

The Behavioral Ecology of Cultural Psychological Variation

Oliver Sng
University of Michigan

Steven L. Neuberg, Michael E. W. Varnum, and
Douglas T. Kenrick
Arizona State University

Recent work has documented a wide range of important psychological differences across societies. Multiple explanations have been offered for why such differences exist, including historical philosophies, subsistence methods, social mobility, social class, climactic stresses, and religion. With the growing body of theory and data, there is an emerging need for an organizing framework. We propose here that a behavioral ecological perspective, particularly the idea of adaptive phenotypic plasticity, can provide an overarching framework for thinking about psychological variation across cultures and societies. We focus on how societies vary as a function of six important ecological dimensions: density, relatedness, sex ratio, mortality likelihood, resources, and disease. This framework can: (a) highlight new areas of research, (b) integrate and ground existing cultural psychological explanations, (c) integrate research on variation across human societies with research on parallel variations in other animal species, (d) provide a way for thinking about multiple levels of culture and cultural change, and (e) facilitate the creation of an ecological taxonomy of societies, from which one can derive specific predictions about cultural differences and similarities. Finally, we discuss the relationships between the current framework and existing perspectives.

Keywords: behavioral ecology, cultural psychology, evoked culture, phenotypic plasticity

In 2011, an earthquake in Japan led to the destabilization of the Fukushima nuclear power plant, leading to the world's worst nuclear disaster since Chernobyl (Bradsher & Tabuchi, 2011). In the midst of evacuation, 50 employees stayed, risking their own lives to prevent a full nuclear meltdown. These individuals have been dubbed the "Fukushima 50," and lauded around the world for their bravery. Halfway around the world, in the mountains of the western U.S., a female Belding's ground squirrel encounters a coyote. She gives off an alarm call, alerting surrounding group members of the approaching predator but putting herself in mortal danger. As the other squirrels scatter in search of cover, the coyote turns its attention toward her.

These individuals, from quite different species, put themselves at risk to save others around them. In what ways are the actions of the Fukushima 50 and the lone ground squirrel, seemingly worlds apart, similar to or different from one another? Could the answer to this question provide insight into the commonalities and differences across human societies?

The ways in which human societies differ have long fascinated scientists across disciplines, including anthropology, sociology, psychology, and genetics. The past two decades in particular have witnessed an explosion of research on cultural psychological differences across societies.¹ A wide variety of differences have been theorized and documented, including individualism-collectivism (Triandis, 1995), independent and interdependent selves (Markus & Kitayama, 1991), social attribution styles (Morris & Peng, 1994), visual attention to context (Nisbett & Masuda, 2003), aggressive reactions to insult (Cohen, Nisbett, Bowdle, & Schwarz, 1996), emotional experience and display (Matsumoto, Yoo, & Nakagawa, 2008), behavior in economic games (Henrich et al., 2005), values (Schwartz & Bilsky, 1990), personality (McCrae & Terracciano, 2005), marital customs and mating preferences (Kenrick & Gomez-Jacinto, 2014), and subjective well-being (Diener, Diener, & Diener, 1995).

Just as wide a variety of factors have been proposed, or found, to underlie these psychological differences. Explanations include dominant philosophies (e.g., Greek vs. Confucian; Nisbett, Peng, Choi & Norenzayan, 2001), climatic and economic stresses (Van de Vliert, 2013), the prevalence of pathogens (Schaller & Murray, 2008), religion (Cohen, 2009), residential mobility (Oishi, 2010), socioeconomic status (Kraus, Piff, Mendoza-Denton, Rheinschmidt, & Keltner, 2012), economic development (Inglehart & Baker, 2000), subsistence activities (Uskul, Kitayama, & Nisbett, 2008; Talhelm et al., 2014), and urbanization (Greenfield, 2013). New frontiers of inquiry continue to emerge, with two notable areas being that of

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Oliver Sng, Department of Psychology, University of Michigan; Steven L. Neuberg, Michael E. W. Varnum, and Douglas T. Kenrick, Department of Psychology, Arizona State University.

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Correspondence concerning this article should be addressed to Oliver Sng, Department of Psychology, University of Michigan, Ann Arbor, MI 48109-1043. E-mail: olisng@umich.edu

¹ Because "culture" can be used to refer to both a specific group (e.g., American Southerners) and the set of shared beliefs or practices that characterizes the group (e.g., culture of honor), for clarity, we differentiate here by referring to the group itself as "society" and the shared beliefs and practices of the group as "culture."

gene-culture interaction—the examination of how the same genes can lead to diverging psychologies when situated in different cultures (Kim & Sasaki, 2014)—and cultural neuroscience—the attempt to understand the neural underpinnings of the above cultural psychological differences (Kitayama & Salvador, 2017; Kitayama & Uskul, 2011).

With the growing body of theory and data, it would be useful to have a unifying framework to bridge the many explanations and approaches, and to address emerging fundamental questions. For example, what are the foundational dimensions of culture: East-West, social class, subsistence method, religion, or something else entirely? Cultures may be psychologically different because different social norms get transmitted within each culture, but this begs a basic question: Where do these different norms come from? What are the fundamental origins of cultural psychological differences across societies?

To examine these questions, we propose a framework grounded in behavioral ecology—the study of how environmental pressures lead to variation in animal behavior (Davies, Krebs, & West, 2012)—with a focus on the idea of adaptive phenotypic plasticity. The proposed framework can be useful in several ways. First, it suggests ecological dimensions that should be linked to cultural variation, but have not yet been explored. Second, it has the potential to integrate diverse existing explanations, suggesting a foundation for many of the existing explanations themselves. Third, it integrates work on nonhuman social groups with psychological thinking about human societies. Fourth, it highlights a way of understanding the influence of multiple levels of culture, and also cultural change.

In all, the framework provides a rich way of conceptualizing the factors driving psychological variation across societies, by characterizing societies in terms of combinations of ecological factors, or ecological profiles. In the sections that follow, we examine these implications in turn, beginning first with a brief overview of some central assumptions and findings from behavioral ecology. We conclude with a brief discussion of the relationship between the current framework and existing perspectives, specifically cultural evolution (Chudek, Muthukrishna, & Henrich, 2015), socio-ecological psychology (Oishi & Graham, 2010), ecological threat approaches (Gelfand et al., 2011; Van de Vliert, 2013), gene-culture interaction (Kim & Sasaki, 2014), intersubjective culture (Chiu, Gelfand, Yamagishi, Shteynberg, & Wan, 2010), and evoked culture (Gangestad, Haselton, & Buss, 2006; Tooby & Cosmides, 1992).

Behavioral Ecology and Adaptive Phenotypic Plasticity

The tiger salamander has two physically distinct larval forms. One form is deemed “typical,” the other “cannibalistic.” The cannibalistic form has a significantly larger mouth and head shape, and, true to its name, it consumes other members of its own species. One factor that influences the frequency of the cannibalistic form is population density. Larvae that grow up in environments where many other larvae are present are more likely to develop into cannibalistic morphs, and this occurs regardless of amounts of food (Collins & Cheek, 1983). However, higher densities do not always lead to greater cannibalism. When larvae grow up in environments that consist of siblings (i.e., individuals from

the same birth clutch), even at high densities the cannibal morph does not increase in frequency (Michimae & Wakahara, 2001).

Belding’s ground squirrels, as described earlier, give off alarm calls that communicate to others the approach of predators. However, female rather than male squirrels are particularly likely to do so. Why? First, the ground squirrels tend to be matrilocal; females upon maturity remain in or close to their birthplaces, whereas males leave. Hence, females are more likely to have kin—genetically related females—in proximity. Furthermore, even among females there is variation in alarm calling: Females who have living mothers, sisters, or daughters are more likely to alarm call than females who do not (Sherman, 1977).

The salamander and squirrel both represent examples of *adaptive phenotypic plasticity*: Individuals with the same genes may exhibit different traits under different environmental conditions (Dingemanse, Kazem, Réale, & Wright, 2010; Piersma & Drent, 2003; Pigliucci, 2005; West-Eberhard, 1989). Such plasticity can be a result of mechanisms that have evolved to be sensitive to environmental changes. The logic is as such: *if* in different environments some behaviors are more biologically adaptive than others, *and* organisms have regularly encountered varying environments (across time or location) in their ancestral history, *then* natural selection should favor the evolution of environmentally sensitive flexibilities.

Consider that, at face, an individual ground squirrel making an alarm call appears to be decreasing its reproductive fitness by putting itself in physical danger. Reproductive fitness, however, involves not just one’s own survival and reproduction but also the survival and reproduction of others who carry one’s genes (i.e., inclusive fitness; Hamilton, 1964). Hence, when a substantial number of genetically related individuals would benefit from the call, greater alarm calling increases inclusive fitness, but when few genetically related individuals would benefit, less alarm calling increases inclusive fitness (reducing personal survival threat). Understanding the tiger salamander example also draws upon inclusive fitness. In high density environments, the cannibal morph is increasing its fitness by removing competition for food and resources. But if the dense environment consists mainly of genetically related individuals, then such cannibalism will instead lower inclusive fitness by removing genes the cannibal shares with its prey.

Many organisms have evolved to be phenotypically plastic, in both their physical (e.g., larval forms) and behavioral (e.g., alarm calling) traits. Moreover, such plasticity has been observed in reaction to diverse ecological factors, including population density, genetic relatedness, disease prevalence, resource and food availability, predation pressures, sex ratio, mortality risks, and geographic isolation (Davies et al., 2012).

What are the implications of this for cultural psychological variation? Given that our human ancestors likely also regularly faced changing ecologies across time and place, our species would also be expected to possess adaptive phenotypic plasticity—flexibilities that react predictably to ecological circumstances. From this, because different societies face varying ecological circumstances, individuals in these societies would also differ in their psychologies and behaviors. And this may then manifest itself as psychological variation at the level of societies. In other words, cultural psychological variation might reflect *different outcomes*

from universal flexibilities that evolved to deal with the adaptive problems posed by specific ecologies.

In the next section, we examine ecological dimensions that have received substantial study in the field of behavioral ecology. We describe some of the ways in which phenotypic plasticity plays a role in how individuals flexibly respond to these ecological conditions (e.g., to environments of high vs. low population density), and derive predictions about how these flexibilities may shape human cultural variation.

Six Ecological Dimensions

In characterizing environments, the field of behavioral ecology has focused on a range of dimensions considered to have substantial implications for biological fitness. We focus on six of these—population density, genetic relatedness, sex ratio, resources, mortality likelihood, and pathogen prevalence—for several reasons. Each has a significant accumulated literature in animal behavior, as we will discuss below, as well as ready parallels in human ecologies. Moreover, they together highlight varying ways in which our proposed framework can be useful. Whereas some of these (e.g., pathogen prevalence) have already been used to enhance understanding of cultural variation, others have remained less explored.

For each ecological dimension, we first briefly review central findings from the behavioral ecological literature. We then outline human parallels of the ecological dimension and derive corresponding predictions about how that dimension might generate psychological variation. A summary of the six dimensions and the general predictions is provided in Table 1.²

Before we begin, two clarifications are useful. First, we focus our theoretical synthesis and prediction more on modern societies and less on small-scale traditional groups (e.g., modern hunter gatherers). We do this because the dominant cultural psychological work has also focused on the former—assessing and theorizing about psychological similarities and differences in modern societies. We are also mindful, however, that the distinction between modern and traditional societies can sometimes have nontrivial implications for the current approach. For example, with respect to the dimension of pathogen prevalence, what “high” pathogen stress means might differ for modern versus traditional societies. In modern societies, pathogen stress, and particularly its lethality, might be less likely to reach extremely high levels, given the availability of modern medical technology. In contrast, for an ecological dimension such as sex ratio, there is no obvious reason to expect such differences (i.e., a female-biased sex ratio is likely qualitatively the same in both traditional and modern societies). Hence, it is useful to attend to how the absolute degrees of an ecological dimension might differ in modern versus traditional societies.

Second, we adopt an evolutionarily inspired approach to highlight potential unexamined areas and hypotheses that may lend themselves to fruitful empirical inquiry. We are not aiming to test evolution itself. The evolutionary approach within psychology is less so a specific theory than a metatheoretical framework, within which multiple theories and ideas can be derived (the behavioral immune system discussed in the “Pathogen Prevalence” section below is a relevant example). Like specific psychological theories derived from other metatheoretical approaches (e.g., social psy-

chology, developmental psychology, cognitive psychology), specific theories and hypotheses derived from the evolutionary metatheory can be, and are regularly, tested and falsified (see Neuberg, Kenrick, & Schaller, 2010, for a discussion of these issues). Relatedly, there are multiple ways in which plasticity might generate adaptive outcomes, especially in a species with as complex a behavioral repertoire as ours. Hence, when testing for the presence of adaptive plasticity with respect to any ecological dimension, it will likely be useful to consider a variety of psychological variables that may be possible outcomes of plasticity. We highlight this below where relevant.

Population Density

Behavioral ecological work. Population density—the number of individuals within a fixed amount of space—received early attention in the behavioral ecology literature (Christian, Flyger, & Davis, 1960), with a focus on how population density influences aggression. Findings were mixed, with some work finding that higher densities lead to increased social aggression and territoriality across species (Kummer & Kurt, 1965; Kwiatkowski & Sullivan, 2002; Southwick, 1969) but other work observing decreased aggression (French & Cade, 1989; Greenfield & Shelly, 1985). The initial idea was that higher densities would lead to greater competition for territory and resources, and that this competition would trigger greater aggression. However, a more sophisticated analysis emerged from considering the costs and benefits of physical aggression (see Knell, 2009, for a review). Engaging in aggressive competition may be dangerous for animals in a very dense environment, as individuals are likely to encounter other competitors after sustaining competition injuries. Hence, the relationship between density and aggression may not be a linear one—aggression is likely highest at moderate densities.

