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Harsh Environments Promote Allomaternal Care Across Human Societies

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B. A., Miami University, 2016

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An abstract of
A thesis submitted to the Faculty of the
James T. Laney School of Graduate Studies of Emory University
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Abstract

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Allomaternal care is central to human life history, which couples exceptionally short interbirth intervals and large birth size with highly dependent juvenility and increased longevity. Formal models and previous comparative research predict higher levels of cooperative childcare in harsher environments, consistent with paleoanthropological evidence suggesting that hominin allomaternal care evolved in response to increased ecological uncertainty. Although this hypothesis remains difficult to test directly, the relative importance of allomaternal care varies across human societies, providing an opportunity to assess how local social and ecological factors influence this behavior. Here we investigate associations among infant allomaternal care and ecology across 141 human societies. In addition to predicting increased infant allomaternal care in harsher environments due to the direct fitness benefits of cooperation, we also predicted that starvation risk would decrease allomaternal care due to prohibitive energetic costs. Using Bayesian phylogenetic multilevel models, we assessed these hypotheses while also accounting for a host of potentially relevant social and ecological factors, as well as population history as described by a supertree combining genetic and linguistic data. Consistent with our hypotheses, we found increased infant allomaternal care in regions characterized by low productivity, diminished biodiversity, and unpredictable climates, but reduced allomaternal care under conditions of greater starvation risk. These findings suggest adaptive plasticity in allomaternal care across ecologies, consistent with expectations based on paleoanthropological evidence. Moreover, our results are comparable to previously observed patterns in avian and mammalian cooperative breeders, suggesting convergent social evolutionary processes.

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Figures and Tables

Introduction

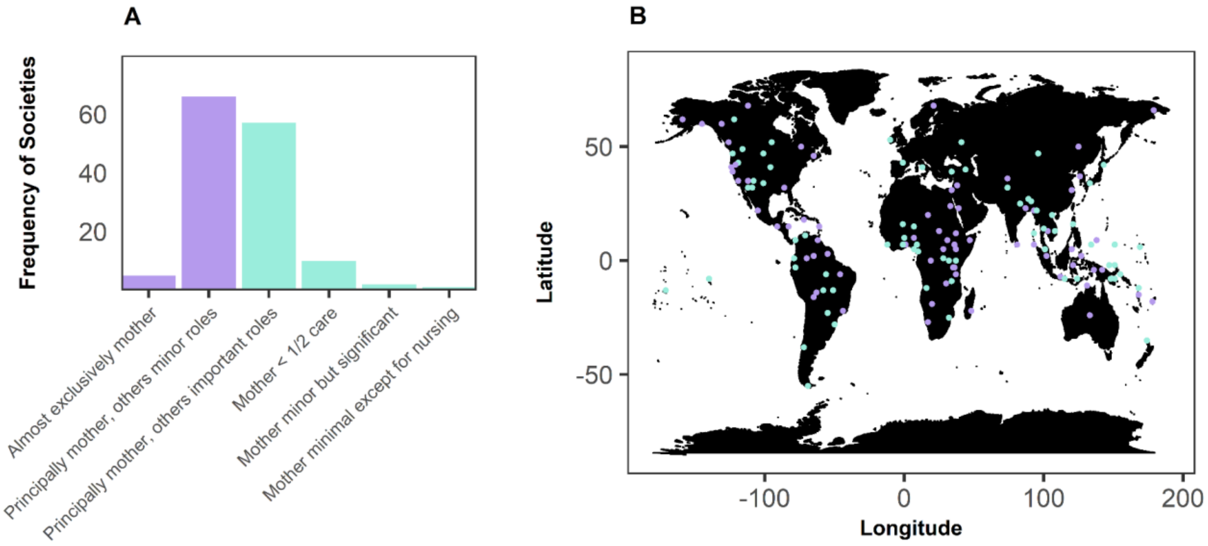
Humans are unique among animals in their tendency to exhibit high degrees of cooperation—encompassing proactive food sharing and child care[1-3], teaching and cultural learning[4,5,6,7], collaborative foraging[8,9], and extensive division of labor[10]—within groups of low average genetic relatedness[11,12] and low frequencies of non-reproductive individuals[13]. Moreover, this propensity toward 'hyper-cooperation'[14] takes place within a rare life history coupling exceptionally short interbirth intervals and large birth size with highly dependent juveniles and a prolonged post-reproductive lifespan[15,16]. Collectively, these traits appear to have facilitated the evolution of humans' large brains and capacity for cumulative cultural learning[17-19], which in turn have given rise to our unprecedented degree of behavioral plasticity and environmental modification[20- 22]. Understanding the emergence and coevolution of human hyper-cooperation, life history, and cumulative culture therefore remains a central explanatory task in evolutionary anthropology.

