



Broadening horizons: Sample diversity and socioecological theory are essential to the future of psychological science

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The present lack of sample diversity and ecological theory in psychological science fundamentally limits generalizability and obstructs scientific progress. A focus on the role of socioecology in shaping the evolution of morphology, physiology, and behavior has not yet been widely applied toward psychology. To date, evolutionary approaches to psychology have focused more on finding universals than explaining variability. However, contrasts between small-scale, kin-based rural subsistence societies and large-scale urban, market-based populations, have not been well appreciated. Nor has the variability within high-income countries, or the socioeconomic and cultural transformations affecting even the most remote tribal populations today. Elucidating the causes and effects of such broad changes on psychology and behavior is a fundamental concern of the social sciences; expanding study participants beyond students and other convenience samples is necessary to improve understanding of flexible psychological reaction norms among and within populations. Here I highlight two examples demonstrating how socioecological variability can help explain psychological trait expression: (i) the role of environmental harshness and unpredictability on shaping time preference and related traits, such as impulsivity, vigilance, and self-efficacy; and (ii) the effects of industrialization, market integration, and niche complexity on personality structure. These cases illustrate how appropriate theory can be a powerful tool to help determine choices of diverse study populations and improve the social sciences.

socioecology | diversity | personality | time preference | cross-cultural

The past four decades have witnessed greater consilience in the understanding of human behavior due to the common thread of evolutionary and ecological theory weaving together the social and life sciences. Recognizing that human psychology and behavior are shaped by similar selection pressures as in other animals is a powerful and humbling starting point when studying the human animal. The existence of population variation, including “cultural differences,” is often believed to complicate the study of humans by obviating generalizability. Instead, variability within and among populations is grist for the theoretical mill. The field of behavioral ecology applies evolutionary and ecological theory to consider adaptive solutions to a wide range of problems typically experienced in the life course of an organism, given competing demands on limited resources. It emphasizes how socioecological factors affect costs and benefits bearing on decision-making. These include factors shaping food acquisition (e.g., patchiness of resources in the environment, technologies available, distance between food patches), marriage and mate choice (e.g., sex ratio, wealth holdings), and social learning (e.g., number and expertise of models, frequency of relevant environmental change), to name a few (1). Given its roots in ecology and ethology, behavioral ecology takes diversity in life and lifeways as fundamental and in need of explanation.

To date, behavioral ecology and related approaches in evolutionary social science (e.g., dual inheritance theory) have

flourished in areas of anthropology and economics, but have had relatively limited impact in psychology. Psychology has been considered more a proximate level explanation detailing mechanism, complementing the ultimate-level functional approach of behavioral ecology. Evolutionary psychology has been remarkably influential in showcasing hypothesized design features of psychological mechanisms, but emphasis in practice has been more on uncovering human universals than explaining variability. The overwhelming emphasis on Western, educated, industrialized, rich, democratic (WEIRD) samples in psychological studies is now well recognized (2), but recognition has had little impact on broadening the sample pools or research directions in much of psychology (3). One strategy to improve representation is to increase sampling of small-scale contemporary hunter-gatherers and horticulturalists, as these populations possess lifeways more similar to our preindustrial past, and thus represent a deep contrast with WEIRD populations. Such inclusion has become more common when testing the universality of different traits or preferences, often revealing noteworthy differences that challenge traditional ideas about human universals (e.g., refs. 4 and 5). For example, working with Tsimane Amerindians of the Bolivian Amazon over the past two decades, colleagues and I have found that Tsimane parents provide minimal infant-directed speech compared with other populations (6), the Big Five personality trait structure fails to replicate (7), there are no midlife psychological crises (8), no sex differences in dead-reckoning skills (9), Tsimane exhibit a highly externalized health locus of control (10), and there is no evidence of heart disease despite high systemic inflammation, a meat-rich diet, and low HDL cholesterol (11). Together, these findings question previously assumed universals in human behavior, psychology, and health.

Diversifying samples is clearly necessary for assessing the universality of traits, or testing any theory about the human phenotype. A second and equally compelling motivation for sampling beyond urban students is to help generate and test theories about human psychology and behavior. In behavioral ecology, the concept of “reaction norms” describes how a phenotype varies in expression across a range of environments and

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conditions. The broad range of physical and social environments the human species has experienced over its evolutionary history leads to a general expectation of a flexible expression of phenotype (i.e., “phenotypic plasticity”) that leads to systematic differences across locales, situations, and over time. Even among hunter-gatherers, many features of subsistence, grouping, mobility, and mating vary in predictable ways along a number of socioecological dimensions (12). Some features of the psychological phenotype are canalized during development (e.g., attachment style, personality), others remain situationally flexible (e.g., loneliness, self-regulation), sometimes varying over the life course (e.g., time preference, libido), while others may show evidence of transgenerational inheritance (e.g., stress reactivity). Diversifying sample pools thus is necessary, not only for assessing trait universality, but for testing causal theories about how the environment shapes human behavior and psychology in systematic, predictable ways.

