

Supplementary Materials for
**Indirect genetic effects among neighbors promote cooperation and accelerate
adaptation in a small-scale human society**

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Supplementary Text

Comparison to other methods.— Our modeling approach, building on standard evolutionary quantitative genetic theory (38-41, 58), ignored how the timing of reproduction may impact the multiplicative fitness of different strategies across generations, due to the benefits of early reproduction in a growing population (97, 98). Ongoing population growth among the Tsimane (59) suggests that heritable variation in women's fertility may, therefore, be a biased indicator of fitness with respect to the long-run population growth rate, as a consequence of unadjusted variation in residual reproductive value across age classes. Methods provided by (99) and (100) can be used to model these age-structured effects using data on survival and reproduction across the lifespan. See (101, 102) for empirical demonstrations of the value of such methods when inferring selection on fitness and mating success in human populations.

We did not employ these prior demographic methods in the present study because our compiled dataset lacked appropriate time depth and age variation within neighborhood and community units to robustly infer age-specific parameters across the lifespan. Instead, we prioritized estimating the magnitude of fertility IGEs expected among neighbors within a selection episode defined by the average time of observed reproduction within a community (9 years). We reduced potential bias by adjusting these estimates for age effects and other causes of spatiotemporal variation within this window of selection. This allowed us to focus attention on the theoretical questions of greatest interest for the present study, which concerned quantitative genetic effects from neighbors on adaptation of the instantaneous growth rate (*Eqs. 15-21*), i.e. the quantity described by Fisher's fundamental theorem (103). Thus, we attempted to make the most of our dataset despite its limitations with respect to quantifying long-term population growth. Clearly, an important goal for future research will be to develop and utilize datasets that are sufficient in both their breadth and depth for synthesizing these approaches, allowing for estimation of context-dependent IGEs on lifetime fitness across multiple categories of social partner with respect to within-lifetime fluctuations in the social environment. To our knowledge, there is no currently available dataset on a human population beyond the present study that provides sufficient scope to study fluctuating IGEs on fitness among both kin and non-kin neighbors in spatiotemporally localized environments.

Tradeoffs and unmeasured IGEs. — The consequences of fluctuating selection for the evolution of social plasticity are likely to differ because of the duration and frequency of selection events. For instance, bet-hedging models suggest that the evolution of adaptive plasticity is contingent on total lifespan and the age at first reproduction, as well as the granularity of spatiotemporal variation (104). Given that women's reproductive careers can extend many years beyond the observed window (59), further unmeasured fluctuations in social plasticity and social selection across women's lifespans may also be acting to inhibit the evolvability of fertility that we estimated among the Tsimane. For example, even in lower density Tsimane neighborhoods, where average selection is expected to promote cooperation in fertility (*Fig. 4*), the positive association between DGEs and IGEs on fertility may be offset by negative associations caused by reduced offspring survival. This highlights a more general limitation of using fertility variation to infer fitness evolution, as any single fitness component may trade off with others and thus provide a biased estimate of individuals' relative fitness (61, 105). Previous research has demonstrated such tradeoffs across Tsimane communities, showing that average community fertility has tended to negatively predict the average probability of offspring survival (106). However, our model adjusted for spatially structured variation in mean fertility rates across communities, so that DGEs and IGEs were marginalized over these environmental effects. Ecologically mediated tradeoffs

between communities were, therefore, unlikely to have biased our results regarding the evolvability of fitness as proxied by fertility. There is also currently no evidence suggesting that women within the same local community are likely to exhibit strong heritable tradeoffs between their relative fertility and offspring survival irrespective of their shared environment. Low rates of offspring mortality during the time period captured by our dataset (*fig. S1*) also strongly suggest against the importance of biasing effects due to putative heritable tradeoffs between women's relative fertility and offspring survival in a shared environment. Instead, they suggest that fertility has become the primary determinant of fitness variation among the Tsimane in recent decades, as has been observed during demographic transitions in other human populations (e.g. *102, 107, 108*).

