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Research with the Tsimane was approved by institutional review boards at UC Santa Barbara and University of New Mexico, and permissions were obtained from the Gran Consejo Tsimane, community leaders and study participants. Research with the Batek was conducted with approval from the Malaysian government and Jabatan Hal Ehwal Orang Asli (formerly Department of Aboriginal Affairs) under permits VC/60050/70; #045847; 581/70, VC/60050; #147485, VC/60050; #4227, VC/60050; 674/90 (KME).

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Code for all analyses and data for the Batek people of Malaysia used in this paper are available at https://osf.io/f95qv/. Tsimane data associated with this paper are not available at this time due to an ongoing assessment of data sovereignty and data sharing guidelines in this population. For more information on this process, please see: https://tsimane.anth.ucsb.edu/data.html.

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Female cooperative labor networks in hunter-gatherers and horticulturalists

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Abstract

Cooperation in food acquisition is a hallmark of the human species. Given that costs and benefits of cooperation vary among production regimes and work activities, the transition from hunting and gathering to agriculture is likely to have reshaped the structure of cooperative subsistence networks. Hunter-gatherers often forage in groups and are generally more interdependent and experience higher short-term food acquisition risk than horticulturalists, suggesting that cooperative labor should be more widespread and frequent for hunter-gatherers. Here we compare female cooperative labor networks of Batek hunter-gatherers of Peninsular Malaysia and Tsimane forager-horticulturalists of Bolivia. We find that Batek foraging results in high daily variation in labor partnerships, facilitating frequent cooperation in diffuse networks comprised of kin and non-kin. In contrast, Tsimane horticulture involves more restricted giving and receiving of labor, confined mostly to spouses and primary or distant kin. Tsimane women also interact with few individuals in the context of hunting/fishing activities and forage mainly with spouses and primary kin. These differences give rise to camp- or village-level networks that are more modular (have more substructure when partitioned) among Tsimane horticulturalists. Our findings suggest that subsistence activities shape the formation and extent of female social networks, particularly with respect to connections with other women and non-kin. We discuss the implications of restricted female labor networks in the context of gender relations, power dynamics, and the adoption of farming in humans.

Introduction

The manner in which organisms acquire food is a major determinant of social organization and structure. The evolution of group size, the most fundamental component of animal social systems, is thought to be driven primarily by two factors: predation risk and resource competition/availability [1]. For example, many ungulate herbivores rely on abundant, evenly-distributed resources and live in large herds that increase protection against predators, whereas the majority of carnivores are solitary and have few social interactions outside of mating [2]. The effect of foraging and the distribution of food resources on social organization and structure has been particularly well-studied among primates [3–8], whose social systems vary tremendously, from graminivorous gelada monkeys living in herds of >1000 individuals to solitary prosimians. According to classic socioecological models [7,9], the evolution of female-bonded groups (where females maintain affiliative bonds with other females and remain in their natal groups) can be explained by differences in the key resources constraining each sex; the distribution and defensibility of food resources serves as the primary determinant of female gregariousness and behavior, and the distribution of females in turn structures the behavior of males, thus linking food resources and central aspects of sociality such as group size, dispersal patterns, and the formation of affiliative bonds.

Human populations similarly exhibit differences in social organization and structure that vary with the distribution of resources in the environment [10]. For example, the availability of abundant, predictable resources is associated with processes of sedentarization and related patterns of increased group size, cooperation, food storage, territoriality, political organization, and demography [11,12]. The relationship between resources and social structure is well-evidenced by ethnographic and archaeological examples, such as complex, sedentary hunter-gatherers utilizing aggregated aquatic resources (e.g., salmon runs) in the Pacific coast of North America. The rise of agriculture and differences in the associated labor inputs and defensibility of cultivated resources has likewise facilitated changes in human social organization [13]. For example, Amazonian horticulturalists tend to live in larger, more closely related groups compared to hunter-gatherers [14].

Underlying macroscopic cross-cultural variation in social structure is the implication that subsistence ecology influences social networks, patterns of interaction, and coalition formation processes that drive human cooperation and competition. The central premise of this paper is that

the opportunity for interactions (or the lack thereof) during subsistence activities represents a key domain structuring how social bonds are formed and maintained. Humans living in subsistence societies devote large amounts of time to food procurement, and these activities are often done in social groups, even when they do not require cooperation to be successful [12,15–18]. Social foraging thus provides critical opportunities for the exchange of information, gossip, prosocial signaling, trust-building, and friendship formation. Most resources targeted by women, including those available during times of scarcity, accommodate social foraging and thus afford the opportunity to develop strong bonds. The influence of foraging on bond formation is demonstrated by differences between our two closest living relatives, chimpanzees and bonobos; whereas chimpanzee females often feed alone, do not develop strong bonds, and are subject to frequent male aggression, differences in the distribution and quality of resources allow female bonobos to feed and travel together with less scramble-competition, leading them to establish strong affiliative bonds and alliances that reduce male aggression toward females [19–21].

Female social bonds in human groups should therefore depend on the interplay between the distribution of food in the environment, interdependence in resource acquisition, and the potential for within-group resource competition. Unlike in other primates, social foraging in humans is less likely to be driven by between-group competition for foraging sites, and is more likely a consequence of the clumped nature of resources targeted by women, protection against predators (or other humans), a high degree of sharing, low within-group competition, and a desire for friendship/company. Theoretical work on optimal foraging group size further predicts that foraging group compositions will depend on the differential costs and benefits of working in groups versus excluding others, as well as shared interests (e.g., kinship) and trust [18,22,23].

The transition to agriculture from hunting and gathering represents a major subsistence shift for human societies. Cultivated food production is broadly associated with sedentarization, food storage, and increased group size and population densities, similar to patterns observed amongst “complex” hunter-gatherers targeting dense, reliable food resources. A less well-appreciated aspect of subsistence transitions, however, are the ways in which the labor requirements of intensive foraging or farming altered human social networks, particularly those of women that are most likely to change in response to food resources. Whereas mobile hunter-gatherers generally form transient, semi-autonomous foraging partnerships, experience little within-group food competition, and are highly interdependent in food acquisition due to large

short-term (daily) risks of food shortfalls, horticulturalists typically form persistent, organized labor partnerships, maintain land-use rights (and compete for land), exhibit greater control of food distribution, and are less interdependent (buffered by food storage).

Importantly, foragers and horticulturalists face different risk profiles that have consequences for cooperation. Hunter-gatherers experience regular short-term *unsycnchronized* variance, which can be buffered by food sharing and frequent cooperation. Horticulturalists are more prone to crop failures and longer-term variance, which is often synchronized regionally, thereby requiring extensive long-distance networks or other mechanisms to avoid shortfalls. Hunter-gatherers are less likely to experience famine than agriculturalists [24] but are more reliant on group members for daily food transfers and in more contemporary contexts may use cultigens as fallback foods to buffer against seasonal shortfalls [25]. As a result, the incentives to cooperate broadly with diverse alters on a daily basis (in social foraging/labor, food sharing, information sharing, etc.) are high among hunter-gatherers. In contrast, as horticulture is less risky over short timescales than foraging activities, the benefits of cooperation in horticultural economies often come from economies of scale in production with turn-taking involving small numbers of reliable partners [26].

A comparison of social foraging in hunter-gatherers and horticulturalists allows us to directly test predictions about social labor networks. Here we compare the social work of hunter-gatherers and horticulturalists by exploring the dynamics of partner choice and cooperative labor networks among two groups inhabiting similar tropical rain forest environments: Batek hunter-gatherers of Peninsular Malaysia and Tsimane forager-horticulturalists of Bolivia. Although both societies rely on human labor to extract food from the environment, they exhibit divergent subsistence strategies that incentivize different conditions for social labor. In light of the differences between hunter-gatherer and horticultural economies discussed above, we compare the size and composition of cooperative female labor partnerships, and group-level network structure in both populations, and make several predictions about the relationship between subsistence strategy and female labor networks. First, despite often living in larger aggregated villages, female horticulturalists are expected to have smaller social networks with less frequent cooperative labor interactions than hunter-gatherer women. Second, we expect farming to be associated with a greater need for stable and reliable labor partnerships due to the potential for reciprocity and defection in help exchanged during key periods of field labor, thereby eliciting

greater reliance on spouses and close kin with high shared interests. Third, group-level labor networks in hunter-gatherers are expected to evince less substructure (lower modularity when partitioned) compared to horticulturalist networks.

Methods

Study populations and cultural background

Batek

The Batek are one of eighteen officially recognized groups of Orang Asli (Malay for "Original People"), the indigenous minorities of Peninsular Malaysia. Before about 1980, roughly 800 Batek were the only permanent residents of a vast area of primary lowland tropical rainforest in the upper Lebir River watershed of Kelantan state and in the northern tributaries of the Tembeling River in the adjacent state of Pahang. Our data stem from research by KME and KLE in 1975-76 focused on the economy and gender relations of Batek people living along the upper Lebir River and its tributaries (K.M. Endicott and K.L. Endicott 2008).

