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.

Main Text

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

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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 (*1–6*). However, this "agri-centric" (*7*) 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 (*7*). 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 (*8–10*). Hunter-gatherers also have large, multilevel relational networks that persist over many generations (*11*). 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 (*12*, *13*). 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 (*12*, *14*, *15*).

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 (*15*, *16*)). 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 (*17*, *18*). Some authors focus on political complexity, excluding many other facets (e.g., population size, economic specialization, residential mobility) (*7*, *19*). Others define complexity in relation to material inequality (*20*) or societal scale. Lack of definitional consensus and inconsistent measurement has produced inconsistent results (*21*) 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 (*22*), although in a sample mostly limited to agricultural societies. In contrast, Chick (*18*) found support for a two-factor model in a more diverse global sample (also see (*23*, *24*)). 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 (*25*, *26*). 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 (*27*, *28*). 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 (*26*, *29*, *30*). Artificially binning continuous measures poses inferential risks such as reduced power and increased false positive rates (*31*), 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) (*32*). 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 (*33*) (see Methods). Using this novel methodology, as summarized in Fig. 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.

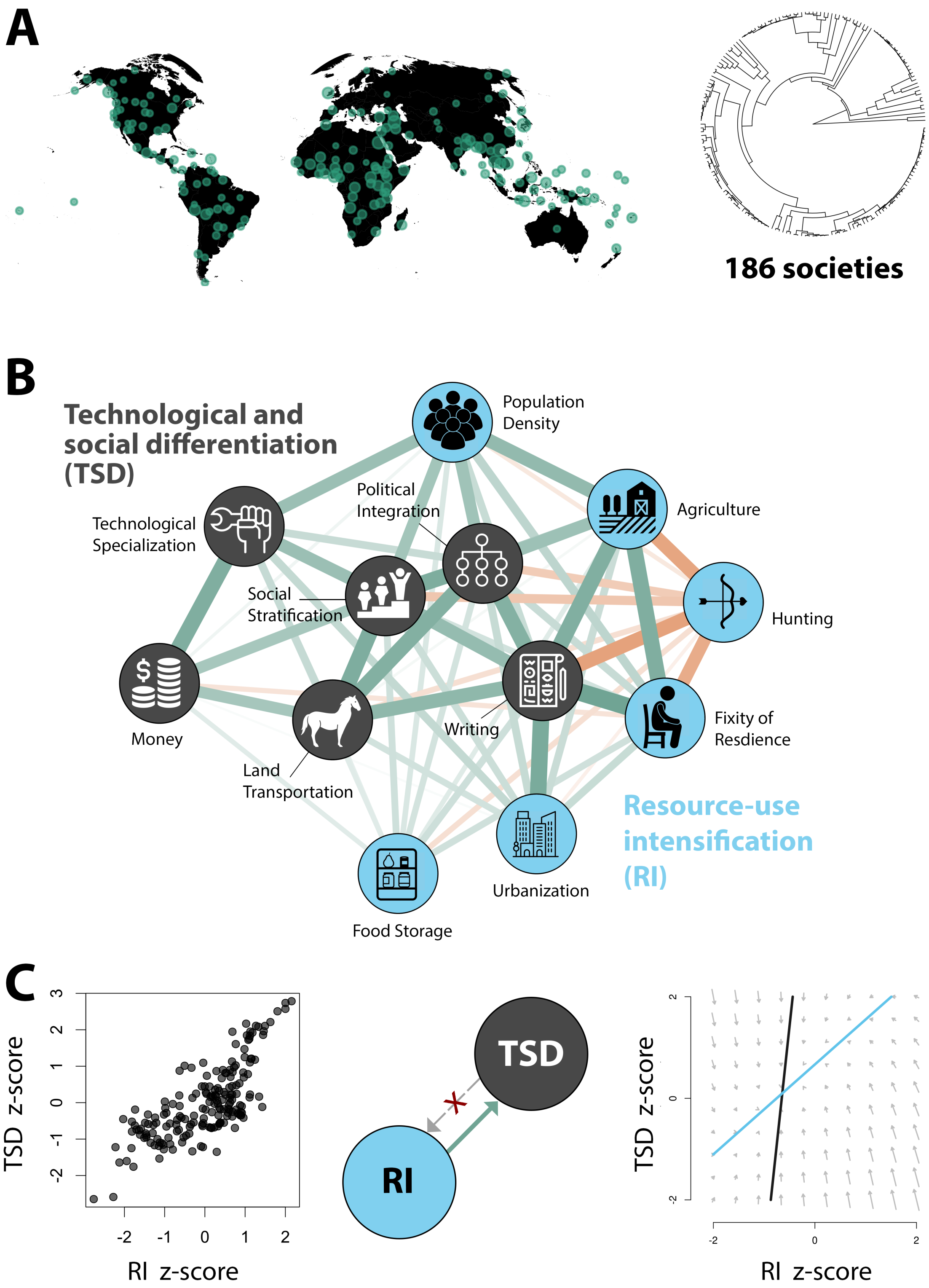

Figure 1: Overview of study approach and main findings. (A)(left) Distribution of study societies; points proportional to log population size. (right) Phylogenetic tree of societies. (B) Phylogenetic correlation network of study variables (depicted as nodes). Edge width/opacity is proportional to correlation 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.

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 (Fig. 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 *a priori*, our approach allowed “complexity” to arise from the correlation structure of the nine individual measures (Fig. 1-2). 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 (*12*). Specifically, greater reliance on hunting should be associated with reduced complexity due to demands on mobility and egalitarian food sharing (*34–37*), whereas food storage allows the breakdown of such sharing (*38*) and facilitates accumulation of surplus as seen in complex hunter-gatherers (*12*).

