



Migliano, A. B., Page, A. E., Gómez-Gardeñes, J., Salali, G. D., Viguier, S., Dyble, M., Thompson, J., Chaudhary, N., Smith, D., Strods, J., Mace, R., Thomas, M. G., Latora, V., & Vinicius, L. (2017). Characterization of hunter-gatherer networks and implications for cumulative culture. *Nature Human Behaviour*, 1, [0043].
<https://doi.org/10.1038/s41562-016-0043>

Peer reviewed version

License (if available):
Other

Link to published version (if available):
[10.1038/s41562-016-0043](https://doi.org/10.1038/s41562-016-0043)

[Link to publication record in Explore Bristol Research](#)
PDF-document

This is the accepted author manuscript (AAM). The final published version (version of record) is available online via Springer Nature at <https://doi.org/10.1038/s41562-016-0043> . Please refer to any applicable terms of use of the publisher.

University of Bristol - Explore Bristol Research

General rights

This document is made available in accordance with publisher policies. Please cite only the published version using the reference above. Full terms of use are available:
<http://www.bristol.ac.uk/red/research-policy/pure/user-guides/ebr-terms/>

1 **Characterisation of hunter-gatherer networks and implications for cumulative**
2 **culture**

3
4
5

6 **Authors**

7 A. B. Migliano^{1*}, A. E. Page¹, J. Gómez-Gardeñes², G. D. Salali¹, S. Viguier¹, M. Dyble¹,
8 J. Thompson¹, Nikhill Chaudhary¹, D. Smith¹, J. Strods¹, R. Mace¹, M. G. Thomas³, V.
9 Latora⁴, L. Vinicius¹

10

11 **Affiliations**

12 ¹Department of Anthropology, University College London, London WC1H 0BW, United
13 Kingdom.

14

15 ²Department of Condensed Matter Physics and Institute for Biocomputation and Physics of
16 Complex Systems, University of Zaragoza, 50009 Zaragoza, Spain.

17

18 ³Department of Genetics, Evolution and Environment, University College London, London
19 WC1E 6BT, United Kingdom.

20

21 ⁴School of Mathematical Sciences, Queen Mary University of London, London E1 4NS, United
22 Kingdom.

23 *Correspondence to: a.migliano@ucl.ac.uk

24

25

26
27 **Social networks in modern societies are highly structured, usually involving frequent**
28 **contact with a small number of unrelated ‘friends’¹. However, contact network structures**
29 **in traditional small-scale societies, especially hunter-gatherers, are poorly characterised.**
30 **We developed a portable wireless sensing technology (motes) to study within-camp**
31 **proximity networks among Agta and BaYaka hunter-gatherers in fine detail. We show**
32 **that hunter-gatherer social networks exhibit signs of increased efficiency² for potential**
33 **information exchange. Increased network efficiency is achieved through investment in a**
34 **few strong links among non-kin ‘friends’ connecting unrelated families. We show that**
35 **interactions with non-kin appear in childhood, creating opportunities for collaboration**
36 **and cultural exchange beyond family at early ages. We also show that strong friendships**
37 **are more important than family ties in predicting levels of shared knowledge among**
38 **individuals. We hypothesise that efficient transmission of cumulative culture³⁻⁶ may have**
39 **shaped human social network and contributed to our tendency to extend networks**
40 **beyond kin and form strong non-kin ties.**

41 We studied in-camp proximity networks (within and between households) as a proxy for
42 social interactions in two hunter-gatherer populations from Africa and Southeast Asia. We
43 developed a portable wireless sensing technology (motes; Figure 1) to record all dyadic
44 interactions within a radius of approximately 3 meters at 2-minute intervals for 15 hours a day
45 (05:00-20:00) over a week, in six Agta camps in the Philippines (200 individuals, 7210 recorded
46 dyadic interactions) and three BaYaka camps in Congo (132 individuals, 3397 dyadic
47 interactions; see Table S1 with descriptive statistics for all camp networks). We built high-
48 resolution proximity networks mapping the totality of close-range interactions within each camp.
49 In hunter-gatherers (who lack technology-aided communication), close proximity is an indicator
50 of joint activities such as foraging⁷, parental care⁸ and information exchange⁴.

51 To investigate a possible relationship between social structure and cultural exchange,
52 we estimated the 'global network efficiency'² of our proximity networks. Global network
53 efficiency is a measure of how the properties of a network can facilitate information flow
54 amongst its individuals (nodes) irrespective of whether exchange of information actually occurs,
55 and is therefore a structural property independent from the nature of the information flow. For
56 example, when planning a new town, engineers may want to compare alternative configurations
57 of road systems and select the one minimising average distance or travelling time between any
58 two points, irrespective of mode of transport. Global network efficiency provides a measure of
59 ease of transmission across a network, and has been applied to studies of social networks as
60 well as power grids, phone networks, neural systems and transportation networks² among
61 others.

62 To estimate global network efficiency, we first built weighted social networks using our
63 notes proximity data from Agta and BaYaka camps (Fig.2A and Fig. S1), and subdivided the
64 networks into three decreasing levels of relatedness: close kin (parents, children, siblings,
65 partners), extended family (grandparents, grandchildren, aunts, uncles, nieces, nephews, first
66 cousins, parents-in-law, siblings-in-law) and non-kin (see Methods for details of kin
67 categorisation, and Tables S2 and S3 for percentages of links for each kin category and age
68 groups). We estimated the contribution of each relatedness level to global network efficiency by
69 comparing our hunter-gatherer network structures to randomly permuted networks (the baseline
70 for estimation of efficiencies of real networks). Our randomisation procedure does not modify
71 the total number of links (edges), sum of all link weights (number of recorded interactions for
72 each dyad) and degree (number of links) of each node, but randomly shuffles links among
73 nodes within each level of relatedness. For example, when randomising the non-kin network, we
74 preserve the number of non-kin links from each individual (number of friends), but redistribute
75 their target nodes (identity of their friends). Since our networks are weighted (as each dyad may
76 have been in close proximity multiple times during the one-week interval), random reshuffling of

77 links also changes the strength of friendships. For each of the three categories of relatedness,
78 we created an ensemble of 1000 randomised graphs (see Methods for procedures). The
79 average global efficiency of the randomised ensemble was then compared to the global
80 efficiency of the corresponding observed networks for each camp.

