RESEARCH ARTICLE

A phylogenetic evaluation of non-random medicinal plants selection around an African biosphere reserve

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Abstract

1. Theory in ethnobiology suggests that the selection of medicinal plants by local people in a given region is not random and evolutionary closely related species may have similar medicinal uses. Additionally, plants selection by local people is often driven by plant therapeutic efficacy, plant availability, plant versatility or local knowledge on medicinal plants.

2. We tested the hypothesis of non-random selection of medicinal plants as well as the potential mechanisms explaining such non-random plants selection. We also tested for phylogenetic signal in medicinal plants. Our study was based in four villages across Benin, West Africa, where the local communities have deep knowledge about medicinal plants. We installed 91 plots around these four villages to establish the total list of plant species and their abundance. We then conducted ethnobotanical surveys in the same villages to identify medicinal plants used in the local pharmacopoeia. To test whether the selection of medicinal plants used in the region was non-random and whether plant selection was driven by plant therapeutic efficacy, plant availability, plant versatility or local knowledge, we used a generalized linear model. Furthermore, we used the D-statistic to test whether evolutionary closely related species are more commonly used as medicinal than other species.

3. We found support for non-random medicinal plant selection. Such a non-random plant selection was driven by plant medicinal versatility. Plant availability and secondary compounds have no significant influence on plant selection. Local people's knowledge on medicinal plants was significantly affected by individuals' literacy but not by their gender, their age or the ethnic group they belong to. We found a weak phylogenetic signal in medicinal plant uses.

4. Our study reveals that the most used families are not necessarily the ones that have more secondary compounds or that are the most available to the local people, but are the most versatile plants. The high level of medicinal flora used at the local scale, which contrasts with the country-level analysis found by previous studies, suggests new methodological guidance in testing the theory of non-random medicinal plants selection.

1 | INTRODUCTION

Humans have always used plants for food, medicine, and as a source of income (Schaal, 2019). In several parts of the world, people still rely on traditional medicine for their primary healthcare (Hamilton, 2004). This is particularly true for rural areas in Africa, Asia, Central and South America, where medicinal plant are widely used (Allkin, 2017). Recent empirical studies demonstrate that the selection of medicinal plants by locals in a given region is often driven by therapeutic efficacy, plant versatility and plant availability but also by recognition by local knowledge (Ford & Gaoue, 2017; Gaoue et al., 2021). However, our understanding of the underlying drivers of non-random plants selection by humans is still limited.

Several hypotheses have been proposed to gain a mechanistic understanding of the selection of plants by local people. The hypothesis of non-random medicinal plants selection predicts that certain plant families are rich in secondary chemistry, and as a result, are overutilised for medicine purpose (Moerman, 1979). Here 'overutilised' does not necessarily mean over-harvested. Overutilised plant families are those that are used more frequently than expected by chance. The basis for the hypothesis of non-random medicinal plants selection is that the number of medicinal plant species per family in a given region can be modelled as a function of the total number of species in the family present in that region (Robles Arias et al., 2019). Furthermore, overutilised families are used more often because most species in these families have secondary chemistry that is known and used by local people to heal disease (Ford & Gaoue, 2017; Hart et al., 2017). In Ecuador, for example, Fabaceae, which has species rich in secondary compounds, is one of the most utilised plant families (Moerman, 1991). However, presence of secondary compounds does not always lead to overutilisation. For instance, a recent study showed that plant families such as Poaceae and Cyperaceae, which are poor in secondary chemistry, are overutilised in Hawaiian pharmacopoeia due to their cultural importance and historical legacy (Ford & Gaoue, 2017).

Beyond the phytochemical basis of medicinal plant overutilisation, the availability hypothesis and the versatility hypothesis have been suggested to explain the selection of medicinal plants by local people. The availability hypothesis proposes that some plant species are overutilised because they are locally more abundant (Ford & Gaoue, 2017; Hart et al., 2017). A meta-analysis using 19 studies showed that indigenous people often used the most available woody plants (Gonçalves et al., 2016). The versatility hypothesis suggests that plants that have a wide range of uses are more likely to be overutilised by local people. Versatility could refer to the use value of a species or the number of diseases a plant can treat. In Ecuador, the selection of medicinal plants was explained by plants versatility (Ford & Gaoue, 2017; Hart et al., 2017).

