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The evolution of daily food sharing: A Bayesian phylogenetic analysis

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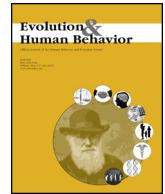
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The evolution of daily food sharing: A Bayesian phylogenetic analysis

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ABSTRACT

Some human subsistence economies are characterized by extensive daily food sharing networks, which may buffer the risk of shortfalls and facilitate cooperative production and divisions of labor among households. Comparative studies of human food sharing can assess the generalizability of this theory across time, space, and diverse lifeways. Here we test several predictions about daily sharing norms—which presumably reflect realized cooperative behavior—in a globally representative sample of nonindustrial societies (the Standard Cross-Cultural Sample), while controlling for multiple sources of autocorrelation among societies using Bayesian multilevel models. Consistent with a risk-buffering function, we find that sharing is less likely in societies with alternative means of smoothing production and consumption such as animal husbandry, food storage, and external trade. Further, food sharing was tightly linked to labor sharing, indicating gains to cooperative production and perhaps divisions of labor. We found a small phylogenetic signal for food sharing (captured by a supertree of human populations based on genetic and linguistic data) that was mediated by food storage and social stratification. Food sharing norms reliably emerge as part of cooperative economies across time and space but are culled by innovations that facilitate self-reliant production.

1. Introduction

1.1. Background

Phylogenetic perspectives on food sharing (hereafter ‘sharing’) highlight that human sharing is unique among primates in its frequency and broad social scope: among hunter-gatherers, sharing often occurs both within and between households on a daily basis (Gurven, 2004; Jaeggi & Gurven, 2013a; Winterhalder, 1996a). This unique pattern is thought to have co-evolved with major derived features of human life histories such as a prolonged juvenile period, late age of peak productivity, and a long post-reproductive lifespan, which depend upon and facilitate intergenerational food transfers, respectively (Hawkes, O’Connell, Blurton-Jones, Alvarez, & Charnov, 1998; Hooper, Gurven, Winking, & Kaplan, 2015; Kaplan, Hill, Lancaster, & Magdalena Hurtado, 2000). Furthermore, inter-household sharing can be an effective strategy to minimize the risk of food shortage, especially when (1) there is high variation in production rates and (2) that variation is relatively uncorrelated among individuals (Winterhalder, 1986). Thus, daily sharing supports our slow life history through intergenerational investment and facilitates exploitation of a risky foraging niche through reciprocal sharing among independent producers (Jaeggi & Gurven,

2013a). In addition, sharing can also act as a costly signal of phenotypic quality or cooperative intent (Hawkes, 1991; Smith & Bliege Bird, 2005), potentially resulting in gains in status and associated fitness benefits (Smith, 2004; von Rueden, Gurven, & Kaplan, 2008; von Rueden & Jaeggi, 2016). As such, sharing food may result in receiving other commodities such as sick care (Gurven, Hill, & Hurtado, 2000) or coalitionary support (Patton, 2005).

Human food sharing is also patterned by a multitude of cultural norms, which specify how to distribute food, who is expected to share with whom, etc. (see Gurven, Allen-Arave, Hill, & Hurtado, 2000; Patton, 2005 for examples). The cultural evolution and enforced maintenance of norms may be a necessary condition for extensive cooperation among unrelated individuals as they offer solutions to group coordination problems (Alvard & Nolin, 2002; Boyd & Richerson, 1994). For instance, Kaplan and Gurven (2005) argue that norms are necessary for extensive communal food sharing networks because they help prevent costly disputes, and that sharing norms change in response to food production and social structure. Thus, we expect cultural norms (which could also be called ‘institutions’) for daily sharing in societies where they can solve recurring problems such as the aforementioned risk of shortfalls or the need to invest in younger families who have yet to reach peak productivity and/or are burdened by highly dependent

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Table 1
Study predictions.

Prediction	Direction	Rationale
1. Hunting	+	Stochastic production; late age of peak production.
2. Animal Husbandry	–	No daily variance in production; smoothing consumption via ‘live-stock.’
3. Food Storage	–	Smoothing consumption via accumulated surplus.
4. Unpredictable Ecology	+	Unpredictable environments ≈ unpredictable production; need for risk-buffering.
5. Labor Sharing	+	Generalized sharing across currencies; cooperative socioecology.
6. External Trade	–	Smoothing consumption via market goods.
7. Community Size	–	Risk of free-riding in larger groups.
8. Social Stratification	–	Skimming of surplus by elites; taxation and redistribution.

offspring.

A recent study demonstrated the ubiquity of beyond-household sharing customs in non-industrial societies and found support for its association with occasional food-destroying natural hazards (Ember, Skogsgard, Ringen, & Farrer, 2018). However, there is tremendous cross-cultural variability in the scope of sharing customs; *daily* sharing among households was relatively rare ($\sim 1/3$ of societies) and was unrelated to those hazards. We suspect that this is because *daily* sharing is only expected in response to *daily* fluctuations in food supply. In particular, we expect *daily* sharing in societies with a high need to buffer the risk of shortfalls associated with certain modes of production and no alternative means for doing so, as well as with a socioecology that facilitates reciprocal cooperation. Below we elaborate our specific predictions for the evolution of *daily* sharing (see Table 1).