81 Our analyses show that randomisation of interactions among either close kin or
82 extended family (including affinal kin) does not affect the global efficiency of hunter-gatherer
83 networks. In contrast, randomisation of non-kin relationships (friends) drastically reduces global
84 network efficiency (Fig.2B, and Fig. S2 for other camps) both in the Congo and the Philippines
85 camps (Fig. 2C). The reason is that randomisation of non-kin links homogenises their weights,
86 eliminating strong friendships from networks. This is not observed in the case of randomisation
87 of close kin and distant kin links, which do not exhibit the same levels of the heterogeneity in
88 strength of links. Therefore, increased global efficiency in our networks results from investing in
89 a few strong 'close friends' in addition to an extended net of social acquaintances, or a
90 combination of strong and weak ties⁹. Controlling for household in randomisations does not
91 change the results (Fig. S3). In summary, a large number of homogeneous links to all unrelated
92 individuals caused by randomisation reduced global network efficiency. In agreement with
93 classic studies of 'small-world networks'¹⁰, our results show that only a few 'shortcuts'
94 (friendships) connecting closely-knit clusters (households consisting mostly of close kin) suffice
95 to significantly reduce the average path length or distance between any two points across the
96 whole network, thus reducing redundancy and the cost of maintaining strong links with a large
97 number of unrelated individuals. Since unrelated individuals often live in different households,
98 they provide a small number of reliable 'shortcuts' between households. Both the Agta and
99 BaYaka had between one to four unrelated 'close friends' whom they interact with as frequently
100 as with close kin (Fig. 3). This number is consistent across ages and camps, and with the
101 finding that people in Western societies are in close contact with an average of four friends¹.
102 Friendships have also been shown to be particularly important in unpredictable environments,

103 and as a special case of reciprocal help¹¹, which is central to hunter-gatherers⁷. We further
104 demonstrated the importance of friendships to cultural transmission through a mixed-effects
105 logistic regression of levels of shared plant knowledge in a dyad against a series of predictors,
106 using our Congo dataset¹². The most important predictor was close friendship, with odds of
107 shared knowledge between close friends of 1.82 (95% CI: 1.32-2.5) , 1.48 (1.26-1.74) between
108 mother-offspring, 1.46 (1.2-1.78) between spouses, and 1.31 (1.11-1.54) between siblings
109 (Table S4).

110 Inequality in link weight distributions is consistently higher among non-kin than among
111 either close kin or extended family members, with Gini coefficients of 0.85, 0.69, 0.72 (Dinipan,
112 Philippines), and 0.92, 0.35 and 0.63 (Ibamba, Congo) respectively (see Table S1 for Gini
113 coefficients in other camps). Heterogeneity in the number of social ties per individual (degree)
114 was previously reported in the Hadza¹³. We extend this finding to the intensity of social
115 interactions (link strength) and demonstrate that the high heterogeneity in the intensity of non-
116 kin social ties is responsible for the increased efficiency of Agta and BaYaka social networks
117 (see Fig. S4 for plots of tie strength distributions of non-kin, close kin and affinal kin ties for each
118 camp). Non-kin interactions also keep transitivity (a measure of the local efficiency or clustering
119 in networks²) consistently higher in Agta and BaYaka networks compared to equivalent
120 randomised networks (Figure 2C; see Fig. S5 for transitivity in other camps, and Methods for
121 details of calculations), in agreement with previous studies of Hadza hunter-gatherers¹³. The
122 combination of high global and local network efficiencies in both Congo and the Philippines is a
123 characteristic of ‘small-world networks’ that allows for efficient information flow, and has been
124 argued to promote creativity¹⁴.

125 We also found evidence that ‘friendships’ are formed early in childhood in both
126 populations. Among the Agta, 27% of interactions of children aged 3 to 7 years occurred with
127 non-kin (Fig. 4A), compared to 32% of interactions with siblings, 13% with mothers, and less
128 than 1% with their grandmothers. Among the BaYaka, 30% of interactions of children aged 2 to

129 7 were with non-kin (Fig. 4B), 30% with siblings, 17% with mothers, and 5% with grandmothers.
130 Between ages 8-12, interactions with non-kin increased to 39% in the Agta and 35% in the
131 BaYaka. Non-kin interactions among children aged between 2 and 12 years were age-
132 assortative (Philippines: $\beta=26.6$, $P<0.001$, 95% CI:14.6-38.67; Congo: $\beta=29.3$, $P<0.001$, 95%
133 CI:18.7-38.8; see Methods).

134 The origin of links with non-kin in early childhood has important implications for our
135 understanding of human life history. We argue that our delayed maturation may facilitate social
136 learning through cultural diffusion in play groups¹⁵, where children are frequently looked after by
137 older children and learn through playing and imitation of role models¹⁶ (see Supplementary
138 Video 1). In Agta and BaYaka play groups, children also establish their first friendships, which
139 may have important consequences in adult life. We show that across age groups people have at
140 any given time a few 'close friends', and this is likely to be one of the conditions for the high
141 between-camp mobility that characterise hunter-gatherers¹⁷, who encounter around ten times
142 more individuals over a lifetime than chimpanzees^{18,19}. We observed that hunter-gatherer
143 households tend to be highly mobile and unrelated to each other^{20,21}, moving between camps on
144 average every 22.8 days in Congo and 12.5 days in the Philippines¹⁷. It should be noted that our
145 analyses of network efficiency focused on within-camp relationships, while between-group
146 structuring was shown to affect cultural innovation at least in an experimental setting²². The new
147 motes technology could therefore be extended to studies of between-band interactions, and
148 performed in parallel with direct measures of cultural transmission in the same networks²³.

149 The observed higher network efficiency of Agta and BaYaka social networks can also
150 impose trade-offs. Friendship choices among urban contemporary Americans, for instance,
151 have been shown to affect not only information exchange but also the spread of diseases²⁴.
152 Such trade-off may be particularly problematic among hunter-gatherers whose population sizes
153 and local genetic diversity are typically low. However, real-world networks are known to be
154 dynamic and adapt to the infection risk status of particular nodes by breaking ties and

155 temporarily reducing transmission efficiency²⁵. For example, we observed a rewiring of proximity
156 networks in one Agta camp, which broke down into two units during a measles outbreak. In
157 addition, although our analyses focused on network efficiency and its potential impact on
158 information flow, other aspects of hunter-gatherer social networks may be shaped by other
159 demands. For example, affinal kinship links may play a potential role in cooperation, coalition
160 formation and marriage rules²⁶, and sex assortativity in offspring care, foraging and access to
161 resources^{7,30}.