The evolution of enhanced food sharing and allomaternal care, which facilitate more consistent energetic input for infants[23] and benefit maternal time and energy allocation[24-27], appears to mark an important transition in the trajectory of cooperative behavior, life history, and cognitive capacity in ancestral hominins[17]. Along with the emergence of a tool-assisted, cooperative foraging niche[28], which is likely to have created surplus production facilitating investment in females and their offspring[16,29], the evolution of cooperative breeding may have allowed initial selection for larger brains and other-regarding, or prosocial, motivations that enhance cooperation and social learning[30]. In extant human populations, an appreciable degree of allomaternal care is observed across most societies, with fathers, older siblings, extended family members, and non-kin providing food, knowledge, and protection to highly dependent offspring[3]. Such cooperatively breeding social structures are rare among primates and mammals more generally[31]. Moreover, compared to other hominids, who exhibit nearly exclusive maternal care[30], human offspring impose appreciably high costs upon their caretakers. For example, while other great apes acquire independent foraging efficiency shortly after weaning[32], humans typically consume more calories than they produce for most of their development, often failing to achieve net productivity and peak foraging efficiency until the second to third decade of life[16,33,34]. Given the prohibitive metabolic costs of extending gestation[35], as well as the necessity of learning to succeed in a skill-intensive foraging niche[33,34,36,37] , much of this energetic input takes place outside the womb and comes from non-maternal caretakers. In particular, for both mothers and their offspring, the decades-long brain and bodily development necessary for navigating human lifeways is contingent upon a steady influx of high quality, macronutrient rich foods[38,39]. What fitness benefits facilitated selection for such a costly life history strategy?

Paleoanthropologists have attempted to explain the evolution of this suite of cooperative behaviors as a response to the environmental volatility of the Plio-Pleistocene period, during which the evolution of early *Homo* took place. The Pleistocene epoch in particular was characterized by high spatiotemporal heterogeneity in habitat quality and protracted intervals of ecological instability and resource uncertainty[40,41], which presumably enhanced the fitness benefits of collaboration and social learning in the face of increasingly harsh environments. Although this hypothesis remains difficult to test directly with the paleoanthropological record, notwithstanding suggestive shifts in hominin life history, brain size, and diet[42,43], empirical data from extant human and animal societies provide important sources of evidence to further assess its predictions. For example, reciprocity and collective action benefits, whereby active coordination and cooperation among group members increases per capita productivity and buffers individual risk, have been suggested to play central roles in the emergence and maintenance of food-sharing practices[1,44,45], leadership[46], social norms[47], religious beliefs[48], and broader biological markets of resource exchange[49]. Similarly, although kin selection is a primary driver of alloparental care across many animal societies[50-52], particularly in the context of small groups of high average relatedness, cooperative breeding is also found to occur in larger social groups of mixed relatedness inhabiting harsher environments[53-55]. Presumably, this pattern reflects increased direct fitness benefits of cooperation in unpredictable, less benign ecologies, which occur independently of genetic relatedness and can facilitate more extensive cooperation in larger groups of both kin and non-kin[56-62]. In contrast to other forms of cooperative behavior, however, research on human allomaternal care has largely emphasized kin-based fitness benefits accrued through grandmaternal[24,63,64] and sibling care[65-69], as well as direct and indirect forms of paternal care[10,70,71]. While kin-directed care is crucial for explaining human life history, non-kin allomaternal care also makes a significant contribution to infant development across many societies[3], suggesting that cooperative childcare in harsh environments may also be an important but relatively understudied source of direct fitness benefits for human alloparents in general.

In the present study, we assessed this environmental harshness hypothesis by taking advantage of variation in infant allomaternal care across human societies. We reasoned that if direct fitness benefits are important for explaining the evolution of cooperative childcare in humans, we should find evidence of increased allomaternal care in contemporary societies occupying harsher environments. In particular, we examined 141 societies from the Standard Cross-Cultural Sample (SCCS) with available ethnographic measures of infant care[72] (**Fig 1**), using multiple climatic, biogeographic, and biodemographic predictors to assess how allomaternal care associates with global variation in ecology. In addition to predicting increased allomaternal care in harsher environments, we also predicted that starvation risk would decrease allomaternal care due to prohibitive energetic costs, consistent with previous simulation studies[62] and research linking rates of infanticide to extreme social and material resource stress[73,74].

Figure 1. Global variation in infant allomaternal care across societies.



Footnote. (**A**) frequency of societies (N = 141 total) scored from 1-6 (verbal description on x-axis) on a standardized measure of allomaternal care, which was subsequently binned into either a minor (purple) or significant (blue) degree of infant allomaternal care. (**B**) global distribution of societies in the present study. Color coded by whether they exhibited minor (purple) or significant (blue) allomaternal care.

Results

To remove collinearity and enhance interpretation, we reduced our primary ecological measures[75-78] to three components using principal component analysis: *environmental productivity* (encompassing temperature predictability [loading = 0.91], annual mean precipitation [0.70], and net primary productivity [0.62]), *biodiversity* (precipitation predictability [0.63] and mammalian and avian species richness [0.87]), and *starvation risk* (higher endemic starvation [0.75], seasonal starvation [0.88], and short-term starvation [0.67]; **Table 1**). We then estimated a Bayesian multilevel phylogenetic regression model to assess our main hypotheses. We included fixed effects for these components, as well as for paternal care[72], pathogen stress[80], the capacity for food storage[81], and reliance on agriculture[82], with random effects for ecological biome[83], primary mode of subsistence[84], and population history as described by a supertree of human populations based on genetic and linguistic data[45,85-87]. In addition to a main effect examining our hypothesis for starvation risk, we further included an interaction effect between environmental productivity and biodiversity to capture variation in environmental harshness caused by the intersection of these factors.