At the same time that work on density and aggression was developing in behavioral ecology, the emergence of a broad framework—life history theory (MacArthur & Wilson, 1967)—contributed another approach to conceptualizing density’s effects. The theory is built upon the premise that each organism, in any species, faces the problem of how to allocate its finite resources (e.g., energy) to survive and reproduce. From the life history perspective, ecological factors can shape a whole host of traits, because of the varying trade-offs of different resource allocation patterns (Del Giudice, Gangestad, & Kaplan, 2015; Roff, 1992; Stearns, 1992).

Drawing upon the same premise that higher densities lead to greater competition for territory and resources, life history theory predicts that individuals may adopt what is referred to as “slower” (as opposed to “faster”) life history strategies in dense ecologies. A slow strategy is characterized by behaviors such as greater investment of energy into growth and bodily maintenance, delayed reproduction but increased effort into accumulating competitive ability and “embodied capital” (e.g., skills and knowledge), and also fewer offspring but greater investment in each individual offspring. The argument is that in dense and thus socially competitive environments, individuals need to invest more in building themselves both physically and mentally to successfully compete

² Because an exhaustive review of the work for each ecological dimension is not feasible in the current article, we highlight, where available, review papers for the interested reader.

Table 1
Summary Table of Ecological Dimensions and Behavioral Ecological Findings

Ecological dimension	Behavioral ecological findings (ecological dimension and corresponding effect)
Population density	Higher density → slower life history Low to moderate density → greater competition/aggression Extremely high density → less competition/aggression
Genetic relatedness	Higher relatedness → prosocial behavior Higher relatedness → alloparenting Higher relatedness → natal dispersal (for one sex)
Sex ratio	More male-biased → mating competition among males More female-biased → mating competition among females
Resource availability/patchiness/unpredictability	Lower availability → decreased reproduction Lower availability → less costly competition Lower availability → resource-seeking behavior Higher patchiness → social competition Higher patchiness → aggression Higher patchiness → territoriality Higher unpredictability → novelty seeking Higher unpredictability → risky exploration Higher unpredictability → storage/hoarding behavior
Mortality (extrinsic)	Higher mortality → faster life history Higher mortality → anti-predator defenses Higher mortality → vigilance Higher mortality → social grouping Lower mortality → boldness
Pathogen stress	Low to moderate pathogen stress → slow life history Extremely high pathogen stress → fast life history Greater pathogen stress → immune function investment Greater pathogen stress → resource seeking behavior

and ultimately reproduce. This logic also applies to offspring, meaning that individuals will tend to have fewer offspring and concentrate their investments on these few, rather than having many offspring and having to spread limited resources across the many. This slower strategy would result in more competitive offspring, again critical in a high density environment.

This seems to be the case. Organisms in populations that are more dense, both naturally and via experimental manipulation, have been generally found to exhibit later sexual maturity, slower reproduction, fewer offspring, greater parental investment in offspring, and larger offspring size (as a result of resources devoted to few, instead of spread over many, offspring; e.g., Adler & Levins, 1994; Allen, Buckley, & Marshall, 2008; Creighton, 2005; Leips, Richardson, Rodd, & Travis, 2009; Meylan, Clobert, & Sinervo, 2007; Sinervo, Svensson, & Comendant, 2000; see Dantzer et al., 2013 for an exception). For instance, female killifish reared in high-density tanks produced fewer but larger offspring compared with fish reared in low-density tanks (Leips et al., 2009). This is evidence for an evolved flexibility sensitive to social density, specifically one that shifts organisms toward a slower life history strategy under higher social density.

Human parallels and predictions. Population density has a straightforward parallel in human societies—the number of people within any given space. It is also an ecological dimension on which societies vary considerably. Early interest in human population density was, interestingly, itself inspired by animal work (Calhoun, 1962). In the now-classic work, rats were allowed to multiply in confined spaces, and their subsequent behaviors were observed. A range of pathological behaviors emerged, such as social disengagement and cannibalism, drawing an ominous picture of how overcrowding might go wrong. With concerns about the societal effects

of overpopulation, early human work also focused on the pathological consequences of high densities on everyday functioning (e.g., Galle, Gove, & McPherson, 1972; Griffitt & Veitch, 1971). However, subsequent reviews of the effects of density in humans showed unclear conclusions, with accumulating evidence that density generally did not lead to social pathologies, contrary to popular intuitions (Freedman, 1979; Lawrence, 1974). Attention to the psychological effects of density in human behavioral science has subsequently waned (for exceptions, see Gelfand et al., 2011; Levine, Martinez, Brase, & Sorenson, 1994).

What predictions might one generate, in light of the behavioral ecological work on density? Life history theory predicts, and the literature demonstrates with nonhuman animals, that organisms adopt a slower life history strategy under higher densities. Do we observe similar plasticity in humans? Initial findings suggest the answer is yes. People in countries with higher population densities do exhibit a range of traits corresponding to a slower life history strategy: They plan more for the future, are more oriented toward long-term romantic relationships, have children later, have fewer children, and invest more in their children’s education (Sng, Neuberg, Varnum, & Kenrick, 2017). Similar patterns emerge when examining cross-state patterns within the U.S.—people living in denser U.S. states exhibit slower life history strategies—even after controlling for potential confounding factors such as urbanization, economic wealth, and cultural tightness-looseness. Furthermore, when individuals are experimentally led to believe that social densities around them are increasing, they also seem to shift toward slower strategies in the moment, such as exhibiting greater delay of gratification and preferring to focus investment in fewer romantic relationships and offspring.

If higher population densities indeed lead to slower life history strategies, other implications follow; we highlight two here. First, a slow life history strategy involves building oneself in ways that increase one's ability to socially compete (e.g., accumulating knowledge and skills). However, to build oneself, one needs to believe that the self *can* be built. Factors that engage different life history strategies might therefore also lead to different implicit theories of the self (Dweck, Hong, & Chiu, 1993). One might thus predict that individuals in high density societies will also be more likely to adopt an incremental theory of the self (e.g., believing that their intelligence can be increased) than an entity theory of the self (e.g., believing that their intelligence is innate and unchangeable). Consistent with this, existing cultural psychological work does suggest that people living in relatively dense societies (e.g., Japan) hold more incremental theories than those living in less dense societies (e.g., North America; Heine et al., 2008). We are, however, unaware of any systematic analysis across populations looking at variation in implicit theories in relation to ecological density.

A second implication relates to friendship styles. As we have seen, a slow life history generally involves prioritizing "quality over quantity" (e.g., having fewer children but investing more in each). One might think of the parallel occurring in friendships. Indeed, a distinction has been made between "shallow" and "deep" friendship styles (Oishi & Kesebir, 2012), with the former being a tendency to have many friendships with relatively low investment in each, and the latter being the tendency to have few friends but investing more in each relationship, consequently building closer ties. A life history approach might thus predict that highly dense societies would lead to inclinations toward deep, instead of shallow, friendship styles.

These predictions about density's effects on societal-level life history strategies, implicit theories, and friendship styles are novel, suggesting the value of adaptive plasticity for better understanding cultural psychological differences.

On a final note, existing work has speculated on the effects of urbanization on cultural practices and behaviors (e.g., Greenfield, 2013). Because urbanized societies also tend to be highly dense, similar predictions could be made about urbanization's effects. However, from a behavioral ecological perspective, density is the critical ecological dimension. One could thus make differentiating density predictions *within* urban environments, such that residents of high-density neighborhoods within urban areas would be expected to exhibit predictably different behaviors than would residents of low-density neighborhoods within those same urban areas, all else equal. In addition, as highlighted earlier, population density is predictive of specific aspects of a slow life history strategy, such as future planning and orientation toward long-term committed relationships, while urbanization itself is *not* (Sng et al., 2017).

In sum, we suggest that the ecological dimension of social density is important for understanding psychological variation between societies. High density societies will tend to have higher levels of social competition, eliciting a wide range of psychological traits and behaviors, including greater delay of gratification, an orientation toward long-term relationships, having children later, having fewer children, and greater parental investment. Density may also have implications for variation in implicit theories of self and friendship styles across societies. To the extent that societies around the world vary in social

density, they should also be predictably different in their psychologies, as outlined here.

Genetic Relatedness

Behavioral ecological work. Ecological genetic relatedness may be generally defined as the extent to which an individual organism is, on average, genetically related to other individuals in its group and immediate surroundings. Within behavioral ecology, genetic relatedness has been of special interest, and is often examined in relation to prosocial behaviors. Across multiple species, animals in proximity of genetically related individuals tend to affiliate more with, and engage in more prosocial behaviors toward, these individuals (e.g., Griffin & West, 2003; Hesse, Bakker, Baldauf, & Thünken, 2012; Holmes, 1995; Komdeur & Hatchwell, 1999; Lihoreau & Rivault, 2009; Mateo, 2010; Russell & Hatchwell, 2001; Sherman, 1977, 1985; Wilkinson, 1985). For instance, urban cockroaches, across all developmental stages, prefer socializing with genetically related individuals (compared with nonrelatives), even when they have never encountered these individuals before (Lihoreau & Rivault, 2009). Like the ground squirrels we mentioned earlier, prairie dogs are more likely to alarm call upon detecting predators when there are genetic relatives in proximity (Hoogland, 1986), and vampire bats are more likely to regurgitate and share blood with related individuals (Wilkinson, 1985).

The genetic relatedness of the local ecology also influences alloparenting—the act of caring for young who are not one's own. The most striking example of this occurs in the social insects, such as the ants, bees, and wasps (Boomsma, 2009; Wilson, 1974; Wilson & Hölldobler, 2005). There is generally only one reproducing individual (the queen) in a group, and all other members of the group aid in helping this individual reproduce. Investing time and energy in helping others reproduce, at the cost of one's own reproduction, only makes adaptive sense when the individuals being helped are genetically related to the helper. Indeed, social insects have a unique genetic structure in which workers are actually more highly related (75%) to their sisters than to their own offspring (50%). It is therefore generally more adaptive for individuals to help raise their sisters than to reproduce on their own. Alloparenting has also been observed in other species, particularly birds, and it is found to vary with genetic relatedness (Cockburn, 1998; Curry, 1988; Emlen, 1978).

Finally, although high genetic relatedness provides opportunities to enhance fitness by helping genetically related individuals, it also poses a unique problem—that of inbreeding depression (Hamilton, 1987; Wildt et al., 1987). One of the mechanisms known to address this problem is sex-biased dispersal. In most sexually reproducing species, one sex tends to leave the group in which they are born upon reaching sexual maturity (Greenwood, 1980; Pusey, 1987). This avoids potential reproduction with relatives in one's natal group. Importantly, dispersal tendencies are also flexible, sensitive to local levels of genetic relatedness. For example, male ground squirrels and voles disperse further from an area in which they are likely to have many female relatives (Holekamp & Sherman, 1992; Lambin, 1994). Hence, high levels of ecological genetic relatedness, to the extent they pose a problem of inbreeding, can lead to greater dispersal by members of one sex.

Human parallels and predictions. Human societies also differ in genetic diversity (e.g., Helgason, Nicholson, Stefánsson, &

Donnelly, 2003; Nelis et al., 2009; The 1000 Genomes Project Consortium, 2015; Van Oven et al., 2011), and one can characterize a high-relatedness ecology as one in which individuals tend to live with or be in close proximity to kin, both immediate and extended. For humans, the concept of *subjective* genetic relatedness may be at least as important. That is, because we are not born with direct knowledge of our genetic kin, we must instead use cues to infer genetic relatedness—cues that ancestrally have been reliable indicators of kinship (see Mateo, 2015, for a review). One such cue is coresidence. People who grow up in close proximity to oneself are likely to be family, particularly siblings. Indeed, having lived in the same place, especially during early developmental life stages, seems to elicit behaviors typically observed between kin. This mechanism has been found in both nonhuman animals (Holmes, 1986; Mateo, 2003) and humans (Lieberman & Lobel, 2012; Lieberman, Tooby, & Cosmides, 2007), and has also been demonstrated across human societies (Szycer, De Smet, Billingsley, & Lieberman, 2016).

Another cue to genetic relatedness is physical similarity. To the extent that morphological similarities reflect shared genes, people should be sensitive to the extent to which another person is physically similar to one's self. This is termed self-phenotype matching in behavioral ecology (Hauber & Sherman, 2001; Mateo, 2010), and there is evidence of it occurring via smell (Mateo, 2009; Olsén, Grahn, Lohm, & Langefors, 1998), sight (Tibbetts & Injaian, 2013), and sound (Rendall, Rodman, & Emond, 1996). In humans, when people are presented with faces of strangers that have been digitally morphed with their own, they tend to exhibit more prosocial behaviors toward these morphed targets (DeBruine, 2005; Krupp, DeBruine, & Barclay, 2008). Such findings suggest the possibility that people can detect relatives by detecting similar facial features. Other work demonstrates that individuals mentally categorize others as kin to the extent they hold similar attitudes, especially if those attitudes are highly heritable ones (Park & Schaller, 2005). In sum, although individuals are not born with knowledge about their actual genetic relatedness to others in their environment, they make inferences about relatedness from cues such as coresidence or morphological similarities.