Sociocultural and demographic characteristics of individuals such as gender, age, and literacy (e.g. having a formal education) are correlated with their level of plant knowledge and could affect how these individuals select plants (Gaoue et al., 2017). Previous studies have shown that higher education level is often negatively correlated with knowledge of medicinal plants (Infield & Namara, 2001). Due to their longer experience, people in their middle age and older tend to know more about medicinal plants than young adults (Caniago & Siebert, 1998). Women tend to have more knowledge of medicinal plants than men (Vodouhê et al., 2009), because in most regions where people rely on medicinal plants, women are the primary healthcare provider.

Phylogenetic niche conservatism in plant medicinal properties is a potential underlying factor explaining non-random plant selection (Saslis-Lagoudakis et al., 2012). Because closed related plant species tend to share similar biochemistry, they are more likely to have similar medicinal properties (Saslis-Lagoudakis et al., 2012). Species belonging to the genus *Pterocarpus* are all used for the same medical purpose across the world (Saslis-Lagoudakis, Klitgaard, et al., 2011; Saslis-Lagoudakis, Williamson, et al., 2011). Furthermore, in the genus *Plectrantus*, most of the species used for medicinal purposes were all clumped in the same clade, indicating a phylogenetic signal in medicinal properties (Lukhoba et al., 2006). However, biochemistry data on plant species is often not available for most species and can be costly to generate. Despite the associated costs, gaining a deep understanding of the phylogenetic signal for a given flora can help predict the potential medicinal value of species for which we lack ethnobotanical or chemical data (Rønsted et al., 2012).

Most tests of the theory of non-random medicinal plants selection present several limitations that can lead to a misclassification of plant families (e.g. over or underutilised). First, using linear regression to model the relationship between the number of medicinal species per plant family and the total number of species per family (e.g. Amiguet et al., 2006; Moerman, 1991) is not appropriate given that the response variable here (the number of medicinal plants per family) is a discrete variable for which a Poisson or negative binomial distribution is recommended (Crawley, 2012; Robles Arias et al., 2019). Second, most tests of the non-random selection hypothesis used country-level plant data (Saslis-Lagoudakis, Klitgaard, et al., 2011; Saslis-Lagoudakis, Williamson, et al., 2011), which can overestimate the number of plant species used at a local level where pharmacopoeia is developed (Robles Arias et al., 2019). Although listed as medicinal plants at the national level, plant species that are only present in protected areas are often not used by locals because the area is not accessible. Using the plant list at the country level is more likely to overestimate overutilised species.

In this study, we tested the hypothesis of non-random selection of medicinal plants and the mechanism explaining plants

selection at the local level, rather than the country, while addressing the limitations of previous studies. We also tested the phylogenetic signal in the medicinal use of species to investigate whether closely related species tend to be medicinal due to their shared evolutionary history. We hypothesized that (i) the selection of medicinal plants is not random in the region, and (ii) plants selection by local people is driven by therapeutic efficacy, plant versatility and plant availability; (iii) there is a strong phylogenetic signal in plant medicinal use in the region; (iv) older people know more medicinal plant species than younger people; women identify more medicinal plant species than men, participants without formal western education recognize more medicinal plant species than those who are literate and there is no difference in local plant knowledge between ethnic groups.

2 | MATERIALS AND METHODS

2.1 | Study system

We tested the hypothesis of non-random selection of medicinal plants and the phylogenetic signal in medicinal plants in four villages (Dassari, Porga, Tanongou and Batia) around the Pendjari biosphere reserve, a place where local communities have accumulated deep knowledge about plant species uses (Samadori et al., 2017). The Pendjari biosphere reserve is located in the northwestern part of Benin in West-Africa and belongs to the Atacora mountain chain, a biodiversity hotspot (Adomou, 2005; Akoègninou et al., 2006). The study area has a tropical climate with a dry season from October to April and a rainy season from May to September. The flora of the Pendjari Biosphere Reserve has 684 plant species belonging to 89 families (Assédé et al., 2012). The population living in the Pendjari Biosphere Reserve was estimated at 27,783 in 2002. Berba (65%) and Gourmantche (23%) are the ethnic groups most represented in the study villages.

