

1 ***Knowledge-sharing networks in hunter-gatherers and the***
2 ***evolution of cumulative culture***

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18 **Summary**

19 Humans possess the unique ability for cumulative culture [1, 2]. It has been argued
20 that hunter-gatherer's complex social structure [3–9] has facilitated the evolution of
21 cumulative culture by allowing information exchange among large pools of individuals [10–
22 13]. However, empirical evidence for the interaction between social structure and cultural
23 transmission is scant [14]. Here we examine the reported co-occurrence of plant uses
24 between individuals in dyads (which we define as their 'shared knowledge' of plant uses) in
25 BaYaka Pygmies from Congo. We studied reported uses of 33 plants of 219 individuals from
26 four camps. We show that 1) plant uses by BaYaka fall into three main domains: medicinal,
27 foraging, and social norms/beliefs; 2) most medicinal plants have known bioactive
28 properties and some are positively associated with children's BMI, suggesting that their use
29 is adaptive; 3) knowledge of medicinal plants is mainly shared between spouses, biological
30 and affinal kin; and 4) knowledge of plant uses associated with foraging and social norms is
31 shared more widely among campmates, regardless of relatedness, and is important for
32 camp-wide activities that require cooperation. Our results show the interdependence
33 between social structure and knowledge sharing. We propose that long-term pair bonds,
34 affinal kin recognition, exogamy and multi-locality create ties between unrelated families,
35 facilitating the transmission of medicinal knowledge and its fitness implications.
36 Additionally, multi-family camps with low inter-relatedness between camp members
37 provide a framework for the exchange of functional information related to cooperative
38 activities beyond the family unit, such as foraging and regulation of social life.

39 **Results**

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

49 ***Uses of plants by BaYaka Pygmies.***

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

58 ***Medicinal properties of plants***

59 Use of similar medicinal plants across cultures would suggest that they have
60 adaptive benefits and real medicinal properties [21–23]. Medicinal plants have already been
61 shown to improve health in other traditional populations with limited access to modern

62 medicine [24]. Out of 33 plants cited by the BaYaka in our interviews, we successfully
63 identified 31 species. Of these, 15 are also used by Baka Pygmies from Cameroon and Gabon
64 [25, 26]. We found a positive correlation between the number of times each of the 15 plants
65 was reported to be used for medicinal purposes by the BaYaka and Baka (Figure 1, $n= 15$,
66 $\beta= 0.81$, $P< 0.01$). Moreover, 26 species in our sample are also used as medicine by at least
67 one other Central African Pygmy population, including the Mbuti and Efe from Democratic
68 Republic of Congo, the Aka from Central African Republic, and the Baka from Cameroon and
69 Gabon [25–27]. Eight species are known to be used as medicine by gorillas [28–30]; and six
70 by chimpanzees [29, 31, 32] (Table S1). Finally, 24 plants (77%) have known bioactive
71 properties (Table S1). These findings indicate that medicinal plant knowledge by the
72 BaYaka is likely to be adaptive.

73 ***Maternal knowledge of medicinal plants affects children's body mass index*** 74 ***(BMI)***

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

84

85 ***Medicinal plant knowledge is shared within families***

86 Mixed effect models revealed that dyads represented by biological or affinal kin ties
87 had increased odds of reporting the same medicinal plant use (Figures 2A and S1A). A 0.25
88 increase in the coefficient of relatedness within a dyad increased the odds of reported co-
89 occurrence of medicinal plant use by 22% (Odds ratio (OR)= 1.22, 95% CI= 1.17, 1.27; Risk
90 ratio (RR)= 1.19; Risk difference (RD)= 3%; Table S2). Breaking down the effects of kinship,
91 dyads including mother and offspring had an increase of 57% in the odds of co-occurrence
92 of medicinal plant use (OR= 1.57, 95% CI= 1.33, 1.84; RR= 1.46; RD= 6%; Figure S1A; Table
93 S2). The effect was much smaller (28%), but still significant for father and offspring (OR=
94 1.28, 95% CI= 1.04, 1.56; RR= 1.23, RD= 3%). Being siblings increased the odds by 40%
95 (OR= 1.40, 95% CI= 1.18, 1.65; RR= 1.33; RD= 5%).