One can generate a range of predictions about psychological variation across societies as shaped by flexibilities sensitive to ecological relatedness. In general, one would expect ecologies characterized by cues to high genetic relatedness (or actual high relatedness) to exhibit higher levels of pro-social behavior, as prosociality in such ecologies leads to a greater increase in inclusive fitness.

For example, in societies where individuals move around less—increasing perceptions of coresidence—one might hypothesize that people will treat one another more like family, showing greater concerns for their welfare and being more attuned to their needs. Indeed, cultural psychological work finds that less residentially mobile societies tend to be more collectivistic (Oishi, 2010). From the current perspective, a finer prediction here is that mobile groups that move in family or kin group units may maintain their ecological relatedness, and subsequently also maintain high levels of collectivism. One might also predict that societies in which geographic factors limit residential mobility (e.g., societies on small islands) are likely to be high in both actual and perceived relatedness and thus also likely to generate within-group collectivistic and prosocial behaviors and norms. Further work finds that

in societies where people are living in groups with a high prevalence of cousin marriages (and hence potentially higher actual levels of genetic relatedness), people report being more willing to risk their lives to fight for their community, a greater trust of neighbors (but not foreigners), and a more interdependently connected self with their community and country (but not with the world; Sng, 2017). Finally, anthropological studies also find that individuals are more likely to form cooperative groups with genetic relatives (Strassmann & Kurapati, 2016), share food with genetic kin (Gurven, Allen-Arave, Hill, & Hurtado, 2001; Nolin, 2011), and side with relatives in coalitional conflicts (Chagnon & Bugos, 1979).

With respect to larger modern societies, a focus on ecological genetic relatedness also enables targeted predictions about *within*-society variation. If genetic homogeneity or perceptions of it increase cooperation and pro-social behavior, this effect should be most pronounced among members of a society who are in the genetic *majority*. This is because the individuals in the society who share fewer genes with those around them are not likely to perceive greater relatedness. To illustrate crudely, imagine two societies: In the first, 80% of the population holds genotype A and 20% holds a different genotype B; in the second, 25% of the population holds each of genotypes A, B, C, and D, all presumably different from one another. One might predict that the first society will be characterized, on average, by higher levels of pro-social behavior. This enhanced prosociality, however, is likely to characterize primarily the subpopulation of individuals holding genotype A (the genetic majority), who are indeed experiencing an ecology of high genetic relatedness, and not the subpopulation of individuals holding genotype B (the genetic minority). This, of course, assumes that social interactions between individuals are not segregated by genotypes. If there is significant social segregation between A and B individuals (or A, B, C, and D individuals in the second society), then each subpopulation is likely to exhibit high levels of intra-group altruism. A consideration of the ecological factor of genetic relatedness thus enables hypotheses about psychological differences both across societies, and within them, based on how genetic variation is distributed within societies.³

Regarding alloparenting, we would predict that societies with higher levels of genetic relatedness will exhibit more alloparenting-related psychologies and behaviors. In a high-relatedness society, given that children in the group are likely to be more related to oneself, one might see a parenting psychology and a general tendency to nurture manifested even among nonparents.

³ Note that greater prosocial behavior under high ecological relatedness does not necessarily imply that individuals are less competitive. In the behavioral ecological literature, related individuals have been found to be just as competitive or aggressive towards one another as unrelated individuals are (Packer & Pusey, 1982; Wahaj et al., 2004), and at times even more so (Bernstein & Ehardt, 1986). This can occur because more genetically related individuals may also draw upon more similar types of resources (Waldman, 1988), leading to greater competition over shared resource pools. In social species, aggressive behavior towards kin may also serve a socialization function (Bernstein & Ehardt, 1986). However, what is crucial is that such aggression and competition between related individuals, even when high, should generally be non-lethal (similar to the suppression of salamander cannibalism when proximal individuals are highly related).

Finally, as mentioned, high ecological relatedness poses a problem of inbreeding. One might therefore predict a stronger psychological tendency in high-relatedness societies for (at least) one sex to leave their natal group upon reaching sexual maturity. In most primates, males disperse. However, in our closest primate relatives—chimpanzees and bonobos—females are the sex more likely to disperse from the natal group (Lawson Handley & Perrin, 2007), and some work in genetics suggests that human females, historically, have also moved between groups more (Seielstad, Minch, & Cavalli-Sforza, 1998). We might thus predict that females (more so than males) in societies characterized by extremely high genetic relatedness might be inclined to disperse from their natal group (i.e., via migration, travel desires), and to do so especially upon sexual maturity when the problem of inbreeding becomes most pertinent. Note that the distance of this dispersal need not be far within large societies—moving to a different town might suffice. Also, this prediction does not preclude individuals from returning to the natal group after successful reproduction. Hence, the prediction about female migration patterns, from the behavioral ecology view, is quite specific.

Dispersal is not the only solution to the problem of inbreeding in highly genetically related societies. Other psychological solutions might include decreased sexual promiscuity (given the high chance of inbreeding from indiscriminate mating), stronger disgust reactions toward incest, or even delayed sexual maturity until highly related individuals move out of the group (evidence for this exists in some mammals; see Waldman, 1988). The problem could also be solved through cultural norms and knowledge. For instance, a system of marriage rules, coupled with genealogical records, may be sufficient to deal with the problem of inbreeding, and we might expect these practices to be more common in societies with high levels of genetic relatedness. Here, cultural practices may emerge to address challenges posed by ecological factors, in support of adaptive flexibilities operating at the individual level.

In sum, ecological genetic relatedness might be represented in multiple ways in human society. There is evidence in both the nonhuman and human literature that individuals are sensitive to variation in ecological relatedness. However, these ideas have yet to be extensively used in thinking about cultural psychological variation. We have proposed hypotheses addressing a range of potential psychologies that might be affected (pro-social behavior, alloparenting, incest avoidance and dispersal) by societal differences in genetic relatedness. The ecological dimension of relatedness also has a potential to integrate a range of important ideas in current cultural psychology, a point we elaborate further in the later section on uniting existing explanations.

Sex Ratio

Behavioral ecological work. Sex ratio has also received much attention in behavioral ecology. Theoretically, what is generally important is not the sex ratio of the entire population but rather the sex ratio of reproductive-aged males and females within that population—known as the operational sex ratio. When sex ratios are biased toward one sex (i.e., male-biased refers to more males than females), the individuals of the more prevalent sex face greater competition for mates (Emlen & Oring, 1977; Kvarnemo & Ahnesjö, 1996), which can shape a wide range of behaviors. For example, under more male-biased sex ratios, male guppies engage

more in sneak mating behaviors (attempting to mate without any prior courtship) whereas females tended to become more selective in choosing mates (Jirotkul, 1999); male garter snakes reduce effort in explicitly courting females, diverting their effort to opportunistic mating strategies (Shine, Langkilde, & Mason, 2003); and male gray mouse lemurs spend more time searching for mates and less time guarding existing mates (Eberle & Kappeler, 2004).

On the other hand, female-biased ecologies can lead to a reversal of sex roles. For example, when sex ratios change from male-biased to female-biased in a natural goby population, male-male competition and courtship behaviors decrease, and are replaced by strong aggression between females and increased female courtship of males (Forsgren, Amundsen, Borg, & Bjelvenmark, 2004). Along similar lines, male milkweed beetles in a female-biased sex ratio ecology become choosier about the females they mate with (Lawrence, 1986).⁴

Human parallels and predictions. Sex ratio has a direct ecological parallel in human societies, and is defined in a similar way (e.g., Secord, 1983). There is considerable variation in sex ratio across societies. For instance, at the country level, Russia has a sex ratio of .86 (i.e., 86 males for every 100 females), whereas Kuwait's sex ratio is 1.43 (Central Intelligence Agency, 2013). Tracking behavioral ecological work, research on the effects of sex ratio on psychological variation across societies and cultures has focused on mating dynamics. Notably, variation in sex ratio within the U.S. has been found to predict differences in inclinations toward monogamy: male-biased populations exhibit lower divorce rates and greater male parental investment (Pedersen, 1991), and higher proportions of young adult men who are married (Kruger & Schlemmer, 2009). Similarly, in hunter-gatherer groups, more male-biased sex ratios are also associated with lower divorce rates (Blurton-Jones, Marlowe, Hawkes, & O'Connell, 2000) and greater paternal investment (Marlowe, 1999). More recent work has also examined how sex ratio, across nations, influences whether individuals are oriented toward more short-term or long-term mating relationships (Schmitt, 2005). In general, under male-biased sex ratios, one sees greater monogamy and tendencies toward long-term mating (Guttenag & Secord, 1983). This reflects the greater intrasexual competition men face in male-biased ecologies, and hence the need to respond by attempting to match female preferences for long-term mating relationships. Experimental work that situationally manipulates perceived sex ratios finds a similar pattern, with males shifting toward greater long-term mating orientations under male-biased sex ratios, and females shifting toward greater short-term mating orientations under female-biased sex ratios (females face greater intrasexual competition in the latter context, hence the shift toward a mating orientation that would appear more attractive to males; Moss & Maner, 2016).

A number of aspects of marital arrangements also appear to be linked to sex ratios (Pollet & Nettle, 2008). In Uganda, polygyny (one man marrying multiple women) is more common in areas with more women, and as the number of men increases, wealthy

⁴ Under certain conditions, skewed sex ratios can lead to the more prevalent sex investing not so much in direct mate seeking behaviors but in parenting effort or in building competitive abilities (Del Giudice, 2012; Kokko & Jennions, 2008). The specific strategy adopted is influenced by the relative costs and benefits of competitive and parenting behaviors within a population.

men are more likely to have multiple wives, and poor men none (Pollet & Nettle, 2009). In China, sex ratios are becoming increasingly skewed (due to selective abortion of female fetuses), and there was by 2006 a surplus of 40 million single men (Chan, Eric, & Chan, 2006). At the same time, the practice of bride price has been increasing in China. In some areas, there has been a fourfold increase in bride price, and half of the men living in rural areas can no longer afford a bride. In Vietnam, men are finding it more difficult to find wives, as men from other countries, with shortages of women, are paying increasingly large sums of bride price to marry Vietnamese women (Belanger & Linh, 2011).

Other indirect effects of changing situational sex ratios have been found, with male-biased sex ratios leading men to increase their spending behaviors for objects that display their wealth and resources (Griskevicius et al., 2012). Such behaviors presumably reflect similarly greater male-male competition in displaying financial resources to potential mates. Given that male-male competition is more likely to involve physical aggression, one might also predict that in societies with male-biased sex ratios that one would observe higher rates of violence. This appears to be the case, as countries that have more male-biased sex ratios have higher rates of homicide and other violent crimes (Barber, 2003; Dreze & Khera, 2000; Hudson & Den Boar, 2005). Female-biased sex ratios, on the other hand, lead women to be more career-driven (Durante, Griskevicius, Simpson, Cantú, & Tybur, 2012), with such a shift ostensibly occurring because of the greater difficulty females face in finding a long-term investing partner when men are scarce. Finally, both men and women have been found to adopt more risky financial investment behaviors under more unfavorable sex ratios (i.e., more individuals of the same sex; Ackerman, Maner, & Carpenter, 2016).

Nonetheless, there is still much to be explored in terms of sex ratio's role in explaining psychological variation across societies and cultures. One possibility is that operational sex ratios may shape the nature of xenophobia and outgroup prejudice. In societies with a strong sex-ratio bias, one might predict greater between-groups prejudice, but specifically between members of the over-prevalent sex. For example, whereas males generally hold stronger outgroup prejudices than females (McDonald, Navarrete, & Van Vugt, 2012), and especially against outgroup men, one might predict that *women* might hold especially strong prejudices against outgroup women within societies with a female-biased sex ratio, as those outgroup women pose mating competition in an already female-competitive ecology. Such a perspective could lend unique insights into cross-society variation in intergroup conflict, and what the specific structure of such conflicts might be.

Finally, there has been recent attention to cultural variation in "tightness-looseness"—with tight societies being those with strong social norms and low tolerance of social deviance (Gelfand et al., 2011). Nations with generally more threatening ecologies (e.g., low resources, frequent natural disasters) tend to have tighter cultures, due to the need for strong norms to facilitate social coordination. The current approach contributes focused predictions about how the sex-ratio within societies might lead to tighter or looser norms *specific* to each sex. For instance, in a society with a male-biased sex ratio, there might be especially strong norms with respect to male-male competition processes (e.g., rules about the permissible types of competitive aggression), because of the need to manage such competition and prevent potential escalation. Note

that the tightness-looseness of norms in this case may not result directly from individuals' sensitivity to sex-ratio per se, but rather from the increased intrasexual competitiveness caused by the adaptive plasticity to sex ratio.

Some of the above ideas converge with existing literature on frontier psychology (Kitayama, Ishii, Imada, Takemura, & Ramaswamy, 2006) and cultures of honor (Cohen & Nisbett, 1994). Frontiers and the ecologies typically associated with cultures of honor typically have a more male-biased sex ratio, and the prevalent psychologies in these societies also seem to reflect strong male-male competition.

In sum, one would expect societies characterized by biases in sex ratio to exhibit psychologies that reflect greater competitiveness among the more numerous sex; males are likely to be especially competitive with one another in societies that are male-biased, whereas females are likely to be especially competitive with one another in societies that are female-biased. The effects of ecological sex ratio are likely to go beyond competition and mating, however, to include society-level psychological differences in prejudices and tightness-looseness.

