Report

Current Biology

Knowledge-Sharing Networks in Hunter-Gatherers and the Evolution of Cumulative Culture

Highlights

- BaYaka Pygmies use plants for medicine, foraging, and social beliefs
- Knowledge of medicinal plant use is shared between spouses and family members
- Plant knowledge related to co-foraging and social beliefs is shared among campmates
- Use of some medicinal plants is positively correlated with children's health

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In Brief

Salali et al. provide empirical evidence on how hunter-gatherer social structure plays a role in the diversification of plant knowledge and cumulative culture. While medicinal knowledge, which has positive effects on offspring health, is shared within families, knowledge about cooperative activities and social norms is shared by campmates.

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Knowledge-Sharing Networks in Hunter-Gatherers and the Evolution of Cumulative Culture

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SUMMARY

Humans possess the unique ability for cumulative culture [1, 2]. It has been argued that hunter-gatherer's complex social structure [3–9] has facilitated the evolution of cumulative culture by allowing information exchange among large pools of individuals [10–13]. However, empirical evidence for the interaction between social structure and cultural transmission is scant [14]. Here we examine the reported co-occurrence of plant uses between individuals in dyads (which we define as their "shared knowledge" of plant uses) in BaYaka Pygmies from Congo. We studied reported uses of 33 plants of 219 individuals from four camps. We show that (1) plant uses by BaYaka fall into three main domains: medicinal, foraging, and social norms/beliefs; (2) most medicinal plants have known bioactive properties, and some are positively associated with children's BMI, suggesting that their use is adaptive; (3) knowledge of medicinal plants is mainly shared between spouses and biological and affinal kin; and (4) knowledge of plant uses associated with foraging and social norms is shared more widely among campmates, regardless of relatedness, and is important for camp-wide activities that require cooperation. Our results show the interdependence between social structure and knowledge sharing. We propose that long-term pair bonds, affinal kin recognition, exogamy, and multi-locality create ties between unrelated families, facilitating the transmission of medicinal knowledge and its fitness implications. Additionally, multi-family camps with low inter-relatedness between camp members provide a framework for the exchange of functional information related to cooperative activities beyond the family unit, such as foraging and regulation of social life.

RESULTS

Studies of cultural evolution have mainly focused on mechanisms such as fidelity, combination, innovation, and modification [15] and rarely investigate how the content and function of cultural information affects knowledge-sharing mechanisms [16, 17]. Because human cumulative culture is diversified into functional domains [16–19], it may also require corresponding differentiation of knowledge-sharing mechanisms and underlying social structure [20]. Here we analyze the reported uses of 33 plants among the Mbendjele BaYaka pygmies from the Republic of Congo. We explored the effects of family and camp ties on the reported co-occurrence of plant use in dyads, which we define as the "shared knowledge" between two individuals.

Uses of Plants by BaYaka Pygmies

Our interviews showed that some plants were used mostly for medicinal purposes, and others for foraging or social beliefs and norms. Most reported medicinal uses were for treating digestive (35%) and respiratory (25%; Table 1) disorders. The BaYaka use some plants for collecting caterpillars or honey and as a poison for killing monkeys or fish; these were classified as foraging uses. Others were used to regulate social life and were classified as social norms and beliefs. For example, some plants are believed to be selectively poisonous to liars, while others are involved in sexual taboos (Supplemental Experimental Procedures, section S1; Table S1).

Medicinal Properties of Plants

Use of similar medicinal plants across cultures would suggest that they have adaptive benefits and real medicinal properties [21–23]. Medicinal plants have already been shown to improve health in other traditional populations with limited access to modern medicine [24]. Out of 33 plants cited by the BaYaka in our interviews, we successfully identified 31 species. Of these, 15 are also used by Baka Pygmies from Cameroon and Gabon [25, 26]. We found a positive correlation between the number of times each of the 15 plants was reported to be used for medicinal purposes by the BaYaka and Baka (Figure 1, $n = 15$, $\beta = 0.81$, $p < 0.01$). Moreover, 26 species in our sample are also used as medicine by at least one other Central African Pygmy population, including the Mbuti and Efe from Democratic Republic of Congo, the Aka from Central African Republic, and the Baka from Cameroon and Gabon [25–27]. Eight species are known to be used as medicine by gorillas [28–30], and six by chimpanzees [29, 31, 32] (Table S1). Finally, 24 plants (77%) have known bioactive properties (Table S1). These findings indicate that medicinal plant knowledge by the BaYaka is likely to be adaptive.