1.2. Predictions

Foraging, in contrast to other forms of subsistence such as horticulture, intensive agriculture, and pastoralism, is characterized by high variance in daily production (return rates). Hunting returns have particularly high variance and zero-return rates (Kaplan, 1985; McElreath & Koster, 2014), and therefore invite reciprocal sharing as a way to buffer risk. Hunting skill also peaks late in life (Gurven, Kaplan, & Gutierrez, 2006; Kaplan et al., 2000) necessitating intergenerational investment, and provides a particularly reliable signal of phenotypic quality, which can be efficiently broadcast through sharing (Gurven et al., 2000; Smith & Bliege Bird, 2005). Lastly, hunted foods come in large packages that may not be economically defensible and thus invite sharing in the form of tolerated theft (Blurton-Jones, 1984; Hawkes, 1993; Winterhalder, 1996b). For all these reasons, we expect that *daily* food sharing norms will be more prevalent among societies that rely more on hunting for subsistence (Prediction 1).

In contrast, food production in subsistence systems based on animal husbandry does not vary on a daily basis and may be more predictable than foraging. Future food supply is embodied in animals (hence the name ‘livestock’), smoothing production and consumption. Moreover, variance in livestock production is more related to inherited wealth and property than the stochastic, skill-intensive prey-encounters of hunting—thus reducing the utility of sharing. While subsistence economies oriented around livestock may benefit from seasonal sharing to increase diet breadth or buffer against unpredictable animal loss (Aktipis, Cronk, & de Aguiar, 2011; Richerson, Mulder, & Vila, 1996), *daily* sharing between households is not expected (Prediction 2).

Sharing is facilitated by stochastic overproduction (e.g., large game) wherein some food would go to waste if the producer did not share. Reciprocal sharing during periods of energetic surplus thus reduces risk at a relatively low cost to the sharer (Cashdan, 1985; Winterhalder, 1996a). However, if the surplus food can be stored and accumulated, then consumption is smoothed, and the producer need not risk defection by their sharing partner; in effect, one can share with one’s future self. Therefore, we predict that *daily* sharing will be less likely in the presence of food storage technology (Prediction 3).

Finally, some extrinsic environmental factors (e.g., climate) can

increase variability in food production and increase the risk of shortage. Thus, we include measures of predictability for precipitation, temperature, and net primary productivity as proxies of unpredictability in subsistence. Assuming that environmental predictability affects the predictability of food production, we expect that *daily* sharing customs will be more likely in less predictable environments (Prediction 4).

In addition to the dynamics of food production, the payoff for sharing may be impacted by social structure, reciprocal exchange of other commodities within the community, and the opportunity for external market exchange. For instance, societies with extensive cooperation in other domains provide the opportunity for trade (e.g., food for sick care, coalitionary support, or labor), and thus generalize the value of sharing. We expect that societies with *daily* labor sharing norms (the only other available measure of *daily* cooperation cross-culturally) will be more likely to also have a *daily* food sharing norm (Prediction 5).

Conversely, participation in external markets may disincentivize sharing by providing alternative means of smoothing consumption without the risk of cheating associated with reciprocity (see Kranton, 1996 for a theoretical model; for empirical examples see Behrens, 1992; Ensminger, 1996; Franzen & Eaves, 2007). We expect that the presence of external trade of food will decrease the likelihood of sharing (Prediction 6). However, see Gurven, Jaeggi, von Rueden, Hooper, and Kaplan (2015) for evidence that market integration need not displace reciprocal exchange.

As the number of group members increases, cooperation based on reciprocity is threatened by heightened risk of free-riding and reduced ability to assess the behavior of partners (Boyd & Richerson, 1988; Kaplan & Gurven, 2005). While we do not have direct measures of the size of sharing networks, we use the mean size of local community as a proxy and expect that smaller communities will be more likely to have *daily* food sharing norms than larger communities (Prediction 7)—insofar as community size is an effective proxy of the size of sharing networks. But note that while reciprocity breaks down in large groups, cooperation based on enforced norms does not (Fehr, Fischbacher, & Gächter, 2002), and thus the strength of this effect should be roughly inverse to the extent that sharing norms are enforced and free-riders punished—data that we lack.

Social stratification could reduce *daily* sharing as surpluses are skimmed off by elites, perhaps in return for other services such as protection (Hooper, Kaplan, & Boone, 2010). Similarly, reciprocity is less common among more hierarchical primate groups as commodities flow up the hierarchy (Barrett, Henzi, Weingrill, Lycett, & Hill, 1999; Jaeggi, Stevens, & Van Schaik, 2010). Thus, we expect that sharing will be less likely in stratified societies than egalitarian societies (Prediction 8). Notably, elites may also skim surplus for purposes of later redistribution, a form of ‘managerial mutualism’ (Smith & Choi, 2007) that could also buffer risk and smooth consumption. However, in this study we focus on inter-household sharing rather than hierarchical redistribution, which is unlikely to be coded as *daily* sharing given our definitions (see 2.1.).

1.3. The comparative method

This study uses the comparative method to test adaptive hypotheses about cross-cultural variation in sharing norms and, like all comparative studies, is subject to a breadth-depth trade off. The advantage of this breadth (a diverse array of non-industrial societies from around the world) is that we can test for the convergent evolution (independent emergence) of cultural norms as general solutions to adaptive problems across time and space (Mace & Pagel, 1994; Nunn, 2011). Worldwide cross-cultural studies can also be construed as testing hypotheses about species-typical reaction norms, or ‘context-dependent human universals’ (Chapais, 2014; Jaeggi, Boose, White, & Gurven, 2016). From either perspective, comparative studies can offer stronger evidence for the adaptive value of a norm than case-studies of single cultures.