Resources: Availability, Patchiness, and Unpredictability

Behavioral ecological work. In behavioral ecology, resources generally refer to food, although the concept encompasses time and energy more broadly. Because limited time and energy is a fundamental problem all organisms face, one might also expect them to possess resource-sensitive plasticities. And as seen below, they do. A behavioral ecological approach also uniquely considers multiple aspects of the resource ecology, beyond simple resource availability. In particular, patchiness and unpredictability are also important aspects. We elaborate on the distinctions below.

First, resource *availability* may be characterized as the absolute amount of resources available in an environment. Plasticity to resource availability has been documented in many species, in both natural and experimentally manipulated environments. The focus of most work has been on reproductive behaviors. For example, when resources are extremely scarce, delayed reproduction and fewer offspring is observed in multiple bird species (e.g., Högstedt, 1980; Martin, Martin, Olson, Heidinger, & Fontaine, 2000; Sofaer, Sillett, Peluc, Morrison, & Ghalambor, 2013). Similar patterns have been found in snakes (Ford & Seigel, 1989; Seigel & Ford, 1991) and lizards (James & Whitford, 1994; Jordan & Snell, 2002). In guppies, resource scarcity leads to more time spent foraging for food and lower levels of aggression (an energetically expensive behavior) among males when competing for mates (Kolluru & Grether, 2005). In general, in extremely resource-scarce ecologies, organisms have less time and energy available for reproduction, and allocate their time and energy toward ensuring survival.

Two environments can hold the same absolute amount of resources but differ in their *patchiness*—the variability in resources across space. An ecology with its resources highly concentrated in some subareas but absent in others is an environment with high resource patchiness. On the other hand, an ecology with the same absolute amount of resources but with its resources evenly distributed across its entire area would have zero patchiness. Differences in resource patchiness are expected to have effects on a range of

behaviors, especially those related to competition. Resources concentrated in specific areas (high patchiness) are easier to monopolize, leading to strong competition between individuals seeking control of these patches. In contrast, resources distributed evenly across space are difficult to monopolize, creating less incentive to defend any specific area and thus leading to lower levels of competition. Indeed, in nonhuman animals, high resource patchiness leads to higher levels of social competition, aggression, and territoriality (Barton & Whiten, 1993; Blanckenhorn, Grant, & Fairbairn, 1998; Grant & Guha, 1993; Magnuson, 1962; Maher & Lott, 2000; Monaghan & Metcalfe, 1985; Sinha, Mukhopadhyay, Datta-Roy, & Ram, 2005; Zahavi, 1971), which in turn leads to defined dominance hierarchies within groups (Isbell, 1991; Koenig, Beise, Chalise, & Ganzhorn, 1998; Sterck, Watts, & van Schaik, 1997; van Schaik, 1989).

Resource *unpredictability* is defined as the extent to which resource availability fluctuates across time. Such unpredictability has also been associated with a wide range of behaviors across nonhuman species, such as a decreased aversion toward novel foods (Greenberg & Mettke-Hofmann, 2001; Liebl & Martin, 2014), more risky exploratory behaviors (Chapman, Morrell, & Krause, 2010), increased bodily storage of fat and other hoarding behaviors (Bednekoff & Krebs, 1995), and a greater likelihood of engaging in hibernation (Munn, Kern, & McAllan, 2010). A decreased aversion to novelty and greater exploratory behavior, even when potentially dangerous, can aid discovery of new food sources. This is particularly important in environments where the availability of existing resources is uncertain. The bodily storing of and the hoarding of resources is especially adaptive in resource-unpredictable ecologies, to buffer against times when resources might be unavailable. Finally, hibernation behaviors help to reduce energy use by the individual, likewise reducing the dangers of an unpredictable energy supply.

Human parallels and predictions. Resource availability, patchiness, and predictability have straightforward parallels in human societies that obtain food directly from the physical environment, and so we would expect humans to show similar flexibility in responses to resource availability, patchiness, and unpredictability. For example, individuals in small-scale societies with poorer nutrition exhibit slower growth and delayed puberty (Walker et al., 2006), tracking the behavioral ecological prediction that low resource availability leads to reduced reproduction. Greater resource patchiness in such groups is associated with greater movement ranges, to cover dispersed resource patches (Smith & Winterhalder, 1992), and also more territorial behaviors (Cashdan et al., 1983). And greater resource unpredictability is associated with more risky resource acquisition behaviors, such as raids on other groups (Winterhalder, Lu, & Tucker, 1999) and warfare (Ember & Ember, 1992).

However, to apply these ideas to modern industrialized human societies requires that we appreciate two distinctions. First, many modern human societies possess wealth, efficient food production and distribution processes, and social welfare systems that mitigate against the severe levels of scarcity (especially with respect to available calories) that can characterize many nonhuman animals and small-scale human societies. Second, the dominant resource in modern human societies tends not to be calories, per se, but rather forms of financial resources that are, in turn, used to gain access to

calories and other social benefits. Nonetheless, important parallels remain.

For example, resource patchiness in modern societies may be represented by the location of available jobs (i.e., the extent to which jobs are highly available in some areas but not others) or levels of income associated with different jobs (i.e., the extent to which certain jobs provide disproportionately higher amounts of financial resources than others). As with nonhuman animals, we would expect patchy ecologies to lead to high levels of social competitiveness, aggression, and territoriality. This could manifest itself in many ways, including social attitudes that favor competition, less tolerance for strangers coming into close proximity (reflecting increasing territoriality), and a higher prevalence or lower threshold of resource-focused emotions such as jealousy and envy (which would facilitate both the identification of “resource patches” and motivate competition for access to them). In extreme cases, one might also predict the emergence of a strong antisocial competitiveness, such as sociopathy and Machiavellianism, implicating moral psychology.⁵ Congruent with this is work showing that income inequality is a strong predictor of homicide rates (e.g., Daly, Wilson, & Vasdev, 2001; Wilson & Daly, 1997), and also creates preferences for high risk, high reward decisions (Payne, Brown-Iannuzzi, & Hannay, 2017).

Equivalents of resource unpredictability in modern human ecologies might include factors such as employment and economic volatility. Moreover, seasonal changes in weather are a source of resource unpredictability and, although these seasonal changes may seem less relevant in many modern societies, our evolved flexibilities might still be sensitive to such factors. Hence, societies and cultures that live in environments with fluctuating employment and economic prospects, and weather conditions, might potentially be characterized as more resource unpredictable.

Societies, cultures, and groups in resource unpredictable ecologies might exhibit a range of psychological traits corresponding to those found in the behavioral ecological literature. For instance, individuals in resource-unpredictable societies may exhibit greater novelty-seeking behavior, higher levels of openness, a higher incidence of pathological hoarding, lower investment in specialized education (which provides access only to limited types of resources, and may not be adaptive under unpredictable conditions), and low delay of gratification (unpredictable resources may disappear if not capitalized on quickly). These effects could spill over to social relationships, with social affiliation and romantic preferences for many (as opposed to few) partners who hold varied traits and skills, to the extent that these other partners might provide resource support for the self under unpredictable conditions.

We note that a considerable body of work has accumulated on the psychological effects of wealth. For instance, across nations, existing work finds that economic development or wealth is associated with greater individualism (Hofstede, 2001),

⁵ It has been proposed that if resources are extremely concentrated (e.g., there is only one patch), the number of competitors attracted to it might be so many that it would be too costly and dangerous for any one individual to attempt to monopolize the patch (Craig & Douglas, 1986). One would therefore expect *lower* levels of competition in such a situation. Although such a pattern has not been observed in non-human animal behavior, the possibility remains.

higher openness (McCrae & Terracciano, 2005), less traditional and survival-oriented values (Inglehart & Baker, 2000), and greater subjective well-being (Diener, Oishi, & Lucas, 2003). Wealthier individuals also make choices that make themselves stand out (Stephens, Markus, & Townsend, 2007), are more likely to engage in delay of gratification and self-control (Li-Grining, 2007), arguably adopt a “broader” friendship style, spreading their resources across a larger social network (Oishi & Kesebir, 2012), and also have different aesthetic preferences (Snibbe & Markus, 2005), among many other differences. We note that much of the existing work on resources has implicitly focused on resource *availability*. As highlighted here, the distinctions between resource availability, patchiness, and unpredictability can potentially lead to a more nuanced understanding of cultural psychological variation.

To take one example, the study of social class is a fast emerging domain, with multiple psychological differences observed between social classes (e.g., Côté, Piff, & Willer, 2013; Kraus et al., 2012; Kraus, Tan, & Tannenbaum, 2013; Varnum, 2016). Although one might most readily associate low social class with low resource availability, our view suggests that there may be multiple, and psychologically distinct, lower social classes defined by the intersections of these three resource dimensions. Consider, for example, low resource availability ecologies that differ in resource predictability. Individuals who live in ecologies *predictably* low in resources (i.e., resources are scarce but predictably so) may be quite different psychologically than individuals who live in ecologies *unpredictably* low in resources. In ecologies carrying few resources—and where it is difficult to predict when these resources will become available—residents might be less likely to delay gratification, consuming resources as they appear and before they are consumed by others. This tracks existing work finding that individuals from lower SES groups are indeed less likely to delay gratification (see Pepper & Nettle, 2017, for a review). However, in ecologies where (even scarce) resources emerge in a predictable manner, residents might instead adopt a planful and future-oriented psychology, timing behaviors to maximize access to resources when they become available. This represents a less examined, and potentially psychologically different, lower social class group.

Or consider residents of two countries that are similarly poor (low resource availability) but differ in resource patchiness. One might predict, at face, that an ecology with few resources would lead to greater territoriality and aggression between individuals as they attempt to protect their scarce resources. However, from the discussion above, we would predict that this would occur specifically when resource distribution is patchy (e.g., where only a small number of jobs have high payoffs). If resources are spread evenly across the ecology, there are few benefits from defending any specific resource. Hence, the relationship between resources and competitive behaviors depends on a consideration of both resource availability and patchiness.

The current framework therefore provides a more complex perspective for thinking about different aspects of human resource ecologies, and their interactive consequences for psychological differences across societies.

Mortality Likelihood

Behavioral ecological work. Death represents the ultimate loss of one’s genes, and mortality likelihood has received considerable attention in the behavioral ecology literature. Ecologies vary in how likely organisms within them will die by a specific point in their life span, and this likelihood is influenced by a range of factors, such as predator pressures, severe lack of food, or the frequency of natural disasters.

Ecologies in which mortality likelihood is high generally trigger faster life history strategies, in which individuals become sexually mature at younger ages, invest less in building embodied capital, have more offspring but invest less in each, among other traits. This is because in an environment where the chance of dying early in life is high, it is more adaptive to reproduce sooner rather than later, to avoid the possibility of dying without reproducing. The same logic applies to having many offspring, as this would reduce the possibility of all of one’s offspring dying. Indeed, the existence of phenotypic flexibilities that shift organisms toward a faster life history strategy under high mortality conditions has been documented across a wide range of species (Benard, 2004; Gross, 1991b; Peckarsky, McIntosh, Taylor, & Dahl, 2002; Roff, 1992; Stearns, 1992).

An important distinction here is that there are two broad classes of mortality, extrinsic and intrinsic, that have differing effects (Promislow & Harvey, 1990). Extrinsic mortality can be understood as mortality resulting from *uncontrollable* environmental factors (e.g., natural disasters, sudden climate change). Extrinsic mortality is relatively independent of the choices made by individual organisms. Intrinsic mortality, on the other hand, can be influenced by the individual, and is formally defined as the costs of reproduction. An extreme illustration of intrinsic mortality is what salmon go through during reproduction, consuming so much of their bodily energetic reserves that they die shortly upon spawning (Berghe & Gross, 1986). Intrinsic mortality is therefore, strictly speaking, less of an ecological factor than extrinsic mortality. And it is specifically *extrinsic* mortality that is predicted to lead to the adaptive shifts toward faster life history strategies, as outlined above.

Beyond the predictions made from life history theory, a body of work has also accumulated with respect to flexibilities that trigger antipredator defenses and behaviors under high predation pressures (Tollrian & Harvell, 1999). These are referred to as inducible defenses, and can manifest in striking ways, including aphids developing wings (Dixon & Agarwala, 1999), mussels thickening their shells (Freeman & Byers, 2006), or wood frogs reducing their size (Relyea, 2004). Given that such defenses cost considerable energy to develop or maintain, one would expect them to emerge only when there is significant predator threat, and that is indeed the case. Predator pressures also shape animal personality, specifically what is referred to as “boldness”—defined as how exploratory an animal is in novel environments and when engaging with novel objects. Higher predator pressures generally lead to lower levels of boldness (Johnson & Sih, 2007; Sih, Kats, & Maurer, 2003). Finally, high levels of predator cues in an ecology are also linked to increased startle responses (Briffa, Rundle, & Fryer, 2008), greater vigilance (Mateo, 2007), and increased social grouping (i.e., shoaling in guppies; Song, Boenke, & Rodd, 2011). Each of these behaviors arguably reduces predation risk.