Table 1. Uses of Plants by Mbendjele BaYaka Pygmies

Category	Subcategory	Percentage in all answers (219 individuals × 33 plants)
Medicinal	digestive	16.60
	respiratory	11.86
	pain and injuries	7.07
	infections	5.77
	wounds	3.27
	genitourinary	1.34
	pregnancy	0.75
	ill-defined	0.32
	skin	0.12
	poisonings	0.06
	circulatory	0.04
	subtotal medicinal	47.20
Beliefs	social norms concerning liars	1.65
	social norms concerning sexual taboos	1.29
	luck in finding a partner	0.35
	luck in hunting	0.32
	luck in fishing	0.32
	better sing	0.06
	better fight	0.03
	for rain	0.03
	better share	0.03
	better work	0.03
	subtotal beliefs	4.08
Foraging	bee plants	0.73
	fish poison	0.62
	caterpillar tree	0.50
	monkey poison	0.48
	subtotal foraging	2.34
Other uses	food	3.45
	mat	1.29
	food additives	0.35
	pirogue	0.32
	firewood	0.14
	uncategorized	0.12
	animal food	0.11
	axe	0.11
	hut	0.10
	avoid animal attacks	0.07
	drum	0.07
	basket	0.03
	subtotal other uses	6.14
Not available		**0.10**
Plant not used		**40.14**
	total	100.00

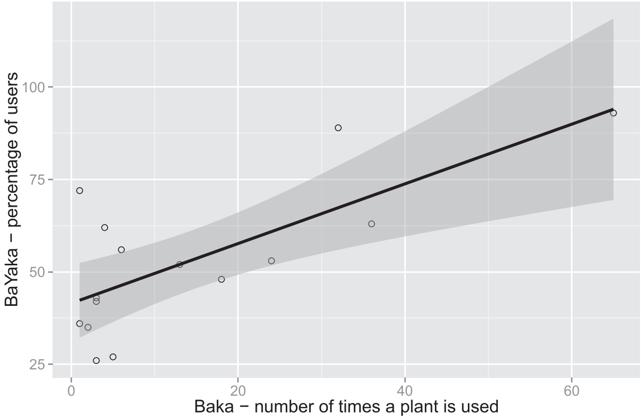

Figure 1. Cross-Population Use of Medicinal Plants

Percentage of Mbendjele BaYaka (n = 219) that used a particular plant as a medicine and the number of times the same plant was used as a treatment by the Baka Pygmies from Cameroon (n = 37, data from [25]) and Gabon (n = 6, data from [26]). Each dot refers to a plant species (n = 15). The shaded area corresponds to 95% confidence interval. See also Table S1.

Maternal Knowledge of Medicinal Plants Affects Children's Body Mass Index

To examine potential health effects of medicinal plant uses, we investigated the 14 most frequently used medicinal species among BaYaka mothers of children aged 0–5 years. Seven plants were used primarily for treating respiratory diseases, and the other seven for digestive system disorders. We found that mothers with higher plant-use scores (calculated as the number of plants used for medicinal purposes by each mother out of the seven possible plants) for treating respiratory system disorders had children with significantly higher body mass index (BMI) (Table 2). However, there was no effect of plant scores for digestive disorders on children's BMI (Table 2). These results indicate that certain medicinal plant uses may provide fitness benefits.

Medicinal Plant Knowledge Is Shared within Families

Mixed-effect models revealed that dyads represented by biological or affinal kin ties had increased odds of reporting the same medicinal plant use (Figures 2A and S1A). A 0.25 increase in the coefficient of relatedness within a dyad increased the odds of reported co-occurrence of medicinal plant use by 22% (odds ratio [OR] = 1.22, 95% confidence interval [CI] = 1.17, 1.27; risk ratio [RR] = 1.19; risk difference [RD] = 3%; Table S2). Breaking down the effects of kinship, dyads including mother and offspring had an increase of 57% in the odds of co-occurrence of medicinal plant use (OR = 1.57, 95% CI = 1.33, 1.84; RR = 1.46; RD = 6%; Figure S1A; Table S2). The effect was much smaller (28%) but still significant for father and offspring (OR = 1.28, 95% CI = 1.04, 1.56; RR = 1.23, RD = 3%). Being siblings increased the odds by 40% (OR = 1.40, 95% CI = 1.18, 1.65; RR = 1.33; RD = 5%).