The disadvantages of this method include, in practice if not necessarily in principle, noisy estimation of data, reliance on proxies rather than the actual phenomena of interest, and loss of within-culture variance. The latter predisposes findings from comparative studies to the ecological fallacy/Simpson’s paradox: correlations at the level of groups need not reflect individual-level processes (Lawson et al., 2015; Pollet, Tybur, Frankenhuys, & Rickard, 2014; Ross & Winterhalder, 2016). This problem is attenuated when studying group-level phenomena (here: sharing norms), but nonetheless we caution that drivers of sharing norms might not always drive variation in sharing behavior among individuals. While comparative studies can avoid these limitations by incorporating individual-level data and testing hypotheses at multiple levels of aggregation (e.g., Ross & Winterhalder, 2016), we lack individual-level sharing data from our sample societies.

Valid inference about convergent evolution relies on observations being statistically independent. Yet, just as there are no independent species, there are no truly independent societies—all populations have some shared history that may affect their current trait values. Failure to take historical relatedness into account can greatly increase false-positive risk, a problem that is well known to evolutionary biologists and routinely controlled for by explicitly modelling the covariance among observations due to phylogeny (Harvey & Pagel, 1991). The history of worldwide cross-cultural research pre-dates the use of phylogenetic regression models, but the non-independence among human societies (‘Galton’s problem’) has been a concern since the inception of the comparative method in anthropology (Tylor, 1889). To overcome this problem in the absence of phylogenetic information, comparative anthropologists have often relied on samples such as the Standard Cross Cultural Sample (SCCS) (Murdock & White, 1969) (of which our dataset is a subset), which attempt to minimize the historical relatedness of sampled societies in hope that societies were sufficiently distant so as to be effectively independent. However, there is accumulating evidence of autocorrelation even in samples such as the SCCS (Dow & Eff, 2008; Minocher, Duda, & Jaeggi, 2019).

To address the problem of non-independence, we utilized a recently published phylogenetic ‘supertree’ (i.e., a tree of trees) of human populations based on genetic and linguistic data (Duda & Zrzavý, 2016, 2019). While many previous cross-cultural studies have employed phylogenetic methods (Mace & Holden, 2005; Mace & Pagel, 1994; Nunn, 2011), a reliable global phylogeny has been lacking. By using this phylogeny, we can not only control for non-independence, but also considerably broaden the sample and leverage the entire breadth of the ethnographic record, thus maximizing the power of the phylogenetic approach to detect convergent evolution.

In addition to phylogeny, we control for non-independence due to the time at which the ethnographic data were collected (the ‘ethnographic present’, median = 1935, range = 1634–1965), which may capture temporal fluctuations in ethnographers’ biases or foci that could affect the likelihood of recording sharing practices. While we initially planned to model the effect of geographic location in addition to phylogeny and ethnographic present, we found that phylogenetic distance and geographic distance were highly correlated (median $\rho = 0.88$, 90%

HPDI = [0.79, 0.99]) creating problems of interpretation and model-fitting. Thus, we excluded geographic location and note that population history cannot be easily disentangled from spatial proximity (Manica, Prugnolle, & Balloux, 2005; Sokal, 1988); both may capture diverse processes generating similarity such as vertical transmission of genes or culture, horizontal transmission (diffusion), niche conservatism or shared ecology. We present results from a model controlling for phylogeny in the main text, and provide results when substituting geographic distance for phylogeny in the supplemental material.

2. Materials and methods

2.1. Data description

Our outcome variable (daily food sharing) and the daily labor sharing predictor come from Ember et al. (2018). In that study, these variables were coded from ethnographic data based on the following criteria:

“Does the typical household share food[labor] with other households or economic units outside the household on a daily or almost daily basis?”
1 = Yes, 0 = No.

Where ‘sharing’ is defined as “the noncoerced giving of aid from one or more household members to one or more individuals within other households.” Sharing norms were coded based on ‘typical’ households, not elites/leaders. This distinction rules out vertical transfers from commoners to elites—or vice-versa, e.g., wealthy Orma pastoralists who gave their surplus milk to the poor (Ensminger, 1996). Coders used eHRAF World Cultures (HRAF, n.d.) and the Human Relations Area Files’ paper collection to find relevant ethnographic materials. See Ember et al. (2018) for additional details of the coding procedure.

We describe all study variables in Table 2. A few of our predictors (food storage, external trade, and social stratification) were dichotomized from their original ordinal scales because we did not believe that their ordinal levels were theoretically relevant for our study. For those variables, we reasoned that dichotomous comparisons (present/absent) were more sensible (but see Section 3.2 for robustness checks).

Before conducting our analyses, we checked for multicollinearity among predictors using the generalized variance inflation factor (GVIF). All GVIF values fell below the commonly used threshold of 10, indicating that our models should not suffer from multicollinearity. While some authors recommend thresholds as low as 3 (Zuur, Ieno, & Elphick, 2010), even a GVIF higher than 10 need not imply serious issues or demand that a predictor be dropped (O’Brien, 2007). Our use of regularizing priors (see Analysis for details) should also reduce variance inflation, as is the case for shrinkage techniques such as ridge regression (Dormann et al., 2013).

2.2. Analysis

2.2.1. Statistical framework

We fit our models and present results in a Bayesian framework (Gelman et al., 2013) where, rather than reporting point estimates and *p*-values, we emphasize effect sizes (Cohen’s *d* on the logit scale), the posterior probability that the effect is in the expected direction, and visualization of model predictions. Posterior predictive plots help the reader understand the impact of a predictor on the probability scale (i.e., the probability of daily sharing as a function of our predictors), whereas Cohen’s *d* on the latent (logit) scale offers a standardized magnitude that can easily be compared to other model parameters and effect sizes from other studies. Unlike the probability scale, latent scale effect sizes are also invariant to the choice of reference category (i.e., the effect size is independent of the intercept). The posterior probability (‘PP’) is calculated as the proportion of the posterior probability distribution that falls on the expected side of 0, which directly expresses our model’s confidence in a given association.