2.2 | Data collection

To estimate the total number of plant species per family (dependent variable), we installed 91 plots of 5 m × 5 m from the center to the edge of each village, ensuring that it covered the habitats utilised by local people. We selected 5 m × 5 m based on previous studies in the same study area (Moutouama & Gaoue, 2022). In each plot, we recorded the botanical name and density of each species. We standardized the names of plant species for each plot using The Plant List (www.theplantlist.org) with the *Taxonstand* package (Cayuela et al., 2019). Species density was also summarized at the family level to estimate family availability. In addition, the number of bioactive elements per family was used as a metric of the richness of the family in secondary compounds.

To estimate the number of medicinal plant species per family (independent variable), we conducted ethnobotanical surveys

with 37 local medicinal plant experts (28 men and 9 women). We surveyed 10 experts per village except for Porga where we only found seven experts. We obtained the list of experts from the local Association of Traditional Medicine. We administered the questionnaire to available experts and to those who consented to take the survey using the local language most spoken by people (Biali and Gourmantche). Before each interview, we briefly explained the purpose of the study and obtained informed consent from the participants. We also obtained local authorization from the village chiefs, to whom we explained the purpose of the study and possible risks and benefits, consistent with the approval of the Internal Review Board (IRB-21-06226-XP, University of Tennessee Knoxville, USA).

For each participant, we recorded age, gender and formal education (western schooling). The average age of the participants was 63 years. Each participant was then asked to list the plant species they used for medicinal purposes by naming the species in their local language (Biali or Gourmantche). We complemented this with walk-in the wood sessions (Phillips & Gentry, 1993) whereby we conducted field trips with each local plant expert to confirm the botanical identity of the plant species they cited during free-listing sessions (Figure S1).

2.3 | Data analysis

2.3.1 | Identifying over- and under-utilised plant families

We developed a generalized linear model with the negative binomial error structure to test the relationships between the number of medicinal plant species per family and the total number of plant species per family in the region. To identify families that are overutilised (more frequently than expected by chance), we used the studentized residuals (Robles Arias et al., 2019) because studentized residuals have constant variance and can be used to test outliers, here the top overutilised plant families. The studentized residuals follow a student's t distribution with $n-k-2$ degree of freedom, where n is the number of observations, and k is the number of predictor variables. We used the qt function to identify the 2.5th and 97.5th percentile quantile for the studentized residuals. We considered the most overutilised plant families as the families for which the studentized residuals are above the 97.5th percentile quantile and the most underutilised families under the 2.5th percentile quantile.

2.3.2 | Drivers of non-random plant selection

For each family, we calculated the mean value of medicinal use (number of diseases treated). We calculated the medicinal use values (UVspecies) of each species for all plant parts using the UV function in the package *ethnobotanyR* (Whitney, 2019) following this formula:

UVspecies=∑UR/number of informants; where the number of UR is the number of uses that mention each informant for the species. Then, we averaged species use values to estimate the mean use values for each family.

To obtain the secondary compound richness for each family, we counted the number of bioactive compounds per family using the literature (Singh & Sharma, 2020). To test whether overutilised families are the most available families in the region, if they are the richest in secondary compounds, or if they are the most versatile (meaning they have the highest use value), we developed a generalized linear model with a binomial error distribution. We used binomial distribution because the response variable (underutilised vs. overutilised) is binary data. We implemented the generalized linear model with the package brms using with three chains, non-informative prior, 4000 iterations, and 1000 warmup. We then used the trace plots (chain mixing and model convergence) to evaluate the quality of the model (Figure S2).

2.3.3 | Sociocultural and demographic influence on experts' knowledge

We conducted a generalized linear model with a negative binomial error distribution to test the effect of age, literacy, gender of the participants on their knowledge of medicinal plants. We chose the negative binomial error distribution because the response variable (the number of diseases cited) is the count data.

