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Kinship ties across the lifespan in human communities

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A hypothesis for the evolution of long post-reproductive lifespans in the human lineage involves asymmetries in relatedness between young immigrant females and the older females in their new groups. In these circumstances, inter-generational reproductive conflicts between younger and older females are predicted to resolve in favour of the younger females, who realize fewer inclusive fitness benefits from ceding reproduction to others. This conceptual model anticipates that immigrants to a community initially have few kin ties to others in the group, gradually showing greater relatedness to group members as they have descendants who remain with them in the group. We examine this prediction in a cross-cultural sample of communities, which vary in their sex-biased dispersal patterns and other aspects of social organization. Drawing on genealogical and demographic data, the analysis provides general but not comprehensive support for the prediction that average relatedness of immigrants to other group members increases as they age. In rare cases, natal members of the community also exhibit age-related increases in relatedness. We also find large variation in the proportion of female group members who are immigrants, beyond simple traditional considerations of patrilocality or matrilocality, which raises questions about the circumstances under which this hypothesis of female competition are met. We consider possible explanations for these heterogenous results, and we address methodological considerations that merit increased attention for research on kinship and reproductive conflict in human societies.

This article is part of the theme issue 'The evolution of female-biased kinship in humans and other mammals'.

1. Introduction

Humans are among the minority of mammalian species in which females exhibit prolonged post-reproductive lifespans [1]. Among anthropologists, adaptive explanations for this life-history strategy have focused on the inclusive fitness benefits of parental and grandparental investment [2,3]. Expanding on these perspectives, Cant & Johnstone [4] observe that in addition to the fitness effects of altruism, conceptual models also need to account for the inclusive fitness consequences of reproductive conflicts. That is, reproductive conflict occurs in social groups, including cooperative groups, when there are limited resources to support reproduction by females in the group. In humans, for instance, increased offspring mortality has been documented when a woman reproduces concurrently with her mother-in-law [5]. Females who are surrounded by fewer genetic kin are predictably more indifferent to the reproductive costs that competition inflicts than females living among many kin [4]. For example, whereas women are typically unrelated to their mother-in-law's offspring, their own offspring will be the genetic grandoffspring of the mother-in-law, who therefore has less to lose by ceding reproductive opportunities. To understand whether the resolution of reproductive conflicts might have shaped the evolution of life-history strategies, we need a better understanding of the kinship structure among interacting females and how this is influenced by demography.

The main factor that influences whether adult females are interacting with close kin is whether and where they move relative to their parents' location [6,7]. In most populations of mammals and birds, there appears to be a strong sex bias in dispersal [8]. Accordingly, populations are generally classified into those where females are philopatric and remain with their kin and those where females disperse and join other, unrelated females. Empirical studies of kinship generally support that in a given population females either remain with kin or not, but also highlight important fluidity in these patterns where only subsets of females remain philopatric [9] or dispersing females end up with kin [10]. Such fluidity in settlement patterns appears to characterize many human populations [11], leading to potential differences between females in their relatedness to other group members depending on their movement history, with corresponding implications for the resolution of reproductive conflicts.

Arguments related to kinship structure among females are further complicated since it is not a static aspect of a female's environment, but changes dynamically across the lifespan [12]. For instance, in human societies that are characterized by male philopatry and female-biased dispersal, younger females are predicted to be surrounded by fewer genetic kin than older females. In this scenario, females leave their kin and join a new group, where they mate with males who are typically related to the older females in the group. Therefore, usually the resulting offspring of these young females exhibit high genetic similarity to the older females (with allowances for paternity uncertainty) such that older females are related to the majority of individuals in their local group. This asymmetry favours younger females in reproductive conflicts with older females because the latter have relatively more to gain via alloparental investment. According to theory, these could be the conditions favouring the evolution of post-reproductive lifespans in females [4].

The conceptual arguments linking kinship structure to residence patterns and age were formalized quantitatively by Johnstone & Cant [1], who derive individuals' relatedness to group members as a function of mating patterns and the dispersal and demography of males and females, respectively. The model provides confirmatory evidence that when females disperse and mating occurs within the local group, the relatedness of females to other group members increases with age as they have sons who remain as breeding members of the group. Given the extent to which female-biased dispersal characterizes hominoid species, this pattern is dubbed the 'ape case' [1]. The model is also flexible enough to accommodate the kinship dynamics of cetaceans, another species with prolonged post-reproductive lifespans. Among killer whales, neither males nor females disperse from their natal group, but because mating occurs with individuals outside the group, females exhibit relatively low relatedness to males other than their sons [13]. As they age and have more sons in the group, female killer whales, therefore, display overall increases in average relatedness to other group members that parallel the aforementioned increases in the ape case [13].

When applied to the evolution of human life-history traits, the female-biased dispersal that typifies African apes has often been assumed to characterize the social organization of human ancestors [4]. By dispersing, young adult females may reside primarily among their mates' female kin, not their own. In that hypothesized scenario, the resulting reproductive conflicts among the females potentially help to explain distinctive human traits, such as prolonged post-reproductive lifespans. However, it is currently difficult to make strong empirical inferences about the social organization of prehistoric hominins, particularly given the flexible residence and dispersal that distinguish contemporary human societies [11]. Heterogeneous residence rules across human societies include patrilocality and matrilocality, which purportedly correspond to the typical dispersal patterns of the ape case and the typical mammalian case, respectively. In addition to cross-cultural variability [14], adherence to normative residence rules within societies is likewise variable. Human couples maintain affiliative bonds with both the husband's and wife's kin, and the ability to move between these groups throughout an individual's life permits flexible residence arrangements that can confound even seasoned ethnographers [15].

Given this diversity and flexibility, empirical research on kinship in human societies is needed to inform our understanding of the potential for reproductive conflict and cooperation among women. In this study, our aim is to investigate the extent to which movement influences kinship patterns across human communities and whether this is associated with predictable variation in individual levels of kinship across female lifespans. Given the expected flexibility in human settlement patterns, and the extent to which individuals adhere to these rules, we consider variation in group kinship across the lifespan for immigrants (of both sexes) in each community, drawing contrasts to natal residents to contextualize these changes. To assess these patterns, we compile genealogical and demographic data from 19 communities to examine age-related variation in relatedness to group members. The study communities vary in terms of settlement history, subsistence strategies,

Table 1. Descriptive statistics for the study sites. Descent rules are reported when known. Sample size corresponds to the number of residents in the communities. Natality status was calculated only among adults (males older than 21 and females older than 18). For each respective sex, the percentages in the table reflect the proportion of adults who are natal members of the study community. For the data on average women per household, the household is considered to be the most relevant resource-sharing units at that locale. For the Gambian study sites, these correspond to multi-family compounds. Blank cells for the descent rules indicate a lack of information.

site number	group	country	descent rule	average relatedness	community size	women per household	per cent natal female adults	per cent natal male adults
1	Savannah Pumé	Venezuela	bilateral	0.085	76	0.90	57.89	14.29
2	Miskito	Nicaragua	bilateral	0.100	92	1.07	53.33	21.43
3	Mayangna	Nicaragua	bilateral	0.044	322	1.88	80.65	38.89
4	Coastal Afro-Colombians	Colombia		0.012	188	1.22	48.15	45.83
5	Inland Afro-Colombians	Colombia		0.006	306	1.11	46.59	47.54
6	Dominica	Dominica		0.017	422	1.33	94.63	96.60
7	Inland Emberá	Colombia		0.048	91	1.00	60.00	61.54
8	Choyeros	Mexico	bilateral	0.054	113	1.19	73.68	81.40
9	The Gambia, 2	The Gambia	patrilineal	0.011	573	1.56	80.50	89.39
10	Mosuo	China	matrilineal	0.014	218	2.13	82.14	91.36
11	Maya	Mexico	bilateral	0.035	544	1.20	84.15	94.74
12	Lamalera	Indonesia	patrilineal	0.005	1216	1.48	83.76	95.43
13	Coastal Emberá	Colombia		0.087	86	1.13	11.76	13.33
14	Maasai	Kenya	patrilineal	0.013	296	1.29	25.93	31.25
15	The Gambia, 1	The Gambia	patrilineal	0.005	1387	5.65	70.23	86.42
16	Mosuo	China	patrilineal	0.024	163	2.27	62.69	88.14
17	Alakāpuram	India	patrilineal	0.004	613	1.33	37.05	85.33
18	Tenpaṭṭi	India	patrilineal	0.004	487	1.27	30.57	91.84
19	Tanna	Vanuatu	patrilineal	0.030	183	2.31	27.03	86.67

population, fertility rates, descent rules and sex biases in dispersal. Given that we also observe flexibility in the dispersal data of the communities in our sample, we are not classifying these along traditional binary lines of matrilocal versus patrilocal. Instead, we explicitly consider the ratio of immigrants in each sex.

Our analysis is framed around the predictions of Johnstone & Cant [1], specifically that individuals who disperse to new communities initially have few kinship ties but progressively exhibit greater relatedness as they have offspring who become members of the group. In this analysis, the outcome variable is the individuals' average relatedness to other community members [13]. Arguably, because sharing and competition over resources may be particularly acute within residential clusters of close kin (i.e. sub-units of the larger community), the measure of community relatedness in this study could be too broad [16]. However, the present compilation of datasets do not permit the identification of relevant subclusters within the communities, a methodological consideration that we address in the discussion. Nevertheless, the numerator in the calculations of average relatedness for a given individual largely reflects the number of close, co-resident kin in the population. Therefore, in larger communities, although most individuals may be distantly related to the individual, variability in average relatedness frequently reflects the presence of close kin and the concomitant opportunities for reproductive conflict and cooperation.[1]

2. Methods

The data for this study were obtained by the authors via censuses and genealogical interviews at their respective field sites (table 1). As noted, the sites exhibit diverse social organization, demography and subsistence strategies (see the electronic supplementary material for brief descriptions of each site). For all living residents in the respective study communities, the authors compiled data on age, sex and whether or not individuals are natal members of the community (figure 1). This latter variable is subject to interpretation, given the diversity of movement patterns in human communities. When groupings are geographically and temporally ephemeral, for example, then it can be challenging to distinguish between natal and non-natal members of the community. In this sample of sites, the Savannah Pumé of Venezuela exhibit such fluidity, and few older residents are therefore considered natal members of the community. Analogously, the Maasai community in this sample is a relatively new settlement that attracted a diverse set of immigrants, resulting in few older residents who are considered natal members of the community. More generally, the co-authors had to categorize individuals such as temporary migrants, children who had relocated with their parents, and foster children. The co-authors attempted to standardize norms about the categorization of such individuals, generally tending toward conservatism in the categorization of natal residents. For instance, children of divorced women who subsequently marry into a new community are generally not considered natal members of the new community. Therefore, relative to immigrants, the comparability of predictions for natal residents is less impacted by the fluidity of residence that characterizes several of the study sites.
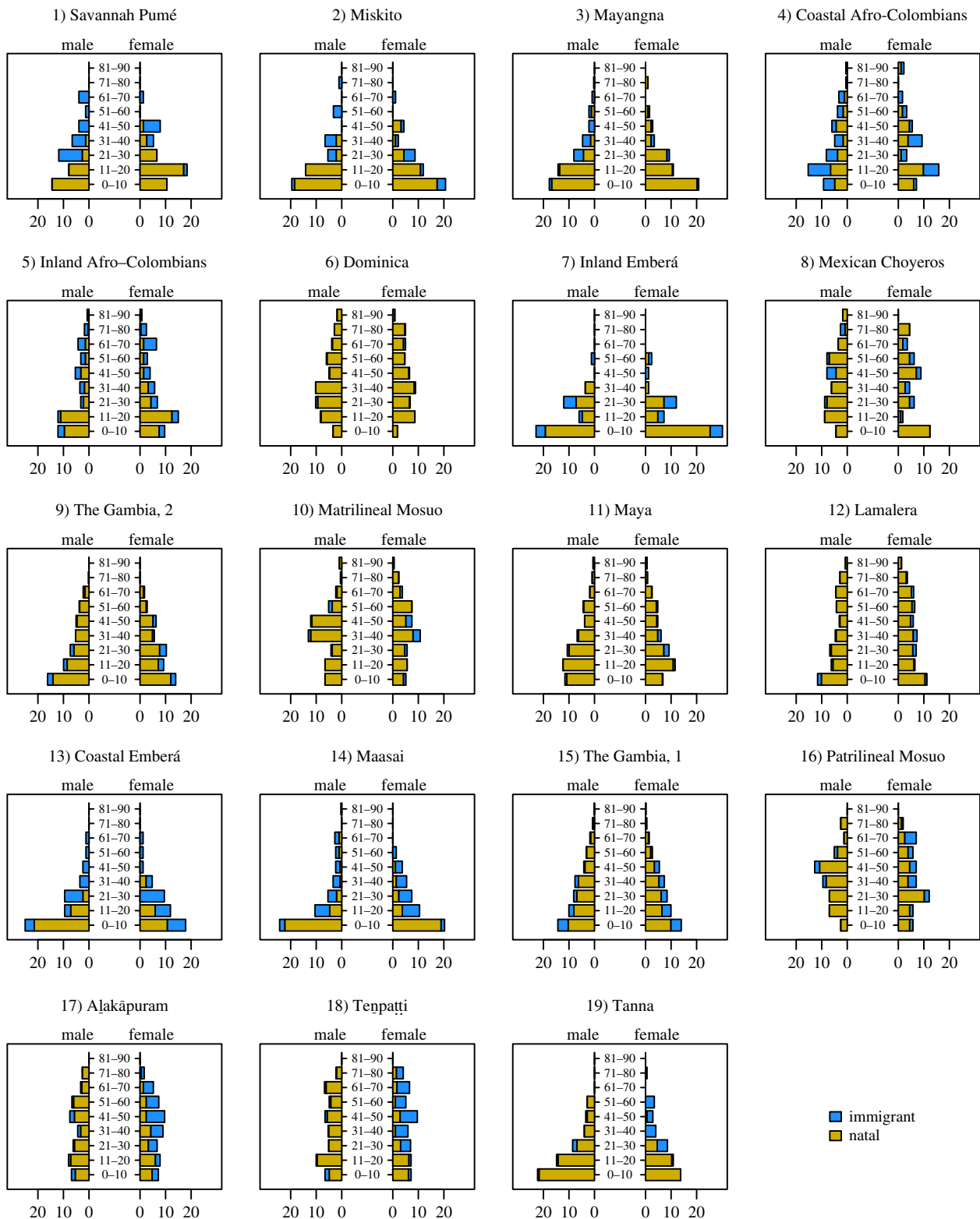
Figure 1. Population pyramids for the study communities. In the plot, sites are ordered in row-wise fashion according to the ratio of adult female natality to adult male natality (the quotient of the respective quantities in table 1). The numbers on the horizontal axes represent the percentage of the total represented by the respective age-sex categories.

