant species used for ethnomedicine in the Ucayali river region of the Peruvian Amazon rainforest. As such, we asked if species that are phylogenetically close tend to have similar use pressure or therapeutic redundancy. Furthermore, we asked if therapeutically redundant species and those that are preferred by local people are more likely to be threatened by high use pressure.

2 | MATERIALS AND METHODS

2.1 | 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 approximately 1,600 mm. The community is approximately 132.3 m above sea level (Casimiro et al., 2013). Approximately 2,000 inhabitants in the community rely on harvesting of economically important trees as well as non-timber forest products for livelihood strategies and medicinal use.

The Shipibo-Konibo community of Paoyhan is located several hours away by boat from larger cities such as Pucallpa where numerous pharmacies are located (approx. 154 km away from the nearest pharmacy). Research demonstrated a direct correlation between the loss of medicinal plant knowledge and the proximity of a given community to a pharmacy (Vandebroek & Balick, 2012; Vandebroek et al., 2004). The location of Paoyhan along with the Shipibo-Konibo's magico-religious beliefs associated with plant medicines and animistic cosmologies is expected to contribute to the persistent use of plant medicines as the primary source of healing and treatment of illnesses within the community. In this context, the majority of the Shipibo-Konibo not only can identify medicinal plants on sight but also prepare remedies from them for treatment. Given the climatic conditions with only two seasons (wet and dry) and cultivation of medicinal plants in *chakras* (local cultivated areas), community members consisting of harvesters, medicinal plant experts and community members with a general knowledge of medicinal plants have access to plants year round. In certain cases where plant phenology (i.e. timing of new growth, flowers, etc.) is important for a given treatment, medicinal plant-derived extracts are often prepared from harvested species' biomass and stored for subsequent therapeutic use. Thus, the constant and sophisticated use of plant medicines within the community provides a context where local knowledge is expected to persist along with its uses for healing. This was critical for investigating how therapeutic value of medicinal plants may influence use pressure and potentially threaten species to extinction.

2.2 | Informed consent, interviews and participant observation

2.2.1 | Triangulation of methods

We used semi-structured interviews and free listing, an elucidation technique commonly used in the social sciences that seeks to identify specific information on a given cultural domain of the investigated community (Albuquerque et al., 2014). As such, each participant was asked to list the medicinal plants they know and their uses for treating illnesses in ethnomedicinal contexts according to the participants' emic perspective. Semi-structured interviews were used because they allow for greater flexibility during the interview process compared to structured interviews and they allow for guided or specific data collection on a given cultural domain compared to unstructured interviews. Furthermore, this approach allowed for more precise data collection as we aimed to get an in-depth understanding of medicinal plant use by knowledgeable participants without having to interview the same participant more than once, which, is not always possible (Albuquerque et al., 2014; Bernard, 2017). These approaches were coupled with focus group discussions supplemented by participant observations and *walk in the woods* (Albuquerque et al., 2014) to collect data that were used 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. The use of such *triangulation of methods* recommended in ethnobiology seeks to ensure the reliability of data collected where one method is used to verify or cross-reference the responses obtained from another elicitation technique (Albuquerque et al., 2014). In addition, some elicitation techniques were used to obtain specific data as we describe below.

2.2.2 | Participant selection

We interviewed 30 participants (13 men and 17 women) at least 18 years old (ages: 25–91) who were all local experts and harvesters using a snowball sampling approach following Albuquerque et al. (2014) and Bernard (2017). Locally recognized participants considered knowledgeable medicinal plant specialists facilitated introductions to adept community harvesters and experts in traditional ethnomedicine employed by the Shipibo-Konibo for healing and treatment of illness. We selected these experts because the goal of the elicitation here was to elucidate the medicinal uses of the plant species in the study area and we need to obtain a reliable sample of the ethnopharmacopoeia used by the Shipibo-Konibo for medicinal purposes.

2.2.3 | Ethical considerations

Fieldwork was conducted between June 2017 and July 2018 (on average 16 days a month). Prior to each interview, we obtained free and prior written informed consent. Participation was voluntary and in accordance with University of Hawaiʻi at Mānoa IRB (CHS#23611). All interviews and focus group discussions were recorded 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. All interview questions were based on medicinal plants that exist in the community or the surrounding area (community territory of Paoyhan).