2.3.4 | Phylogenetic signal test for medicinal plant selection

To test for phylogenetic signal in medicinal plants selection, we estimated the D-statistic, which is a more appropriate metric of phylogenetic signal for binary traits (here medicinal or non-medicinal) (Fritz & Purvis, 2010). We calculate the D-statistic in three steps. First, we used the most recent and largest dated phylogeny for seed plants, GBOTB (Smith & Brown, 2018) as backbone phylogeny to prune our phylogenetic tree using a list of 158 species. Specifically, we used the nodes.info.1 option and scenario 3 of the *phylo.maker* function in the package *V.PhyloMaker* (Jin & Qian, 2019) on angiosperms species to generate the phylogenetic tree (Figure S3). Second, we created a data frame in which we specified whether the species is used for medicinal purposes or not. Finally, we combined the species-level phylogenetic tree and the data frame on the medicinal selection of the species (medicinal or non-medicinal) to estimate the D-statistic using the package *caper* (Orme, 2013). D values closer to 1 suggest a weak phylogenetic signal, which aligns with a 'random' distribution of plant selection for medicinal use. D values closer to 0 imply a phylogenetically clumped distribution of medicinal plant selection as if it had evolved under a Brownian motion model (Fritz & Purvis, 2010).

All analyzes were performed in R 4.2.4 (R Core Team, 2019).

3 | RESULTS

The number of medicinal plant species per family was positively associated with the total number of plant species per family around the biosphere reserve ($\beta=1.086\pm0.0142$; $p<0.001$, Figure 1). Sixteen of the 49 families identified in the region were overutilised more than expected by chance (Table S1): Rubiaceae, Apocynaceae, Sapotaceae, Meliaceae, Moraceae, Rhamnaceae, Rutaceae, Fabaceae,
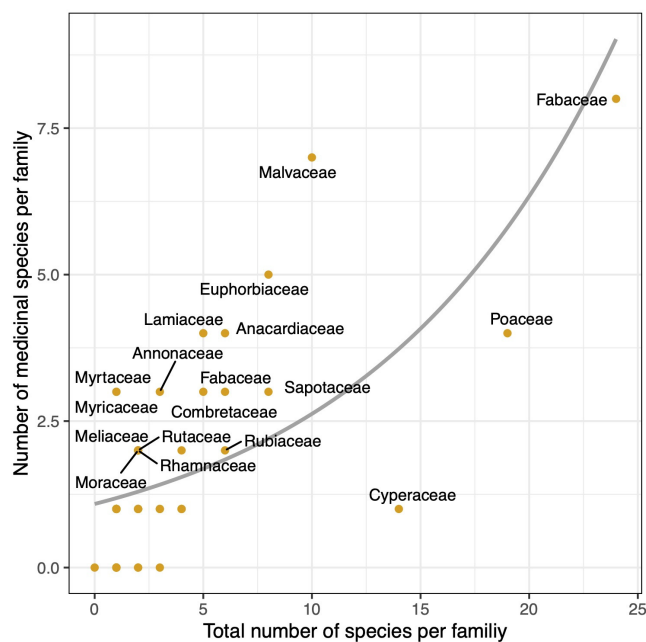

