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Developing a Modern Toolkit to Study the Co-evolution of Human Subsistence & Social Behavior

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Doctor of Philosophy

Anthropology

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An abstract of
a dissertation submitted to the Faculty of the
James T. Laney School of Graduate Studies of Emory University
in partial fulfillment of the requirements for the degree of
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Abstract

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By Erik J. Ringen

This dissertation aimed to develop a modern theoretical and computational toolkit for comparative research, with applications to three studies of the co-evolution of human subsistence and social behavior. In Chapter 2, I drew on a cross-cultural sample of 73 societies and a phylogenetic supertree of human populations to assess how cross-cultural variation in food sharing norms map onto differences in human subsistence economies and social organization. Consistent with a risk-buffering function, sharing was found to be less likely in societies with alternative means of smoothing production and consumption such as animal husbandry, food storage, and external trade. In Chapter 3, I introduced a new method for testing coevolutionary hypotheses with phylogenetic data and applied it to the question of how ‘complex’ societies evolved. I found that subsistence intensification is a leader, not a follower, in the rise of 'complex' societies worldwide. In Chapter 4, I investigated the social structure of dietary variation among Tsimane of lowland Bolivia, developing a modeling framework to estimate multilevel cultural variation from fine-grained behavioral datasets. I found that most dietary variation is structured at the household and local network level, rather than at the individual or community level. These chapters exemplify the potential for a revitalized comparative method to investigate the co-evolution of human subsistence and social behavior and offer innovations that are relevant for the study of human evolution and cross-cultural variation more broadly.

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Acknowledgements

“Wishing you godspeed, glory
There will be mountains you won't move
Still, I'll always be there for you
How I do

I let go of my claim on you, it's a free world
You look down on where you came from sometimes
But you'll have this place to call home, always”

- Frank Ocean, “Godspeed”

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Chapter 1: Introduction

Dissertation Overview

The goal of this dissertation is to develop a modern theoretical and computational toolkit for comparative research, with particular attention to the co-evolution of human subsistence and social behavior. This dissertation is written in a three-paper format with the intention of publishing each paper in a peer-reviewed journal. In the first section of this introductory chapter, I trace the history of the comparative method in anthropology and address major critiques of cross-cultural comparison. I illustrate both the importance of the comparative method for anthropology as a discipline and for inference about human variation broadly. In the second section, I focus on how the comparative method can be used to study the co-evolution of subsistence (i.e., the "how" and "what" of obtaining food) and social behavior (with an emphasis on cooperation and social structure). I provide theoretical background and aims for the three studies that comprise the body of this dissertation, each of which offer methodological innovations and demonstrate the potential of a modern comparative approach to shed light on human evolution and cross-cultural variation.

Section 1: The Comparative Method in Anthropology

The history of the comparative method is part and parcel with the history of anthropology as a science which, unlike other social sciences, is uniquely informed by ethnographic records from diverse societies around the world. In this section, I review how anthropologists since the late-19th century have used cross-cultural data to make inferences about cultural change and behavioral variation. Moreover, I highlight some major critiques of the comparative method that remain relevant for cross-cultural research.

E.B. Tylor's Big-Data

Systematic cross-cultural research began in 1889: Edward Burnett Tylor, speaking to the Royal Anthropological Institute of Great Britain and Ireland, declared that ". . . it has become evident that the great need of anthropology is that its methods should be strengthened and systematized" (Tylor 1889, 245). Tylor had spent years collecting information on marriage, residence, and descent rules from hundreds of societies, and tabulating these customs to assess the correlations (called 'adhesions' in Tylor's paper) between them. Attendees congratulated Tylor on applying a coherent statistical method to comparative research, which had previously only been attempted in qualitative terms, but there was also serious critique. William Henry Flower suggested that, when groups of communities exhibit very similar customs, they should be counted as one unit rather than many (272). Francis Galton expressed concern that "...some of the concurrences might reflect descent from a common source, so that a single character may be counted several times from its mere duplicates." These critiques, referred to as the 'units of analysis problem,' (M. Ember & Ember, 2000; Korotayev & De Munck, 2003) and 'Galton's problem' (Dow et al., 1984; Naroll, 1961) respectively, are about statistical non-independence, also called autocorrelation or pseudoreplication. To understand why these arcane-sounding statistical concepts matter for anthropology, we have to consider two interrelated ideas: generalizability and convergent evolution.

Generalizability means that results obtained from a study of some population holds elsewhere—insights from one sample of humans ought to tell us something about humans more generally. Rather than simply assume that findings generalize and wait for other researchers to conduct replication studies, generalizability and cross-cultural variation is inherent to the comparative method, which aims to sample broadly. However, it is important not to conflate broad samples with large samples. For example, in 2021 Delphi-Facebook ran a large (~250,000 responses per week), but non-representative poll on vaccine uptake in the United States that had double digit errors when compared to actual vaccination rates. In contrast, the much smaller Axios-Ipsos poll (~1000 responses per week) made highly accurate predictions because the pollsters took care to make their design representative of the U.S. population (Bradley et al., 2021). Facebook's poll did not produce generalizable knowledge about vaccinations in the U.S., and having a large sample arguably made things worse because of the illusory precision of their model's confidence intervals. This phenomenon has been called the Big-Data Paradox: the more data, the surer that we fool ourselves (Meng, 2018).

The connection between Covid vaccine pollsters and Tylor's cross-cultural sample of in-law avoidance is that both had to grapple with the generalizability of their data. Just as Facebook's poll was inflated by oversampling college-educated white citizens, Tylor was criticized by Galton and Flowers for oversampling closely-related and neighboring populations. In each case, unmeasured confounders (socio-demographics in the former, history and geography in the latter) put the generalizability of these studies into jeopardy. Was Tylor learning about human cultures in general, or simply describing the patterns in his sample?

This problem is not unique to anthropology. Evolutionary biologists often seek evidence for convergent evolution, or the emergence of similar phenotypes in *independently evolving* lineages to perform similar functions in response to similar environmental pressures (Losos, 2011; Mahler et al., 2017). Why independently evolving lineages? Evolution is often a slow, gradual process, so descendants often retain the traits of their ancestors regardless of current environmental conditions. Thus, similarity in phenotypes within a clade of related species does not necessarily imply instances of evolutionary change. Counting them as such might mislead us into thinking some phenotype-environment correlation was general, when in fact it may have only evolved once and then replicated in descendant species (note that this is just Galton's problem re-stated). It is easy to stack the deck in favor of our preferred hypotheses by oversampling certain groups. Simple random sampling from the tree of life would not fix the problem either, because some taxa have many more species than others (e.g., >14,000 species of ant). The solution to the problem of non-independence in biological data is to construct an explicit model of the *phylogenetic* relationships (tree-like descriptions of evolutionary history) between populations. In contemporary research, this is usually accomplished via statistical adjustment using phylogenetic trees derived from molecular data (Garamszegi, 2014; Harvey et al., 1991). Just as there are no independent species, there are no completely independent human groups–all populations have some shared history that may influence their current traits, which has been shown to increase the risk of false-positive *and* false-negative results in cross-cultural studies that ignore autocorrelation (Dow & Eff, 2008; Minocher et al., 2019). In recent years, phylogenetic methods have become widely used in comparative anthropology as a solution to Galton's problem (Mace et al., 1994; Nunn, 2011).

It is evident that cultural/behavioral traits are not merely transmitted from ancestor to descendent, but also shared among contemporaries. Innovations and ideas move horizontally between populations, complicating the tree-like pattern of cultural change (Boyd et al., 1997; Evans et al., 2021; Greenhill et al., 2009; Lukas et al., 2021). This undeniable fact was leveraged to critique the comparative method in anthropology and inspired the "diffusionism" approach, which attempted to trace the transmission of cultural traits across world regions (Bock, 1966). These critiques suffused cultural anthropology in the 20th century, and the study of discrete culture units came to be viewed as naive at best. Some tried to rehabilitate the culture concept by changing their units of analysis to larger, interconnected "culture areas" (Kroeber, 1939) or "interaction spheres" in archeology (Hayden & Schulting, 1997). But others more radically rejected the study of 'cultures,' instead turning their attention towards regional and global processes of exchange, industrialization, and colonization of peoples that would go on to become ethnographic subjects (Gupta & Ferguson, 1997; Sahlins, 1992; Wolf, 1982).

As these critiques accumulate, the barriers to comparative research can feel insurmountable. However, as we saw with the development of phylogenetic methods in biology, it can be helpful to step outside of anthropology to see how similar problems are handled in other disciplines. For example, the 'units of analysis' problem (neighboring groups have similar trait values, possibly due to diffusion/horizontal transmission) can also be reframed as a special case of "spatial autocorrelation," which has been studied in fields such as ecology, geography, and economics (Cliff, 1973; Getis, 2007; Legendre, 1993). The key insight of spatial autocorrelation is often summarized as the 'first law of geography': "Everything is related to everything else, but near things are more related than distant things." (Tobler, 1970). Practically speaking, this means that we can incorporate the geographic distance between populations (or any other unit) into our analyses to attempt to adjust for statistical non-independence due to proximity. Contemporary cultural evolutionists are actively developing methods using both geographic distance and culture history to model global cultural change (Giuliano & Nunn, 2020; Matthews et al., 2016; Ruck et al., 2020; Schulz et al., 2019).

Cross-Cultural Research Goes Pro

Comparative work in anthropology floundered for some decades after Tylor's seminal paper. This was partly due to the aforementioned critiques, and the rejection of evolutionism by Franz Boas and his students (Boas, 1896). But the lack of momentum in comparative work was also due to the logistics of conducting systematic cross-cultural studies: how could a lone scholar organize and read all of the relevant ethnography from around the world? This problem motivated a group of researchers in anthropology, sociology, and developmental psychology to found the Institute of Human Relations at Yale University in 1935. This marked the beginning of a new, highly productive era for the comparative method, in which it was possible to make, "...on a large scale and using quantitative methods…scientific generalizations of a universally human or cross-cultural character" (Murdock, 1940). The goal of the Institute of Human Relations was to facilitate cross-cultural research by compiling cultural data (mostly ethnography from social anthropologists) from diverse societies. The Human Relations Area Files (HRAF) succeeded the Institute of Human Relations in 1949, and as of 2017, approximately 700,000 pages of ethnography from more than 300 cultures are available online, with new material added annually. These advancements have been indispensable in the growth of cross-cultural research during the 20th century.

One major barrier to conducting comparative research was accessing the vast cross-cultural library of texts. Another related problem was locating the relevant information from ethnographic texts: ethnography is generally not formatted to facilitate retrieval of specific data, so a prospective cross-cultural researcher might need to read entire texts to ensure that they were not overlooking relevant information. Given that the relevant information for any particular study might be confined to just a few pages or a few paragraphs, a whole-text survey is extremely inefficient. Additionally, it was unclear how one might produce an unbiased, globally representative sample of world cultures. George "Pete" Murdock, a key figure at the institute, tried to address these problems with two systems: the Outline of Cultural Materials and the Cross-Cultural Survey. Without these two systems, countless comparative studies, including Chapters 2 and 3 of this dissertation, would not have been possible.

The Outline of Cultural Materials (OCM) is a subject indexing system for ethnographic texts. Each paragraph is coded for the presence of more than 700 subjects, such as “Marriage Practices,” “Kinship,” or “Diet” (Human Relations Area Files, August 03 2017). Researchers interested in these subjects can jump directly to the relevant paragraphs rather than having to sift through entire texts, greatly reducing the burden on individual scholars. The Cross-Cultural Survey consisted of several hundred societies chosen to be representative of all major types and levels of culture. Having both a ready-made worldwide sample and an indexing system greatly empowered cross-cultural researchers, and set the stage for a productive era of comparative research.

While the comparative method was growing in accessibility and popularity, researchers sought to address Galton’s problem via sampling methods that minimize autocorrelation. While some cross-cultural samples, such as (Murdock, 1967) Ethnographic Atlas aim to be comprehensive surveys of all well-described societies, these are generally too large for most researchers to utilize, and some societies may be only scantly described. Moreover, they contain many closely related societies, as per Galton’s criticism. Thus, there was a need for cross-cultural surveys that: 1) were globally representative, 2) consisted of societies that were relatively well-described, and 3) not closely related.

The Standard Cross-Cultural Sample (SCCS) (Murdock & White, 1969) is by far the most popular answer to these criteria (but also see (Naroll, 1967)). The SCCS includes one society from 186 different ‘world-areas’ demarcated by Murdock and White, selected for global-representation, cultural diversity, adequate levels of description, and maximal historical independence[1]. World-areas were designated as cultural and geographic clusters of closely related societies, and for each world area one society was (more-or-less) randomly sampled[2]. Another desirable feature of the SCCS is the designation of a time-place focus (ethnographic present, e.g., the !Kung San in 1950) for each society. When testing cross-cultural correlations, it is important that each variable is synchronic–from the same time and place, not just from an ethnography with the same culture name. Since its inception, hundreds of studies have been conducted using the SCCS. As a consequence, and due to the collaborative ethos of many comparative researchers, a massive number of pre-coded variables (more than 2000) from the SCCS are available and published periodically in the Standard Cross-Cultural Sample Codebook (Divale, 2004).

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[1] As noted in the previous section, there are no truly independent human societies, and thus the SCCS also suffers from some problems with statistical non-independence despite the efforts of Murdock and White (Dow & Eff, 2008; Minocher et al., 2019).

[2] Taking a step back, it is clear that the SCCS is a solution to sampling problems only insofar as we take seriously the arbitrary demarcations of world culture as understood and legitimated by mid 20th century comparative anthropologists. But we should not be too quick to dismiss attempts to develop globally-representative surveys. All sampling designs are to some degree subjective, and in their absence we fall back onto convenience samples—which are often taken for granted in even the most prestigious contemporary cross-cultural research (H. C. Barrett, 2020).

Facilitated by these methodological advances, the body of comparative research grew exponentially during the mid 20th century (Schaefer & Levinson, 1977). As of 2017, more than 900 worldwide cross-cultural studies had been produced (Explaining Human Culture, n.d.). Early exemplars include (Murdock, 1949) Social Structure, which tests dozens of hypotheses related to kinship, social organization, and sex. Social Structure established “Main sequence” kinship theory, which posits that postmarital residence patterns follow from the division of labor in subsistence activities. Another classic cross-cultural study from this era is (C. R. Ember, 1978) “Myths about hunter-gatherers,” which, using systematic survey methods, demonstrated that several (at the time) popular assumptions about hunter-gatherers do not hold up to cross-cultural scrutiny. Articles such as this exemplify the value of cross-cultural surveys, which can challenge assumptions based on case studies or convenience samples pulled from the anthropologist's bookshelf.

Franz Boas and the mechanisms of cultural evolution

In the previous section, I alluded to Boas as an opponent of Tylor's comparative approach. In this section I delve into some subtleties of his critique, which extend beyond opposition to 19th-century evolutionism and hit upon general problems with using cross-sectional, group-level data to test evolutionary hypotheses. As before, I relate these anthropological debates to broader issues in statistics and causal inference. Finally, I consider how these problems can be addressed using modern comparative methods.

Franz Boas was initially inspired by Tylor’s method, enthused by its potential to test anthropological hypotheses. However, his enthusiasm waned as he came to see Galton’s problem as a fatal flaw ((Lowie, 1946) cited in (Naroll, 1961)). In addition to the problem of non-independence, Boas leveled another critique against the comparative method: equifinality. In “The limitations of the comparative method of anthropology,” Boas (1896) challenged the notion that cultural traits evolve the same way everywhere, asserting that “...no such proof can be given. Even the most cursory review shows that the same phenomena may develop in a multitude of ways” (902-903). Traits and covariance between traits can emerge via many different pathways, and thus synchronic/cross-sectional data should not be used to infer historical processes. To study cultural evolution, you need to actually observe culture evolving. Boas asserted that anthropologists had little justification to conduct ambitious comparative work until they could scientifically explain culture in even a single society[3].