Table 2
Description of study variables.

Name	Original Source	Original Scale	Transformation
Hunting	(Murdock & Morrow, 1970)	Ordinal scale from 0 to 100% dependence, with deciles as cutpoints.	Centered and standardized by 2 SD
Animal Husbandry	(Murdock & Morrow, 1970)	Ordinal scale from 0 to 100% dependence, with deciles as cutpoints.	Centered and standardized by 2 SD
External Trade	(Murdock & Morrow, 1970)	1 = No Trade 2 = Food Imports absent although trade present 3 = Salt or Minerals only 4 ≤ 10% of food (90% from local extractive sources) 5 ≤ 50% of food, and less than any single local source 6 ≥ 50% of food	Dichotomized into present (5–6 on original scale) or minimal/absent (1–4 on original scale).
Food Storage	(Murdock & Morrow, 1970)	1 = None 2 = Individual Households 3 = Communal Facilities 4 = Political agent controlled repositories 5 = Economic agent controlled repositories	Dichotomized into food storage present (2–4 on original scale) or food storage absent (1 on original scale).
Social Stratification	(Murdock & Provost, 1973)	1 = Egalitarian 2 = Hereditary Slavery 3 = 2 social classes, no castes/slavery 4 = 2 social classes, castes/slavery 5 = 3 social classes or castes, with or without slavery	Dichotomized into egalitarian (1 on the original scale) and stratified (2–5 on the original scale).
Community Size (mean size of local community)	(Gray, 1999)	1 = Fewer than 50 2 = 50–99 3 = 100–199 4 = 200–399 5 = 400–1000 6 = 1000 without any town of > 5000 7 = One or more towns of 5000–50,000 8 = One or more cities of > 50,000	Centered and standardized by 2 SD
Precipitation Predictability	Kirby et al., 2016), based upon Colwell's (1974) information theoretic index.	Continuous measure between 0 and 1	Centered and standardized by 2 SD
Temperature Predictability	Kirby et al., 2016), based upon Colwell's (1974) information theoretic index.	Continuous measure between 0 and 1	Centered and standardized by 2 SD
Net Primary Productivity (NPP) Predictability	Kirby et al., 2016), based upon Colwell's (1974) information theoretic index.	Continuous measure between 0 and 1	Centered and standardized by 2 SD

2.2.2. Model definition

We model sharing using logistic multilevel regression models, utilizing regularizing priors to impose conservatism on parameter estimates. Phylogenetic distance and similarity in the ethnographic present are captured by pairwise distance matrices, which can be modeled as continuous random effects using Gaussian Process regression (McElreath, 2016; Rasmussen & Williams, 2006). This approach leverages the standard multilevel strategy of pooling variance and regularizing hyper-parameters, while expanding upon the more commonly used discrete random effects (like individual, group, or location ID) for which the distance, and thus expected covariance, between categories is unknown. The full model, including random effects for phylogeny and ethnographic present, was defined as:

Daily Sharing~Bernoulli(p)

$$\text{logit}(p) = \beta_0 + \gamma_{\text{Phylogeny}} + \gamma_{\text{EP}} + \beta_1 \text{Hunting} + \beta_2 \text{Food Store} + \beta_3 \text{Strat} \\ + \beta_4 \text{External Trade} + \beta_5 \text{Animal Hus} + \beta_6 \text{Precip Pred} \\ + \beta_7 \text{Temp Pred} + \beta_8 \text{NPP Pred} + \beta_9 \text{Labor Sharing} \\ + \beta_{10} \text{Comm Size}$$

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

$$\gamma \sim \text{MVNormal}(0 \dots N \text{ Societies}, K)$$

$$K_{ij} \sim \eta \exp(-\rho D_{ij})$$

$$\eta \sim \text{Exponential}(0.5)$$

$$\rho \sim \text{Exponential}(0.5).$$

Sharing is modeled as a Bernoulli distribution where the probability of sharing is a logit-linear function of main effects β and random effects γ . The number of random effects for phylogeny and ethnographic present is equal to the number of societies, and the variance of these random effects is pooled according to the Gaussian Process covariance function K . K states that the maximum covariance between any two societies η declines exponentially at rate ρ as the distance (patristic/temporal) between societies grows. This covariance function is akin to an Ornstein-Uhlenbeck (OU) model of evolution (see Fig. 2). We prefer these functions over the more commonly employed Brownian Motion (BM) models because BM assumes that variance is proportional to time, and thus phenotypic variance would become infinitely large as time approaches infinity. OU models simply add ‘friction’ to the random walk process of BM models, which can reflect realistic phenotypic constraints. OU models of evolution have also performed well in empirical studies when compared to alternative models of phenotypic change (Butler & King, 2004; Gartner et al., 2009). See Nunn (2011) for discussion of different models of evolutionary change in the context of

the comparative method and McElreath (2016) for a practical introduction to Gaussian Process covariance functions.

Priors for the Gaussian Process function are modeled as coming from the exponential distribution with rate parameter = 0.5. It is easiest to understand these priors in terms of the covariance function parameterized by η and ρ . The function is regularized in the sense that small values for the maximum covariance are more likely than large values, and covariance is more likely to decline rapidly with distance than slowly. Distance values were standardized by their respective maxima so that all values fell in the interval [0,1]. See Supplement A for visualization of the posterior covariance functions for phylogeny and ethnographic present.

Priors for main effects are modeled as a normal distribution centered on 0 and with a standard deviation of 2. On the logit scale, these are weakly-regularizing priors, in that the probability mass is highest for small values, and little probability is afforded to very large values. Using such priors greatly reduces both Type-S (inferring the wrong sign for an effect) and Type-M error (inferring that an effect is of greater magnitude than it is) (Gelman & Carlin, 2014; Gelman & Tuerlinckx, 2000). The use of regularizing priors is analogous to ‘penalized likelihood’ approaches in non-Bayesian frameworks (Green, 1998).