Affinal ties were also important in explaining co-occurrence of medicinal plant uses (Figure 2A; Table S2). The odds of co-occurrence of medicinal plant use increased by 61% between spouses (OR = 1.61, 95% CI = 1.32, 1.96; RR = 1.49; RD = 7%). Even distant affinal kin were more likely to report similar

Table 2. Mixed-Effects Linear Regression Models

	Respiratory Uses							
	Model 1-1		Model 1-2		Model 1-3		Model 1-4	
	Coefficient (SE)	p Value	Coefficient (SE)	p Value	Coefficient (SE)	p Value	Coefficient (SE)	p Value
(Intercept)	−0.84 (0.67)	0.22	−1.24 (0.54)	0.03	−0.3 (0.31)	0.35	−0.37 (0.32)	0.26
Use score	0.21 (0.1)	0.04	0.2 (0.09)	0.05			0.1 (0.08)	0.21
Age 25–35	−0.28 (0.48)	0.56						
Age 35–45	−0.34 (0.51)	0.51						
Age 45–55	0.26 (0.79)	0.74						
Forest camp 2	0.61 (0.5)	0.23	0.55 (0.47)	0.25	0.73 (0.49)	0.15		
Forest camp 3	1.51 (0.54)	0.01	1.47 (0.54)	0.01	0.88 (0.49)	0.08		
Town camp	0.4 (0.4)	0.32	0.44 (0.38)	0.26	0.13 (0.37)	0.73		
Sex: male	−0.46 (0.3)	0.14						
AIC	119.83		117.64		120.36		120.17	
N observations	42		42		42		42	
N groups	33		33		33		33	
	Digestive Uses							
	Model 2-1		Model 2-2		Model 2-3			
	Coefficient (SE)	p Value	Coefficient (SE)	p Value	Coefficient (SE)	p Value		
(Intercept)	0.35 (0.65)	0.59	−0.3 (0.31)	0.35	−0.04 (0.34)	0.91		
Use score	−0.03 (0.13)	0.85						
Age 25–35	−0.51 (0.5)	0.32						
Age 35–45	−0.54 (0.54)	0.33						
Age 45–55	0.09 (0.89)	0.92						
Forest camp 2	0.9 (0.54)	0.11	0.73 (0.49)	0.15	0.7 (0.48)	0.15		
Forest camp 3	0.92 (0.52)	0.09	0.88 (0.49)	0.08	0.86 (0.48)	0.08		
Town camp	0.15 (0.41)	0.72	0.13 (0.37)	0.73	0.05 (0.36)	0.89		
Sex: male	−0.36 (0.34)	0.31			−0.46 (0.28)	0.15		
AIC	125.41		120.36		119.52			
N observations	42		42		42			
N groups	33		33		33			

Models 1-1 to 1-4: mothers' use score of seven plants for respiratory-system disorders on children's (aged 0 to 5) z-BMI. Models 2-1 to 2-3: mothers' use score of seven plants for digestive-system disorders on children's z-BMI. Control variables: mother's age group, camp residence, and children's sex. The models were fit by maximum likelihood. Models 1-1 and 2-1 were the full models.

For respiratory use score, the optimum model was Model 1-2, which included mother's use score for respiratory problems and her camp residence. Dropping the variable *Use score* from Model 1-2 significantly decreased the model fit (for Models 1-2 and 1-3: $P[\chi^2(1) > 4.72] < 0.05$). For digestive use score, the optimum model was Model 2-2, which included mother's camp residence. Dropping the variable *Sex* from Model 2-2 did not affect the model fit (for Models 2-2 and 2-3: $P[\chi^2(1) > 2.84] = 0.09$). Coefficient is the regression coefficient obtained from the model, and SE is its standard error.

medicinal uses of plants (Figure 2A). The odds of co-occurrence of medicinal plant use increased by 41% (OR = 1.41, 95% CI = 1.26, 1.58; RR = 1.34; RD = 6%) between an individual and their spouse's primary kin and increased by 24% (OR = 1.24, 95% CI = 1.17, 1.31; RR = 1.20; RD = 3%) between an individual and their spouse's distant kin. We also observed spouses collecting medicinal plants and preparing medicines together (Movie S1).