In 1975-6 the upper Lebir Batek were living by a combination of hunting-and-gathering and trading forest products—mainly rattan—to Malay traders (>60% of total calories consumed at the time were from wild foods). The resources the Batek depended upon for survival—such as wild yams, monkeys, squirrels, fish, and turtles—were widely dispersed, and some—including wild fruits, nuts, and honey—were seasonal. Having limited means for preserving and storing food, people worked at food-getting almost every day. They established temporary camps where they thought food might be available, either because the area contained known sources of seasonal foods (e.g., fruit trees) or because they had lived there a few years earlier and expected the nonseasonal food sources to have regenerated. They also obtained some foods, such as rice and salt, and metal tools, cloth, etc. from Malay traders in exchange for rattan. When the rate of food acquisition declined to a certain level, residents would abandon the camp, some moving to a more promising location and some joining other existing camps. On average, these camps lasted 8.2 days (range = 3-24 days) (Venkataraman et. al 2017: 3098).

Camps consisted of between two and thirteen thatched lean-to shelters, each housing a conjugal family, a widow or widower, an unmarried adult of either sex, or adolescents. The upper Lebir population was usually spread between two and four separate camps. Average camp size was 34.2 individuals (K.M. Endicott 1984). Shelters were clustered together and freely open

to view. People sometimes visited other camps during the day, and occasionally families moved to another camp. Although only some camp members were close biological or affinal kin, people treated all the occupants of a camp much like an extended family (cf., Bird-David 2017). Most adults knew each other well since childhood. Batek shared food they obtained in excess of their immediate family's needs widely with other camp members and provided many other forms of help, such as caring for children left in camp when their parents were away, without expectation of compensation (K.M. Endicott 1988, 2011; K.M. Endicott and K.L. Endicott 2008). Camp members also freely shared information about newly found sources of food and trade goods and no one had the authority to claim ownership over land or unharvested resources.

With regards to cooperative foraging, no individual played the role of organizer, although occasionally someone might ask someone else to do something for him or her, such as an elderly mother asking a daughter to get something she wanted. This pattern is reflective of the broader gender and politically egalitarian social system of the Batek [27]. Batek ethics emphasized both the freedom of individuals to do whatever they wanted to do and the obligation to help other camp members as needed, what has been referred to as "cooperative autonomy" (K.M. Endicott 2011).

The Batek have a gendered division of labor, although there were no prohibitions on people of either sex performing the activities normally done by the other. Most foraging practices did not require cooperation but were done with companions for pleasure or for safety from predators, such as tigers and leopards. The division of labor took into consideration strength, safety, and compatibility with childcare. Men and boys did almost all the tree climbing and hunting, as people said that males had more strength for climbing and stronger breath for shooting poisoned blowpipe darts at arboreal game than did women. Men usually hunted in groups of two or three for safety (from predators or getting lost) and cooperation in finding and sneaking up on animals (K.M. Endicott 1979). Group hunting also served as an important training opportunity for young male apprentices. Hunters did not take their children with them because the noise made by the children would scare away the game. Digging tubers, on the other hand, could be done by large, noisy groups—in fact, the noisier, the safer—so groups of women often worked together with infants and young children in tow. Men sometimes also dug tubers, even when out on hunting trips. Both men and women dug up small burrowing animals, such as bamboo rats, and chopped nesting animals, such as bats, out of holes in trees using machetes.

Both men and women fished with wooden poles and traded hooks and lines, while men did most of the spear fishing, net fishing, and fishing with traps. Both men and women also participated in collecting firewood and water, processing foods, and cooking. Women tended to do most of the weaving of pandanus leaves into sleeping mats and carrying baskets, while some men made open-work split rattan baskets for leaching poison out of poisonous tubers and nuts. Men and boys did most of the collecting of rattan for trade, which required some tree climbing, although a few young women without children might go along to help.

A few foraging processes involved specialized roles and cooperation. Members of both sexes cooperated in poisoning fish, some people pounding the sap out of poisonous tree bark, others arranging sticks into weirs, and others collecting the stunned fish in baskets. The most complicated division of labor was the gathering of honey from bees' nests high in the forest canopy. A group consisting mostly of men would prepare the torches, bark baskets, and rattan vine ladders in the trees bearing the nests. After dark a man would climb up to a perch below the nest carrying a leaf torch and dragging a rattan cord connected to a honey basket. He would then use the smoking torch to stun the bees, cut the nest free, put it in the basket, and lower it to the ground. Both men and women might carry the honey-filled baskets back to camp, where all camp members would take a share of the honey, larvae, and wax comb.

Although most women's work did not require joint or coordinated efforts, women usually carried out their tasks together with companions. Women socialized with each other in numerous ways while working together. They would chat about various family and group concerns, share news of happenings in other camps, discuss the things they wanted to do, comment on the behavior of others, sing songs and tell stories to each other's children, etc. Perhaps the most distinctive characteristics of Batek women's work were the great flexibility in how it was carried out and the personal control each woman had over what she did, where, when, and with whom. Normally, women (and men) would discuss what the needs of the group were—such as getting more tubers, processing poisonous tubers, getting pandanus leaves to make sleeping mats, getting fish, looking after children, etc.—before forming work groups for the day. Women chose their companions themselves, sometimes different ones on different days for different tasks. Some companions were kin but others just friends.

Tsimane of Bolivia

The Tsimane are a population of ~17,000 subsistence forager-horticulturalists living in the lowland Amazonian region of Bolivia [28]. Over 90 villages, containing 50-500 individuals, are spread along regional rivers and roads and are comprised of multi-generational households and kin-intensive social networks. Work effort and allocation is typically organized within these household clusters with little influence from individuals outside the family, lending a strong sense of economic independence at the level of the nuclear family and extended Tsimane household. Like many tropical horticulturalists, Tsimane subsistence emphasizes the slash-and-burn cultivation of multiple crops (e.g. plantains, sweet manioc, corn, rice), supplemented by hunting, fishing, and gathering of wild foods. Sex roles are well-defined, with women processing and preparing food, taking care of children, and making chicha (local fermented beverage), while men hunt, chop trees, and do wage labor. Both sexes fish, collect fruit and honey, fetch wood and water, and work in horticultural fields [29].

Nuclear families or groups of nuclear families coresiding in a compound are typically the units of production, particularly for garden foods. Family members may coordinate work activities in the early morning, especially if one member intends to make a trip to a distant field or to a fishing location by canoe. Hunts are often planned the day before, although the final decision to hunt may depend on weather, physical state of the hunter, and whether or not the hunter had an ominous dream during the previous night. Consumption occurs within extended family units living in close proximity to each other.

Each family has its own set of fields, and sometimes individuals within families own specific fields. Fields are usually small (<1 hectare) and are left to fallow after several years of use, with new fields created based on availability and ownership based on usufruct. New fields in the dry season are started by clearing primary (preferred) or secondary forest of small shrubbery, vines, and small trees using a machete (*fetsaqui*). Then, larger trees are felled (*pacan*) using a hand axe (though chain saws are becoming more common). The fields are left to dry for several weeks to a month and then burned, releasing nutrients into the leeched Amazonian soil. If the burn is not successful, unburned detritus is gathered into piles and re-burned. After a successful burning, new fields are planted, typically with rice (*arrosh*) and corn (*tara'*), though some manioc (*o'yi*) and plantains (*pe're*) may be interspersed. The latter are commonly planted in older fields and fallows, along with other roots and crops. The planting process and timing of seasonal agricultural tasks is crop specific, with rice and corn being planted mainly in August-

October whereas manioc and plantain are cultivated year-round. Fields are later weeded using a hoe, machete or by hand.

Help is commonly solicited from other individuals at multiple stages of the agricultural process. This is especially true during the clearance of undergrowth, felling of large trees, and harvesting of rice and corn. For field clearance and tree felling, the size of the desired field defines the amount of help solicited. Help for these two tasks is typically solicited from men and often from sons-in-law as a form of informal bride service. The organizer of field construction specifies the boundaries of the desired field and work is done semi-autonomously. Because of the dangers of tree felling, individual workers spread themselves out over the field area. Help with felling is occasionally compensated for with money, but it is common for reciprocal help to be provided in field construction. Assistance is more broadly solicited from individuals of all ages during the harvesting of rice and corn in the short window between crop maturity and the potential loss to rot. Such help is often reciprocated when the helper's crops are mature, or helpers are given some portion of the crop they harvest. Children as young as 5 are often brought to the field during the harvesting season to "help" with the harvest.

Hunting with shotguns, rifles, and bow and arrow is common in interfluvial villages. Single-day hunting is usually done alone or with 2-4 partners, usually a sibling, son, in-law, or age-mate [30]. Young adults will often hunt with more experienced hunters. Sometimes several men will participate in extended hunting trips or entire families in interior forest villages will go on trips that can last anywhere from two days to several months. These longer excursions typically involve establishing a base camp with individuals hunting in separate areas around the central camp. Information is exchanged at camp and hunters coordinate their plans for the day. Help is exchanged in instances when a hunter makes a kill and needs help processing/carrying out the game.

Fishing is common in all Tsimane villages located near water rivers, oxbow lakes, or lagoons. The Tsimane fish using a variety of methods including hook and line, bow and arrow, net, and using poison from native plants to incapacitate the fish. Fishing is a common activity for both young and old, men and women. Except for poison fishing, and to lesser extent, net fishing, Tsimane fishing does not require a significant amount of cooperation or coordinated effort. During group fishing events, several families, or sometimes entire villages, use plant poisons to fish in closed-off sections of rivers, streams, and lagoons. Several men perform all of the work

(acquiring the plant poisons, closing off the body of water, pounding the poison), and many more individuals, including women and children, harvest the fish with bow and arrow, machete, or knife. In contrast to Batek poison fishing, there typically is an individual or a household cluster that organizes and coordinates the poison fishing event including the collection of poison and the building of weirs. Neighbors and friends are invited to participate. Typically, the spoils of the poison fishing event go to the person/household that collected the specific fish.