FIGURE 1 Negative binomial regression of the number of medicinal species per family predicted by the total number of species per family around the Pendjari biosphere reserve. The grey line represents the negative binomial fit line predicted by the generalized linear model.
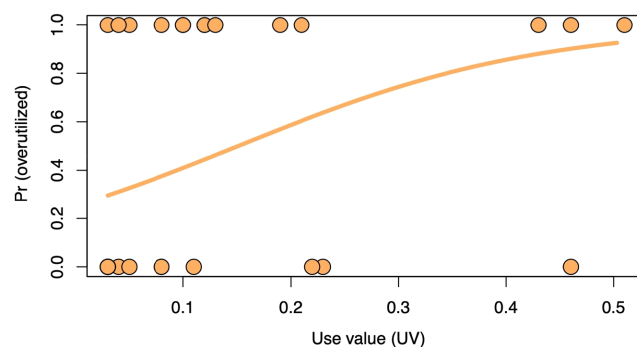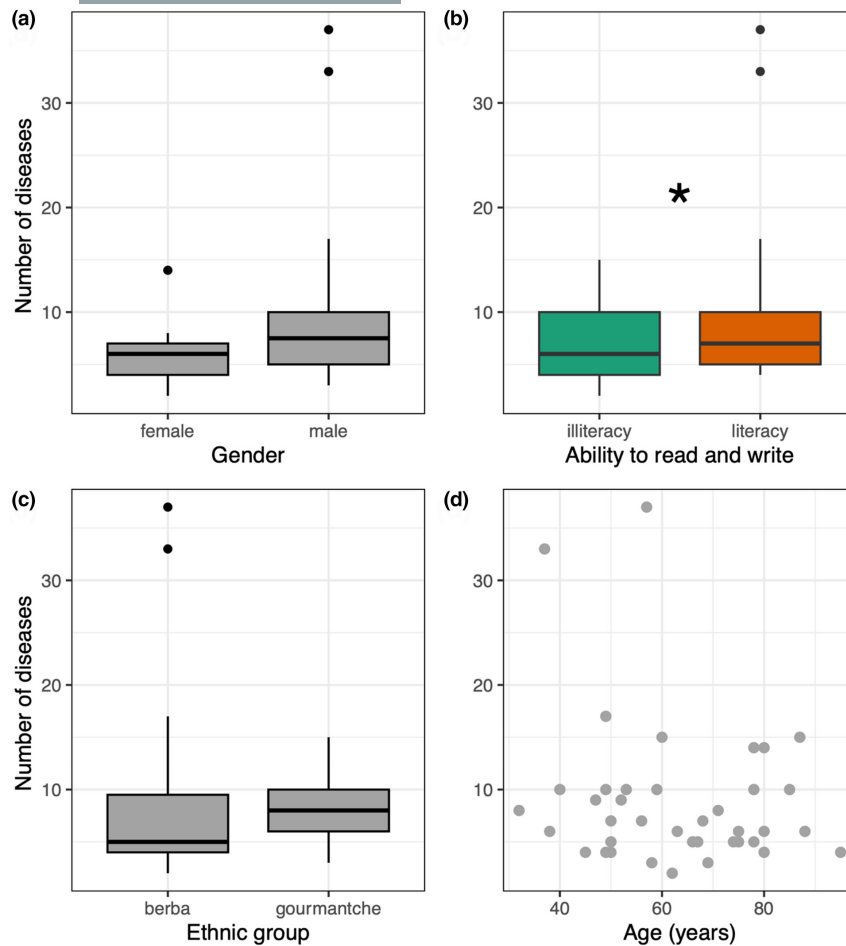

FIGURE 2 Result of the logistic regression showing relation between the probability of being overutilised and medicinal use value. Plant families with the highest medicinal usage values were more likely to be overutilised than plant families with the lowest medicinal usage values around the Pendjari biosphere reserve.

FIGURE 3 Sociocultural and demographic drivers of individuals' knowledge of medicinal plants illustrating the effect of (a) gender (male and female), (b) level of education (literate and non-literate), (c) ethnic group (Berba or Gourmantche) and (d) age on individuals' knowledge about medicinal plants. '*' indicates a significant difference between groups.

Combretaceae, Annonaceae, Anacardiaceae, Myricaceae, Myrtaceae, Lamiaceae, Euphorbiaceae, and Malvaceae. The likelihood of a family being overutilised increased significantly with its medicinal use value ($\beta=6.91$; 95% CI: 0.50 to 14.89, Figure 2). However, the most available plant families were not necessarily the most overutilised ($\beta=00$; 95% CI: 0 to 0). Similarly, families rich in secondary compounds were not the most overutilised families ($\beta=0.01$; 95% CI: −0.01 to 0.02). Contrary to our expectation, gender ($\beta=0.47\pm0.24$, $p=0.06$, Figure 3a), ethnic groups ($\beta=-0.12\pm0.21$, $p=0.56$, Figure 3c) and age ($\beta=-0.01\pm0.01$, $p=0.16$, Figure 3d) did not affect local people knowledge on medicinal plants. However, literate participants recognize more medicinal plant species than those without formal western education ($\beta=0.41\pm0.20$, $p=0.04$, Figure 3b).