2.3 | Estimating species use values

During the semi-structured interviews, we asked each of the 30 participants to free list the medicinal plant species they know and their therapeutic uses. This resulted in a list of medicinal plant species cited by each participant and the medicinal uses listed for each species (Albuquerque et al., 2014). This approach was coupled with a *walk in the woods* and a standardized format for semi-structured interviews where we asked the participants follow-up questions 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. To gain a deeper understanding of medicinal plant use among the Shipibo-Konibo, participant observation was employed to observe medicinal plant harvest, preparation and species use in ritual (Albuquerque et al., 2014) which allowed for a more enriching data collection. In doing so, we used notes, audio recordings and photographs to aid in the data collection. The goal of the complementary participant observation and *walk in the woods* or *guided tour* (Albuquerque et al., 2014) was to verify the botanical identity of medicinal plants cited by participants in situ with one or more participants considered local medicinal plant experts. These guided tours were also used to collect botanical specimens cited by participants during interviews and to observe the biomass they harvested for each species. Medicinal plants cited by participants were later taxonomically identified and deposited in the UNAP (Universidad Nacional de la Amazonia Peruana) Herbarium.

The list of medicinal plant species cited by each participant was used to estimate a species use value index ($UV = \Sigma U_i/n$) adapted from Phillips and Gentry (1993b). This index, UV, estimates the relative importance of each plant species cited from a local perspective (Albuquerque et al., 2014; Lucena et al., 2007). In the formula, U_i is the number of uses cited for a given species by each participant i and n is the total number of participants. As such, UV is the average number of therapeutic uses participants cited for a given species.

2.4 | Measuring therapeutic redundancy

For each medicinal plant species cited by participants during interviews, we also recorded their local medicinal uses. This was used to determine the local therapeutic categories and disease classifications for the study region. 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). 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 & Oliveira, 2007), these approaches may be limited by subjectivity due to authors directly assigning weight to levels of redundancy (e.g. where *highly redundant* represented >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, we calculated species therapeutic redundancy as $R = (\Sigma S_i/n) \times W$. In this formula, ΣS_i is the sum of the total number of plant species that can be used to treat a given illness or fulfil a given therapeutic function across therapeutic functions cited for a single species, n is the total number of species cited by participants and W is the total number of therapeutic functions fulfilled by a given species. It is important to mention that species therapeutic redundancy is estimated here as the total therapeutic redundancy of each species in an existing pharmacopeia cited by participants in accordance with the utilitarian redundancy model (Albuquerque & Oliveira, 2007). For example, if species x is cited to treat cataracts and nausea, it fulfils two therapeutic functions and there are two species totally cited to treat cataracts and three species totally cited to treat nausea out of 62 species cited by participants, then redundancy equals: $((2 + 3)/62) \times 2) = 0.161$ units. Therapeutic redundancy estimates for medicinal plant species cited by participants ranged between a low of 0.032 units and a high of 5.8 units.

2.5 | Estimating species use pressure and preference

We used focus group discussions (Bernard, 2017) to estimate the use preference and the local perspective of use pressure for all the medicinal plant species that were previously free listed. Following initial interviews among the general community, 10 participants consisting of local experts and community harvesters were selected for two focus group discussions regarding species use pressure and use preference (Albuquerque et al., 2014). Each focus group discussion was approximately 90 min in duration. The first focus group consisting of participants with expert medicinal plant knowledge was conducted to elucidate the use preference for medicinal plants fulfilling 31 therapeutic functions cited by participants. The second focus group consisting of harvesters and participants with expert medicinal plant knowledge was conducted to elucidate species use pressure for 62 medicinal plant species cited by participants. Furthermore, all final responses elucidated during the focus group discussions were considered a consensus by community members according to the emic perspective.

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. Although this approach may be limited in terms of a direct measure of species harvest or use pressure, our intention of this study was not to evaluate the conservation status of species per se. Rather, it was to evaluate the relationship between the local perspective of use pressure and species preference. Given that 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. Although harvesters in the community of Paoyhan often employ subsistence strategies involving the additional harvest of economically important trees and other non-timber forest products for local sale or commercial use, our use pressure estimates are based solely on medicinal plant species use in ethnomedicine at a community level.