Rather than relying on null hypothesis tests and arbitrary designations of statistical significance, we provide multiple measures to summarize and draw inferences from our posterior model estimates[88,89]. In particular, to interpret the strength and uncertainty of estimated regression effects, we used the posterior log odds (β), the median absolute deviation (MAD) as a robust measure of dispersion, the 90% quantile-based credible interval (CI), and the probability of observing a positive or negative effect, i.e. the proportion of the posterior probability greater or smaller than 0 ($p_{<0}$ or $p_{>0}$). Note that, in contrast to classical *p*-values, the reported $p_{<0}$ and $p_{>0}$ directly estimate the probability in support of a positive or negative effect. In addition, we calculated Cohen's *d* standardized mean difference effect sizes for our fixed effect predictors, estimated the total variance explained (R^2) by our fixed and random effects, and further examined the change in model quality following removal of each parameter using the Watanabe-Akaike information criterion (WAIC)[90]. Posterior medians are denoted throughout by tilde accents (i.e. $\tilde{\beta}$, $\tilde{d}$, and $\tilde{R}^2$), while MAD are presented in brackets.

Table 1. Components of ecological measures.

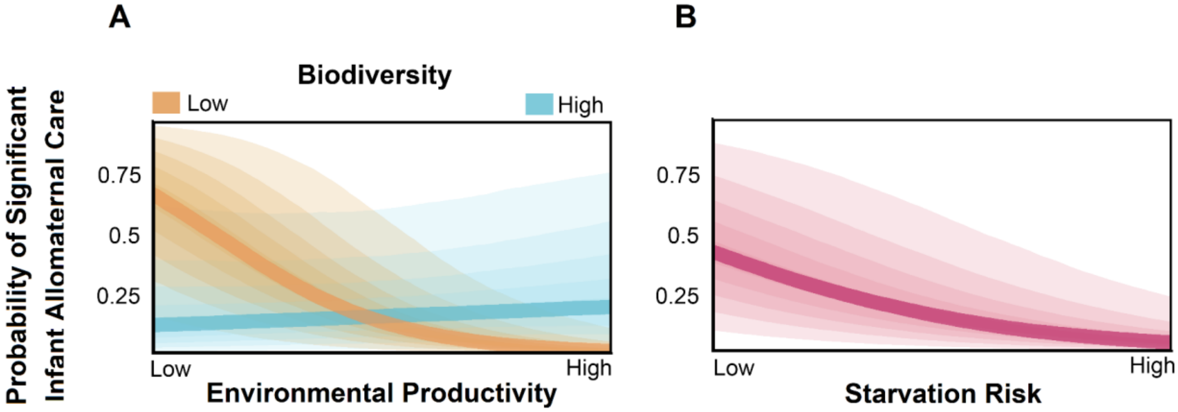
Variable	Productivity [a]	Biodiversity [a]	Starvation
Temp predictability	**0.91**	0.21	—
Temp mean	**0.86**	0.03	—
Temp variance	**-0.84**	-0.16	—
Precipitation predictability	0.09	**0.63**	—
Precipitation mean	**0.70**	0.29	—
Precipitation variance	**0.56**	0.16	—
Net primary productivity	**0.62**	0.46	—
Plant species richness	**0.65**	0.48	—
Amphibian species richness	0.27	**0.84**	—
Mammal species richness	0.24	**0.87**	—
Avian species richness	0.27	**0.87**	—
Endemic starvation	—	—	**0.75**
Short-term starvation	—	—	**0.67**
Seasonal starvation	—	—	**0.88**

Footnote. Loadings greater than 0.50 (i.e. component describes +25% original measure variance) are bolded. Dashes indicate that the third principal component was independently derived due to greater missing data across societies. [a] Components were rotated using the Quartimax criterion to enhance interpretability.

We find a clear main effect of environmental productivity ($\tilde{\beta}$ = -1.17 [0.60], $\tilde{d}$ = -0.65 [0.33], 90% CI [-2.36, -0.28], $p_{>0}$ = 0.98), as well as a strong interaction effect with biodiversity ($\tilde{\beta}$ = 1.58 [0.76], $\tilde{d}$ = 0.87 [0.42], 90% CI [0.47, 3.00], $p_{>0}$ = 0.99), such that significant infant allomaternal care was more likely to occur in societies occupying regions characterized by low temperature and precipitation predictability, low net primary productivity, and low biodiversity (**Fig. 2A**). Conversely, greater starvation risk predicted reduced infant allomaternal care ($\tilde{\beta}$ = -1.53 [0.46], $\tilde{d}$ = -0.84 [0.25], 90% CI [-2.58, -0.91], $p_{>0}$ = 0.99; **Fig 2B**). Highly uncertain effects were observed for agricultural development ($\tilde{\beta}$ = 0.93 [1.11], $\tilde{d}$ = 0.51 [0.61], 90% CI [-1.01, 2.79], $p_{>0}$ = 0.80), pathogen stress ($\tilde{\beta}$ = 0.19 [0.49], $\tilde{d}$ = 0.10 [0.27], 90% CI [-0.65, 1.04], $p_{>0}$ = 0.75) and food storage capacity ($\tilde{\beta}$ = 0.25 [0.65], $\tilde{d}$ = -0.07 [0.14], 90% CI [-0.87, 1.34], $p_{>0}$ = 0.69).

