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Characterisation of hunter-gatherer networks and implications for cumulative culture

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Social networks in modern societies are highly structured, usually involving frequent contact with a small number of unrelated 'friends'[1]. However, contact network structures in traditional small-scale societies, especially hunter-gatherers, are poorly characterised. We developed a portable wireless sensing technology (motes) to study within-camp proximity networks among Agta and BaYaka hunter-gatherers in fine detail. We show that hunter-gatherer social networks exhibit signs of increased efficiency[2] for potential information exchange. Increased network efficiency is achieved through investment in a few strong links among non-kin 'friends' connecting unrelated families. We show that interactions with non-kin appear in childhood, creating opportunities for collaboration and cultural exchange beyond family at early ages. We also show that strong friendships are more important than family ties in predicting levels of shared knowledge among individuals. We hypothesise that efficient transmission of cumulative culture[3-6] may have shaped human social network and contributed to our tendency to extend networks beyond kin and form strong non-kin ties.

We studied in-camp proximity networks (within and between households) as a proxy for social interactions in two hunter-gatherer populations from Africa and Southeast Asia. We developed a portable wireless sensing technology (motes; Figure 1) to record all dyadic interactions within a radius of approximately 3 meters at 2-minute intervals for 15 hours a day (05:00-20:00) over a week, in six Agta camps in the Philippines (200 individuals, 7210 recorded dyadic interactions) and three BaYaka camps in Congo (132 individuals, 3397 dyadic interactions; see Table S1 with descriptive statistics for all camp networks). We built high-resolution proximity networks mapping the totality of close-range interactions within each camp. In hunter-gatherers (who lack technology-aided communication), close proximity is an indicator of joint activities such as foraging[7], parental care[8] and information exchange[4].

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

To estimate global network efficiency, we first built weighted social networks using our motes proximity data from Agta and BaYaka camps (Fig.2A and Fig. S1), and subdivided the networks into three decreasing levels of relatedness: close kin (parents, children, siblings, partners), extended family (grandparents, grandchildren, aunts, uncles, nieces, nephews, first cousins, parents-in-law, siblings-in-law) and non-kin (see Methods for details of kin categorisation, and Tables S2 and S3 for percentages of links for each kin category and age groups). We estimated the contribution of each relatedness level to global network efficiency by comparing our hunter-gatherer network structures to randomly permuted networks (the baseline for estimation of efficiencies of real networks). Our randomisation procedure does not modify the total number of links (edges), sum of all link weights (number of recorded interactions for each dyad) and degree (number of links) of each node, but randomly shuffles links among nodes within each level of relatedness. For example, when randomising the non-kin network, we preserve the number of non-kin links from each individual (number of friends), but redistribute their target nodes (identity of their friends). Since our networks are weighted (as each dyad may have been in close proximity multiple times during the one-week interval), random reshuffling of links also changes the strength of friendships. For each of the three categories of relatedness, we created an ensemble of 1000 randomised graphs (see Methods for procedures). The average global efficiency of the randomised ensemble was then compared to the global efficiency of the corresponding observed networks for each camp.