For each site, the data also includes genealogical relationships that were elicited via interviews with informants. These genealogies permit the calculation of relatedness among individual residents of the communities. These calculations employ standard methods for estimating the coefficient of relatedness from genealogies [17]. For any given dyad, the coefficient is therefore constrained to lie between 0 and 1, which we anticipate to provide a useful approximation of genetic similarity. The genealogies from our study sites include

at least three generations of depth for residents, typically permitting us to distinguish cousins and closer genealogical relationships. As shown by Pemberton [18], pedigrees of three generations capture much of the variation in genetic relatedness among individuals. Some datasets provide even greater depth, and this varying thoroughness introduces between-site variation into the sample. In some communities, most notably the matrilineal Mosuo community, women were often unable to reliably indicate the father of their children. The data are

cross-sectional and represent the composition of the community at a single point in time.

In our primary analysis, we examine the average relatedness of adults to other adult residents in the community. A focus on adults has parallels to the ethological literature and its attention to inbreeding avoidance among reproductively mature individuals [19]. Accordingly, we consider females to be adults when they are 18 years or older and males to be adults when they are 21 years or older. These ages align with evidence that Aché women typically give birth the first time at 19 years old and that men in natural fertility populations are commonly 3 years older than women when their first child is born [20,21].

The analysis is oriented primarily toward illuminating demographic patterns within the respective study sites. We therefore model average relatedness at each site separately using regression models with the main effects and interaction terms of the three predictor variables: age, sex and natality. In some datasets, there were missing values for individuals' age and natality. Typically, these individuals were not permanent residents of the respective communities, so although their genealogical connections were included in the calculations of dyadic relatedness, the average relatedness of these individuals were not included in the statistical models. Because the outcome variable, average relatedness, is bounded to lie between 0 and 1, we use beta regression models [22]. Since average relatedness for some individuals is zero, we add a constant (0.0001) to all values for identifiability of model parameters.[2] We interpret the models graphically, plotting their predictions as a function of age interacted with the categorical predictors, sex and natality. As a supplemental analysis, we model average relatedness among all individuals in the study communities, including children. We also consider a multilevel analysis of the aggregated cross-cultural dataset, and we evaluate simpler site-specific models that omit sex as a predictor.

Models are fit with Markov chain Monte Carlo estimation using functions from the *Rstan* package [23] and auxiliary functions from the *rethinking* package [24]. Weak regularizing priors are implemented for all model parameters. We do not adopt any particular threshold for statistical significance, but we make sure to note the effects for which the models consistently predict age-related increases or decreases in the posterior samples. Data and coding scripts are available as supplemental files on the Open Science Framework (https://osf.io/h8cqr/).

3. Results

Our models examine the average relatedness of individual adults to all other adults in the community. Model predictions for each site are plotted in figure 2 (see also electronic supplementary material, table S1). Before interpreting predictions for specific sites, it is important to acknowledge that the confidence in predictions is a reflection of varying sample sizes, both across sites and across demographic subclasses within sites. In smaller communities, such as the Emberá sites, the predicted slopes may exhibit high heterogeneity, but there is little confidence that the slopes are conclusively positive or negative, nor are the slopes for demographic subclasses distinguishable from each other. The uncertainty relates in part to the small size of these communities, though another consideration is the high mobility and dispersal rates that characterize these sites. That is not to say that age-related variation in relatedness cannot be discerned in small communities. The Savannah Pumé community is also small, but for immigrant females, the model confidently predicts an increase in relatedness with age. Similarly, low sample sizes within demographic subclasses can also

reduce confidence in the corresponding model predictions. At the patrilineal Mosuo site, for example, the predicted effects of age are roughly comparable for male and female immigrants. However, there are substantially more female immigrants than male immigrants. Consequently, there is relatively more confidence in predictions for the average female immigrant.

In larger communities, individuals exhibit minimal relatedness to most of the other residents. This lowers the average relatedness among residents, and slopes in these communities typically seem relatively flat. Because of the larger sample size in communities, however, there is higher confidence in the predicted means (e.g. the downward trends in Lamalera). On the other hand, a comparison of the predicted values to the empirical data shows that age and the moderating effects of sex and natality typically explain only a modicum of the variation in average relatedness in large communities.

With those caveats in mind, we assess model predictions. Initially, we focus on age-related increases in average relatedness given the importance of such increases in recent theorizing of reproductive conflict [1]. For natal residents, increases with age are rare and evident primarily among males and females in the Mayangna community (site 3) and the female residents of the Coastal Afro-Colombian community (site 4) and the Mexican *choyero* community (site 8). For immigrants, increases are relatively more common and apparent among female immigrants in the patrilineal communities of Lamalera (site 12), the patrilineal Mosuo (site 16), Aḻakāpuram (site 17), Teṉpaṭṭi (site 18) and Tanna (site 19). Similar age-related increases for female immigrants are evident in two communities characterized by bilateral descent and female philopatry, the Savannah Pumé (site 1) and Mayangna (site 3). For male immigrants, conclusive age-related increases are evident primarily in the Mayangna community.[3] Collectively, these results accord with expectations from Johnstone & Cant [1] that adult immigrants initially have few kin in the community, but then their relatedness increases over time as they have descendants who join them as residents in the group.

Although prevailing theories focus on age-related increases in relatedness over time, declines are also interesting because they imply a different set of tradeoffs that merit theoretical attention. In this sample, declines in average relatedness are evident in several communities. For instance, the statistical models predict decreases for both natal females and males in Lamalera (site 12) and Aḻakāpuram (site 17). There is a decrease with age for natal males in Teṉpaṭṭi and a decrease for natal females in the smaller Gambian community (site 9). There is also moderate evidence for a decline in relatedness with age among natal residents of both sexes in the larger Gambian community (site 15). For natal females in Dominica (site 6), the predicted relationship with age also trends negative. Among immigrants, however, there is little evidence for decreases in relatedness with age at any of the sites.

(a) Supplemental analyses
For a supplementary analysis of age-related variation in relatedness, we also calculated and modelled average relatedness among all individuals in the community, including both adults and children (electronic supplementary material,
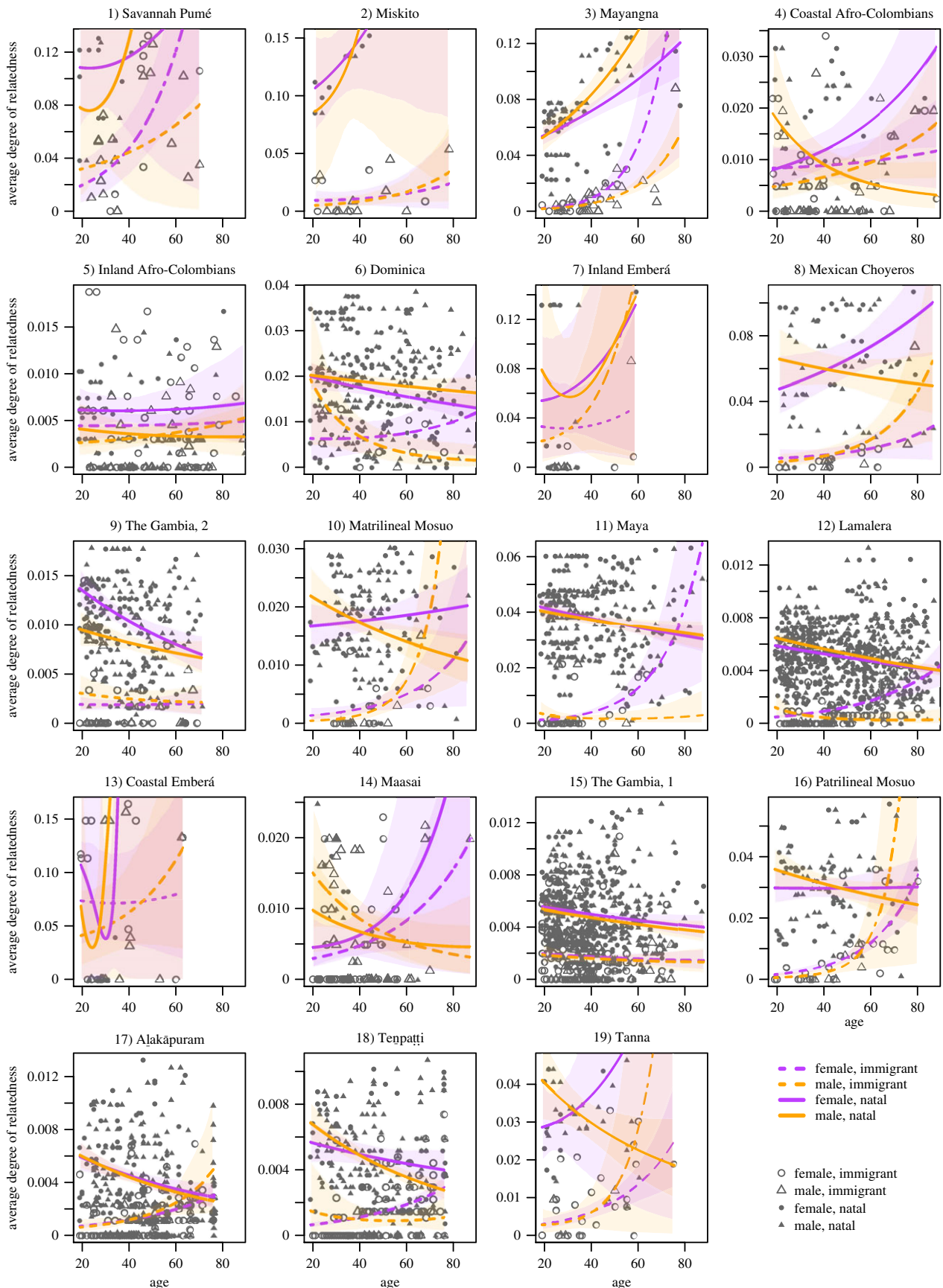
Figure 2. Model predictions for adults' relatedness to all other adults in the study communities, which is expected to vary as a function of individuals' age, sex and natality status. All predictions are based on beta regression models with three-way interaction terms (and the corresponding two-way interactions) between these variables. Shaded intervals depict 89% confidence intervals around model predictions. Note that the scale of the vertical axis changes for each community. Sites are ordered in row-wise fashion according to the ratio of adult female natality to adult male natality (the quotient of the respective quantities in table 1).

figure S1 and table S2). In general, the predictions from these models resemble the models for relatedness among adults. Noteworthy differences include the flattening of slopes for

female immigrants in Lamalera (site 12), the Maasai (site 14), Alakāpuram (site 17) and Tenpaṭṭi (site 18). This preliminarily suggests that juvenile female immigrants to

these communities have more kin ties (potentially including siblings) than women who arrive as adults. There is also clearer evidence for age-related increases in relatedness among natal males and females in the Miskito community (site 2).

As an additional supplementary analysis, we aggregated and analysed the cross-cultural dataset using a multilevel beta regression model. For this analysis, we calculated the proportion of adult males and females in each community who are natal residents to reflect patrilocal or matrilocal biases (these quantities are reported in table 1). These 'contextual effects' are then separately interacted with the individual-level effects, *age*, *sex* and *natality*. The purpose of these models is to assess whether matrilocal and patrilocal biases in the communities moderate the age-related variation that is evident among individuals. Perhaps because they are overparametrized, these statistical models largely recapitulate our prior findings, revealing few noteworthy differences that vary as a function of the residence biases that characterize the study communities (electronic supplementary material, figure S3). Overall, in these aggregated models, the most consistent difference is between the average relatedness of natal residents and immigrants. As in the model of Johnstone & Cant [1], the philopatric sex consistently exhibits higher relatedness to group members.

Finally, we view these analyses primarily as descriptive and exploratory, which initially led us to consider the full three-way interactions between *age*, *sex* and *natality*. However, visual inspection of the predictions in figure 2 reveals that, conditional on *age* and *natality*, there are few differences between males and females. In the supplemental file, we consider simpler models that omit *sex* as a predictor and moderator. These models often receive greater Watanabe–Akaike information criterion weight than the models presented here. In other words, in models that include *age* and *natality* as predictors, *sex* typically explains little variation in average relatedness (electronic supplementary material, table S4).

4. Discussion

Our analyses show age-related increases in relatedness among immigrants in several of the study communities that conform to predictions [1]. That is, immigrants of the more commonly dispersing sex initially have low relatedness, but they accrue more kinship ties as they age and reproduce. These increases are evident both among immigrant females to societies in which most males remain in their natal locality (patrilocal communities) and among migrating males in societies in which most females do not move (matrilocal communities). Not all communities show this pattern, however, and exceptions occur especially among the Gambian communities and the small communities with fluid residence patterns and unstable settlement histories. This fluidity also suggests that traditional labels of matrilocality versus patrilocality do not fully capture the diversity of migration patterns across human communities. Nevertheless, our results provide partial support for the prediction that average relatedness of immigrants to other group members increases as they age. That is, in societies where immigrants exhibit changes in relatedness that vary as a function of age, the effects are positive, not negative. However, the predicted positive effects are not evident at all study sites. In the

following, we discuss additional factors that were not modelled in this analysis, but that potentially shape the observed variation in kinship ties across the lifespan.

In this analysis of community relatedness, age is seldom associated with increases in average relatedness among natal members of the community. A notable exception is the Mayangna site in Nicaragua. The increase for females in this community is noteworthy because there are biases toward matrilocality and dispersal by males. This result therefore departs from the conceptual model advanced by Johnstone & Cant [1], which anticipates that females in such circumstances would start to show gradual declines in average relatedness as they age. To explain this departure, a factor to consider is the high fertility rate and population growth in this indigenous Nicaraguan community. As a matriline expands, older women are increasingly surrounded by daughters ($r = 0.5$) and nieces ($r = 0.25$).[4] By contrast, for younger females in an expanding population, a high proportion of their peers are cousins ($r = 0.125$). To some extent, therefore, the effects of age on relatedness at this site may be a by-product of the population growth rate, which is considerably higher than the long-term growth rates that characterized Paleolithic and Neolithic human populations [25].[5] Conversely, decreases in age-related relatedness were observed for natal residents of several communities that have a lower ratio of younger to older individuals (e.g. Alakāpuram), which suggests a potential need to account for demographic non-stationarity in populations when conducting comparative research on kinship (see [26] for a similar argument).