The key concern with WEIRD samples is that they often reflect a limited and largely unrepresentative portion of the world population. However, within industrialized countries typically labeled as WEIRD, there are large, understudied rural, working class, and ethnically diverse subpopulations (i.e., “inconvenient” samples), whose inclusion could greatly benefit the social sciences. To the extent that WEIRDness is unrepresentative of most of our species history and much of the current world population, a critical question to consider is how WEIRDness and global “WEIRDification” itself affects psychology and behavior. Indeed, different versions of this question have pervaded the social sciences and humanities for several centuries. For example, the institutional and individual changes in behavior associated with a “great transformation” from personalized exchange and reciprocity to formal markets pervades the early work of political economist Karl Polanyi (13) and anthropologist Charles Erasmus (14). Polanyi (13) described how Market Society not only changed laws but altered economic mentalities with the rise of capitalism, while Erasmus (14) focused on greater implications of the replacement of cooperative farm labor with wage labor throughout western South America. The sociologist Max Weber proposed that post-Reformation Protestant ethics and ideas advanced modern capitalism by promoting cultural values of long-term planning and investment, individualism, and wealth accumulation (15).

The German sociologist and philosopher Ferdinand Tönnies developed the concepts of *Gesellschaft* (“society”) and *Gemeinschaft* (“community”) in the late 19th century to contrast urban, cosmopolitan, industrialized societies characterized by impersonal, monetized social relations and rational self-interest, with premodern rural peasant societies valuing family, neighborhoods, and personal social relationships (16). I supplement the *Gesellschaft* prototype with additional WEIRD characteristics: high levels of formal schooling, frequent one-shot interactions with strangers, greater individualism, commercialized market-based interactions, high reliance on efficient technology, and *Gemeinschaft* with the opposite (Fig. 1). Although simplified, the contrast captures key distinctions between WEIRD and many traditional subsistence societies. The contrast can also be made based on the underappreciated (and undersampled) variability within high-income countries. This spatial cross-sectional approach of “reading history sideways” by comparing populations and subgroups within and among countries provides critical variation, although caution is warranted in interpretation given that relationships can vary over space and time (17). Thus, assessing temporal changes experienced in WEIRD countries over the past several centuries, and ongoing transformations occurring in most small-scale populations today, can provide additional opportunities for evaluating causal effects of changes in *Gesellschaft* traits or features.

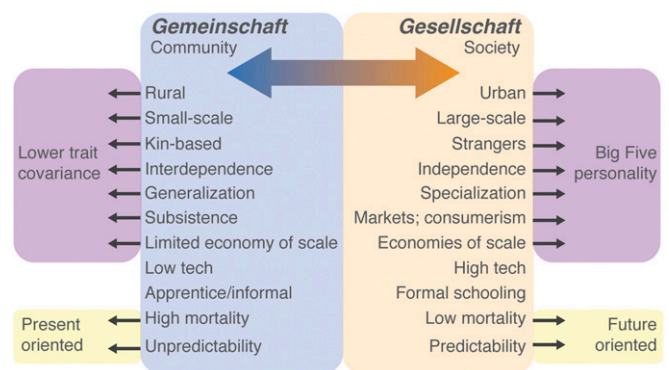


Fig. 1. Schematic framework contrasting *Gemeinschaft* (community) characteristics with those of *Gesellschaft* (society). Adapted from ref. 21. *Gesellschaft* characteristics mirror those reflected by the WEIRD acronym, while *Gemeinschaft* reflect preindustrial Europe and low income countries, and anthropological populations. Text in purple and yellow boxes refer to examples described in the text.

Changes along the dimensions shown in Fig. 1 can be expected to have important impacts on numerous traits. For example, greater abstract representation, innovation, and less “scaffolded guidance” were found among Zinacantec Mayan weavers shifting from subsistence agriculture and minimal schooling to wage labor and increased schooling over a period of four decades (18, 19). Another study in Mexico found that children were less cooperative and more competitive using the same experimental design over several decades in the same communities (20). Some have argued that separate *Gesellschaft* dimensions are all part of the same sociocultural complex, wherein movement along distinct dimensions are expected to have identical effects on development (e.g., ref. 21). However, there are no a priori theoretical reasons to expect separate dimensions to exhibit similar effects on many psychological traits, nor at the same pace of change. Indeed, greater schooling might help promote use and abilities employing abstract logic, whereas more exposure to strangers or an increasingly monetized economy might not. There is also no reason to expect change along a particular dimension to have the same effect everywhere. Thus, understanding how distinct aspects of WEIRDification affect psychology and behavior requires a richer body of theory and empirical studies to assess the separate and synergistic effects of schooling, urbanization, commercialization, and cosmopolitanism. However, the relatively uniform samples comprising most studies in psychology obstruct progress. The subfield of cultural psychology is an exception, but it is often marginalized within the larger psychology discipline, and has focused on limited domains: for example, group differences in individualism and collectivism (22, 23), and strength of social norms and tolerance of deviance (loose vs. tight cultures) (24, 25). Explanatory frameworks rooted in evolutionary and ecological theory have not typically been a part of cultural psychology. However, some research highlights the importance of practice in shaping values and beliefs (26), and how adaptive behavior in different (economic) contexts might help explain differences in perceptions and cultural values (27–29). Usually though, ecology, culture, and history are ignored in most psychological research.