96 Affinal ties were also important in explaining co-occurrence of medicinal plant uses
97 (Figure 2A, Table S2). The odds of co-occurrence of medicinal plant use increased by 61%
98 between spouses (OR= 1.61, 95% CI= 1.32, 1.96; RR= 1.49; RD= 7%). Even distant affinal
99 kin were more likely to report similar medicinal uses of plants (Figure 2A). The odds of co-
100 occurrence of medicinal plant use increased by 41% (OR= 1.41, 95% CI= 1.26, 1.58; RR=
101 1.34; RD= 6%) between an individual and their spouse's primary kin, and 24% (OR= 1.24,
102 95% CI= 1.17, 1.31; RR= 1.20; RD= 3%) between an individual and their spouse's distant
103 kin. We also observed spouses collecting medicinal plants and preparing medicines together
104 (Supplemental Movie 1).

105 Unlike the large effect of family ties, camp ties (when the two individuals in the dyad
106 reside in the same camp) increased odds of co-occurrence of medicinal plant use by only
107 6% (Figure 2A; OR= 1.06, 95% CI= 1.04, 1.08; RR= 1.05; RD= 1%; Table S2). Dyads where
108 individuals belonged to the same age group had increased odds of reporting the same

109 medicinal plant use by 36% (Figure 2A; OR= 1.36, 95% CI= 1.33, 1.39; RR= 1.30; RD= 4%;
110 Table S2). Female-female dyads had increased odds of co-occurrence of medicinal plant use
111 compared to female-male dyads, but the effect size (7%) was small (Figure 2A; OR= 1.07,
112 95% CI= 1.05, 1.09; RR= 1.06; RD= 1%; Table S2).

113 ***Plant knowledge related to cooperative foraging and social beliefs is shared***
114 ***among campmates***

115 Unlike medicinal plant knowledge, plant uses related to foraging and social
116 norms/beliefs co-occurred more frequently among camp members, regardless of family ties
117 (Figures 2B and S1B). Kin and non-kin effects on odds of reporting similar plant uses were
118 similar in the two categories (Tables S3-4), which were therefore merged. Being from the
119 same camp increased the odds of co-occurrence of plant use in foraging and social norms
120 and beliefs by 84% (Figure 2B; OR= 1.84, 95% CI= 1.72, 1.97; RR= 1.83; RD= 0.3%; Table
121 S3). In contrast, neither relatedness (Figure 2B; OR= 0.91, 95% CI= 0.78, 1.06; RR= 0.92;
122 RD= 0%; Table S3) nor spousal ties had an effect on odds (Figure 2B, OR, RR= 0.82; RD=
123 0.1%; Table S3). The odds of co-occurrence of plant use decreased by 26% between a
124 person and his/her spouse's distant kin (OR, RR= 0.78, 95% CI= 0.64, 0.96; RD= 0.1%).
125 Similarity in age group (OR, RR= 1.51; RD= 0.02%) and sex (for male-male dyads: OR= 1.13;
126 RR= 1.12, RD= 0.01%; for female-female dyads: OR= 0.91; RR=0.92; RD= 0%) had
127 significant effects, but the effect sizes for sex were small (Figure 2B and Table S3). Patterns
128 of co-occurrence of plant use are similar for foraging and social norms and beliefs, as they
129 both refer to camp wide activities. As an example, we observed multi-family groups fishing
130 with plant poison (Supplemental Movie 2).

131 **Discussion**

132 Our results showed that family ties have a significant effect on variation in medicinal
133 plant uses among BaYaka hunter-gatherers, while camp co-residence has the strongest
134 effect on variation in plant knowledge related to foraging and social norms and beliefs. We
135 suggest that this pattern is a consequence of two unique aspects of human social structure:
136 pair-bonding with affinal kin recognition, and co-residence with unrelated individuals in
137 camps. Joint-production of medicine by parents (Supplemental Movie 1) is consistent with
138 the frequent co-occurrence of medicinal plant uses between spouses. Information exchange
139 between families is also likely to be valuable since mothers with higher medicinal plant use
140 scores had healthier children. We also observed grandmothers (maternal and paternal)
141 preparing medicines, which creates additional opportunity for transmission of medicinal
142 knowledge to grandchildren exposed to treatment.