To explain cross-cultural heterogeneity in relatedness across the lifespan, we argue that there are likely to be recursions between relatedness and demographic outcomes. In other words, the fertility, mortality and dispersal of individuals plausibly vary in response to the presence of kin in the group. Over time, variation in these outcomes can consequently amplify or reduce relatedness to other group members. For instance, high average relatedness among older individuals could indicate greater longevity or fertility due to support from kin, possibly augmented by the dispersal of individuals with few local kinship ties. Effects of kin on fertility and mortality have received substantial attention from human behavioural ecologists [27,28]. By comparison, dispersal in human populations has received less attention [29,30]. Studies of non-human mammals provide evidence of facultative dispersal strategies as a function of the presence and rank of local kin [31–34]. Comparable anthropological research is empirically challenging, but ethnographers who conduct longitudinal studies can potentially examine decisions about residence and dispersal as kin availability fluctuates. In addition, there is an opportunity for theoretical models and simulations that allow demographic outcomes to vary non-randomly and dynamically in response to local kinship ties. In particular, whereas the theoretical model of Johnstone & Cant [1] assumes that all individuals have equivalent probabilities for reproduction, dispersal and mortality, it is beneficial to consider models in which these probabilities depend in part on an individual's relatedness to others in the group.

Whereas adult immigrants frequently show increases over time in average relatedness, these effects were not apparent in the Gambian communities, which were previously analysed by Mace & Alvergne [16]. Polygyny is the norm in this

setting, and men and their wives live in extended family compounds. For females at this study site, although there were minimal changes in average relatedness with age when examining kinship among all members of the community, their relatedness to other adults in the compound increased as their offspring reached adulthood.[6] In other words, whereas the predicted effects were not evident in our community-level analysis, age-related variation in relatedness to other compound members accords with expectations from the Johnstone & Cant [1] model.

The discrepancy from the Gambia between relatedness in compounds and communities provides a cautionary note regarding the interpretation of the results of this study. That is, reproductive conflict is expected to be acute when individuals are drawing on the same resources. For example, the killer whales studied by Croft *et al.* [13] live in pods composed of closely related individuals who share access to harvested food resources. Ethnographically, there are analogous examples of human communities that share food resources communally, including indigenous South Americans who collectively prepare and consume meals as a community [35]. More commonly, however, residents of human communities share preferentially with subsets of co-residents, including close kin [36–39]. Whereas our analysis helps to substantiate the asymmetries of relatedness that distinguish young immigrants from older affinal kin, this does not necessarily imply that these respective individuals are drawing on the same resources. In some settings, it is plausible that humans facultatively employ behavioural strategies to minimize such reproductive competition.

In communities that are characterized by discriminative sharing, research would ideally be directed at the dynamics of kinship within resource-sharing subgroups [40,41]. In most ethnographic settings, however, there are methodological challenges that hinder such analyses, particularly the task of distinguishing the boundaries of the subgroups. At most of our study sites, individuals are organized in small households, usually occupied by a single adult woman (table 1). As a result, there are minimal opportunities for reproductive competition within females in the same household. Yet, households often maintain strong cooperative ties to other households in the community. The pooling of resources among households produces the conditions in which reproduction competition could be pronounced [1]. A key challenge is that these inter-household ties are rarely evident when using standard demographic and census methods. As a possible alternative, a combination of social network surveys [17] and community detection algorithms [42,43] could potentially provide opportunities to identify the subgroups in which reproductive competition is especially relevant for life-history strategies.[7]

5. Conclusion

In this study, we have considered a cross-cultural sample of sites with heterogeneous patterns of residence and dispersal. The sample includes sites at which dispersal is biased toward females (e.g. Tenpaṭṭi) or males (e.g. Mayangna). At other sites, including several of the larger communities, the majority of residents of both sexes are natal members of the community. There are also sites, including those affected by political disruptions (e.g. Colombia), at which most adults of both sexes are immigrants. Amid this variability, several study sites feature increases in relatedness that support

prevailing conceptual models [1]. That is, immigrants of the more commonly dispersing sex tend to show increases in local relatedness as they get older. There are noteworthy exceptions to this generalization, and given the limitations of the sample, it is premature to assume that this pattern typifies the majority of human communities. Furthermore, the demographic variables in this analysis usually explain only a minority of the observed variation in relatedness, which implies opportunities for additional variables to explain heterogeneity in kin ties. Nevertheless, evidence of the predicted asymmetries in relatedness are apparent in multiple settings, reinforcing the potential value of additional empirical research on inter-generational reproductive conflict [5,46–48].

More generally, this cross-cultural study reveals surprisingly diverse relationships between age and kinship in human communities. These results reinforce perspectives on the flexible kinship that distinguishes humans from other hominoids [11]. There are pitfalls to reasoning from ethnographic analogy, but this flexibility motivates a reconsideration of human kinship and life-history strategies. Currently, research is directed toward discerning the social structure of prehistoric hominins with the assumption that distinctive life-history traits evolved partly as a consequence of this social organization [1]. From this perspective, the emergence of flexible kinship arrangements in human societies is largely an epilogue that postdates the evolution of more remarkable human traits. However, the malleability of human kinship enables diverse adaptive responses to socio-ecological challenges. It is worthwhile to consider scenarios in which life-history traits evolved concurrently with the ability to reside and cooperate with different classes of kin throughout one's lifetime.

In terms of female-biased kinship, the theme of this special issue of *Philosophical Transactions*, this cross-cultural study underscores the importance of dispersal as a determinant of kin availability. In most cases, young adult immigrants to new communities have fewer co-resident kin than their same-aged natal counterparts. Although female immigrants can maintain intermittent affiliative ties to family members from their natal communities [49], women who do not disperse can expect to be surrounded by kin more consistently during their reproductive years. Therefore, in combination with broader debates about descent rules and daughter-biased inheritance [50], heterogeneity in female philopatry has a key role to play in evolutionary accounts of human social organization. A contribution of this study is that dispersal tendencies vary not only across societies, but also within populations. Dispersal is seldom obligatory, and a mixture of natal male and female adults is observable in nearly all study communities (see also [51]). Decisions about dispersal impose trade-offs on individuals, and society-level variation in residence rules may be explained in part by unidentified individual-level predictors that capture heterogeneous effects both across and within the sexes.

Maasai (M.C.), Alakāpuram and Tenpaṭṭi (E.P.) and Tanna (E.M., A.R. and S.M.). All authors read and commented on the manuscript.

Endnotes

[1]Whereas we follow Croft et al. [13] by focusing on average relatedness as our outcome variable, we include a supplemental analysis in which we model the number of close kin in the community as the outcome variable.

[2]Alternatively, fitting the models as zero-augmented (hurdle) beta regression models provides qualitatively similar predictions.

[3]There is also moderate evidence for a positive slope for male immigrants in several additional communities, including the Mexican choyero community (site 8), the two Mosuo communities (sites 10 and 16) and Alakāpuram (site 17). However, the low number of male immigrants in these communities precludes strong conclusions about this demographic subgroup.

[4]These coefficients of relatedness assume monogamous mating.

[5]Bottom-heavy population pyramids are evident at other study sites (e.g. Maasai) without accompanying age-related increases in average relatedness, which suggests that other factors can potentially counteract the age-related accumulation of close kinship ties in expanding populations.

[6]The dataset for that paper is the same used for the Gambian sites in this paper. Unlike the 2012 paper, however, the present study depicts results separately for each community rather than modelling individuals in an aggregated dataset.

[7]In addition to the Social Relations Model that has been used by evolutionary anthropologists (e.g. [44]), there are related statistical models that permit the identification of block structures in social network data, including models that permit the inclusion of covariates (e.g. [45]).

References

1. Johnstone RA, Cant MA. 2010 The evolution of menopause in cetaceans and humans: the role of demography. Proc. R. Soc. B 277, 3765–3771. (doi:10.1098/rspb.2010.0988)

2. Williams GC. 1957 Pleiotropy, natural section, and the evolution of senescence. Evolution 11, 398–411. (doi:10.1111/evo.1957.11.issue-4)

3. Hawkes K. 2003 Grandmothers and the evolution of human longevity. Am. J. Hum. Biol. 15, 380–400. (doi:10.1002/(ISSN)1520-6300)

4. Cant MA, Johnstone RA. 2008 Reproductive conflict and the separation of reproductive generations in humans. Proc. Natl Acad. Sci. USA 105, 5332–5336. (doi:10.1073/pnas.0711911105)

5. Lahdenperä M, Gillespie DOS, Lummaa V, Russell AF. 2012 Severe intergenerational reproductive conflict and the evolution of menopause. Ecol. Lett. 15, 1283–1290. (doi:10.1111/j.1461-0248.2012.01851.x)

6. Hamilton WD. 1972 Altruism and related phenomena, mainly in social insects. Annu. Rev. Ecol. Syst. 3, 193–232. (doi:10.1146/annurev.es.03.110172.001205)

7. Clutton-Brock TH, Lukas D. 2012 The evolution of social philopatry and dispersal in female mammals. Mol. Ecol. 21, 472–492. (doi:10.1111/j.1365-294X.2011.05232.x)

8. Greenwood PJ. 1980 Mating systems, philopatry and dispersal in birds and mammals. Anim. Behav. 28, 1140–1162. (doi:10.1016/S0003-3472(80)80103-5)

9. Kirkpatrick RC. 2007 Asian colobines: diversity among leaf-eating monkeys. In Primates in perspective (eds CJ Campbell, A Fuentes, KC MacKinnon, N Panger, SK Bearder), pp. 186–200. New York, NY: Oxford University Press.

10. Bradley BJ, Doran-Sheehy DM, Vigilant L. 2007 Potential for female kin associations in wild western gorillas despite female dispersal. Proc. R. Soc. B 274, 2179–2185. (doi:10.1098/rspb.2007.0407)

11. Chapais B. 2013 Monogamy, strongly bonded groups, and the evolution of human social structure.

Evol. Anthropol. 22, 52–65. (doi:10.1002/evan.21345)

12. Silk JB, Altmann J, Alberts SC. 2006 Social relationships among adult female baboons (Papio cynocephalus) I. Variation in the strength of social bonds. Behav. Ecol. Sociobiol. 61, 183–195. (doi:10.1007/s00265-006-0249-2)

13. Croft DP et al. 2017 Reproductive conflict and the evolution of menopause in killer whales. Curr. Biol. 27, 298–304. (doi:10.1016/j.cub.2016.12.015)

14. Marlowe FW. 2004 Marital residence among foragers. Curr. Anthropol. 45, 277–284. (doi:10.1086/382256)

15. Goodenough WH. 1956 Residence rules. Southwestern J. Anthropol. 12, 22–37. (doi:10.1086/soutjanth.12.1.3628856)

16. Mace R, Alvergne A. 2012 Female reproductive competition within families in rural Gambia. Proc. R. Soc. B 279, 2219–2227. (doi:10.1098/rspb.2011.2424)

17. Koster JM. 2018 Family ties: the multilevel effects of households and kinship on the networks of individuals. R. Soc. Open Sci. 5, 172159. (doi:10.1098/rsos.172159)

18. Pemberton JM. 2008 Wild pedigrees: the way forward. Proc. R. Soc. B 275, 613–621. (doi:10.1098/rspb.2007.1531)

19. Clutton-Brock TH. 1989 Female transfer and inbreeding avoidance in social mammals. Nature 337, 70–72. (doi:10.1038/337070a0)

20. Hill K, Hurtado AM 1996 Ache life history: the ecology and demography of a foraging people. London, UK: Routledge.

21. Fenner JN. 2005 Cross-cultural estimation of the human generation interval for use in genetics-based population divergence studies. Am. J. Phys. Anthropol. 128, 415–423. (doi:10.1002/ajpa.20188)

22. Ferrari S, Cribari-Neto F. 2004 Beta regression for modelling rates and proportions. J. Appl. Stat. 31, 799–815. (doi:10.1080/0266476042000214501)

23. Stan Development Team. 2018 RStan: the R interface to Stan. R package version 2.17.3. See http://mc-stan.org.

24. McElreath R 2015 Statistical rethinking: a Bayesian course with examples in R and stan. Boca Raton, FL: CRC Press.

25. Wells JCK, Stock JT. 2007 The biology of the colonizing ape. Am. J. Phys. Anthropol. 134, 191–222. (doi:10.1002/(ISSN)1096-8644)

26. Beckerman AP, Sharp SP, Hatchwell BJ. 2011 Predation and kin-structured populations: an empirical perspective on the evolution of cooperation. Behav. Ecol. 22, 1294–1303. (doi:10.1093/beheco/arr131)

27. Sear R, Mace R. 2008 Who keeps children alive? A review of the effects of kin on child survival. Evol. Hum. Behav. 29, 1–18. (doi:10.1016/j.evolhumbehav.2007.10.001)

28. Kramer KL. 2010 Cooperative breeding and its significance to the demographic success of humans. Annu. Rev. Anthropol. 39, 417–436. (doi:10.1146/annurev.anthro.012809.105054)

29. Towner MC. 2001 Linking dispersal and resources in humans. Hum. Nat. 12, 321–349. (doi:10.1007/s12110-001-1002-1)

30. Kramer KL, Schacht R, Bell A. 2017 Adult sex ratios and partner scarcity among hunter-gatherers: implications for dispersal patterns and the evolution of human sociality. Phil. Trans. R. Soc. B 372, 20160316. (doi:10.1098/rstb.2016.0316)

31. Chapais B. 1983 Matriline membership and male rhesus reaching high ranks in natal troops. In Primate social relationships: an integrated approach (ed. RA Hinde), pp. 171–175. Sunderland, MA: Sinauer Associates.

32. Moore J. 1993 Inbreeding and outbreeding in primates: what's wrong with 'the dispersing sex'. In The natural history of inbreeding and outbreeding (ed. N Wilmsen Thornhill), pp. 392–426. Chicago, IL: University of Chicago Press.

9

royalsocietypublishing.org/journal/rstb   Phil. Trans. R. Soc. B 374, 20180069

33. Armitage KB, Van Vuren DH, Ozgul A, Oli MK. 2011 Proximate causes of natal dispersal in female yellow-bellied marmots, *Marmota flaviventris*. *Ecology* **92**, 218–227. (doi:10.1890/10-0109.1)

34. Hoogland JL. 2013 Prairie dogs disperse when all close kin have disappeared. *Science* **339**, 1205–1207. (doi:10.1126/science.1231689)

35. Beckerman S, Valentine P, Eller E. 2002 Conservation and native Amazonians: why some do and some don't. *Antropologica* **96**, 31–51.