During the focus group discussion, participants consisting of harvesters and local experts were asked to estimate how much biomass was harvested per month at the community level for each medicinal species cited to fulfil a given therapeutic function during the free listing and semi-structured interviews. To elucidate a single value representing the use pressure of a given species, participants discussed use pressure estimates and established a consensus for a final response. As such, use pressure for a given species was estimated as kilograms of biomass (the local unit of measurement) harvested per month by the community. Use pressure estimates ranged between 0.5 and 110 kg of biomass harvested per month by the community.

To estimate the use preference for the 62 medicinal plant species cited by participants, we asked the 10 local experts in the focus group discussion which species were preferred over others to treat a given illness according to traditional ethnomedicine practiced by the community. To elucidate a single value representing a preferred species over others fulfilling a given therapeutic function, participants discussed their preference and established a consensus for a final response. During the focus group discussion, the preference of a given species over others to treat 31 cited therapeutic functions were elucidated. To ensure objectivity and reduce the potential for researcher biases, all data on species cited as preferred to fulfil a given therapeutic function were ranked as binary where a value of 1 = preferred and 0 = not preferred.

All data collected during free listing, semi-structured interviews, walk in the woods and focus group discussions were used to compile a database that was subsequently imported into analytical software described below.

2.6 | Data analysis

To test the effects of species use preference, redundancy and use values, on species use pressure, we used general linear models (GLM) and phylogenetic generalized least squares (PGLS) in R 3.4.3 (R Development Core Team, 2019). Because our response variable, use pressure, was estimated as a measurement (biomass), we used a Gaussian error structure for both models (Crawley, 2013). Prior to running our models, we tested for a correlation between predictor variables and excluded any that were significant (McGarigal et al., 2013). The PGLS model in addition to testing the effects of preference, redundancy and use values, also controlled for phylogenetic relatedness between medicinal plant species. We compared outcomes of both models to understand role of species shared evolutionary history (Heinrich & Verpoorte, 2012) on the prediction of species use pressure. Controlling for species evolutionary relatedness in our models allows us to account for non-independence between observations due to phylogenetic history between species (Mundry, 2014). This allowed us to provide a direct test of our predictor variables on medicinal plant species use pressure.

To develop the PGLS model, we built a phylogeny of medicinal species cited by participants using the *S. PhyloMaker* function in R (Jin & Qian, 2019; Qian & Jin, 2016). Our phylogenetic tree was built by pruning a mega-tree comprised of molecular data from GenBank, phylogenetic data from the Open Tree of Life and fossil records. It includes all plant families, approximately 10,000 genera and 70,000 species of vascular plants in the world. As such, our phylogenetic tree generated by the *S. PhyloMake*r function consists of plant species cited by participants where all plant families and the majority of genera were resolved (Jin & Qian, 2019). For both GLM and PGLS models, we started with a saturated model that included all the three predictors (preference, redundancy and use value), and developed subsequent nested models' candidates by sequentially removing one of the predictors. To select the best fitting models, we estimated the ΔAIC (Akaike information criterion) for each model (Crawley, 2013) as the difference in the AIC between each model and the model with the lowest AIC. We then selected models with $\Delta AIC < 2$.

The distribution of plant secondary chemistry depends on plant family and shared evolutionary history (Ford & Gaoue, 2017; Heinrich & Verpoorte, 2012; Moerman, 1979; Souza et al., 2018). This could drive species use preference and therapeutic redundancy. As such, we asked if species that are phylogenetically close tended to have similar use pressure or therapeutic redundancy. To gain better insights into such processes, we tested for a phylogenetic signal in species therapeutic redundancy and use pressure using the *phylosig* function of the R package PHYTOOLS (Revell, 2012). The phylogenetic signal describes the degree to which closely related species share similar traits (Blomberg et al., 2003). We estimated Pagel's λ, which ranges from 0 (no phylogenetic signal) to 1 (strong phylogenetic signal) (Pagel, 1999). We then used a log likelihood ratio test to examine if λ was significantly greater than zero.

3 | RESULTS

3.1 | Correlated predictors

We found species use value was strongly correlated with redundancy ($r^2 = 0.80$). Subsequently, we excluded use value as a predictor of species use pressure in our GLM and PGLS models.