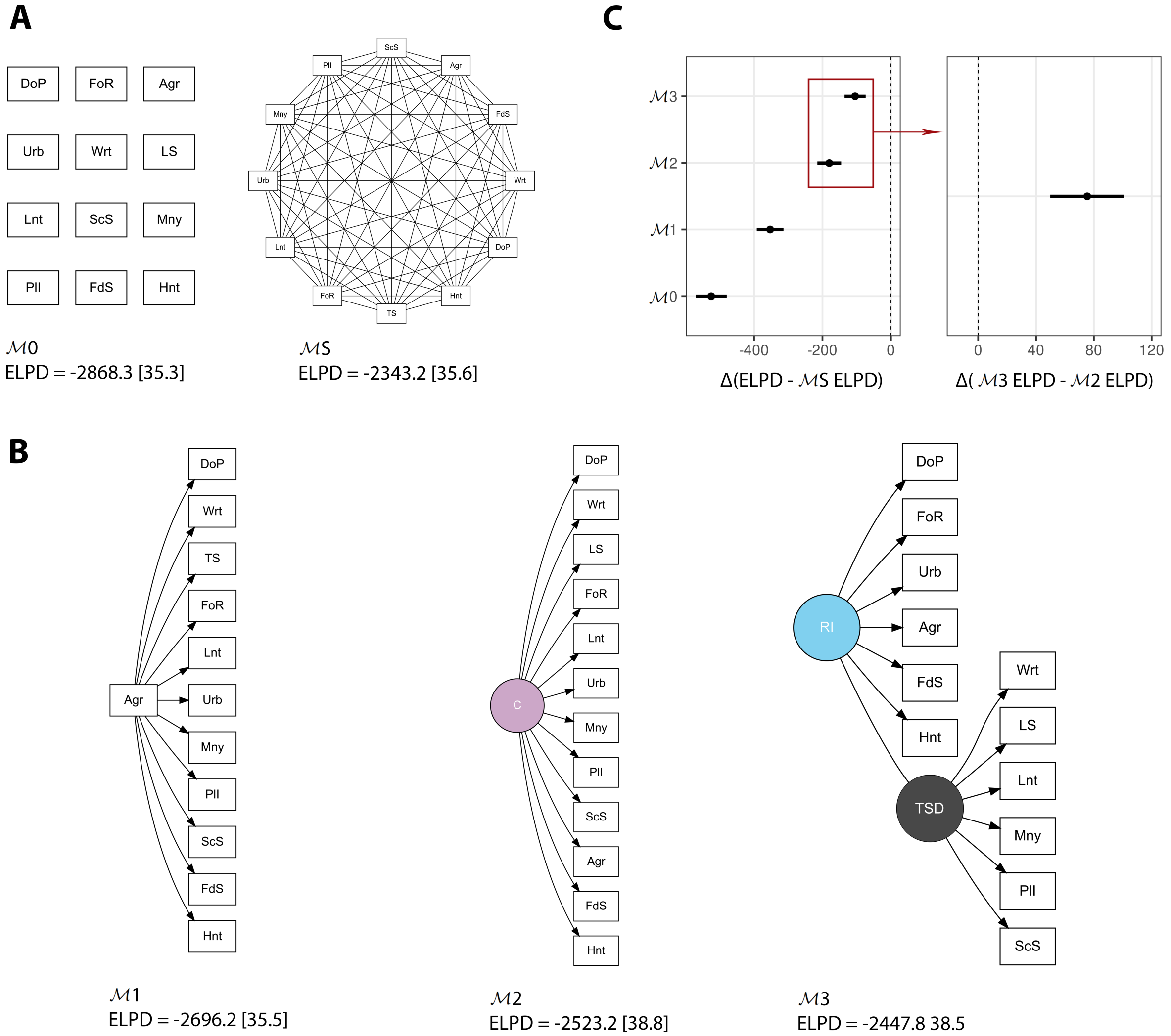

Figure 2: Comparing different causal models of complexity and its relation to subsistence. (A) M0 and MS, which serve as low and high-end model performance benchmarks, respectively. Higher expected log predictive density (ELPD) indicates greater performance. (B) Candidate models (M1 − M3) and their ELPD. 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 Fig. 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 (*39*) 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 (*33*), which simply sums all measures. This model is also consistent with Turchin et al.'s (*22*) 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 (*18*) analysis of the SCCS, which distinguished between societal "scale" and "technology" and has been conceptually replicated in other samples (*23*, *24*). 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).

$\mathcal{M}S$ 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 an *a priori* causal model. We used it as our high-end performance benchmark, which is best practice in structural equation modeling (*40*, *41*).

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)	–	0.59 [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]	–

Table 1: Correlations (ρ) between latent and manifest variables, on the latent scale. Values indicate the posterior median ρ and 90% HPDI.

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 (*42*). 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 Fig. 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 ρ = 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 1. Predicted effects of the latent variables on the observed variables are visualized in Appendix A.

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). The phylogenetic correlation between them was 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 (*43*). Time-calibrated phylogenetic trees, such as the one in this study (*44*), 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 (*27*) and implemented in the software BayesTraits (*45*), 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 (*26*). However, the focus on binary traits is a clear limitation. While it is possible to generalize beyond two traits (*46*), 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 (*47*), 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 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 that gains in RI caused increases in TSD, but changes in TSD did not affect RI (Fig. 1C, Fig. 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.). The relative strength of drift was also greater for RI than TSD (Fig. 4), suggesting that most changes in resource-use intensification were exogenous.