Our analyses show that randomisation of interactions among either close kin or extended family (including affinal kin) does not affect the global efficiency of hunter-gatherer networks. In contrast, randomisation of non-kin relationships (friends) drastically reduces global network efficiency (Fig.2B, and Fig. S2 for other camps) both in the Congo and the Philippines camps (Fig. 2C). The reason is that randomisation of non-kin links homogenises their weights, eliminating strong friendships from networks. This is not observed in the case of randomisation of close kin and distant kin links, which do not exhibit the same levels of the heterogeneity in strength of links. Therefore, increased global efficiency in our networks results from investing in a few strong ‘close friends’ in addition to an extended net of social acquaintances, or a combination of strong and weak ties[9]. Controlling for household in randomisations does not change the results (Fig. S3). In summary, a large number of homogeneous links to all unrelated individuals caused by randomisation reduced global network efficiency. In agreement with classic studies of ‘small-world networks’[10], our results show that only a few ‘shortcuts’ (friendships) connecting closely-knit clusters (households consisting mostly of close kin) suffice to significantly reduce the average path length or distance between any two points across the whole network, thus reducing redundancy and the cost of maintaining strong links with a large number of unrelated individuals. Since unrelated individuals often live in different households, they provide a small number of reliable ‘shortcuts’ between households. Both the Agta and BaYaka had between one to four unrelated ‘close friends’ whom they interact with as frequently as with close kin (Fig. 3). This number is consistent across ages and camps, and with the finding that people in Western societies are in close contact with an average of four friends[1]. Friendships have also been shown to be particularly important in unpredictable environments, and as a special case of reciprocal help[11], which is central to hunter-gatherers[7]. We further demonstrated the importance of friendships to cultural transmission through a mixed-effects logistic regression of levels of shared plant knowledge in a dyad against a series of predictors, using our Congo dataset[12]. The most important predictor was close friendship, with odds of shared knowledge between close friends of 1.82 (95% CI: 1.32-2.5) , 1.48 (1.26-1.74) between mother-offspring, 1.46 (1.2-1.78) between spouses, and 1.31 (1.11-1.54) between siblings (Table S4).

Inequality in link weight distributions is consistently higher among non-kin than among either close kin or extended family members, with Gini coefficients of 0.85, 0.69, 0.72 (Dinipan, Philippines), and 0.92, 0.35 and 0.63 (Ibamba, Congo) respectively (see Table S1 for Gini coefficients in other camps). Heterogeneity in the number of social ties per individual (degree) was previously reported in the Hadza[13]. We extend this finding to the intensity of social interactions (link strength) and demonstrate that the high heterogeneity in the intensity of non-kin social ties is responsible for the increased efficiency of Agta and BaYaka social networks (see Fig. S4 for plots of tie strength distributions of non-kin, close kin and affinal kin ties for each camp). Non-kin interactions also keep transitivity (a measure of the local efficiency or clustering in networks[2]) consistently higher in Agta and BaYaka networks compared to equivalent randomised networks (Figure 2C; see Fig. S5 for transitivity in other camps, and Methods for details of calculations), in agreement with previous studies of Hadza hunter-gatherers[13]. The combination of high global and local network efficiencies in both Congo and the Philippines is a characteristic of ‘small-world networks’ that allows for efficient information flow, and has been argued to promote creativity[14].

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

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

The origin of links with non-kin in early childhood has important implications for our understanding of human life history. We argue that our delayed maturation may facilitate social learning through cultural diffusion in play groups[15], where children are frequently looked after by older children and learn through playing and imitation of role models[16] (see Supplementary Video 1). In Agta and BaYaka play groups, children also establish their first friendships, which may have important consequences in adult life. We show that across age groups people have at any given time a few 'close friends', and this is likely to be one of the conditions for the high between-camp mobility that characterise hunter-gatherers[17], who encounter around ten times more individuals over a lifetime than chimpanzees[18,19]. We observed that hunter-gatherer households tend to be highly mobile and unrelated to each other[20,21], moving between camps on average every 22.8 days in Congo and 12.5 days in the Philippines[17]. It should be noted that our analyses of network efficiency focused on within-camp relationships, while between-group structuring was shown to affect cultural innovation at least in an experimental setting[22]. The new motes technology could therefore be extended to studies of between-band interactions, and performed in parallel with direct measures of cultural transmission in the same networks[23].

The observed higher network efficiency of Agta and BaYaka social networks can also impose trade-offs. Friendship choices among urban contemporary Americans, for instance, have been shown to affect not only information exchange but also the spread of diseases[24]. Such trade-off may be particularly problematic among hunter-gatherers whose population sizes and local genetic diversity are typically low. However, real-world networks are known to be dynamic and adapt to the infection risk status of particular nodes by breaking ties and temporarily reducing transmission efficiency[25]. For example, we observed a rewiring of proximity networks in one Agta camp, which broke down into two units during a measles outbreak. In addition, although our analyses focused on network efficiency and its potential impact on information flow, other aspects of hunter-gatherer social networks may be shaped by other demands**.** For example, affinal kinship links may play a potential role in cooperation, coalition formation and marriage rules[26], and sex assortativity in offspring care, foraging and access to resources[7,30].