Data

Batek

During a 5-month period between September 1975 and June 1976, KLE and KME lived with a focal group of Batek foraging nomadically. Foraging activities of all Batek individuals (n_{women}= 19, n_{men}= 25) in camp were recorded daily (n = 93 days). Specifically, the type of foraging activity, time out of camp, total foraging returns (measured using a spring scale), and the composition of foraging groups were recorded for all major activity bouts. The activities undertaken during out-of-camp bouts were further assessed via post-facto conversations.

Cooperative foraging data (involving multiple individuals traveling together to perform a foraging activity such as hunting, fishing, gathering, or collecting forest products) were extracted from hand-written records and organized into undirected daily social networks of individuals present in camp for a given day, with a tie representing a binary indication of cooperation within a dyad [31]. Due to camp movement, the number of available alters changed daily. Custom algorithms were written to tabulate the cumulative number of unique cooperative foraging alters that each ego encountered over the days ego was observed in camp. Finally, extensive genealogical records on the Lebir Batek were used to characterize the genetic and affinal relationships between dyads.

Tsimane

Data on field (horticultural) labor were collected in targeted interviews from 1171 individuals (n = 1576 interviews) between 2005-2019. Participants were asked about the number of fields maintained, new fields cleared and planted, the primary crops planted in each field, estimated yields, and the names of individuals with whom the participant either received help from or provided help to with field labor in the past year. Although data were collected on the

stage of field labor for which help was exchanged (e.g., clearing, weeding, harvest), the number of days of help given, and whether or not payment was exchanged, this information was aggregated into a binary measure of help given/received across an entire horticultural cycle (past year) for analysis.

Data on hunting/fishing labor partnerships were collected as part of a separate food production interview in which participants were asked about any hunting and fishing activities undertaken in the two previous days (n=1380 individuals, 2721 interviews collected in 2010-2014). For each instance of hunting or fishing, participants were queried regarding the identity of and kin relationships with other accompanying individuals. Because production interviews were conducted over many years, between 1 and 8 longitudinal interviews were available per participant, allowing for 2-16 observation days over which to assess the interaction of egos with unique alters in the context of foraging.

For both horticultural and hunting/fishing data, the number of unique cooperative labor partners was calculated across cumulative observation days. Dyadic affinal and genetic relationships were drawn directly from interviews (cross-referencing with a long-term demographic database indicated accurate reporting of relationships). Repeat interviews conducted with individuals generally took place over long interim periods and thus cumulative observation days do not correspond to consecutive days.

Analysis

To compare the number of cooperative labor partners between Batek and Tsimane despite different data types, we compared the number of unique alters encountered by each Batek ego over increasing observation days (up to 84 days) with a similar measure from Tsimane hunting/fishing interviews (up to 16 days), as well as the number of alters with whom Tsimane egos gave/received horticultural labor help to/from (over the past year). To characterize population-averages for Batek foraging and Tsimane hunting/fishing, we fit random-slopes GLMMs (zero-inflated Poisson error distribution, random slopes for cumulative number of observation days by individual) with a fixed effect for the interaction between sex and observation day. Values of zero for the number of labor partners can result from two distinct processes in this context: non-foraging (an individual does not engage in a foraging activity on a given day) and solo foraging (an individual engages in a foraging activity alone). Given the

different time scales of these measures, Batek foraging and Tsimane hunting/fishing are compared using estimates extrapolated to the same number of days (84) from model fits, whereas number of horticultural partners were tallied over a longer time period and thus are expected to be higher all else equal.

The composition of female cooperative labor partnerships was studied as a function of alter sex and kinship. Alter sex was determined from the identity of partners. Genetic and affinal dyadic relationships were characterized as both specific associations (e.g., parent-offspring, parent/offspring-in-law, etc.) and kin category groupings following Hill et al. [32].

To investigate how cooperative labor partnerships shape community-level differences in network structure, we assessed the modularity of Batek cooperative foraging and Tsimane horticultural labor networks. Modularity is a network property that compares the proportion of existing ties within pre-defined clusters to those expected under a random distribution of edges [33,34]. Modularity therefore captures the extent to which networks are composed of distinct subgroupings.

For Batek, we compiled daily networks across the entire study period into a cumulative network of all individuals present for at least 20 study days (1 individual excluded), with binary ties between individuals that foraged together at least once. For Tsimane, complete networks were not observed for any villages, and thus we used partially sampled ego network data to simulate complete networks for villages in which at least 30 interviews were conducted. Specifically, we used observed egocentric properties of mean degree, ego sex, sex homophily, age homophily, spousal relationship, genetic kinship, and affinal kinship as target statistics to parameterize exponential family random graph models (ERGMs) from which complete village networks could be simulated (which reproduce target statistics in expectation) on a population with known attributes from community censuses [35].

Stochastic network models are known to produce networks with appreciable modularity [36]. Comparisons of modularity in observed Batek and simulated Tsimane networks were therefore compared with that of networks with equal size and density simulated under Erdos-Renyi random graph null models. In all cases, we estimated network modularity using the *modularity* function from the *igraph* package [37] based on clusters defined by the "fast-greedy" community detection algorithm of [34]. A higher modularity score for a network and given partitioning reflects denser connections between nodes in the same community and sparser

connections between nodes in different communities, leading to greater substructure in the network.

All analyses were conducted using R (version 4.1.2). Models were fit using *brms* (version 2.16.3) [38] and ERGM simulations were conducted using the *statnet* [39]and *ergm* (version 4.1.2).

Results

Breadth of labor networks

Batek women and men both collaborated frequently with others while foraging (Figure 1; Table S1). Predicted values from GLMMs estimate that after 84 observation days, women and men foraged with an average of 10.3 and 10.6 unique alters, respectively. These numbers correspond to a high proportion of total available adult alters (~25%), a conservative estimate given that not all dyads were present in camp together each day (some dyads may rarely have been in camp together). Batek women and men had similar numbers of labor partners (sex x cumulative day interaction: ß = -0.02, 95% CI = [-0.03, 0.00]). Batek also tend to hunt and fish in larger groups than Tsimane (Table S1).

In contrast, Tsimane women and men's subsistence networks are more restricted (Figure 1). During horticultural labor, Tsimane women and men reported a median of 3 and 5 labor partners, respectively (mean difference between the sexes = 1.6, t_{df}=1517.7, $P < 0.001$). These low numbers include alters encountered over an entire horticultural cycle (a time period much longer than the 84 observation days among Batek) and reflect both field help given and received. On average, focals reported receiving help from more alters than they gave help to (Figure S1). Similarly, cooperative hunting/fishing appears to be rare among Tsimane (Figure 1). Predicted values from GLMMs fit to data collected over 2-16 observation days suggest that after 84 observation days one would expect the average Tsimane woman and man to have engaged in cooperative foraging with 0.56 and 1.04 unique alters, respectively. Importantly, these data were collected in Tsimane villages consisting of 50-500 individuals, and family members sometime travel from surrounding villages to aid in field labor; the numbers of alters reported for both

horticultural labor and hunting/fishing therefore represent an extremely small proportion of the total alters potentially available.

Qualitative observations further suggest that whereas Batek fluidly form foraging work groups among camp members on a daily basis, Tsimane individuals are relatively unlikely to undertake either collaborative field labor or to hunt/fish with many others on any given day. The frequency of cooperative labor interactions, and not just the breadth of individual labor networks, is therefore also likely to be much higher among Batek than Tsimane. Taken together, these observations suggest that labor networks are both larger and more flexible among Batek hunter-gatherers as compared to Tsimane forager-horticulturalists.

Labor network composition

We assessed the composition of female Batek and Tsimane labor networks in terms of alter sex and dyadic kin relationships. Foraging networks of Batek women included a substantial proportion of ties with unrelated individuals (32% of dyads), spouses (23%), primary kin (19%) and distant kin (19%) (Figure 2). In contrast, Tsimane women had far fewer ties with unrelated individuals for both horticultural labor (1%) and hunting/fishing (0%), and a far greater proportion of ties with primary kin (horticulture: 55%, hunting/fishing: 40%). Spousal partnerships were also much more common within Tsimane hunting/fishing labor (42%) than Batek foraging or Tsimane horticulture, but such interactions are still relatively rare due to the low absolute frequency of such cooperation (Figure 1).

With the exception of spouses (who were all male), the majority of alters that Batek women interacted with were other women (69%). This proportion was similarly high for interactions with unrelated Batek individuals (70%). On the other hand, Tsimane women interacted with substantially fewer women in both horticultural (42%) and hunting/fishing (47%) activities, a number that is even lower relative to Batek when considering that spousal partnerships are also more common among Tsimane (Figure 2).

Analysis of more specific dyadic relationships shows that Batek foraging involves not only more cooperative labor partnerships with unrelated individuals than Tsimane horticultural labor, but also a much smaller proportion of parent-offspring, grandparent-grandchild, and parent/offspring-in-law dyads, and a higher frequency of cousin and sibling dyads (Figure 3).

This difference reflects a higher frequency of within-family cooperative labor occurring between similarly aged individuals among Batek compared with Tsimane.