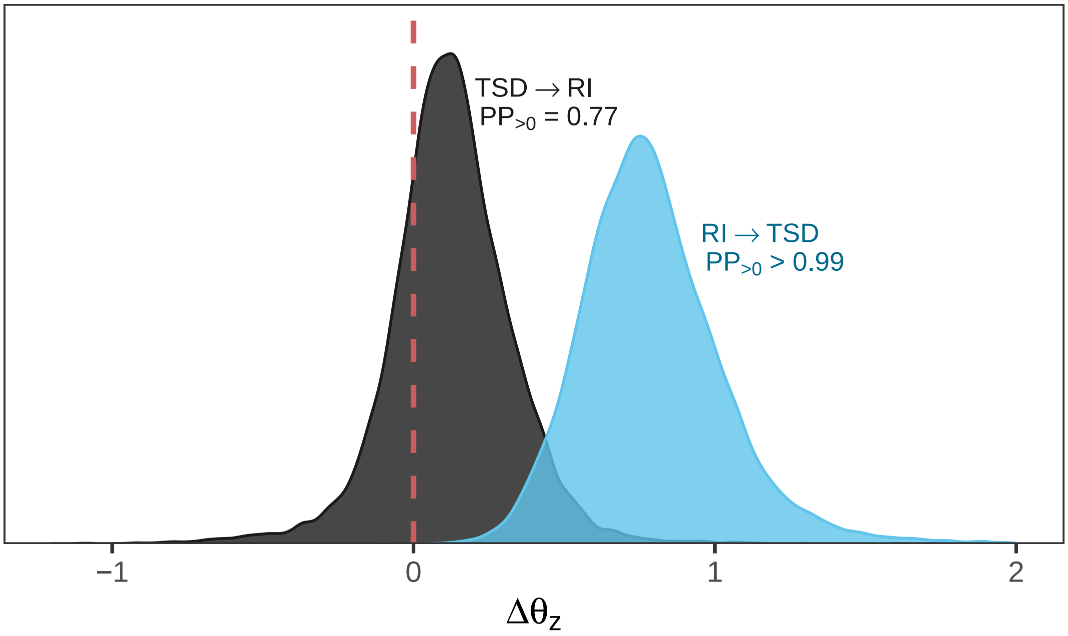

Figure 3: Change in the equilibrium trait value θ of resource-use intensification (RI) and technological and social differentiation (TSD) in response to a 1 standardized unit increase in the other trait. Posterior probabilities (PP) denote the probability that increases in RI leads to increases in TSD, and vice-versa. Values were scaled by the median absolute deviation, which is less sensitive to outliers than the standard deviation.

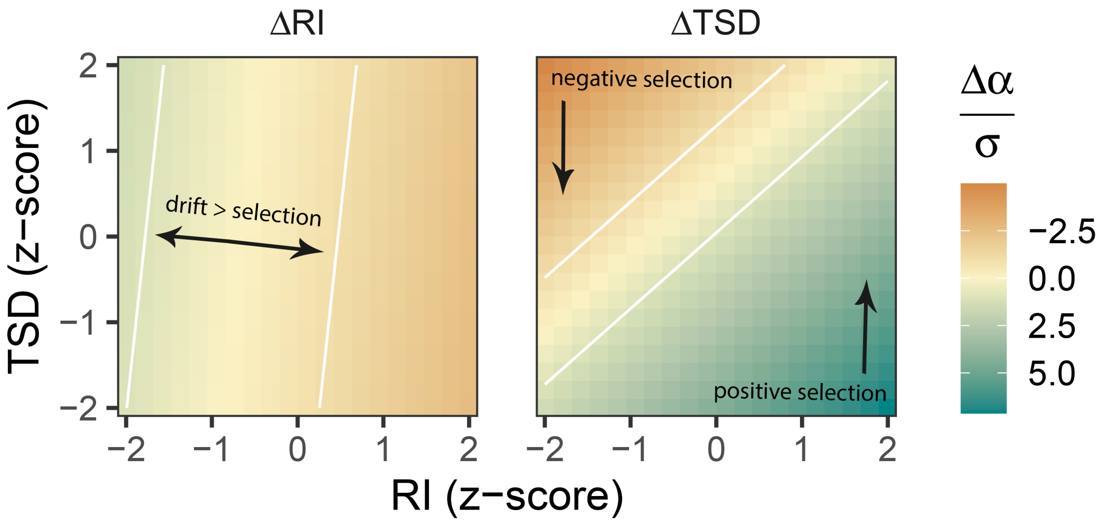

Figure 4: Selection gradients for RI and TSD, given different combinations of trait values, scaled by the strength of drift σ. Absolute values less than 1 are encompossed by white countour lines and indicate parameter space where the change due to stochastic drift σ is greater than change due to deterministic 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 (*2*, *4*, *6*, *48*). 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 (*49*). Many aspects of social structure and subsistence are highly interrelated (see Fig 1B), so analyses that focus on just one measure may dramatically overestimate their importance in explaining cross-cultural variation (but see (*50*), 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 (*42*, *51*, *52*), and dynamical phylogenetic models (*53–55*). 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 (*56*). 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 (*12*, *57*, *58*). 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 (*25*), 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 (*59*), property rights (*60*), and tighter political integration (*61*). Intensification and technological innovations may also exacerbate inequality as material wealth becomes more important and transmitted intergenerationally (*50*, *56*, *62*). 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 (*63*, *64*). Additionally, population growth may increase technological innovation rates (*65*) and expand the number of socio-ecological niches available to individuals (*66*).