It is tempting to dismiss this critique as not specific to the comparative method. Equifinality is a concern in virtually all observational studies (B. J. Barrett, 2019; Kandler et al., 2017), and many mechanisms will remain opaque even in the most detailed case study. Proponents of the comparative method would also argue that comparison aids in interpreting individual studies, because repeatable cross-cultural patterns are more likely to be correct than culture-bound theory overfit to particular cases (Bloch, 2005; Harris, 2001). Nonetheless, Boas's critique hit upon an important point about how cross cultural data can mislead us and create illusory correlations. Comparative studies are vulnerable to the 'ecological fallacy' (also known as Simpson's paradox), wherein unmeasured group-level confounders affect both the exposure and the outcome (Pollet et al., 2014). At a minimum, this means that it is important not to extrapolate group-level findings to individual-level processes. Simpson's paradox can also be

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[3] This line of reasoning also inspired the ‘method of controlled comparison’ (Eggan, 1954), wherein closely related societies from particular regions are compared on traits of interest, because they are assumed to be more directly comparable than a global sample.

resolved by increasing the resolution of your data. For example, Ross and Winterhalder refuted previous associations between parasite prevalence and violent crime rates (Thornhill & Fincher, 2011), showing these correlations do not hold—or even reverse—at the individual level after accounting for structural deprivation (C. T. Ross & Winterhalder, 2016). Similarly, Lawson and colleagues found that while polgyny is associated with poor child health and food insecurity at the village level across Tanzania, these associations do not hold within villages (Lawson et al., 2015). Thus, these problems can be addressed with a combination of individual-level data and multilevel modeling techniques that allow us to test hypotheses at multiple levels of aggregation.

In addition to the incorporation of individual-level data, we can also make our comparative analyses more robust with longitudinal data. Time series provide the evidence Boas insisted on (actual documentation of cultural change) and can offer stronger tests of theory (in particular, the direction of causality) than static, cross-sectional correlations (Chrisomalis, 2006; C. R. Ember, 2009). Recent examples include studies conducted with the longitudinal database Seshat, which collates historical and archeological records (Collins et al., 2020; Turchin et al., n.d., 2015). In addition to population-level time series, mechanisms of behavioral change can be elucidated using longitudinal data of individuals over time (Koster et al., 2019; Redhead et al., 2019). Finally, while phylogenetic relationships are often treated as a nuisance variable or confounder in comparative studies, they actually offer an opportunity to extract longitudinal insights from cross-sectional data. This is because a phylogeny represents a special kind of time series, where the past can be probabilistically reconstructed using present trait values and, if available, historical data (Jordan et al., 2009; Lukas et al., 2020; Mace & Holden, 2005). Chapter 3 develops a new method for assessing causality in phylogenetic analyses, which generalizes current approaches that are limited to two binary traits to any number of traits of any distribution.

The Future of the Comparative Method

Recent years have seen an uptick in comparative projects in anthropology. Some involve small-teams opportunistically pooling data to answer comparative questions, often with subjective coding of culture-level variables by the ethnographers (Borgerhoff Mulder et al., 2009; Lew-Levy et al., n.d.; Smith et al., 2016), others take meta-analytic approaches (Von Rueden & Jaeggi, 2016), or apply sophisticated computational approaches to analyze ethnographic materials (Garfield et al., 2020; Martin et al., 2020; Mehr et al., 2019). There are also large teams working together with standardized collection protocols[4] and to test hypotheses about group-level differences (Bryant et al., 2018; Henrich et al., 2006; Scelza et al., 2019). Central planning for large-scale comparative projects has been supported by the Max Planck Institute for Evolutionary Anthropology (McElreath, 2018). In addition to evolutionary anthropology, the use of secondary data is increasingly recognized as useful in addressing big questions in human biology (Hruschka & Hadley, 2016; Rosinger & Ice, 2019). Psychologists and other social scientists rattled by the replication crisis have also turned to cross-cultural samples as a means to increase the reliability and generalizability of their studies (Moshontz et al., 2018; Open Science Collaboration, 2015; Simons et al., 2017; Tiokhin et al., 2019). Beyond simply demonstrating that cross-cultural variability exists, many investigators are trying to understand how socioecological differences map onto behavioral variation (Amir et al., 2019; M. D. Gurven, 2018; Smaldino et al., 2019). Renewed interest in cross-cultural research in

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[4] The earliest such project that I know of was Beatrice and John Whiting's "Children of Six Cultures" study, which documented universals and variation in the development of social behavior around the world (Whiting & Whiting, 1975).

evolutionary anthropology and other fields means that there is an urgent need to establish methodological best practices and make statistical innovations—advanced modeling techniques are often needed to analyze complex, multilevel cross-cultural datasets.

Section 2: Background & Overview of Dissertation Studies

> *"Overall, I would say that the collected evidence justifiably casts the evolutionary history of primates in largely dietary terms" (Milton, 1993)*

Katherine Milton's assertion about the primacy of diet reflects the vast body of research that connects changes in non-human primate and hominin subsistence to changes in life history, morphology, cognition, and behavior (Aiello & Wheeler, 1995; Carmody & Wrangham, 2009; Crittenden & Schnorr, 2017; DeVore et al., 1968; Kaplan et al., 2000; Leonard & Robertson, 1997; Regan et al., 2001; Ungar, 1998). Primate "socioecological" models highlight the interplay between subsistence strategies and social organization across primate species (Clutton-Brock & Janson, 2012; Snaith & Chapman, 2007; Sterck et al., 1997; Terborgh & Janson, 1986; Thierry, 2008). A parallel literature in humans examines how human subsistence relates to both our species-typical life-history traits and cross-cultural variation in social behavior (reviewed below). My dissertation chapters contribute to this literature while also offering methodological innovations that address limitations of previous comparative work. Taken together, I hope that this dissertation demonstrates the potential of the comparative method for studying the coevolution of subsistence and social behavior.

Chapter 2 Background: Diet, Cooperation, and Life History Evolution

Evolutionary anthropologists have filled many volumes trying to understand the unique constellation of human life history features. Namely, our slow physical growth, extended juvenile period of low productivity, longer life-spans, high totality fertility rates, and large brains compared to our closest nonhuman primate relatives (Bogin, 1997; M. Gurven & Walker, 2006; Jones, 2011; Konner, 2010). An influential theory by Kaplan and colleagues suggests that human subsistence plays a central role in explaining these traits. They argue that our long juvenile period serves as a period for acquiring the knowledge, skill, and physical strength ("embodied capital") to acquire high-quality but difficult-to-acquire food resources, like large game and tubers (Kaplan et al., 2000). Humans trade-off early life production and reproduction for returns later in life, which necessitates intergenerational resource transfers to dependent offspring (Hooper et al., 2015).

Human subsistence is not only skill-intensive, with peak productivity typically obtained in late adulthood (M. Gurven et al., 2006; Kaplan et al., 2000; Koster et al., 2019), but also high-variance and *risky* (Winterhalder, 1986). For example, among the Ache of Paraguay nearly half of all hunting trips result in zero-returns, even at peak skill (McElreath & Koster, 2014). Conversely, a successful hunt might result in overproduction, with more food than a forager and their family can eat. Food sharing between households is an effective way of pooling risk that smoothes production and consumption: foragers and their families that are unlucky on a given day don’t go hungry, and the surplus from successful hunts does not go to waste. This pattern of sharing increases fitness interdependence between households and expands the scope of cooperation. Other types of ecological risks, such as food-destroying natural disasters and environmental harshness, promote forms of cooperation such as labor sharing and alloparenting (C. R. Ember et al., 2018; Martin et al., 2020). Varied forms of cooperation (labor, child care, sick care) co-occur with food sharing in networks of reciprocal exchange in societies such as Tsimane in Bolivia (Jaeggi et al., 2016). Thus, human's reliance on risky, skill-intensive food resources may help explain both our unique life history features as well as key aspects of our social organization and cooperation.

Data from contemporary foraging populations plays a vital role in testing and refining theory about coevolution of subsistence and social behavior. However, for topics such as food sharing, the literature is primarily driven by formal mathematical models, experiments, and in-depth case studies among a few extensively studied populations such as Ache and Tsimane. While these case studies are invaluable, we must also keep in mind the Big-Data Paradox (Meng, 2018). Large, high-quality food sharing datasets from single populations are valuable, but not sufficient for assessing cross-cultural generalizability. Therefore, in chapter 2, I utilize a worldwide sample to test risk-buffering hypotheses of inter-household food sharing.

Chapter 2 Aims

Chapter 2 draws on ethnographic data from 73 societies to ask: what types of socioecologies promote or erode norms of daily inter-household sharing? Crucially, human foragers target food resources that are nutritionally dense but difficult-to-acquire and unpredictable. This means that a forager might produce a large surplus on one day, but come home empty-handed the next. Food sharing may play an important part in this story because it buffers against the risk of nutritional shortfalls and fosters interdependence among households. We can indirectly assess risk-buffering hypotheses by looking at how cross-cultural variation in food sharing norms map onto differences in human subsistence economies and social organization. This study demonstrates how behavioral variation among human societies can be linked to differences in socioecology (such as food storage technology, population size, social stratification, and market integration), which can then be used to assess the testable principles underlying evolutionary hypotheses. It also provides a statistical toolkit for dealing with some common problems in cross-cultural research, such as missing data and multivariate predictors, and allows for the tandem examination of long-term population history along with local adaptation.

Chapter 3 Background: Complex Societies and Causal Inference

While Chapter 2 addresses the Plio-Pleistocene transition to a skill-intensive and risky foraging niche, Chapter 3 considers a more recent transition: the rise of "complex" agricultural societies during the Holocene. During the last 12,000 years, human populations have become larger and more sedentary, with greater inequality, expanded political hierarchy, and more labor specialization (Carneiro, 2001; Richerson & Boyd, 1999; Turchin & Gavrilets, 2009). These characteristics are collectively referred to as "societal complexity." It is widely argued that increases in complexity were caused by the adoption of agriculture. Variations on this core idea have pervaded anthropology since the time of Lewis Henry Morgan (1877), growing to become a foundational assumption about human cultural evolution (Carneiro, 2001; Johnson & Earle, 2000; Mattison et al., 2016; Richerson & Boyd, 1999).

However, some hunter-gatherer populations exhibit social inequality, economic specialization, and high population densities, despite relying on foraging for subsistence (Ames, 1994; Johnson & Earle, 2000; Singh & Glowacki, n.d.). Conversely, some small-scale agricultural societies maintain relatively egalitarian social structures (M. Gurven et al., 2010; von

Rueden, 2020). Are these observations incompatible with the widely held belief that agricultural intensification is the cause of increases in complexity?

Chapter 3 Aims

In this chapter, I utilize a globally-representative sample of 186 nonindustrial societies and a phylogenetic supertree (Duda & Zrzav\`y, 2019) to disentangle the causal, co-evolutionary relationship between subsistence and complexity. Explaining variation in societal complexity is a contentious topic that has been addressed in recent high-profile studies (Borgerhoff Mulder et al., 2009; Currie et al., 2010; Sheehan et al., 2018; Turchin et al., 2018; Whitehouse et al., 2019). However, all previous comparative studies of complexity have been limited in one or more of the following ways:

(i) they focused on just one or two measures of complexity and/or they were limited to samples of societies in relatively small geographic regions, which limits the generality of results

(ii) they were conducted in samples of societies that already had agriculture to begin with, excluding hunter-gatherers, which limits their ability to detect an influence of subsistence on complexity

(iii) if the direction of causality between complexity and subsistence was addressed at all, existing phylogenetic methods forced authors to artificially dichotomize these traits (e.g. complexity: yes/no, agriculture: yes/no), which can lead to loss or distortion of information and thereby false inference

Chapter 3 addresses the first two limitations by retaining 12 different measures of complexity and subsistence in a globally representative sample that includes hunter-gatherer subsistence, intensive agriculture, and everything in-between. To address the third limitation, I introduce a new phylogenetic method for causal inference that can assess the direction of causality between more than two variables and can be used with any type of data (continuous, binary, ordinal, categorical, etc.). Because phylogenies represent a time series, they can be used to infer the direction of causality in cultural and biological evolution. Many authors in both anthropology and evolutionary biology have used a type of model, developed by Mark Pagel (Pagel, 1994; Pagel & Meade, 2006), to move beyond correlations and directly assess causality in topics ranging from the evolution of social stratification in humans (Watts et al., 2016) or social organization in primates (Opie et al., 2013; Shultz et al., 2011) to cooperative breeding in birds (Cornwallis et al., 2017). But these models have a clear limitation in that the traits must be binary and are typically limited to only two variables. I draw upon recent advances in Bayesian dynamic multilevel structural equation models (Driver & Voelkle, 2018) to lift these restrictions, greatly expanding the horizon of future comparative research.

Chapter 4 Background: Multilevel population structure of diet

Thus far, we have considered the co-evolution of human foraging and social behavior, as well as the causes and consequences of more recent transitions to agriculture. However, the diversity of human subsistence strategies extends well beyond the foraging spectrum and the use of domesticates. Our species has been characterized as a 'generalist-specialist' because in aggregate, humans consume countless varieties of foods, while each population specializes on a relatively narrow dietary subset (Hardesty, 1975; Harris & Ross, 1987; Roberts & Stewart, 2018). We rely on cumulative cultural knowledge of how to subsist and what to eat, a remarkable form of plasticity that allows us to inhabit every environment on Earth (Boyd et al., 2011; Henrich & Henrich, 2010). However, there may actually be more dietary variation within populations than between them, as evinced by cross-national comparisons of diet that use individual-level data (Arimond & Ruel, 2004; Naska et al., 2006). Structured variation within populations (e.g., among individuals, families, or within social networks) allows the maintenance of behavioral and cultural diversity, which can accelerate the rate of innovation and act as a buffer against risk in unpredictable environments (Derex & Boyd, 2016; C. R. Ember et al., 2020; Migliano et al., 2020; Scaggs et al., 2021). The relative amount of variation between vs. within groups also determines the scope for multilevel selection to act on cultural traits such as diet (Bell et al., 2009; Smaldino, 2014). Identifying how dietary variation is structured within societies is crucial to understanding the evolutionary processes that allow humans to subsist in a staggering array of environments, ranging from tropical rainforests to arid deserts and frozen tundras.

Chapter 4 Aims

Chapter 4 investigates the social structure on diet among Tsimane farmer-foragers in lowland Bolivia. Tsimane are an ideal population for this study due to their small-scale social organization, and a diet that is composed mostly of foraged food and horticultural crops. Rather than large-scale patterns of cultural macroevolution, this study engages in within-society comparison, combining fine-grained behavioral, demographic, and spatial data (N = 4474 eating observations spread across 961 individuals in 226 families from 8 communities) with a Bayesian multilevel model. I provide a model-based method to estimate "Cultural FST" (i.e., the proportion of dietary variance that is between-groups) (Bell et al., 2009; Muthukrishna et al., 2020; R. M. Ross et al., 2013) at the individual, household, network, and community level. Variable degrees of market integration also offers an opportunity to explore the impact of industrialization on intra-cultural differentiation (i.e., does proximity to markets increase or decrease dietarily variability within communities?). As discussed in Section 1, human behavioral and cultural variation is not confined to discrete "societies." Instead, it is massively multilevel, varying across individuals, families, social networks, and communities. This study develops a modeling framework to partition behavioral variation across levels of social organization, respecting the unique multilevel structure of human societies that generates food traditions and other forms of cumulative culture (Derex & Boyd, 2016; Hamilton et al., 2007; Migliano et al., 2020).

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Chapter 2: 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.

Introduction

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 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, Skoggard, Ringen, & Farrer, 2018). However, there is tremendous cross-cultural variability in the scope of sharing customs; daily sharing among households was relatively rare (~ ⅓ 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 2.1).

Table 2.1: 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.

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 (Pre- diction 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 *Data description*).

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, Frankenhuis, & 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.

Materials and methods

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.

Figure 2.1: Global distribution of daily food sharing norms in our sample (N = 73 societies). Black dots indicate presence (19/73 societies), red dots indicate absence.

We describe all study variables in Table 2.2. 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 *Exploratory results* 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 (Dorrmann et al., 2013).