143 We also show that co-residence of unrelated families in camps is associated with
144 camp-specific plant uses in the domains of foraging and social norms and beliefs.
145 Differences in foraging uses may reflect distinct levels of foraging activities in each camp
146 [33, 34]. For example, people from the Minganga region (where camps one and two were
147 located) are known as “children of the flowers” because they are known to be forest-
148 oriented and good honey collectors [33]. Social norms and beliefs on the other hand help to
149 regulate camp-wide processes, such as social conflict resolution, punishment of cheaters,
150 and coordination of cooperation through rituals (Table 1). Camp-dependence on social
151 norms and beliefs regardless of family ties (Figure 2B) may favour cultural drift in plant
152 knowledge, exemplified by the distinct ritualistic ‘forest spirit’ dances across Pygmy groups
153 [35]. A second example is that only people from the Ibamba camp are known as “people
154 who can fly” due to their particularly rich rituals [33].

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

171 Social interactions create the conditions for cultural transmission through various
172 modes of social learning [38]. Among the BaYaka, social learning predominantly happens
173 through observation and imitation (a young woman observing her mother preparing a
174 medicine), through being a recipient of actions relying on cultural knowledge (a child being
175 treated with a particular medicine by parents), or through sharing experiences (co-
176 participation in rituals). Active teaching is also present, although learning through
177 observation, participation and practice is more common among African Pygmies [38, 39]. In
178 this context, it must be noted that social learning and cultural transmission are not

179 exclusively human traits. Some African apes also use medicinal plants for similar diseases to
180 humans, and may acquire plant knowledge through observation and imitation of other
181 individuals [28, 29], as well as through asocial learning. The fact that eight plants are
182 medicinally used by gorillas [28–30] and six by chimpanzees [29, 31, 32] makes it unlikely
183 that learning happens solely through trial-and-error in those species. However, their
184 medicinal plant uses are not comparable to the vast diversity of plants used by the BaYaka
185 and other human populations. The close match between hunter-gatherer multi-level social
186 structure and diversification of medicinal plant knowledge indicates that the complex
187 structure of pair bonding, affinal kin recognition, and co-residence of multiple nuclear
188 families created an environment for cultural transmission as well as knowledge
189 specialisation and innovation exclusive to humans. In addition, co-residence of multiple
190 families allows for the transmission and accumulation of plant knowledge related to group-
191 wide activities such as foraging and rituals, which enhance group coordination. All these
192 factors may have contributed to the adaptive differentiation of cultural domains and the
193 diversity of human cumulative culture.

194 ***Experimental Procedures***

195 All experiments and procedures were approved by the UCL Ethics Committee
196 (UCLEthicscode3086/003).

197 **Study population.** Mbendjele BaYaka hunter-gatherers are a subgroup of the BaYaka
198 Pygmies whose residence spans across the rainforests of the Republic of Congo and Central
199 African Republic. The BaYaka live in multi-family camps consisting of a number of huts in
200 which nuclear families reside. Social ties among camp members affect food sharing patterns
201 [40] and individuals' fitness [41, 42].

202 We visited four BaYaka camps in the Republic of Congo; three in the forest (Longa: n
203 = 59, Masia: n = 22, Ibamba: n= 31), and one in a logging town (Sembola: n = 107;
204 Supplemental Experimental Procedures, section S2).

205 **Measuring plant knowledge and use.** 15 adult informants (10 men, 5 women)
206 were asked to list the names of plants they used for any purpose. We then chose a subset of
207 33 plants that are used by the population and asked another 219 individuals (118 women,
208 101 men) across four campsites whether they knew each of the 33 species, and if so,
209 whether they used it for any purpose (Supplemental Experimental Procedures, section S1).
210 Later, we classified plant uses into four categories: medicinal, social norms and beliefs,
211 foraging, and other. Each category had sub-categories (Table 1). We used the Economic
212 Botany Data Standard for sub-categories of medicinal uses [43].