2.2.3. Missing data

For some predictors, the number of observations was less than the number of observed outcomes. Rather than performing complete-case analysis, i.e. excluding all societies with missing values, which implicitly assumes that data are missing at random, we utilized Bayesian imputation for the missing values (which also assumes missing at random). Bayesian imputation replaces the missing values with a parameter (or, in the case of discrete missing values, marginalizes over the possible outcomes), which propagates uncertainty in parameter estimation and allows us to use the full dataset. We use all other observed variables, including the outcome, to predict missing observations—an approach that minimizes bias in imputation and parameter estimates (Bartlett, Frost, & Carpenter, 2011; Collins, Schafer, & Kam, 2001). Our imputation procedure thus makes better use of the valuable ethnographic record and imposes no additional assumptions on missingness than would be implied by a complete-case analysis.

2.2.4. Model comparison and Bayesian R^2

To evaluate whether including phylogeny and ethnographic present improved model performance, we fit three nested submodels of the model defined in section 2.2.2. These models were (i) main effects and phylogeny, (ii) main effects and EP, and (iii) main effects only. Using the Watanabe-Akaike Information Criterion (WAIC), we calculated model weights—the probability that a given model will perform best on new data, relative to other candidate models (McElreath, 2016).

Additionally, recent extensions of the coefficient of determination R^2 or ‘variance explained’ generalize the familiar statistic to non-Gaussian distributions (Gelman, Goodrich, Gabry, & Ali, 2017; Nakagawa, Johnson, & Schielzeth, 2017) and allow us to partition the proportion of variance captured by our main theoretical variables (fixed effects) and the variance captured by phylogeny and ethnographic present (EP). We use these statistics to evaluate the relative importance of each in explaining sharing variation in our sample. We also examined whether phylogenetic (or temporal) signal was mediated by other predictors, fitting a model with phylogeny and EP but no fixed effects.

2.2.5. Exploratory analyses

While we designed our models to provide the clearest tests of our hypotheses (conditional on the constraints of our data), some of our analytic decisions were subject to ‘researcher degrees of freedom,’ (Simmons, Nelson, & Simonsohn, 2011) in the sense that reasonable alternative analytic decisions could have been made that could plausibly affect our inferences. These decisions include our choice of phylogenetic tree, the decision to use phylogenetic distance rather than

geographic distance, and the way that we transformed a few of our predictors. To check the robustness of our results, we conducted extensive exploratory analyses varying each of these decision points, holding everything else in the analysis constant. We also ran (i) a bivariate model where hunting was the only predictor and (ii) substituted dependence on hunting for dependence on foraging more broadly (hunting, gathering, and fishing) as alternative tests of Prediction 1. Finally, to test whether our measures of environmental predictability map on to the predictability of actual subsistence (which is what should predict sharing), we utilized data from a new cross-cultural study of foraging returns (Koster et al., 2019). Specifically, we explored the association between hunting success (i.e., a non-zero return) and environmental predictability.

2.2.6. Model fitting

All analyses were run in R 3.4.4 (R Core Team, 2017) and all models were fit using the RStan package (Stan Development Team, 2018), which fits Bayesian models using Hamiltonian Markov Chain Monte Carlo. Markov chain convergence was assessed using standard diagnostics (number of effective samples, the Gelman-Rubin diagnostic, and visual inspection of trace plots). Data and code for reproducing this analysis and all figures are available at <https://github.com/erik-ringen/phylo-foodsharing>.

3. Results

3.1. Main results

Prediction 1 was not supported as dependence on hunting was not associated with sharing (median $d = -0.21$, $PP = 0.34$; see Fig. 3). Thus, our main proxy for various proposed functions of sharing (risk-buffering, kin investment, costly signaling) failed to predict sharing. Other aspects of subsistence were consistent with our predictions: societies with external trade of food ($d = -0.68$, $PP = 0.90$), and dependence on animal husbandry ($d = -1.08$, $PP = 0.99$) were less likely to have a daily sharing norm, indicating that alternative means of smoothing consumption decreased sharing. Labor sharing ($d = 1.14$, $PP > 0.99$) and absence of food storage ($d = -1.06$, $PP = 0.98$) were also strong predictors of food sharing. Sharing may be less likely in societies with large community sizes ($d = -0.36$, $PP = 0.72$) and social stratification ($d = -0.28$, $PP = 0.72$), which are potential obstacles to reciprocal cooperation, though there was high uncertainty in those estimates. Our reference categories were egalitarian, without food storage, external trade, or labor sharing, and with all continuous predictors set to their mean values; a society with these traits had a 0.50 probability of sharing. Adding food storage, external trade, and social stratification jointly decreased the probability to 0.02, while adding labor sharing raised it to 0.88 (see Fig. 3 for uncertainty in estimates). (See Fig. 4.)

Contrary to our expectations, all three measures of environmental predictability were positively associated with sharing, albeit with varying degrees of certainty ($d = 0.24$, 0.71 , and 1.3 for precipitation, temperature, and NPP predictability, respectively; $PP = 0.32$, 0.11 , 0.01). Thus, sharing was more likely in predictable environments.