36. Gurven M. 2004 To give and to give not: the behavioral ecology of human food transfers. *Behav. Brain Sci.* **27**, 543–559. (doi:10.1017/S0140525X04000123)

37. Allen-Arave W, Gurven M, Hill K. 2008 Reciprocal altruism, rather than kin selection, maintains nepotistic food transfers on an Ache reservation. *Evol. Hum. Behav.* **29**, 305–318. (doi:10.1016/j.evolhumbehav.2008.03.002)

38. Nolin D. 2011 Kin preference and partner choice. *Hum. Nat.* **22**, 156–176. (doi:10.1007/s12110-011-9113-9)

39. Koster J, Leckie G. 2014 Food sharing networks in lowland Nicaragua: an application of the social relations model to count data. *Soc. Netw.* **38**, 100–110. (doi:10.1016/j.socnet.2014.02.002)

40. Frank SA 1998 *Foundations of social evolution*. Princeton, NJ: Princeton University Press.

41. West SA, Pen I, Griffin AS. 2002 Cooperation and competition between relatives. *Science* **296**, 72–75. (doi:10.1126/science.1065507)

42. Girven M, Newman MEJ. 2002 Community structure in social and biological networks. *Proc. Natl Acad. Sci. USA* **99**, 7821–7826. (doi:10.1073/pnas.122653799)

43. Aven BL. 2015 The paradox of corrupt networks: an analysis of organizational crime at Enron. *Organiz. Sci.* **26**, 980–996. (doi:10.1287/orsc.2015.0983)

44. Koster J, Aven B. 2018 The effects of individual status and group performance on network ties among teammates in the National Basketball Association. *PLoS ONE* **13**, e0196013. (doi:10.1371/journal.pone.0196013)

45. Sweet TM. 2015 Incorporating covariates into stochastic blockmodels. *J. Educat. Behav. Statist.* **40**, 635–664. (doi:10.3102/1076998615606110)

46. Ji T, Wu J, He Q, Xu J, Mace R, Tao Y. 2013 Reproductive competition between females in the matrilineal Mosuo of southwestern China. *Phil. Trans. R. Soc. B* **368**, 20130081. (doi:10.1098/rstb.2013.0081)

47. Snopkowski K, Moya C, Sear R. 2014 A test of the intergenerational conflict model in Indonesia shows no evidence of earlier menopause in female-dispersing groups. *Proc. R. Soc. B* **281**, 20140580. (doi:10.1098/rspb.2014.0580)

48. Pettay JE, Lahdenperä M, Rotkirch A, Lummaa V. 2016 Costly reproductive competition between co-resident females in humans. *Behav. Ecol.* **27**, 1601–1608. (doi:10.1093/beheco/arw088)

49. Scelza BA. 2011 Female mobility and postmarital kin access in a patrilocal society. *Hum. Nat.* **22**, 377–393. (doi:10.1007/s12110-011-9125-5)

50. Mattison SM. 2011 Evolutionary contributions to solving the 'Matrilineal Puzzle'. *Hum. Nat.* **22**, 64–88. (doi:10.1007/s12110-011-9107-7)

51. Walker RS *et al.* 2012 Living with kin in lowland horticultural societies. *Curr. Anthropol.* **54**, 96–103. (doi:10.1086/668867)

Kinship Ties Across the Lifespan in Human Communities
Supplemental Material

Koster et al.

Introduction

This supplemental file contains four sections: (1) Descriptions of the study sites, (2) a supplemental figure depicting model predictions on a dataset that includes all community residents, not just adults, (3) the results of a multilevel analysis of the aggregated, cross-cultural data, (4) the results of site-specific models in which *sex* is deemphasized as a predictor variable, and (5) the results of analyses in which we model the number of close kin who co-reside with individuals in the communities, which provides an alternative to the outcome variable of average relatedness that was used in the main analysis.

Site descriptions

1) Savanna Pumé

The Savanna Pumé are mobile hunter-gatherers indigenous to the *llanos* (savannas) of west-central Venezuela. At the last complete census, the Savanna Pumé numbered 670, dispersed in 24 bands over a 2800 km^2 area. Because of the region's political instability, their geographic isolation and a poor terrestrial environment, the Savanna Pumé are largely buffered from outside encroachment and continue to live a hunting and gathering way of life. The bands that are part of this study have lived in their current foraging area since the mid 1960's, having migrated from foraging communities 50 km south along the Cinaruco River. Kin relations and marriage partner exchange are maintained between these regions, and this fission settlement pattern is an ancestral aspect of their long-term mobility. The Savanna Pumé are related to the River Pumé, their horticultural neighbors, with whom they exchange some goods, and infrequently marriage partners. The census for this study was collected in 2007 as part of a 20-year longitudinal demographic and life history project.

   The Savanna Pumé move 5-6 times a year in response to changes in rainfall and the water table. During the six-month dry season, food is relatively abundant and subsistence centers on aquatic resources and wild fruit. When the *llanos* flood during the wet season, fish are difficult to locate and the subsistence base shifts to terrestrial game and tubers. Males, both adults and children, almost exclusively fish and hunt, while women and girls gather tubers and do most of the food processing. Both males and females collect wild fruit. Male-foraged and female-foraged foods are both critical to the diet and are widely shared within and across families. Women and children provide most of the childcare, with males providing about 8%. The Savanna Pumé have no schools, access to health care, or market foods.

   Pumé kinship organization is primarily bilateral. Marriages tend to be endogamous, with 66% of first marriages and 57% of second marriages occurring among individuals of the same community. Most individuals maintain life-long relationships with their natal bands and multilocality is common. The Savanna Pumé use kin terms, rather than names, in speaking about and identifying each other. While about 30% of women and men are polygynously married at some point during their lives, most marriages are serially monogamous; 20% of adults remarry due to divorce (about 10%) and spousal death (10%). Childcare is fluid. Of the care that in infant receives, 65% comes from someone other than the mother. Allocaretakers include close kin, more distant bilateral kin, and nonkin.

   Savanna Pumé females marry on average at age 15.1 (SD ±2.5; n=59) and males at age 18.0 (SD ±4.3; n=51). Although first marriages are often arranged, young people are not obliged to accept these matches, and have autonomy about when and whom they marry. A couple is recognized as

married if they engage in conjugal relations, whereupon they cohabit. Consequently, birth occurs within the context of marriage and co-residence. Divorce may be instigated by either spouse. Marriage to non-Pumé has not been documented. Mothers who survive their reproductive careers have on average 7.0 ±1.29 live births. However in this high pathogenic and seasonally food-limited environment, 35% of children born do not survive infancy, and 45% do not survive to reproductive age. No evidence exists for sex-biased investment in children (mortality; treatment, work load).

2) Miskito

The Miskito community is located in Nicaragua's Bosawas Biosphere Reserve, part of Central America's largest rain forest. The community was settled prior to 1960, vacated during the Contra War in the 1980s, and occupied again since the early 1990s. Data for this study were collected in 2013, building on earlier demographic and genealogical research conducted with community members. In terms of subsistence, the community relies primarily on horticulture with supplements from hunting, fishing, and animal husbandry. Gold panning and non-local wage labor are the leading sources of monetary income, which is used to purchase mercantile products. There is a pronounced sexual division of labor, and men are responsible for most of the agricultural work whereas women assume most domestic tasks. Both sexes engage in fishing and gold panning, sometimes cooperatively with spouses or other family members.

As with the Mayangna, descent is traced bilaterally, and Eskimo kinship terms have largely supplanted a more complex indigenous kinship terminology. Marriages to cousin are largely proscribed. If prospective mates are not present locally, males typically travel to other communities, often staying with extended kin to facilitate their search. Once married, young couples typically reside with the woman's parents for multiple years, often until at least two children have been born and the couple decides to build a new house nearby. For older women, including formerly divorced women, there tends to be more flexibility in their residence decisions, and relocating to the husband's natal community is not uncommon. In general, couples benefit from the alloparental investment of extended families, who provide benefits such as childcare and cooperative labor. At the time of data collection, fertility was high, with total fertility rates exceeding 8 births per woman. There is little evidence for sex-biased investment in offspring.

3) Mayangna

The Mayangna community is located in Nicaragua's Bosawas Biosphere Reserve, part of Central America's largest rain forest. The community was settled prior to 1960, vacated during the Contra War in the 1980s, and occupied again since the early 1990s. Data for this study were collected in 2016 as part of a longitudinal study of subsistence and social support networks. Subsistence strategies the community revolve around horticulture with supplements from hunting, fishing, and animal husbandry. Gold panning and non-local wage labor are the leading sources of monetary income, which is used to purchase mercantile products. A minority of residents maintain salaried positions as government-funded schoolteachers. There is a pronounced sexual division of labor, and men are responsible for most of the agricultural work whereas women assume most domestic tasks. Both sexes engage in fishing and gold panning, sometimes cooperatively with spouses or other family members.

As with the Miskito, descent is traced bilaterally, and Eskimo kinship terms have largely supplanted a more complex indigenous kinship terminology. Marriages to cousin are largely proscribed. If prospective mates are not present locally, males typically travel to other communities, often staying with extended kin to facilitate their search. Once married, young couples typically reside with the woman's parents for multiple years, often until at least two children have been born and the couple decides to build a new house nearby. For older women, including formerly divorced women, there tends to be more flexibility in their residence decisions, and relocating to the husband's natal community is not uncommon. In general, couples benefit from the alloparental investment of extended families, who provide benefits such as childcare and cooperative labor. At the time of data collection, fertility was high, but hormonal contraception was becoming available via government-funded clinics.

4) Coastal Afrocolombians

This community is located on the Pacific coast of Colombia. This community, like many other communities in the region, has been affected by Colombia's internal conflicts, and violence from guerilla and paramilitary groups—especially in the late 1990s and early 2000s. Many current residents are considered internally displaced persons within Colombia, having settled here after being forced from their natal communities. Data for this study were collected in the winter of 2016, through structured interviews. In terms of subsistence, the community relies primarily on a mixture of fishing and local wage labor. Hunting, horticulture, and animal husbandry are also practiced. There is a general sexual division of labor, where men engage in most of the fishing and women assume most domestic tasks, but exceptions are not infrequent. Relationships are formed based on personal preferences. Once married, couples typically form their own residential units near kin. Marriages are not generally stable for long periods of time, with adults over age 45 having a mean of 2.1 total marriages. In general, couples benefit from the alloparental investment of extended families, who provide benefits such as childcare and material support. At the time of data collection, fertility was high, with mean fertility exceeding 8.5 births per woman, for those women age 50 or older.

5) Inland Afrocolombians

This Afrocolombian community is located in the rainforests of western Colombia. This community, like many other communities in the region, has been affected by Colombia's internal conflicts, and violence from guerilla and paramilitary groups—especially in the late 1990s and early 2000s. Many current residents are considered internally displaced persons within Colombia, having settled here after being forced from their natal communities. Others, who were once residents of this community, were displaced during periods of local unrest to other regions inside of Colombia. Data for this study were collected in the spring of 2017, through structured interviews. In terms of subsistence, the community relies primarily on a mixture of horticulture and local wage labor (most frequently as laborers on road construction projects). Hunting, fishing, and animal husbandry are also practiced, as is small-scale gold panning. There is a general sexual division of labor, where men engage in most of the horticultural work, and women assume most domestic tasks and do most of the gold panning, but exceptions are not infrequent. Once married, couples typically form their own residential units near kin. Marriages are not generally stable for long periods of time, with adults over age 45 having a mean of 2.4 total marriages—though some stable lifelong partnerships do occur. In general, couples benefit from the alloparental investment of extended families, who provide benefits such as childcare and material support. At the time of data collection, fertility was high, with mean fertility exceeding 7 births per woman, for those women age 50 or older.

6) Dominica

The study community is located on the remote windward coast of Dominica. The community population includes about 110 households with 400 to 600 residents depending on the time of year and vagaries of overseas migration from year to year. Inhabitants are a mix of African, Native American, and European descent. Data for this study were collected between 1993 and 2010 and supplemented with parish records going back to the 19th Century, and preliminary genealogies collected by Mark Flinn in 1988. Livelihoods are varied including a mixture of subsistence gardening, fishing, commercial bay oil production, wage labor, and small-scale businesses such as local dry goods, and rum shops. There are pronounced gender cultures with gender-specific models of behavior in various domains; however, the division of labor is not strict, and it is mostly due to requirements for upper body strength for certain tasks. Descent is traced through patrilineages. However, ego-centric kindreds are also important, and kin related through unnamed matrilineages cooperate in several spheres. Marriage is an institution in decline. Most conjugal unions consist of a common-law couple. Conjugal unions are generally fluid with "visiting" relationships commonplace. After the birth of a first child, however, a mother and father may live together for decades in a stable union. Conjugal families tend to reside neolocally or patrilocally, but many households are best described as matrifocal in which none of the children has a co-resident father. As of the year 2004 about 30% of mothers were in long-term conjugal unions. Alloparenting is extensive in matrifocal and conjugal households. Mean surviving offspring for people over 50 in 2004 was 5.5

(SD=3.0) offspring for women, and 4.6 (SD=3.5) for men. Many women have children with mates from outside the community. In recent years hormonal contraception has been common.

7) Inland Emberá

This community is located in the rainforests of western Colombia and has been affected by Colombia's internal conflicts. This small community is composed of several families affected by displacement. Individuals in this community have used the group terms *Emberá Chamí* and *Emberá Katío* when self identifying. Data for this study were collected in spring 2017, through structured interviews. In terms of subsistence, the community relies primarily on a mixture of horticulture, wage labor (most frequently as laborers on road construction projects), and artisinal crafting (production of glass-bead necklaces). Hunting, fishing, and animal husbandry are also practiced. There is a general sexual division of labor, where men engage in most of the wage labor, and women assume most domestic tasks and produce most of the necklaces. Both men and women take part in horticultural activities. Once married, couples typically form their own residential units. Marriages are generally stable for long periods of time, with married adults over age 30 having a mean of 1 total marriages. In general, couples benefit from the alloparental investment of extended families, who provide benefits such as childcare and material support. At the time of data collection, fertility was high, with mean fertility exceeding 7.5 births per woman, for those women age 30 or older.

8) *Los Choyeros* of Mexico

The *Choyero* community is located in a southern portion of the Sierra de La Giganta mountain range of Baja California Sur, Mexico. The population is descended from Euro-American colonists who first settled the region alongside Jesuit missionaries in 1741 AD followed by two additional waves of colonization following the expulsion of the Jesuits (1768 AD) and Mexican independence (1821 AD). Data for this study were collected in 2017, building on earlier genealogical research conducted with community members in 2015. *Choyero* subsistence is primarily based on goat and cattle husbandry, which is used for meat and cheese production for personal and local consumption, as well as for sale on regional commercial markets. In addition to the sale of animals and their byproducts, non-local wage labor has become a secondary source of income for most families. Households also supplement their diet through a governmental sponsored food program (i.e. CONASUPO) and via goods purchased in regional markets (e.g., Las Pocitas, Ciudad Constitución, and La Paz). There is a pronounced sexual division of labor, with men responsible for animal husbandry and women responsible for domestic tasks and cheese production. Both sexes engage in artisanal craft production; however, the types of crafts produced differ by sex. Males engage in leather tanning, metal smithing, and heritage crop production, while women engage in basketry and crochet.