162 We propose that high global efficiency of social networks is important to multiple aspects
163 of human cumulative culture, including the spread of social norms¹⁷, diffusion of technological
164 innovations²², among others. Efficient hunter-gatherers networks depend on the existence of a
165 few close friends linking households and enabling the flow of information among them. The role
166 of friendship ties in promoting cumulative culture in hunter-gatherers is further supported by the
167 fact that close friends have increased shared plant knowledge as compared to spouses, siblings
168 and parent-offspring dyads in our Congo dataset. ‘Small-world’ properties (such as the
169 combination of high global and local efficiency) and the tendency to share and exchange
170 information with unrelated individuals are features previously identified in online communities²⁸
171 and even the World Wide Web^{1,2,29}. We have presented evidence that those properties are also
172 found in two hunter-gatherer populations. Details of the evolutionary links among network
173 structures, strong friendships and cumulative culture require further investigation. However, the
174 evidence presented in our study suggests an explanation for why people are keen to socialise,
175 cooperate and exchange information with unknown individuals, from isolated tribes seeking
176 contact³⁰ to global-scale social networks on the World Wide Web.

177

178

179 **Materials and Methods**

180

181 **Experimental Design**

182

183 **1. Sample.** We studied two populations of hunter-gatherers: Agta (Philippines) and Mbedjele
184 BaYaka pygmies (Congo). Research started in 2011, while proximity notes data were collected
185 between March and September 2014.

186 *1.1. Agta.* Agta hunter-gatherers subsist on terrestrial, river and coastal marine resources. They
187 live in North East Luzon within the Northern Sierra Madre Natural Park, Municipality of Palanan,
188 Isabela and speak Agta Paranan (an Austronesian Language). Population is estimated in 1000
189 individuals in Palanan³¹. We studied 200 individuals of all ages from six camps. They live in
190 small bands of 49 ± 22 people on average. Some camps have semi-permanent houses while in
191 others households mover more regularly between camps. Across camps, 80.4% of food is
192 produced by foraging (fishing, hunting and gathering) and the remaining by cultivation. The Agta
193 trade some fish and vegetables for rice and occasionally engage in cash labour (between 0 and
194 12% of their time, depending on camp). Rice is consumed in 44% of meals, but there is
195 significant variation across households (from 12.5% to 75%). Therefore, activity and production
196 patterns still reflect a foraging lifestyle, while diet composition depend on the fraction of rice
197 traded by households^{32,33}.

198 *1.2. Mbendjele BaYaka.* The Mbendjele (a Bantu language) are a subgroup of the BaYaka
199 pygmy hunter-gatherers. BaYaka subsistence includes hunting, trapping, fishing, gathering and
200 honey collecting. They span across Congo-Brazzaville and Central African Republic forests,
201 where their population is around 30,000. Our study population lives in Sangha and Likuoala. We
202 studied 132 Mbendjele of all ages from three camps (with 10-60 individuals; mean= 44 ± 24).
203 Nuclear families live in langos (multi-family camps consisting of 'fumas' or huts). Some live near
204 mud roads opened by logging companies and move between camps depending on food
205 resources, trading some meat and forest products for farmer products and occasionally
206 engaging in cash labour.

207

208 **2. Portable wireless sensing technology (motes).**

209 *2.1. Motes.* Recent progress in embedded electronics has led to compact (50 mm*35 mm*15
210 mm with casing) and affordable wearable devices with sensors. For this study, we selected
211 devices supporting TinyOS, an operating system developed at the University of California,
212 Berkeley. Our device (Fig. 1) is a customised UCMote Mini with main processor, wireless
213 communication module, memory storage unit and a four-week battery (software-optimised for
214 low energy consumption). We deployed 200 motes in the Philippines and 200 in Congo.

215 *2.2. Software.* We wrote the embedded software in *C* and *nesC* following an iterative process to
216 optimise parameters (frequency of beacons, strength of wireless communications, length of
217 sleep phases). Each device sends beacons every 2 minutes, receiving beacons from other
218 devices within a 3-meter range and storing them in long-term memory. At the end of the
219 experiment, device memories were downloaded via a PC side application written in JAVA.

220 *2.3. Range and calibration.* Radio links were adjusted to allow recording of other radio signals
221 within 3 meters. A specific radio transmission technique (low power listening) was used to
222 reduce battery usage. We calibrated radio links by testing devices on a range of situations and
223 environments, in the UK and in the field.

224 *2.4. Motes utilisation.* After being waterproofed with cling film, motes were sealed into
225 wristbands or armbands (for babies). We studied one camp at a time in the Philippines and
226 Congo. After explaining methods and discussing data anonymity through presentations and
227 posters in local languages, each participant agreeing to participate and signing the informed
228 consent form received a mote. Each motes received an ID number and coloured string.
229 Individuals wore motes uninterruptedly from four to nine days depending on the camp, but only
230 data collected between 05:00 and 20:00 were analysed. Individuals arriving at camp during the
231 experiment were given a mote and an entry time; those leaving camp before the end of the
232 experiment had their exit time recorded. A small compensation (thermal bottle or cooking

233 utensils) was given to each participant at the end. We regularly checked for armband swaps.
234 Mote numbers were also checked upon return, alterations recorded and adjustments made prior
235 to data processing.

236 *2.5. Ethical approval.* Research project and fieldwork were approved by the UCL Ethics
237 Committee in 2011 for the period between 2011 and 2016 (code 3086/003, Leverhulme Trust
238 grant RP2011-R-045, 2011-2016) and carried out after informed consent was obtained from all
239 participants. In order to establish a fair process of understanding within the communities, we
240 presented posters with pictures and drawings explaining the purpose of our research project.
241 Subsequently, procedures and the technology (motes) were described to the whole community
242 in multiple presentations. Later, we obtained consent from tribal elders, and then from each
243 individual; parents gave consents for their children. Only 2-3 individuals from each camp
244 preferred not to participate in the study and were excluded.

245 *2.6. Data recovery.* Raw data were run through a stringent data-processing system in *Python* to
246 leverage the filtering power of MySQL databases and prevent data corruption. Following basic
247 checks, data were matched to ID numbers (preserving anonymity) and to start-stop times of
248 each mote. We then created a matrix containing the number of recorded beacons for all
249 possible dyads (i.e. frequency of close-range interactions) in each camp. A proportional
250 correction was made for late entries or early exits.

251 *2.6. Motes validation (focal follows).* To validate our methodology, we compared motes and
252 observational data from eight children aged between 3-5 years. We conducted 'focal follows' for
253 a total of nine hours over three non-constitutive days, observing all individuals present within
254 three meters of each child every 30 seconds³⁴. This produces 1080 observational points per
255 child over three days (one every 30 seconds), compared to an average of 3150 emitted motes
256 points over one week (1 every 2 minutes). However, since multiple ties are captured with each
257 observation or motes recording, there is on average 3850 mote points compared to 3080
258 observational points per child.