I propose that theoretical frameworks using evolutionary theory, optimality principles, cost-benefit analysis, trade-offs, and socioecological factors are necessary to better understand variability in cultural norms, psychological traits, and behavior, and are necessary for increasing consilience with the life sciences and the study of nonhuman variability. Here I outline two directions for considering how socioecological differences may shape several psychological traits. The first highlights the role of environmental unpredictability and harshness on time preference,

impulsivity, self-efficacy, and related traits. The second focuses on the role of social and economic niche complexity in shaping the structure and diversity of personality. Sketching out the framework and some predictions for these two cases illustrates how theory can help explain population variation, and further justifies why the selection of more diversified study populations—within high income countries characterized by high levels of socioeconomic and ethnic diversity, and among small-scale populations undergoing socioeconomic change—is quintessential for expanding the scientific study of human nature and its manifest expression.

Unpredictability, and Psychological Signature of Fast Life-History Pace

Socioeconomic status (SES) is one of the most commonly used measures in the social sciences, meant to proxy wealth and social status, but it is a “black box” that alone provides little insight above and beyond a general access to knowledge and resources (30). Objective SES indicators are indirect, and may depart from perceived status, standing, and well-being in local communities. SES thus taps into multiple dimensions of “lived experience” that can vary substantially within and among populations.

Two of these perceived dimensions related to SES are environmental harshness and unpredictability. Whereas much research in the social sciences has focused on the amount of social and economic resources, the predictability (i.e., stability) of resource access is a relatively underappreciated component underlying decision-making, with pervasive effects on evolved life history and psychological traits. A species’ life history reflects the effects of selection on the timing and duration of life stages and its events, including juvenile development, age of first reproduction, and rate of senescence. Living in harsh, unpredictable environments characterized by resource insecurity, ecological uncertainty, volatile safety nets, and unsafe neighborhoods can foster a present-oriented disposition that favors short-term benefits despite long-term costs, while discounting long-term benefits that carry short-term costs (31, 32). Present-oriented time preference reflects a “fast” life history. While species vary along a slow–fast life-history continuum as a function of mortality risks and predictability, similar logic and testing finds individuals in the same species varying in life-history pace as well. According to this view, people who perceive themselves living under harsh conditions that are difficult to control are more likely to abstain from healthy habits, including routine physical activity, a healthy diet, physician check-ups, and preventative care, not because of poor understanding of the health consequences of such abstention, but because other uses of time and money may take precedence if chronic disease risks at later ages are discounted (31, 33). Cigarette smoking, alcohol consumption, drug use, criminal behavior, overeating, risk taking, and other activities that provide short-term gains but long-term costs have all been associated with (perceptions of) living in an unpredictable, high-mortality environment (34, 35). Medical treatment compliance, safer sexual practices, regular physical exercise, and other activities that may provide long-term benefits but have immediate costs are instead associated with a predictable, low-mortality environment (36, 37). Faster life histories where future prospects look dim are also expected to shift priorities toward earlier and greater reproductive effort, including earlier sexual maturity, sexual activity and reproduction, greater short-term mating, and higher total fertility (38, 39).

Rural, underserved populations rarely studied in psychology are disproportionately affected by poor living conditions, high rates of disease, adverse effects of climate change, natural disasters, and displacement by governments or foreign entities. These and other cues of harsh environments tend to be associated with more present-oriented time preferences, as short-term

fitness considerations may outweigh potential long-term gains that may never be realized (40). Consistent with this notion, young adults living in slums (*favelas*) of Rio de Janeiro were found to discount the future more heavily than age-matched Brazilian university students (41). Across 46 nations, those with greater life expectancy (proxy for better conditions) were more willing to wait for a larger but delayed reward (i.e., less present-oriented) (42).