Furthermore, we found a weak phylogenetic signal for medicinal plants selection around the Pendjari Biosphere Reserve ($D=0.76$, p ($D<1$)<0.05 and p ($D>0$)$=0$; Figure 4). However, some clades had more medicinal plants than others (Figure 5).

4 | DISCUSSION

Our study tested the theory of non-random plants selection in an understudied region of tropical Africa, while addressing recurrent limitations in previous tests of this theory. We showed that plants selection is not random in that region of Africa. Some plant
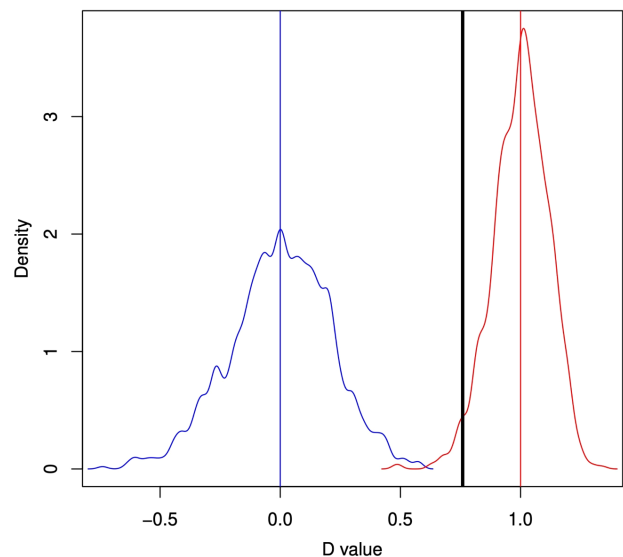
FIGURE 4 Results of the tests of the phylogenetic signal in medicinal plants using the Fritz and Purvis (2010) D-statistic. The blue line represents the distribution of D values assuming a Brownian motion (BM) model and the blue vertical line indicates $D=0$ (when the phylogenetic distribution of a parameter is not different from BM). The red line represents the distribution of D values assuming a random model and the red vertical line indicates $D=1$ (when the phylogenetic distribution of a parameter is not different from random). The bold black vertical line indicates the mean D value observed.
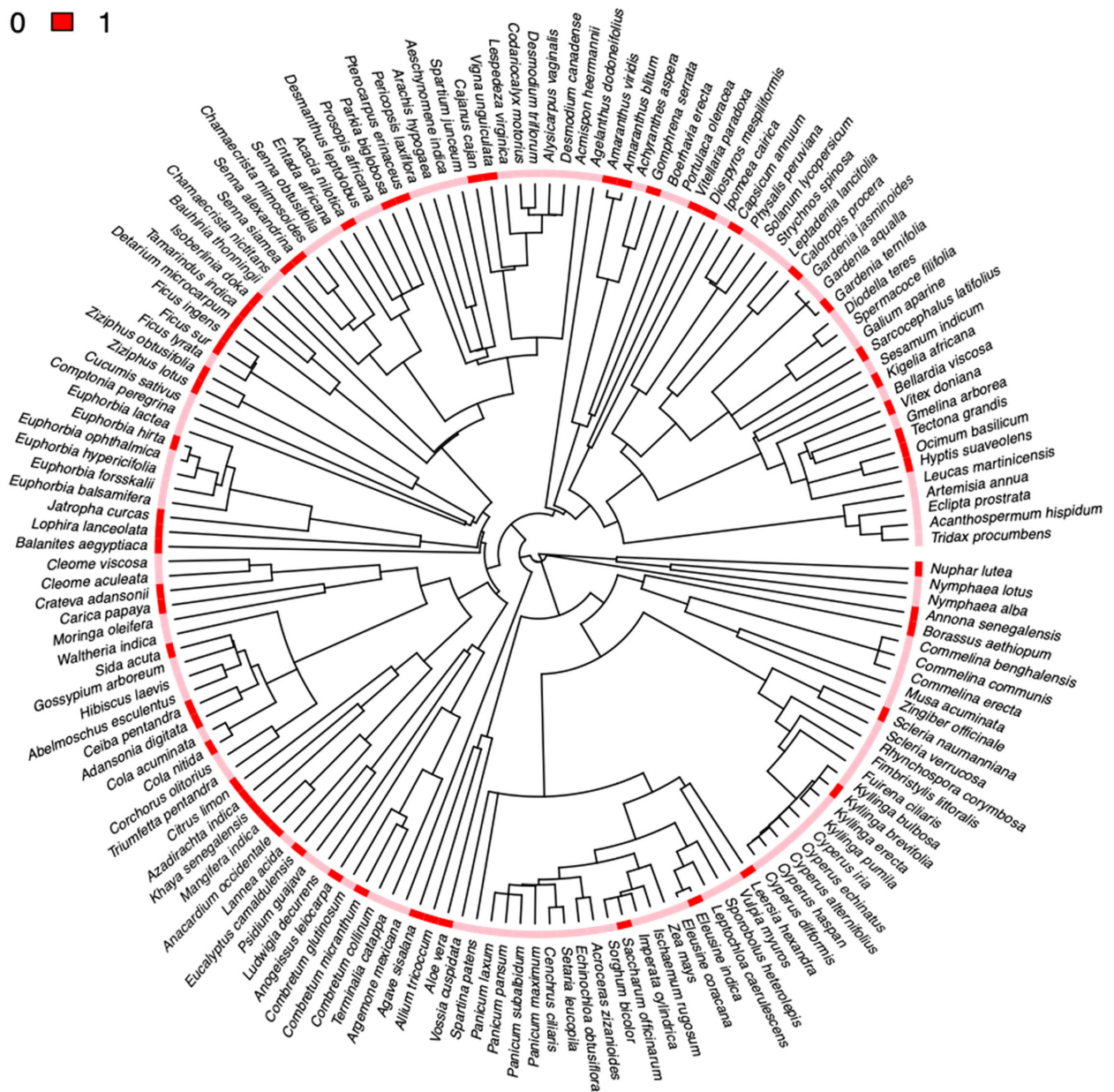
FIGURE 5 Distribution of 159 medicinal plant species across the phylogeny indicating that some clades have more medicinal species than others. The red colour suggests that the species is used for medicinal purposes, and the pink colour indicates that the species is not used for medicinal purposes.