259 To compare notes and focal follows data, we produced average proportions of time
260 spent by children with specific kin categories. Differences between averages were minimal, as
261 well as the distribution of observations with specific kin types. Notes recorded an average of
262 34% of time spent with mothers, 11% with fathers, 24% with siblings and 6%, 7% and 23% for
263 grandparents, other kin ($0.125 \leq r \leq 0.25$) and non-kin ($r < 0.125$), respectively. Focal follows
264 recorded 37% of time spent with mothers, 19% with fathers, 24 % with siblings and 2 %, 7% and
265 24% of their time with grandparents, other kin and non-kin, respectively. Small differences are
266 most likely caused by notes covering a full week, and focal follows only nine hours. Note that
267 the total proportions do not add up to 100% as multiple people can be found simultaneously
268 within the three-meter range. Overall, this demonstrates that notes data accurately represent
269 proximity patterns.

270 *2.7. Notes validation (camp scans).* We also ran camp scans four times a day for a week in
271 some camps. In the Philippines, people were found together 'resting in silence' (activity
272 categories 'resting together' plus 'sleeping close to each other during the day') only 5.6% of the
273 time. The most frequent activity categories were 'chatting' (25.7%), playing together (16%),
274 looking after children together (11.5%), cooperating in food-related activities such as hunting,
275 gathering, food processing, cooking and eating (17.4%); together, they represent 70% of
276 activities done in close proximity. The remaining 24.4% also refer to social interactions and joint
277 activities (building houses, fixing tools, washing clothes, tending fire, trading, logging,
278 participating in religious ceremonies). Therefore people in close proximity are generally involved
279 in social interactions and joint activities.

280

281 **3. Genealogical data and kin definition.** We collected genealogies over three generations for
282 all individuals, and built relatedness matrices based on kin categories (mother, father, son,
283 daughter, spouse, brother, sister, uncle, aunt, niece, nephew, cousin, grandparents,
284 grandchildren, parents-in-law, children-in-law, brother/sister-in law, other kin, other affines, and

285 unrelated individuals). We defined 'primary kin' as parents, children, siblings and partners.
286 'Extended family' included distant kin (grandparents, grandchildren, aunt, uncle, niece, nephew,
287 first cousins, parents-in-law, siblings-in-law). 'Unrelated individuals' are all other individuals, also
288 including more remotely related individuals (such as the ego's wife's brother's wife's sister)
289 eligible for marriage in these populations, and therefore better interpreted as friends than
290 extended family members.

291

292 **Statistical Analyses**

293 **4. Multi-level modelling of age assortativity.** We tested for age assortativity in dyadic
294 interactions using a mixed-effects linear regression. The number of recorded interactions for a
295 dyad was the response variable. To control for pseudoreplication we defined dyad, ego ID and
296 camp as hierarchically structured random effects, and 'same age' as a binary (yes/no) fixed
297 effect. Each individual was allocated an age group: infant (under 2 years old); child (2-12 years);
298 teenager (13-18 years); reproductive adults (18-45 years); and post-reproductive adults (46 and
299 over). If both individuals in a dyad were in the same age group, the variable 'same age' was
300 given the value 'yes'.

301

302 **5. Dyadic predictors of shared plant knowledge.** We ran a mixed-effects logistic regression
303 of shared plant knowledge¹² in dyads (binary response; shared=1, non-shared=0) on various
304 binary predictors. If a dyad consisted of a father-offspring pair, the predictor 'father' was coded
305 as '1' and otherwise as '0'; the same for predictors 'mother', 'sibling', 'spouse', 'sibling's primary
306 kin', 'siblings distant kin', and 'close friend'. 'Close friend' was any dyad whose weight (link
307 strength) was higher than the average weight of a close kin dyad in the same camp. Ego ID,
308 'same camp' and 'same age group' (five-year intervals) were entered as random factors. Our
309 sample consists of dyads for which both data on proximity and plant knowledge were available.
310 A total 824 dyads were analysed, 16 of which were close friends. Each was assessed for

311 shared knowledge 33 times (the number of plants each individuals was asked about), totalling a
312 sample of 27192 regression data points.

313

314 **6. Social Network Analysis.** We used proximity data to build nine undirected weighted graphs
315 G describing the social interaction networks for each of camps (Figure 1A and Fig. S1). The N
316 nodes of each network represent the individuals in the camp, while the undirected link (i,j)
317 between node i and j indicates the presence of proximity interactions between individual i and
318 individual j . The weight w_{ij} of link (i,j) is the frequency of interaction between two individuals,
319 measured by the number of recorded interactions (beacons) between their notes. The weights
320 ranged from the smallest possible non-zero value of $w_{ij}=238$ to $w_{ij}=20,876$ beacons. Each graph
321 is described by the $N \times N$ symmetric and weighted adjacency matrix $W=\{w_{ij}\}$, with $i,j=1,2,\dots,N$.
322 Entry w_{ij} is equal to zero if individuals i and j had no close-range social contacts, and by
323 definition also when $i=j$. For each graph, an unweighted adjacency matrix $W=\{w_{ij}\}$, with
324 $i,j=1,2,\dots,N$, can be defined by setting $w_{ij}=1$ if w_{ij} is different from zero, and $w_{ij}=0$ otherwise. The
325 total number of links in the graph is equal to $K = \frac{1}{2} \sum_{i=1}^N \sum_{j=1}^N w_{ij}$. The degree k_i of a node i is
326 defined as $k_i = \sum_{j=1}^N w_{ij}$, and is equal to the number of its first neighbours, while its strength s_i is
327 equal to the sum of node weights $s_i = \sum_{j=1}^N w_{ij}$. Finally, the average node degree is $\langle k_i \rangle = 2K/N$.

328 *6.1. Link weight distribution and Gini coefficient.* The heterogeneity in the distribution of weights
329 among the links of a graph can be quantified by the Gini coefficient g , an index used in
330 economics and ecology to measure inequalities of a given resource among individuals³⁵. It is
331 obtained by comparing the Lorenz curve of a ranked empirical distribution (i.e. a curve that
332 shows, for the bottom $x\%$ of individuals, the cumulative percentage $y\%$ of the total size) with the
333 line of perfect equality. In our case, we obtain the Lorenz curve by plotting the percentage $y\%$ of
334 the total weights held by the $x\%$ of links considered, sorted in increasing value of weights. The
335 Gini coefficient ranges from a minimum value of zero, when all individuals are equal, to a

336 theoretical maximum value of 1 in a population in which every individual except one has a size
337 of zero.