Network structure

We compared modularities of a cumulative Batek labor network constructed over the whole study duration and simulated complete Tsimane village horticulture networks with random graphs of the same size and density. Both Batek and Tsimane labor networks exhibited greater modularity than expected based on random graphs (*Figure 4*). However, the difference in modularity between the empirical Batek network and average of simulated random graphs (0.298 vs. 0.263, difference = 0.035, one-sample *t*-test $P < 0.001$) was less than that between simulated Tsimane horticulture networks and comparable random graphs (paired (by village) *t*-test mean difference = 0.064, $P < 0.001$). This result suggests that although both Batek and Tsimane labor networks exhibit detectable clustering, Batek foraging networks are more diffuse and contain less substructure than Tsimane horticulture networks, as predicted based on the expectation that field labor requires a smaller number of more reliable partners. Given that Tsimane horticulture networks were simulated based on egocentric data without reference to specific alters or alter-alter edges (using only attribute mixing terms), it is likely that our estimates of Tsimane horticulture networks are conservative underestimates of modularity due to unobserved friendships, household proximity, and other factors that drive clustering.

Discussion

We found that the cooperative labor networks of female Batek hunter-gatherers and Tsimane forager-horticulturalists differed in accord with predictions based on socioecological differences between these populations. We found that (1) Batek women had larger labor networks with more frequent interactions than Tsimane women, (2) Batek women engaged in cooperative labor with more unrelated individuals, more female alters, and fewer primary kin than Tsimane women, and (3) composite group-level Batek labor networks were more modular than those of Tsimane horticulturalists. Tsimane women therefore have fewer opportunities than Batek women to develop and strengthen social bonds with others during work activities, especially other women and individuals outside of the immediate family. These differences are striking given that Tsimane villages (and the broader population) are much larger than Batek

forest camps, and thus the numbers presented here reflect smaller network sizes despite access to more potential alters.

We suggest that this contrast in labor networks reflects differences in the demands of alternative subsistence economies. The most common foraging activities of Batek women are gathering (mainly tubers and fruit) and fishing, and these are usually done semi-independently in medium-sized same-sex groups without within-group competition between foragers. Because food is shared widely in-camp, there is substantial collective interest and interdependence with respect to risk-reduction and division of labor with economies of scale [22]. Batek women derive both potential economic and social benefits from cooperative labor; foraging in groups offers protection from predators, information about the location of productive food patches, companionship, and access to gossip or other information. In many cases men are not present during these interactions. As a result, cooperative foraging among Batek women occurs fluidly at little cost to participants, and with little incentive for defection.

In contrast, Tsimane women rarely forage in groups (Figure 1) and have fewer cooperative foraging partners than men, corroborating other studies of fishing among Tsimane [40]. Cooperative horticultural labor involves directed work invested into fields that while having specific owners, yields harvesting rights to collaborators, as well as the subsequent sharing of the resulting produce between households, with strong biases towards kin [41]. Field ownership, which applies to both Tsimane men and women, creates a context in which reciprocal labor partnerships are critical (e.g., for labor-intensive and time-limited tasks, such as rice harvest and clearing). In an environment where flooding and pests pose risk to crops, Tsimane practice several methods that promote buffering against crop failure, including distributing fields across locations, intercropping, and overplanting. As these risk buffering steps can be taken largely independently by households, labor needs can often be met by just a few other helpers outside the immediate household. With a high potential for defection or unequal labor inputs, labor partner characteristics become critical. As such, Tsimane women tend to share labor with a smaller network of trustworthy and dependable partners, primarily spouses and close kin split fairly equally between male and female alters (Figure 2, Figure 3). A similar pattern was reported among Ache hunter-gatherers adopting incipient horticulture in a semi-sedentary reservation, as compared to active hunting and gathering during forest treks; food sharing, especially of subsistence crops, was more restricted to close kin and neighbors on reservations,

and consistent with reciprocity, while both labor and sharing networks were more diffuse on forest treks [42]. The directed nature of horticulture labor provided to Tsimane field owners is further reflected by the fact that 12% (weighted by number of helping days) of reported female labor interactions involved payments of cash or food, many of which involved Tsimane working for unrelated *napo* (non-Tsimane Bolivians). Given recent increases in *napo* living in the region, it is likely that Tsimane womens' labor networks included even fewer non-relatives in the past.

Food acquisition involves a significant social component and is intimately intertwined with status and social relationships [43]. The restricted nature of female Tsimane labor networks and the relative lack of partnerships with non-relatives compared to Batek women suggests that agriculture may reduce a key domain of female interaction and potential social bond and alliance formation. Tsimane women do visit and form friendships with other women in the village, but this occurs as a form of leisure, and the relationships lack the kind of economic interdependence more typical of foragers like the Batek.

Our findings provide preliminary support for an expanded socio-ecological model with relevance to humans. Unlike some non-human primates for whom food distribution and predation may be keystone features [7,9], social bonds between human females are further shaped and constrained by complex social systems that vary within our species, including divisions of labor, sharing, and cooperative allocare. Nevertheless, characteristics of targeted food resources, like patchiness, abundance, predictability, divisibility, and extent of processing required, affect how women spend their time and the social interactions that occur during work activities which make up a substantial portion of the day in subsistence societies [44]. The resulting networks have downstream implications for cooperation, alliance formation, and social organization more broadly. For example, changing labor network structure may work in concert with other pathways that are strongly influenced by food distribution and subsistence strategies, such as reduced mobility and increased population density, which have been linked with increased political and economic inequality [45] and gender inequality [46,47].

Female social bonds driven by subsistence may be a key driver of other important social traits, such as reduced male aggression. According to the "self-domestication" hypothesis, selection for cooperative, non-aggressive males leads to a suite of morphological, physiological, behavioral, and psychological changes that mirror those observed in domestic animals [21]. This process has been invoked to explain derived differences between congeneric chimpanzees and

bonobos. Hare et al. [21] hypothesize that bonobos form more stable parties wherein females are more gregarious than males due to differences in feeding ecology and reduced scramble competition, possibly as a result of higher densities of terrestrial food and the absence of gorillas south of the Congo river [48,49]. In comparison to chimpanzees, the existence of stable parties in bonobos thus favors female-female alliances that allow for effective suppression of male aggression, reduced efficacy of male coercion of females, and reduced value of male rank [50–52].

Several lines of evidence going back to Darwin [53] suggest that a self-domestication process has also influenced human evolution [54–56]. Numerous hypotheses have been presented to explain selection against reactive violence in humans [57]. Of these, Tomasello's "interdependence hypothesis" [58] posits that an ecological shift to foods that were not individually obtainable drove increased interdependence and selection for less selfish, more cooperative foraging partners. Although Wrangham [59] discounts this hypothesis and a "female-choice" hypothesis primarily on the assumption that a despotic male could still use aggression to commandeer food and mates in the absence of coalitions, the evidence presented here suggests that resources which elicit low within-group competition for and accommodate stable social foraging among females and mixed-sex groups have the potential to drive the formation of "coalitions of the weak" that could enforce social selection. The underlying logic is the same as that for female bonobos that form both strong female-female and male-female alliances given resource distributions that promote stable parties. The data presented here suggest that hunting and gathering is amenable to social foraging amongst stable groups of females, potentially aiding in a process of self-domestication, although later changes in subsistence ecology (e.g., farming) may have further changed labor network structures.

The hypotheses and results presented here also have implications for understanding cross-cultural differences in gender relations and egalitarianism. Female social contacts developed during cooperative labor provide an avenue for social support, time to develop trust and to transmit information, and opportunities for coalition-building. Absence of these opportunities can facilitate male control over women and a lack of recourse in response to male aggression, as evidenced by the observation that intimate partner violence and other forms of abuse in industrialized societies often involve attempts to isolate victims from their networks, such as those developed at work [60–63]. Employment, and the networks developed therein, can

be protective against intimate partner violence [64,but see 65]. In support of this idea, gendered violence is virtually unknown amongst the Batek [27], whereas intimate partner violence is not uncommon amongst Tsimane [66]. We therefore suggest that economic systems which stymie the participation of women promote power differentials between the sexes via not only asymmetries in resource access, but also access to valuable social interactions.

This paper has several important limitations. First, we have only examined a single domain of social interaction: cooperative subsistence labor. Although subsistence populations spend many hours per day in subsistence activities, female hunter-gatherers and horticulturalists alike maintain social networks that span a variety of other relevant domains that merit study, such as cooperative child care, food sharing, co-residence, and other subsistence-related tasks like food processing and tool manufacture [67]. Second, our analytical focus on the number of unique alters in labor networks and not the frequency of interactions targets the breadth, but not depth, of cooperative labor. A follow-up analysis of repeated interactions over time would be instructive as it could reveal population differences in the strength of ties that might accompany reduced network sizes among Tsimane women. Third, our sample of Batek foragers is small given high inter-individual variation in cooperative foraging. Finally, we are only using data from two populations Though both inhabit tropical forests, Batek and Tsimane differ in many ways beyond subsistence strategy, and these examples cannot be taken to typify "hunter-gatherers" or "horticulturalists", nor can any two populations be representative. Progress in testing the hypotheses presented here will require going beyond forager-farmer comparisons, exploring cross-cultural variation in multiplex social networks and female social bonds. As food production strategies vary in relation to local ecology, social organization, mating system, technology, and cultural preferences, so should the size, strength and composition of female social networks.