Descent is traced bilaterally and Eskimo kinship terminology predominates. While cousin marriage is not proscribed, only a small percentage of the population engages in it. If prospective mates are not present locally, males and females either wait for a partner to reach marriageable age locally or they travel to regional festivals and weddings to find a partner. Males also report they search for mates in distant communities when they travel on horseback looking for their livestock. Post-marital residence is flexible and young couples may reside with the groom or bride's family, near the groom or bride's family, or in a separate location altogether. However, historically it was common for young couples to reside with the groom's family following marriage and currently, many males state a preference for this outcome. Although there is a strong independent ethos centered at the ranch-level, extended family members and neighbors, who are often kin, provide childcare and cooperative labor. Fertility has been on the decline for several decades and there is little evidence for sex-biased investment in offspring.

9) The Gambia, 2

The data from this rural community in Gambia come from a longitudinal dataset collected by the UK Medical Research Council, initiated by the late Sir Ian McGregor in 1949. He studied four villages in total, collecting demographic and some anthropometric and health data on all inhabitants for nearly 25 years. Until 1975, this population lived in a largely 'natural fertility' and 'natural mortality' environment, albeit with some medical care available on occasions when McGregor and others were residing in the village. Deaths due to malaria and other infections

were commonplace, with only 45% of children surviving to their fifth birthday. After 1975, a permanent medical centre opened in one of the villages and mortality declined markedly. Modern contraception was also introduced, and has gradually been adopted. The data in this compilation focus primarily on the period 1950-1975, when mortality was still high. Compounds were areas where people lived together in a cluster of households. Compounds often comprise a patrilineal group (fathers, brothers and sons and their spouses and children), although more distant relatives or unrelated families may reside in the same compound. The society is polygynous and co-wives usually inhabit the same compound. Divorce and remarriage do occur, in which case women move compounds (but often leave weaned children in their natal compound with their patrilineal kin). However compound residents can include more distantly related or unrelated families. Because these compounds are matters of historical record, we do not know exactly how individuals shared work on fields or how they shared food within these compounds or who owned what land. Women often remained in their husbands' households for life, but occasionally started to reproduce with another man in another compound even if their first husband was alive, at which point we assumed divorce and remarriage and relocation to the new husband's compound had occurred. Women do not remain single for long in this society, and on widowhood remarry quickly, often marrying their late husband's brother through the levirate system. *Note that this paper includes data from two of the communities studied by McGregor, and the same description is used for both.*

10) Matrilineal Mosuo

The Mosuo, numbering approximately 40,000, live in the Hengduan mountains in the foothills of the Himalayas in Southwest on the border of Sichuan and Yunnan Provinces. Ethnographic accounts suggest that they migrated to this area from northern China before the thirteenth century. There are approximately 18,000 Mosuo residing in the Yongning Basin in Yunnan province where we performed our study. Normatively, the Yongning Mosuo are matrilineal, conferring descent and inheritance to daughters and their children, and natalocal. They are known for their lack of institutionalized marriages, engaging instead in "walking marriage", whereby women engage in non-exclusive, impermanent romantic partnerships with men from other clans. Such arrangements are still common, but bilateral families and institutional marriages have become increasingly popular following the rapid development of ethnic tourism beginning in the late 20th century.

The Yongning Mosuo traditionally rely on agriculture and animal husbandry, including a heavy reliance on domesticated pigs, cattle, and water buffalo, for subsistence. A relative abundance of farmlands (when compared with neighboring areas) allows for rice cultivation, but yields are not high due to the high elevation at which the Mosuo reside (upwards of 2,650 meters). There is a strong sexual division of labor in the Yongning Mosuo. Specifically, women engage in most of the day-to-day tasks associated with planting and harvesting crops, while men are involved in less frequent bouts of heavy labor associated with home construction and agricultural activities. Some families supplement household income by working in tourist towns nearby; some work as drivers and tour guides while some engage in day labor in construction sites. Data for this study were collected in 2017 and 2018.

11) Maya

Maya subsistence farmers live in the tropical forests of the Puuc region of the Yucatan Peninsula, Mexico. The village was established in its current location about 100 years ago when dispersed local hamlets aggregated at two abandoned colonial wells following the Caste Wars. Most villagers are descendants from these few founder families. The census for this study was collected in 2017, as part of an ongoing longitudinal demographic and life history project. When first documented in the early 1990s, the population was 300, and today is about 550. The majority of the Maya diet comes from of maize, and to a lesser extent from beans, squash, domesticated and hunted animals. Few market foods are consumed, those that are largely in the form of soda. Electricity, running water, a rudimentary health clinic, primary schools, mechanized farming and cash cropping have been introduced over the past decade due to the recent road construction linking this isolated community to the region. In 2017 most households made their living from farming. Wage work is available only outside the community, and few household heads (15%) are full time wage laborers. Recent regional market access has been accompanied by a change in the division of labor. While adult nonnursing women and children used to spend about 10% to 15% of their time, respectively, in agricultural labor, women in particular spend much less time in the fields or forest following the

introduction of mechanized farming. While mothers and children provide most of the childcare, because agricultural labor is more expedient, men now spend more time at home caring for their children and helping with domestic tasks. Both unmarried men and women engage in unskilled wage labor. However, at marriage, women quit these jobs, while men do not necessarily. Most of the few skilled wage laborers live outside the village.

The Maya trace descent bilaterally, and maintain close relations with their natal families throughout their lives. At birth, children are given two traditional Maya surnames, the first is their mother's paternal last name, and the second their father's paternal last name. Neither males nor females change their names when they marry. The *ejido* land tenure system, which was instituted following the Mexican Revolution, proscribes that agricultural land be communally held, and is not inheritable. Because there is also little heritable material wealth, inheritance rules are not well established. Upon marriage, young couples frequently reside with the husband's family for some years before they cut their own fields, have the resources to build and maintain an independent household. However, there are many exceptions to this pattern of transient patrilocality. Most villagers marry endogamously, though in-marriage and out-marriage is increasing. The Maya are monogamous, with no incidence of divorce or unwed motherhood recorded in the 100 years of reproductive histories. This, however, is likely to change with market integration. Most childcare and domestic work occur within biological families (mother, father, children), although agricultural profits, labor and other economic gains are shared across extended families in 33% of households (extended families are usually composed of a biological family and an elderly parent, or young recently married sons). At the community level, mean completed fertility slightly declined over the past 20 years from 7.5 to 6.1 children. However, within-population variance has significantly increased. There is no evidence (birth weight, education, work load, or survivorship) for sex-biased investment in offspring.

12) Lamalera

Lamalera is a fishing and sea hunting community located on the south coast of the island of Lembata in southeast Indonesia. In 2006 (the year these data were collected) the resident population numbered 1,227 people in 317 households (excluding two historically separate agricultural hamlets now under Lamaleran village administration). The village is famous for being one of the last remaining traditional whaling societies in tropical waters. Villagers grow little food of their own; instead women trade marine resources for agricultural produce from the shifting cultivators of the interior. Patrilineal kinship (with Omaha terminology) is the key organizing principle for boat-owning corporate groups and hunting crew formation. Marriage was traditionally exogamous by lineage and endogamous within the village, with clans related in permanent wife-giving and wife-taking relationships to each other in an asymmetric marriage alliance system. Since the mid-20th Century, this system seems to have broken down under the influence of the Catholic Church, though marriage still defines relationships of social dominance and deference between clans and individuals. Post-marital residence was traditionally virilocal though the Church successfully promoted a shift to neolocal residence beginning in the 1930s. When marriages take place between communities it is nearly always the woman that moves to her husband's village.

Lamalera was the site of the first Catholic mission on Lembata, and consequently the site of the first schools. At the time of the study, the village was the site of two elementary schools, and the only junior high school on the south coast of the island. The latter attracted a handful of students from other villages, who stayed either in a small dormitory or as borders with local families. The best students may go on to high school in the main town of Lewoleba on the north side of the island. Both junior high and high school provide opportunities for young people to meet potential spouses from other communities. Trade trips accompanying mothers into the interior or to the weekly market town may provide additional opportunities. The schools themselves are staffed in part by outsiders from other communities, who are sometimes already married with families of their own. Outside-born adult women tend to have married into the village and permanently reside there. Outside-born adult men tend to be either temporary residents working as teachers, or men born outside the village to Lamaleran parents who later returned.

13) Coastal Emberá

This community is located on the Pacific coast of Colombia. It has been heavily affected by Colombia's internal conflicts and displacement—with a large fraction of this population being

internally displaced residents, forced from their natal communities by violence. Individuals in this community primarily use the group term *Emberá Chamí* when self identifying. Data for this study were collected in winter 2016, through structured interviews. In terms of subsistence, the community relies primarily on a mixture of horticulture and wage labor. Hunting, fishing, and animal husbandry are also practiced. There is a general sexual division of labor, where men engage in most of the wage labor, and women assume most domestic tasks. Both men and women take part in horticultural activities. Once married, couples typically form their own residential units. Marriages are generally stable for long periods of time, with married adults over age 30 having a mean of 1.4 total marriages. In general, couples benefit from the alloparental investment of extended families, who provide benefits such as childcare and material support. At the time of data collection, fertility was high, with mean fertility exceeding 8 births per woman, for those women age 30 or older.

14) Maasai

The Maasai community is located in the Serengeti ecosystem within Simanjiro District in northern Tanzania. The community was recognized as a sub-village in the 1990's although the area is a traditional grazing area for Maasai herds. Data from this study were collected in 2017 as part of a cross-cultural study of social networks and wealth. Subsistence patterns within the community remain centered around maintaining a pastoralist livelihood although the community has expanded reliance on crops, particularly maize and beans. A small number of men also participate in the Tanzanite trade and non-local wage labor, mostly as security guards for banks and safari companies. The division of labor is pronounced with men tending livestock and participating in business affairs while women perform most domestic tasks although women are increasingly working in crop fields. Descent is traced patrilineally with traditional kinship terms generally similar to the Omaha system. Polygyny is still commonly practiced with marriages structured by patrilocal residence and clan exogamy. Once married, young couples usually reside in bomas with brothers of the husband. Young divorced women usually return to the boma of their father and older divorced women go to their brother's boma. Widowed women often stay at the boma although remarriage is uncommon in older women. Alloparental investment is common in childcare and cooperative labor, largely provided by co-wives and wives of husband's brothers in the boma. At time of collection, fertility rates among Maasai women remained high with total fertility rates around 6 per woman. There is some evidence of sex-biased investment in offspring with males completing primary and secondary schooling at a considerably higher rate although sex ratios favor females.

Broadly speaking, Maasai pastoralist communities are more recently established compared to neighboring farming populations given their history of transhumance. Consequently, it is common for male heads of Maasai bomas to be born outside of the community where they currently reside. Decisions to settle on a particular community depended upon several factors, including availability of forage and water, family ties, and more recently, access to villages. In addition, many Maasai communities were established relatively more recently due to pressures from Tanzanian government policies that forbid inhabitation/use of national parks (e.g., Serengeti National Park), which resulted in the relocation of Maasai across vast regions of northern Tanzania. Several families in the current community were those pressured to relocate, either directly or indirectly from population pressure in other regions. Furthermore, the area does not contain large amounts of foraging areas for livestock so the area has attracted households willing to invest more in agriculture. The decision for a household to focus on agriculture meant that some bomas became separated with other boma members and related bomas moving/staying in areas with better forage and water.

15) The Gambia, 1

The data from this rural community in Gambia come from a longitudinal dataset collected by the UK Medical Research Council, initiated by the late Sir Ian McGregor in 1949. He studied four villages in total, collecting demographic and some anthropometric and health data on all inhabitants for nearly 25 years. Until 1975, this population lived in a largely 'natural fertility' and 'natural mortality' environment, albeit with some medical care available on occasions when McGregor and others were residing in the village. Deaths due to malaria and other infections were commonplace, with only 45% of children surviving to their fifth birthday. After 1975, a permanent medical centre opened in one of the villages and mortality declined markedly. Modern contraception was also introduced, and has gradually been adopted. The data in this compilation

focus primarily on the period 1950-1975, when mortality was still high. Compounds were areas where people lived together in a cluster of households. Compounds often comprise a patrilineal group (fathers, brothers and sons and their spouses and children), although more distant relatives or unrelated families may reside in the same compound. The society is polygynous and co-wives usually inhabit the same compound. Divorce and remarriage do occur, in which case women move compounds (but often leave weaned children in their natal compound with their patrilineal kin). However compound residents can include more distantly related or unrelated families. Because these compounds are matters of historical record, we do not know exactly how individuals shared work on fields or how they shared food within these compounds or who owned what land. Women often remained in their husbands' households for life, but occasionally started to reproduce with another man in another compound even if their first husband was alive, at which point we assumed divorce and remarriage and relocation to the new husband's compound had occurred. Women do not remain single for long in this society, and on widowhood remarry quickly, often marrying their late husband's brother through the levirate system. *Note that this paper includes data from two of the communities studied by McGregor, and the same description is used for both.*

16) Patrilineal Mosuo

Approximately 4,000 Mosuo live in the area surrounding Labai Township, a mountainous region at slightly lower elevation, but with far steeper terrain, to the west of the Yongning basin. The Labai Mosuo are said to have migrated from Yongning in search for gold by the Jinsha River. Unlike their Yongning counterparts, they practice patrilineal descent, patrilocal post-marital residence, and ultimogeniture. Institutional marriage is the norm and cross-cousin marriage is not infrequent. Some Mosuo reason that the rugged mountainous landscape and distance between villages have prevented frequent spousal visitations and hence deterred natalocal residential arrangements that correspond to walking marriage.

Population and farmland in Labai (amounting to less than 5000 acres in total) are sparsely distributed along the steep mountainous terrain. The Labai Mosuo keep pigs and farm cash crops such as walnuts, peppercorns, and tobacco. Nevertheless, due to the limited size of their farms, many import rice and animal fodder from Yongning. Labai was accessible only on horseback before a road was built in 2011 and its infrastructure (including availability of private toilets and electricity) has only developed significantly in the last several years. The Mosuo population in Labai declined from 4,319 in 2006 to 4,199 in 2015 (official statistics), due in part to out-migration in search for economic opportunities. Data for this study were collected primarily in 2018, with supplementary information drawn from a demographic survey conducted in 2017.

17) Aḻakāpuram

The village of Aḻakāpuram (a pseudonym) is located in the Indian state of Tamil Nadu, near the Vaigai River. The village is many generations old, well beyond the memory of residents, and occupied continuously. Data for this study were primarily collected as part of a demographic household census between 2011 and 2013, and further updated in 2017. Inclusion in the dataset used here reflects residence in 2017. Residents include a mix of different religious (Hindu, Catholic, and Protestant) and caste groups (primarily Scheduled Castes (esp. Paḷḷar and Paṟaiyar) and some Backward Castes (esp. Yātavar and Tēvar)). Two hamlets are at slight remove from the main village, with one occupied exclusively by Hindu Yātavars, and the other primarily by Protestant (Church of South India) Paṟaiyars.