3.2 | Medicinal plant species and illnesses

In all, 62 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. In all, 31 local therapeutic categories were cited by participants. Most plant species were often used to treat the following illnesses: diarrhoea (n = 17 species), rheumatism (n = 17 species), clean wounds and cuts (n = 15 species) and body pain (n = 13 species) (Figure 1a). In contrast, fewer plant species were used to treat AIDS (n = 2 species), heal or remove scars (n = 2 species), as an anti-purgative (n = 2 species), and to treat cataracts (n = 2 species) (Figure 1a). The species with the highest level of therapeutic redundancy were *Jatropha curcas* L. (j. cur) with 8.13 units, *Ocimum campechianum* Mill. (o. camp) with 5.87 units and *Maytenus krukovii* A.C. Sm. (m. kruk) with 5.48 units (Figure 1b). This indicates these species are among the most versatile medicinal plants within Shipibo-Konibo ethnomedicine in that they share several similar therapeutic functions with other species. In contrast, species with the lowest level of therapeutic redundancy were *Cyperus* sp. (c. sp.1) with 0.04 units, *Paspalum conjugatum* P.J. Bergius (p. conj) with 0.03 units and *Abuta grandifolia* (Mart.) Sandwith (a. gran) with 0.03 units (Figure 1b) suggesting these species fulfil unique or non-redundant therapeutic functions within Shipibo-Konibo ethnomedicine.

3.3 | Do species therapeutic redundancy and use preference affect species use pressure?

The main effect of species use preference on use pressure was marginally significant ($\beta_{PGLS} = 9.86 \pm 5.32$, $t_{PGLS} = 1.85$, $p_{PGLS} = 0.069$; Table 1). The main effect of species therapeutic redundancy on use pressure was significant ($\beta_{PGLS} = 13.25 \pm 3.29$, $t_{PGLS} = 4.03$, $p_{PGLS} = 0.0002$) suggesting species therapeutic redundancy may drive species use pressure. Species use preference and therapeutic redundancy interactively had a significant effect on species use pressure ($\beta_{PGLS} = -9.27 \pm 3.57$, $t_{PGLS} = -2.60$, $p_{PGLS} = 0.0018$; Table 1; Figure 2). This suggests that the relationship between therapeutic redundancy and medicinal species use pressure is stronger for non-preferred species than preferred species. As such, therapeutically redundant species that are less preferred over other species to treat a given illness experienced the highest level of use pressure whereas less therapeutically redundant species may experience a higher level of use pressure if they are preferred over other species to treat a given illness (Table 1; Figure 2).