Table 2.2: Description of Study Variables

Name	Original Source	Original Scale	Transformation
Hunting	(Murdock & Morrow, 1970)	Ordinal scale from 0-100% dependence, with deciles as cutpoints.	Centered and standardized by 2 SD
Animal Husbandry	(Murdock & Morrow, 1970)	Ordinal scale from 0-100% 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	Dichotomized into food storage present (2-4 on original scale) or food storage

		repositories 5 = Economic agent controlled repositories	absent (1 on original scale).
Social Stratification	(Murdock & Morrow, 1970)	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 = 1,000 without any town of more than 5000 7 = One or more towns of 5,000-50,000 8 = One or more cities of more than 50,000	Centered and standardized by 2 SD
Precipitation Predictability	Kirby et al., 2016), based upon Colwell's	Continuous measure between 0 and 1	Centered and standardized by 2 SD

	(1974) information theoretic index.		
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

Analysis

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.

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:

$$\text{Daily Sharing} \sim \text{Bernoulli}(p)$$

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

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

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

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

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

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

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 Figure 2.2). 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.

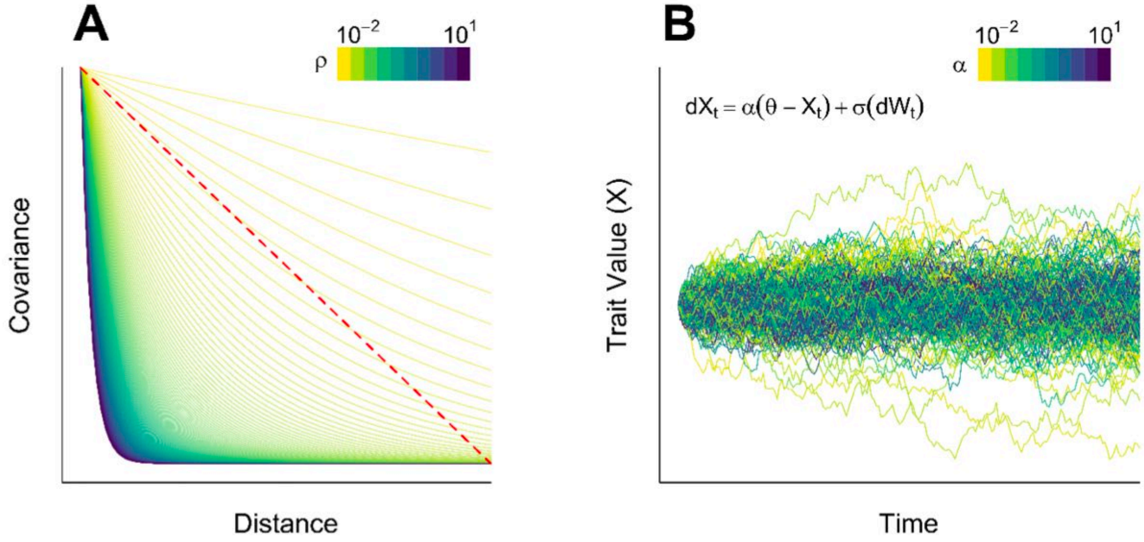

Figure 2.2: Correspondence between GP Covariance Function and OU Model of Evolution. *A*: Simulated Gaussian Process (GP) covariance functions, as described in our model definition. Darker lines denote larger values of ρ, where the covariance between societies declines rapidly with phylogenetic/temporal 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.

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 like-likelihood' approaches in non-Bayesian frameworks (Green, 1998).

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 para- meter 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.

Model comparison and Bayesian R^2

To evaluate whether including phylogeny and ethnographic present improved model performance, we fit three nested submodels of the previously defined model. 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.

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 bi-variate 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.

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.

Results

Main results

Prediction 1 was not supported as dependence on hunting was not associated with sharing (median d = −0.21, PP = 0.34; see Figure 2.3). 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 Figure 2.3 for uncertainty in estimates).

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.

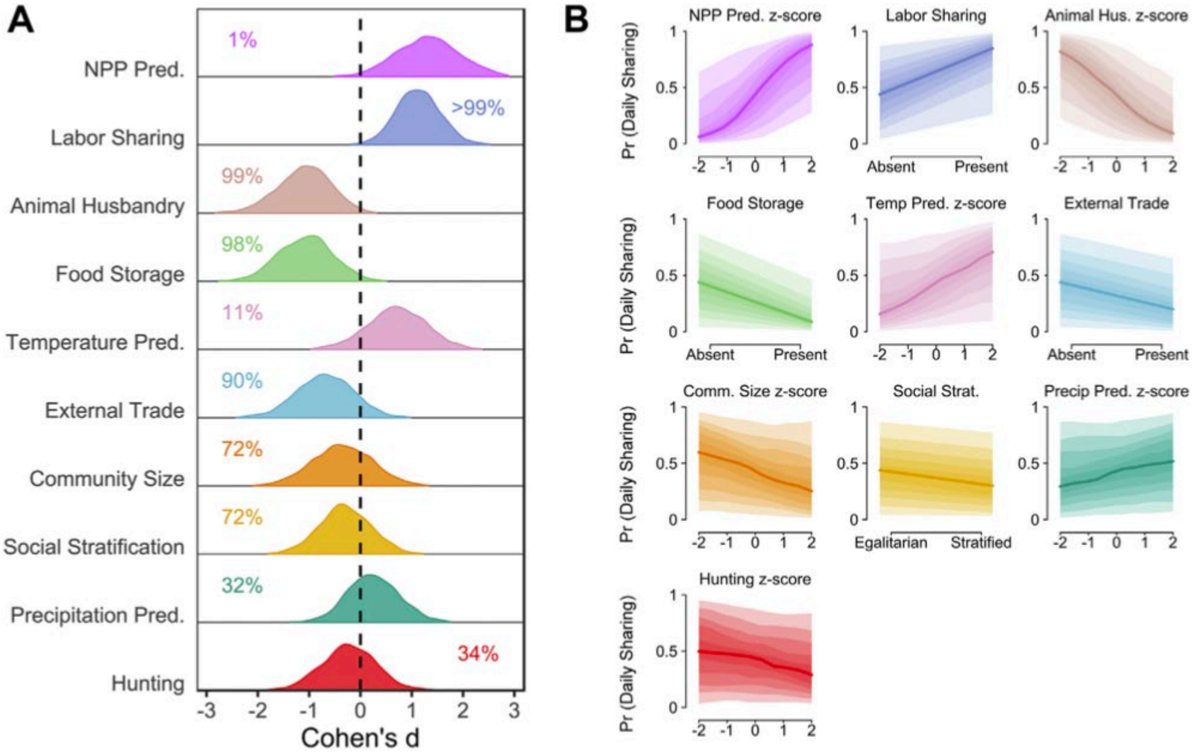

Figure 2.3: Predictors of sharing. *A*: Posterior distribution of effect sizes on the logit scale, sorted by the absolute value of the effect size. Percentages indicate the proportion of the posterior that was in the predicted direction. Effect sizes were converted from the logit scale to Cohen's d following 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.

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 Figure 2.4).

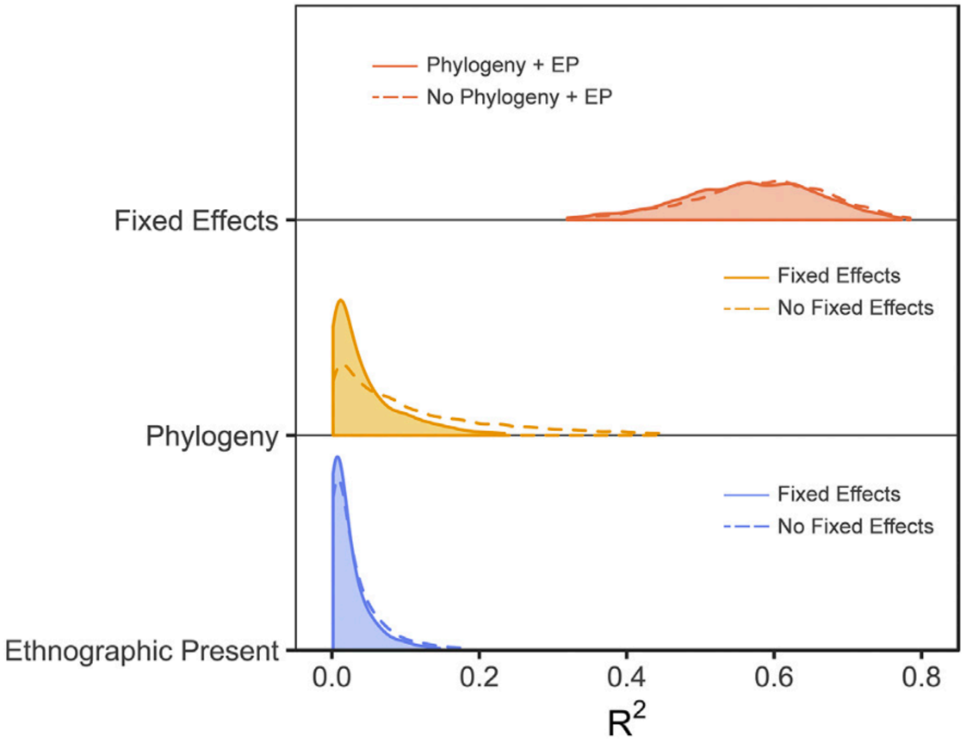

Figure 2.4: Variance Captured by fixed effects, phylogeny, and ethnographic present.

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 R2 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.

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 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.

Table 2.3: Model Comparison using WAIC. 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).

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

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 (Figure 2.1).

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.

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 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 un- measured 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 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 ex- tended 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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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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Chapter 3: Novel phylogenetic methods reveal that resource-use intensification drives the evolution of “complex” societies

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Abstract

Explaining the rise of large, sedentary populations, with attendant expansions of socio-political hierarchy and labor specialization (collectively referred to as “societal complexity”), is a central problem for social scientists and historians. Adoption of agriculture has often been invoked to explain the rise of complex societies, but archaeological and ethnographic records contradict simple agri-centric models. Rather than a unitary phenomenon, “complexity” may be better understood as a network of interacting features, which in turn have causal relationships with subsistence. Here we use novel comparative methods and a global sample of 186 nonindustrial societies to infer the role of subsistence practices in shaping complexity. We also introduce a phylogenetic method for causal inference that generalizes beyond two binary traits, lifting a major constraint on comparative research. We found that, rather than agriculture alone, a suite of resource-use intensification variables leads to broad increases in technological and social differentiation. Our study provides evidence that resource intensification is a leader, not a follower, in the rise of complex societies worldwide.

Introduction

For most of our species' history, humans lived as hunter-gatherers in *relatively* mobile, egalitarian societies. The Holocene epoch brought the widespread emergence of both intensive agriculture and large socially stratified societies with dense, sedentary populations. These transitions were also associated with expanded political hierarchy, labor specialization, and technological innovation–features collectively referred to as "societal complexity." Many scholars argue that the adoption of agriculture caused these changes (R. Carneiro 2001; Johnson and Earle 2000; Richerson and Boyd 1999; White 1943). However, this "agri-centric" (Arnold et al. 2016) account has been challenged by ethnographic, historical, and archaeological records that suggest alternative pathways to societal complexity. These alternative paths are exemplified by so-called complex hunter-gatherers. For instance, the Calusa of Florida had extensive craft specialization and the coastal Peruvians' burial records suggest long-standing sociopolitical inequality (Arnold et al. 2016). Ethnographic accounts of Northwest Coast peoples also depict social stratification, permanent settlement, economic specialization, and relatively high population density such that some communities exceeded 1000 individuals (Ames 1994; Arnold 1996; Sassaman 2004). Hunter-gatherers also have large, multilevel relational networks that persist over many generations (Bird et al. 2019). This is not to deny the influence of subsistence on social organization; Sedentism and inequality among foragers, for example, is facilitated by technology such as food storage and by the defensibility of food resources (Kelly 2013; Rueden 2020). Nevertheless, given their reliance on foraging rather than farming, complex-hunter gatherers demonstrate that intensive agriculture is not necessary for the emergence of some features traditionally associated with complex societies (Bailey and Milner 2002; Kelly 2013; Singh and Glowacki 2021).

This leads us to ask two questions: First, what exactly is “complexity” and how does it relate to subsistence? Second, what is the direction of causality in the co-evolutionary relationship between complexity and subsistence? “Complexity” itself is an ethnocentric construct invented by anthropologists and historians. Popular notions of complexity privilege social structures and technologies that remind us of the great civilizations, those powerful states that get to write their own histories. In contrast, foraging populations are cast as the basal “simple” society, the point where cultural evolution begins. This position has been widely rejected by social scientists, who no longer believe that cultural evolution is a progressive, unilineal process. In its contemporary usage, complexity is a descriptive, diminutive term broadly related to a suite of major transitions that are thought to have occurred during the Holocene (but see (Singh and Glowacki 2021; Graeber and Wengrow 2018)). Stripped of its original conceptualization as an all-encompassing evolutionary force, complexity has taken on a variety of different meanings between studies and between disciplines (R. L. Carneiro 1962; Chick 1997). Some authors focus on political complexity, excluding many other facets (e.g., population size, economic specialization, residential mobility) (Arnold et al. 2016; Price and Brown 1985). Others define complexity in relation to material inequality (McGuire 1983) or societal scale. Lack of definitional consensus and inconsistent measurement has produced inconsistent results (Tosh, Ferguson, and Seoighe 2018) that ultimately cannot resolve debates about the rise of complex societies. Rather than defining complexity *a priori*, one alternative approach is to infer dimensions of complexity in a more “bottom-up” way. For instance, a recent cross-cultural and historical study concluded that various measures of complexity were well-described by a single latent dimension (Turchin et al. 2018), although in a sample mostly limited to agricultural societies. In contrast, Chick (Chick 1997) found support for a two-factor model in a more diverse global sample (also see (Peregrine 2018; Miranda and Freeman 2020)). One problem with a completely bottom-up approach however is that it is not constrained by prior theory on the causal relationships among variables. Here we compare different causal models of the relationship between complexity and subsistence in a globally representative sample of subsistence societies (Part 1).

The second important question is whether changes in subsistence came before or after increases in population density, socio-political hierarchy, and other traits typically associated with complex societies (Boserup 2011; Sheehan et al. 2018). In a sample of Austronesian societies, Sheehan et al. tested the causal relationship between agricultural intensification and social stratification and found evidence for reciprocal coevolution. However, a general limitation of this approach is that the standard method currently used for testing causal coevolutionary relationships is limited to two binary traits (Pagel 1994; Pagel and Meade 2006). This problem, which applies broadly to all phylogenetic comparative analyses (across species or societies), means that continuously varying, multivariate traits like societal complexity or subsistence intensification have to be artificially dichotomized in many studies (Sheehan et al. 2018; Watts et al. 2016, 2015). Artificially binning continuous measures poses inferential risks such as reduced power and increased false positive rates (Royston, Altman, and Sauerbrei 2006), which can exacerbate inconsistency across studies. Here we introduce a novel phylogenetic method that generalizes the classic test for causal coevolution to any number of traits, categorical or continuous, following any distribution. We use this method to model the coevolutionary dynamics between the complexity-subsistence dimensions inferred by our model comparison (Part 2).

In sum, we employ a diverse global sample of societies and novel phylogenetic methodology to (1) infer the structure of complexity and its relationship with subsistence, and (2) test whether changes in subsistence precede changes in complexity or vice versa. Specifically, our methods (i) retain diverse aspects of complexity using a multivariate approach, (ii) compare different causal models of the relationship between complexity and subsistence, and (iii) generalize Pagel's method for causal coevolutionary relationships from binary to continuous traits. We develop a fully Bayesian implementation of this approach and provide R code for others to use. To maximize the scope and generalizability of our analyses, we utilized the globally representative Standard Cross-Cultural Sample (SCCS) (Murdock and White 1969). The SCCS comprises 186 societies that include a great diversity of subsistence modes - including foragers, pastoralists, and agriculturalists with varying degrees of intensification. Societal complexity was described by nine individual measurements that are commonly used in cross-cultural research (Murdock and Provost 1973) (see Methods). Using this novel methodology, as summarized in Figure 3.1, we found that complexity was best described by 2 correlated latent variables, broadly characterized as "resource-use intensification", which encompasses both agriculture and other subsistence systems that allow for dense, sedentary populations, and "technological and social differentiation", which encompasses social stratification, political integration, labor specialization, and technology. Moreover, we found that increases in resource-use intensification lead to increases in technological and social differentiation over evolutionary time, but not vice-versa.