Model comparison provided additional evidence that the hypothesized effects appreciably enhanced prediction of infant allomaternal care, while no clear support was found for the inclusion of any additional fixed effects (**Table 2**). Random intercept effects for biome ($\tilde{R}^2$= 0.02 [0.03]), subsistence mode ($\tilde{R}^2$ = 0.05 [0.06]), and population history ($\tilde{R}^2$ = 0.30 [0.27]) also accounted for a small to moderate degree of variance in infant allomaternal care. Taken together, the fixed effects also explained a moderate degree of variance ($\tilde{R}^2$ = 0.34 [0.12]), with all model parameters collectively accounting for a large proportion of total variance ($\tilde{R}^2$ = 0.82 [0.12]).

Figure 2. Predicted effects of ecology on infant allomaternal care.



Footnote. The model predicted probability (y-axis) of allomaternal care making a significant contribution during infancy, as a function of variation in the hypothesized predictors (x-axis). (**A**) The observed interaction between environmental productivity (x-axis) and biodiversity, visualized here at low (-1; orange) and high (+1; blue) values of the biodiversity component; (**B**) The influence of starvation risk (x-axis; low= -1, high = +1) on allomaternal care. Shaded bands indicate posterior probabilities of the model predictions across 5 intervals ranging from p = 0.12-0.88% credible intervals from darkest to lightest, respectively. Model predictions are generated conditional on expected covariate values for a society without agriculture and food storage, marginalizing over random effects.

Table 2. Parameter-specific model comparisons.

Model comparison	$\mathrm{WAIC}_{\mathrm{reduced}} - \mathrm{WAIC}_{\mathrm{full}}$
– productivity*biodiversity	**11.08 (5.55)**
– productivity*biodiversity – productivity – biodiversity	**16.76 (7.16)**
– starvation	**32.24 (9.06)**
– agriculture	0.24 (1.45)
– pathogen stress	0.37 (0.90)
– food storage	0.80 (0.99)
– primary subsistence mode	**6.68 (3.04)**
– biome	1.92 (2.05)
– phylogeny	**13.51 (3.87)**

Footnote. The Watanabe-Akaike information criterion (WAIC) provides a fully Bayesian criterion for model comparison. Similar to other indices, lower values indicating greater relative model quality and ±2 indicating minimal evidence for a difference in quality (row in bold). Comparisons are made between a model without a parameter ($\mathrm{WAIC}_{\mathrm{reduced}}$) and the full model with all parameters included ($\mathrm{WAIC}_{\mathrm{full}}$), so that positive values indicate reduced model quality following removal of a predictor. Posterior expectations are reported, with standard errors in parentheses.

Discussion

Overall, we find strong support for our hypotheses, suggesting adaptive plasticity in infant allomaternal across ecological contexts. Consistent with paleoanthropological evidence[42,43], formal models[56.62], and empirical patterns discovered in other cooperatively breeding taxa[53-55], we observed greater allomaternal care in human societies occupying harsher environments (i.e. regions of lower productivity and biodiversity; **Fig 2A**), which presumably result in more stochastic patterns of resource availability and production. Although our measure of biodiversity does not directly capture variation in resource acquisition, this interpretation is supported by previous work demonstrating that reduced biodiversity leads to diminished population density in regions of low primary productivity[94], as well as the positive relationship between species diversity and dietary quality[95]. We therefore find support for convergent social evolutionary processes[91,93] influencing allomaternal care across human and other animal societies. While clearly facilitated by indirect fitness benefits[63-68], human allomaternal care may therefore also be promoted by direct fitness benefits in the face of unpredictable climates and reduced resource biodiversity. This finding is consistent with broader behavioral ecological theory emphasizing the importance of collective action and reciprocity for maintaining various other cooperative behaviors and institutions, such as interhousehold food sharing and biological markets[44,45,49], leadership[46], social norms[47], and religious beliefs[48]. While previously supported by suggestive climate data and concurrent shifts in hominin life history, foraging practices, and brain size[17,28,41,42,43], our results provide strong and more direct support for the claim that human allomaternal care has been adapted to buffer against the risks of volatile ecological contexts.

In addition, while harsher environments appear to elicit higher rates of allomaternal care, we also observed that greater starvation risk has a strong negative effect on infant allomaternal care (**Fig 2B**). Our finding is consistent with previous research demonstrating that extreme resource stress is associated with increased rates of infanticide[73,74], as well as formal models that predict reductions in cooperative breeding when the costs of childrearing become increasingly prohibitive[62]. This suggests that although cooperative childcare can provide direct fitness benefits under harsh conditions, allomaternal care can also become exceedingly costly if subsistence practices and/or social structure do not sufficiently offset the risks of extreme malnourishment. It is important to emphasize, however, that our models do not directly disentangle alternative causal hypotheses relating allomaternal care and ecology. In particular, while we expect starvation risk to decrease the expression of infant allomaternal care, observed starvation risk may itself be a function of reduced allomaternal care in response to alternative ecological factors. Similarly, while the observed associations between allomaternal care, productivity, and biodiversity are expected to arise from adaptive plasticity in response to ecological conditions, as suggested by the environmental harshness hypothesis[56-62], societies with high infant allomaternal care may also exhibit increased rates of successful migration into harsh environments, as was recently found across avian cooperative breeders[54]. The results of the present study therefore provide a crucial starting point for further investigation of these processes.