Human parallels and predictions. As a species currently at the top of the food chain, few modern humans live in ecologies characterized by high levels of nonhuman predation pressure. But many of us do live in ecologies in which *other humans* are predators. Indeed, violent conflict between groups has been a recurrent feature of our ancestral history, with evidence that it exists both within our primate relatives (Goodall, 1986; Wilson & Wrangham, 2003) and modern hunter-gatherers (Chagnon, 1988; Ferguson, 1984; Haas, 1990). From this, one might view modern human societies with high levels of violent intergroup conflict (and resulting mortality) as high predation ecologies. Extrinsic mortality in human ecologies can also result from disasters of nature (e.g., flooding, earthquakes). One might therefore expect societies that experience high levels of violent intergroup conflict or frequent natural disasters to exhibit a psychology corresponding to a fast life history strategy (i.e., early reproduction, short-term relationship strategies, low parental investment, present-focused time orientation). Congruent with this, populations with lower life expectancies have indeed been found to have earlier ages of first birth, in both modern and small-scale societies (Low, Hazel, Parker, & Welch, 2008; Nettle, 2010; Walker et al., 2006; Wilson & Daly, 1997) and societies that experience higher levels of warfare also exhibit lower levels of parental investment (Quinlan, 2007).

Moreover, building on findings about nonhuman defenses in high-predation ecologies, we might expect humans in high (human) predator ecologies to be especially attentive and vigilant to their surroundings, exhibit heightened sensitivity to movement (which might cue an approaching aggressor), or startle more readily. Because of the potential threats posed by outgroups, individuals in these ecologies might be less inclined to travel or move too far away from their home group.⁶ Inhabitants of such ecologies might also experience heightened chronic fear, or lowered thresholds for experiencing fear, given that fear facilitates behaviors that help avoid physical threats.

Existing work provides initial evidence for such adaptive flexibilities. For instance, individuals become more socially conforming after imagining themselves in a physically dangerous situation (Griskevicius, Goldstein, Mortensen, Cialdini, & Kenrick, 2006). Converging with this, individuals in countries with higher levels of military spending (an indicator of an ecology facing high levels of cross-country conflict) are more agreeable, but only toward familiar (but not unfamiliar) others (White et al., 2012). Such findings suggest adaptive flexibilities that facilitate affiliation with one's ingroup as one way of coping with extrinsic physical threats.

In sum, societies and cultures characterized by higher levels of extrinsic mortality are likely to exhibit psychological and behavioral inclinations that correspond to a faster life history strategy. These groups are also likely to engage psychological traits that serve "anti-predator" functions, helping individuals avoid relevant dangers. This can include heightened vigilance, chronic fear, and within-group conformity.

Pathogen Prevalence

Behavioral ecological work. The final ecological factor we discuss is pathogen prevalence. In the animal literature on adaptive plasticity, pathogen stress has generally been found to lead to accelerated reproduction (Agnew, Koella, & Michalakis, 2000;

Bonneaud, Mazuc, Chastel, Westerdahl, & Sorci, 2004; Michalakis & Hochberg, 1994). Relating back to life history theory, when pathogens lead to a decrease in life expectancy, this should lead to resource allocation toward faster reproduction, to avoid dying before reproducing. For instance, Tasmanian devil populations infected by a highly lethal cancer exhibited an almost 16-fold increase in the number of precocial breeders (Jones et al., 2008), crickets experimentally infected with bacteria laid more eggs after infection (Adamo, 1999), and freshwater snails carrying more parasites reproduced at younger ages (Jokela & Lively, 1995).

Although parasite stress can lead to accelerated reproduction and increased investment in reproductive effort, this is not always the case. Plasticity to pathogens seems specific to the nature of the pathogen threat. If a pathogen reduces life expectancy, and the host organisms are unable to effectively stop or suppress it, this should lead to accelerated reproduction. However, if organisms are likely to recover, that should lead to the opposite—diversion of energy away from reproduction toward bolstering immune function and defense (Bocher, Tirard, & Doums, 2007; Rosengaus et al., 2017). Indeed, some evidence suggests that this occurs. For instance, female voles and mice delay reproduction when experimentally infected with cowpox (Telfer et al., 2005), an acute infection that can be recovered from. Hence, pathogen threats may take the form of either extrinsic (lethal) or intrinsic (curable) mortality threats, with the former leading to accelerated reproduction and a faster life history strategy, and the latter leading to a slower strategy instead.

The availability of resources also plays an important role in disease plasticity. High levels of pathogen stress, when coupled with low resource availability, can lead to a diversion of time and energy away from reproduction to resource acquisition. In support of this, male guppies infected with parasites decreased time spent on courtship and competing with other males, and increased time spent foraging (Kolluru, Grether, Dunlop, & South, 2009). This effect was attenuated when infected guppies were given extra food provisions. Similarly, rainforest frogs infected with fungus were less likely to call for mates than uninfected frogs, but specifically if their bodily condition was poor (Roznik, Sapsford, Pike, Schwarzkopf, & Alford, 2015).

Human parallels and predictions. Infectious diseases are widespread in our own species, have accompanied us through our evolutionary history, and continue to be a significant source of mortality (Ewald, 1993; Wolfe, Dunavan, & Diamond, 2007). Hence, evolution is likely to have selected for mechanisms to deal with this recurrent adaptive problem. Our complex biological immune systems are one testament of our long struggle with pathogens. More recently, however, a *behavioral* immune system has also been proposed (Schaller & Duncan, 2007). The underlying argument is that activating our physiological immune system incurs considerable costs. If individuals are able to detect, and

⁶ A limited movement range might have secondary effects on other ecological dimensions, such as resource availability and predictability, or even density and genetic relatedness (to the extent that group members now remain within close proximity of one another). Also, although not a direct outcome of plasticity, the low levels of intergroup contact in physically threatening ecologies might over time lead to greater diversity in practices and languages between groups, as each develops in relative isolation from others.

preemptively avoid or minimize exposure to pathogens through specific behaviors, this would minimize energetic costs. Indeed, there is now considerable accumulated evidence for the existence of such a system, sensitive to the ecological prevalence of pathogens, shifting individual behaviors in ways that facilitate coping with pathogen threat. When these ideas are extended to thinking about how societies and cultures varying in pathogen prevalence adopt different behaviors, they form a foundation for what is referred to as the parasite-stress theory of sociality (Fincher & Thornhill, 2012).

Variation in parasite stress across cultures indeed predicts a diverse range of behaviors. Higher pathogen prevalence across societies is associated with higher fertility (Guégan, Thomas, Hochberg, de Meeûs, & Renaud, 2011), greater prioritization of physical attractiveness in mates (Gangestad et al., 2006), lower extraversion, openness, and sexual promiscuity (Schaller & Murray, 2008), more authoritarian personalities and government systems (Murray, Schaller, & Suedfeld, 2013), greater traditionalism (Tybur et al., 2016), greater collectivism (Fincher & Thornhill, 2012), and reduced individual movement between communities (Cashdan & Steele, 2013). Findings that higher pathogen prevalence leads to higher fertility are consistent with life history theory: High pathogen stress is a form of high extrinsic mortality and thus, like predation and similar threats, is likely to shift individuals toward a faster life history strategy. The increased mate preference for physical attractiveness reflects an adaptive flexibility that, when confronted by high pathogen loads, puts a premium on selecting mates possessing cues to disease resistance. Low levels of extraversion, openness, and sexual promiscuity all presumably function to avoid exposure to infectious diseases in the high pathogen ecology—an interpretation also supported by experimental work in which making disease threats salient leads to lower levels of extroversion and approach inclinations (Mortensen, Becker, Ackerman, Neuberg, & Kenrick, 2010). Authoritarian inclinations and political systems promote conformity to tradition (including rituals that have been adapted over time to reduce infection threats), and thus also partially serve a disease-avoidance function. Collectivism, by drawing distinct boundaries between the ingroup and outgroup, facilitates the avoidance of outgroup pathogens that one's body may not be adapted to cope with (Fincher & Thornhill, 2012; although also see Tybur et al., 2016). Finally, less movement between communities also arguably helps avoid exposure to unfamiliar pathogens.

Although findings are generally consistent with parasite stress theory, there are some exceptions. For instance, in a large scale study of provinces within China, pathogen prevalence was unrelated to nepotism and was seemingly related in the opposite direction with cognitive styles associated with collectivism (e.g., holistic thinking; Talhelm et al., 2014). Other analyses within the Standard Cross-Cultural Sample also did not find a relationship between pathogens and ingroup loyalty (Cashdan & Steele, 2013). Finally, in a reanalysis of Fincher and Thornhill's (2012) data, Hruschka and Hackman (2014) find that the cross-societal correlation between pathogen prevalence and collectivism seems primarily driven by the difference between Western countries and everyone else. When the relationship between pathogen prevalence and collectivism is examined within Western countries, and within non-Western ones, no significant effect is observed in each of the two groups of countries. From this, the authors argue that the

cross-national relationship observed between pathogen prevalence and collectivism may not necessarily be a result of the behavioral immune system responding independently in each society to its specific pathogen levels (if this was so, one would also have observed the predicted correlations within non-Western and Western countries). Instead, it may be more a result of unique historical events that Western cultures experienced that, simultaneously, led to both improvements in public health and a rise in individualism.

Work on ecological pathogen prevalence and cultural psychological variation has generated considerable discussion (e.g., Hruschka & Hackman, 2014; Pollet, Tybur, Frankenhuys, & Rickard, 2014; Thornhill & Fincher, 2013), much of which revolves around issues of how cross-cultural associations should be interpreted, the methodological difficulties that emerge, and alternative explanations. It is nevertheless important to note that even where alternative explanations for a proposed ecological effect might exist, the alternative is often likely to remain an ecological hypothesis of some form (Nettle, 2009). For instance, in a reexamination of the relationships between pathogen prevalence and a host of variables (e.g., family ties, homicide) across the U.S. states, it has been found that other life history factors may better explain the cross-state patterns than parasite stress theory (Hackman & Hruschka, 2013). In particular, when relevant ecological factors such as mortality likelihood are taken into account, the relationship between pathogen levels and its related variables generally disappears (although also see Varnum, 2014, for an exception). Instances like this highlight the need for a fuller consideration of multiple ecological factors in thinking about cultural variation, a point we return to later.

Examining the interplay between mortality risk and pathogen prevalence, within a life history framework, is likely to be important for future work in this area. The earlier distinction between extrinsic and intrinsic mortality will be especially useful in understanding the links between pathogens and life history strategies (see Hill, Boehm, & Prokosch, 2016, for a discussion). When pathogen stress reaches levels so high that it becomes a source of mortality organisms have little control over (extrinsic mortality), this should trigger faster life history strategies. However, if pathogen threat is moderate enough that it can be addressed through increasing energetic investment in relevant capacities (e.g., immune function), then slower life history strategies may emerge. Thus the relationship between pathogens and life history may not always be linear.

There is some evidence for this. Specifically, across human societies, pathogen stress has been found to have a quadratic association with parental investment (Quinlan, 2007). From low to moderate levels of pathogen stress, parental investment increases, presumably because parental care is able to exert a protective effect on offspring when pathogen stress is within manageable limits. At extremely high levels of pathogen stress, however, parental investment decreases, reflecting the fast life history tendency to invest less in each individual offspring and to invest instead in having more offspring (given the high chances of any one child dying from infections). This highlights a broader point that plasticity need not exhibit a linear function (e.g., Dینگemane et al., 2010). Future work might distinguish between the effects, on societal-level psychologies and cultural practices, of pathogens that are lethal and unpredictable versus those that can be countered with sufficient investment in immune function. Also, as high-

lighted above in the behavioral ecology disease literature, the amount of energetic resources available for coping with disease stress will likely also play an important role.

In sum, the body of work on pathogen prevalence represents a mature example of the value of thinking about how phenotypic plasticity, in response to different ecologies, may shape psychological and cultural variation across societies. Many novel empirical discoveries about cultural differences have followed from applying the idea of phenotypic plasticity to variations in ecological disease. We suggest that there may be a similar richness waiting to be uncovered by exploring each of the other ecological dimensions highlighted by the current framework.

Summary

We have discussed six broad ecological dimensions: density, relatedness, sex ratio, resources, mortality likelihood, and disease. In each, we have highlighted relevant work in the behavioral ecology literature, drawn parallels with human ecologies, and outlined a range of predictions about how each ecological dimension might lead to human cultural psychological variation as outcomes of adaptive plasticity.

Density, genetic relatedness, and mortality likelihood vary considerably across societies yet remain largely unexplored as drivers of psychological differences. Sex ratio has received more empirical attention, yet many of its links to behavior remain unexamined. One valuable feature of sex ratio as an ecological dimension is its clear ability to make predictions not just about variation between societies but also *within* them (i.e., different effects for each sex). A behavioral ecological perspective on resources highlights nuanced conceptions that stem from considering how distinct features of resources—their availability, patchiness, and unpredictability—may uniquely and interactively shape psychology and behavior. Finally, the attention already paid to pathogen prevalence represents a powerful example of the empirical potential of adaptive plasticity in thinking about cultural variation.

Returning to a point we made earlier, one might ask: why focus on *these* six dimensions? Why not focus, instead, on other dimensions, such as desert versus plains versus mountainous ecologies? Again, we note that each of the six dimensions (a) connect to accumulated behavioral ecological literatures, giving them substantial evidentiary foundations, (b) have clear implications for biological fitness, and (c) have ready parallels in human ecology. This allows for inferences about relevant adaptive plasticities in humans. Although it may be that differences between desert, plains, and mountainous ecologies also shape human behavior, we are unaware of substantial nonhuman animal plasticity research that documents systematic plasticity in response to such differences. That said, we are not suggesting that the six current ecologies are the only ones that matter. Instead, we see these six as a relatively parsimonious yet comprehensive starting point for thinking and theorizing about a wide variety of cultural groups.