Many subsistence populations today are currently experiencing rapid changes in livelihood strategies and other aspects of risk management that likely impact women's social networks. Understanding the social consequences of changing labor networks in these transitional economies will require the simultaneous assessment of gender inequality, isolation from social support, and power dynamics in relation to changing network structures. A research agenda that examines links between available resources, social labor networks, and gender relations may find parallels between patterns observed among subsistence societies like the

Batek and Tsimane and those observed in industrialized economies; for example, the social ramifications of the socioeconomic changes wrought by the Industrial Revolution were profound, instigating a precipitous decline in the percentage of married women working outside the home in 19th century England [68,69]. The identification of a common phenomenon will help identify whether major economic shifts have led to the contraction of female social networks not only through separation from primary economic production, but also via the direct loss of relational capital.

Competing Interests

The authors declare that they have no competing interests.

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Authors' Contributions

TSK conceived the study and wrote the paper. MG, DC, KLE, KME, and VVV contributed text. TSK analyzed the data. KLE, KME, TSK, VVV, DC, ES, HK, BB, SA, PH, BCT, JS, and MG collected and organized the data. All authors contributed ideas and gave final approval for publication.

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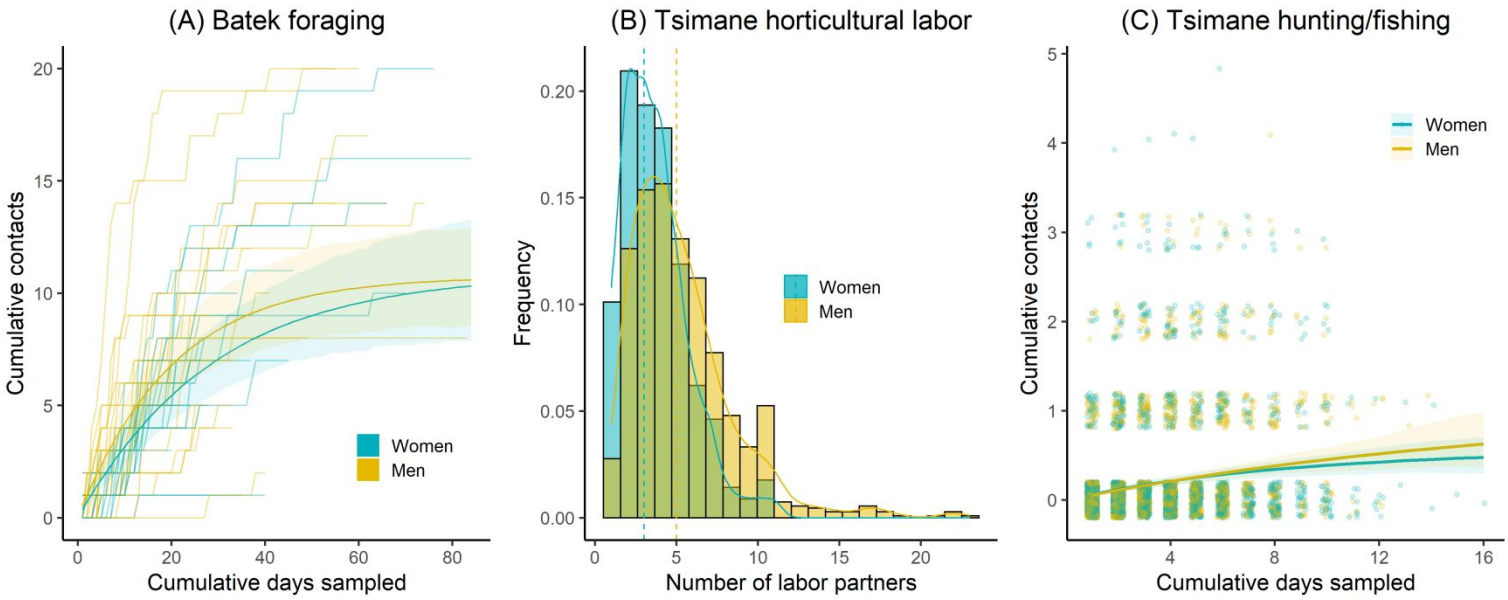

Figure 1: (A) Cumulative number of unique foraging partners observed among Batek foragers over an 84 day period in 1975/76. High mobility causes changes in camp composition leading to variation in the number of observation days across individuals. Semi-transparent lines represent observed data from individual foragers. Solid lines and shaded areas represent posterior median and 95% highest density interval for a zero-inflated random slopes model fit to data with an interaction between cumulative days sampled and sex (see methods). (B) Reported number of Tsimane horticulture labor partners (unique individuals whom ego either received help from or provided help to for field labor) over the past year for men (yellow) and women (blue). Solid lines indicate density overlay and dotted lines represent median values. (C) Cumulative number of unique hunting/fishing partners as a function of number of sampling days for Tsimane men and women combined. Solid lines (shaded intervals) denote posterior 95% highest density interval for a zero-inflated random slopes model fit to data (see methods). Note that sampling days for a given individual are not necessarily consecutive and derive from repeat interviews conducted over longer time periods.

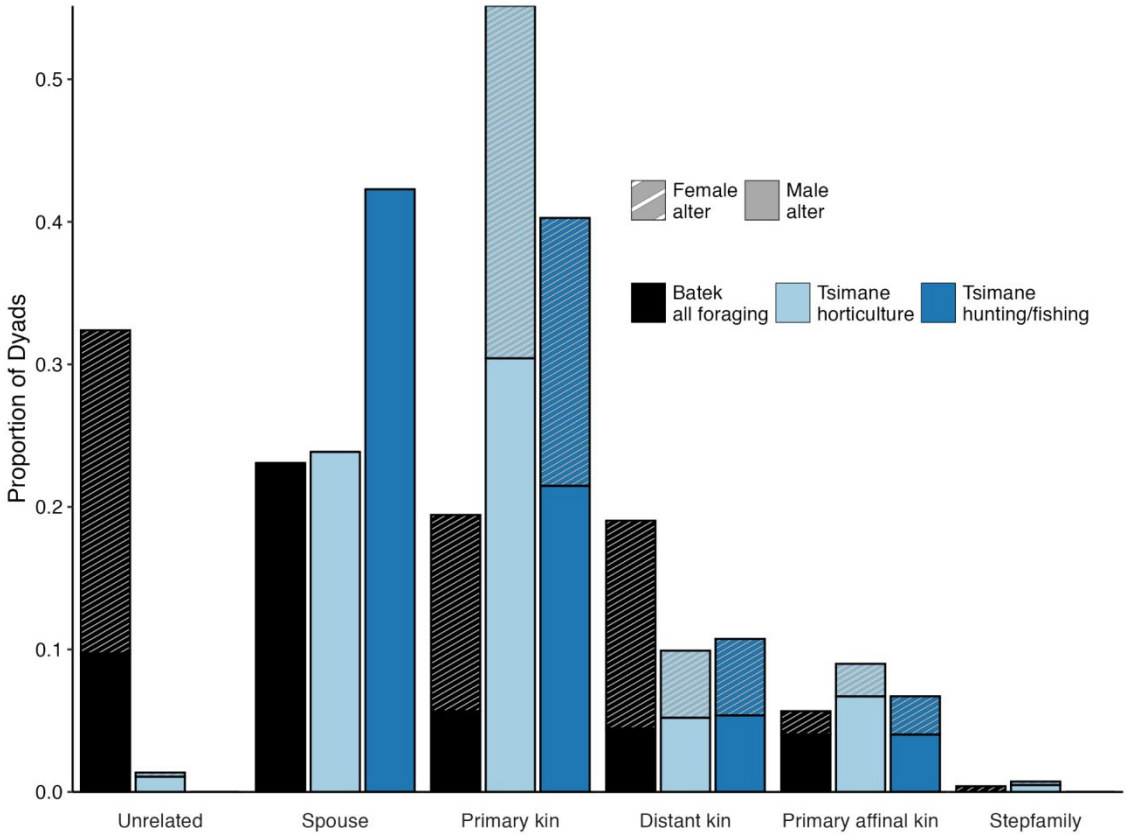

Figure 2: The proportion of cooperative labor dyads for Batek (black) and Tsimane women (light blue = horticulture, dark blue = hunting/fishing), separated by relationship to alter (x-axis categories) and sex of alter (hashed = female, solid = male).