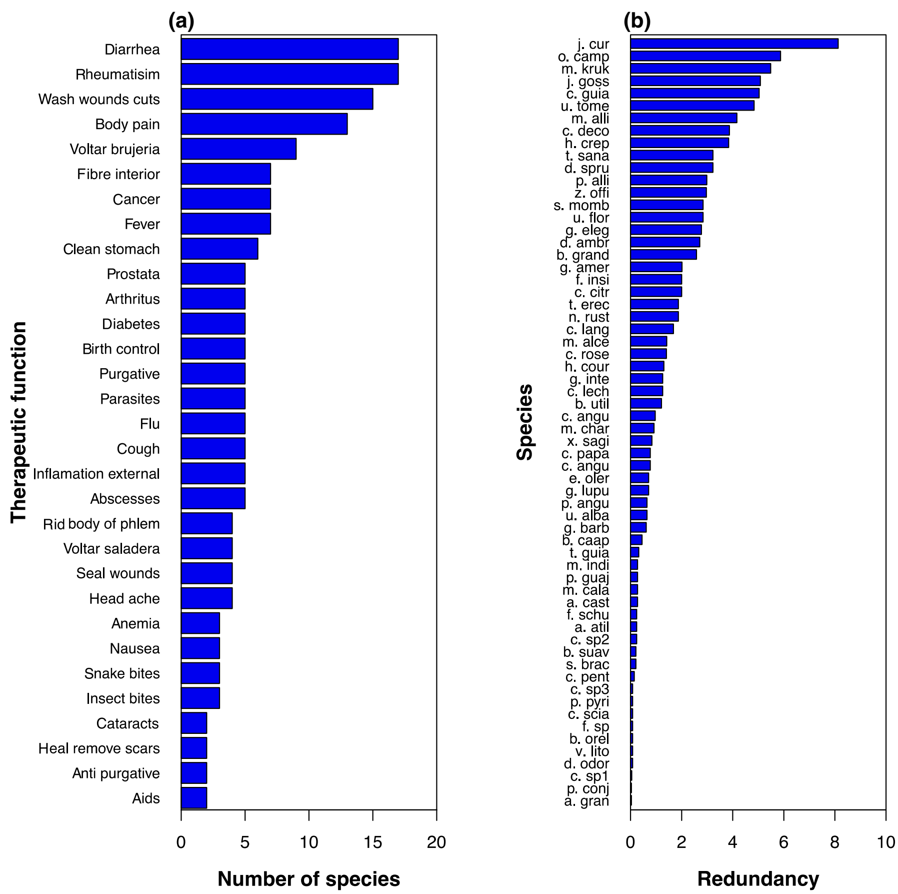

FIGURE 1 Species therapeutic redundancy according to the Shipibo-Konibo community of Paoyhan. (a) The total number of species cited to fulfil a given therapeutic function in Shipibo-Konibo ethnomedicine. (b) Species redundancy for 62 plant species cited by participants in the Shipibo-Konibo community of Paoyhan. Latin binomials are abbreviated

TABLE 1 Results of phylogenetic generalized least squared models (model selection) to test the effects of species use preference and species therapeutic redundancy on the use pressure of medicinal plants used by the Shipibo-Konibo community of Paoyhan. This model controls for species evolutionary relatedness of medicinal plants cited by participants. Significant predictors are in bold

	Estimate	*SE*	*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**	

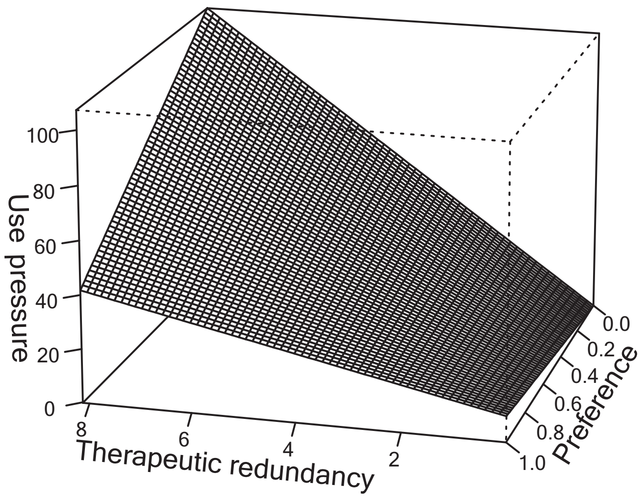

FIGURE 2 Perspective plot of the relationship between species use pressure (*z*) and species use preference (*y*) and species therapeutic redundancy (*x*) predicted via the phylogenetic generalized least squares model

TABLE 2 Results of generalized linear models (model selection) to test the effects of species use preference and species therapeutic redundancy on the use pressure of medicinal plants used by the Shipibo-Konibo community of Paoyhan. This model does not control for species evolutionary relatedness of medicinal plants cited by participants. Significant predictors are in bold

	Estimate	*SE*	*t* value	*p*	AIC
Intercept	9.569	3.415	2.802	0.006824	550.84
Preference	9.761	5.785	3.620	**0.000606**	

3.4 | Does phylogeny affect the predictive power of the drivers of species use pressure?

Controlling for evolutionary relatedness between species resulted in a difference in our models by 8 units of AIC (AIC_{PGLS} = 558.45 vs. AIC_{GLM} = 550.84; Tables 1 and 2). Not controlling for phylogeny masked the interactive effects between species use preference and therapeutic redundancy (Table 2). Furthermore, because use pressure estimates are done at a species level, failure to control for species' shared evolutionary history (as in GLM models) would violate statistical assumptions due to phylogenetically driven non-independent residuals and may lead to misleading conclusions.

3.5 | Are therapeutically redundant species more likely to be phylogenetically clustered?

There was a strong phylogenetic signal for therapeutic redundancy indicating therapeutically redundant species were more phylogenetically close than not (pagel's $\lambda = 0.79$, $p = 0.003$). This is consistent with our redundancy ranking where several moderate-to-highly therapeutically redundant species were found to be closely related such as the phylogenetic clade containing *Hura crepitans* L., *Jatropha gossypifiolia* L., *Jatropha curcas* L. and *Croton lechleri* Mull. Arg. (Figure 2b). Another example of closely related and moderate-to-highly therapeutically redundant species were found in the phylogenetic clade containing *Genipa americana* L., *Capirona decorticans* Spruce, *Uncaria tomentosa* (Willd. ex Schult.) DC. and *Tabernaemontana sananho* Ruiz & Pav. Furthermore, closely related species found within the clade including *Gallesia integrifolia* (Spreng.) Harms, *Dysphania ambrosioides* (L.) Mosyakin & Clemants, *Petiveria alliacea* L. *and Gomphrena elegans* Mart. all were moderately redundant (Figure 3b).