To summarize so far, the current framework provides multiple novel insights. It highlights unexamined ecological dimensions that might underlie cultural differences. It generates predictions not just about variation on traits studied in the cultural psychological literature but also about variation on traits less examined. It provides specific hypotheses regarding the people within a society who are especially likely (or unlikely) to be affected by these

ecological dimensions. And it offers a textured conception of seemingly simple ecological dimensions. Over and above all of this, the proposed framework also has broad potential implications for existing theory and data in cultural psychology, a point we turn to now.

Connecting Cultural and Ecological Dimensions

In this section, we highlight four implications of the current framework for existing thinking about psychological variation across cultures. Specifically, we propose that the current framework can (a) connect existing explanations of cultural differences and similarities, (b) provide a foundation for many existing explanations, (c) provide a way of thinking about multiple levels of culture, and (d) provide a framework for understanding cultural change. We elaborate on each with specific examples.

Connecting Existing Explanations

Thinking about culture in terms of behavioral ecology could help unite seemingly disparate explanations. Consider the heavily studied cultural dimension of individualism-collectivism and its effects on many aspects of cognition and behavior (e.g., Markus & Kitayama, 2010; Triandis, 1995). Briefly defined, individualistic cultures are those in which members focus on their individual goals and independence (Oyserman, Coon, & Kemmelmeier, 2002), whereas collectivistic cultures are those in which members place group interests above those of the self and focus on the maintenance of harmonious interpersonal relations within the group. In collectivistic cultures, the ingroup-outgroup distinction is relatively stronger than in individualistic cultures (Markus & Kitayama, 2010). Closely related to this are notions of independent and interdependent selves (Cross, Hardin, & Gercek-Swing, 2011; Markus & Kitayama, 2010). An independent self is one in which the individual sees herself as unique and distinct from others, whereas an interdependent self is one in which the individual sees herself as connected inextricably to others. Independent self-concepts are often associated with individualistic cultures, and interdependent selves with collectivistic cultures.

A wide range of factors have been associated with cultural variation in collectivism and self-construal. Early work centered around differences between East Asia and the West, with the former being more collectivistic (Nisbett, Peng, Choi, & Norenzayan, 2001). The difference was thought to be due in part to historical differences in philosophies (Confucian vs. Greek) that had exerted long-lasting psychological influences. More recent work has found roles for other factors. To the extent that dominant subsistence activities require high levels of social cooperation and coordination (e.g., cultivating rice vs. wheat), the psychology of a group is inclined toward collectivism (Talhelm et al., 2014). A high prevalence of contagious diseases also predicts greater collectivism, with a strong social boundary between the ingroup and outgroup ostensibly functioning to reduce exposure to novel diseases (Fincher & Thornhill, 2012). Social class has also been hypothesized to shape collectivist tendencies, with individuals of lower social class holding more interdependent self-concepts, because such individuals face more situational constraints (e.g., lack of resources) and uncertain environments, thereby increasing the value of an interdependent orientation (Kraus et al., 2012). Geo-

graphic regions that have been more recently settled (i.e., frontiers) tend to be more individualistic (Kitayama et al., 2006; Varnum & Kitayama, 2011), presumably as a result of both self-selection (those who choose to move are more independent) and the often harsh conditions of frontiers (which necessitates self-reliance). Finally, in a similar vein, communities for which there are high levels of residential mobility tend to promote more individualistic selves, given the greater difficulty of building stable social relationships (Oishi, 2010).

One sees, then, myriad potential explanations for differences in individualism and collectivism across groups. Might there be a common thread, drawing upon the idea of phenotypic plasticity, that unites these apparently disparate explanations?

Recall our earlier discussion of how ecologies with higher genetic relatedness elicit greater pro-social behavior, because of an adaptive plasticity sensitive to ecological relatedness. To the extent, then, that collectivism involves prosocial acts of sacrificing oneself for the group's interest (Singelis, Triandis, Bhawuk, & Gelfand, 1995), we suggest that differences in collectivism may result from this same sensitivity to levels of genetic relatedness. Eastern societies may be more collectivistic than Western cultures because individuals in Eastern societies live with and interact more frequently with genetic relatives (e.g., Yasuda, Iwai, Yi, & Xie, 2011), hence inhabiting an ecology of high relatedness. People at frontiers may be less collectivistic because, in moving to a frontier, they have presumably left their kin, close or extended, essentially creating for themselves a low-relatedness environment. Rice farmers may be more collectivistic than wheat farmers because rice farmers, given the need for cooperative help, are more likely to be surrounded by relatives. Individuals of lower social class may be more collectivistic because they are more likely to live in proximity of kin than are upper-class individuals, both because they have more children (and thus larger kin networks) and because a lack of resources may restrict residential movement. In sum, we propose that plasticity to variation in ecological relatedness may underlie, and thereby conceptually unite, seemingly disparate existing explanations for cultural variations in individualism and collectivism. And supporting this, individuals who live in high relatedness societies do seem to exhibit a range of behaviors that correspond to a more collectivistic and interdependent psychology, trusting and feeling more connected to typical ingroup (but not outgroup) members (Sng, 2017). Our broader suggestion is that other psychological differences across cultures and societies, similarly predicted by multiple cultural dimensions, may also find unifying explanations based on adaptive plasticity in other ecological factors. Consequently, the current framework may help "carve culture at its joints."

A Foundation for Existing Explanations

The second potential utility of the current approach is the ability to account for existing explanations themselves. As mentioned, an early explanation for East–West differences in individualism–collectivism was cultural philosophy (Nisbett et al., 2001), with the historical philosophies of the East being Confucian and of the West being Greek. But one could logically conceive of a West that embraced a Confucian-like philosophy, and an East that favored a Greek-like one. Why, then, is the East philosophically Confucian

and the West philosophically Greek? These differences in cultural philosophy themselves require explanation.

It seems likely that a range of philosophies emerged in both the East and West, but that the ones that ultimately persisted were those congruent with the psychologies triggered by the specific ecologies characterizing the East and West. In ancient China, this indeed seemed to be the case. The historical period of the Hundred Schools of Thought was a time during which many philosophies emerged (Feng, 1983). Alongside Confucianism, which places great value on the family, there existed the School of Names, a philosophy that focused on logic and definition, and Mohism, which advocated universal impartiality. However, it was Confucianism that has been most widely received and that has persisted over time. Why? Part of the reason may be the presence of an already high relatedness ecology, which triggers more prosocial psychologies. Such psychologies are then, in turn, more compatible with and subsequently prefer the collectivistic practices promoted by Confucianism relative to other philosophies.

Or consider that farmers are more socially interdependent than herders, because farming requires more group cooperation than herding (Uskul et al., 2008). Again, however, one might logically conceive of individuals who exhibit the opposite traits—herders who are highly *interdependent*. Why, then, are herders relatively independent? Recall that movement in and out of groups may serve as a cue to ecological relatedness, with high levels of movement implying lower relatedness, and that people respond to lower perceived relatedness with more individualistic orientations. Because the very task of herding requires greater mobility than does the task of farming, and thus a likelihood of encountering members of distant, less related individuals, one might expect herders to perceive their ecology to be of lower genetic relatedness and therefore adopt more independent psychologies and behavioral strategies.

Thus we are suggesting that, by understanding underlying ecologies and how people flexibly respond to them, one might be able to predict the emergence, persistence, or change of important cultural philosophies, practices, and norms.

Note that we are not saying that cultural transmission processes are unimportant; individuals obviously adopt the practices and beliefs of others in their society, as either active or passive learners (Boyd & Richerson, 1985). Hence, farmers learn the cooperative practices and behaviors of other farmers. However, because cultural transmission processes require something to be transmitted *in the first place*, such processes alone cannot account for the origin of specific patterns of cultural differences. Of course, some cultural practices may primarily be the products of historical accident. For instance, the historical adoption of the plow versus hoe in agriculture is associated with contemporary differences in gender norms (Alesina, Giuliano, & Nunn, 2013), and historical exposure to the slave trade (as a function of proximity to slave trader raiding routes) predicts current public mistrust in Africa (Nunn & Wantchekon, 2011).

Our suggestion, however, is that adaptive plasticity responses to ecological variation can provide explanations for *nonaccidental origins* of cultural differences, as well as for why some cultural beliefs and practices are more likely to transmit and persist (see "Adaptive Plasticity and Cultural Evolution" section below for further discussion). This perspective can be particularly useful when attempting to not just understand current cultural psycho-

logical diversity, but when predicting future differences. By their very nature, one cannot anticipate historical accidents. But one can anticipate, at least to some extent, changes in ecologies. This should not be taken to imply that historical accidents are therefore less important than ecological changes (think Chicxulub meteor).

Considerations of adaptive plasticity therefore provide what is termed an ultimate (compared with proximate) functional explanation (Scott-Phillips, Dickins, & West, 2011) for understanding psychological similarities and differences across cultures.⁷ Such an explanation allows for integration between disciplines, connecting the nonhuman animal and human literatures on psychological and behavioral differences between groups. It is important to note that ultimate explanations complement, not contradict, proximate ones. The two types of explanations are simply acting as explanations at different levels of analysis. Ultimate explanations provide foundational answers to the “why” question, when the question is pushed.

Multiple Levels of Culture

Beyond integrating and providing a foundation for existing explanations, the current framework also has implications for conceptualizing subcultures—cultures within cultures (e.g., Fine & Kleinman, 1979; Frost, Moore, Louis, Lundberg, & Martin, 1985; Scherer, 1974)—that include, for example, cultures of race, social class, religion, principles of honor, and organizations.

From an ecological perspective, the distinction between culture and subcultures may be unnecessary. This is because “subculture” could simply be conceived of as the outcome of ecological effects more immediately proximate to the individual (e.g., density in one’s town), whereas “culture” could be conceived of as the outcome of ecological effects at a larger scale (e.g., overall density of one’s country). This does not necessarily imply that subcultures, being more proximate ecologies, will always exert greater psychological effects than the more distal culture. From the current perspective, the relative psychological influence of subculture and culture might depend on the variability in underlying ecological dimensions. For example, if followers of two different religions within a country generally live in similar ecologies, then one might correspondingly see fewer psychological differences between the two religious groups (Cohen, Kenrick, & Li, 2006). Conversely, two religious groups that share similar origins may be psychologically quite different if they are now situated in two countries that have large ecological differences. For example, Roman Catholics living in the high-density, low-relatedness urban area of New York City might have more in common with Jews living there than with Catholics living in a low-density, high-relatedness agricultural village in Southern Italy.

This suggests a potentially interesting interplay between culture and subcultures. From an ecological approach, to the extent that a single unit of culture is ecologically *heterogeneous*, then one might expect there to be a large number of distinct “subcultures” existing within it, due to each subculture emerging as a result of distinct psychologies triggered by its unique proximate ecology. For instance, if a national culture spans a geographic space containing considerable ecological variability (e.g., some regions are much denser than others, or some have sex ratios skewed in opposite directions), then one would expect the national culture to contain many subcultures (potentially corresponding to each ecologically distinct region) in which residents of one region are psychologi-

cally different than those living in other regions. In addition, the more that the ecology of a specific subculture deviates from the average ecological circumstances of its umbrella culture (e.g., one region is exposed to an exceptionally high level of pathogen threat relative to other regions), the more one might expect psychological tensions between members of the subculture and members of the culture-at-large. This is because the psychologies triggered by the subculture’s quite distinct ecology will also deviate substantially from the average psychology of individuals in the rest of the culture.

Cultural Change

Finally, in addition to explaining patterns of cultural variation across societies, an ecological framework may also help us understand the causes of specific patterns of change over time within societies (Varnum & Grossmann, 2017). For example, changes in levels of gender equality in the US and U.K. over the past 6–7 decades appear to be driven in part by reductions in the prevalence of infectious diseases, an effect mediated by a shift toward slower life history strategies (Varnum & Grossmann, 2016). Rising individualism in the United States over the past 100–150 years appears to be linked to increases in resource levels (Grossmann & Varnum, 2015), as do more global shifts in the past 50 years toward individualistic values and practices (Santos, Varnum, & Grossmann, 2017). Also, as noted earlier, changes in bride price and dowry customs in Asian societies have been linked to changes in sex ratios (Kenrick & Gomez-Jacinto, 2014). Hence, the ecological framework can help us understand not only current patterns of cultural variation across space but also cultural shifts across time.

In sum, a behavioral ecological emphasis on adaptive plasticity has the potential to integrate multiple explanations of psychological variation across societies; where multiple explanations for a specific psychological difference exist, they may be united by common ecological factors. Second, the approach can provide a foundational, ultimate level of explanation: Existing explanations for psychological differences across societies may themselves need explanation and the idea of plasticity may provide that explanation. Third, the current approach offers a way of understanding the effects of multiple levels of culture, by conceptualizing them in terms of relatively proximate or distal ecological influences. And finally, one can use the current framework to generate predictions about changes in culture from changes in ecologies.

Characterizing Cultures as Ecologies in Interaction

Returning to our central thesis, we propose that psychological variation across societies and cultures can be conceptualized as the outcomes of evolved flexibilities reacting to ecological circumstances. But because cultures are embedded in ecologies characterized by *multiple* ecological dimensions, to fully understand such patterns of psychological variation one needs to consider how

⁷ The term “function” is also used in cultural psychological literature, but in reference to behaviors that fit cultural norms (e.g., Cohen, 2007; Mesquita & Walker, 2003). The use of it here refers specifically to biologically adaptive function, which in some cases is also culturally adaptive (Kitayama & Uskul, 2011), but need not be.

these ecological dimensions may interact with one another. Here we consider how such interactions might emerge from our proposed framework, using several illustrations.