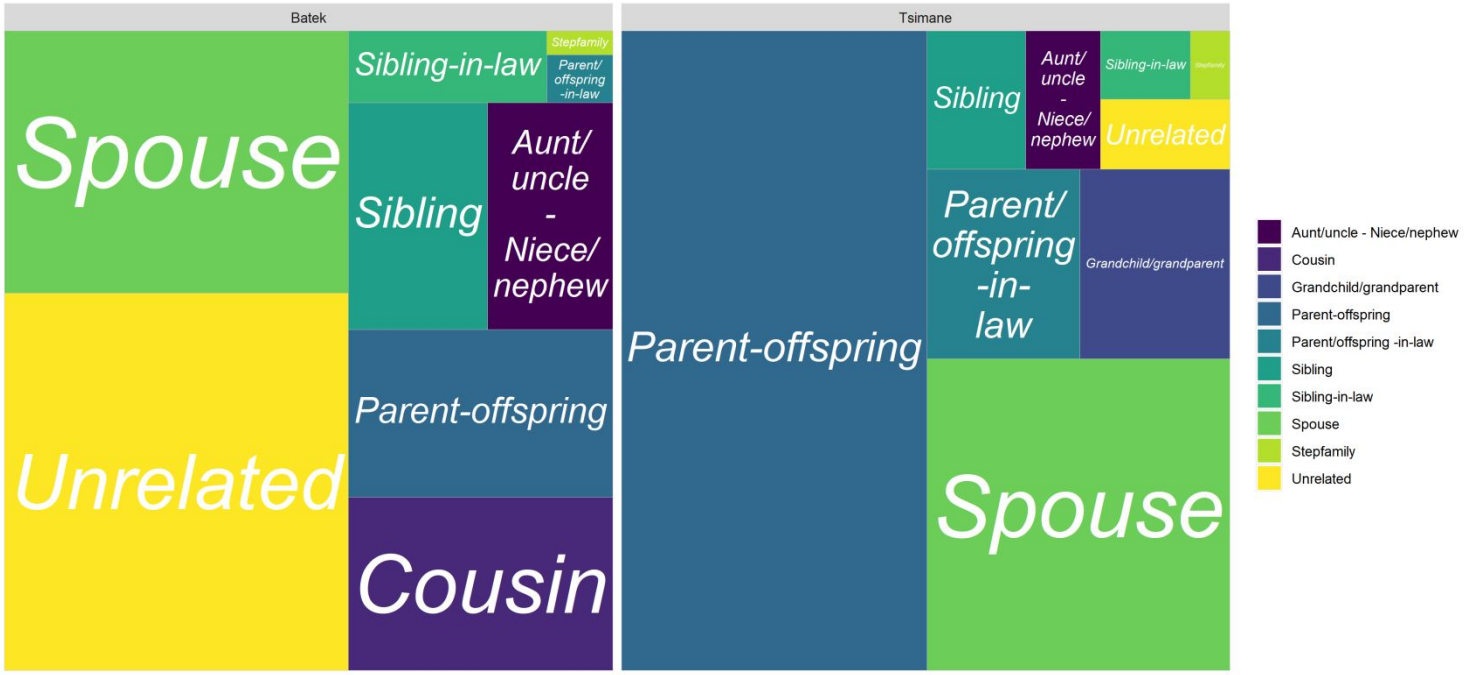

Figure 3: Treemap plot of the relationship between alter and ego in cooperative labor dyads for Batek (left) and Tsimane (right) women. Tsimane dyads represent horticultural labor partnerships reported for field help given and received. To focus on female networks, dyads were only counted for Batek if they involved a woman, and Tsimane only if the ego interviewed was a woman. The size of boxes corresponds to the proportion of dyads for a given type.

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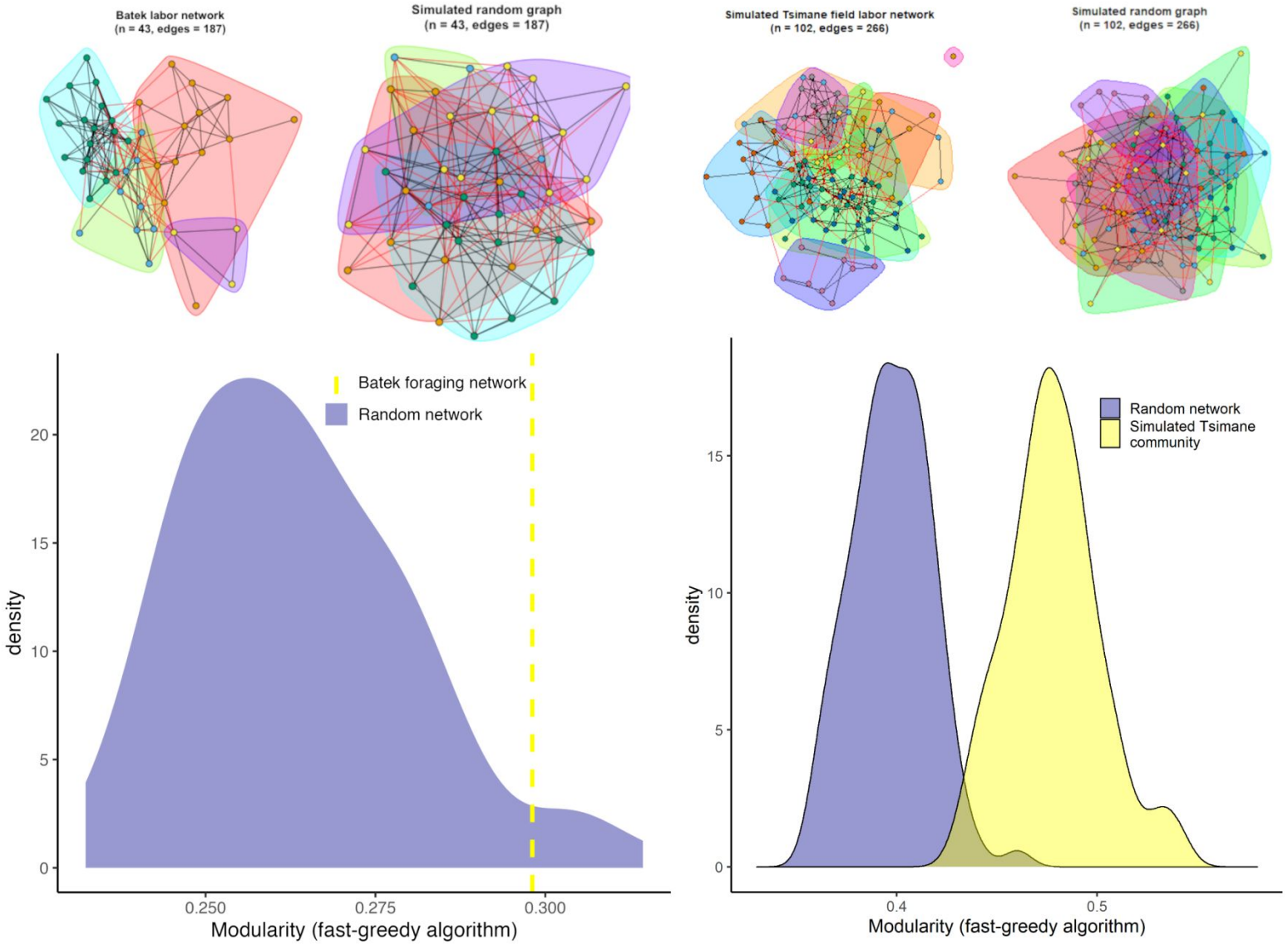

Figure 4: Network modularity for the Batek foraging network (left; non-valued, cumulative across 84 days including all individuals present for at least 20 days) and Tsimane horticultural labor networks (right; 100 simulated networks of one Tsimane village from an ERGM parameterized to reproduce target statistics from empirical egocentric network data) compared to random networks with equal size and density. Network graphs in the top row show examples of networks with overlaid communities from a fast-greedy community detection algorithm (nodes are colored by community, red and black ties represent between- and within-community ties, respectively).