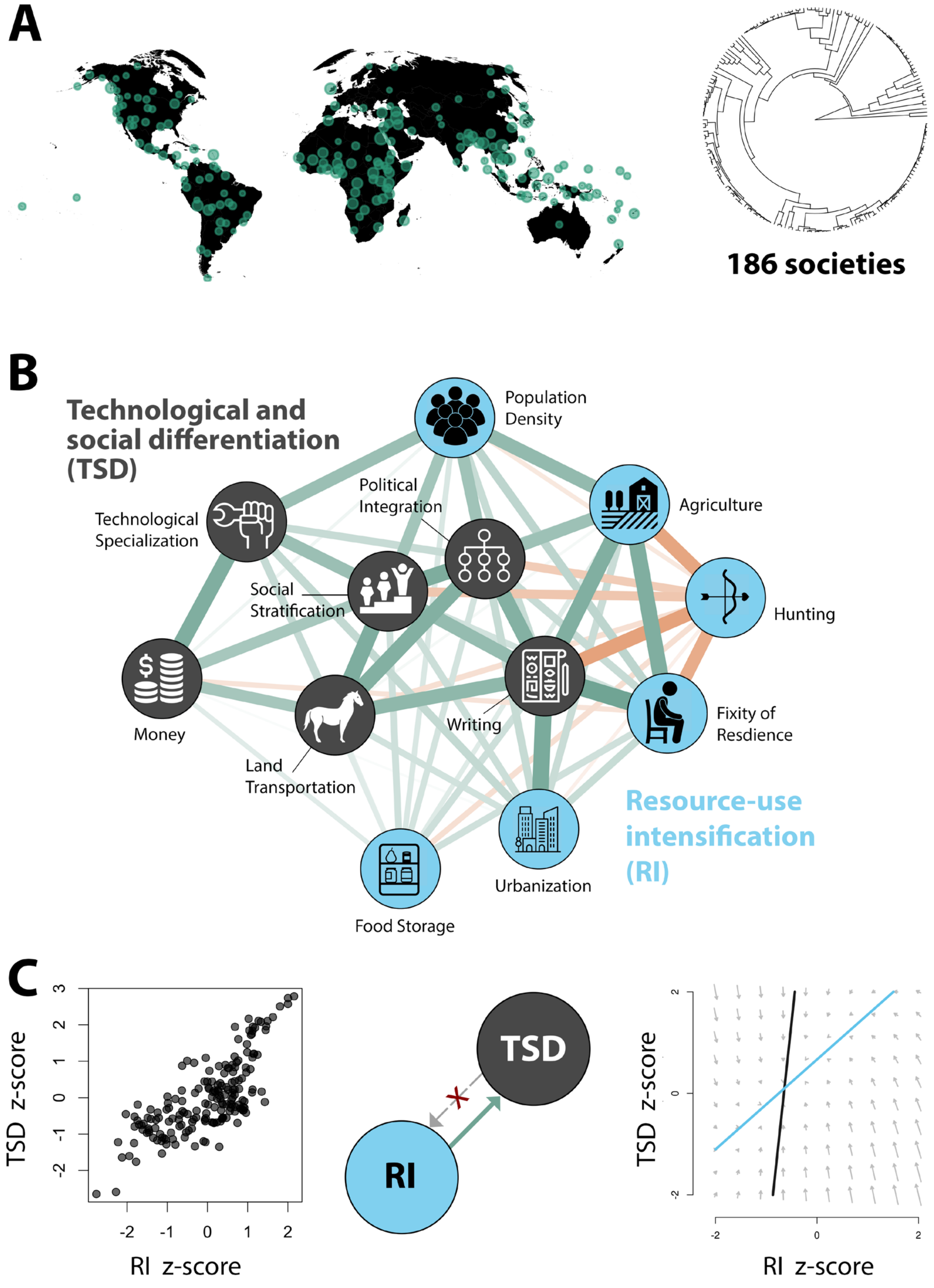

Figure 3.1: Overview of study approach and main findings. (A)(left) Distribution of study societies; points proportional to log population size. (right) Phylogenetic tree of societies. (B) Phylogenetic correlation network of study variables (depicted as nodes). Edge width/opacity is

proportional to correlation size; green edges represent positive correlations and red edges represent negative correlations. Nodes are colored according to our two-factor model (M2). (C) (left) Correlation between the latent variables resource-use intensification (RI) and technological and social differentiation (TSD). (middle) Inference from our dynamic co-evolution model, which suggests that increases in RI lead to greater TSD, but not vice-versa. (right) Flow-field depicting the expected change in RI and TSD depending on their current states. Solid lines are nullclines where RI (blue) and TSD (grey) are at equilibrium, depending on the state of the other.

Part 1: Inferring complexity and its causal relationship with subsistence

First, we compared three competing causal models to assess how well each predicted the global distribution of complexity (Figure 2), wherein the structure of "complexity" itself was inferred from several distinct variables rather than defined *a priori*. Although causal inference in observational settings is generally difficult, causal models imply specific–but not unique–patterns of conditional independence between traits that can be statistically compared. Rather than choose a single definition of complexity, our approach allowed "complexity" to arise from the correlation structure of the nine individual measures (Figures 3.1 and 3.2). Subsistence was measured using an agricultural intensification scale (how much a society depends on agricultural crops, and technological modifications to enhance productivity), as well as measures of hunting dependency and food storage, as both have been theoretically linked to societal complexity (Kelly 2013). Specifically, greater reliance on hunting should be associated with reduced complexity due to demands on mobility and egalitarian food sharing (Jaeggi and Gurven 2013; Lewis et al. 2014; Winterhalder 1986; Woodburn 1982), whereas food storage allows the breakdown of such sharing (Ringen, Duda, and Jaeggi 2019) and facilitates accumulation of surplus as seen in complex hunter-gatherers (Kelly 2013).

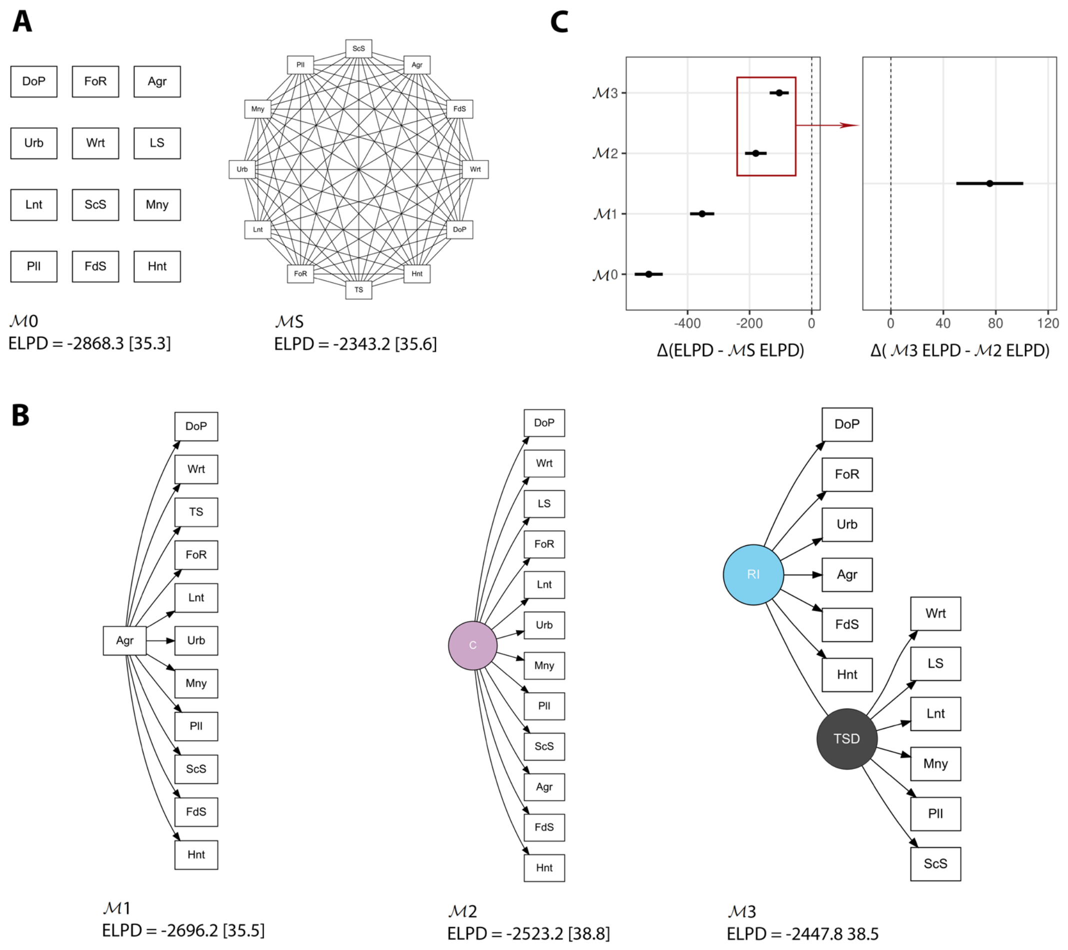

Figure 3.2: Comparing different causal models of complexity and its relation to subsistence. (A) M0 and MS, which serve as low and high-end model performance benchmarks, respectively. Higher expected log predictive density (ELPD) indicates greater performance. (B) Candidate models (M1 – M3) and their ELPD. M1 is an “agri-centric” model where agriculture directly causes every dimension of complexity. M2 includes a single latent factor causing every dimension of complexity and subsistence. M3 includes two latent factors, “resource-use intensification” (RI) and “technological and social differentiation” (TSD), which cause distinct

dimensions of complexity and subsistence. (C) ELPD comparison of candidate models with MS, the high-end benchmark indicated by the dashed line (left), and comparison between M3 and M2 (right). Error bars indicate +/- 2 SE. Agr = Agriculture; DoP = Density of Population; FoR = Fixity of Residence; FdS = Food Storage; Hnt = Hunting; LnT = Land Transportation; Mny = Money; PlI = Political Integration; ScS = Social Stratification; LS = Labor Specialization; Urb = Urbanization; Wrt = Writing; C = Complexity latent variable ("c-factor"); RI = Resource-use intensification latent variable; TSD = technological and social differentiation latent variable.

Below we describe our candidate list of causal models, which are also displayed in Figure 3.2, and mathematically described in Methods:

$\mathcal{M}0$ is a phylogenetic null model where each dimension of complexity and subsistence evolves independently. This model was used as a low-end performance benchmark for model comparison.

$\mathcal{M}1$ is an "agri-centric" model where agriculture directly causes every dimension of complexity. Agriculture was an ordinal measure, so we parameterized it to have monotonic but potentially non-linear effects (Bürkner and Charpentier 2020) on the complexity variables.

$\mathcal{M}2$ is a latent variable model where a single "c-factor" causes every dimension of complexity and subsistence. This is the causal model implicit in Murdock and Provost's summary score of complexity (Murdock and Provost 1973), which simply sums all measures. This model is also consistent with Turchin et al.'s (Turchin et al. 2018) recent study, which used principal component analysis to infer a single latent dimension of complexity.

$\mathcal{M}3$ is a two-variable latent factor model, where the two factors are correlated. This model is based on Chick's (Chick 1997) analysis of the SCCS, which distinguished between societal "scale" and "technology" and has been conceptually replicated in other samples (Peregrine 2018; Miranda and Freeman 2020). We extend this model by including hunting and food storage, and estimating the correlation between the two latent factors rather than assuming that they are orthogonal. One latent variable, which we label "resource-use intensification," (RI) is a common cause of agricultural intensification, fixity of residence, density of population, urbanization, hunting, and food storage. RI thus jointly indicates (i) whether societies are dense and sedentary and (ii) their subsistence practices. The other latent variable captures all of the remaining complexity measures, which we broadly characterize as “technological and social differentiation” (TSD).

$\mathcal{MS}$ is a correlation network where every measure of complexity and subsistence has potential pairwise interactions–everything causes everything else. This “saturated” model provides a complete description of the multivariate network but is not itself a causal model. We used it as our high-end performance benchmark, which is best practice in structural equation modeling (Skrondal and Rabe-Hesketh 2004; Pavone et al. 2020).

We compared the performance of each model using approximate leave-one-out-cross-validation (PSIS LOO-CV), a recent information criterion that outperforms classical criteria such as AIC in terms of out-of-sample prediction (Vehtari, Gelman, and Gabry 2017). We evaluated the difference in expected log predictive density (ΔELPD) between MS and each of our candidate models. Relative model performance is visualized in the top-right of Figure 2C. Note that larger values (i.e., closer to 0, the ELPD of $\mathcal{MS}$) indicate better model performance.

As expected, the null model ($\mathcal{M}0$) performed the worst (ΔELPD = -525.16, SEΔ = 22.60), indicating that different facets of complexity are not evolving independently. However, neither the agri-centric model ($\mathcal{M}1$) (ΔELDP = -352.99, SEΔ = 19.56), nor the c-factor only model ($\mathcal{M}2$) (ΔELDP = 180.03, SEΔ = 17.42) came close to describing the actual covariance structure (i.e. the MS benchmark). The two factor model ($\mathcal{M}3$) performed the best (ΔELDP = -104.59, SEΔ = 15.41) and clearly outperformed $\mathcal{M}2$ (ΔELPD[$\mathcal{M}3$ - $\mathcal{M}2$] = 75.43, SEΔ = 12.77). Thus, a two-factor model that differentiates between “resource-use intensification” (agricultural intensification, fixity of residence, density of population, urbanization, reduction in hunting, and food storage) and “technological and social differentiation” (land transportation, money, political integration, social stratification, technological specialization, and writing) better predicted the global distribution of societal complexity than unidimensional or agri-centric models. Although the phylogenetic correlation between the two latent variables is strong (median $\rho = 0.64$, 90% HPDI = [0.41,0.84]), the greater performance of M3 supports the contention that some facets of societal complexity can increase without attendant changes in subsistence practices, as empirically demonstrated by complex hunter-gatherers. Correlations between the latent variables RI and TSD and the manifest variables are reported in Table 3.1. Predicted effects of the latent variables on the observed variables are visualized in Appendix A.

Table 3.1: Correlations (ρ) between latent and manifest variables, on the latent scale. Values indicate the posterior median ρ and 90% HPDI.

Variable	ρ(**RI**)	ρ(**TSD**)
Agriculture (Agr)	0.70 [0.63,0.75]	–
Fixity of Residence (FoR)	0.81 [0.75,0.87]	–
Density of Population (DoP)	0.85 [0.8,0.9]	–
Urbanization (Urb)	0.60 [0.51,0.69]	–
Writing (Wrt)	–	0.72 [0.63,0.79]
Labor Specialization (LS)	–	.59 [0.49,0.68]

Money (Mny)	–	0.68 [0.59,0.75]
Political Integration (PlI)	–	0.78 [0.71,0.83]
Social Stratification (ScS)	–	0.81 [0.76,0.87]
Hunting (Hnt)	-0.79 [-0.73,-0.84]	
Food Storage (FdS)	0.50 [0.36,0.63]	

Part 2: Dynamic coevolutionary model

Our model comparison found that the global distribution of complexity was well-described by two correlated latent variables: resource-use intensification (RI) and technological and social differentiation (TSD). But to advance long-standing debates about the origins of complex societies (i.e., whether intensification is a leader or a follower in the coevolutionary process), we needed to directly assess the direction of causality using a dynamical model. More concretely, while causality in the previous section was expressed as a specific covariance structure that may or may not be consistent with the observed data, here we detect causation through the influence of one variable on another in a time series (i.e., does knowing the state of y_1 at time t predict the state of y_2 at time $t+1$?), which is called “Granger causality” in economics (Granger 1969). Time-calibrated phylogenetic trees, such as the one in this study (Duda and Zrzavỳ 2019), have branch lengths that are proportional to time, allowing us to quantify the shared history of sample societies.