Most residents engage in a combination of agriculture and wage labor. Most people grow rice paddy, and so are reliant on irrigation waters being released upstream (which does not materialize in some years). A few wealthier families have bore wells and grow other crops such as sugar cane, bananas, cotton, and vegetables. Wage labor work includes construction, wood collection (for coal factories), and participation in a government program that guarantees 100 days of work to each household. In most households, all adults work. Wages for women (even when doing comparable work) are often slightly lower than what men earn. Government programs provide many basic necessities and services (basic foodstuffs, medical care, free lunches for students, etc.).

Inheritance of most property and land is patrilineal, though daughters receive substantial transfers from their parents at marriage. Marriages are almost always arranged by parents and are within the same caste group. Close kin marriages (especially to cross cousins (mother's brother's children or father's sister's children) or maternal uncles) are traditionally preferred. Increasingly,

however, "stranger" marriages (still arranged, with connections typically made through kin and close acquaintances) are becoming common. Residence is generally patrilocal, with new married couples now typically establishing a new household near the husband's parents (co-residence does sometimes occur, though resources are not typically pooled). A significant number of married women end up residing in their natal village, however; this is usually because they have married locally, or because of employment (either the wife is living in her natal village while her husband works elsewhere (often abroad), or both are residing there because of better proximity to work opportunities). Divorce does occur, and though remarriage is seen as being unlikely, it does happen. The village has undergone the demographic transition, with women now typically having two children (assisted by active government family planning policies).

18) Teṉpaṭṭi

The village of "Teṉpaṭṭi" (a pseudonym) neighbors "Alakāpuram" in the Indian state of Tamil Nadu, near the Vaigai River. The village is many generations old, well beyond the memory of residents, and occupied continuously. Data for this study were primarily collected as part of a demographic household census between 2011 and 2013, and further updated in 2017. Inclusion in the dataset used here reflects residence in 2017. Residents include a mix of different religious (Hindu and Catholic) and caste groups (primarily Backward Castes (esp. Yātavar, Tēvar, and Acāri) and some Scheduled Castes (esp. Paḷḷar and Aruntatiyar)).

As in "Alakāpura," most residents engage in a combination of agriculture and wage labor. Most people grow rice paddy, and so are reliant on irrigation waters being released upstream (which does not materialize in some years). A few wealthier families have bore wells and grow other crops such as sugar cane, bananas, cotton, and vegetables. Wage labor work includes construction, wood collection (for coal factories), and participation in a government program that guarantees 100 days of work to each household. In most households, all adults work. Wages for women (even when doing comparable work) are often slightly lower than what men earn. Government programs provide many basic necessities and services (basic foodstuffs, medical care, free lunches for students, etc.).

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19) Tanna

Tanna is an island in the Melanesian nation of Vanuatu. Tannese data were collected from Ikakahak, the largest village in the Green Point region, located in the southwest of the island, during June and July of 2018. Green Point was settled prior to historical records, but pieces of oral histories discussed during data collection indicate that it was settled some time in the 1700s-1800s by migrants from further north. Tanna itself was first settled circa 420 B.C.E. Green Point has played an important role in Tannese history, because it was there that John Frum appeared and started his traditionalist movement; local elders say that the region was named "Green Point" by John Frum himself.

Subsistence is based primarily on horticulture in nearby gardens, supplemented by occasional meat from domesticates and foraged meat from wild birds and shellfish. The primary subsistence crops are manioc, yam, and taro root, with manioc predominating because it can be grown year-round. Since the introduction of imported goods, rice has also become a staple of the local diet. Male heads of house are typically responsible for tending gardens, often in cooperation with their

patrilineal male relatives. It is common for women to assist their husbands in agricultural labor, and women with dead or absent husbands maintain their own gardens.

Residence is virilocal and descent and inheritance are patrilineal, though there is significant flexibility in kinship, including via adopting children of patrikin. It is nonetheless common for women to maintain cooperative relationships with their natal kin. A historical preference for cross-cousin marriage has recently been replaced by love marriage. Polygyny is allowed, but the vast majority of marriages of marriages are monogamous, and all marriages in the sampled community are monogamous. Affairs and divorce are common, and when a relationship dissolves the children usually go with the mother, who returns to live with her parents or brothers.
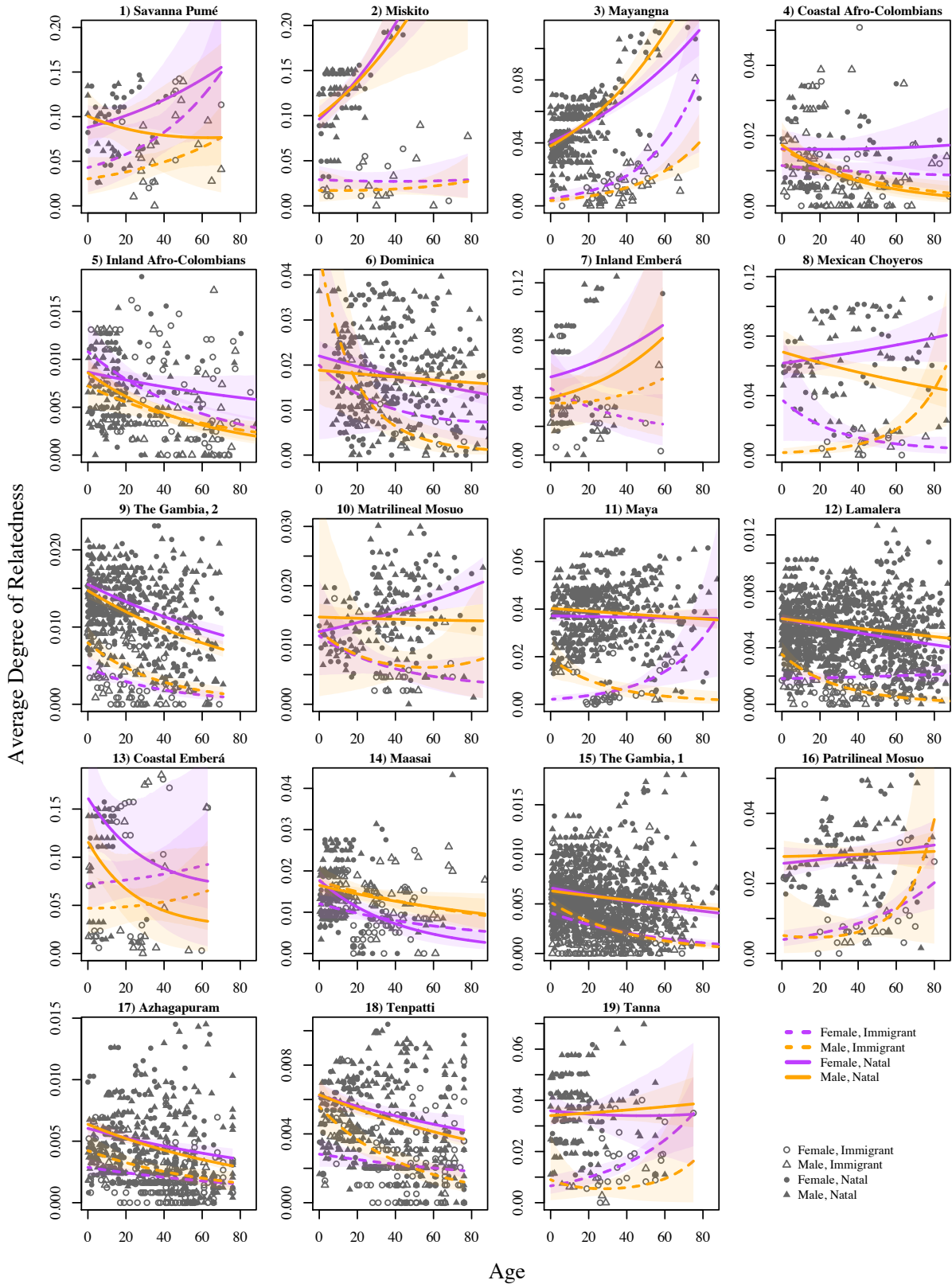
Figure S1: Model predictions for adults' relatedness to other community members in the study communities, including juveniles. All predictions are based on beta regression models with three-way interaction terms of age, sex, and natality (versus immigrants). Shaded intervals depict 89% confidence intervals around model predictions. Note that the scale of the vertical axis changes for each community. In the plot, sites are ordered in row-wise fashion according to the ratio of adult female natality to adult male natality (the quotient of the respective quantities in Table 1).

Table S1: Coefficients for the beta regression models that are depicted in Figure 2 of the main text. The outcome variable is the average relatedness of individual i to other adults in the community. The quantities depicted in the table are the posterior means, with posterior standard deviations in parentheses. Note that asterisks denote interaction terms of the corresponding main effects.

Site	Intercept	Age	Male	Natal	Age * Male	Age * Natal	Male * Natal	Age * Male * Natal
Savanna Pumé	-3.042 (0.321)	0.051 (0.018)	-0.044 (0.363)	0.942 (0.544)	-0.032 (0.022)	-0.049 (0.034)	-0.097 (1.142)	0.055 (0.086)
Miskito	-4.577 (0.458)	0.009 (0.026)	-0.19 (0.491)	2.819 (0.508)	0.022 (0.033)	0.012 (0.033)	0.224 (0.719)	0.005 (0.074)
Mayangna	-4.666 (0.243)	0.079 (0.022)	-0.49 (0.28)	2.101 (0.247)	-0.019 (0.024)	-0.064 (0.023)	0.657 (0.299)	0.028 (0.025)
Coastal Afro-Colombians	-4.738 (0.214)	0.004 (0.01)	-0.287 (0.265)	0.289 (0.252)	0.014 (0.015)	0.016 (0.014)	0.02 (0.374)	-0.064 (0.028)
Inland Afro-Colombians	-5.417 (0.178)	0.001 (0.007)	-0.378 (0.268)	0.302 (0.207)	0.008 (0.013)	-0.001 (0.012)	-0.153 (0.354)	-0.013 (0.019)
Dominica	-5.1 (0.395)	0.008 (0.019)	0.053 (0.573)	1.069 (0.398)	-0.052 (0.033)	-0.014 (0.02)	0.031 (0.578)	0.054 (0.034)
Inland Emberá	-3.515 (0.595)	0.008 (0.035)	0.393 (0.76)	0.869 (0.767)	0.044 (0.057)	0.009 (0.051)	-0.817 (1.421)	-0.076 (0.108)
Mexican Choyeros	-4.955 (0.34)	0.021 (0.021)	-0.093 (0.537)	2.167 (0.355)	0.026 (0.028)	-0.008 (0.021)	0.122 (0.562)	-0.043 (0.029)
The Gambia, 2	-6.296 (0.184)	0 (0.012)	0.255 (0.306)	1.737 (0.188)	-0.007 (0.019)	-0.013 (0.013)	-0.49 (0.319)	0.013 (0.02)
Matrilineal Mosuo	-6.031 (0.263)	0.033 (0.018)	-0.613 (0.611)	2.003 (0.268)	0.049 (0.041)	-0.03 (0.018)	0.597 (0.619)	-0.063 (0.042)
Maya	-5.527 (0.185)	0.055 (0.013)	-0.845 (0.528)	2.293 (0.187)	-0.079 (0.044)	-0.06 (0.014)	0.834 (0.531)	0.08 (0.044)
Lamalera	-6.941 (0.113)	0.03 (0.006)	-0.728 (0.389)	1.693 (0.115)	-0.07 (0.037)	-0.035 (0.006)	0.797 (0.392)	0.068 (0.037)
Coastal Emberá	-2.637 (0.434)	-0.001 (0.021)	-0.152 (0.456)	2.298 (3.737)	0.026 (0.034)	0.372 (0.474)	-2.027 (6.477)	-0.311 (0.557)
Maasai	-5.356 (0.213)	0.025 (0.015)	0.586 (0.229)	0.239 (0.397)	-0.051 (0.021)	-0.006 (0.036)	-0.48 (0.494)	0.016 (0.043)
The Gambia, 1	-6.345 (0.084)	-0.005 (0.007)	-0.082 (0.149)	1.054 (0.09)	-0.001 (0.012)	0 (0.007)	0.028 (0.158)	0 (0.012)
Patrilineal Mosuo	-5.437 (0.2)	0.052 (0.008)	-0.816 (0.5)	1.951 (0.21)	0.04 (0.045)	-0.051 (0.01)	0.864 (0.513)	-0.047 (0.046)
Alakāpuram	-6.711 (0.093)	0.025 (0.005)	-0.02 (0.215)	1.318 (0.109)	0.011 (0.019)	-0.038 (0.007)	-0.006 (0.231)	-0.013 (0.02)
Tenpaṭṭi	-6.778 (0.105)	0.026 (0.005)	-0.277 (0.51)	1.474 (0.129)	-0.024 (0.029)	-0.033 (0.007)	0.261 (0.519)	0.015 (0.03)
Tanna	-5.099 (0.205)	0.039 (0.011)	-0.16 (0.668)	1.75 (0.492)	0.01 (0.056)	-0.029 (0.029)	0.023 (0.809)	-0.035 (0.063)

Table S2: Coefficients for the beta regression models that are depicted in Figure S1 of the supplemental material. The outcome variable is the average relatedness of individual i to other members of the community, including children. The quantities depicted in the table are the posterior means, with posterior standard deviations in parentheses. Note that asterisks denote interaction terms of the corresponding main effects.