Unlike the large effect of family ties, camp ties (when the two individuals in the dyad reside in the same camp) increased odds of co-occurrence of medicinal plant use by only 6% (Figure 2A; OR = 1.06, 95% CI = 1.04, 1.08; RR = 1.05; RD = 1%; Table S2). Dyads in which individuals belonged to the same age group had increased odds of reporting the same medicinal plant use by 36% (Figure 2A; OR = 1.36, 95% CI = 1.33, 1.39; RR = 1.30; RD = 4%; Table S2). Female-female dyads had increased odds of co-occurrence of medicinal plant use compared to female-male dyads, but the effect size (7%) was small (Figure 2A; OR = 1.07, 95% CI = 1.05, 1.09; RR = 1.06; RD = 1%; Table S2).

Plant Knowledge Related to Cooperative Foraging and Social Beliefs Is Shared among Campmates

Unlike medicinal plant knowledge, plant uses related to foraging and social norms and beliefs co-occurred more frequently among camp members, regardless of family ties (Figures 2B and S1B). Kin and non-kin effects on odds of reporting similar plant uses were similar in the two categories (Tables S3 and S4), which were therefore merged. Being from the same camp increased the odds of co-occurrence of plant use in foraging and social norms and beliefs by 84% (Figure 2B; OR = 1.84, 95% CI = 1.72, 1.97; RR = 1.83; RD = 0.3%; Table S3). In contrast, neither relatedness (Figure 2B; OR = 0.91,

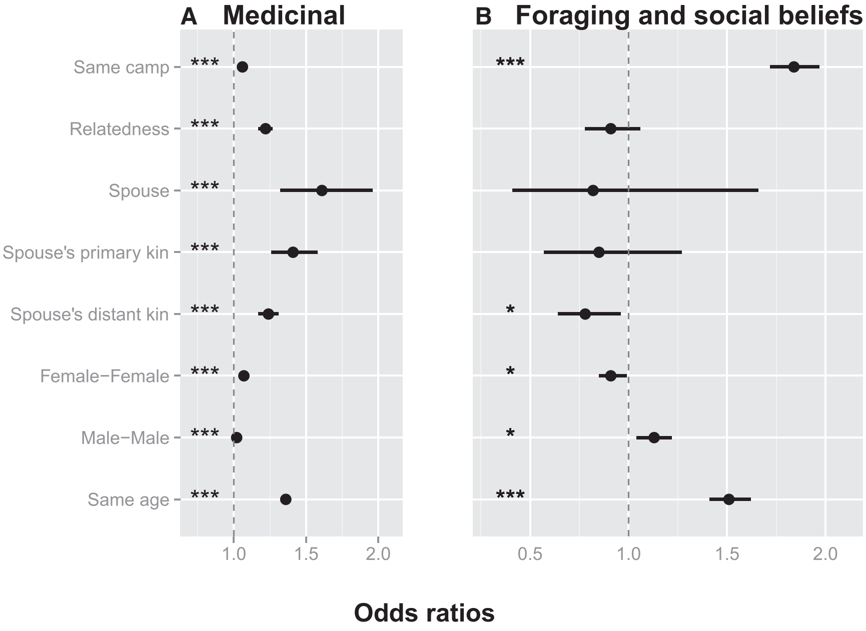

Figure 2. Odds Ratios for the Predictor Variables

Odds ratios are calculated based on mixed-effects logistic regression models (Tables S2 and S3, full models). Response variable is reported co-occurrence of plant use for (A) medicinal purposes or (B) purposes related to foraging and social beliefs. The dots show the odds of co-occurrence of plant use when individuals in a dyad belong to the same camp; are genetically related (odds ratio calculated for a 0.25 increase in coefficient of relatedness); have one of the following affinal kin ties: spouse, spouse's primary kin, or spouse's distant kin; are females; are males; or belong to the same age group. Error bars show 95% confidence intervals. ***$p < 0.001$, *$p < 0.05$. See also Figure S1, Tables S2–S4, and Movies S1 and S2.