Importantly, the initial causes of resource intensification are exogenous in our model. Resource-use intensification, and agriculture specifically, were only possible in certain environments (*57*, *67*, *68*). 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 (*69*). 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) (*70*, *71*). 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. We believe that this risk is lower in the Standard Cross Cultural Sample, because the societies were chosen to minimize relatedness and geographic proximity (*32*). 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

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 = Hereditary slavery; 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 (*44*, *72*, *73*).

Model Definitions

M0-MS

$\mathcal{M}0$

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

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

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:

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

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 $\mathbf{M}$ is a matrix of mean values, $\mathbf{U}$ is a matrix of among-row (society) covariances, and $\mathbf{V}$ is a matrix of among-column (variable) covariances. $\mathbf{U}$ and $\mathbf{V}$ 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 $\mathbf{X}$ of independent, normal samples with unit variance and dimensions $[N, J]$, such that:

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

Where $\mathbf{A}$ and $\mathbf{B}$ are lower triangle Cholesky decompositions of the covariance matrices $\mathbf{U}$ and $\mathbf{V}$.

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

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

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

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

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 $\mathbf{M} = 0 \ \forall \ n \in N$. HalfNormal$(0, 1)$ and LKJ(2) are generic regularizing priors that impose conservatism on parameter estimates and facilitate model convergence. The structure and priors of subsequent models ($\mathbf{M}1 - \mathbf{M}3$) 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 (*39*).

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

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

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

Where $\beta_{[\mathrm{AGR}]}$ is the effect of moving from the lowest scale of agricultural intensification to the highest and $\mathbf{S}$ 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 $\mathbf{C}$ only, rather than for each variable.

$$\eta = \mathbf{M}$$

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

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

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

$\mathcal{M}3$

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.

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

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

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

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

$\mathcal{MS}$

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.

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

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

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

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

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" (*53*, *74*). 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) (*53*, *75*). 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 (*53*), and a Bayesian implementation for RStan (*47*) was developed by Ross et al (*54*).

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 (*27*) with binary traits but without restrictions on the type or number of traits.

We describe our implementation below and visualize our approach in Fig. 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 (*55*, *76*) 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 $\mathbf{A}$ 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 $\eta_{[TSD]}$). $\mathbf{b}$ 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 $\mathbf{Q}$ 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 $\mathbf{Q}$ (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 $\mathbf{A}$, so in our model we assume that they are 0. This assumption is equivalent to the one made in Pagel's discrete method (*27*), where it is assumed that multiple traits do not transition together instantaneously.

Following (*55*), the solution to this equation for any time interval $t - t_0$ is:

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

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

$A_{\#} = A \otimes I + I \otimes A$, 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 (*55*).

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:

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

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 ($\mathbf{b}_{\Delta\infty}$)(*55*), 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 Algorithm 1, 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.

Algorithm 1: Phylogenetic mvSDE

```
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
```

Model Fitting

All analyses were run in R 4.0.0 (*77*) and all models were fit using the "rstan" package (*47*), 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 (*78*), 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" (*79*), "phytools" (*80*), "deSolve" (*81*), "phaseR" (*82*), "geosphere" (*83*), "tidyverse" (*84*), "qgraph" (*85*), "igraph" (*86*), "loo" (*87*), "sf"