338 *6.2. Calculating network efficiency.* Network global efficiency of graph G (Figure 1A and Fig. S1)
339 was calculated as follows. First, we created weighted networks using the notes data. This
340 means that a dyad observed 100 times in close proximity is connected by a link 100 times
341 stronger than a dyad only observed once in close proximity. Our procedure assumes that a
342 frequent or strong link reflects a ‘close’ link, i.e. the two points are separated by a short distance
343 in the network. We implement this relationship by defining the length of a link as the inverse of
344 its weight. Weighted shortest paths were computed for each couple of nodes in G, assuming
345 that the length l_{ij} of an existing link (i,j) is equal to the inverse of the weight w_{ij} , and using
346 standard algorithms to solve the all-shortest-path problem in weighted graphs. The distance d_{ij}
347 between nodes i and j is defined as the sum of the link lengths over the shortest path
348 connecting i and j. The efficiency ϵ_{ij} in the communication from i to j over the graph is then
349 assumed to be inversely proportional to the shortest path length, i.e. $\epsilon_{ij}=1/d_{ij}$. When there is no
350 path linking i to j we have $d_{ij}=+\infty$ and the efficiency in the communication between i and j is set
351 equal to 0. The global efficiency of graph G is defined as the average of ϵ_{ij} over all couples of
352 nodes:

$$353 \quad E(G) = \frac{1}{N \cdot (N-1)} \cdot \sum_{\substack{i,j \in G \\ i \neq j}} \epsilon_{ij} = \frac{1}{N \cdot (N-1)} \cdot \sum_{\substack{i,j \in G \\ i \neq j}} \frac{1}{d_{ij}}$$

354 In the case of unweighted graphs, global efficiency E assumes values from 0 to 1, while
355 in weighted graphs the values of $E(G)$ depend on the typical weights associated to the links. It is
356 therefore very useful to compare the global efficiency of a given weighted network to the global
357 efficiency of a randomised version of the network.

358 6.3. *Network randomisation*. We constructed randomisations for each of the nine undirected
359 weighted graphs G describing a proximity network. The aim is to randomise each graph by
360 maintaining some of its original properties, such as the total number of links, the sum of all the
361 weights, and the degree of each node, and then randomising such links and nodes at each level
362 of relatedness. To that purpose we divided the ties into close kin, extended family, and lastly
363 non-kin. Then, for each camp, we considered first a network with only close-kin links, and we
364 compared it to its randomised versions. The randomisation procedure consists in the following
365 two stages.

366 Stage A: changing the adjacency matrix of close-kin ties.

367 1) Take a node i and a close-kin node j .

368 2) Choose with uniform probability a node l in a close-kin relation with node i (excluding node j),
369 and a node m in a close-kin relation with node l .

370 3) If there are no links already between node i and node m , or between node j and node l , and if
371 nodes i and m are close kin, and node j and l are also close kin, swap the two links by
372 connecting node i to node m and node j to node l .

373 4) If any of the conditions in point 3 are not verified, repeat the search with another couple of
374 nodes l and m , up to M times. If after M times the conditions have not been fulfilled, the link
375 between node i and node j is left unaltered.

376 Stage B: redistributing weights to the new adjacency matrix.

377 5) Each node i has a total number of beacons equal to its strength s_i (the sum of the weights of
378 all its links). Each of these beacons is randomly reallocated with uniform probability to one of the
379 k_i new neighbours.

380 Steps (1-5) are repeated for each node and for each of its links.

381 Next, we considered the network with close kin and extended family links, and then randomised
382 only extended family links according to the procedure above. Finally, we considered the network
383 with close kin, extended family and non-kin links, and randomised only non-kin links. For each

384 of the three cases, we used $M=100$ iterations and we created an ensemble of 1000 randomised
385 graphs. The average global efficiency obtained for the ensemble of randomised graphs was
386 compared to the global efficiency of the real networks at the three relatedness levels for each
387 camp. We also performed randomisations preserving household structure, where for each level
388 of dyadic relatedness (close kin, extended family and non-kin) we checked whether the original
389 dyad was within or between households, and only allowed randomisation to occur respectively
390 within or between households. Results remained mostly unchanged (Fig. S3).

391 *6.4. Network Transitivity.* Since our networks are weighted, we have measured transitivity (a
392 measure of local efficiency) as the total strength of the triads found in our network. To do
393 this, we have calculated the third power of the weighted adjacency matrix. The element i,j of
394 the resulting matrix A^3 measures the strength of the walks of length 3 starting from node i
395 and reaching node j . In this way, the i -th element of the diagonal of matrix A^3 gives the total
396 strength of a closed triad starting and ending at node i . Summing all the elements of the
397 diagonal (i.e. computing the trace of A^3) and dividing by 6, since each triad is counted twice
398 (once in each direction) for each of its three nodes, we obtain the total strength of the triads,
399 i.e. the transitivity of the weighted network:

$$T = \frac{1}{6} \sum_{i=1} A_{ii}^3$$

400 As in the case of global efficiency, the values of network transitivity of the hunter-gatherer
401 real networks have been compared to the averages obtained for randomised ensembles.

402

403 **7. Data availability.** The data that support the findings of this study are available from the
404 corresponding author (ABM) upon request.

405

406

407

408

409 **References**

410

- 411 1. Saramäki, J., Leicht, E.A, Lopez, E., Roberts, S.G.B., Reed-Tsochas, F. & Dunbar R.
412 Persistence of social signatures in human communication. *Proc. Natl. Acad. Sci. USA* **111**, 942-
413 947 (2014)
- 414 2. Latora, V. & Marchiori, M. Efficient Behavior of Small-World Networks. *Phys. Rev. Lett.* **87**,
415 198701 (2001)
- 416 3. Rendell, L. et al. Why Copy Others? Insights from the Social Learning Strategies
417 Tournament. *Science* **328**, 208-213 (2010)
- 418 4. Powell, A., Shennan, S. & Thomas, M. G. Late Pleistocene Demography and the Appearance
419 of Modern Human Behavior. *Science*, **324**, 1298-1301 (2009)
- 420 5. Feldman, M. W. & Laland, K. N. Gene-culture coevolutionary theory. *Trends Ecol. Evol.* **11**,
421 453-457 (1996)
- 422 6. Henrich, J. *The secret of our success: How culture is driving human evolution, domesticating*
423 *our species, and making us smarter*. Princeton University Press, Princeton (2015)
- 424 7. Jaeggi, A.V. & Gurven, M. Natural cooperators: food sharing in humans and other primates.
425 *Evol. Anthropol.* **22**, 186-195 (2015)
- 426 8. Kramer, K.L. The evolution of human parental care and recruitment of juvenile help. *Trends*
427 *Ecol. Evol.* **26**, 533-540 (2011)
- 428 9. Granovetters, M. The Strength of Weak Ties. *Am. J. Sociol.* **78**, 1360-80 (1973)
- 429 10. Watts, D.J. & Strogatz, S.H. Collective dynamics of 'small-world' networks. *Nature* **393**, 440-
430 442 (1998)
- 431 11. Hruschka, D. J. *Friendship: Development, Ecology, and Evolution of a Relationship*.
432 University of California Press, Berkeley (2010)