95% CI = 0.78, 1.06; RR = 0.92; RD = 0%; Table S3) nor spousal ties (Figure 2B; OR, RR = 0.82; RD = 0.1%; Table S3) had an effect on odds. The odds of co-occurrence of plant use decreased by 26% between a person and his or her spouse's distant kin (OR, RR = 0.78, 95% CI = 0.64, 0.96; RD = 0.1%). Similarity in age group (OR, RR = 1.51; RD = 0.02%) and sex (for male-male dyads: OR = 1.13; RR = 1.12, RD = 0.01%; for female-female dyads: OR = 0.91; RR = 0.92; RD = 0%) had significant effects, but the effect sizes for sex were small (Figure 2B and Table S3). Patterns of co-occurrence of plant use are similar for foraging and social norms and beliefs, as they both refer to camp-wide activities. As an example, we observed multi-family groups fishing with plant poison (Movie S2).

DISCUSSION

Our results showed that family ties have a significant effect on variation in medicinal plant uses among BaYaka hunter-gatherers, while camp co-residence has the strongest effect on variation in plant knowledge related to foraging and social norms and beliefs. We suggest that this pattern is a consequence of two unique aspects of human social structure: pair-bonding with affinal kin recognition, and co-residence with unrelated individuals in camps. Joint production of medicine by parents (Movie S1) is consistent with the frequent co-occurrence of medicinal plant uses between spouses. Information exchange between families is also likely to be valuable because mothers with higher medicinal plant-use scores had healthier children. We also observed grandmothers (maternal and paternal) preparing medicines, which creates additional opportunity for transmission of medicinal knowledge to grandchildren exposed to treatment.

We also show that co-residence of unrelated families in camps is associated with camp-specific plant uses in the domains of foraging and social norms and beliefs. Differences in foraging uses may reflect distinct levels of foraging activities in each camp [33, 34]. For example, people from the Minganga region (where camps one and two were located) are known as "children of the flowers" because they are known to be forest oriented and good honey collectors [33]. Social norms and beliefs, on the other hand, help to regulate camp-wide processes, such as social conflict resolution, punishment of cheaters, and coordination of cooperation through rituals (Table 1). Camp dependence on social norms and beliefs regardless of family ties (Figure 2B) may favor cultural drift in plant knowledge, exemplified by the distinct ritualistic "forest spirit" dances across Pygmy groups [35]. A second example is that only people from the Ibamba camp are known as "people who can fly," due to their particularly rich rituals [33].

Overall, our results suggest that variation in plant knowledge across families and camps cannot be explained purely by ecological variation. If similar plant uses were a result of local variation in plant availability, camp co-residence would have an equal effect on the distribution of all types of plant knowledge. However, residing at the same camp had a very small effect on similarities in medicinal plant use. We propose instead that a multi-layered social structure provides underlying channels for cultural transmission and diversification of plant knowledge among the BaYaka. This is suggested by the correlations we found between social structure (family ties and camp ties) and plant uses. Attempts to detect patterns and direction of cultural transmission by asking people from whom they learned particular information (the "retrospective method") are known to be problematic, as they are affected by memory biases and social norms [19, 36]. For this reason, assessing similarity of cultural knowledge among individuals is seen as a better way of mapping pathways of cultural transmission [18, 37]. By mapping dyadic correlations (or co-occurrence) in plant uses between individuals onto the underlying social structure, we could reveal the roles of biological kin, marriage, and camp ties on the diversification of plant knowledge.

Social interactions create the conditions for cultural transmission through various modes of social learning [38]. Among the BaYaka, social learning predominantly happens through observation and imitation (a young woman observing her mother preparing a medicine), through being a recipient of actions relying on cultural knowledge (a child being treated with a particular medicine by parents), or through sharing experiences (co-participation in rituals). Active teaching is also present, although learning through observation, participation, and practice is more common among African Pygmies [38, 39]. In this context, it must be noted that social learning and cultural transmission are not exclusively human traits. Some African apes also use medicinal plants for similar diseases as humans and may acquire plant knowledge through observation and imitation of other individuals [28, 29], as well as through asocial learning. The fact that eight plants are medicinally used by gorillas [28–30] and six by chimpanzees [29, 31, 32] makes it unlikely that learning happens solely through trial and error in those species. However, their medicinal plant uses are not comparable to the vast diversity of plants used by the BaYaka and other human populations. The close match between hunter-gatherer multi-level social structure and diversification of medicinal plant knowledge indicates that the complex structure of pair bonding, affinal kin recognition, and co-residence of multiple nuclear families created an environment for cultural transmission, as well as knowledge specialization and innovation, exclusive to humans. In addition, co-residence of multiple families allows for the transmission and accumulation of plant knowledge related to group-wide activities such as foraging and rituals, which enhance group coordination. All of these factors may have contributed to the adaptive differentiation of cultural domains and the diversity of human cumulative culture.