	Intercept	Age	Male	Natal	Age * Male	Age * Natal	Male * Natal	Age * Male * Natal
Savanna Pumé	-2.422 (0.196)	0.021 (0.013)	-0.559 (0.25)	0.413 (0.296)	-0.005 (0.017)	-0.012 (0.016)	0.018 (0.551)	-0.012 (0.024)
Miskito	-3.613 (0.279)	-0.001 (0.01)	-0.376 (0.363)	2.235 (0.313)	0.008 (0.018)	0.023 (0.011)	0.286 (0.437)	-0.011 (0.02)
Mayangna	-3.968 (0.176)	0.037 (0.011)	-0.485 (0.204)	1.359 (0.181)	-0.005 (0.013)	-0.023 (0.011)	0.617 (0.221)	0.009 (0.014)
Coastal Afro-Colombians	-4.629 (0.156)	-0.003 (0.006)	-0.226 (0.213)	0.512 (0.195)	-0.014 (0.01)	0.003 (0.009)	-0.622 (0.312)	-0.008 (0.014)
Inland Afro-Colombians	-5.14 (0.092)	-0.015 (0.004)	-0.316 (0.151)	0.198 (0.131)	0.002 (0.006)	0.01 (0.005)	-0.18 (0.211)	-0.015 (0.008)
Dominica	-4.62 (0.329)	-0.011 (0.016)	-0.498 (0.477)	0.591 (0.332)	-0.035 (0.026)	0.005 (0.016)	0.49 (0.481)	0.038 (0.026)
Inland Emberá	-3.685 (0.364)	-0.015 (0.014)	0.484 (0.564)	1.135 (0.465)	0.019 (0.023)	0.023 (0.017)	-0.737 (0.754)	-0.017 (0.029)
Mexican Choyeros	-4.473 (0.275)	-0.025 (0.017)	-0.531 (0.488)	1.876 (0.28)	0.071 (0.024)	0.028 (0.017)	0.297 (0.497)	-0.08 (0.024)
The Gambia, 2	-6.31 (0.186)	-0.024 (0.008)	0.435 (0.263)	1.843 (0.189)	-0.002 (0.011)	0.016 (0.008)	-0.589 (0.269)	-0.001 (0.011)
Matrilineal Mosuo	-5.131 (0.171)	-0.014 (0.013)	0.088 (0.324)	0.98 (0.178)	0.011 (0.026)	0.02 (0.013)	-0.168 (0.33)	-0.017 (0.027)
Maya	-4.974 (0.155)	0.032 (0.011)	-0.231 (0.377)	1.704 (0.158)	-0.063 (0.018)	-0.032 (0.011)	0.27 (0.378)	0.061 (0.018)
Lamalera	-6.247 (0.071)	0.002 (0.004)	-0.741 (0.25)	0.968 (0.072)	-0.035 (0.009)	-0.007 (0.004)	0.801 (0.251)	0.037 (0.009)
Coastal Emberá	-2.428 (0.228)	0.004 (0.009)	-0.484 (0.349)	-0.054 (0.677)	0 (0.017)	-0.024 (0.023)	-0.342 (1.021)	-0.012 (0.035)
Maasai	-4.829 (0.127)	-0.01 (0.007)	0.476 (0.151)	-0.124 (0.236)	0.003 (0.008)	-0.013 (0.009)	0.107 (0.283)	0.014 (0.011)
The Gambia, 1	-6.174 (0.079)	-0.017 (0.003)	-0.032 (0.132)	0.94 (0.084)	-0.007 (0.005)	0.011 (0.003)	0.049 (0.138)	0.008 (0.005)
Patrilineal Mosuo	-4.757 (0.14)	0.021 (0.007)	-0.399 (0.381)	1.211 (0.151)	0.012 (0.035)	-0.019 (0.008)	0.405 (0.39)	-0.013 (0.035)
Alakāpuram	-6.181 (0.06)	-0.008 (0.004)	0.202 (0.134)	0.806 (0.081)	-0.004 (0.007)	0.001 (0.004)	-0.278 (0.152)	0.001 (0.007)
Teṉpaṭṭi	-6.102 (0.066)	-0.006 (0.004)	0.079 (0.169)	0.818 (0.084)	-0.015 (0.007)	0 (0.004)	-0.143 (0.182)	0.013 (0.007)
Tanna	-4.161 (0.124)	0.023 (0.008)	-1.116 (0.679)	0.795 (0.246)	-0.025 (0.038)	-0.025 (0.011)	1.193 (0.709)	0.028 (0.039)

Aggregated Analysis

In our main analysis, we separately modeled the data from each study community. The rationale for this modeling approach is that our cross-cultural sample is relatively small ($n = 19$) and not necessarily representative of ethnographically documented societies. Therefore, attempts to generalize from the sample to an "average" human society are potentially misleading. Having emphasized those important caveats, we consider additional statistical models in which data from all communities are combined for an aggregated analysis. This analysis considers the extent to which matrilocal and patrilocal tendencies within communities affect the age-related variation in relatedness among individuals. For a practical example, this implies that immigrant females in matrilocal societies may exhibit different changes in relatedness with age when compared to immigrant females in patrilocal societies. We examine these questions by including site-level averages as "contextual effects." For each study site, we therefore calculate the percentage of adults of each sex who reside in their natal community (these same quantities appear in Table 1 in the main manuscript). We then consider multilevel beta regression models in which these contextual effects are included as predictors of adults' relatedness to other adults in their respective communities. Hereafter these variables are described as *percent born female* and *percent born male*. They are included in statistical models both as main effects and as moderators in interaction terms that also include the three primary individual-level variables, age, sex, and natality.

In notational form, a candidate model was the following:

$$
\begin{aligned}
\text{relatedness}_{ik} &\sim \text{Beta}(p, \theta) \\
\text{logit}(p) &= \alpha + \beta_1 Age_{ik} + \beta_2 Male_{ik} + \beta_3 Natal_{ik} \\
&\quad + \beta_4 PercentFemale_k + \beta_5 PercentMale_k + \beta_6 PopulationSize_k \\
&\quad + \beta_7 Age_{ik} Male_{ik} + \beta_8 Age_{ik} Natal_{ik} + \beta_9 Male_{ik} Natal_{ik} \\
&\quad + \beta_{10} PercentFemale_k Age_{ik} + \beta_{11} PercentFemale_k Male_{ik} + \beta_{12} PercentFemale_k Natal_{ik} \\
&\quad + \beta_{13} PercentMale_k Age_{ik} + \beta_{14} PercentMale_k Male_{ik} + \beta_{15} PercentMale_k Natal_{ik} \\
&\quad + \beta_{16} Age_{ik} Male_{ik} Natal_{ik} \\
&\quad + \beta_{17} PercentFemale_k Age_{ik} Male_{ik} \\
&\quad + \beta_{18} PercentFemale_k Age_{ik} Natal_{ik} \\
&\quad + \beta_{19} PercentFemale_k Male_{ik} Natal_{ik} \\
&\quad + \beta_{20} PercentMale_k Age_{ik} Male_{ik} \\
&\quad + \beta_{21} PercentMale_k Age_{ik} Natal_{ik} \\
&\quad + \beta_{22} PercentMale_k Male_{ik} Natal_{ik} \\
&\quad + \beta_{23} PercentFemale_k Age_{ik} Male_{ik} Natal_{ik} \\
&\quad + \beta_{24} PercentMale_k Age_{ik} Male_{ik} Natal_{ik} \\
&\quad + v_{intercept[k]} + f_{age[k]} Age_{ik} + g_{male[k]} Male_{ik} + h_{natal[k]} Natal_{ik}
\end{aligned}
$$

$$
\begin{pmatrix} v_{intercept[k]} \\ f_{age[k]} \\ g_{male[k]} \\ h_{natal[k]} \end{pmatrix} \sim \text{Normal} \left\{ \begin{pmatrix} 0 \\ 0 \\ 0 \\ 0 \end{pmatrix}, \begin{pmatrix} \sigma_v^2 & & & \\ \sigma_{vf} & \sigma_f^2 & & \\ \sigma_{vg} & \sigma_{fg} & \sigma_g^2 & \\ \sigma_{vh} & \sigma_{fh} & \sigma_{gh} & \sigma_h^2 \end{pmatrix} \right\},
$$

where the outcome variable is the average relatedness of adult individual i to other adults in community k. The model includes four effects that vary by study site, including a varying intercept (v_k) and varying slopes for age (f_{ik}), sex (g_{ik}), and natality (h_{ik}). In addition to the main effects, there are two separate four-way interaction terms between *percent born female* and *percent born male* and the individual-level main effects for age, sex, and natality status. Finally, a variable for the number of adults in the community is included given the expectation that larger communities exhibit lower average relatedness.

In addition to the above model, we also specified three additional beta regression models of the aggregated dataset: (1) a base model that excludes the contextual effects altogether, (2) a model that includes the contextual effects as "main effects" but not in interaction terms, (3) a highly parameterized model that includes the five-way interaction of the three individual-level variables and the two sex-specific contextual effects. The random effects structure remains constant across all of these models.

Table S3: WAIC comparisons of four statistical models of the aggregated cross-cultural dataset. Lower WAIC values indicate models with greater generalizability. Within the comparison set, a model's weight is an estimated probability that will generate the best predictions on new datasets. Four models are included in the comparison set with varying use of the contextual effects, *percent born female* and *percent born male* (referenced in the table as "effects," though note that the individual-level predictors and their interactions are included in all models). The code and data to reproduce these models are included as supplemental files.

Model Description	WAIC	Weight
No effects included	-33556.40	0.91
Effects included only as main effects	-33551.70	0.09
Effects included as moderators in separate 4-way interactions	-33544.70	0.00
Effects included in 5-way interaction terms	-33541.10	0.00

We use WAIC comparisons to evaluate the fit of these models (Table S1). These comparisons suggest that the most basic model, which lacks the contextual effects of *percent born female* and *percent born male*, receives the strongest support. The only other model that receives any WAIC weight is the model that includes the contextual effects only as main effects, not in interaction terms. Overall, this evidence suggests that age-related variation in relatedness among individuals is evidently not moderated by the proportion of males and females who are natal residents of the communities.

Although the model receives minimal statistical support, we plot the predictions of the model notated above in order to visually assess the evident lack of moderating effects (Fig S2). We organize our plots to align with the quantitative model of Johnstone and Cant (2010), depicting predictions at high and low combinations of male and female dispersal, respectively. Within any particular combination, these plotted predictions generally show few differences in the age-related variation of immigrants.[1] We hesitate to draw further inferences from these predictions in part because of the small sample size of communities. For instance, the predictions for the "High Female, Low Male" combination largely recapitulate the patterns in the Miskito and Mayangna communities. In the main text, we noted that the age-related increases for both immigrants and natals in those communities seemingly stem from high population growth rates that our statistical models do not address. Future analyses of age-related variation in kinship ties would benefit from the inclusion of predictor variables that account for demographic heterogeneity across sites. It is less clear how statistical models might account for communities that are characterized by unstable settlement histories, such as the Maasai and coastal Colombian sites in the present sample.

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[1]Note that the model with the five-way interaction terms generated qualitatively similar predictions.
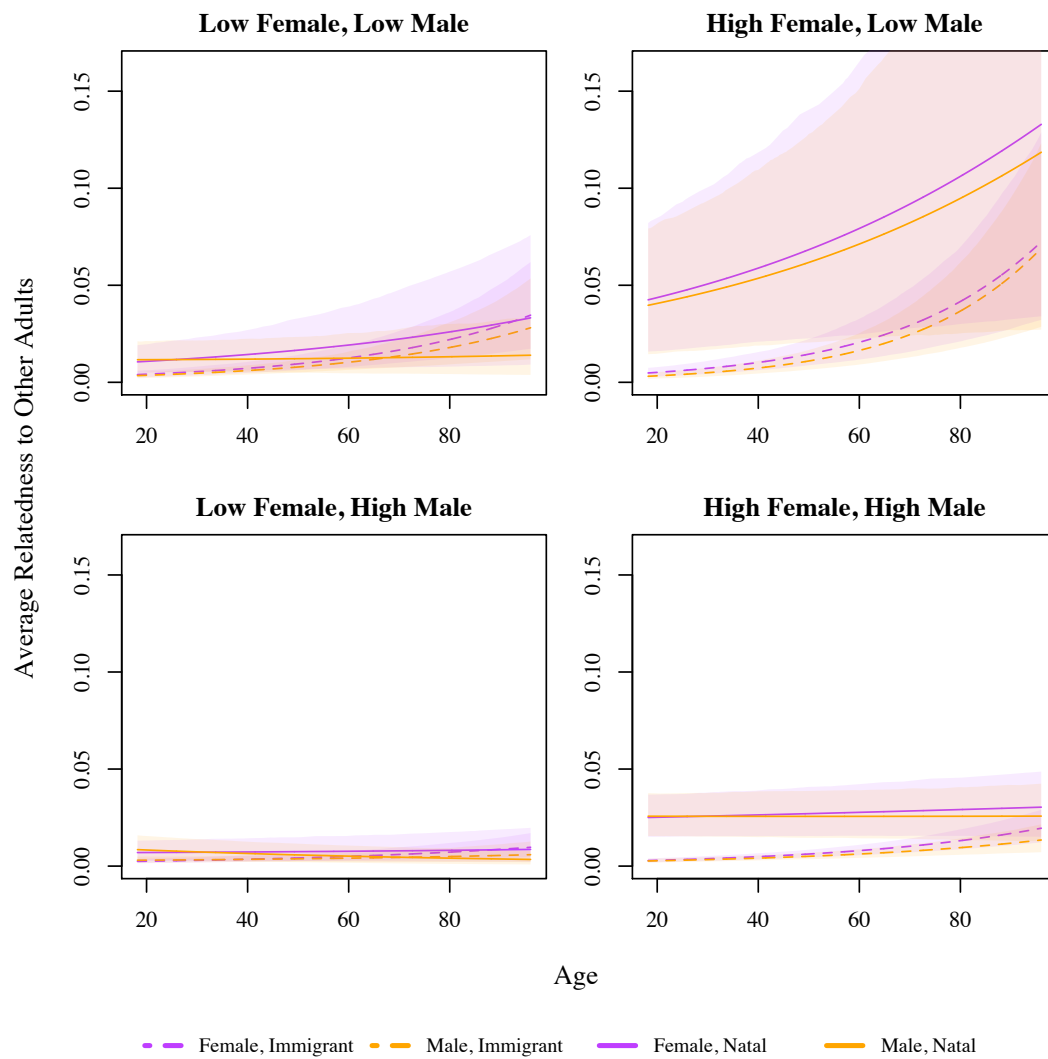
Figure S2: Model predictions from an analysis of the aggregated dataset. The four panels depict varying combinations of high and low *percent born female* and *percent born male*, which moderate the individual-level predictors. For high levels of these variables, predictions are based on a value of 0.75. For low levels, predictions are based on a value of 0.25. The predictions further assume a population size of 100 adults, and predictions are based only on the fixed effects. In other words, these predictions assume a society with values of 0 for all of the random effects. Shaded intervals depict 89% confidence intervals around model predictions.

Simplifying Models and Sex as a Predictor

In our main models, we had included *sex* (coded as 1 for males) as a main effect and as a moderator of the other individual-level covariates, It is evident from the posterior predictions plots in Figure 2, however, that the predictions of males and females overlap considerably. Within many study sites, that is, male and female immigrants exhibit similar age-related variation, as do male and female natal residents. This led us to consider additional statistical models for each site. Compared to the models that are depicted in Figure 2 and reported in Table S1, we specified models that (1) excluded *sex* altogether as a predictor, and (2) included *sex* as a main effect, but not as a moderator of the other terms in the model (it was included only as a main effect, in other words). We then compared these models using WAIC (Table S4).