Although less explored, these proxies of a faster life-history trajectory can be linked to other psychological traits. Dispositional attributes shaped by living under resource-insecure conditions include not only steep temporal discounting, but also higher impulsivity, less self-regulation, low self-efficacy, and an externalized locus of control: that is, believing that one’s own efforts may have only marginal effects on well-being (43). Thus, in terms of motivation to improve one’s health, a relatively stable environment with predictable resources and low extrinsic mortality risk should favor greater self-efficacy and a more internalized health locus of control orientation due to the payoffs from successful planning in matters of health. Such planning requires a sense of control and an ability to self-regulate in ways that help attain delayed gains at short-term cost, especially in the presence of numerous stressors. On the other hand, an environment characterized by resource unpredictability and high exogenous mortality risks should favor a more externalized locus of control orientation, greater temporal discounting, and lower self-efficacy in terms of health care decision-making. Consistent with this line of reasoning, experimental evidence reveals that low levels of control lead to a lower ability to focus on concrete goals (44), a belief that goals are not attainable (45), less motivation to realize goals (46), and greater future discounting (47). Across 43 nations using a World Values Survey, lower income within and among countries was associated with lower perceived control, intrinsic motivation, trust, and prosocial attitudes (48). Across countries, low income conditions also reduce self-efficacy, and increase vigilance and impulsivity (49, 50). Among seven postcommunist countries, the effects of SES and material deprivation on health were mediated largely by perceived control (49). Thus, resource limitation, harsh environment, and uncertainty about the future may lead to undervaluing long-term health. Further support is evident in a recent study of Tsimane Amerindians, who exhibit less internal and more external locus of control than representative, age-matched samples from the United Kingdom and Japan; Tsimane with external locus orientation are less likely to seek medical attention for common illnesses (10).

To date, the few experiments testing effects of harshness on time preference and other psychological traits reveal similar findings as in observational and comparative studies. Inducing cues of poverty among Chinese students revealed more impulsivity and present-oriented preferences (51). Envisioning one’s future self, through letter-writing and virtual reality representation, also appears to reduce support for risky and delinquent behavior (52). Additional experiments show parallel relationships beyond humans. For example, European starlings in poorer condition (proxied by greater telomere attrition) act more impulsively, while having lower energy reserves resulted in steeper time discounting (53). Thus, observational and experimental evidence supports patterned variability in several psychological risk-related attributes that affect decision-making as coherent, functional responses to cues of socioecological context. Development of these psychological traits guiding preferences and decision-making may be especially shaped by exposures early in life (54), although additional changes over the life course as circumstances improve have also been observed (55).

Living in poverty with many stressors and low sense of power is also believed to induce greater “cognitive load,” and hence greater susceptibility to cognitive biases and poor decision-making (50).

But in contrast to this “deficit” model where adverse environments are believed to result only in impairments and underachievement, an adaptive flexibility approach considers that individuals groomed in adverse or high-stress conditions develop traits that are better suited to managing these conditions (56). Indeed, evidence to date suggests enhanced abilities among vulnerable and at-risk populations or even when such stressful conditions are artificially induced in the laboratory. These include greater attention-shifting (57), memory for negative events (58), rapid tracking (56), recognition of angry and fearful faces (59), enhanced learning about animal dangers (60), enhanced early-life memory retention (61), and empathic accuracy (62). Understanding that different cognitive “biases” may be adaptive responses to sustained living under difficult conditions has important implications for what constitutes appropriate interventions in educational and employment settings (56).

This theoretical approach relating life-history pace, time preference, and psychological traits presents a promising direction for further exploration of population differences in a growing number of psychological and behavioral traits. Most critically, it requires sampling individuals from a wide range of socioeconomic backgrounds and developmental histories in WEIRD populations. For example, a study of urban middle school students in the industrial city of Flint, Michigan, showed that perceptions of a harsh neighborhood and social environment were associated with more present-oriented time preference, and itself associated with greater participation in risky behaviors, such as physical aggression and property crime (63). Similarly, community college students with shorter perceived time horizons and greater perceived future unpredictability engaged in more risk-taking behavior in areas of safety, health, sexual behavior, finances, and social relationships (40). Contrasting environments characterized by uncertainty, harshness, poverty, and danger with those distinguished by predictability, abundance, comfort, and safety requires that researchers sample beyond the university, broadly within one’s state and country, in addition to greater sampling of low-income countries.

The studies mentioned here represent just the beginning of a nascent life-history and socioecological approach to understanding plasticity in psychological traits. Exciting directions abound. For example, with improved health infrastructure and other forms of socioeconomic development occurring globally but at different rates, perceptions of uncertainty and environmental harshness should shift accordingly, with concomitant impacts on psychological traits affecting behavior. Natural disasters and other unexpected traumatic events can temporarily shift perceptions in the opposite direction, even in high-income countries. Indeed, exposure to catastrophes is associated with altered time and risk preferences (64). In low-income countries, floods and other disasters can lower aspirations and affect risk and time preferences in ways that help explain the difficulty of escaping poverty (65). Even when individuals experience similar traumas or inhabit similar environments, individual perceptions of events and future prospects can vary in key ways that affect decision-making related to resilience. This new body of research highlights the need to better understand how perceptions are formed in the first place. The question of perception formation and updating is especially relevant in the context of rapid cultural, socioeconomic, and political change.