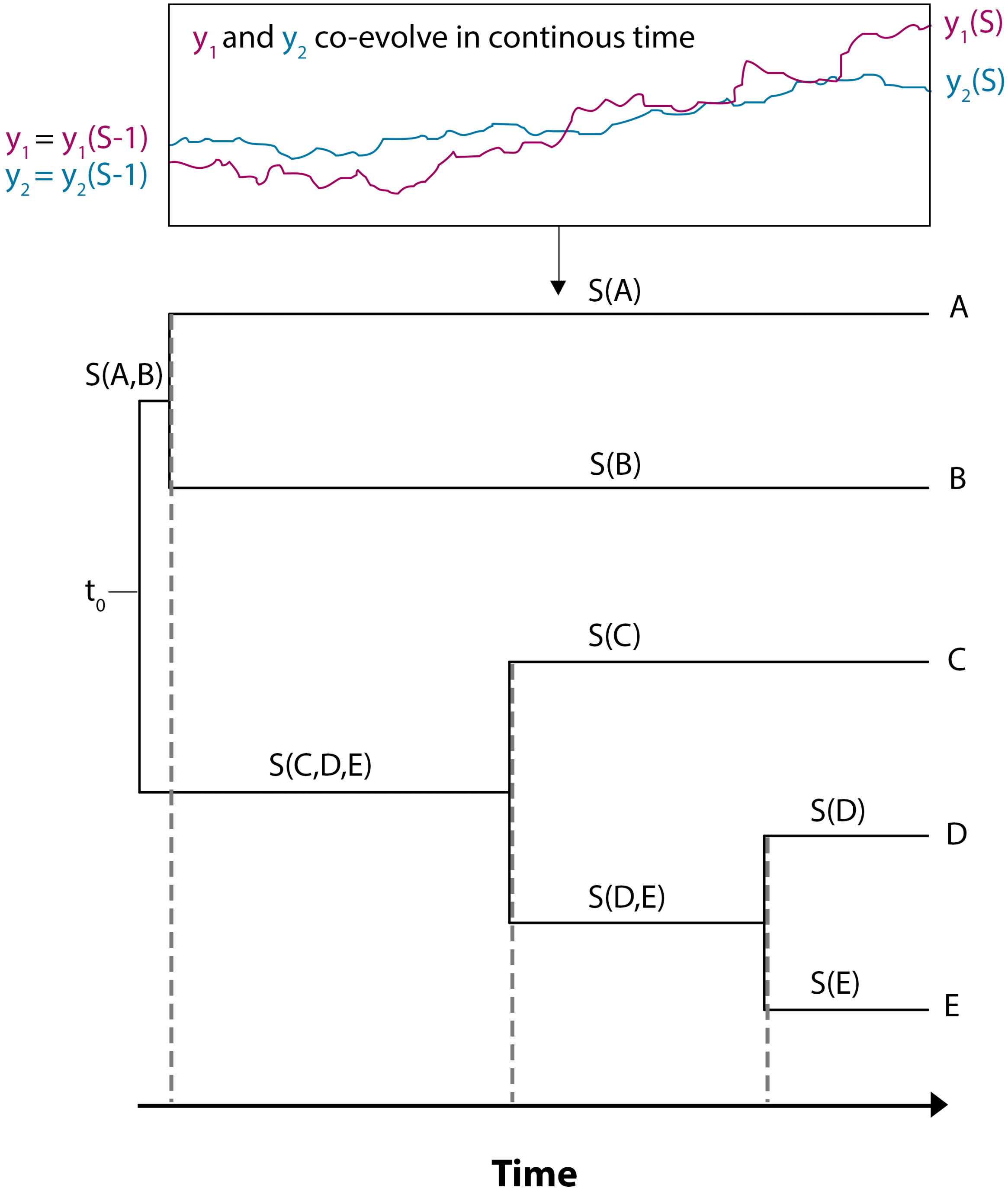

Figure 5: Example of how our phylogenetic algorithm works. The evolutionary history of each tip (A-E) is described as a time series starting at t_0 and comprised of a set of segments S. The OU process runs over each segment in order, where the initial trait values for any segment s are the terminal values 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.