Our inability to directly partition distinct sources of allomaternal care represents an important limitation of the present investigation, as we cannot confidently differentiate between alternative but potentially complementary forms of allomaternal care that may facilitate and lead to variation in the observed effects across societies. Indeed, independent of the highly uncertain effects of agriculture and the capacity for food storage, infant allomaternal care was found to exhibit non-trivial differences across primary modes of subsistence (**Fig S1**), with conserved population history also accounting for a moderately high degree of variance. This suggests that unmeasured predictors may be important for further differentiating the specific factors influencing care in the presence of differential agricultural development, as well as among societies primarily reliant on distinct forms of foraging such as fishing or hunting. Nonetheless, given higher rates of fertility following the onset of agricultural practice[96,97], there may also be strong benefits for parents to attain additional allomaternal care in the presence of agriculture, either through kin such as older siblings[25,26,92], interhousehold care, or trade. Future research should therefore seek to disentangle how these distinct pathways to enhanced infant allomaternal care may manifest and interact across societies. While our study emphasizes reciprocity and collective action benefits, other forms of direct benefit such as monetary compensation are likely to be important motivators of cooperative childcare in market-integrated societies.

In conclusion, our study provides strong evidence for the sensitivity of infant allomaternal care to variation in local ecology. The consistency of these patterns has now been demonstrated across a broad range of species, with our findings for human societies complimenting previous work linking cooperative breeding to unpredictable, arid climates in both mammalian and avian taxa[53-55]. These data collectively demonstrate that harsh environments play a central role in the evolution of cooperative breeding. Therefore, while to some degree unique in its proximate manifestation and social structure[98-101], our results nonetheless demonstrate that human allomaternal care is congruent with expectations of broader social evolutionary theory[56,91,93]. Moreover, our findings provide indirect support for paleoanthropological evidence emphasizing the importance of ecological volatility for promoting cooperative behavior during hominin evolution in the Pleistocene[41-43]. More nuanced investigation into the effects of environmental harshness on cooperative breeding, using quantitative measures of infant care for distinct caretakers both across and within societies, remains an important testing ground for further examining the suggestive results of the present study. Th direct benefits of cooperation in the face of common threat, as in many other domains of human behavior, appear to be central to infant allomaternal care across societies—providing a fundamental source of stability for the maintenance of our costly life history strategy, and in turn promoting our unprecedented degree of biodemographic success[3].

Methods

Sample

All measures utilized in the present study were retrieved from the Database of Places, Language, Culture and Environment (D-PLACE)[78]. We examined data on infant care available for 141 contemporary societies drawn from the SCCS, which was compiled as one of the first representative samples for systematic investigations of cross-cultural variation across six major world regions[101]. These societies were selected from the larger set for which infant allomaternal care measures are available due to the availability of measures for both allomaternal and paternal infant care, as discussed further below. We investigated the "Non-maternal relationship, infancy" measure (SCCS v51)[72], which is a standardized 6-point scale capturing the degree of infant-directed allomaternal care described in ethnographies for each society, with a value of 1 indicating "Almost exclusively mother" and a value of 6 indicating "Mother minimal except for nursing" (see **Fig 1**). Due to low counts of primary allomaternal care (13 societies scored 4 or above), we binned our scale into a binary measure of whether a society exhibited a minor (1-2) or important (3-6) role for allomaternal care during infancy. We focused our analysis on infant allomaternal care due to the particularly high energetic demands that mothers face during this period[102]. Moreover, we did not analyze codes for early childhood allomaternal care because of reduced variation in the degree of care exhibited across societies (i.e. no societies in the SCCS are coded for minor rates of early childhood allomaternal care). This likely reflects the inclusion of more indirect or low-cost forms of care that are typical of early childhood development (e.g., mixed-age and -sex play groups[103]).

Social and ecological predictors

For our primary hypotheses, we extracted multiple climatic and biogeographic measures[75,76] and indices of starvation risk (endemic, SCCS v1261; short-term, v1262; and seasonal, v1263)[77] from D-PLACE (**Table 1**). Principal component analysis (PCA) was conducted to reduce multicollinearity and enhance interpretation. Given differential missingness across our predictors, we conducted two distinct PCAs to avoid unnecessary data imputation: the first capturing climatic and biodiversity measures (N = 107 societies; 67% variance described), and the second capturing measures of starvation risk (N = 83 societies; 60% variance). We used a Quartimax rotation[104] for the first analysis to produce two orthogonal components and enhance interpretation.

Three measures were included in our analysis to account for variation due to subsistence practices. In addition to primary subsistence mode (SCCS v820)[84], we also included a measure of reliance on agriculture (SCCS v151)[82], as agriculture may influence allomaternal care through its positive effects on fertility[96,97]. Food storage capacity (SCCS v20)[81] was also modelled as it has been previously demonstrated to reduce the probability of daily food sharing[45], suggesting that this factor may smooth food consumption through accumulated surplus and thus reduce the benefits of cooperation in harsher environments. In addition to these measures, total pathogen stress (SCCS v1260)[80] was also included for comparison with recent work on factors influencing forager population density[94].