Many authors have used a class of phylogenetic models, developed by Mark Pagel (Pagel 1994) and implemented in the software BayesTraits (Pagel and Meade 2013), that empower researchers to assess both directionality (A → B vs. B → A) and contingencies (A, then B) in the evolution of two binary traits by treating a phylogeny as a time series. This method has greatly improved causal inference and helped advance theory in many domains, including the coevolution of subsistence and social stratification (Sheehan et al. 2018). However, the focus on binary traits is a clear limitation. While it is possible to generalize beyond two traits (Burin et al. 2016), these models are still limited to discrete variables (with associated crudeness and difficulties in coding), and involve large transition matrices that suffer from sparsity and lead to poor model identification. Moreover, when measurements are noisy (of particular concern when continuous traits are dichotomized), state-space models will propagate error, undermining causal inference. To overcome these limitations and facilitate causal inference about the coevolution of subsistence and societal complexity, or any other set of continuous traits, we introduce a flexible modeling approach that should be widely applicable for phylogenetic analyses. Our approach, as implemented in RStan (Team et al. 2016), can accommodate an arbitrary number of co-evolving variables from any probability distribution (i.e., it is not limited to discrete or Gaussian outcomes), and permits flexible model structures.

Based on our model comparison results (Part 1), we treat resource use intensification (RI) and technological and social differentiation (TSD) as two latent variables that co-evolve as a multivariate stochastic differential equation. These latent variables were identified by their loadings onto the observed complexity and subsistence variables from the previous section (see graphical representation in Figure 3.2B). This model describes the continuous-time evolution of traits under the influence of both “selection” (i.e., tendency towards a central position or optimum, denoted as) and “drift” (i.e., Gaussian noise, which may represent exogenous forces), represented by the parameters α and σ, respectively. Change in the trait values of RI and TSD depend on each other and themselves, which allowed us to assess the directional influence of each factor on future change in the other factor.

We found strong evidence that gains in RI caused increases in TSD, but only very weak evidence that gains in TSD caused increases in RI (Figure 3.1C, Figure 3.3). In other words, higher values of RI earlier in the phylogeny led to higher values of TSD later but not vice-versa. In the absence of increased intensification, gains in TSD are unstable and will revert over time. We quantified the magnitude of these effects in terms of change in the equilibrium trait value θ (Fig 3.3). The relative strength of drift was also greater for RI than TSD (Figure 3.4), suggesting that most changes in resource-use intensification were exogenous.

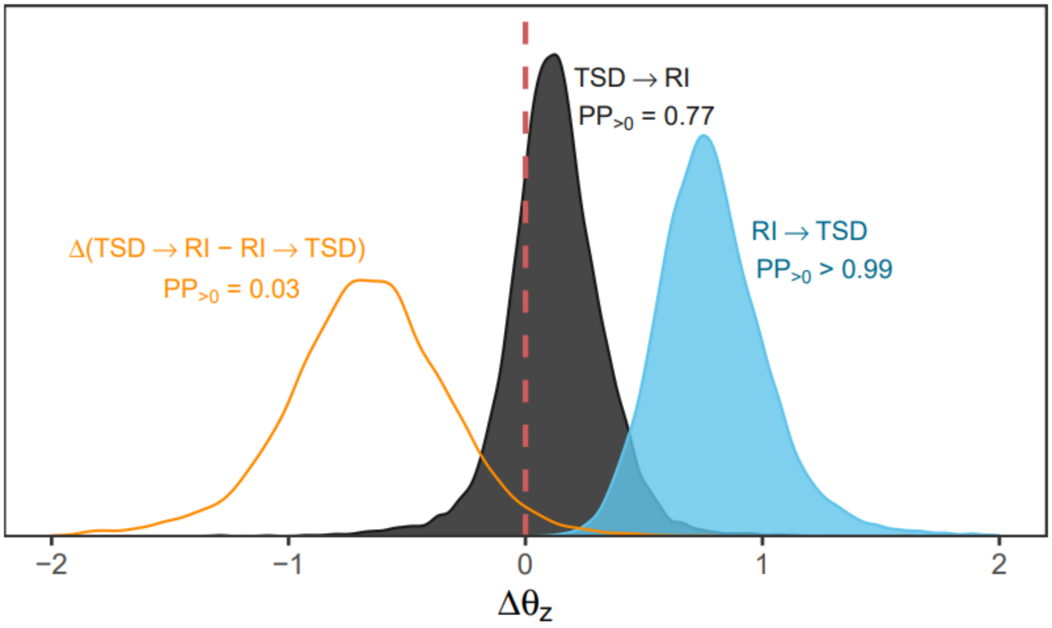

Figure 3.3: Change in the equilibrium trait value θ of resource-use intensification (RI) and technological and social differentiation (TSD) in response to a 1 standardized unit increase in the other trait. Posterior probabilities (PP) denote the probability that increases in RI leads to increases in TSD, and vice-versa. Values were scaled by the median absolute deviation, which is less sensitive to outliers than the standard deviation. Although we cannot conclude that there is zero effect of TSD on RI, our model strongly suggests that TSD → RI is smaller than RI → TSD (PP = 0.03).

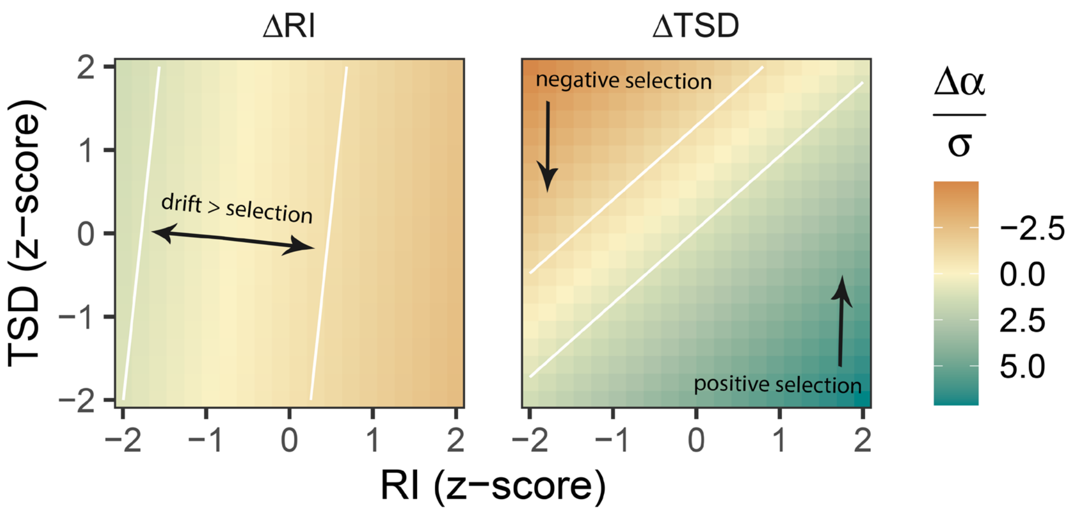

Figure 3.4: Selection gradients for RI and TSD, given different combinations of trait values, scaled by the strength of drift σ. Absolute values less than 1 are encompossed by white countour lines and indicate parameter space where the change due to stochastic drift σ is greater than change due to deterministic selection on the trait $\Delta\alpha$. Values were standardized by the median and median absolute deviation as robust meausures of central tendency and variability, respectively.

Discussion

Explaining the rise of "complex" societies is a centuries old problem that spans across a variety of disciplines. Our study suggests that a suite of interrelated political and technological variables (technological and social differentiation) increase together in response to resource-use intensification. For more than a century, social scientists have argued for or against this conclusion, typically relying on case studies or informal comparative methods (White 1943; Sahlins 2017; Diamond 2002). Previous quantitative comparative studies were limited in their ability to assess causation and/or restricted to single world regions and binary measures of complexity and subsistence. In contrast, we employed novel comparative methods to test competing causal models of the co-evolution of subsistence and social complexity across diverse lifeways on a global scale. Our study has important methodological and theoretical implications for the complexity concept and comparative research more broadly.

Some previous comparative studies have addressed just one aspect of "complexity" (such as political organization, material inequality, or societal scale) at a time. As a result, many different predictors are tested independently in different studies, and all appear to have large effects. But it is implausible that all those effects (i.e., individual complexity relationships) could co-exist, because they would be expected to interfere with each other (Gelman 2017). Many aspects of social structure and subsistence are highly interrelated (see Fig 3.1B), so analyses that focus on just one measure may dramatically overestimate their importance in explaining cross-cultural variation (but see (Haynie et al. 2019), for a recent application of structural equation modeling to cross-cultural data). Conversely, the notion that societies can be characterized by a single dimension of complexity is often taken for granted across the social and behavioral sciences. Cross-cultural researchers often "control for complexity" as if it were a routine sociodemographic variable like age or sex. Indeed, in our study and others a positive manifold emerges (i.e., all complexity dimensions are positively correlated with each other). But positive manifolds are patterns, not processes. The descriptive validity of latent factors should not distract our attention from the additional causal, pairwise relationships among variables that play out over the course of many generations. Integrating these multiple causal pathways to complexity is crucial for explaining unique empirical patterns observed across the historical and ethnographic record, such as complex hunter-gatherer societies that contradict a generalized, agri-centric model of societal complexity.

Here we strike a balance between investigating pairwise relationships on the one hand, and broad statistical summation of the data on the other. We make substantial methodological advances by combining Bayesian model comparison via approximate leave-one-out cross validation (Vehtari, Gelman, and Gabry 2017; Epskamp, Rhemtulla, and Borsboom 2017; Martin et al. 2019), and dynamical phylogenetic models (Butler and King 2004; Ross et al. 2016; Driver, Oud, and Voelkle 2017). This toolkit allowed us to decompose the complexity construct and make causal inference with phylogenetic data in a much more flexible manner than would have been afforded by older approaches, which remain limited to the coevolution of two binary traits. Adopting our approach should empower comparative researchers to better assess multiple competing coevolutionary models.

On its face, our results may resemble "agric-centric" models that nominate agriculture as driving the rise of complex societies. However, we specifically identified the combination of agriculture, fixity of residence, density of population, and urbanization (which we jointly labeled "resource use intensification") as a causal factor. Amazonian horticulturalists practice small-scale agriculture (e.g., swidden gardens) yet maintain a relatively egalitarian social organization and low levels of inequality, perhaps due to abundant but difficult-to-defend food resources (Gurven et al. 2010). In contrast, complex hunter-gatherers rely on relatively stationary but highly productive and defensible resources (e.g., marine foraging, salmon runs, oak groves) which favors sedentism and population growth (Bettinger, Richerson, and Boyd 2009; Kelly 2013; Kennett and Winterhalder 2006). In general, populations are expected to become sedentary and grow larger over time when mobility is limited by resource scarcity and/or inter-group competition. From this perspective, intensive agriculture is sufficient but not necessary for increases in societal complexity.

But how does intensification lead to rises in technological and social differentiation? Population size and subsistence technology may co-evolve to sustain increasingly dense and productive populations (Boserup 2011), but there are large material and labor costs associated with such technologies. The coordination necessary to create and maintain subsistence innovations (e.g., irrigation, fishing weirs, paddy fields) may lead to expansion of leadership roles (Hooper, Kaplan, and Boone 2010), property rights (Pryor 2005), and tighter political integration (Harner 1970). Intensification and technological innovations may also exacerbate inequality as material wealth becomes more important and transmitted intergenerationally (Borgerhoff Mulder et al. 2009; Gurven et al. 2010; Haynie et al. 2019). For example, historical and archaeological records suggest that growing populations coupled with increasing levels of agricultural intensification led to the emergence of stratified chiefdoms in the Hawaiian Islands (Boone 1992; Earle 1978). Additionally, population growth may increase technological innovation rates (Kline and Boyd 2010) and expand the number of socio-ecological niches available to individuals (Smaldino et al. 2019).

Importantly, the initial causes of resource intensification are exogenous in our model. Resource-use intensification, and agriculture specifically, were only possible in certain environments (Bellwood 2005; Bettinger, Richerson, and Boyd 2009; Vilela et al. 2020). We do not extrapolate past environments from current societies. Instead, we use phylogenetic information, reflecting shared population history, as a time-series to investigate how different societal features co-evolve. In principle, archaeological and paleoclimatic data could be incorporated into future analyses as ancestral states and exogenous variables, respectively (Kavanagh et al. 2018). One concern in all phylogenetic studies of cultural evolution is that horizontal transmission between societies means that trait evolution is not strictly tree-like (vertical) (Greenhill, Currie, and Gray 2009; Lukas, Towner, and Mulder 2020). In principle, horizontal transmission should not bias our results: we estimated how changes in RI affect TSD, which does not depend on the mechanism of cultural change being vertical. However, the risk of false-positives would be inflated if societies from different cultural lineages changed due to common horizontal diffusion, because that implies fewer instances of convergent cultural evolution. Finally, we emphasize that comprehensive explanations of individual societies or world regions demand particularistic attention. But our aim in this study was to give a generalizable, macroscopic account of the co-evolution of subsistence and societal complexity, and we found strong evidence that intensification precedes the rise of "complex" societies.

Methods

Study Data

Table 3.2: Description of study data

Variable	**Measure**	**Original Scale**	**Transformation**
Writing	[SCCS149]	1 = None; 2 = Mnemonic devices; 3 = Nonwritten records; 4 = True writing, no records; 5 = True writing, records	None
Fixity of Residence	[SCCS150]	1 = Nomadic; 2 = Semi-nomadic; 3 = Semisedentary; 4 = Sedentary, impermanent; 5 = Sedentary	None

Agriculture	[SCCS151]	1 = None; 2 = <10% food supply; 3 = >10%, secondary; 4 = Primary, not intensive; 5 = Primary, intensive	None
Urbanization	[SCCS152]	1 = fewer than 100 persons; 2 = 100-199 persons; 3 = 200-399 persons; 4 = 400-999 persons; 5 = 1000+ persons	None
Labor Specialization	[SCCS153]	1 = None; 2 = Pottery; 3 = Loom weaving; 4 = Metalwork; 5 = Smiths, weavers, and potters	None
Land Transport	[SCCS154]	1 = Human only; 2 = Pack animals; 3 = Draft animals; 4 = Animal-drawn vehicles; 5 = Automotive vehicles	None
Money	[SCCS155]	1 = None; 2 = Domestically usable articles; 3 = Alien currency; 4 = Elementary forms; 5 = True money	None
Density of Population	[SCCS156]	1 = less than 1 person/sq mi; 2 = 1-5 sq/mi; 3 = 5.1-25 sq/mi; 4 = 26-100 sq/mi; 5 = 100 sq/mi	None

Political Integration	[SCCS157]	1 = None; 2 = Autonomous local communities; 3 = 1 level above community; 4 = 2 levels above community; 5 = 3 levels above community	None
Social Stratification	[SCCS158]	1 = Egalitarian; 2 = Status and wealth inequality; 3 = 2 social classes, no castes/slavery; 4 = 2 social classes, castes/slavery; 5 = 3 social classes or castes	None
Hunting	[SCCS204]	0 = 0-5% dependence; 1 = 6-15%; 2 = 16-25%; 3 = 26-35%; 4 = 36-45%; 5 = 46-55%; 6 = 56-65%; 7 = 66-75%; 8 = 76-85%; 9 = 86-100%	None
Food Storage	[SCCS20]	1 = None; 2 = Individual households; 3 = Communal facilities; 4 = Political agent controlled repositories; 5 = Economic agent controlled repositories	0 = absent; 1 = present

Phylogeny

We used a time-calibrated phylogenetic "supertree" (a tree of trees) based on many published genetic and linguistic phylogenies (Duda and Zrzavý 2019; Hrnčíř et al. 2020; Minocher, Duda, and Jaeggi 2019).