(*88*), “ggtree” (*89*), and “rworldmap” (*90*). Data and code for reproducing these analyses are available at https://github.com/erik-ringen/complex_coev_sccs./

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Appendix A

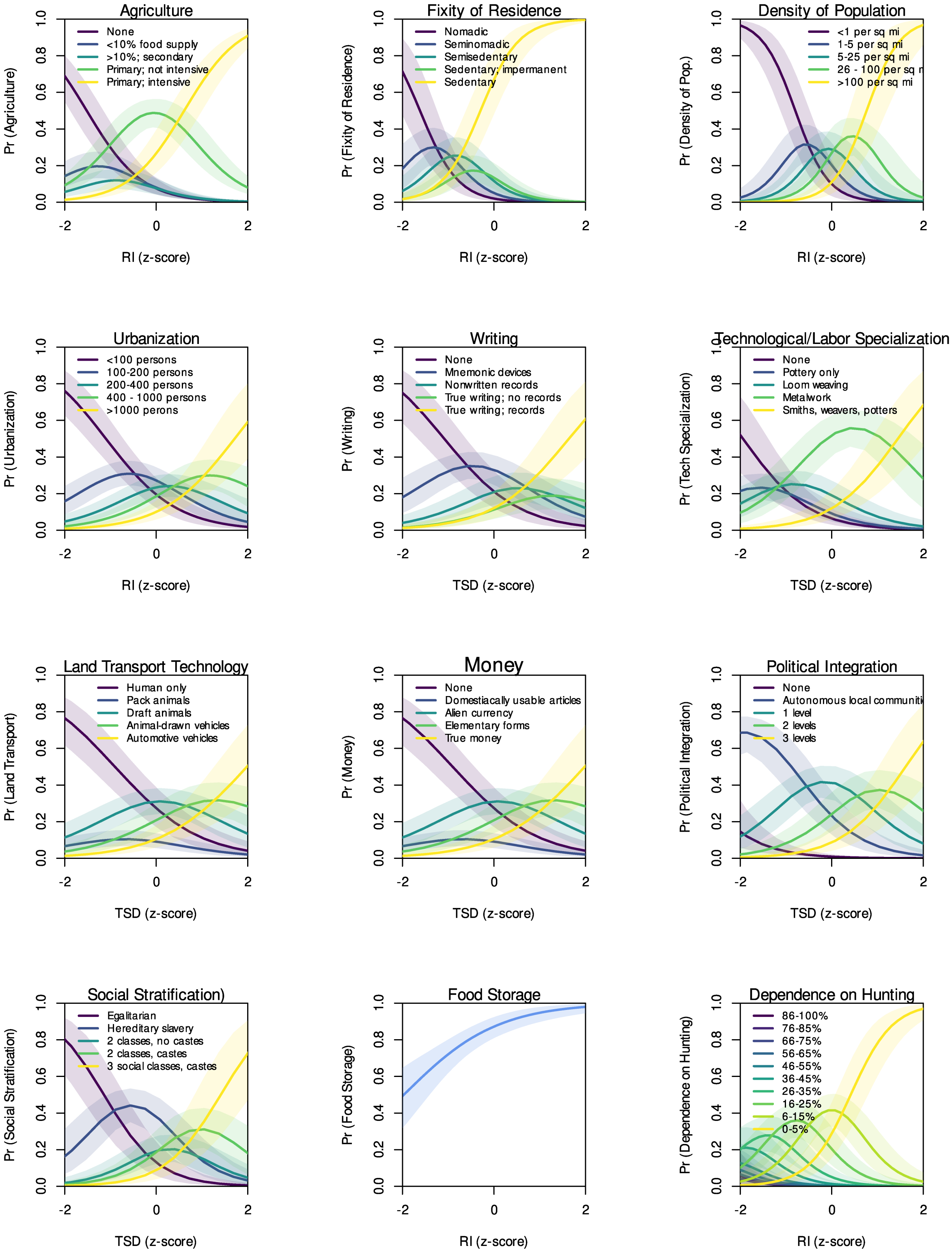

Figure 6: Predicted probabilities of study variables on their original measurement scales, given different values of the latent variables RI and TSD.