While fathers are an important source of offspring care and energetic input across many human societies[10,71], we controlled for paternal infant care (SCCS v53)[72] as a covariate rather than a separate outcome measure in our analysis. This choice was made to ensure that our allomaternal care measure accurately reflected alloparenting, rather than being confounded by potentially distinct influences on paternal investment[70,105], as well as to facilitate more direct comparison with the broader literature on non-human cooperative breeders. A strong relationship was observed between the paternal and allomaternal infant care ($\tilde{\beta}$ = 2.71 [1.17], $\tilde{d}$ = 1.50 [0.65], 90% CI [0.86, 4.90], $p_{<0}$ = 0.99, $\mathrm{WAIC}_{\mathrm{reduced}} - \mathrm{WAIC}_{\mathrm{full}}$ = 5.35 [4.29]), further supporting this analytic decision. The biome[83] occupied by each society was also included to estimate any ecological heterogeneity relevant to allomaternal care that was not captured by our principal components. Finally, we utilized a human supertree for the SCCS that combines genetic and linguistic data, which allowed us to avoid the potential pitfalls of pseudoreplicability due to shared population history[85- 87].

Statistical analysis

A Bayesian multilevel phylogenetic regression model was fit to assess our main hypotheses for the Bernoulli response of minor or significant allomaternal care, using the 'brms' package[106] for R statistical environment[107]. Regularizing priors—$\beta \sim \mathrm{Normal}(0,2)$ for fixed effects, $\sigma \sim \mathrm{Half-Cauchy}(0,2)$ for random effects—were placed on all model parameters to penalize extreme estimates and reduce our risk of inferential error[88]. We used a fully predictive Bayesian imputation procedure to infer missing values for the components, which avoided systematic bias in our estimates due to the incorrect assumption of missing completely at random (MCAR) data[108]. All ordinal variables were accurately represented as such using monotonic effects[109]. Please see **Appendix S1** for further details on our statistical models, effect size calculations, and results without imputation supporting the robustness of our findings.

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Appendix SI

Supplementary Methods and Results

Descriptive statistics

Our climate predictability measures were drawn from the Database of Places, Language, Culture and Environment (D-PLACE) and are based on information criteria proposed by Colwell[1], which capture predictability due to both climate constancy (stability across seasons) and contingency (stability in seasonality). Temperature constancy was positively associated with environmental productivity (r = 0.84) and biodiversity (r = 0.44) but negatively associated with starvation risk (r = -0.25). Both environmental productivity (r = -0.69) and biodiversity (r = -0.50) negatively correlated with temperature contingency, while starvation had a small positive correlation (r = 0.23). Precipitation constancy was negatively associated with productivity (r = -0.23), positively associated with biodiversity (r = 0.35), and had a weak association with starvation (r = -0.11). Finally, precipitation contingency positively correlated with productivity (r = 0.42) and biodiversity (r = 0.25) but had no zero-order correlation with starvation (r = -0.01). Societies high in both productivity and biodiversity were more likely to experience high temperatures and low temperature seasonality, as well as high precipitation seasonality.

Latitude was negatively correlated with productivity (r = -0.64) and biodiversity (r = -0.41) and had a weak positive correlation with starvation risk (r = 0.16). Longitude positively associated with productivity (r = 0.42) and had weak negative associations with biodiversity (r = -0.13) and starvation (r = -0.12).

Calculation of effect sizes

Bayesian R^2 estimates were calculated as the variance explained by fixed or random effects divided by the sum of these components and the logit-scale variance $\pi^2/3$. The variance of fixed effects was calculated as the variance in model predicted logit-scale outcomes for our dataset, marginalizing over random effects[2]. Cohen's *d* was calculated for fixed effects as the posterior log odds (*β*) divided by the logit-scale standard deviation $\pi/\sqrt{3}$. This standardized mean difference measure provides a comparable effect size across studies using distinct data structures and link functions[3].

Statistical models

The findings reported in the main text can be replicated using the 'brms' R package[1] interfacing with the Stan statistical programming language[4]. All results were estimated based on the following model for society *i*

$$\text{Infant allomaternal care}_i \sim \text{Bernoulli}(p_i)$$

$$\text{logit}(p_i) = A_i + B_i$$

$$A_i = \alpha_0 + \alpha_1 \text{biome}_{[i]} + \alpha_2 \text{subsistence}_{[i]} + \alpha_3 \text{society}_{[i]}$$

$$B_i = \beta_1 \text{Productivity} + \beta_2 \text{Biodiversity} + \beta_3 \text{Productivity} * \text{Biodiversity} + \beta_4 \text{Starvation} +$$
$$\beta_5 \text{Parental care} + \beta_6 \text{Agriculture present} + \beta_7 \text{Storage present} + \beta_8 \text{Pathogen stress}$$

with priors:

$$\alpha_1, \alpha_2 \sim \text{Normal}(\alpha_0, \sigma)$$

$$\alpha_3 \sim \text{Normal}(\alpha_0, \mathbf{A_{SCCS}})$$

$$\alpha_0, \beta \sim \text{Normal}(0,2)$$

$$\sigma \sim \text{Half} - \text{Cauchy}(0,2)$$

where *p* is the probability of observing significant allomaternal care (3+ on original scale), α_0 and α_{1-3} are population-level and random intercepts respectively, β are fixed effects coefficients, and $\mathbf{A_{SCCS}}$ is the expected phylogenetic covariance matrix. See **Fig S1** for a visualization of the random effects for subsistence mode.