Model Definitions

M0-MS

$\mathcal{M}0$

For each society $n \in N$, each variable $j \in J$ was modelled:

$$y_{[n,j]} \sim f_{[j]}\left(\theta_{[j]}\right)$$

Where f is a probability mass function (Bernoulli or Ordinal) and θ is a vector of parameters. The latent scale expected value μ is a function of θ and defined as:

$$g_{[j]}\left(\mu_{[n,j]}\right) = \alpha_{[j]} + \eta_{[n,j]}\lambda_{[j]}$$

Where g is a link function (e.g., logit, log), α is an intercept, λ is a factor loading that scales the relationship between each latent variable η and the observed variables. The latent variables η were modeled as a matrix normal distribution, which is a generalization of the multivariate normal that allows us to simultaneously capture among-society and between-variable covariance.

$$\begin{bmatrix} \eta_{[1,1]}, \eta_{[1,2]}, \cdots, \eta_{[1,J]} \\ \eta_{[2,1]}, \eta_{[2,2]}, \cdots, \eta_{[2,J]} \\ \vdots \\ \eta_{[N,1]}, \eta_{[N,2]}, \cdots, \eta_{[N,J]} \end{bmatrix} \sim \mathcal{MN}(\mathbf{M},\mathbf{U},\mathbf{V})$$

Where M is a matrix of mean values, **U** is a matrix of among-row (society) covariances, and **V** is a matrix of among-column (variable) covariances. **U** and **V** are linear combinations of different sources of variance, which in M0 comes only from phylogeny. The phylogenetic distance (patristic distance) between societies is incorporated via Gaussian process (GP) functions with exponential kernels. The exponential GP corresponds to an Ornstein Uhlenbeck model of evolution.

We first draw a matrix **X** of independent, normal samples with unit variance and dimensions $[N, J]$, such that:

$$\eta = \mathrm{M} + \mathbf{A}_{[\mathrm{PHY}]}\mathbf{X}_{[\mathrm{PHY}]}\mathbf{B}_{[\mathrm{PHY}]}$$

Where **A** and **B** are lower triangle Cholesky decompositions of the covariance matrices U and V.

$$\mathbf{A}_{[\mathrm{PHY}]}\mathbf{A}_{[\mathrm{PHY}]}^{\top} = \exp\left(-\rho_{[\mathrm{PHY}]}D\right)$$

$$\mathbf{B}_{[\mathrm{PHY}]} = \sigma_{[\mathrm{PHY}]}\mathrm{L}\left(\Omega_{[\mathrm{PHY}]}\right)$$

$$\rho_{[\mathrm{PHY}]}, \sigma_{[\mathrm{PHY}]} \sim \mathrm{HalfNormal}(0,1)$$

$$\Omega_{[\mathrm{PHY}]} \sim \mathrm{LKJ}(2)$$

Where ρ controls how quickly covariance declines with the pairwise distance between societies, denoted D, σ is the standard deviation, and Ω is a correlation matrix. Finally, we set $\mathbf{M} = 0 \ \forall \ n \in N$. $\mathrm{HalfNormal}(0,1)$ and $\mathrm{LKJ}(2)$ are generic regularizing priors that impose conservatism on parameter estimates and facilitate model convergence. The structure and priors of subsequent models ($\mathcal{M}1 - \mathcal{M}3$) are the same unless otherwise stated.

$\mathcal{M}1$

In this model we treat agriculture as a common cause of all other subsistence and complexity variables. SCCS151 is an ordinal variable where the levels encode increasing, but not linear, amounts of agricultural intensification. To accommodate the non-linearity of this variable, we modeled agriculture as a monotonic function where the “dose-response” effect of intensification on each η is estimated from the data (Bürkner and Charpentier 2020).

$$\mathbf{M}_{[n,j]} = \beta_{[\mathrm{AGR,j}]} \sum_{\mathrm{AGR}=1}^{\mathrm{AGR}[n]} \mathrm{S}_{[j]}$$

$$\beta_{[\mathrm{AGR}]} \sim \mathrm{Normal}(0,1)$$

$$\mathbf{S} \sim \mathrm{Dirichlet}(2,2,2,2,2)$$

Where $\beta_{[\mathrm{AGR}]}$ is the effect of moving from the lowest scale of agricultural intensification to the highest and **S** is a simplex that controls the relative effect of each intermediate step.

$\mathcal{M}2$

In this model, a single latent “c-factor” is a common cause of all subsistence and complexity variables. Taking the implications of this model seriously, we include phylogenetic covariance for the latent **C** only, rather than for each variable.

$$\eta = \mathrm{M}$$

$$\mathrm{M}_{[n,j]} = \beta_{[C,j]}\mathrm{C}_{[n]}$$

$$\mathbf{C} \sim \mathrm{Normal}\big(0, \sigma_{[\mathrm{C}]}\big)$$

$$\sigma_{[\mathrm{C}]} \sim \mathrm{HalfNormal}(0,1)$$

$\mathcal{M}3$

In this model, variables are caused by either a resource-use intensification (RI) or technological and social differentiation (TSD) latent factor. We model the correlation between these two factors, but do not include any cross-factor loadings.

$$\eta = \mathbf{M} + \mathbf{A}_{[\mathrm{PHY,RI:TSD}]}\mathbf{X}_{[\mathrm{PHY,RI:TSD}]}\mathbf{B}_{[\mathrm{PHY,RI:TSD}]}$$

$$\mathbf{M}_{[n,j]} = \begin{cases} \beta_{[RI,j]}\mathbf{RI}_{[n]}, & \text{if } j \in \mathbf{RI} \\ \beta_{[TSD,j]}\mathbf{TSD}_{[n]}, & \text{if } j \in \mathbf{TSD} \end{cases}$$

$$\mathbf{RI},\mathbf{TSD} \sim \mathrm{MVNormal}\left(\begin{bmatrix} 0,0 \\ 0,0 \\ \vdots \\ N,N \end{bmatrix}, \Sigma_{[RI:TSD]}\right)$$

$$\Sigma_{[RI:TSD]} = \sigma_{[RI:TSD]}\Omega_{[RI:TSD]}\sigma_{[RI:TSD]}$$

$\mathcal{MS}$

This model is “saturated” in the sense that each variable is correlated with every other variable at both the phylogenetic and observation (denoted “RES”, as shorthand for residual) level.

$$\eta = \mathbf{M} + \mathbf{A}_{[\mathrm{PHY}]}\mathbf{X}_{[\mathrm{PHY}]}\mathbf{B}_{[\mathrm{PHY}]} + \mathbf{A}_{[\mathrm{RES}]}\mathbf{X}_{[\mathrm{RES}]}\mathbf{B}_{[\mathrm{RES}]}$$

$$\mathbf{A}_{[\mathrm{RES}]} = I$$

$$\mathbf{B}_{[\mathrm{RES}]} = \sigma_{[\mathrm{RES}]}\mathrm{L}\left(\Omega_{[\mathrm{RES}]}\right)$$

$$\Omega_{[\mathrm{RES}]} \sim \mathrm{LKJ}(2)$$

Where I is an identity matrix.

Dynamic co-evolutionary model

Our co-evolutionary model is driven by a multivariate stochastic differential equation, similar to a multivariate Ornstein-Uhlenbeck (OU) process. We begin by describing the basic OU model and then relate its components to our own implementation, which permits greater model complexity and flexibility.

OU is a mean-reverting, stationary Gauss-Markov process. It describes change in a trait due to both Gaussian noise and reversion towards some central value. In some fields, such as economics, the mean-reversion component is called "drift" and the stochastic noise is called "diffusion" (i.e., the Vasicek model). In evolutionary biology, the mean-reverting quality is loosely interpreted as "selection" and accordingly the Gaussian noise is labeled "drift" (Lande 1976; Butler and King 2004). The basic OU form is:

$$dy(t) = \alpha(\theta - y_t)dt + \sigma dW(t)$$

Where α controls the strength of mean-reverting selection, θ is the mean trait value, and σ controls the strength of drift. When $\alpha = 0$, the model is pure drift Brownian Motion. The simplest OU models assume a single evolutionary optimum (θ), or estimate an ancestral optimum along with a global optimum. More elaborate OU models imagine that θ changes as a function of other variables, turning it into a co-evolutionary process with varying selection regimes (i.e., the Hansen model) (Hansen 1997; Butler and King 2004). These approaches exploit the fact that, if selection regimes are piecewise-constant (the optimum is the same within each segment of the phylogenetic tree, but allowed to vary at branching points), the OU process can be discretized, giving the expectation and covariance matrix of a trait a closed-form solution. Butler and King provided a maximum-likelihood algorithm for this approach (Butler and King

2004), and a Bayesian implementation for RStan (Team et al. 2016) was developed by Ross et al (Ross et al. 2016).

Depending on the research question, the piecewise constant assumption can be quite restrictive and a poor approximation when tree segments are long. Our approach arose from two complementary goals: first, to extend previous Bayesian implementations of the multivariate OU model such that the optimal trait value θ is updated dynamically (rather than assuming piecewise constant). Second, we wanted a general form of θ that could be used to assess directionality (A → B vs. B → A) and contingencies (A, then B) in evolution, akin to Pagel's popular method (Pagel 1994) with binary traits but without restrictions on the type or number of traits.

We describe our implementation below and visualize our approach in Figure 5. Rather than estimating a phylogenetic variance-covariance matrix, we partition the deterministic and stochastic components of the co-evolutionary process, adapting the continuous time structural equation modeling approach of Driver and colleagues (Driver, Oud, and Voelkle 2017; Driver and Voelkle 2021) to the phylogenetic context. The evolutionary history of any society is modeled as a time series where the deterministic dynamics of the OU play out over the length of each tree segment, and the stochastic drift components (which are by definition orthogonal to selection) are added to the end of each segment as independent samples from the standard normal distribution, scaled by the expected covariance for a given segment duration $t(s)$.

$$d\eta(t) = (A\eta(t) + \mathbf{b})dt + \mathbf{G}dW(t)$$

Where $\eta(t)$ is a vector of the latent variables at time t. The matrix **A** represents "selection" with autoregressive terms on the diagonal equivalent to α in the OU process and the off-diagonals representing the effect of each latent variable on the others (e.g., if η_1 is **RI** and η_2

is **TSD**, then $\mathbf{A}[2,1]$ represents the effect of $\eta_{[RI]}$ on $\eta_{[TSD]}$). b is a vector of continuous time intercepts that, along with A, determine the asymptotic values of η. **G** is the Cholesky decomposition of the "drift" covariance matrix $\mathbf{Q} = \mathbf{G}\mathbf{G}^{\top}$, which scales the stochastic Weiner process. The square root of the diagonals in matrix **Q** are equivalent to σ in the OU process. Although in other types of time-series analyses it is possible to estimate the off-diagonals of **Q** (i.e., the covariance of the stochastic drift terms), it is not possible to simultaneously estimate them in the phylogenetic context while also estimating the off-diagonals of **A**, so in our model we assume that they are 0. This assumption is equivalent to the one made in Pagel's discrete method (Pagel 1994), where it is assumed that multiple traits do not transition together instantaneously.

Following (Driver, Oud, and Voelkle 2017), the solution to this equation for any time interval $t - t_0$ is:

$$\eta(t) = e^{\mathbf{A}(t-t0)}\eta(t_0) + \mathbf{A}^{-1}\left[e^{\mathbf{A}(t-t_0)}\right]\boldsymbol{b} + \int_{t_0}^{t} e^{\mathbf{A}(t-s)}\,\mathbf{G}dW(s)$$

$$\operatorname{cov}\left[\int_{t_0}^{t} e^{\mathbf{A}(t-s)}\,\mathbf{G}dW(s)\right] = \operatorname{irow}\left(\mathbf{A}_{\#}^{-1}\left[e^{\mathbf{A}_{\#}(t-t_0)} - I\right]\operatorname{row}(\mathbf{Q})\right)$$

$\boldsymbol{A}_{\#} = \boldsymbol{A} \otimes \boldsymbol{I} + \boldsymbol{I} \otimes \boldsymbol{A}$, where $\otimes$ denotes the Kronecker-product, **I** is an identity matrix, row is an operation that takes elements of a matrix rowwise and puts them in a column vector, and irow is the inverse of the row operation (Driver, Oud, and Voelkle 2017).

In the OU process, $\frac{dy}{dt} = 0$ when $y = \theta$. Equivalently, we can calculate the equilibrium trait value θ for each latent variable η_i as:

$$\theta_{\eta_i} = \frac{-\left(\sum_{j \neq i} \mathbf{A}\,[i,j]\eta_j + b_i\right)}{\mathbf{A}[i,i]}$$

In the main text we report the standardized difference θ_z, which is the standardized difference in the equilibrium trait value given a standardized increase (we used +1 median absolute difference) in another trait. Note that the vector θ_η does not equal the time asymptotic trait values for the system as a whole ($\mathbf{b}_{\Delta\infty}$) (Driver, Oud, and Voelkle 2017), which are:

$$\mathbf{b}_{\Delta\infty} = -\mathbf{A}^{-1}\mathbf{b}$$

Our method of mapping of this model onto a phylogenetic tree is described in Figure 3.5, and additional computational details are available in our Stan code. Our implementation is flexible and can be used to bridge the gap between static and dynamic models. We were able to transform the static two-factor model $\mathcal{M}3$ into a dynamic model by treating RI and TSD as co-evolving variables rather than simply correlated latent factors, all the while retaining the original model structure that accounts for heterogeneous measurements, missing data, and measurement error. In previous comparative work, researchers might first run intricate multivariate regression models, but then dichotomize their data into a 2x2 contingency table when the time comes to infer co-evolutionary dynamics. With our method, we have made the second step unnecessary. You can simultaneously make full use of the comparative record and make phylogenetic casual inferences.

```
for $n \in N$ do
    Divide the evolutionary history of $n$ into $S$ segments, where each segment starts with a parent node and ends with a child node or tip.
    Calculate the length of each segment $s \in S$, i.e., duration of time between the parent and child nodes.
    Initialize the ancestral trait values $\eta_0$.
    for $s \in S$ do
        Solve for $\eta(s)$:
            $\eta(s) = e^{\mathbf{A}(t(s))}\eta(s-1) + \mathbf{A}^{-1}[e^{\mathbf{A}(t(s)-t(s-1))}]b + \int_{t(s-1)}^{t(s)} e^{\mathbf{A}(t(s-1)-t(s))}\mathbf{G}dW(t(s))$
    end
end
```

Figure 3.5: Algorithm describing the dynamical phylogenetic model.

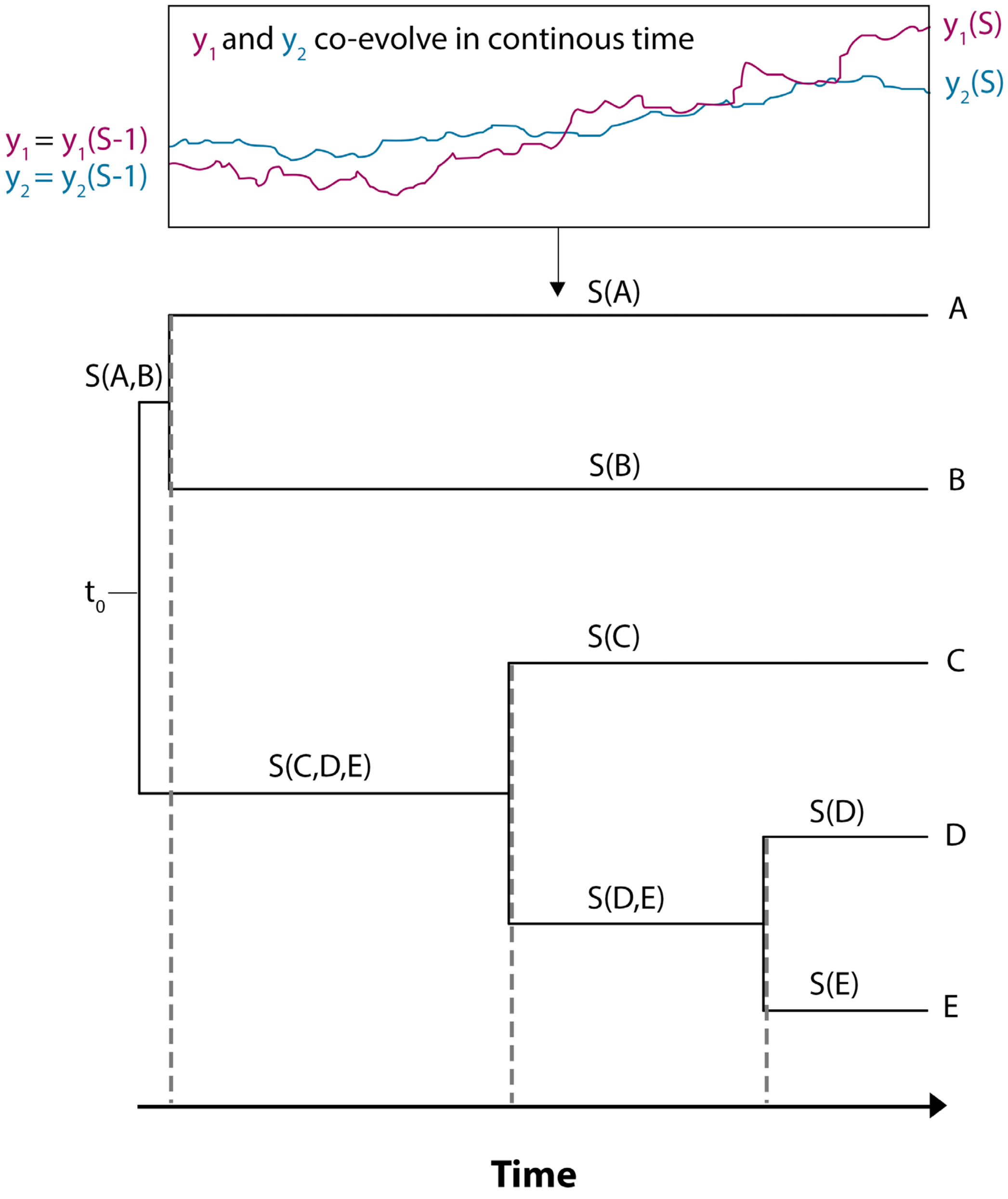

Figure 3.6: Illustration of how our phylogenetic algorithm works. The evolutionary history of each tip (A-E) is described as a time series starting at t_0 and comprised of a set of segments S. The OU process runs over each segment in order, where the initial trait values for any segment s are the terminal values from $s - 1$. Each sequence is a combination of shared segments (where tips are evolving together) and unshared segments (where tips are evolving independently). For

example, S(A) and S(B) start with the same trait values because they both descend directly from the parent segment S(A,B). But further evolution along S(A) and S(B) happens independently. Dashed lines indicate segment split points.