- 433 12. Salali, D.S., Chaudhary, N., Thompson, J., Grace, O.M., van der Burgt, X.M, Dyble, M.,
434 Page, A., Smith, D., Lewis, J., Mace, R., Vinicius, L. & Migliano, A.B. Knowledge-sharing
435 networks in hunter-gatherers and the evolution of cumulative culture. *Cur. Biol.* **26**, 2516-2521.
436 13. Apicella, C. L., Marlowe, F. W., Fowler, J. H. & Christakis, N. A. Social networks and
437 cooperation in hunter-gatherers. *Nature* **481**, 497–501 (2012)
438 14. Uzzi, B & Spiro, J. Collaboration and creativity: The small world problem. *Am. J. Sociol.* **11**,
439 447-504 (2005)
440 15. Warneken, F., Steinwender, J., Hamann, K. & Tomasello, M. Young Children's Planning in a
441 Collaborative Problem-Solving Task. *Cog. Dev.* **31**, 48–58 (2014)
442 16. Whiten A. & Flynn E. The transmission and evolution of experimental microcultures in
443 groups of young children. *Develop. Psych.* **46**, 1694-709 (2010)
444 17. Lewis, H.M., Vinicius, L., Strods, J., Mace, R. & Migliano, A.B. High mobility explains
445 demand sharing and enforced cooperation in egalitarian hunter-gatherers. *Nature Comm.* **5**,
446 5789 (2014)
447 18. Hill, K. R., Wood, B. M., Baggio, J., Hurtado, A. M. & Boyd, R. T. Hunter-Gatherer Inter-
448 Band Interaction Rates: Implications for Cumulative Culture. *PLoS ONE* **9**, e102806 (2014)
449 19. Dunbar, D. *How Many Friends Does One Person Need? Dunbar's Number and Other*
450 *Evolutionary Quirks*. Harvard University Press, Cambridge MA (2010)
451 20. Dyble, M. et al. Sex equality can explain the unique social structure of hunter-gatherer
452 bands. *Science* **348**, 796-798 (2015)
453 21. Hill, K. R. et al. Co-residence patterns in hunter-gatherer societies show unique human
454 social structure. *Science* **331**, 1286–1289 (2011)
455 22. Derex, M. & Boyd, R. Partial connectivity increases cultural accumulation within groups.
456 *Proc. Natl. Acad. Sci. USA* **113**, 2982-2987 (2016)
457 23. Aplin, L. M. et al. Experimentally induced innovations lead to persistent culture via
458 conformity in wild birds. *Nature* **518**, 538-541 (2015)

- 459 24. Fowler, J. H., Dawes, C. T. & Christakis, N. A. Model of genetic variation in human social
460 networks. *Proc. Natl. Acad. Sci. USA* **106**, 1720-1724 (2009).
- 461 25. Gross, T., D'Lima, C. J. D. & Blasius, B. Epidemic dynamics on an adaptive network. *Phys.*
462 *Rev. Lett.* **96**, 208701 (2006).
- 463 26. Macfarlan, S. J., Walker, R. S., Flinn, M. V. & Chagnon, N. A. Lethal coalitionary aggression
464 and long-term alliance formation among Yanomamö men. *Proc. Natl. Acad. Sci. USA* **113**,
465 16662-16669 (2014)
- 466 27. Burkart, J. M., Hrdy, S. B. & van Schaik, C. P. Cooperative breeding and human cognitive
467 evolution. *Evol. Anthropol.* **18**, 175-186 (2009)
- 468 28. Wohlgemuth, J. & Matache, M.T. Small-World Properties of Facebook Group Networks.
469 *Complex Systems* **23**, 3 (2012)
- 470 29. Albert, R., Jeong, H. & Barabási, A.-L. Diameter of the world wide web. *Nature* **401**, 130-131
471 (1999)
- 472 30. Lawler, A. Making contact. *Science* **348**, 1072-1079 (2015)
- 473 31. Minter, T. *The Agta of the Northern Sierra Madre. Livelihood strategies and resilience*
474 *among Philippine hunter-gatherers*. Institute of Cultural Anthropology and Development
475 Sociology, Leiden University (2010)
- 476 32. Page, A. E., Viguier, S., Dyble, M., Smith, D., Chaudhary, N., Salali, G. D., Thompson, J.,
477 Vinicius, L., Mace, R. & Migliano, A. B. Reproductive trade-offs in extant hunter-gatherers
478 suggest adaptive mechanism for the Neolithic expansion. *Proc. Natl. Acad. Sci. USA* **113**, 4694-
479 4699 (2016)
- 480 33. Dyble, M., Salali, G. D., Chaudhary, N., Page, A. E., Smith, D., Thompson, J., Vinicius, L.,
481 Mace, R. & Migliano, A. B. Multi-level social organisation facilitates food sharing among small-
482 scale hunter-gatherers. *Cur Biol.* **26**, 2017-2021 (2016)
- 483 34. Meehan, C. L., Quinlan, R. & Malcom, C. D. Cooperative breeding and maternal energy
484 expenditure among Aka foragers. *Am. J. Hum. Biol.* **25**, 42-57 (2013)

485 35. Dagum, C. The generation and distribution of income, the Lorentz curve and the gini ratio.

486 *Écon. Appl.* **33**, 327–367 (1980)

487

488

489 **Competing interests.** The authors declare no competing interests.

490

491 **Correspondence.** Requests should be addressed to Andrea B. Migliano: a.migliano@ucl.ac.uk

492

493 **Acknowledgments.** We thank J. Lewis and R.K. Schlaepfer for help in the field. We thank

494 Rodolph Schlaepfer and RKSmedia for producing the accompanying movies, and Robert Foley

495 and Jaume Bertranpetit for useful comments. We also thank our assistants in Congo and the

496 Philippines, as well as the Agta and BaYaka communities. This project was funded by the

497 Leverhulme Trust grant RP2011-R-045 to A.B.M., M.T. and R.M. R.M. also received funding

498 from European Research Council Advanced Grant AdG 249347. The funders had no role in

499 study design, data collection and analysis, decision to publish, or preparation of the manuscript.