Socioecological Complexity and Personality Diversification

A major area of psychology addresses the content of personality structure. The Five Factor Model (i.e., “Big Five”: openness, conscientiousness, extraversion, agreeableness, neuroticism/emotional stability) is often claimed to be the universal structure of human personality that transcends language, culture, history, economy, and ideology (66, 67). Although other structures have been described (e.g., ref. 68), with more or fewer factors, most

are similar to the Big Five. It is largely non-WEIRD samples that to date have deviated most from the Big Five. For example, Tsimane personality structure supports two factors combining features across the Big Five: prosociality/leadership and industriousness (7). The failure of the Big Five to replicate among the Tsimane could not be explained by addressing the usual methodological culprits. Stratifying by sex, cohort, schooling, and Spanish fluency made little difference, nor did accounting for acquiescence and confirmation bias; spousal reports also showed a similar two-factor structure. Other findings with indigenous populations are instructive. For example, failure to demonstrate the Big Five has also been recently shown among both rural and urban Mossi in Burkina Faso (69). Among 12 isolated languages, including Maasai, Fijian, and Enga, a lexical approach documenting universal attribute concepts highlighted just two dimensions of dynamism and social self-regulation (70).

Without a theory of personality formation, it is unclear whether different environments should generate true differences in personality structure in the first place. An evolutionary hypothesis proposes that temporally stable aspects of affect, cognition and behavior (i.e., personality) are adaptations that over generations tended to maximize biological fitness. However, this middle-range expectation alone does not carry enough specificity to guide research on personality variation across populations. Thus, it is critical to understand how low-order traits are coordinated to assemble into higher-order factors. The Big Five’s successful replication in many countries could be an artifact of living in a large urban, literate population. Even in prior studies demonstrating cross-population evidence for the Big Five, low congruence scores were obtained in samples in India, Botswana, Morocco, and Nigeria (66). An old but still unstudied question thus is to ask whether and why personality and its structure might differ substantially among populations. Levels of specific traits, such as extraversion and openness, certainly vary among populations (71), but the notion that the number and content of factors itself might vary is more complicated to resolve.

A behavioral ecological perspective would suggest that personality items should covary to the extent that they act synergistically to help individuals achieve fitness-relevant goals. Fitness effects of particular trait covariance structures should vary across socioecological environments with distinct ways of gaining status, obtaining mates, caring for children, producing and defending resources. Big Five personality covariance will be greater to the extent that meeting these goals requires facets cross-cutting the five factors. With this guiding logic, my colleagues and I recently proposed a hypothesis that greater societal complexity, defined by a greater number of diverse specialized social and occupational niches, should favor more weakly inter-correlated higher-order personality factors in a population. This “socioecological complexity hypothesis” (72) suggests that beginning with the Neolithic agricultural revolution, life in large, dense, and stratified populations became increasingly marked by greater niche diversification and divisions of labor; later technological and industrial revolutions, and expansion of markets in a monetized economy further expanded the number and specialized character of niches. More niches means more ways of being successful, and of maximizing fitness or proxies of fitness, such as wealth and prestige. Urbanization intensifies labor, mating, and social markets by concentrating larger numbers of people, and by incentivizing novel forms of specialization (73). Whereas hunter-gatherers are more likely to be “Jacks and Jills of all trades,” industrialized populations rely on highly specialized roles for producing goods and services. Personality diversification should map onto this high degree of occupational and social diversification if phenotypic specificity favors a more optimal performance within specialized niches. Another possibility is that having a greater number of niches open to individuals loosens whatever constraints on personality expression that

might otherwise arise with having fewer options. For example, successful leaders in small-scale horticulturalist populations, such as the Tsimane, must not only be gregarious, but also generous, agreeable, hard-working, conscientious, and emotionally stable; under such conditions, we might expect greater interfactor correlations among the traditional Big Five factors, as is found among Tsimane. In industrialized populations, a project leader on an engineering project could be highly organized and creative, but shy, introverted, and unpleasant. Thus, a straightforward prediction is that populations characterized as having greater socioecological complexity should show greater personality diversification. In terms of the Big Five, we would expect lower correlations among the factors in more complex societies.

The first test of this hypothesis, by my colleagues and me, compared 55 nations (comprising 17,637 adults) tested using the same Big Five Inventory (72). Socioecological complexity was operationalized as a composite of three variables: human development index (United Nations index that combines data on levels of education, gross domestic product, and life expectancy), urbanization (percentage of nation's population living in an urban vs. rural setting), and sectoral diversity (a measure of a country's volume and diversity of exported products). Complex countries have citizens who are relatively, wealthy, literate, long-lived, residing in cities, and both producing and exporting a large and diverse set of goods and products. According to this composite measure, Japan, Belgium, and the United States are on the high end of socioecological complexity, while Ethiopia, Tanzania, and Bangladesh are on the low end. We found that a nation's socioecological complexity was inversely associated with its average interfactor Big Five correlation (Pearson's $r = -0.54$, $P < 0.001$). The average Big Five interfactor correlation spans from 0.14 (France) to 0.45 (Tanzania) across the 55 countries. For comparison, Tsimane horticulturalists, the only small-scale society studied using the same personality instrument, had an average interfactor correlation of 0.54 (7). Accounting for differences in sample size, geography, literacy, acquiescence, negative item, and evaluative bias did not substantially reduce the magnitude or significance of the relationship between socioecological complexity and interfactor correlation (72). It is notable that the Big Five factor combinations whose associations diminished most strongly with greater socioecological complexity tended to involve openness and conscientiousness more than emotional stability, agreeableness, or extroversion.