These models show that *sex* often explains little of the variation in average relatedness to other adults in the community. For 12 of the 19 study sites, the models with the greatest WAIC weight are those in which *sex* is omitted altogether as a predictor. And across all site, the inclusion of *sex* either as a main effect or a moderator rarely has a substantial impact on model fit. That is, even for sites like the Mayangna (site 3), although the greatest weight is evident for the full model presented in the main text, this model is largely indistinguishable from the other models presented here. (These comparisons rely on the heuristic that superior models are distinguished by a WAIC score that differs from scores of other models by 2 or more.) In summary, in models that include *age*, *natality status*, and the interaction of those effects, then the inclusion of *sex* as a predictor seemingly explains little variation in average relatedness. Note that we did not consider models that omit other predictors and/or their interactions, though it is possible that other statistical models would compare favorably to those we have presented.

Table S4: WAIC comparisons of three candidate models for each study site. Like the models presented in Figure 2, there is a separate set of models for each study site. In the "Sex Absent" models, *sex* is omitted altogether as a predictor, leaving only parameters for *age*, *natality status*, and their interaction. In the "Sex Main" models, *sex* is added only as a main effect (these models differ from the "Sex Absent" models only by a single parameter). Bold values signify the model that receives the strongest support at each site, though we note again that differences between most models are modest.

Site number	Site	Sex Absent	Sex Main	Sex Moderator
1	Savanna Pumé	**-141.60**	-140.30	-135.30
2	Miskito	**-182.20**	-181.10	-174.90
3	Mayangna	-713.20	-712.00	**-713.70**
4	Coastal Afro-Colombians	-818.40	-818.80	**-819.80**
5	Inland Afro-Colombians	-1346.10	**-1350.80**	-1346.50
6	Dominica	**-1873.30**	-1872.50	-1870.10
7	Inland Emberá	**-186.20**	-183.80	-178.70
8	Mexican Choyeros	**-397.70**	-393.50	-393.70
9	The Gambia, 2	-2349.80	**-2355.00**	-2351.80
10	Matrilineal Mosuo	**-1159.50**	-1157.50	-1157.00
11	Maya	**-1954.50**	-1952.60	-1952.90
12	Lamalera	-7589.20	-7588.80	**-7590.30**
13	Coastal Emberá	**-196.00**	-194.10	-190.30
14	Maasai	-938.50	-941.70	**-942.40**
15	The Gambia, 1	**-6787.80**	-6786.80	-6780.70
16	Patrilineal Mosuo	**-829.60**	-827.30	-825.50
17	Alakāpuram	**-4399.10**	-4396.50	-4392.00
18	Teṉpaṭṭi	-3440.00	-3439.40	**-3440.90**
19	Tanna	**-459.50**	-458.60	-453.60

Modeling the Number of Close Kin

In the main text of the paper, we noted: "The numerator in the calculations of average relatedness for a given individual largely reflects the number of close, co-resident kin in the population. Therefore, in larger communities, although most individuals may be distantly related to the individual, variability in average relatedness frequently reflects the presence of close kin and the concomitant opportunities for reproductive conflict and cooperation."

As an alternative to using average relatedness, it may be worthwhile to consider the number of close consanguineal kin with whom individuals co-reside in human communities. Therefore, for each individual at the respective study sites, we summed the number of close *primary* kin and also the number of close *secondary* kin. Primary kin are defined as dyads in which the putative degree of relatedness is 0.50 or greater. This category therefore includes dyads of full siblings and dyads of parents and offspring. Secondary kin are defined as dyads in which the degree of relatedness is 0.25 or greater, but less than 0.50. In this category, there are half-siblings, aunts and uncles and their nieces and nephews, and dyads of grandparents and grandoffspring. The analysis presented here is based on calculations from dyads in which both individuals are adults, as defined in the main text.

We model the counts of these kin using Poisson regression models with specifications that follow the modeling approach from the main text. That is, we model the counts as a function of the three-way interactions of *age*, *sex*, and *natality*. At some sites, low variation and low representation of individuals in these demographic categories is challenging for the estimation (for example, when there are very few male immigrants with kin, as in Lamalera, the patrineal Mosuo community, and Teṉpaṭṭi, the statistical models end up overfitting on the available data). Accordingly, the plotted model predictions should be interpreted cautiously, particularly since we supplied only weakly regularizing priors on the parameters of the model. The data and coding scripts for these supplemental analyses are available as supplemental files (https://osf.io/h8cqr/). The outcome variables for these analyses are titled *primary* and *secondary* in the corresponding site-specific data files.

In general, these models tend to provide similar inferences to the models featured in the main text (Fig S3 and (Fig S4). These results are unsurprising given the assumption that variation in average relatedness is determined in large part by variation in the number of close, co-resident kin in the community.

Another preliminary inference from this supplemental analysis is that demographic effects are potentially evident in the ratio of primary to secondary kin. In the main text, that is, we noted that the high fertility rate in the Mayangna community (site 3) was seemingly associated with the high average relatedness of older, natal residents. In this analysis, the plots of the empirical data suggest that the number of kin is highest among middle-aged individuals, whose co-residents in the community often include ample full siblings and offspring. As individuals get older, however, potentially the availability of primary kin declines as full siblings die. Although the statistical model did include the estimation of curvilinear effects for age, it is possible that such models would better fit the data for primary kin in some of the communities. Meanwhile, although elderly individuals may co-reside with few primary kin, there are sites in which the highest counts of secondary kin are evident among the older individuals. The Mayangna (site 3) and Maya (site 11) are particularly noteworthy in this regard. This variation plausibly reflects the bottom-heavy population pyramids in these communities, implying that older individuals are likely to co-reside with many grandchildren.

This latter observation is potentially relevant for research on the investment strategies of grandparents. In settings where older individuals co-reside with relatively few grandoffspring, it may be favorable for them to direct their investment to those specific individuals. By contrast, when older individuals live close to many grandoffspring, it may be more effective for them to invest in collective goods that simultaneously benefit all of their respective grandchildren.
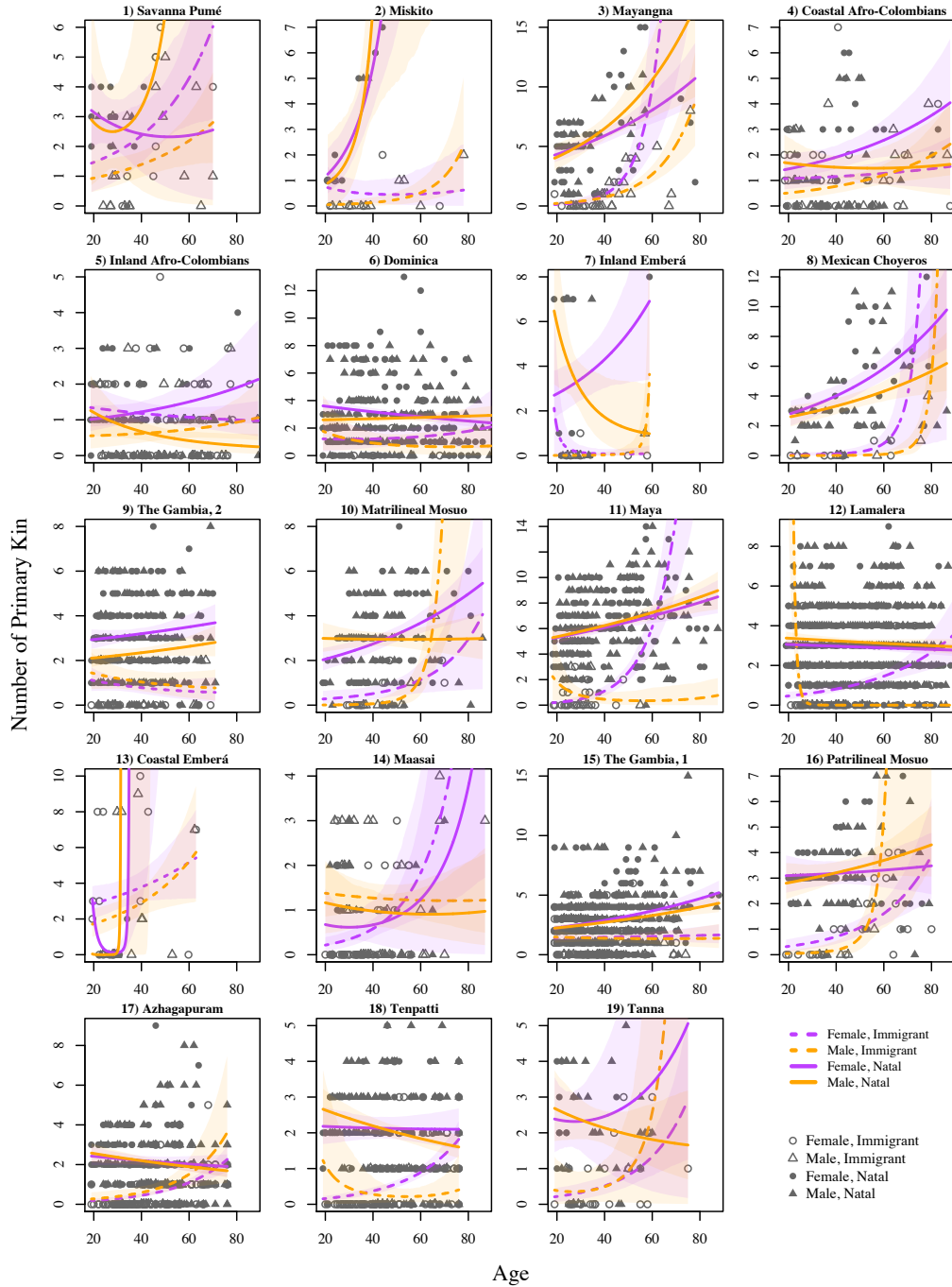
Figure S3: Model predictions for the number of adult primary kin who co-reside with individual adults in the study communities. All predictions are based on Poisson regression models with three-way interaction terms of *age*, *sex*, and *natality* (versus immigrants). Shaded intervals depict 89% confidence intervals around model predictions. Note that the scale of the vertical axis changes for each community. In the plot, sites are ordered in row-wise fashion according to the ratio of adult female natality to adult male natality (the quotient of the respective quantities in Table 1). See the text for important caveats about the model predictions of demographic categories that exhibit small sample sizes and minimal variation in the number of co-resident kin.
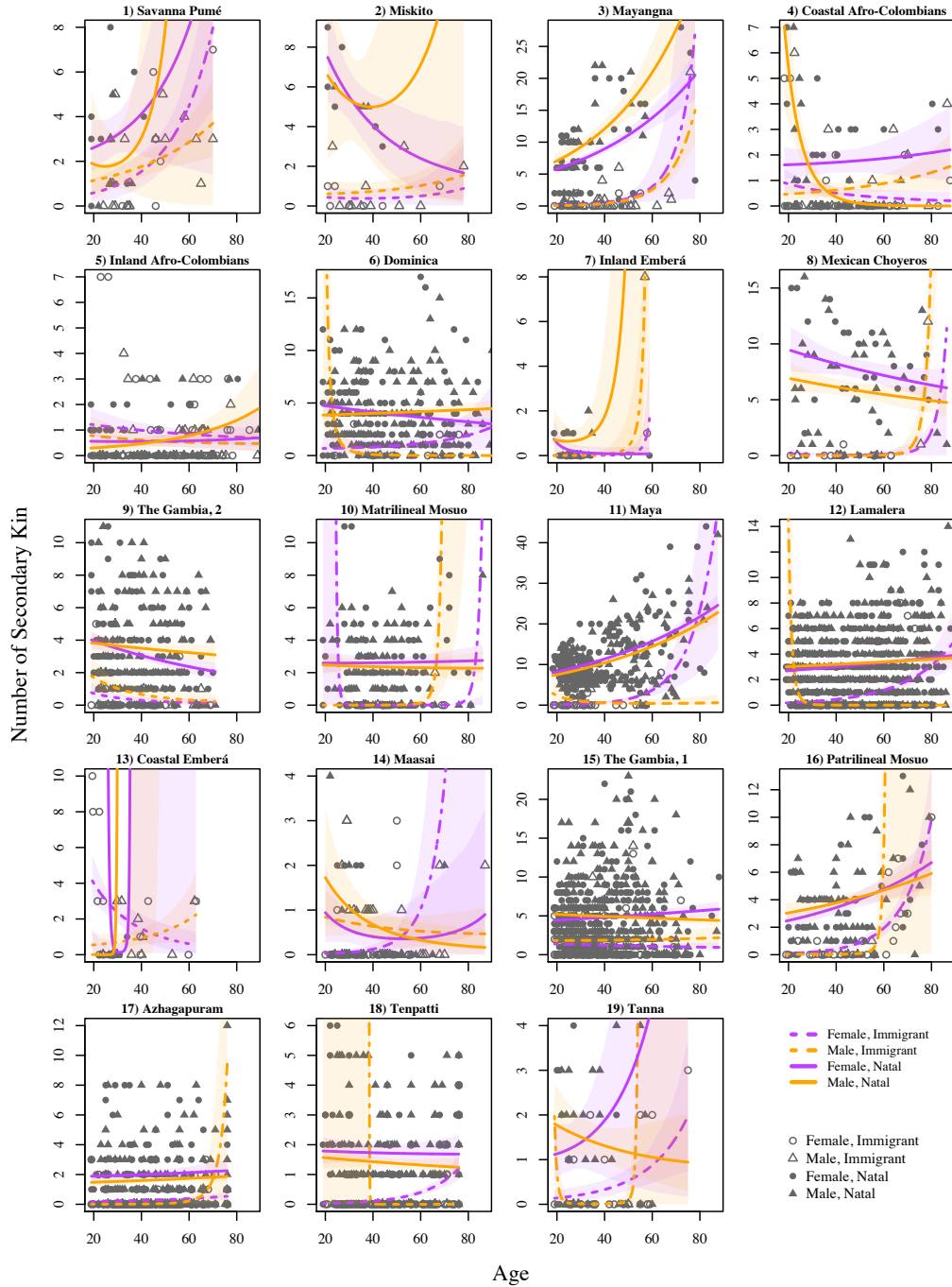
Figure S4: Model predictions for the number of adult secondary kin who co-reside with individual adults in the study communities. All predictions are based on Poisson regression models with three-way interaction terms of *age*, *sex*, and *natality* (versus immigrants). Shaded intervals depict 89% confidence intervals around model predictions. Note that the scale of the vertical axis changes for each community. In the plot, sites are ordered in row-wise fashion according to the ratio of adult female natality to adult male natality (the quotient of the respective quantities in Table 1). See the text for important caveats about the model predictions of demographic categories that exhibit small sample sizes and minimal variation in the number of co-resident kin.