Missing values were imputed for the rotated and principal component scores using fully predictive models. By using Bayesian imputation, we were able to estimate the imputation models simultaneously with our main model, such that uncertainty in imputation was propagated and accounted for in the main model estimates[5]. The following model structure was used for the missing value of society *i*, with notation as above.

$$\text{Component score}_i \sim \text{Normal}(\mu_i, \sigma_{\text{residual}})$$

$$\mu_i = A_i + B_i$$

$$A_i = \alpha_0 + \alpha_1 \text{biome}_{[i]} + \alpha_2 \text{subsistence}_{[i]}$$

$$B_i = \beta_1 \text{allomaternal care} + \beta_2 \text{Parental care} + \beta_3 \text{Agriculture present} +$$

$$\beta_4 \text{Storage present} + \beta_5 \text{Pathogen stress}$$

$$\alpha_1, \alpha_2 \sim \text{Normal}(\alpha_0, \sigma_{\text{random}})$$

$$\alpha_0, \beta \sim \text{Normal}(0,2)$$

$$\sigma_{\text{random}} \sim \text{Half} - \text{Cauchy}(0,2)$$

$$\sigma_{\text{residual}} \sim \text{Student} - \text{t}(3,0,10)$$

Random slopes for primary subsistence mode

The model reported in the main text assumes a constant slope for the change in infant allomaternal care across the main and interaction effects of productivity and biodiversity, while accounting for random variation in the average degree of allomaternal care across societies primarily reliant upon agricultural, foraging, horticulturalist, and pastoralist modes of subsistence. Model comparison suggested that estimating different slopes in these parameters across modes of subsistence appreciably reduced the predictive quality of the model, both with ($\text{WAIC}_{\text{reduced}} - \text{WAIC}_{\text{full}} = -124.22$ [14.06]) and without ($\text{WAIC}_{\text{reduced}} - \text{WAIC}_{\text{full}} = -101.06$ [10.69]) correlations estimated between random slopes and intercepts. Statistical power was low for estimating these effects, however, given how few societies in our sample were primarily horticulturalists (N = 13) or pastoralists (N = 9). In addition, there may be meaningful heterogeneity within these categories, such as between societies reliant upon distinct forms of foraging or agricultural development. This finding is therefore preliminary and should be cautiously interpreted.

Complete case analysis

This imputation procedure facilitates more robust inferences in comparison to complete-case analysis, as the latter makes the stringent and unrealistic assumption that data are missing completely at random (MCAR) and can therefore be omitted from the model without consequence. Previous research suggests that this assumption is generally unsafe and can dramatically bias statistical results[6,7]. Moreover, it often results in a dramatic loss of statistical power, further inhibiting accurate inference. Nonetheless, it is useful to compare results obtained with imputation to those obtained solely through measured complete case analysis, which can be used to determine whether effects are contingent upon particular features of the imputation model.

We therefore estimated each of our hypothesized effects independently without imputation, otherwise including all main model effects, for the 107 and 60 SCCS societies without missing values for the productivity + biodiversity and starvation risk components, respectively. Consistent with our predictions, we continued to observe the expected main effect for environmental productivity ($\tilde{\beta}$ = -0.70 [0.43], $\tilde{d}$ = -0.39 [0.24], 90% CI [0.-1.48, -0.02], $p_{<0}$ = 0.96) and its interaction with biodiversity ($\tilde{\beta}$ = 1.04 [0.63], $\tilde{d}$ = 0.57 [0.34], 90% CI [0.07, 2.17], $p_{>0}$ = 0.96). After further regularizing model parameters to achieve convergence and adequate sampling using $\beta \sim \mathrm{Normal}(0,1)$ for fixed effects and $\sigma \sim \mathrm{Half-Cauchy}(0,1)$ for random effects, we also observed the expected main effect for starvation risk ($\tilde{\beta}$ = -0.49 [0.29], $\tilde{d}$ = -0.27 [0.16], 90% CI [-1.04, -0.03], $p_{<0}$ = 0.96). These findings further bolster the robustness of the results reported in the main text, which do not rely on the biasing assumption of MCAR data and are more inferentially reliable in virtue of the greater statistical power used to estimate them.