We propose that high global efficiency of social networks is important to multiple aspects of human cumulative culture, including the spread of social norms[17], diffusion of technological innovations[22], among others. Efficient hunter-gatherers networks depend on the existence of a few close friends linking households and enabling the flow of information among them. The role of friendship ties in promoting cumulative culture in hunter-gatherers is further supported by the fact that close friends have increased shared plant knowledge as compared to spouses, siblings and parent-offspring dyads in our Congo dataset. ‘Small-world’ properties (such as the combination of high global and local efficiency) and the tendency to share and exchange information with unrelated individuals are features previously identified in online communities[28] and even the World Wide Web[1,2,29]. We have presented evidence that those properties are also found in two hunter-gatherer populations. Details of the evolutionary links among network structures, strong friendships and cumulative culture require further investigation. However, the evidence presented in our study suggests an explanation for why people are keen to socialise, cooperate and exchange information with unknown individuals, from isolated tribes seeking contact[30] to global-scale social networks on the World Wide Web.

Materials and Methods

Experimental Design

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

1.1. Agta. Agta hunter-gatherers subsist on terrestrial, river and coastal marine resources. They live in North East Luzon within the Northern Sierra Madre Natural Park, Municipality of Palanan, Isabela and speak Agta Paranan (an Austronesian Language). Population is estimated in 1000 individuals in Palanan[31]. We studied 200 individuals of all ages from six camps. They live in small bands of 49±22 people on average. Some camps have semi-permanent houses while in others households mover more regularly between camps. Across camps, 80.4% of food is produced by foraging (fishing, hunting and gathering) and the remaining by cultivation. The Agta trade some fish and vegetables for rice and occasionally engage in cash labour (between 0 and 12% of their time, depending on camp). Rice is consumed in 44% of meals, but there is significant variation across households (from 12.5% to 75%). Therefore, activity and production patterns still reflect a foraging lifestyle, while diet composition depend on the fraction of rice traded by households[32,33].

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

2. Portable wireless sensing technology (motes).

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

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

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

2.4. Motes utilisation. After being waterproofed with cling film, motes were sealed into wristbands or armbands (for babies). We studied one camp at a time in the Philippines and Congo. After explaining methods and discussing data anonymity through presentations and posters in local languages, each participant agreeing to participate and signing the informed consent form received a mote. Each motes received an ID number and coloured string. Individuals wore motes uninterruptedly from four to nine days depending on the camp, but only data collected between 05:00 and 20:00 were analysed. Individuals arriving at camp during the experiment were given a mote and an entry time; those leaving camp before the end of the experiment had their exit time recorded. A small compensation (thermal bottle or cooking utensils) was given to each participant at the end. We regularly checked for armband swaps. Mote numbers were also checked upon return, alterations recorded and adjustments made prior to data processing.

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

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

2.6. Motes validation (focal follows). To validate our methodology, we compared motes and observational data from eight children aged between 3-5 years. We conducted ‘focal follows’ for a total of nine hours over three non-constitutive days, observing all individuals present within three meters of each child every 30 seconds[34]. This produces 1080 observational points per child over three days (one every 30 seconds), compared to an average of 3150 emitted motes points over one week (1 every 2 minutes). However, since multiple ties are captured with each observation or motes recording, there is on average 3850 mote points compared to 3080 observational points per child.

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

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

3. Genealogical data and kin definition. We collected genealogies over three generations for all individuals, and built relatedness matrices based on kin categories (mother, father, son, daughter, spouse, brother, sister, uncle, aunt, niece, nephew, cousin, grandparents, grandchildren, parents-in-law, children-in-law, brother/sister-in law, other kin, other affines, and unrelated individuals). We defined ‘primary kin’ as parents, children, siblings and partners. ‘Extended family’ included distant kin (grandparents, grandchildren, aunt, uncle, niece, nephew, first cousins, parents-in-law, siblings-in-law). ‘Unrelated individuals’ are all other individuals, also including more remotely related individuals (such as the ego’s wife’s brother’s wife’s sister) eligible for marriage in these populations, and therefore better interpreted as friends than extended family members.