In the absence of any fixed effects, phylogeny accounted for a moderate amount of variance (median = 0.14 , 90% HPDI = $[0,0.52]$), but EP did not (median = 0.02 , 90% HPDI = $[0,0.11]$). After adding fixed effects, the phylogenetic signal was reduced to 0.03 $[0,0.12]$. The majority of variance was captured by the fixed effects (median = 0.57 , 90% HPDI = $[0.32,0.69]$). Food storage and social stratification were likely mediators of the effect of phylogeny on sharing, because those variables also showed phylogenetic signal and had direct effects on sharing (see Supplement G for details) (See Fig. 4).

Model comparison using the Watanabe-Akaike Information Criterion (WAIC) suggested that including phylogeny and EP offered little improvement in predictive power (Table 3). ‘Fixed Effects’ had the

Table 3
Model comparison using WAIC.

Model	WAIC	ΔWAIC	pWAIC	Weight
Fixed Effects	72.5	0	10.5	0.33
Fixed Effects + EP	72.6	0.1	11.5	0.32
Fixed Effects + Phylogeny + EP	73.6	1.1	13.3	0.19
Fixed Effects + Phylogeny	74	1.5	12.5	0.15

Watanabe-Akaike Information Criterion (WAIC) values for models that include phylogenetic and ethnographic present (EP) random effects, phylogenetic random effects, EP random effects, or only fixed effects (no control for phylogeny/EP). ΔWAIC is the difference between a given model and the model with the lowest WAIC. pWAIC is the effective number of parameters in each model. WAIC weights are the probabilities that a given model will perform best with new data, relative to the other candidate models (McElreath, 2016).

lowest WAIC/highest weight, followed closely by ‘Fixed Effects + EP’. None of the models clearly outperformed the others. Combined with the small conditional R^2 for both phylogeny and EP, this suggested that there is not much residual autocorrelation in our sample, at least not due to population history and time.

3.2. Exploratory results

We found that our main results are robust to (i) the use of an alternative phylogeny based on lexical data (Jäger, 2018), (ii) substituting phylogenetic distance for geographic distance, and (iii) treating social stratification and external trade as continuous predictors and log-transforming community size. We did not explore the effect of treating food storage as continuous because the higher levels of the variable (e.g., ‘Political agent controlled repositories’ vs ‘Economic agent controlled repositories’) were not theoretically relevant for our study. See Supplement sections B–D for details (Fig. 1).

Replacing hunting with foraging more broadly (i.e., hunting, gathering, or fishing) did not substantially change our results (median $d = -0.16$, $PP = 0.40$). However, in a bivariate model where hunting was the only main effect, we found that hunting was positively associated with sharing (median $d = 0.58$, $PP = 0.96$). See Supplement E for details.

While environmental predictability was positively associated with food sharing, our analysis of foraging return data from 40 foraging societies (Koster et al., 2019) offered contradictory results. Precipitation predictability was positively associated with hunting success rate, consistent with our predictions, (median $d = 1.14$, $PP = 0.98$). Temperature predictability was negatively associated ($d = -1.09$, $PP = 0.11$), and NPP predictability was unassociated with hunting

success ($d = -0.28$, $PP = 0.37$). Methodological differences in the way that zero-returns were recorded across societies limits our confidence in these findings, but, at a minimum, this suggests that our measures of environmental predictability may be poor proxies for the predictability of actual subsistence. See Supplement F for details.

4. Discussion

Food sharing is a perennial topic in the study of evolution and human behavior, but it is still important to interrogate the generalizability of theory beyond formal models and case studies. Our study leveraged the ethnographic record to test how sharing norms are affected by subsistence and socioecology in 73 nonindustrial societies. Our findings generally support risk-buffering hypotheses: sharing was most likely when individuals cannot store food, engage in external markets, or retain surplus in the form of livestock. A positive association between labor and food sharing suggests the possibility of exchange between multiple currencies in cooperative socioecologies (e.g., Hames, 1987; Jaeggi, Hooper, Beheim, Kaplan, & Gurven, 2016). Thus, (daily) sharing norms emerge as part of cooperative economies across time and space but are culled by innovations that facilitate self-reliant production and by social structures that hinder reciprocity (e.g., large community sizes, social stratification, and external trade). These findings are largely consistent with formal models of sharing and case studies in small-scale subsistence economies (Gurven, 2004; Hooper et al., 2015; Kaplan et al., 1985; Winterhalder, 1986), and support the generalizability of their predictions.

Surprisingly, sharing was not associated with hunting once other predictors were included, even though reliance on hunting should capture not only the need for risk-buffering but also investment in younger kin, opportunities for costly signaling, and low economic defensibility. This finding is somewhat difficult to interpret as few if any societies rely to a large degree on hunting and have the traits here found to reduce sharing (food storage, animal husbandry, etc.), hence this counterfactual might not be meaningfully estimated. If real, this finding would imply that the production of foods with sharing-prone features (high yield/high variance, late age of peak production, high levels of skill required, low economic defensibility) in and of itself does not necessarily lead to daily sharing between households in the presence of food storage, animal husbandry, etc., and that the bivariate effect of hunting may be capturing the absence of these traits rather than a direct effect of hunting on sharing (in Supplement E we explore the bivariate relationships between hunting and all other predictors). However, the essence of resource production with high yield/high variance does spontaneously lead to reciprocal sharing in virtual



Fig. 1. Sample societies and distribution of daily sharing.

Global distribution of daily food sharing norms in our sample ($N = 73$ societies). Black dots indicate presence (19/73 societies), red dots indicate absence.