500

501 **Author contributions.** A.B.M. conceived the project, S.V. designed the notes, A.B.M., M.D.,

502 J.T., A.E.P., D.S., G.D.S., N.C., S.V. collected data, G.D.S. provided video images from Congo

503 and collected data on plant knowledge, J.G.-G., V.L. performed social network analysis, J.G.-G.,

504 S.V., A.E.P., M.D., D.S., N.C., J.S., J.T., V.L., L.V. and A.B.M. analysed the data, and A.B.M.,

505 L.V., M.T. and V.L. wrote the paper with the help from all other authors.

506

507
508 **Fig. 1. Pictures of motes (left), and of Agta hunter-gatherers (Philippines) wearing motes**
509 **in armbands (right).** Credit: Rodolph Schlaepfer and Sylvain Viguier.

510
511
512 **Fig. 2. Global network efficiency and clustering depend on non-kin ties.** (A) Diagrams (G
513 graphs) of networks for two camps in the Philippines (top: Dinipan, N=33 people) and Congo
514 (bottom: Ibamba, N=47 people). Nodes: individuals. Node colours: households. Red ties
515 represent close kin or extended family, and blue ties connect unrelated individuals. Tie
516 thickness: intensity of relationship (number of recorded close-range interactions). Graphs
517 display the 60% strongest links. (B) Global network efficiency (y axis) was compared among
518 close kin, extended families and non-kin (x axis). Global network efficiency (a measure of ease
519 of information flow across a network; see main text and methods for formal definition) was
520 compared in real (solid circles) and randomised networks of the same size and properties (open
521 circles; see Materials and Methods for randomisation procedure). Randomisation of non-kin ties
522 in real networks causes dramatic reduction in global efficiency, in contrast to randomisation of
523 close kin and extended family ties. We calculated averages over 1000 different randomisations.
524 Error bars for randomisations represent standard error of mean, but are small and
525 imperceptible. All differences are statistically significant ($P < 0.001$). Ratios of global network
526 efficiencies, E , and transitivities, T , in real vs. randomised networks for each Agta and BaYaka
527 camp (coloured bars). Ratios of global efficiencies and transitivities are greater than 1 (vertical
528 line) in all camps, indicating that real camp networks have increased global efficiency and
529 transitivity in comparison to equivalent random networks. All ratios are significantly greater than
530 1 ($P < 0.001$).

531

532 **Fig. 3. Frequency of close-range interactions with close kin and unrelated individuals.**
533 Top row, Philippines (all camps); bottom row, Congo (all camps). (A) children (2-12 years), (B)
534 teenagers (13-17) (C) reproductive adults (18-45), (D) post-reproductive adults (46 or over).
535 Red bars: from left to right, proportion of interactions with mother, father and siblings (A and B);
536 or sons, daughters and siblings (C and D). Blue bars: proportion of interactions with unrelated
537 individuals ranked from left to right by frequency of interactions, up to the 10th strongest
538 relationship. Spouses and affines were excluded. Shaded area represents the range of
539 frequency of interactions with close kin. In all plots, error bars represent plus and minus one
540 standard deviation. In both camps and across all age groups, people interact with from one to
541 four unrelated individuals as closely as with their close kin.

542

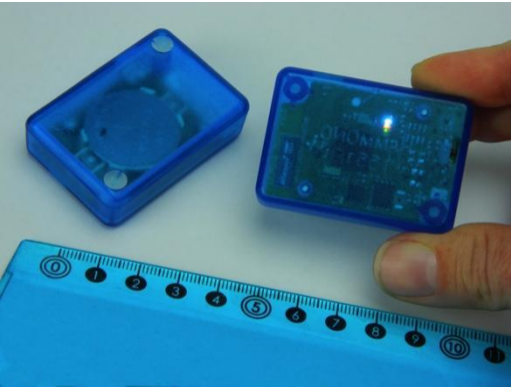
543

544 **Fig. 4. Proportion of interactions by age group and relatedness category.** Colours
545 represent relatedness categories (close kin: mother, father, siblings, spouse, offspring;
546 extended family: grandparents, grandchildren, aunt, uncle, niece, nephew, first cousins,
547 parents-in-law, siblings-in-law; non-kin: all other individuals). (A) Philippines, all camps. (B)
548 Congo, all camps. From an early age, weaned children (aged 2-7) exhibit a large frequency of
549 interactions with unrelated individuals in play groups (see main text).

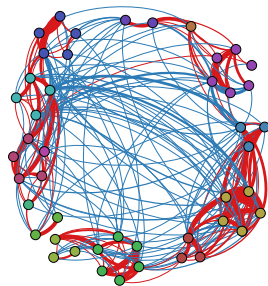
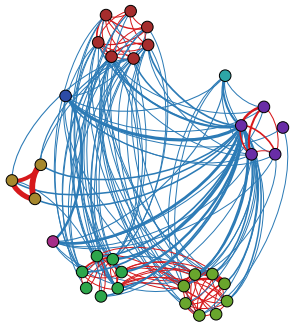
550

551

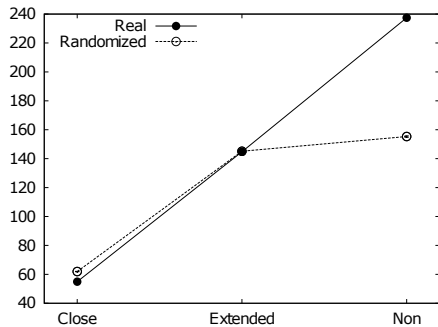
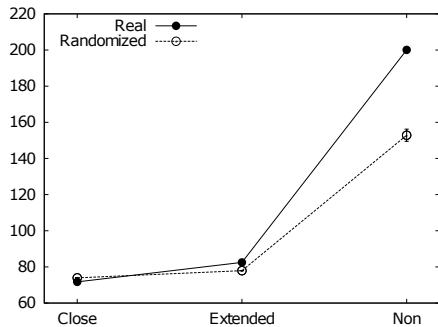
552