3.6 | Are phylogenetically closed species more likely to experiencing similar use pressure?

Interestingly, the phylogenetic signal for species use pressure was weak indicating species experiencing high use pressure were not phylogenetically close (pagel's $\lambda = 6.77 \times 10^{-5}$, $p = 1$). However, participant ranking indicated several clusters of closely related species experienced moderate-to-high levels of use pressure (Figure 3a). This was the case for the phylogenetic clade including *Phthirusa pyrifolia* (Kunth) Eichler, *Gallesia integrifolia* (Spreng.) Harms, *Dysphania ambrosioides* (L.) Mosyakin & Clemants, *Petiveria alliacea* L. *and Gomphrena elegans* Mart. Similarly, closely related species within the clade consisting of *Genipa americana* L., *Capirona decorticans* Spruce and *Uncaria tomentosa* (Willd. ex Schult.) DC. all experienced moderate-to-high levels of use pressure (Figure 3a). This was also the case for closely related species within the clade containing *Ceiba pentandra* (L.) Gaertn., *Gossypium barbadense* var. sp. and *Malachra alceifolia* Jacq. In contrast, participant ranking suggests several closely related species within the clade consisting of *Gouania lupuloides* (L.) Urb., *Artocarpus altilis* (Parkinson ex F.A. Zorn) Fosberg, *Cecropia sciadophylla* Mart., *Brosimum utile* (Kunth) Oken, *Ficus sp.*, *Ficus insipida* Willd. and *Ficus schultesii* Dugand all experienced low use pressure. This was also the case for the clade consisting

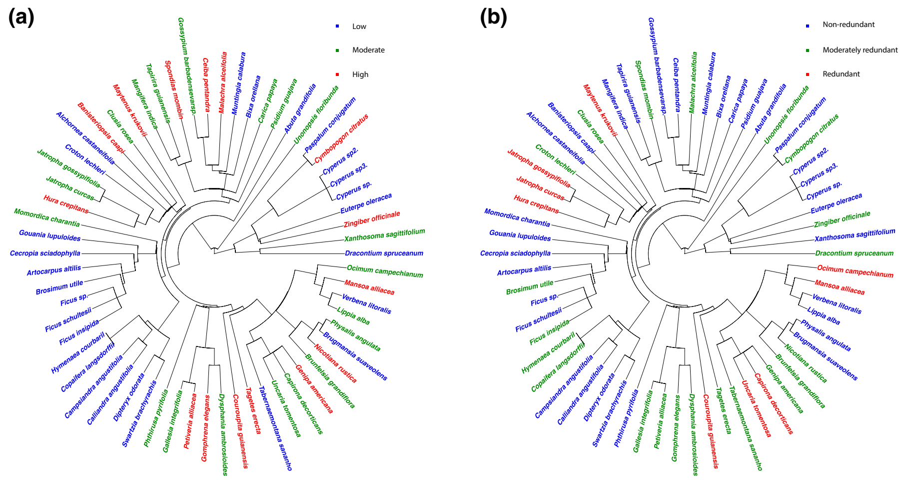

FIGURE 3 Phylogeny of plant species cited for medicinal use by participants of the Shipibo-Konibo community of Paoyhan. In all, 62 medicinal plant species belonging to 33 families and 57 genera. This phylogenetic tree was developed using the *S. PhyloMaker* function in R (Qian & Jin, 2016). It was constructed from a comprehensive phylogeny for vascular plants (Jin & Qian, 2019) consisting of 31,389 tip labels and 31,387 internal nodes. The resulting phylogenetic tree contains 62 tips and 59 internal nodes. (a) Species evolutionary relatedness and use pressure ranking. Use pressure rankings were consistent with the participant emic perspective as follows where 0.5–9 kg/month = low and represents the amount of biomass generally used to provide one to several therapeutic treatments for most plant species, 10–29 kg/month = moderate and represents the amount of biomass generally used to provide several to many therapeutic treatments, 30 or more kilograms/month = high and represents the amount of biomass generally used to provide numerous therapeutic treatments. Latin binomials are colour coded to represent species experiencing low, moderate and high use pressure. (b) Species evolutionary relatedness and therapeutic redundancy ranking. The level species therapeutic redundancy was ranked corresponding to a posteriori of therapeutic use of medicinal plant species among the Shipibo-Konibo from the etic approach guided by the researcher's perspective as follows: 0.032–1.0 units = non-redundant, 1.1–3.2 units = moderately redundant, 3.3 units or more = redundant. Latin binomials are colour coded to represent species that have non-redundant, moderately redundant and high therapeutic redundancy. Use pressure and redundancy rankings were coupled with statistical analyses where we used the *phylosig* function of the R package PHYTOOLS to test whether species therapeutic redundancy and species use pressure had a significant phylogenetic signal