Personality trait covariance among Big Five at the nation level may reflect other aspects of national character or personality that are not typically studied by considering socioecological underpinnings. One achievement of cultural psychology has been to develop country-specific measures describing different aspects of

culture, including "tightness," "individualism," and "power distance." For example, cultural tightness reflects having many strong social norms and low tolerance of deviant behavior (74), while power distance describes the extent to which a community accepts and endorses authority, power differences, and status privileges. I expect personality trait covariance to be higher in places identified as tight, ranking low in individualism and high in gender egalitarianism. Indeed, Table 1 reports significant positive correlations between nation-level personality trait covariance and cultural tightness, and negative associations with Hofstede's Individualism Index and GLOBE's Gender Egalitarianism Values. Though not explicitly predicted, trait covariance also associated positively with Hofstede's Power Distance Index and GLOBE's Assertiveness Values Index. Adjusting for gross domestic product (GDP) reduces but does not eliminate many of these associations. Thus, even after accounting for the fact that trait covariance is greater in low-income countries, nations with higher trait covariance have greater cultural tightness, less cultural emphasis on gender egalitarianism, and more cultural emphasis on the role of assertion and confrontation in social relationships.

Despite the usual limitations of country-level comparative studies, together these findings introduce important questions about how personality structure might vary among populations in ways that have yet to be addressed, due in part to assumptions and repeated claims about universal structure. Greater sampling of diversity is needed on several empirical fronts. First, more research is needed among populations varying widely in socioecological dimensions. Second, populations experiencing rapid changes over time in socioecology (Fig. 1) could be sampled throughout this process to determine whether personality structure shifts accordingly. Along these lines, it will be interesting to assess Tsimane personality structure again in another decade after further modernization and acculturation. Third, children of immigrants who migrated from areas of lower to higher or higher to lower socioecological complexity may expect to show reflective differences in personality structure compared with their parents. Fourth, developmental research will need to focus on how coordinated traits might be facultatively calibrated in different environments during childhood and adolescence. Some evidence supports this view: Tsimane men and women who are physically stronger or obtain schooling are more likely to be extraverted (75). Similarly, exposures to stressors early in life may calibrate one's later susceptibility to stress, possibly reflecting differences in neuroticism (76). Finally, formal models will be necessary to more explicitly consider the verbal argument about the evolution of personality structure described here,

Table 1. Relationship between dimensions of national character and Big Five trait covariance

Cultural variable	Definition	Pearson correlation with Big Five trait covariance	Pearson correlation, adjusting for GDP
Tightness Index (24)	Having many strong social norms and low tolerance of deviant behavior	$r = 0.419$, $P = 0.042$, $n = 24$	$r = 0.437$, $P = 0.037$, $n = 24$
Hofstede's Individualism Index (90)	Degree to which people in a society are integrated into groups.	$r = -0.349$, $P = 0.034$, $n = 37$	$r = -0.190$, $P = 0.266$, $n = 37$
Hofstede's Power Distance Index (90)	The extent to which the community accepts and endorses authority, power differences, and status privileges.	$r = 0.301$, $P = 0.071$, $n = 37$	$r = 0.133$, $P = 0.441$, $n = 37$
GLOBE's Gender Egalitarianism Values (91)	The degree to which a collective minimizes (and should minimize) gender inequality.	$r = -0.423$, $P = 0.013$, $n = 34$	$r = -0.334$, $P = 0.058$, $n = 34$
GLOBE's Assertiveness Values (91)	The degree to which individuals are (and should be) assertive, confrontational, and aggressive in social relationship	$r = 0.451$, $P = 0.007$, $n = 34$	$r = 0.440$, $P = 0.010$, $n = 34$

Adjustments made for 2001 GDP (Pearson's r between GDP and personality covariance = -0.326 , $P = 0.015$).

especially the role of feedback effects between successful specialized role fulfillment and trait-related behaviors.

Socioecology and Culture

Calls to diversify samples in the social sciences are poised to expand the range of cultural diversity. My emphasis and the two examples discussed in this paper, however, focused on socioecological factors as key drivers of population variability, rather than any explicit consideration of culture. Many socioecological characteristics directly or indirectly affect the expression of cultural traits. There is a long history of modeling cultural traits as adaptations to social and physical environment in small-scale societies, and socioecological features figure prominently in studies of the historical origins of cultural institutions in large-scale societies. For example, a history of defending herds among mobile pastoralists in the absence of police authorities has been linked to the cultural complex of honor in the United States South and elsewhere (28). The cultural legacy of agriculture, however, is not uniform, but depends on how crops are produced. A history of rice farming requiring cooperative irrigation and intensive labor in southern China was associated with more interdependent cultural traits, whereas wheat farming requiring minimal cooperation was associated with traits emphasizing independence (27). Countries with a heritage of capital- and strength-intensive plow agriculture with gendered divisions of labor show less-equal gender norms, whereas those with a history of shifting cultivation have norms and practices emphasizing greater gender equality (77). Operational sex ratio has also been shown to affect a variety of norms related to marriage, mating, and relationship dynamics (78).