213 **Dyadic sample.** From 219 individuals we obtained 23,871 dyads. Each dyad had
214 responses for uses of 33 plants, resulting in possible 787,743 data points. In 151,038 data
215 points (19%) neither individual used a given plant and these points were omitted, resulting
216 in a sample of 636,705 data points and 23,868 dyads.

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

223 **Statistical analysis.** Because we had 33 responses for each dyad, we used mixed
224 effects logistic regression to predict the reported co-occurrence of plant use in a dyad. Our

225 fixed predictors were biological kin ties (measured first as coefficient of relatedness, and
226 subsequently as presence of a specific biological kin tie, e.g. mother-offspring; we analysed
227 and described models based on each measure separately), affinal kin ties, camp ties
228 (residing in the same camp), age group and sex. We used dyad id as a random effect. We
229 performed separate analyses for three categories of plant use (medicinal, foraging, and
230 social norms and beliefs).

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

239 **Author contributions**

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

245

246 **Acknowledgements**

247 Many thanks to all the Mbendjele BaYaka participants for their hospitality and
248 sharing their knowledge of the forest; Bakima Arnaud, Ngulawe and Fongola for showing us
249 trees in the forest; Aude Rey and our Mbendjele translators Nicolas, Gifhanou, and Paul for
250 their help in data collection. This project was funded by the Leverhulme Trust grant
251 RP2011-R-045 to A.B.M. and R.M. R.M. also received funding from European Research
252 Council Advanced Grant AdG 249347, and G.D.S. from Funds for Women Graduates,
253 Foundation Main Grant 156240.

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374 **Figure legends and tables**

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376 **Figure 1. Cross Population Use of Medicinal Plants.** Percentage of Mbendjele BaYaka (n=
377 219) that used a particular plant as a medicine and the number of times the same plant was
378 used as a treatment by the Baka Pygmies from Cameroon (n= 37, data from Betti 2004 [23])
379 and Gabon (n= 6, Betti et al. 2013 [24]). Each dot refers to a plant species (n= 15). The
380 shaded area corresponds to 95% confidence interval. See also Table S1.

381 **Figure 2. Odds Ratios for the Predictor Variables.** Odds ratios are calculated based on
382 mixed effects logistic regression models (Tables S2-3, full models). Response variable is
383 reported co-occurrence of plant use for (a) medicinal purposes or (b) purposes related to
384 foraging and social beliefs. The dots show the odds of co-occurrence of plant use when
385 individuals in a dyad belong to the same camp; are genetically related (odds ratio calculated
386 for a 0.25 increase in coefficient of relatedness); have one of the following affinal kin ties:
387 spouse, spouse's primary kin, or spouse's distant kin; are females; are males; belong to the
388 same age group. Error bars show 95% confidence intervals. *** $P < 0.001$, * $P < 0.05$. See also
389 Figure S1, Tables S2-4, and Movies S1-2.

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394 Table 1. Uses of plants by Mbendjele BaYaka Pygmies

Category	Sub category	% Percentage in all answers (219 individuals x 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
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
	uncategorised	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

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396 **Table 2. Mixed-effects linear regression models.** Models 1-1 to 1-4: mothers' use score of
397 7 plants for respiratory system disorders on children's (aged 0 to 5) z-BMI. Models 2-1 to 2-
398 3: mothers' use score of 7 plants for digestive system disorders on children's z-BMI. Control
399 variables: mother's age group, camp residence, and children's sex.

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

400 The models were fit by maximum likelihood. Models 1-1 and 2-1 were the full models.
401 For respiratory use score, the optimum model was Model 1-2 which included mother's use
402 score for respiratory problems and her camp residence. Dropping the variable *Use score*
403 from Model 1-2 significantly decreased the model's fit (for Model 1-2 and 1-3: $P[\chi^2(1) >$
404 $4.72] < 0.05$). For digestive use score, the optimum model was Model 2-2 which included
405 mother's camp residence. Dropping the variable *Sex* from Model 2-2 did not affect the model
406 fit (for Model 2-2 and 2-3: $P[\chi^2(1) > 2.84] = 0.09$). Coefficient is the regression coefficient
407 obtained from the model and SE is its standard error.

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