Model Fitting

All analyses were run in R 4.0.0 (R Core Team 2020) and all models were fit using the "rstan" package (Team et al. 2016), 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). We validated our OU algorithm using simulation-based calibration (Talts et al. 2018), first simulating data using a random phyloygenetic tree and prior draws from our generative model and then comparing the posterior distribution of parameter values to the prior simulated parameters. Simulation results suggest the algorithm returns unbiased posterior samples of model parameters.

We relied on convenience functions from the R packages "rethinking" (McElreath 2020), "phytools" (Revell 2012), "deSolve" (Soetaert, Petzoldt, and Setzer 2010), "phaseR" (Grayling 2014), "geosphere" (Hijmans 2017), "tidyverse" (Wickham et al. 2017), "qgraph" (Epskamp et al. 2012), "igraph" (Csardi and Nepusz 2006), "loo" (Vehtari, Gelman, and Gabry 2018), "sf" (Pebesma 2018), "ggtree" (Yu et al. 2017), and "rworldmap" (South 2011). Data and code for reproducing these analyses are available at https://github.com/erik-ringen/complex_coev_sccs.\

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Chapter 4: Multilevel structure of diet among Tsimane forager-farmers

Introduction

Humans rely on cumulative cultural knowledge of how to subsist and what to eat, a remarkable form of plasticity that allows us to inhabit every environment on Earth (Boyd et al., 2011; Boyd & Richerson, 1988; Henrich & Henrich, 2010). Our species has been characterized as a 'generalist-specialist' because in aggregate, humans consume countless varieties of foods, while each population specializes on a relatively narrow dietary subset (Hardesty, 1975; Harris & Ross, 1987; Roberts & Stewart, 2018).[5] Consequently, the foods that people consume (or avoid) often serve as strong indicators of social identity and group membership (Appadurai, 1981; Counihan et al., 2018; Rozin, 1996; Smith, 2006). However, despite the salience of group differences in diet, there may be more dietary variation within populations than between them (Arimond & Ruel, 2004; Naska et al., 2006). Structured variation within populations (e.g., among individuals, families, or within social networks) allows the maintenance of behavioral and cultural diversity, which can accelerate the rate of innovation and act as a buffer against risk in unpredictable environments (Derex & Boyd, 2016; Ember et al., 2020; Migliano et al., 2020; Scaggs et al., 2021). The relative amount of variation between vs. within groups also determines the scope for multilevel selection to act on cultural traits such as diet (Bell et al., 2009; Smaldino, 2014). Therefore, identifying how dietary variation is structured within societies is crucial to

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[5] For example, the Ache of Paraguay derive 98% of their calories from only 17 food sources, despite living in a hotspot of biodiversity (Hill & Hurtado, 1989, cited in Meyer-Rochow, 2009). Lee (1968) notes that, of the 223 plant and animal species known by the !Kung Bushmen, only 54 are classified as edible. While Marlowe (2005) reports more than 880 species included in the Hadza diet, he notes that only a small subset accounts for most consumption, and that many possible prey species are not exploited by the Hadza, either due to explicit taboos or simply being ignored (p. 102, 126).

understanding the evolutionary processes that allow humans to subsist in a staggering array of environments, ranging from tropical rainforests to arid deserts and frozen tundras.

Many different mechanisms can create within-population heterogeneity in diet, including selective social learning (Cruwys et al., 2015; Liberman et al., 2016; Salali et al., 2016), cooperative production and sharing networks (Díaz-Reviriego et al., 2017; Dyble et al., 2016; Reedy & Maschner, 2014), and unequal access to food along geographic and sociodemographic gradients (Darmon & Drewnowski, 2008; Grigsby-Toussaint et al., 2010; Walker et al., 2010). Regardless of mechanism, previous work has clearly demonstrated that: (1) there are repeatable individual differences in diet, and (2) the diets of social partners tend to be correlated (Fletcher et al., 2011; Larsen et al., 2015). These findings demonstrate that there is structured variation in diet *within* human populations. However, these studies are limited in that they tend to focus on just one level of population structure at a time (i.e., just parent-child relationships, or just peers), Additionally, the vast majority have been conducted in wealthy, industrialized nations where children receive formal education about food and are dietarily limited by market offerings rather than local ecology (but see (Aunger, 2000) for a notable exception). Understanding human's evolved pattern of dietary adaptation requires studying subsistence populations where production and consumption are still coupled, and where it is possible to measure several different levels of social organization.

In this study, we quantify the multilevel population structure of diet among Tsimane farmer-foragers of Bolivia using cultural F_{ST} values (CF_{ST}) (Bell et al., 2009; Muthukrishna et al., 2020). CF_{ST} is a standardized measure that tells us to what extent subpopulations are culturally differentiated. We present estimates of dietary CF_{ST} derived from Bayesian multilevel models, which allow us to adjust for confounders and measurement error.

Materials and Methods

Study population

Tsimane live in lowland Bolivia, mostly in settlements along the Maniqui river, with a population of more than 16,000 (Gurven et al., 2017). Tsimane diet is composed primarily of horticultural crops, fish, meat, and gathered plant foods. Market foods account for less than 10% of the diet on average, but this varies between individuals and communities (Kraft et al., 2018). The central form of social organization is the extended family, with kin and neighbors engaging in frequent food sharing, childcare, and other forms of labor sharing—forming small cooperative social networks (Hooper et al., 2015; Jaeggi et al., 2016). Communities range in size from a few dozen to 500 people and are composed of residential clusters formed by 3-4 households of extended kin. In addition to variable population size and river access, communities have differential access to education, healthcare, wage labor opportunities, and market foods from the nearby towns San Borja and Yucomo. Previous research has demonstrated substantial inter-community variation in cooperative behavior (Gurven et al., 2008), health-related phenotypes (Jaeggi et al., 2021; Nyberg et al., 2012; Sprockett et al., 2020), ethnobiological knowledge (Reyes-García et al., 2004, 2014), and diet (Kraft et al., 2018; Reyes-García et al., 2005). Thus, there is ample evidence for behavioral/cultural variation across multiple nested levels of Tsimane social organization (individuals within households, within residential networks, within communities).

Data collection

Behavioral data were collected using random scan-sampling of residential clusters. Observers recorded the behavior of each individual in the cluster every 30 minutes for a period of 2-3 hours. See Cristia et al. (2019) for additional details on the collection of behavioral data, which were collected periodically from 2002-2007. In this study, we use only the subset of observations where individuals were eating (N = 4474 observations, spread across 961 individuals in 226 families from 8 communities, with a median of 4 observations per person). Each observation constitutes the food category (e.g., tapir, plantains, rice) that an individual was eating at a given time. Due to the observational data-collection, these data are not sufficient to comprehensively describe an individual's diet—but that is not our goal. Instead, these data offer unbiased 'snapshots' of what people are eating in a particular time and place and are not subject to the selective reporting/recall bias that often plagues dietary surveys (Coughlin, 1990). Proximity between households was precisely measured using the GPS coordinates of each home, which were then used to calculate within-community distance matrices.

Statistical analysis

CF_{ST}

We used Cultural FST (CF_{ST}) to quantify dietary differentiation across multiple levels of Tsimane social structure (individuals, households, neighbors, communities). CF_{ST}, like genetic F_{ST}, is defined as the ratio of between-population variance to total variance, σ_P^2/σ_T^2. CF_{ST} would be 0 if variation in diet was distributed equally across subpopulations, while larger values of CF_{ST} indicate that diet varies among subpopulations. This statistic has previously been used to quantify cultural distance between societies (Bell et al., 2009; Muthukrishna et al., 2020; Ross et al., 2013) and at multiple levels of aggregation within societies (i.e., village, clan, ethnicity) (Handley & Mathew, 2020; Tucker et al., 2021).

Most authors calculate CF_{ST} directly from their data, which can be problematic because both the sample subpopulation variance and sample total variance may differ systematically from the population they are meant to describe. By definition, CF_{ST} is sensitive to *all* sources of variance, even those that we might consider 'noise'. For example, consider that some foods are only available seasonally. If subpopulations are unevenly sampled with respect to time, this will induce a spurious correlation between subpopulation membership and dietary variation, inflating CF_{ST}. Similarly, because food resources are not evenly available across space, clinal variation in availability may induce correlations between dietary variation and population structure (Ross et al., 2013; Ross & Atkinson, 2016). Measurement error in the data can also distort estimates, for example when a study instrument (i.e., a norms questionnaire, a behavioral ethogram) imperfectly captures an underlying latent variable (Gustafson, 2003; Loken & Gelman, 2017). Therefore, it is useful to use statistical models to adjust for non-relevant sources of variance, confounders, and measurement error. The parameters from these models can then be used to calculate more accurate estimates of CF_{ST} between subpopulations. Bayesian multilevel models are particularly well-suited for this purpose: partial-pooling improves estimates of subpopulation trait values and accommodates unbalanced sampling design, and poststratification offers a principled approach to generalizing from sample to population while propagating uncertainty (Deffner et al., 2021; Gelman & Hill, 2006).

Model Definition

Our outcome variable is categorical (which food type is individual j eating during observation i) with repeated observations of the same individuals, families, and communities. Due to the difficulty of parameter estimation for rarely observed foods, we retained only the top

31 foods (shown in Figure 4.1), which together account for ~80% of all observations and were each observed at least 30 times. All others were collapsed into "other food," which served as the reference category in our model.

For every observation i from individual j:

$$y_{ij} \sim \text{Categorical}\left(\text{softmax}(\beta_{ij})\right)$$

Where β_{ij} is a vector of log-odds scaled probabilities that the food eaten (y) in a given observation i is food category $k \in K$, such that $\sum_{k=1}^{K} \frac{\exp(\beta_{ij})}{\sum_{k=1}^{K} \exp(\beta_{ij[k]})} = 1$. We set the "other foods" category as the reference and fixed its value on the latent scale to 0.

We model β_{ij} as a linear combination of $\text{adjusted effects}_{ij}$ and population structure random effects (v_j):

$$\beta_{ij} = \text{adjusted effects}_{ij} + v_{\text{PID}[j]} + v_{\text{HH}[j]} + v_{\text{RC}[j]} + v_{\text{Comm}[j]}$$

Adjusted effects include the global intercept, age, sex, time (time of day, day of week, and date), and geographic location of community. We adjust for these variables in our model because they are potential sources of variation in diet that are not attributable to population structure. For example, without adjustment, individual variation in diet might be driven largely by differences in age and sex. Continuous predictors (age, date, weekday, hour of day) were standardized before model fitting to have mean = 0 and standard deviation = 1.

$$\begin{aligned}&\text{adjusted effects}_{ij}\\&= \alpha + \beta_{\text{age}}\text{age}_{ij} + \beta_{\text{age}^2}\text{age}_{ij}^2 + \beta_{\text{sex}}\text{sex}_j + \beta_{\text{date}}\text{date}_{ij} + \beta_{\text{date}^2}\text{date}_{ij}^2\\&+ \beta_{\text{weekday}}\text{weekday}_{ij} + \beta_{\text{weekday}^2}\text{weekday}_{ij}^2 + \beta_{\text{hour}}\text{hour}_{ij} + \beta_{\text{hour}^2}\text{hour}_{ij}^2\\&+ v_{\text{geo}[j]}\end{aligned}$$

$$v_{\text{geo}} \sim \text{MultiNormal}\left(\begin{bmatrix}0\\ \vdots \\ 0\end{bmatrix}, \sigma_{\text{geo}}\text{D}_{\text{geo}}\right)$$

Where D_{geo} is the expected variance covariance matrix under a Brownian motion model. While v_{geo} is a community-level random effect that captures geographic covariance, v_{comm} is i.i.d. and represents the residual community-level variance that is not due to geographic proximity.

It is straightforward to calculate adjusted CF_{ST} using the population structure parameters. For example, $\text{CF}_{\text{ST(adj)}}$ for households is given by:

$$\frac{v_{\text{HH}}^2}{v_{\text{PID}^2} + v_{\text{HH}^2} + v_{\text{RC}^2} + v_{\text{Comm}^2} + \frac{\pi^2}{3}}$$

Where $\frac{\pi^2}{3}$ is the distribution-specific variance (Nakagawa et al., 2017). CF_{ST} for other levels of social organization follow the same structure. Note that while this formulation represents the *average* CF_{ST}, this model could also be used to calculate specific sets of pairwise cultural distance between individuals, households, and communities.

Model Fitting

All analyses were run in R (version 4.2.0) and all models were fit using the RStan package (Team & Others, 2016), which fits Bayesian models using Hamiltonian Markov Chain Monte Carlo. We employed regularizing priors for all parameters to reduce overfitting and facilitate model convergence. Markov chain convergence was assessed using standard diagnostics (number of effective samples, the Gelman-Rubin diagnostic, and visual inspection of trace plots).

Results

On average, CF_{ST} was greatest between residential clusters (posterior median = 0.363, 90% credible interval (CI) = [0.274,0.460]) and between households (median = 0.2, 90% CI = [0.154,0.253]). CF_{ST} was low between communities (median = 0.013, 90% CI = [0.001,0.076] and effectively zero between individuals (median = 0.000, 90% CI = [0.000, 0.001]). The magnitude of household vs residential cluster differences varied across food items, but individual and community levels were consistently low (see Fig 4.1). Averaging over diet items, adjusted effects (age, sex, location, time) accounted for ~30% of the variance in the data (median R^2 = 0.302, 90% CI = [0.086,0.741]). In contrast, population structure random effects (individual, household, residential cluster, and community) accounted for ~39% of the variance (median R^2 = 0.416, 90% CI = [0.140,0.632]).