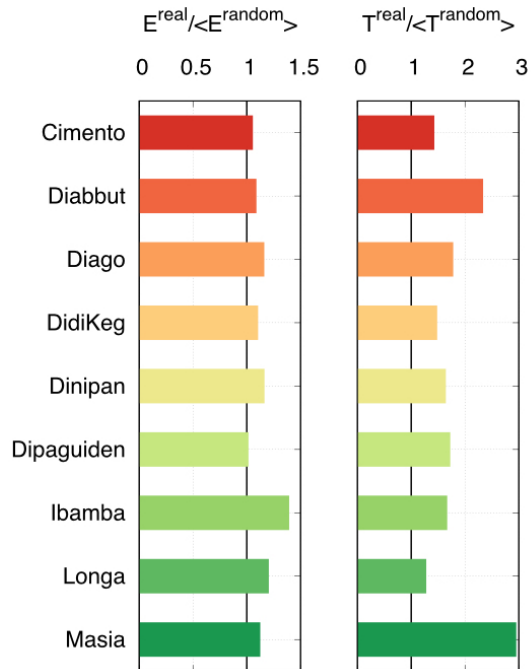
A



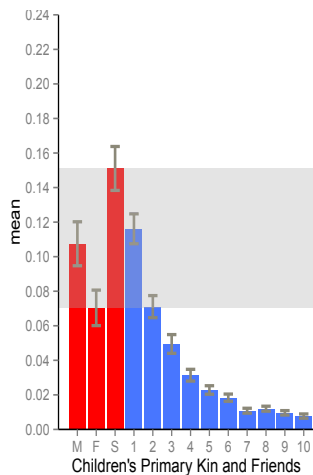
B



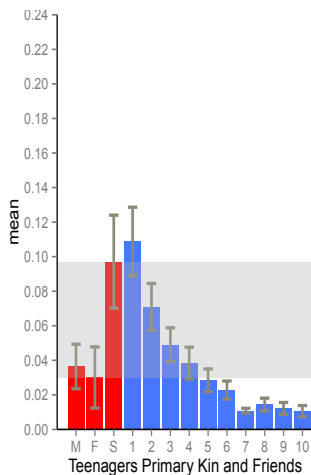
C



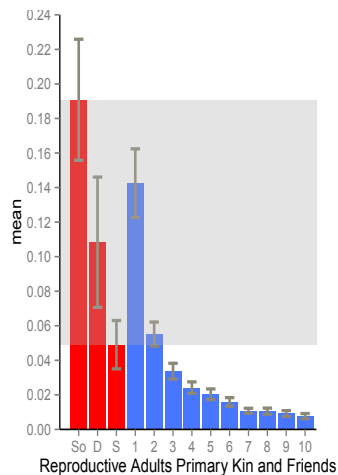
A



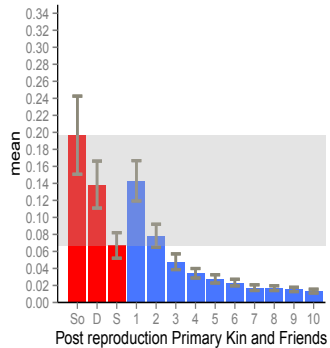
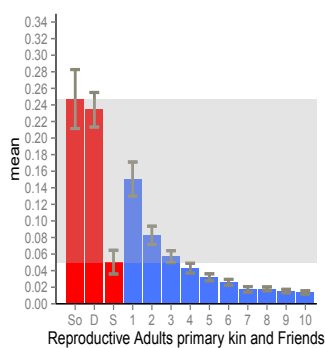
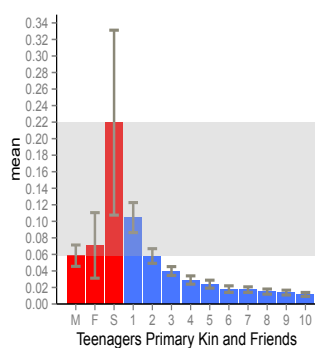
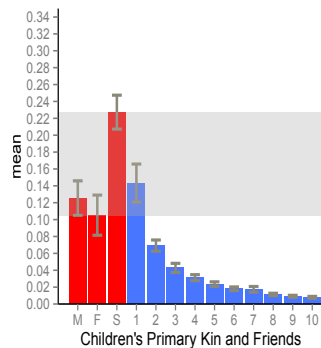
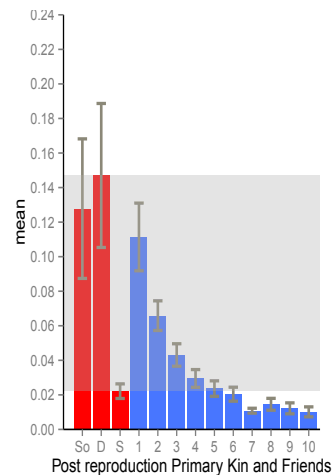
B



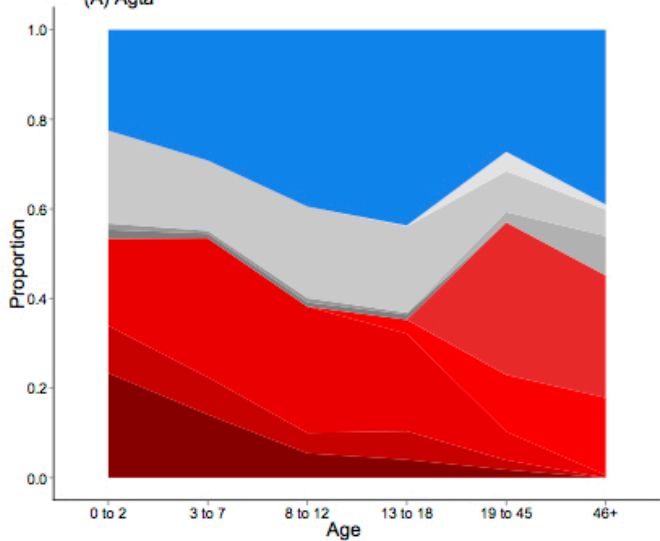
C



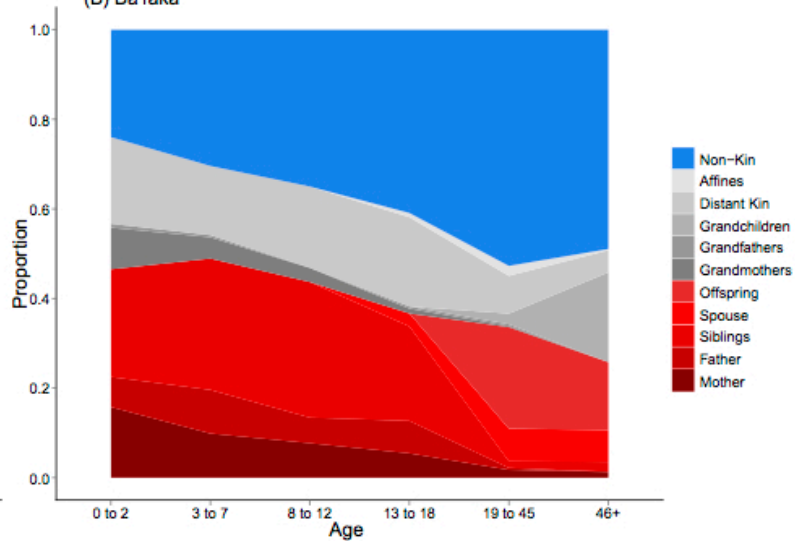
D



(A) Agta



(B) BaYaka



- Non-Kin
- Affines
- Distant Kin
- Grandchildren
- Grandfathers
- Grandmothers
- Offspring
- Spouse
- Siblings
- Father
- Mother