Statistical Analyses

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

5. Dyadic predictors of shared plant knowledge. We ran a mixed-effects logistic regression of shared plant knowledge[12] in dyads (binary response; shared=1, non-shared=0) on various binary predictors. If a dyad consisted of a father-offspring pair, the predictor ‘father’ was coded as ‘1’ and otherwise as ‘0’; the same for predictors ‘mother’, ‘sibling’, ‘spouse’, ‘sibling’s primary kin’, ‘siblings distant kin’, and ‘close friend’. ‘Close friend’ was any dyad whose weight (link strength) was higher than the average weight of a close kin dyad in the same camp. Ego ID, ‘same camp’ and ‘same age group’ (five-year intervals) were entered as random factors. Our sample consists of dyads for which both data on proximity and plant knowledge were available. A total 824 dyads were analysed, 16 of which were close friends. Each was assessed for shared knowledge 33 times (the number of plants each individuals was asked about), totalling a sample of 27192 regression data points.

6. Social Network Analysis. We used proximity data to build nine undirected weighted graphs G describing the social interaction networks for each of camps (Figure 1A and Fig. S1). The N nodes of each network represent the individuals in the camp, while the undirected link (i,j) between node i and j indicates the presence of proximity interactions between individual i and individual j. The weight w_{ij} of link (i,j) is the frequency of interaction between two individuals, measured by the number of recorded interactions (beacons) between their motes. The weights ranged from the smallest possible non-zero value of $w_{ij}=238$ to $w_{ij}=20,876$ beacons. Each graph is described by the N x N symmetric and weighted adjacency matrix $W=\{w_{ij}\}$, with $i,j=1,2,\ldots,N$. Entry w_{ij} is equal to zero if individuals i and j had no close-range social contacts, and by definition also when i=j. For each graph, an unweighted adjacency matrix $W=\{w_{ij}\}$, with $i,j=1,2,\ldots,N$, can be defined by setting $w_{ij}=1$ if w_{ij} is different from zero, and $w_{ij}=0$ otherwise. The 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 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 equal to the sum of node weights $s_i = \sum_{j=1}^{N} w_{ij}$. Finally, the average node degree is $<k_i>=2K/N$.

6.1. Link weight distribution and Gini coefficient. The heterogeneity in the distribution of weights among the links of a graph can be quantified by the Gini coefficient g, an index used in economics and ecology to measure inequalities of a given resource among individuals[35]. It is obtained by comparing the Lorenz curve of a ranked empirical distribution (i.e. a curve that shows, for the bottom *x*% of individuals, the cumulative percentage *y*% of the total size) with the line of perfect equality. In our case, we obtain the Lorenz curve by plotting the percentage *y*% of the total weights held by the *x*% of links considered, sorted in increasing value of weights. The Gini coefficient ranges from a minimum value of zero, when all individuals are equal, to a theoretical maximum value of 1 in a population in which every individual except one has a size of zero.

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

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

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

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

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

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

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

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

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

Stage B: redistributing weights to the new adjacency matrix.

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

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

Next, we considered the network with close kin and extended family links, and then randomised only extended family links according to the procedure above. Finally, we considered the network with close kin, extended family and non-kin links, and randomised only non-kin links. For each of the three cases, we used M=100 iterations and we created an ensemble of 1000 randomised graphs. The average global efficiency obtained for the ensemble of randomised graphs was compared to the global efficiency of the real networks at the three relatedness levels for each camp. We also performed randomisations preserving household structure, where for each level of dyadic relatedness (close kin, extended family and non-kin) we checked whether the original dyad was within or between households, and only allowed randomisation to occur respectively within or between households. Results remained mostly unchanged (Fig. S3).