Earlier, we discussed the tiger salamander, which develops a cannibalistic form under higher population densities, but not when surrounded by genetically related individuals. This example suggests that one might predict that population density and genetic relatedness will *interact* to shape human psychology. We hypothesized earlier that people in highly dense cultures and societies are likely to be more competitive. Such competitiveness may take the form of antisocial behaviors, including Machiavellianism, sociopathy, or traits that decrease social competition by hurting others (the human equivalent of salamander cannibalism). Our more specific prediction, however, is that, as with the tiger salamander, such effects will *not* emerge in societies that are also characterized by high genetic relatedness. Density's effects on antisocial competitiveness may only emerge, or emerge more strongly, in societies with low levels of relatedness. We represent this prediction in a simple ecological matrix below (see Figure 1).

A second example relates to predictions from life history theory. As mentioned earlier, higher population densities seem to lead to a slower life history strategy, consisting of traits such as a greater future orientation, investment in high commitment relationships, delayed reproduction, and greater parental investment. Such traits arguably facilitate successful competition in a denser environment. So, for instance, the slow strategy of delaying reproduction allows individuals more time to build their abilities and resources before engaging in mate competition and investing in potential offspring. But such a strategy is really most viable when individuals are in a *low* extrinsic mortality environment (Ellis, Figueredo, Brumbach, & Schlomer, 2009). If individuals are instead living in a dense, *high* extrinsic mortality environment, adopting a slow strategy will likely be maladaptive, as a slow strategy of delayed reproduction may lead to individuals dying before reproduction. Indeed, if the high mortality is driven by factors that would be further amplified by high densities (e.g., lethal disease, violent competition), we would expect population-dense societies in which there is high extrinsic mortality to be characterized by *faster*, not slower, life history strategies (see Figure 2).

For another example, consider cultural variation in tightness-looseness (Gelfand et al., 2011). A threatening ecology is theorized to lead to tight norms and low tolerance of social deviance due to the greater pressures on smooth social coordination. From the various ecological dimensions presented earlier, though, a specific ecology can pose multiple kinds of threats, and affect very specific norms. For instance, a society within a resource-scarce ecology might have strong norms about resource sharing, reciprocity, individual investment in cooperative tasks, and in general, rules that affect social cooperation and resource distribution. In contrast,

	Low Density	High Density
Low Relatedness	Low competition	High competition, including lethal forms
High Relatedness	Low competition	Moderate competition

Figure 1. Genetic relatedness and population density predicting social competition.

	Low Density	High Density
Low Extrinsic Mortality	Fast Life History (due to low density)	Slow Life History (due to high density)
High Extrinsic Mortality	Fast Life History (due to high mortality)	Very Fast Life History (due to density amplifying mortality)

Figure 2. Extrinsic mortality and population density predicting life history strategy.

threats posed by sex-ratio imbalances might suggest quite different implications for tightness-looseness. For instance, in ecologies where there are more females than males (female-biased ratio), one finds higher levels of sexual promiscuity and a greater orientation toward short-term mating (Schmitt, 2005). This is attributable to a scarcity of males which gives males greater power in the mating market, allowing them to impose a more short-term mating orientation typically associated with men.

From this, one might construct yet another ecological matrix (see Figure 3). Societies within a low resource and female-biased ecology would likely have tight norms regarding social cooperation and resource distribution, but *loose* mating and marriage norms (given higher promiscuity in such an ecology); societies within a low resource and male-biased ecology would have stricter norms in general; societies within a high resource availability and female-biased ecology would have generally looser norms; and societies within a high resource and male-biased ecology would have loose resource distribution and cooperation norms but tight mating and marriage norms. This represents an example where the consideration of interacting ecologies may lead to finer distinctions within existing cultural psychological phenomenon.

A final example turns to another important psychological difference across societies: collectivism. Collectivism seems, at face, characterized by positivity toward the ingroup and negativity toward outgroups. It is, however, not necessary that ingroup favoritism and outgroup prejudice have to exist together. In fact, they frequently do not (Brewer, 1999; Cashdan, 2001; Struch & Schwartz, 1989). As mentioned earlier, pathogen prevalence predicts outgroup prejudice because distancing from outgroup individuals facilitates the avoidance of unfamiliar pathogens. Yet, the influence of pathogen prevalence on *ingroup loyalty* is less consistent (Cashdan & Steele, 2013). One might consider the role of genetic relatedness, which predicts that people are especially favorable to highly related individuals. From this, another ecological matrix emerges (see Figure 4): A society that experiences high pathogen prevalence and low within-group genetic relatedness will exhibit a high degree of outgroup prejudice but low ingroup favoritism; a society that experiences low pathogen prevalence and high genetic relatedness, on the other hand, will exhibit low

	Male-Biased Sex Ratio	Female-Biased Sex Ratio
Low Resource	Tight Norms in General	Tight Resource Norms Loose Mating Norms
High Resource	Loose Resource Norms Tight Mating Norms	Loose Norms in General

Figure 3. Resource availability and sex ratio predicting tightness-looseness of different norms.

	Low Pathogen	High Pathogen
Low Relatedness	Low Ingroup Favoritism Low Outgroup Prejudice	Low Ingroup Favoritism High Outgroup Prejudice
High Relatedness	High Ingroup Favoritism Low Outgroup Prejudice	High Ingroup Favoritism High Outgroup Prejudice

Figure 4. Genetic relatedness and pathogen prevalence predict ingroup favoritism and outgroup prejudice.

outgroup prejudice but high ingroup favoritism; and a society situated in a high pathogen and high relatedness environment will most strongly discriminate between groups, exhibiting both strong ingroup favoritism and outgroup prejudice.

The above examples illustrate that certain combinations of ecological factors likely interact to create, across societies, distinct but predictable psychological and behavioral patterns. More generally, one can use these ecological factors to create ecology-based profiles of societies. For example, East Asian societies might be characterized by an ecological profile of relatively high genetic (actual or perceived) relatedness, high densities, low extrinsic mortality, and somewhat male-biased sex ratios. The U.S. might be characterized by high resource availability, low relatedness, moderate density, a balanced sex ratio, and low pathogen prevalence. A frontier settlement might be characterized by extremely low relatedness, very low density, high extrinsic mortality, high resource patchiness and unpredictability, and male-biased sex ratios. Lower social class groups, as noted earlier, may be represented by multiple, alternative ecological profiles: Although, in general, these groups might be characterized by low resource availability, high relatedness, and high pathogen prevalence, they might vary considerably in resource predictability, density, and mortality. In Table 2, we outline a preliminary taxonomy of the ecological factors characterizing various cultural groups that have received substantial attention in the literature. The current approach also encourages and provides a framework for the examination of other kinds of cultural groups that have been less studied (also see Kitayama & Salvador, 2017), to the extent that such groups may also inhabit different ecologies.

In sum, the current framework's explicit consideration of multiple interacting ecological dimensions offers a uniquely rich way of thinking about cultural psychological variation that does not necessarily emerge from existing approaches. By creating reliable

ecological profiles for existing cultural groups, and tapping into the literature on adaptive plasticity (see Table 1), one can generate hypotheses about a wide range of potential cultural differences and similarities.

Adaptive Plasticity and Cultural Evolution

In this section, we discuss the connections between the current approach and another major perspective at the intersection of culture and evolution: cultural evolution. Cultural evolution is a perspective that extends the application of evolutionary principles, beyond genes, to units of culture (e.g., beliefs and practices; see Boyd & Richerson, 1985; Chudek et al., 2015; Henrich, 2016; Mesoudi, 2016; Richerson, & Christiansen, 2013). Traditional biological evolution requires three conditions to be fulfilled: (a) There exists individual variation, (b) such variation is heritable (genetically) across generations, and (c) some variants survive and reproduce more successfully than others. Such logic also applies to units of culture, except that their transmission need not rely on genetically heritable variation.

As one example, consider god beliefs in traditional small-scale societies and modern large-scale ones (Norenzayan et al., 2016). In traditional hunter-gatherer groups, gods are viewed as typically distant and disinterested in the morality of human actions. The god of the Kalahari Kung hunter-gatherers, Gao!Na, for instance, is described as relatively unconcerned with the punishments of human wrong-doings. This is in contrast to the "Big Gods" of the Abrahamic religions, which are typically viewed as omniscient, omnipotent, and moralizing. Why the difference?

As human groups grew larger and more complex, social coordination became more difficult. Those groups that held beliefs promoting intragroup cooperation and cohesion—better enabling social coordination—gained advantages in intergroup competition, thereby enabling them to survive and spread over time. Through this cultural group selection process, the cooperation-promoting beliefs and practices held by these groups were passed on and gradually refined. Because beliefs in all-powerful, punishing supernatural observers encourage pro-social behavior and discourage free-riding, societies with Big God religions and associated cultural traits were more likely to succeed in intergroup competition. Via cultural evolutionary processes, then, Big Gods became more common with increasing societal size and complexity (Roes & Raymond, 2003). Hence, cultural evolution is one set of processes through which cultural psychological variability emerges.

Table 2

Prominent Cultural Groups in the Literature and Preliminary Ecological Profiles

Cultural group	Ecological profile (relative to comparison group)
East Asia (relative to West)	High density, High relatedness, Potential male-biased sex ratio, High pathogens
Farming communities (relative to herding)	High density, High relatedness, High resource patchiness
Frontiers (relative to non-frontiers)	Low density, Low relatedness, Male-biased sex ratio, High resource patchiness/unpredictability, High mortality
Honor cultures (relative to non-honor cultures)	Low density, High resource patchiness/unpredictability, High mortality, High pathogens
Residentially mobile (relative to residentially stable)	Low relatedness, High resource unpredictability, High pathogens
Social class, lower (relative to upper)	High relatedness, Low resource availability, Potential high resource unpredictability, High pathogens
Urban (versus rural)	High density, Low relatedness, High resource availability, High pathogens

How does adaptive plasticity connect to cultural evolution? In the following sections, we discuss (a) how variation in cultural learning strategies might itself be an outcome of plasticity, with certain learning strategies becoming more dominant in different ecologies, (b) how adaptive plasticity and cultural evolution process may be differentially important under specific conditions, and finally (c) how the evolution of plasticity might be shaped by cultural practices.

Variation in Learning Biases as Plasticity

One necessary element of cultural evolution is cultural learning, which is required for the transmission of culture. But learning is not random. Importantly, from a cultural evolution perspective, there exist several key learning biases (Chudek et al., 2015). Specifically, people preferentially learn from prestigious models (i.e., models who have demonstrated prior skill and success), similar models (i.e., models who are similar to the learner in ways that may indicate experience with similar adaptive problems), and more frequent models (i.e., adopting the beliefs and practices most prevalent in others). Importantly, there are significant individual differences in cultural learning strategies (e.g., individuals with high IQ are less likely to adopt social learning; Muthukrishna, Morgan, & Henrich, 2016). Such individual differences might themselves be outcomes of adaptive plasticity. Just as certain phenotypes may be more or less adaptive in different ecological conditions, certain *learning strategies* may be more or less adaptive in different ecologies. Hence, evolution should have also selected for adaptive shifts in learning strategies depending on the current ecology. Indeed, recent work in behavioral ecology suggests that individual learning strategies are influenced by ecological circumstances (e.g., conformity in foraging choices, Webster & Laland, 2008; learning from parents vs. other adults, Farine, Spencer, & Boogert, 2015; see Mesoudi, Chang, Dall, & Thornton, 2016, for a review). We highlight a few potential predictions about how ecology might affect learning biases in humans.

First, consider conformist transmission, also referred to as frequency bias. As noted earlier, individuals are more likely to hold conformist attitudes under disease threats (Murray & Schaller, 2012), and are also more agreeable toward ingroup members in ecologies with high levels of intergroup conflict (White et al., 2012). One might thus predict that conformity/frequency biases will be stronger in ecologies with high levels of disease and mortality (as driven by intergroup aggression), and that this might particularly apply to learning from ingroup models.⁸

Consider next the prestige bias. Earlier, we discussed the distinction between fast and slow life history strategies. Slow strategists invest more in learning skills and knowledge (embodied capital) that have immediate costs but future benefits. If prestigious individuals represent individuals who have successfully accumulated skills useful for survival and reproduction, one might expect slow strategists to also exhibit a strong tendency to learn from prestigious targets. From this, the same ecological conditions discussed earlier that should lead to a slower life history strategy, should also lead to stronger prestige biases (e.g., high population density, low extrinsic mortality).

Finally, for the similarity bias, consider two individuals similar in traits such as sex, age, skills, and knowledge. To the extent that both face similar adaptive problems, it would indeed be useful to learn from one another. But if the resource ecology is a highly

patchy one, for instance, one individual might find him- or herself in a much more resource rich patch than the other. The resource acquisition practices of one may then be ineffective for the other, and the similarity learning bias may not be particularly adaptive. More generally, for groups that live in highly heterogeneous ecologies (e.g., some individuals encounter one ecology, whereas others encounter a very different one), similarity biases may not be prevalent. Alternatively, consider individuals who live in a high relatedness ecology: To the extent that genetically related individuals might be more likely to face similar problems (e.g., preferring the same kinds of resources, being susceptible to the same kinds of diseases), one might see strong similarity biases.

In sum, the learning strategies that form the foundation of cultural evolution may be tied to ecological conditions, to the extent that individual differences in learning are outcomes of adaptive plasticity. This represents an area in which future empirical work would benefit greatly from attention by researchers in both the behavioral ecological and cultural evolutionary traditions.