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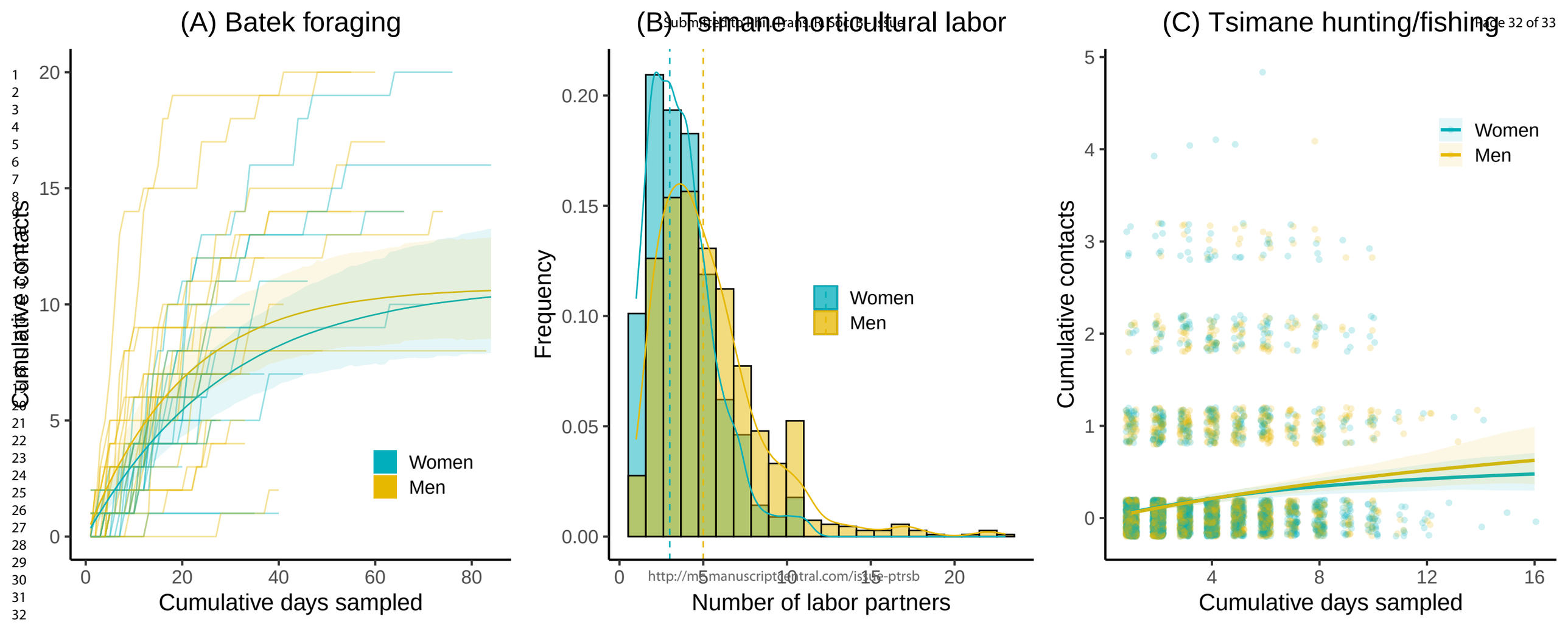
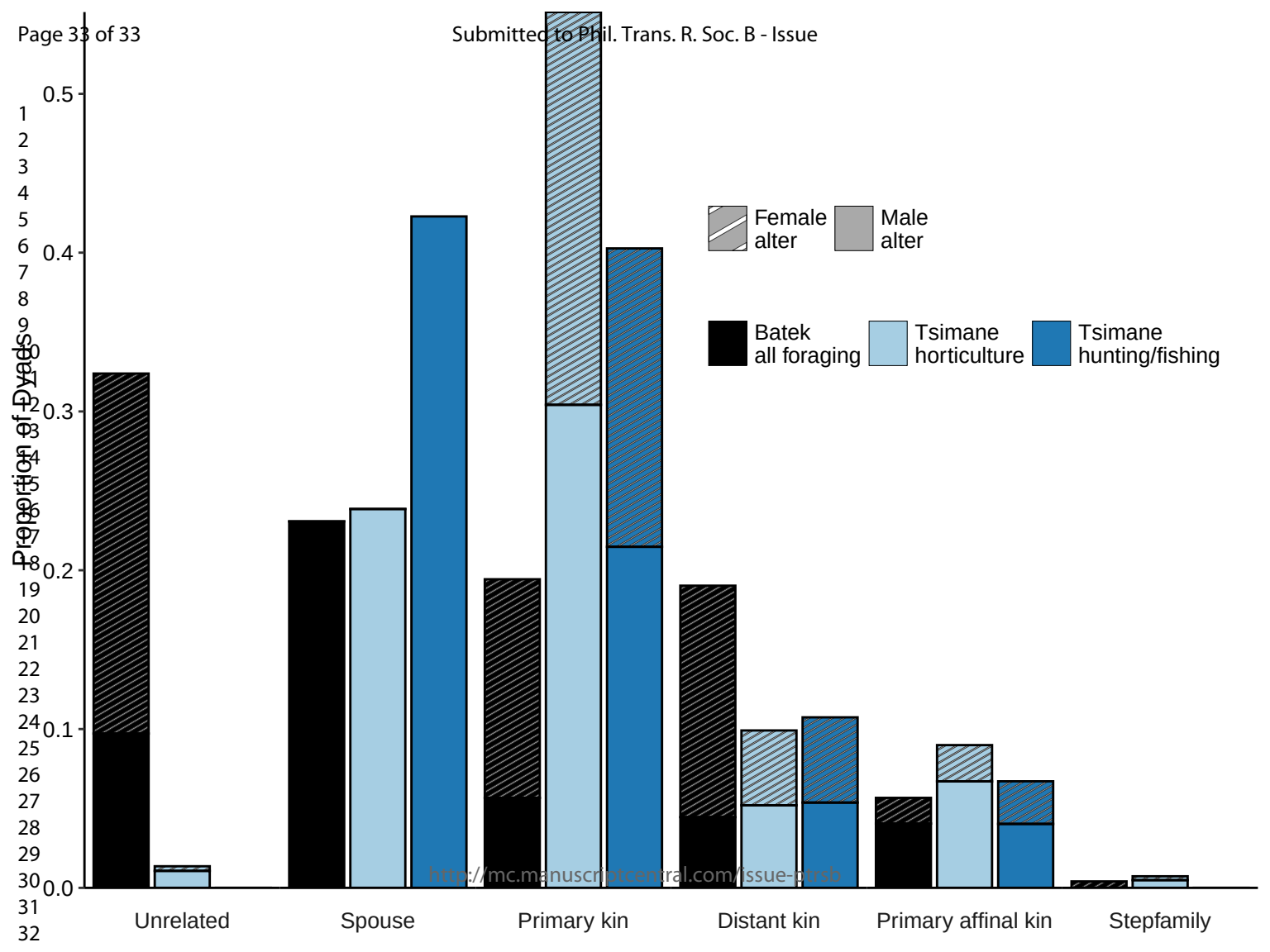

(A) Batek foraging
Cumulative contacts
Cumulative days sampled
Women
Men
(B) Tsimane horticultural labor
Frequency
Number of labor partners
Women
Men
(C) Tsimane hunting/fishing
Cumulative contacts
Cumulative days sampled
Women
Men



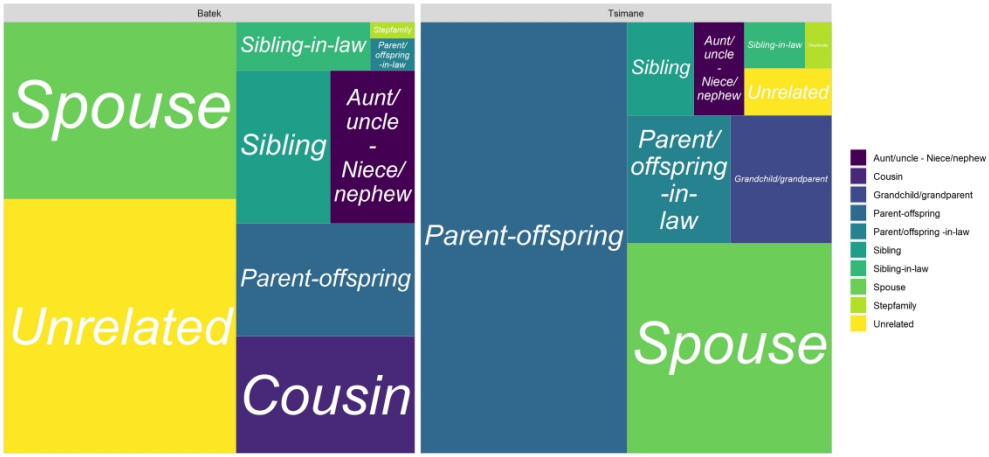
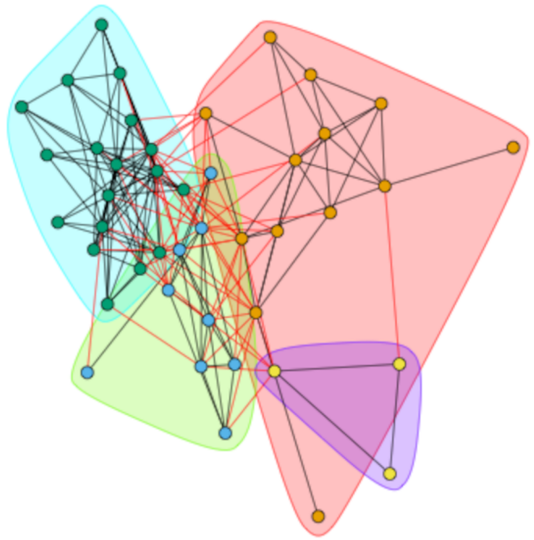
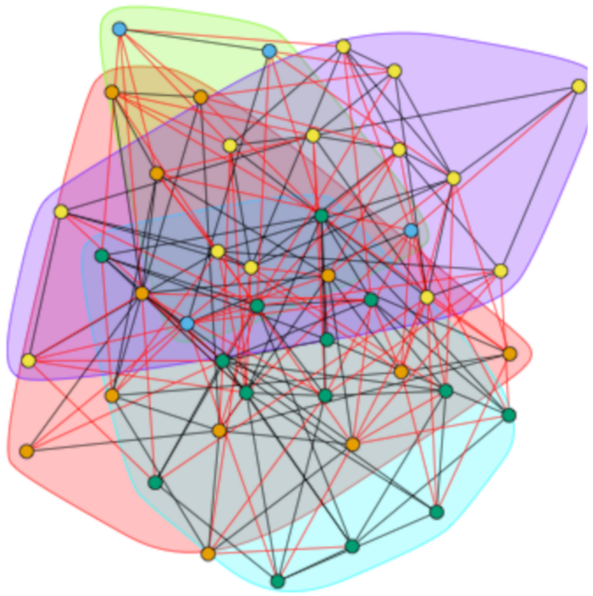
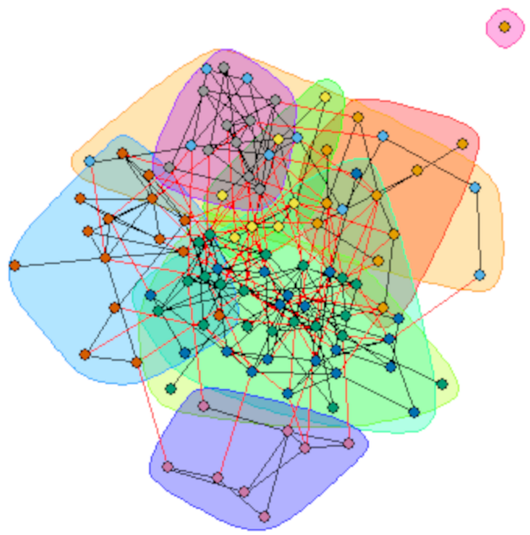


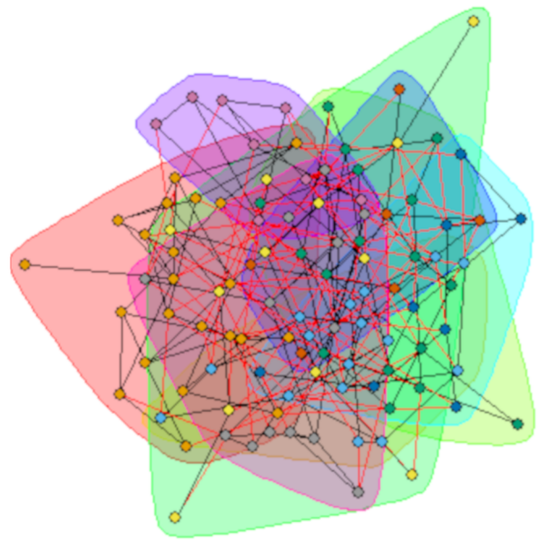
Figure 3: Treemap plot of the relationship between alter and ego in cooperative labor dyads for Batek (left) and Tsimane (right) women. Tsimane dyads represent horticultural labor partnerships reported for field help given and received. To focus on female networks, dyads were only counted for Batek if they involved a woman, and Tsimane only if the ego interviewed was a woman. The size of boxes corresponds to the proportion of dyads for a given type.