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

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

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

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

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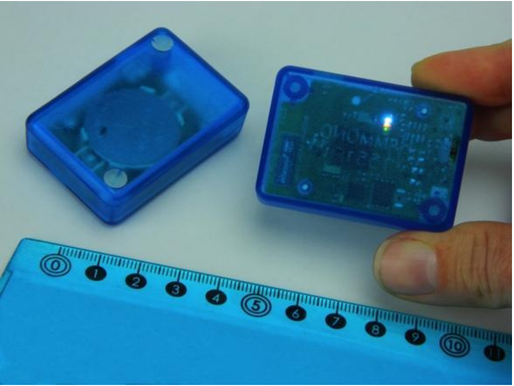
Author contributions. A.B.M. conceived the project, S.V. designed the motes, A.B.M., M.D., J.T., A.E.P., D.S., G.D.S., N.C., S.V. collected data, G.D.S. provided video images from Congo and collected data on plant knowledge, J.G.-G., V.L. performed social network analysis, J.G.-G., S.V., A.E.P., M.D., D.S., N.C., J.S., J.T., V.L., L.V and A.B.M. analysed the data, and A.B.M., L.V., M.T. and V.L. wrote the paper with the help from all other authors.

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

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

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

Fig. 4. Proportion of interactions by age group and relatedness category. Colours represent relatedness categories (close kin: mother, father, siblings, spouse, offspring; extended family: grandparents, grandchildren, aunt, uncle, niece, nephew, first cousins, parents-in-law, siblings-in-law; non-kin: all other individuals). (A) Philippines, all camps. (B) Congo, all camps. From an early age, weaned children (aged 2-7) exhibit a large frequency of interactions with unrelated individuals in play groups (see main text).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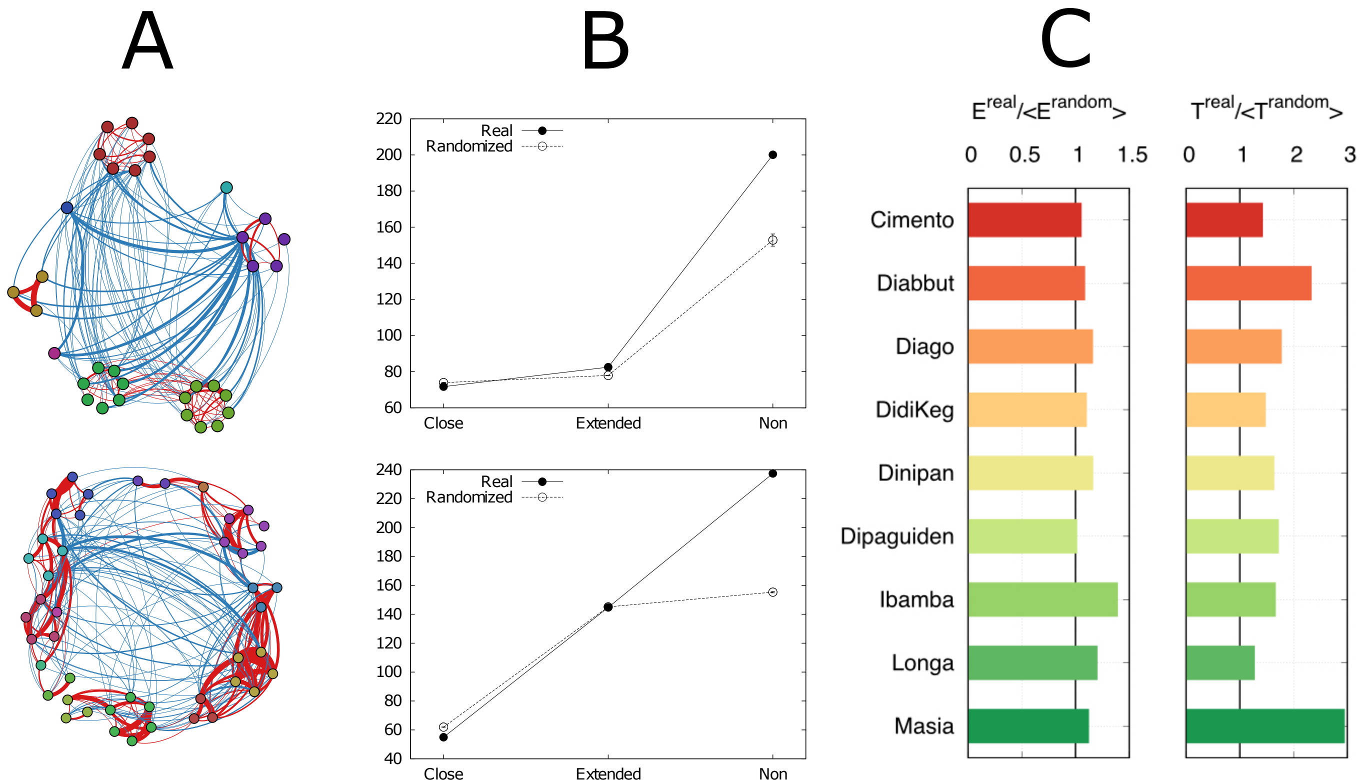