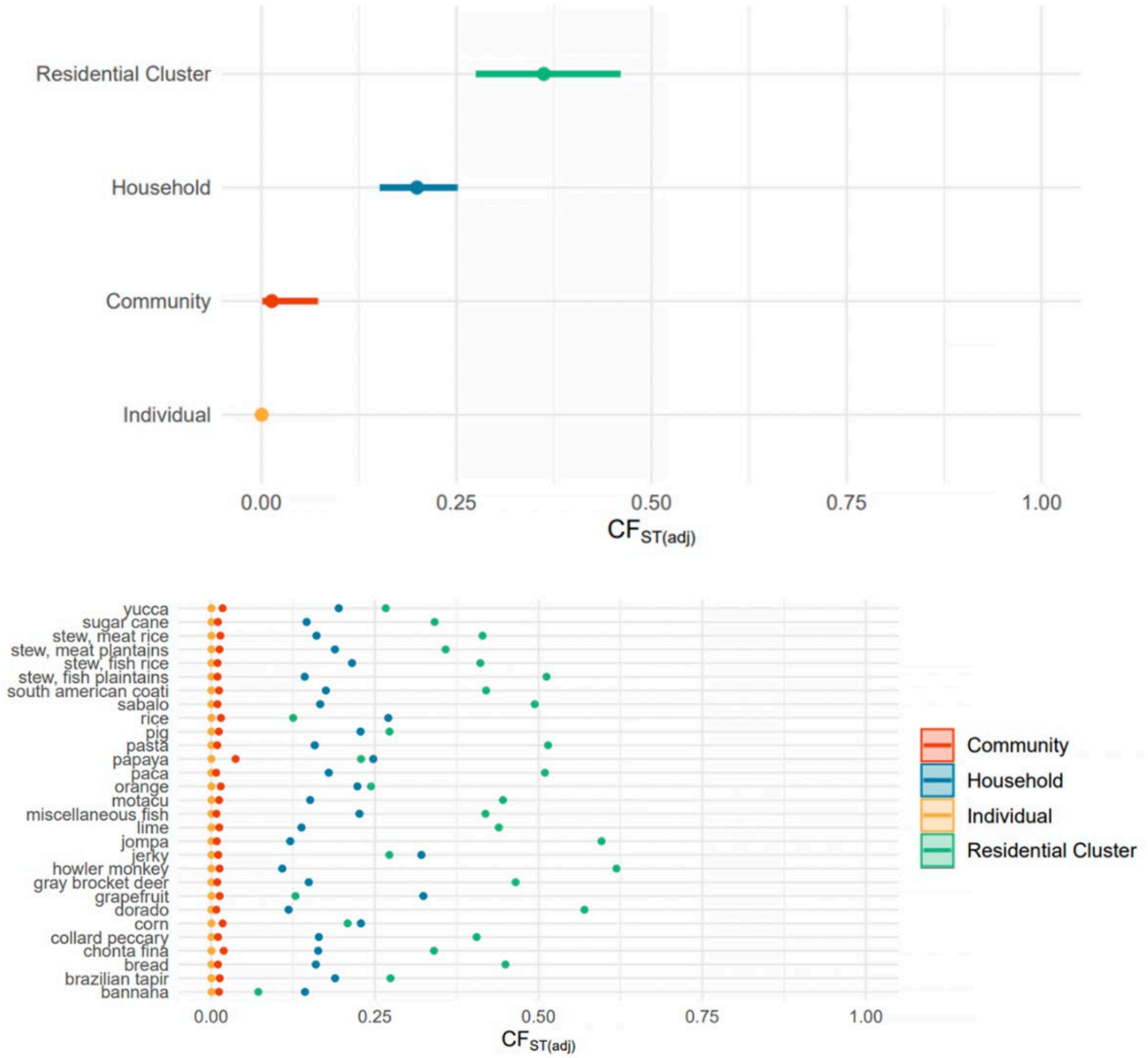

Figure 4.1: (top) Adjusted dietary CF_{ST} across four levels of Tsimane population structure, averaging over food category. Points are posterior median values and error bars denote 90% CI. (bottom) Posterior median dietary CF_{ST} across food categories.

Discussion

This study used naturalistic data and the CF_{ST} statistic to assess the multilevel population structure of diet among Tsimane farmer-foragers. We found that there was substantial CF_{ST} between households and between residential clusters, but minimal differentiation between individuals and between communities. Taken together, around 42% of variance in diet was captured by population structure, suggesting substantial cultural clustering that is not attributable to geographic location, time, or demographic factors. We note that the social structure of dietary variation corresponds closely to the cooperative kin-based networks where Tsimane live, work, produce and consume together (Hooper et al., 2015; Stieglitz, 2009). Across foraging societies, social organization is deeply intertwined with labor and subsistence (Dyble et al., 2016; Jaeggi et al., 2016; Kelly, 2013; Kramer & Ellison, 2010). Identifying the socioecological factors that create and maintain cultural variation within subpopulations is important for understanding how macroscopic cross-cultural differences in diet and subsistence emerge (Boyd & Richerson, 1988; Ross et al., 2013). Previous work has demonstrated that when cultural variation (such as diet and subsistence practices) is maintained in subpopulations, this diversity may lead to more population-level innovations and accelerate the process of cumulative cultural evolution (Derex & Boyd, 2016; Migliano et al., 2020). Thus, the local, kin-based cooperative networks that structure social life in populations such as Tsimane may be primary drivers of cultural change.

Our findings also put the study of social influences on diet in industrial societies in a new light (Cruwys et al., 2015; Zhang et al., 2018). Among Tsimane, we found that individual differences in diet are minimal, after accounting for variation due to age and sex. Tsimane individuals eat whatever those in their households and residential clusters eat. Such small-scale cooperative production and consumption networks were likely important (albeit variable) features of human societies for most of our evolutionary history. When then, did we come to think of eating as an individualistic activity that is "influenced" by our social partners? And what forms of social organization are most influential in populations where most people do not produce their own food?

An important limitation is that the dietary variation considered here is all restricted to variability within Tsimane, over a period of only 5 years. Follow-up studies could "scale up" the investigation of the population structure of diet by including comparison with the diets of neighboring populations in lowland Bolivia such as Mosten (Kraft et al., 2018), as well as investigating how the multilevel structure of diet may have changed over time along with other shifts in lifestyle and nutrition. Future work could also investigate cultural differentiation in other dimensions of human diet, such as quantity of food rather than just type.

The modeling framework presented here opens many possibilities for estimating cultural distance for complex, multi-dimensional phenotypes like diet. The ability to estimate cultural distance from naturalistic data also makes the CF_{ST} statistic relevant for the study of animal "cultures" and food traditions (Avital & Jablonka, 2000; Laland et al., 2009; Laland & Janik, 2006; Whiten & van Schaik, 2007). For example, many primatologists routinely collect the type of data used here to infer dietary CF_{ST} among Tsimane. Our modeling approach, which separates distinct sources of variance and accounts for heterogeneity in availability of food resources across time and space, could be fruitfully applied in animal behavior more broadly. Such comparative study of the population structure of diet could help us understand the evolution of humans' unique capacity to subsist in every environment on Earth.

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Chapter 5: Conclusion

Introduction

This dissertation aimed to develop a modern theoretical and computational toolkit for comparative research, with applications to three studies of the co-evolution of human subsistence and social behavior (Chapters 2-4). In Chapter 2, I drew on a cross-cultural sample of 73 societies and a phylogenetic supertree of human populations to assess how cross-cultural variation in food sharing norms map onto differences in human subsistence economies and social organization. Consistent with a risk-buffering function, sharing was found to be less likely in societies with alternative means of smoothing production and consumption such as animal husbandry, food storage, and external trade. In Chapter 3, I introduced a new method for testing coevolutionary hypotheses with phylogenetic data and applied it to the question of how complex societies evolved. I found that subsistence intensification is a leader, not a follower, in the rise of 'complex' societies worldwide. In Chapter 4, I investigated the social structure of dietary variation among Tsimane of lowland Bolivia, developing a modeling framework to estimate multilevel cultural variation from fine-grained behavioral datasets. I found that most dietary variation is structured at the household and local network level, rather than at the individual or community level. These chapters exemplify the potential for a revitalized comparative method to investigate the co-evolution of human subsistence and social behavior, and offer innovations that are relevant for the study of human evolution and cross-cultural variation more broadly.

In the remainder of this dissertation, I reflect on some outstanding problems for the comparative method in anthropology, as well as some promising future directions. I consider how the methodological innovations from Chapters 2-4 can help resolve these problems—and where they fall short.

Individual vs Group Level Data

In Chapter 1, I discussed the limitations of using averaged, group-level data to test hypotheses about individual-level processes. Simpson's paradox, also called the ecological fallacy, occurs when unmeasured confounding creates spurious, or even reversed, correlations at the group level. For this reason, individual-level data is often considered more decisive or robust. My dissertation engages with this tension most obviously in Chapter 4, where I attempt to partition dietary variation at multiple levels of social organization. Multilevel modeling allows us to avoid premature averaging of data and identify distinct sources of variance rather than assuming the prominence of one level over another. In that chapter, I found that most variation was between households, likely reflecting the Tsimane pattern of cooperative production and consumption. If I had ignored household clustering in my analyses, it would have appeared that most dietary variation was at the individual level.

Thus, the primacy of individual level data is complicated by the facts that: (i) groups exist, and (ii) groups are more than just the average of their constituents. The second point is particularly important when measurements are not the same at different levels of aggregation. For example, a recent study using individual-level data in Cebu, Philippines found that harsh environments do *not* promote alloparental care (Rosenbaum et al., 2022), contrary to previous comparative work that utilized group-level data on allocare and environmental harshness (Martin et al., 2020). While individual data is often held as decisive, it is important to note that the construct of "harshness" means something very different at the individual vs group levels.

"Harshness" in the Martin et al. study is related to shared ecological challenges that increase fitness interdependence, not individual-level developmental adversity and socioeconomic status. We need to be cautious of over-extending predictions from one level of analysis to the other, and that caveat cuts in both directions.

Chapter 2 offers an example of how data at multiple levels of aggregation can be used in a complementary way to better understand study results. We predicted that environmental predictability (temperature, precipitation, and net primary productivity) would be negatively correlated with daily food sharing, due to decreased need to buffer against shortfalls in predictable environments. Contrary to expectations, we found that 2 of these predictability measures were *positively* correlated with sharing. I suspected that these extrinsic predictability measures might be poor proxies of the predictability of actual food production. Therefore, I used a large cross-cultural dataset of foraging returns (Koster et al., 2019) to assess whether populations living in unpredictable environments (measured by the same ecological variables used in the food sharing study) have a greater rate of 'zero-return' trips (measured from individual hunting bouts)--a test of whether these variables capture unpredictability in subsistence. I found no consistent association between hunting success and our measures of predictability. These predictability variables likely capture a more complex pattern of unmeasured environmental variation that cannot be easily interpreted in relation to the "riskiness" of human subsistence.

The Geography of Phylogeny

Much ink has been spilled in the evolutionary human sciences over the relative importance of "cultural" vs "ecological" factors in explaining cross-cultural variation and adaptation (Barkow et al., 1992; Beheim & Bell, 2011; Borgerhoff Mulder, 2013; Boyd et al., 2011; Guglielmino et al., 1995; Mathew & Perreault, 2015; Minocher et al., 2019; Pinker, 2010; Smith, 2000). Comprehensive discussion of this debate is beyond the scope of this chapter, but the core question is to what extent human differences in human behavior are due to species-typical responses to the current environment (i.e., reaction norms, evoked culture) as opposed to cumulative, culturally transmitted information. Here I comment on what I perceive to be an underappreciated nuance to this debate: niche conservatism.

Adaptations, whether genetically or culturally inherited, can be thought of as *strategies* that specify how an organism should develop and behave in the set of different situations they might encounter (Hammerstein et al., 2006; Laubichler et al., 2006). Crucially, this set of situations should reflect not just the current fitness-relevant environment, but that of future generations. If offspring were not born into environments that resembled those of their parents, Darwinian adaptation would be impossible. This micro-evolutionary truism also manifests in macro-evolution, where descendant species tend to live in ecological niches similar to ancestral species ("niche conservatism") (Peterson, 2011; Peterson et al., 1999; Wiens, 2004).

Niche conservatism is relevant for the comparative method in anthropology because human populations also tend to live in environments similar to their ancestors. Variance partitioning approaches that attempt to cleanly separate socioecology from phylogeny (such as those I myself advocate for in Chapters 2-4) are complicated by the fact that ecology mediates the relationship between phylogeny and behavior (see Figure 5.1). In Chapter 2, I found that the correlation between geographic distance and phylogenetic distance among societies in the Standard Cross Cultural Sample (SCCS) was nearly 0.9, making it problematic to include both in the same model due to multicollinearity. In other samples, such as the Pultulo Austronesian database, the correlation is more moderate (cite personal comm here). In Chapter 3 (which also used SCCS data) I noted this problem and alluded to the fact that the inability to adjust for geographic distance *and* phylogeny means that our models do not account for horizontal transmission.

Modeling horizontal transmission, too, is complicated by the tangled web of phylogeny and ecology. For example, a popular approach to adjust for "horizontal transmission" is to include a random effect that captures trait covariance based on geographic distance, i.e., spatial autocorrelation (Gavin et al., 2018; Hooper et al., 2021; Lukas et al., 2021; Ringen et al., 2019)[6]. This makes sense only given a narrow interpretation of horizontal transmission as cultural transmission that occurs within rather than between generations (Cavalli-Sforza & Feldman, 1981). However, because it is ahistorical, this approach fails to capture all the instances of horizontal transmission that occurred in the past. Dynamical network-based methods, used in conjunction with traditional vertical models of transmission, may provide a promising way forward (Gray et al., 2010; Heggarty et al., 2010; Youngblood et al., 2021).

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[6] For example, a regression of the form:

y ~ (1|phylogenetic distance) + (1|geographic distance)

This parameterization implies that "horizontal transmission" is all the similarity between neighbors after accounting for population history.

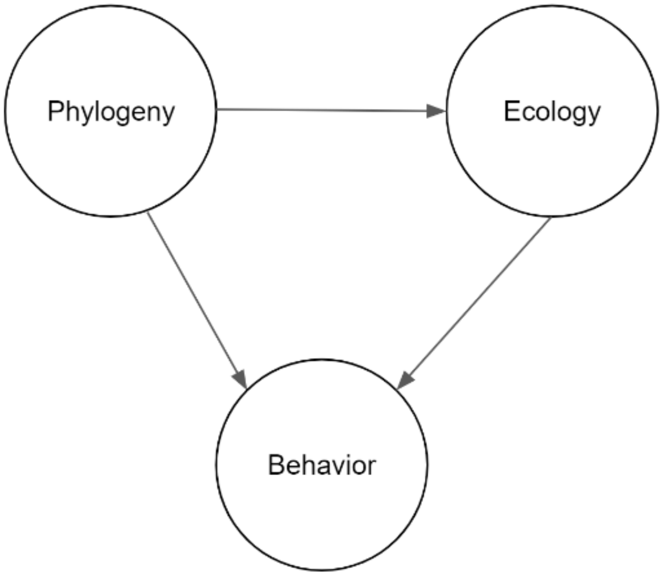

Figure 5.1: Causal diagram of niche conservatism.

B.B.M.B.

In this dissertation I've argued that I can reinvigorate the comparative method, making it Bigger, Better, and More Bayesian (B.B.M.B.). In Chapters 2-4, I presented innovative modeling approaches that expand the horizon of comparative research in anthropology and beyond. These studies also offer insights into the co-evolution of human subsistence and social behavior. However, I suspect that my approach is most persuasive to those who were already on board with the comparative method. Epistemological tensions linger, such as the difficulties of causal inference and the breadth-depth trade-off that inevitably occurs when we do cross-cultural comparison, and —even if our models are B.B.M.B..

My mind is also increasingly drawn to ethical considerations in the production of cross-cultural research—namely, who gets to do it. In evolutionary anthropology and related fields, high-income country-based researchers are the disproportionate beneficiaries of prestigious comparative projects reliant on data collected in low- and middle-income countries (Clancy & Davis, 2019; Nordling, 2020; Urassa et al., 2021). Norms of collaboration, capacity-building, and engagement with local research infrastructure are weak in our field, but it is possible to do better. Increasing the diversity of perspectives in research should also change the questions we ask and make for better science. But even if it didn't (from our vantage point), it would still be the right and equitable thing to do. As norms change for the better in cross-cultural research, an outstanding question is: how do we engage with the comparative record of the past, with data collected under circumstances we would deem unethical today?

Overall, the more time I spend conducting comparative research, the more sobered I am by its limitations. But despite this hard-earned skepticism, I continue to believe in the comparative method as an indispensable tool for understanding human variation and adaptation. I hope that this dissertation honors the legacy of comparative research while also pushing it in constructive new directions.

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