of *Hymenaea courbaril* L., *Copaifera langsdorffii* Desf., *Campsiandra angustifolia* Benth, *Calliandra angustifolia* Benth, *Dipteryx odorata* (Aubl.) Willd. and *Swartzia brachyrachis* Harms (Figure 3a).

4 | DISCUSSION

Our study has shown that species therapeutic redundancy can predict species use pressure. Although this is consistent with the utilitarian redundancy model, our findings indicate therapeutically redundant species experienced greater use pressure than less therapeutically redundant species when preference is not considered. This is in contrast to the central prediction of the utilitarian redundancy model. However, we have demonstrated as preference increases, the use pressure of less therapeutically redundant medicinal plant species increases, thus supporting the central prediction of the utilitarian redundancy model (Albuquerque & Oliveira, 2007). As such, we have highlighted the complex interplay between species therapeutic redundancy and use preference suggesting that the effect of therapeutic redundancy on the use pressure of medicinal plant species depends on preference. Surprisingly, this suggests an alternative understanding of utilitarian redundancy and use preference of ethnomedicinal species use patterns that both supports and is in contrast to the central prediction of the utilitarian redundancy model (Albuquerque & Oliveira, 2007).

Our results demonstrate also the complexity involved in understanding medicinal plant use and species use pressure within a diverse ethnopharmacopeia. Several plant species were cited by the Shipibo-Konibo as preferred to treat more than one illness while for some therapeutic functions, multiple species were cited as preferred and used concomitantly to treat an illness. Thus, we expected some medicinal plants may experience greater use pressure despite their level of therapeutic redundancy 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. Our results indicating significant interactive effect of species use preference and therapeutic redundancy on species use pressure was primarily in contrast to these predictions (Table 1; Figure 2). For example, *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. These species experienced moderate use pressure (Figures 1b and 3a,b). However, *Uncaria tomentosa* Willd. ex Schult. DC. and *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 moderate-to-high levels of use pressure (Figures 1b and 3a,b).

We demonstrated the importance of considering shared species evolutionary history in understanding the patterns and processes surrounding medicinal plant species use pressure. If we had not controlled for phylogenetic relatedness between the medicinal plant species used by the Shipibo-Konibo community of Paoyhan, we would have wrongly suggested that the main effect of species use preference solely drives species use pressure. In contrast to other studies that have solely shown support for preference as a driver of use pressure (Ferreira Júnior et al., 2012), our 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. Furthermore, 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. This was demonstrated by our PGLS models and tests for a strong phylogenetic signal. As such, taxonomically related species within a given phylogenetic clade may be more likely to be harvested primarily because they share evolutionary traits with other medicinally important species rather than a shared level of redundancy or preference.