EXPERIMENTAL PROCEDURES

All experiments and procedures were approved by the UCL Ethics Committee (UCL Ethics code 3086/003).

Study Population

Mbendjele BaYaka hunter-gatherers are a subgroup of the BaYaka Pygmies whose residence spans across the rainforests of the Republic of Congo and Central African Republic. The BaYaka live in multi-family camps consisting of a number of huts in which nuclear families reside. Social ties among camp members affect food-sharing patterns [40] and individuals' fitness [41, 42].

We visited four BaYaka camps in the Republic of Congo: three in the forest (Longa: n = 59, Masia: n = 22, Ibamba: n = 31), and one in a logging town (Sembola: n = 107; Supplemental Experimental Procedures, section S2).

Measuring Plant Knowledge and Use

Fifteen adult informants (10 men, 5 women) were asked to list the names of plants they used for any purpose. We then chose a subset of 33 plants that are used by the population and asked another 219 individuals (101 men, 118 women) across four campsites whether they knew each of the 33 species, and if so, whether they used it for any purpose (Supplemental Experimental Procedures, section S1). Later, we classified plant uses into four categories: medicinal, social norms and beliefs, foraging, and other. Each category had sub-categories (Table 1). We used the Economic Botany Data Standard for sub-categories of medicinal uses [43].

Dyadic Sample

From 219 individuals we obtained 23,871 dyads. Each dyad had responses for uses of 33 plants, resulting in a possible 787,743 data points. In 151,038 data points (19%), no individual used a given plant, and these points were omitted, resulting in a sample of 636,705 data points and 23,868 dyads.

Measuring Co-occurrence of Plant Use, or "Shared Knowledge"

For each dyad, if individual A and individual B reported the same use for a given plant, their dyadic response was coded as 1 ("shared knowledge"). For all other cases (when individuals reported different uses, or when one of them did not report any uses), the dyadic response was coded as 0. When multiple uses were reported by the same individual, we only included the first use (which occurred in only 2% of the responses).

Statistical Analysis

Because we had 33 responses for each dyad, we used mixed-effects logistic regression to predict the reported co-occurrence of plant use in a dyad. Our fixed predictors were biological kin ties (measured first as coefficient of relatedness, and subsequently as presence of a specific biological kin tie, e.g., mother-offspring; we analyzed and described models based on each measure separately), affinal kin ties, camp ties (residing in the same camp), age group, and sex. We used dyad id as a random effect. We performed separate analyses for three categories of plant use (medicinal, foraging, and social norms and beliefs).

Maternal Medicinal Plant Use and Child BMI

We calculated z scores of BMI (body mass index) using 1-year intervals for children aged 0 to 5 to compare their health status. Plant-use scores were calculated by summing the number of plants used by a mother out of the seven most commonly used plants for treating respiratory or digestive system disorders. We used linear mixed-effects models for testing the effect of plant-use score of each mother on offspring BMI (response variable), controlling for mother's age, camp residence, id (as there were 33 mothers and 42 children, random effect), and sex of the child (Table 2).

SUPPLEMENTAL INFORMATION

Supplemental Information includes Supplemental Experimental Procedures, one figure, four tables, and two movies and can be found with this article online at http://dx.doi.org/10.1016/j.cub.2016.07.015.

AUTHOR CONTRIBUTIONS

A.B.M. conceived the project; G.D.S designed the research and collected the data; G.D.S., A.B.M., R.M., N.C., J.T., M.D., A.E.P., and D.S. helped with protocol design and data collection; O.M.G. and X.M.vdB. identified the plant species and helped with the plant literature research; G.D.S. analyzed the data with several contributions of A.B.M. and L.V.; J.L. assisted in fieldwork; G.D.S., A.B.M., and L.V. wrote the manuscript with the help of all other authors.

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