families were used more than others not because of their secondary compound richness or high availability, but because of their medicinal therapeutic versatility. This result is consistent with previous studies on traditional Ecuadorian medicinal plants that highlight the importance of species versatility on plant selection (Hart et al., 2017). It has also been suggested that people tend to be more likely to retain knowledge, use, and access to plant species with many applications for humans (Alencar et al., 2010). Most studies on the theory of non-random medicinal selection failed to directly test the drivers of family overutilisation (Ford & Gaoue, 2017; Moerman, 1979). As a result, these studies often

speculate that family richness in secondary chemistry and species availability for local people explain non-random plant selection. Here, we found that most of the available families or families rich in secondary compounds are not necessarily over-utilised. We recommend more rigorous local-level tests of the theory of non-random medicinal plant selection to directly elucidate the drivers of family overutilisation.

The Malvaceae and Euphorbiaceae families, which we found to be overutilised across the four villages in Benin, were also among the most overutilised in other areas such as Amazon (Moerman et al., 1999). Species in the Malvaceae family, such as

the Bombacoideae subfamily which is common in the study area, have antimicrobial activities. Additionally, vitamins C, steroids, and flavonoid extract of *Adansonia digitata* are antioxidant, analgesic, antidiarrheal, anti-inflammatory and bronchial asthma (Sundarambal et al., 2015). Furthermore, *Hibiscus* genus of the Malvaceae family is also common in the study area and is used for medicinal purposes. The genus is rich in polyphenolic compounds (Gene et al., 2010). Euphorbiaceae is one of the largest dicot families (Webster, 1994). The Euphorbiaceae family is also rich in antioxidant and antiproliferative activities (Nascimento et al., 2013). The roots and leaves extraction of the Euphorbiaceae contains a high proportion of flavonoid and phenolic secondary metabolites (Saleem et al., 2019). The family is also rich in alkaloids and tannins (Mali & Panchal, 2017).