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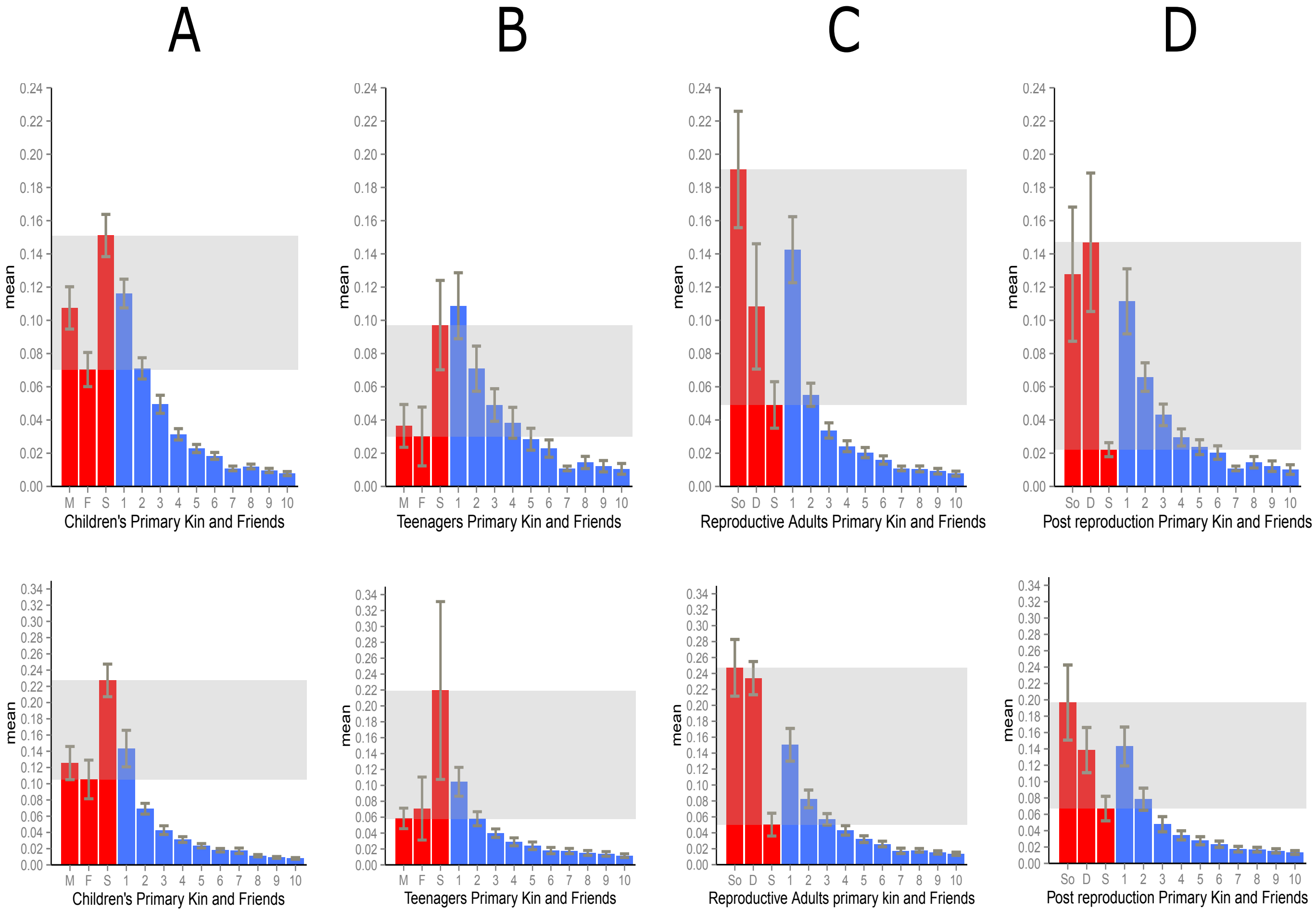
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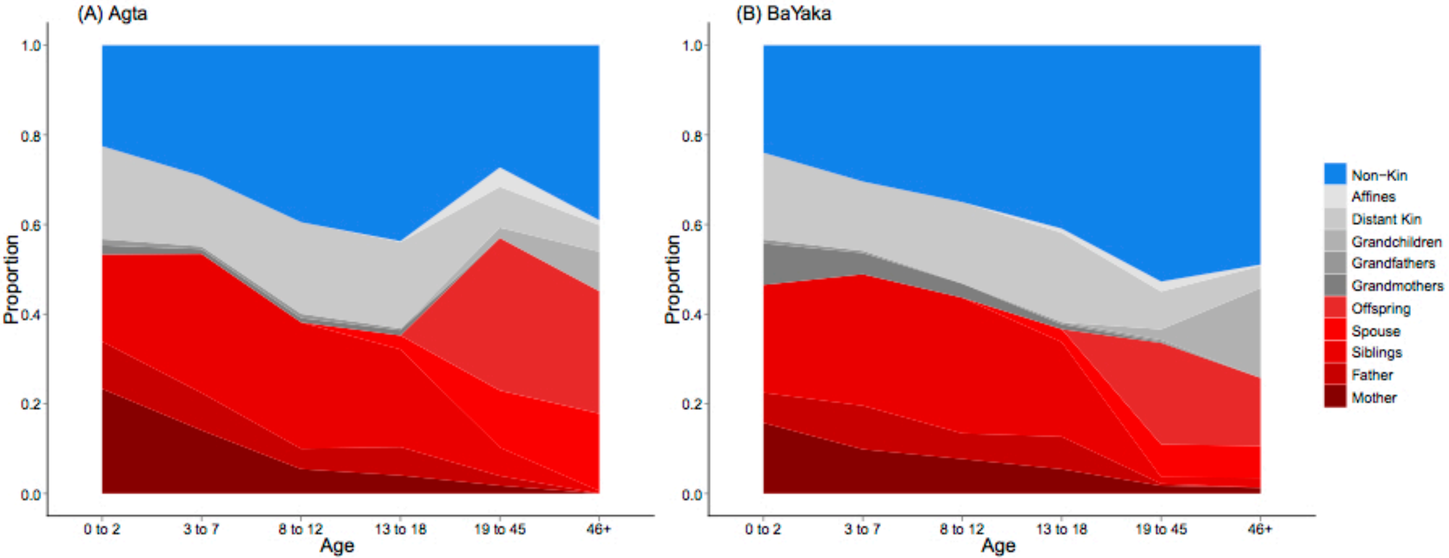
Children's Primary Kin and Friends
Teenagers Primary Kin and Friends
Reproductive Adults Primary Kin and Friends
Post reproduction Primary Kin and Friends
Children's Primary Kin and Friends
Teenagers Primary Kin and Friends
Reproductive Adults primary kin and Friends
Post reproduction Primary Kin and Friends



(A) Agta
(B) BaYaka
Proportion
0.0
0.2
0.4
0.6
0.8
1.0
Age
0 to 2
3 to 7
8 to 12
13 to 18
19 to 45
46+
Non−Kin
Affines
Distant Kin
Grandchildren
Grandfathers
Grandmothers
Offspring
Spouse
Siblings
Father
Mother