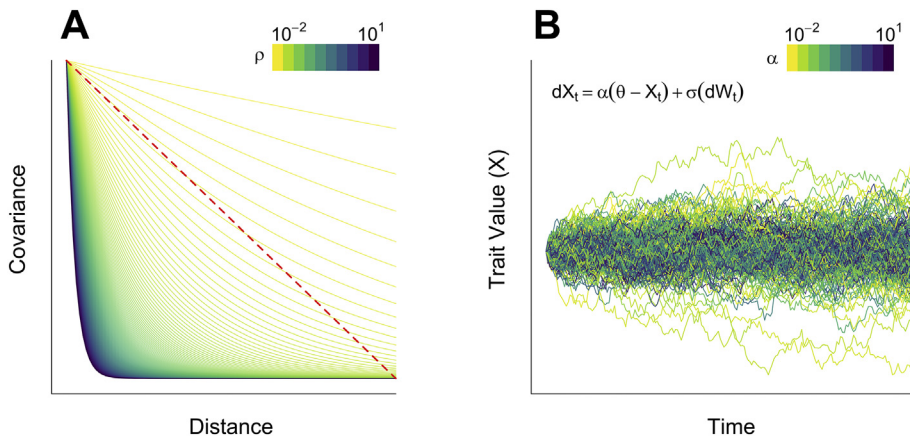


Fig. 2. Correspondence between GP Covariance Function and OU Model of Evolution.

A: Simulated Gaussian Process (GP) covariance functions, as described in our model definition. Darker lines denote larger values of ρ , where the covariance between societies declines rapidly with phylogenetic/temporal distance. The dashed diagonal line represents a linear covariance function, which is assumed by Brownian Motion (BM) models of trait evolution. **B:** Simulated evolution of a trait following an Ornstein-Uhlenbeck model of evolution, which is the implicit process model of our covariance function. Darker lines denote larger values of α (which is analogous to ρ in the GP covariance function), where the trait does not drift as far away from the optimal trait value θ . W_t denotes the BM process of drift. For both sets of simulations, we set the variance/drift parameters (η and σ , respectively) equal to 1.

foraging experiments (Kaplan, Schniter, Smith, & Wilson, 2012; Kaplan, Schniter, Smith, & Wilson, 2018), and hunted game typically does come in large packages that are not economically defensible (Blurton-Jones, 1984; Hawkes, 1993; Winterhalder, 1996b), which makes sharing inevitable (at least in the absence of strong property rights). Thus, the overall weight of theory, ethnography, and experiments still strongly predicts that a greater reliance on hunting, or other risky foods, should increase sharing.

Contrary to Prediction 4, we found that environmental predictability was positively associated with sharing. This reversal of expectations is puzzling, but these measures may be poor proxies of the

predictability of actual food production, which is the construct we sought to measure. To illustrate this point, variance in food availability need not imply variance in actual food intake among highly-encephalized species. For instance, large-brained catarrhines have consistent food consumption even in variable environments ('cognitive buffering') (van Woerden, Willems, van Schaik, & Isler, 2012). These predictability measures also likely capture a large amount of unmeasured ecological variation, confounding interpretation. While more precise measures of subsistence predictability could be derived from quantitative data (e.g., zero-return rates, inter-household variance in production), most ethnographic sources are insufficient to estimate

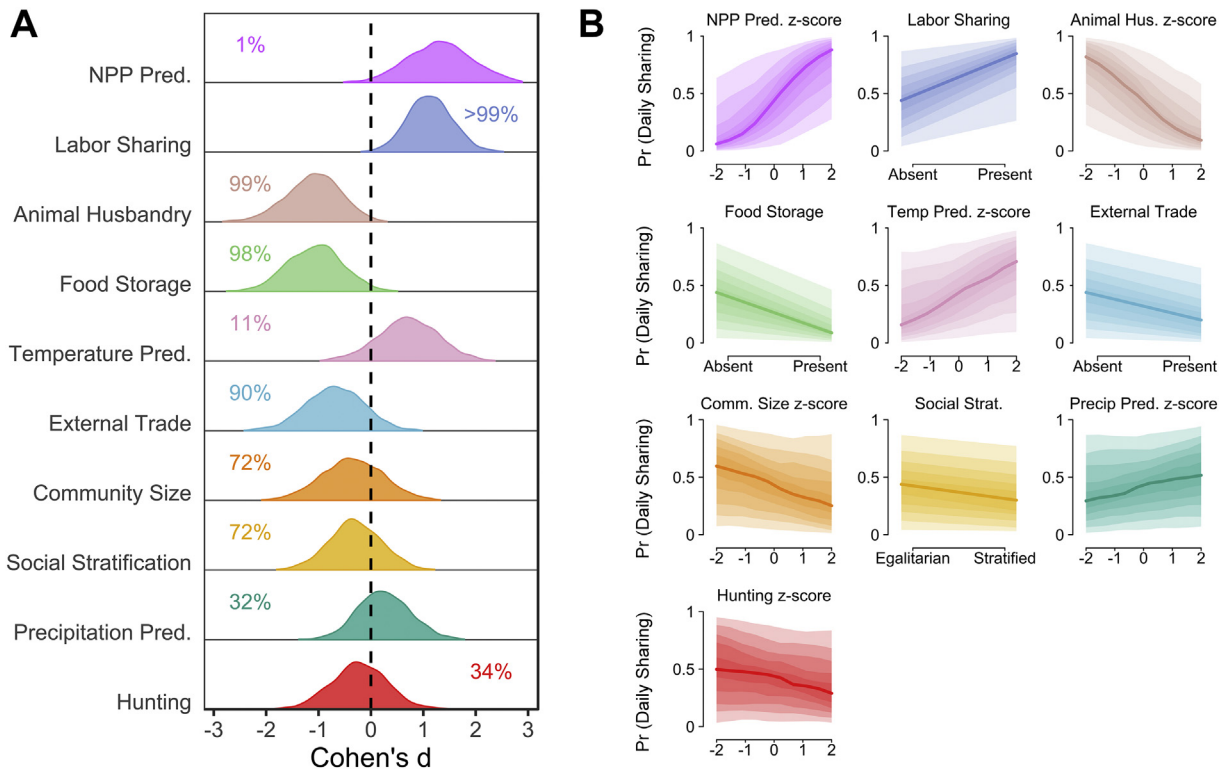


Fig. 3. Predictors of sharing.