Parental care

As described in the main text, we included infant parental care as a covariate rather than a separate outcome measure in our main model so as to properly assess alloparental care, as well as to avoid confounding potentially distinct influences on paternal and other allomaternal caregivers. As an additional exploratory supplementary analysis, however, we estimated a model for infant parental care with the same effects used to predict allomaternal care. In addition, we included a measure of the degree of polygeny within a society (SCCS v860)8 to assess how parental investment varies as a function of marriage practices. In contrast to allomaternal care, infant parental care was not meaningfully associated with productivity ($\tilde{\beta}$ = 0.39 [0.33], $\tilde{d}$ = -0.22 [0.18], 90% CI [-0.18, 0.93], $p_{>0}$ = 0.87), biodiversity ($\tilde{\beta}$ = 0.21 [0.28], $\tilde{d}$ = 0.12 [0.15], 90% CI [-0.25, 0.67], $p_{>0}$ = 0.78), or their interaction ($\tilde{\beta}$ = 0.03 [0.49], $\tilde{d}$ = 0.02 [0.27], 90% CI [-0.74, 0.84], $p_{>0}$ = 0.53). Similar to infant allomaternal care, however, starvation risk was found to reduce parental care ($\tilde{\beta}$ = -0.41 [0.20], $\tilde{d}$ = -0.23 [0.11], 90% CI [-0.76, -0.07], $p_{<0}$ = 0.97). Agriculture also had a small and highly uncertain effect ($\tilde{\beta}$ = -0.15 [0.79], $\tilde{d}$ = -0.09 [0.44], 90% CI [-1.37, 1.23], $p_{<0}$ = 0.58). Consistent with prior research[9], pathogen stress had a clear negative effect on parental care ($\tilde{\beta}$ = -0.50 [0.29], $\tilde{d}$ = -0.28 [0.16], 90% CI [-0.99, -0.01], $p_{<0}$ = 0.95), along with modest and moderately uncertain negative effects for food storage ($\tilde{\beta}$ = -0.57 [0.39], $\tilde{d}$ = -0.32 [0.21], 90% CI [-1.20, 0.06], $p_{<0}$ = 0.93) and polygeny ($\tilde{\beta}$ = -0.77 [0.66], $\tilde{d}$ = -0.43 [0.36], 90% CI [-1.84, 0.27], $p_{<0}$ = 0.89).

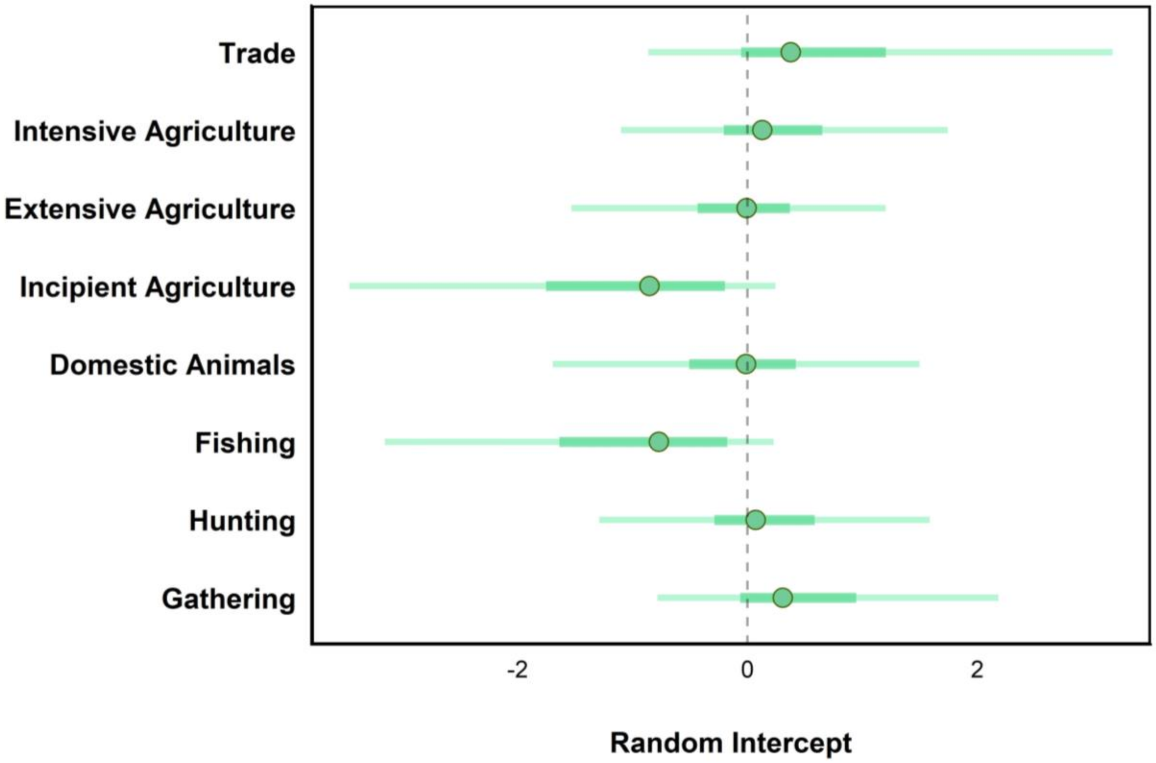

Fig. S1. Random intercepts for primary subsistence mode. Predicted link-scale deviations from the population-level intercept for primary subsistence mode. Note that the presence of agriculture is controlled for as a fixed effect in the main model, such that the agricultural deviations presented here are independent of this main effect. Circles represent the expected posterior value, with 50% and 90% credible intervals indicated by the thicker and thinner bars, respectively.

Appendix SI References

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