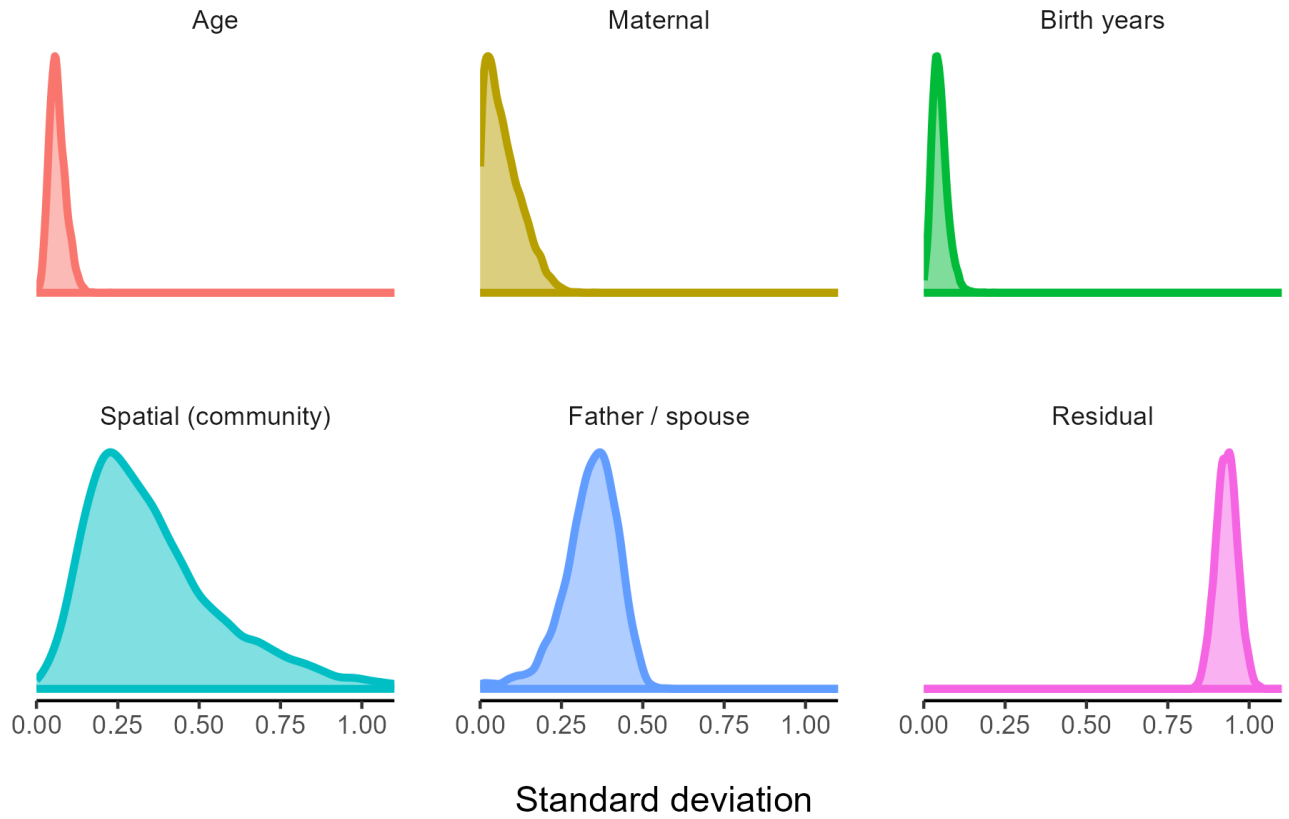
It is also possible that our estimates of evolvability may be under- rather than overestimating the total effect of IGEs with respect to women's reproductive success across their lifespan, which as described above could not be effectively partitioned into sources of variation due to community- and neighbor-specific interactions. Previous work has documented extensive intrafamilial and spousal cooperation among the Tsimane (*60, 66, 67*), which would be expected to only further accelerate the predicted rate of adaptation. Given that previous phenotypic studies among the Tsimane have shown positive associations between cooperative production and family size among spouses (*66*), it is particularly plausible that unmodelled IGEs from spouses similarly accelerate the evolvability of Tsimane women's fertility, consistent with findings in other human populations (*47, 48*). Biparental care may also buffer tradeoffs with other fitness components such as offspring survival and growth (*109*), further potentiating social drive via cooperation in reproduction. We adjusted for the total phenotypic effects of spouses in the current analysis, which explained a non-trivial proportion of variation in fertility outcomes (*fig. S2*), to more directly isolate genetic effects attributable to neighbors. While paternal care has likely played a crucial role in human life history evolution (*110*), the most unique and difficult to explain features of human sociality concern the rapid expansion of our cooperation in larger social groups beyond the nuclear family, motivating our attention to the specific effects of neighbors. Nevertheless, in future research, we intend to investigate how spousal IGEs also shape women's lifetime reproduction, a scale at which neighbor effects cannot be directly quantified in our dataset (see above). Relatedly, it is also important to bear in mind that 'small-scale' societies such as the Tsimane are still nonetheless underpinned by highly distributed and dynamic social networks (*111*). Thus, our analyses are likely to also have missed important fitness-relevant social interactions that occur among Tsimane women outside of the semi-arbitrary boundaries of neighborhoods and communities that we have defined here.

Figure S1. Mortality risk for young Tsimane children and older adults.



Mortality rates are plotted for (left) 0- to 4-years old children and (right) 60- to 69-years-old adults across the time period captured by THLHP data collection. The dotted orange line indicates the earliest birth years recorded in the fertility dataset used for the present study, which shows that the survival probability for infants and juveniles remained very high throughout the study period, providing increasingly limited scope for selection on fitness via offspring mortality. This suggests against the importance of tradeoffs between survival and fertility as constraints on the contemporary adaptation of fitness. Survival for adult women was also very high throughout the study period, with the mortality risk of elderly post-reproductive individuals providing an upward bound estimate with an annual probability of approximately < 0.05 . As in any ecological study of fitness variation, prenatal viability selection could not be quantified for both ethical and pragmatic reasons, as well as any viability selection acting on mothers prior to the onset of the study period. These selection effects could potentially bias our evolutionary predictions if the alleles under selection have pleiotropic effects on both early life viability and survival and/or reproduction in later life (i.e. the invisible fraction problem, *112*). However, our goal in the present study was not to develop the most accurate possible estimate for quantitative microevolution of the population growth rate among the Tsimane, but rather to generate valid inferences about the direction and proportional impact of fitness IGEs resulting from social interactions among reproductively active neighbors.

Figure S2. Environmental effects on fertility variation.



Posterior distributions are shown for the variation in fertility explained by the environmental predictors, scaled to standard deviations. See *Eq. 1* and accompanying text for further details on these fixed and random predictors.

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