My point here is that a renewed focus on the socioecological drivers of culture permits an initial framework for considering cultural variation. Sampling across the spectrum of socioecological conditions within and among populations therefore ensures a wider range of cultural variation as well. That being said, cultural evolution can direct norms and behavior in non-adaptive or maladaptive directions, or lead to multiple adaptive equilibria depending on initial conditions (79). In the examples above, the legacy of historical economic practices affects cultural traits in the present, despite massive changes in economic livelihoods over the past few centuries. Thus, even when socioecological conditions change, certain cultural traits and behavioral expression are less flexible and show path-dependence. The opposite scenario is also not uncommon: even when socioecological conditions are relatively uniform, distinct patterns of behavior may exist among subpopulations. For example, distinct fairness norms and cooperative behavior were found to exist among Tsimane villages, despite these villages inhabiting a very similar cultural and ecological environment (80). These cases where similar behaviors are found in distinct socioecologies, or where disparate behaviors are encountered in similar socioecologies, suggest that direct consideration of social learning and cultural transmission using the tools and methods of cultural evolutionary theory will be necessary to explain these discrepancies (79, 81). Sampling across populations identified as having distinct (similar) cultures despite sharing similar (distinct) socioecological features could lead to new insights about how ethnohistorical trajectories and transmission dynamics shape psychology and behavior.

Discussion

Nontraditional samples—that is, moving beyond students, cities, and western borders—are critical for generating a broader understanding of human nature and its multifaceted psychological and behavioral manifestation. Although greater sampling of humanity in the social and behavioral sciences may be warranted for ethical and moral reasons alone, I have argued here that deeper scientific understanding of psychological and behavioral

reaction norms can only be gained by considering the socioecological factors underlying behavioral and cultural variation, which leads naturally to deliberate sampling across a broader range of human socioecology. This includes the so-called anthropological populations of foragers, farmers, and herders, but also city dwellers and rural poor in low-income countries, and rural poor, factory workers, wealthy engineers, and other non-student populations in high-income countries. Regional variation is important, especially when historical origins, selective migration, and experience help shape aspects of culture and psychology. For example, English residents living in areas with a history of large-scale coal-based industry and economic hardship were more likely to have markings of present-day psychological adversity (e.g., lower conscientiousness, higher neuroticism) (82).

Sampling beyond the WEIRD should not be relegated to subfields of social science dealing more directly with cultural differences, such as anthropology, cultural psychology, and development economics, but needs to be applied in all social science disciplines aiming to understand human nature and its variable expression. The tendency to contrast samples from traditional small-scale populations with urban WEIRD samples has resulted in important discoveries (e.g., ref. 4). Just as there are poor, rural, and uneducated subpopulations living in countries glossed with the “WEIRD” label, traditional populations everywhere are experiencing rapid changes in their lifeways. Ripe sampling opportunities should include groups experiencing cultural and socioeconomic change. Even hunter-gatherers are exposed to myriad aspects of globalization, although modern exposures are often ignored or given only brief attention, and rarely treated as a useful source of variability. Groups undergoing changes are especially relevant for exploring contrasts between the polar extremes of *Gemeinschaft* and *Gesellschaft* (Fig. 1). Longitudinal studies of these populations, using ethnography to complement traditional psychological experiments, will be vital to improve understanding of the psychological determinants of behavioral change. A few instructive examples act as models for the future (e.g., refs. 18 and 20).

Moving from description of population differences in psychological traits to theory-driven empiricism is an effortful but exciting challenge. As a preliminary nod in this direction, I presented two manifestations of variation in psychological phenomena along the *Gemeinschaft/Gesellschaft* continuum: the role of environmental harshness and unpredictability on dispositional traits of present-orientation, impulsivity, and self-efficacy; and the effects of markets, specialization, economies of scale, and urbanization on personality structure. Both examples employ evolutionary and ecological theory, thereby unifying the current exercise with logic used in the life and natural sciences (and with nonhumans). A fuller elaboration of these and other examples addressing additional topics in psychology will require broader interdisciplinary training, empirical (inconvenient) sampling, and more sophisticated theory tailored to specific domains.