A: Posterior distribution of effect sizes on the logit scale, sorted by the absolute value of the effect size. Percentages indicate the proportion of the posterior that was in the predicted direction. Effect sizes were converted from the logit scale to Cohen's d following Borenstein, Hedges, Higgins, and Rothstein (2011). Effect sizes for binary predictors represent presence/absence and effect sizes for continuous predictors represent a + 2 standard deviation increase to facilitate comparison between discrete and continuous effect sizes (Gelman, 2008). A small number of posterior samples from the extreme tails were suppressed to enhance visualization. **B:** Posterior-predictive plots on the probability scale. Shaded intervals of increasing opacity represent quantiles of the 90% credible interval, with darker shades reflecting the relative increase in probability mass. 'Z-score' axes indicate standard deviations. Our reference categories were: egalitarian, without food storage, external trade, or labor sharing, and with all continuous predictors set to their mean values.

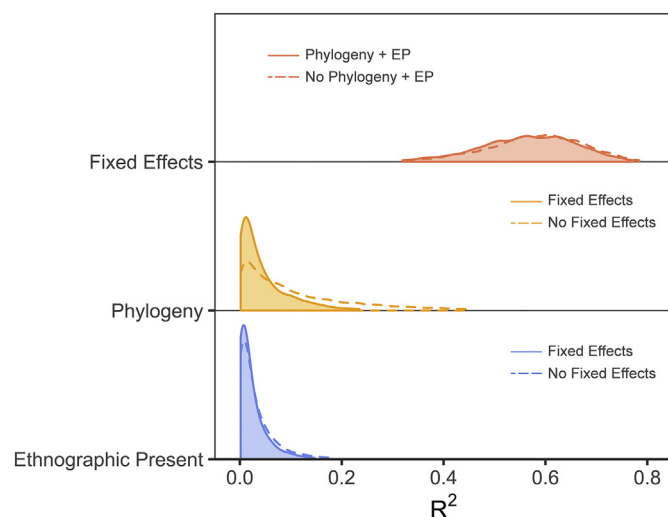


Fig. 4. Variance Captured by fixed effects, phylogeny, and ethnographic present.

Variance captured by all fixed effects, phylogeny, and ethnographic present. The denominator of these statistics includes all three sources of variance, plus the latent scale variance of the Bernoulli distribution that arises from the logit link. Dashed lines represent each R^2 in the absence of phylogeny/EP or in the absence of the fixed effects. The variance captured by phylogeny was mediated by fixed effect predictors.

these rates. In our exploratory analysis of foraging returns in 40 societies (Koster et al., 2019), we found that the associations between hunting success rates and environmental predictability were inconsistent with our food sharing results, casting doubt on the usefulness of those measures as proxies of subsistence predictability (Supplement F). Previous cross-cultural studies have found subtle interactions between environmental predictability and other ecological variables (Botero et al., 2014), but we abstained from further analyses in the absence of clear theoretical predictions.

It is important to note that our findings are not inconsistent with some other evolutionary theories of food sharing. Some of our findings, such as the negative association between animal husbandry and sharing, could also be driven by the stability of group structure. When group membership is unstable (as is the case for some pastoralists), reciprocal sharing can break down due to ephemeral interactions and an inability to punish free-riders (Smith et al., 2016). Thus, while our results are congruent with risk-buffering theories, they do not rule out competing or complementary explanations of sharing. Data on intra-societal variation or changes in socioecology over time would be particularly useful in parsing out the importance of factors such as group stability.

The limited role of phylogeny suggests that sharing norms adapt rapidly to local socioecologies. This finding contrasts with marriage norms, which show a strong phylogenetic signal in the SCCS (Minocher et al., 2019), but is congruent with a meta-analysis of food sharing which found virtually no phylogenetic signal for reciprocal sharing (Jaeggi & Gurven, 2013b), as well as with case studies where sharing norms change rapidly depending on socioecological context (e.g., Ache in forest vs reservation (Gurven, Hill, & Kaplan, 2002); !Kung vs //Gana Bushmen [Cashdan, 1980]). That said, the relationship between evolutionary rate and phylogenetic signal is not linear. We also reiterate that it is difficult to disentangle population history from geographic proximity—which means that ‘phylogeny’ might also capture horizontal transmission/diffusion and unmeasured environmental similarity. Indeed, our findings were qualitatively the same when substituting phylogenetic distance for geographic distance.

We emphasize two major methodological limitations in this study: cross-sectional data and Simpson's paradox. With diachronic data, we

could infer how sharing norms change within societies over time and gain insights into the actual process of cultural change. The danger of Simpson's paradox (an ecological fallacy) comes from conflating group-level patterns with individual processes. While sharing norms are reasonably construed as group-level phenomena, some of our predictions come from a behavioral ecology literature focused on the strategic sharing behavior of individuals. Our inferences cannot be safely extended to individual behavior nor individual endorsement of cultural norms. A productive future direction would be to explore the cross-cultural congruence between group-level sharing norms and individual endorsement of or adherence to the norms. Despite these limitations, consistent cross-cultural correlations offer strong evidence for adaptive hypotheses, and thus our results can guide future studies of human cooperation by highlighting some principal drivers of variation in sharing.

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Declaration of interests

The authors declare no competing interests.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.evolhumbehav.2019.04.003>.

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