In our study area, a previous study revealed that Bombacoideae, a Malvaceae subfamily, and Euphorbiaceae were the most used families (Vodouhê et al., 2009). However, the reasons for such a high preference for species belonging to this family were not investigated. Gaoue et al. (2021) who conducted a country-level analysis in Benin where the study was carried out showed that the Euphorbiaceae family was underutilised by local people. This contrasting result in the same study country is most likely due to differences in the scale of the studies and the data collection method. We analysed medicinal flora at the local level, where we directly interview local experts in traditional medicine. In contrast, as it is common for most studies, Gaoue et al. (2021) analysed data collected at the country level (e.g. Benin's flora data). This suggests that the scale of analysis is vital in classifying over and under-utilised species.

Despite the weak phylogenetic signal in medicinal plant use, we found a phylogenetic clump for some genera, suggesting that for some clades, closely related species have similar uses. These results agree with previous studies that found a phylogenetic signal in local pharmacopoeia (Zhu et al., 2011). Our results here suggest that around the Pendajari biosphere, the medicinal properties of the plant are not evenly distributed throughout the phylogeny. Some genera contain more species of medicinal plants than others. One might claim that the observed phylogenetic signal can be explained by phylogenetic conservatism (Losos, 2008). However, we did not analyse the secondary compounds of plants to draw such a conclusion, and this is one of the limitations of our study (Zhang et al., 2021). The data we used were based on local medicinal plant therapeutic experts. Relying on experts could underestimate or overestimate the strength of the phylogenetic signal within certain clades (Saslis-Lagoudakis, Klitgaard, et al., 2011; Saslis-Lagoudakis, Williamson, et al., 2011). The results we provided could be used as a basis on which other studies could explore the phytochemistry of these medicinal plants and identify species that produce similar chemical compounds.

We found no difference in medicinal plant knowledge between older and younger people and between women and men. This contrasts with our initial prediction and previous studies suggesting that knowledge accumulates over time, and older people and women are more likely to have more knowledge of medicinal plants than young

people (De Albuquerque et al., 2011; Torres-Avilez et al., 2016). Similarly, there was no variation in knowledge about medicinal plants between ethnic groups. However, our analysis was based on numbers of species used and not the frequency of use. These results could be explained by the fact that most of the participants in our interview were experts in traditional medicine. Thus, for these experts, age and gender do not confer greater knowledge, particularly in a region where a very high proportion of the medicinal flora is utilised. However, experts with formal western education were more likely to cite more diseases than those who were illiterate. This result contrasts with previous studies showing that the more people are educated, the less they know about medicinal plants (Voeks, 2007). Perhaps, experts who are literate and possibly have more resources, learned additional medicinal plants from accessing a variety of sources including a wide range of other experts they have consulted.

5 | CONCLUSIONS AND RECOMMENDATIONS

Our study revealed that certain plant families were more utilised than expected by chance, supporting the theory of non-random plant selection. The therapeutic versatility of plants was the main driver of such a non-random selection of plants. We also showed that the ethnopharmacopeae of the population at the local level does not have a strong phylogenetic basis. Furthermore, we demonstrated that smaller-scale tests of ethnobiological theories can yield contrasting results compared to larger-scale country-level studies. There are a number of gaps in our knowledge around the hypothesis of non-random plants selection that follow from our findings and would benefit from further research. For example, understanding how the difference in sociodemographic groups knowledge affects plants selection could help to gain insight. Analysis of local plant secondary compounds will help reveal if phylogenetics could serve as a guide for investigating potential species to use for drug discovery.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The anonymized data used in this analysis are available on figshare at https://figshare.com/s/26a08524d50004457e82.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1: Number of species cited by the experts per village.

Figure S2: Smoothed density plots on the left panel.

Figure S3: Phylogenetic tree of the species used in the manuscript.

Table S1: Studentized residuals showing the most used family.