Contrary to our predictions in alignment with the use pressure rankings, the weak phylogenetic signal for use pressure indicates that high use pressure observed for some species is more related to other drivers than their evolutionary link with other valuable species. In contrast, our findings also demonstrate several closely related species with moderate-to-high levels of therapeutic redundancy were more phylogenetically close (Figure 3a,b) than expected at random indicating these species likely exhibit similar medicinal properties that, in turn, make them therapeutically redundant. Given the strong phylogenetic signal in species therapeutic redundancy, it is likely the selection of therapeutically redundant medicinal plants may in part be driven by a given species shared evolutionary history which resulted in the production of similar plant secondary compounds among closely related medicinal plants. Although the relationship between plant secondary chemistry and taxonomically related species has been demonstrated (Rønsted et al., 2012) along with discussions on their possible roles in driving species therapeutic redundancy (Reinaldo et al., 2020), further research including a direct test of this hypothesis is warranted. Thus, we anticipate future considerations of species shared evolutionary history including traits favourable to traditional ethnomedicine such as the presence or lack of suites of plant secondary compounds will likely prove informative. Therefore, we 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 fulfilled redundant therapeutic functions and were not preferred over other species to treat a given illness. Surprisingly, this is in contrast to the central prediction of the utilitarian redundancy model in that species fulfilling less redundant therapeutic functions likely experienced greater use pressure only when they were preferred over other species to treat a given illness (Albuquerque & Oliveira, 2007). In contrast to previous studies (Albuquerque & Oliveira, 2007; Ferreira et al., 2012; Ferreira Júnior et al., 2012), we found, when controlling for phylogeny, the main effect of species use preference alone only marginally affected 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, our analyses indicated species use value was strongly correlated with redundancy. Thus, we excluded use value as a predictor of species use pressure. However, we found some species with low-to-moderate use value experienced greater use pressure. For example, *Nicotiana rustica* L. and *Banisteriopsis caapi* Spruce ex. Griseb. which had low-to-moderate use values and therapeutic redundancy are frequently used in ritual for ethnomedicinal purposes (Coe & McKenna, 2017; Luna, 1986) and as a result were cited by participants to experience high levels of use pressure. We acknowledge the high use pressure of medicinal plant species such as *Nicotiana rustica* L. and *Banisteriopsis caapi* Spruce ex. Griseb. or *ayahuasca* may be driven also by a compounding effect such as local use and the globalization and use of these species beyond traditional ethnomedicine (see e.g. Luna & White, 2017; 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 & 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). We suggest a greater understanding of the demography of medicinal plant species experiencing higher levels of use pressure will likely inform sustainable management practices. However, we also acknowledge understanding the impacts of use pressure on the conservation status of medicinal species used by the Shipibo-Konibo community of Paoyhan is likely challenging due to the fact that some of the plants highlighted in this study are cultivated.

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 our findings suggest species that fulfil redundant therapeutic functions are likely candidates for management and conservation efforts, we caution that our results and conclusions are limited to the Shipibo-Konibo community of Paoyhan. Furthermore, research in other geographical locations should be conducted to provide comparable results and thus inform robust management and conservation efforts.

It is important to highlight all therapeutic 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, resins or latexes) with potentially higher concentrations of plant secondary compounds are utilized (Coe & Gaoue, 2021, unpublished data) most often for adults. Thus, our 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 *Maytenus krukovii* A.C. Sm. or *chuchuwasa* was cited as preferred to treat diarrhoea for adults and although not included in this study, children with diarrhoea in the Shipibo-Konibo community are often treated with a remedy combining the leaves of several species including *Psidium guajava* L., *Mangifera indica* L. and *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 ethnopharmacological research on the concentration of secondary compounds in plant parts used in treatments for adults versus children would likely yield informative results on the patterns and processes surrounding medicinal plant use and selection among the Shipibo-Konibo. We acknowledge our estimates of medicinal plant species use pressure solely based on the *emic* perspective are limited. Therefore, we suggest future estimates of species use pressure including both the *emic* and *etic* perspective are warranted. Use pressure estimates based on combining local knowledge of harvesters and the demography of medicinal plant species will add to the reliability of these measures.

We also acknowledge various individual sociocultural and socioeconomic factors including age, gender, formal educational and literacy levels are all correlated with a given person's level of medicinal plant knowledge (Albuquerque et al., 2011; Gaoue et al., 2017; Hanazaki et al., 2013; McCarter & Gavin, 2015; Souto & Ticktin, 2012; Voeks, 2007; Voeks & Leony, 2004). These factors coupled with culturally defined gender dynamics are likely to affect our understanding of the community-level dynamics surrounding species use pressure, preference, species use value and therapeutic redundancy.

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CONFLICT OF INTEREST

The authors report no conflict of interest.

AUTHORS' CONTRIBUTIONS

M.A.C. and O.G.G. conceived of the idea for the paper and outlined and structured its content; M.A.C. collected and analysed the data with contribution from O.G.G.; M.A.C. wrote the first draft of the manuscript with additional edits from O.G.G. All authors read and approved the final manuscript.

DATA AVAILABILITY STATEMENT

The data generated and analysed for the current study are available in the Dryad Digital Repository https://doi.org/10.5061/dryad.69p8cz91x (Coe & Gaoue, 2021).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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