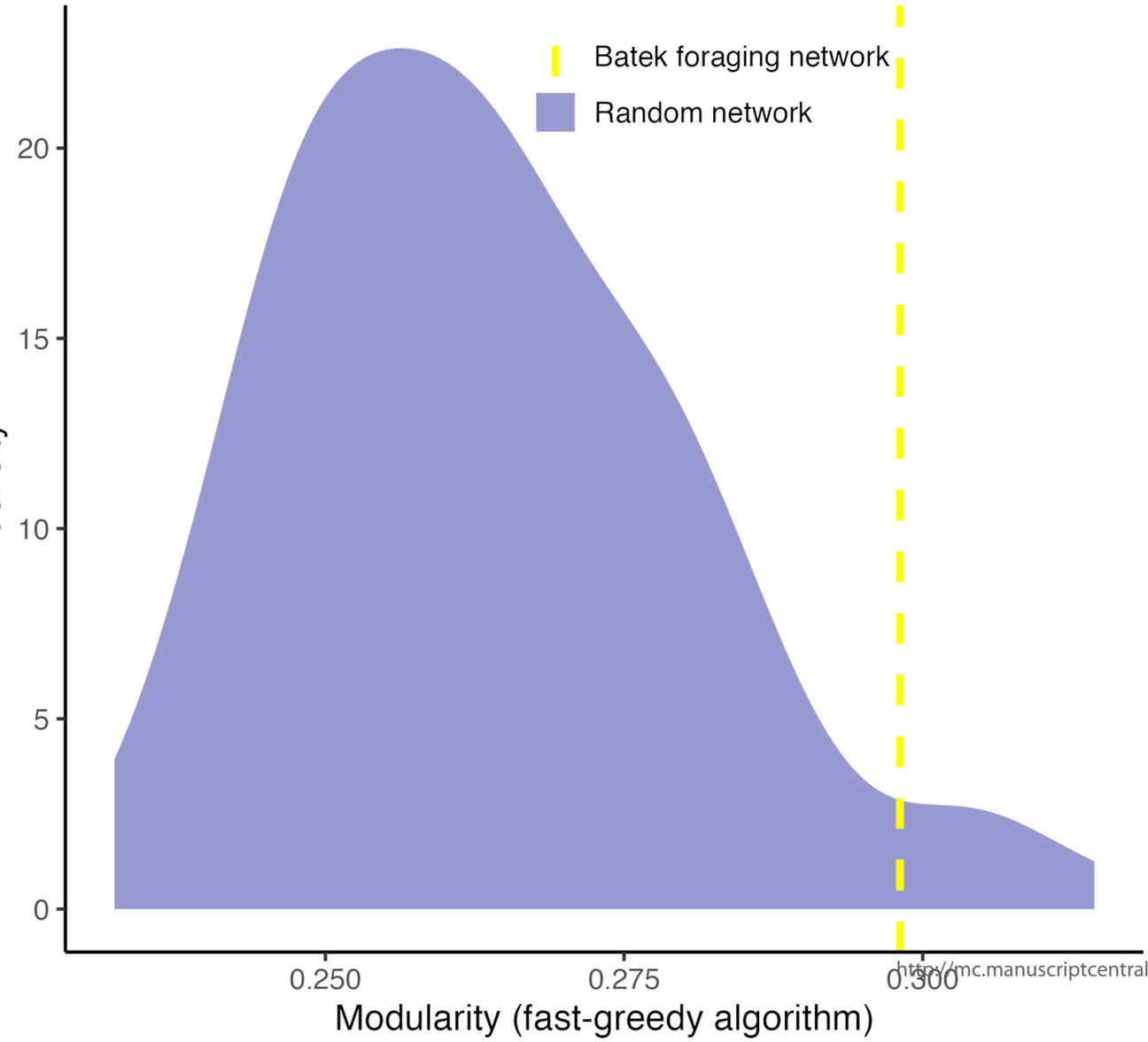
839x387mm (118 x 118 DPI)

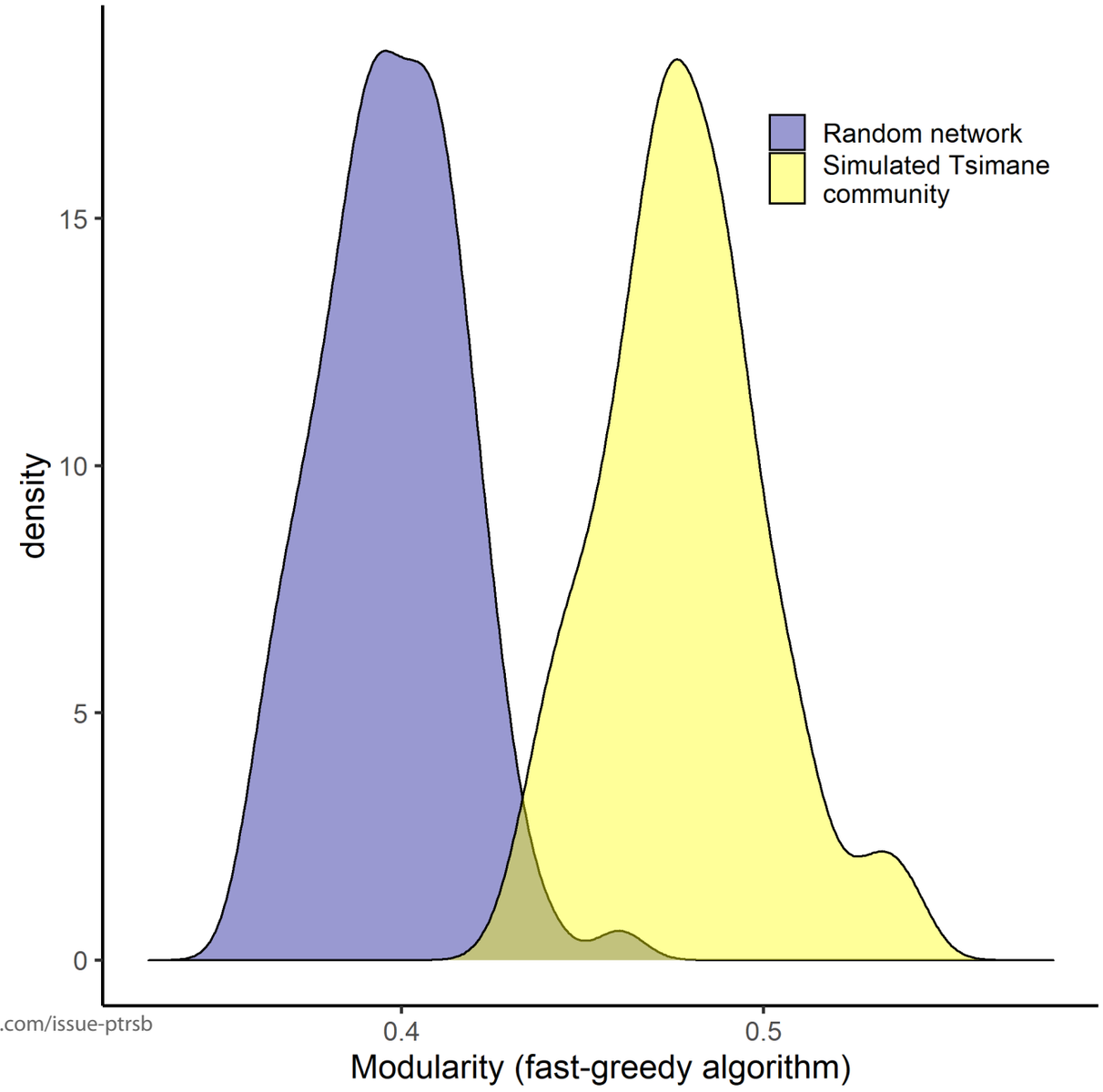

Batek labor network
(n = 43, edges = 187)


Simulated random graph
(n = 43, edges = 187)


Simulated Tsimane field labor network
(n = 102, edges = 266)


Simulated random graph
(n = 102, edges = 266)


Batek foraging network
Random network
density
20
15
10
5
0
0.250
0.275
0.300
Modularity (fast-greedy algorithm)


Random network
Simulated Tsimane community
density
15
10
5
0
0.4
0.5
Modularity (fast-greedy algorithm)