Life-history theory's broad applicability to explaining variation in demographic traits across and within species is an attractive midrange theory applied here to help explain time preference, self-control, vigilance, patience, and impulsivity. Many more questions stemming from this approach remain to be studied. For example, how does direct experience at different life stages shape perceptions of risk and uncertainty in harsh environments? Are there critical developmental windows for calibrating personality to one's socioecological environment? How do perceptions of social support and other kinds of buffering build resilience in high-risk contexts? Given the ubiquity of social comparison for gauging relative standing, wealth, and other markers of success and security, how are reference groups chosen? That perceptions may be based in part on relative comparison complicates studies of trait differences between populations. For example, if social comparison occurs primarily with local

reference groups (83), high-status Bolivian Tsimane comparing themselves to poorer Tsimane may discount the future less than people living in low-income Flint, Michigan neighborhoods who compare themselves to wealthy Americans, despite the higher absolute mortality risks in Bolivia. Perhaps independently of absolute risks, greater inequality within populations may lead to greater time discounting and related psychological traits among those in the lower-status stratum. In high-income countries with great wealth inequality (e.g., United States, Switzerland, United Kingdom), it is possible that poorer people may discount the future more than expected based only on objective nation-level metrics of life expectancy and well-being. Finally, understanding how cultural workarounds and other strategies help individuals attain long-term goals in harsh environments where more present-oriented valuations may be favored is important. Hunter-gatherers invest in social relationships with long-term gain, farmers plant seeds that bear fruit harvested after substantial delay, and complex food-storage traditions developed in many coastal foragers of the United States Northwest, all despite environmental conditions being relatively harsh compared with those in WEIRD populations.

Behavioral ecology's focus on tradeoffs, functional design, and its borrowing of economic principles of division of labor, complementarity, specialization, and biological markets helps set up a framework for modeling the relationship between components of socioecological complexity and personality structure. Consideration of reaction norms also holds promise for parsing variability within populations due to facultative calibration to phenotypic condition, such as physical strength, body size, and embodied capital (i.e., knowledge, skills, or somatic traits that increase future expected fitness) (75, 84). Those in better condition can either afford to express certain personality traits or benefit preferentially from them. Among Tsimane horticulturalists, personality traits related to prosociality, cooperation, emotional stability, and the pursuit of leadership are positively associated with an individual's embodied capital, measured as level of schooling and physical strength (75). Interestingly, physical strength was associated with prosocial personality traits in both men and women among Tsimane, with similar findings among Aka Pygmy foragers (85), whereas studies in the United States hold only for males.

One obstacle to cross-cultural personality research is judging whether differences are genuine or instead artifacts due to methodological inconsistencies (69). For example, failures of samples in low-income countries to replicate the Big Five structure have been blamed on inconsistent response styles of participants. Indeed, negative item bias and evaluative bias (assessed by agreeableness) were positively associated with Big Five interfactor correlations in the 55-nation example described in ref. 72, although acquiescence bias was not. However, although one can sometimes adjust for these types of response bias, adjustment ignores the possibility that response bias itself may be an important aspect of personality or communication style that can vary culturally. Evidence supports the notion of multiple biases forming a general response-style factor that varies systematically

among populations, in accordance with other personality characteristics, such as dominance in interpersonal relationships and competitive emotion (86).

Finally, it is worth stating that emphasizing differences wherever they exist does not necessarily contradict notions of universality nor mean we should avoid generalization. Identifying and explaining similarities in effects even across distinct socioecological settings is equally instructive as explaining differences. For example, despite their unique personality structure and highly externalized locus of control, the Tsimane show age profiles of fluid and crystallized cognitive abilities similar in shape to those observed in WEIRD populations (87). Tsimane extraversion is also greater among physically stronger men and women, as similarly observed in the United States (75). Similarly, despite their relatively egalitarian social and political structure, Tsimane men of higher social status had lower levels of the hormone cortisol and better health than men of low status, similar to findings in WEIRD populations with more rigid stratification (88).

Conclusion

The two presented examples demonstrate how socioecological principles and evolutionary theory can be positioned to help explain diverse psychological trait expression among and within populations. Increasing sample diversity along relevant socioecological (and cultural) dimensions is an essential part of this exciting scientific mission. Additional theoretical coherence should also help improve replicability of scientific studies in the social sciences by requiring hypotheses and predictions be derived from a larger body of theory shared across the life sciences. Greater attention to socioecological drivers underlying variability in psychological traits and behavior should also help improve study replicability. One reason why some studies replicate poorly is the implicit and perhaps erroneous assumption that samples are homogenous, carrying the same treatment effect despite variable sample composition on numerous (often unspecified) dimensions. In other words, most studies assume universality without stating this assumption. Thus, while the Reproducibility Project found that only 39% of 100 studies published in top psychology journals could be unambiguously reproduced, a reexamination revealed that studies dealing with topics that are contextually sensitive (to time, place and culture) were less likely to replicate successfully (89). Explicit consideration of the effects of context, and sample characteristics should not only help improve transparency, but also help uncover "hidden moderators" that affect psychological and behavioral expression. Failed replications provide an opportunity to explore reasons for poor generalizability. Indeed, one lesson here is that a complete understanding of many traits may not be possible without considering socioecological, cultural, and historical context.

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