The Scope of Cultural Evolution and Adaptive Plasticity

Cultural evolution models have shown that social learning (compared with asocial learning) is more adaptive under some conditions than others (e.g., Boyd & Richerson, 1985; Nakahashi, Wakano, & Henrich, 2012). If environmental conditions are relatively stable across time, for instance, then genes that directly produce adaptive behavior would be more efficient than energetically expensive cognitive mechanisms for cultural learning. However, when environments fluctuate too much in relatively short periods of time (e.g., within two generations), then cultural practices of the previous generation may also not be particularly useful, and copying them will not be an ideal strategy. Hence, cultural learning is likely to be especially adaptive within ecologies that fluctuate in moderate extents. Also, as highlighted above in the Big Gods example, intergroup competition is a factor that is necessary for cultural group selection to occur.

Similarly, behavioral ecologists have outlined the limits of plasticity (e.g., DeWitt, Sih, & Wilson, 1998). One prerequisite is sufficient and recurrent ecological variation. If a certain aspect of the ecology does not vary at all, then evolution will not be able to select for sensitivity to that ecological dimension. Beyond actual ecological variation, another important condition is the reliability of ecological information. If it is difficult for individuals to gather reliable ecological information (e.g., other conspecifics are hard to detect and hence population density is difficult to estimate), or gathering ecological information is particularly expensive and risky (e.g., estimating the prevalence of deadly predators), then relevant adaptive plasticities will be less likely to evolve. Finally, plasticity itself also has costs, as energy is required for building mechanisms that gather the necessary ecological information to inform plasticity.

⁸ Note that the traditional psychological concept of conformity is not identical to the conformist bias, which is formally defined as the learning probability of a cultural variant increasing with its frequency (e.g., a practice performed by 60% of the population is learned by observers 90% of the time). Existing psychological findings on conformity may or may not reflect frequency biases *per se*, but are likely to nonetheless lend some insights.

Taking the above considerations into account, then, one might generally expect cultural evolution processes to play a key role in driving psychological variation when there are moderate amounts of environmental change (but not so much that accumulated cultural information loses its relevance quickly) and when there are high levels of intergroup competition. When ecological conditions are highly fluctuating, then adaptive plasticity might play a more important role, assuming that these ecological dimensions also varied in our evolutionary history. For evolutionarily novel kinds of “ecologies” (e.g., the Internet), given the greater speed of cultural evolutionary processes, cultural evolution might play a larger role than plasticity in predicting psychological variation across different societies. Finally, for ecologies that do not fluctuate much, neither cultural evolution nor adaptive plasticity may be very relevant frameworks for predicting cultural psychological variation.

It has also been argued that cultural evolutionary approaches may be particularly useful for understanding behaviors that seem maladaptive (Richerson & Boyd, 1989). Consider the demographic transition—the unexpectedly low fertility rates in industrialized and high income societies. Cultural evolutionists have proposed that this may be driven by prestige biases (Richerson & Boyd, 2005). In modern societies, individuals with high status often achieve that status through sacrificing personal reproduction, investing instead in building skills and knowledge that increase prestige. From this, prestige learning biases will result in much lower fertility than expected. Indeed, the influence of cultural transmission on fertility is strong (e.g., Newson, Postmes, Lea, & Webley, 2005; Shenk, 2009). That said, we earlier reviewed ecological findings showing that high population density also predicts low fertility rates (Sng et al., 2017). Moreover, behavioral ecologists have proposed that the demographic transition may be the result of adaptive plasticity being now *mismatched* to modern resource ecologies, where indefinite amounts of wealth (e.g., land, money) can be accumulated outside one’s body (e.g., Borgerhoff Mulder, 1998; Kaplan, Lancaster, Tucker, & Anderson, 2002). Indeed, existing work finds that both cultural transmission and ecological plasticity independently contribute to variation in fertility (Shenk, 2009). Understanding such complex phenomena will likely require an integrative consideration of multiple perspectives including behavioral ecological and cultural evolutionary ones (see McAllister, Pepper, Virgo, & Coall, 2016, for a review).

Plasticity and Gene–Culture Coevolution

To the extent that cultural practices and innovations exert evolutionary pressures on genes themselves, the outcome is the co-evolution of genes and culture (see Laland, Odling-Smee, & Myles, 2010, and Janicki & Krebs, 1998, for reviews). The classic example here is the spread of alleles for lactose tolerance. In general, the ability to digest lactose in our species decreases significantly after infancy. Yet, the ability to digest lactose in adulthood, and its associated genetic traits, is prevalent in certain populations around the world. Multiple lines of evidence show that this resulted from the spread of dairying practices (e.g., Burger, Kirchner, Bramanti, Haak, & Thomas, 2007; Holden, & Mace, 1997). The reasoning is that in cultures that historically practiced dairying, individuals who were able to digest lactose in adulthood would obtain a substantial nutritional benefit relative to those who did not have this ability. Over time, the former would be more

likely to survive and reproduce, and genes that enabled lactose tolerance would then spread throughout such populations.

If cultural practices have shaped our genes, and plasticity itself is genetically coded (Scheiner, 1993), then cultural practices might also exert evolutionary pressures that alter the nature of plasticity. Plasticity itself can vary in its strength and structure, referred to formally as a *reaction norm* (Dingemans et al., 2010). Crudely, one might imagine two individuals who are both sensitive to changes in ecological mortality. The first individual might increase her fertility by four times for a single “unit” increase in mortality, whereas the second individual might increase her fertility by two times for the same mortality increase. Both exhibit adaptive plasticity, but the two reaction norms are different. The first individual might be thought of as holding a steeper reaction norm (or greater flexibility), given a greater change in fertility in response to the same ecological difference.

Building on this, cultural practices might alter the nature of plasticity. For instance, the ability to preserve and cook foods allows individuals to maintain a more consistent food supply over time. This may, in turn, reduce the selection pressure for plasticities that react to resource predictability (insofar as resource is defined as food). More generally, if cultural innovations remove (experienced) ecological variation, plasticity may become irrelevant. In particular, if latent plasticity is also costly (e.g., energetic resources are required for building and maintaining plasticity mechanisms), and there are no longer any adaptive benefits, then plasticity itself will be selected against over time, ultimately leading to the evolution of populations that are insensitive to ecological fluctuations.

More interesting would be the emergence of new kinds of plasticity, to the extent that cultural innovations generate novel selection pressures. For instance, the invention of agriculture has vastly increased the carrying capacity (i.e., the number of individuals a fixed land area can support given its resource providing potential) of inhabited land. Coupled with modern food transportation and processing technologies, extremely dense human populations that would have never been sustainable in our evolutionary history are now commonplace. Over time, this might shape a plasticity that reacts to extremely high density conditions. An even more recent cultural innovation is the Internet. The Internet is an evolutionarily novel medium in which social behaviors that have actual fitness consequences play out (e.g., learning, resource acquisition, mate seeking). However, the Internet ecology might often not match individuals’ actual physical ecology (e.g., one sees cues of mortality from disease outbreaks/disasters happening halfway across the world). Over time, this may create selection pressures for a plasticity that distinguishes Internet-mediated information from physically immediate information, adjusting phenotypes in specific ways. How plasticity might evolve in response to the Internet (assuming people continue to inhabit its ecology) will be a fascinating area for future research.

In sum, we briefly outlined several ways in which adaptive plasticity and cultural evolutionary processes may relate to one another. First, key cultural learning biases may be influenced by adaptive plasticity, such that different learning biases may be more or less prominent in different ecologies. Second, adaptive plasticity and cultural evolution processes may vary in their relative importance under different conditions. And finally, in connecting adaptive plasticity to gene-culture coevolution, the evolution of plasticity might itself be influenced by recurrent cultural practices.

Connections With Relevant Frameworks

Beyond cultural evolution, how does our framework connect with other prominent approaches to explaining cultural psychological variation—socioecological psychology, ecological threat approaches, gene-culture interaction, intersubjective culture, and evoked culture?

Socioecological psychology (Oishi, 2014; Oishi & Graham, 2010) is an approach that “investigates how mind and behavior are shaped in part by their natural and social habitats and how natural and social habitats are in turn shaped partly by mind and behavior” (Oishi, 2014, p. 582). Socioecological psychology has its roots in early ecological and environmental psychology (Barker, 1968; Stokols, 1978), and is described as sharing similarities with multiple disciplines, including behavioral ecology itself. There is indeed overlap between the socioecological perspective and behavioral ecology, with both emphasizing the importance of ecological influences. Socioecological psychologists describe the difference between the two as being that a socioecological approach focuses on psychological mechanisms (e.g., emotions), whereas behavioral ecology focuses on biological mechanisms (e.g., hormones; Oishi, 2014). Behavioral ecology, as per its name, has indeed focused less on psychological mechanisms, and more on predicting behavior. But this is not because behavioral ecology is *unable* to make predictions about psychological mechanisms. Rather, this is because evolution acts on behavior: If a trait or characteristic is not expressed behaviorally (or externally in some way), evolutionary forces cannot select for or against it. Hence, if a specific adaptive plasticity exists, it is presumed to have the predicted behavioral outcome. Beginning with predictions about behavior—what has been labeled the *phenotypic gambit* (Nettle, Gibson, Lawson, & Sear, 2013)—provides initial insight into the presence of hypothesized underlying mechanisms. Behavioral ecologists can make predictions about psychological mechanisms, and indeed have (e.g., time preferences in starlings: Bateson, Brilot, Gillespie, Monaghan, & Nettle, 2015; novelty-seeking in sparrows: Liebl & Martin, 2014).⁹

Importantly, the behavioral ecological perspective, particularly the notion of evolved plasticity, provides a foundation for *why* such psychological mechanisms should exist: They exist because they facilitate adaptive behavior for a species that has encountered recurrent ecological variation. Therefore, the current framework is complementary with a socioecological perspective, as the latter examines the function of psychological mechanisms in their ecologies, whereas the former provides a theoretical rationale for why such ecologically sensitive mechanisms exist in the first place. This is related to the distinction between proximate and ultimate levels of explanation (Mayr, 1961; Scott-Phillips et al., 2011), as described earlier. The current framework also highlights unique ecological dimensions that might underlie cultural psychological variation (e.g., density, genetic relatedness, resource patchiness) that do not clearly emerge from a socioecological perspective. Finally, the current approach is also coupled with a theoretical architecture that encourages the consideration of the effects of multiple ecological dimensions in combination.

Also relevant to the current framework are perspectives that adopt a general conception of ecologies as threats. Two dominant approaches are climato-economic theory (Van de Vliert, 2013) and tightness-looseness (Gelfand et al., 2011; Witkin & Berry, 1975).

Climato-economic theory proposes that climatological conditions, in tandem with available economic resources, influence the needs and goals of individuals in varying environments. Specifically, in physiologically demanding climates (very cold or hot), monetary resources can serve as a buffer to the harsh conditions posed by such climates. This generates more growth-oriented needs and self-expression goals. However, when monetary resources are lacking in such conditions, people instead seek to satisfy more survival-oriented needs and goals. Finally, in more temperate climates, regardless of economic resource levels, people are likely to have more “easygoing” goals, given low climatological stress (Van de Vliert, 2013). Work on tightness-looseness considers ecological threat broadly, conceiving of high population densities, resource scarcity, high disease prevalence, and a high frequency of natural disasters as representing threatening ecologies. In general, in societies with high levels of ecological threat, one observes greater tightness—strong social norms and low tolerance of deviant behaviors (Gelfand et al., 2011). Cultural tightness is particularly important in such ecologies because the threats impose barriers to smooth social coordination, resulting in the need for strict adherence to established practices and the policing of deviations from them.

The current framework does not limit itself to an exploration of threatening ecological features. Indeed, some ecological dimensions (e.g., genetic relatedness, sex ratio) do not fit neatly within a general threat perspective. Sex ratio, for instance, might be considered as threatening for the overprevalent sex but as opportunity-providing for the scarcer sex. Moreover, the behavioral ecological approach enables unique predictions even for ecological dimensions of common interest to these approaches. For instance, that higher population densities lead to a slower life history strategy emerges naturally from the current framework but not from tightness-looseness theorizing. The current framework also goes beyond a consideration of general resource scarcity, to make unique predictions about resource patchiness and unpredictability. Finally, as highlighted in the ecological matrix examples (see Figure 3), the current framework can also generate varying predictions about tightness-looseness of specific norms (e.g., resource distribution vs. mating). That said, the current approach does share, with both perspectives, an emphasis on the importance of considering multiple ecological factors simultaneously to understand the complexities of cultural variation.

Another recent framework that has been highly productive is gene-culture interaction (Kim & Sasaki, 2014), which examines how the same genes can lead to different outcomes when situated in different cultures. This approach builds on ideas of gene-environment interaction, but distinguishes itself through its consideration of culture as a unique form of environment, characterized by collectively shared values and patterns of action. For instance, one study examines the serotonin gene 5-HTTLPR, finding that Japanese with the SS genotype detect the disappearance of smiles more quickly compared with Japanese with SL and LL genotypes (Ishii, Kim, Sasaki, Shinada, & Kusumi, 2014). Amer-

⁹ This behavioral ecological approach has an interesting parallel with the distinction between Stage 1 and 2 research described in cultural psychology (Heine & Norenzayan, 2006), with the initial stage establishing where cultural differences are, followed by an examination of the mechanisms underlying such differences.

icans, on the other hand, showed the opposite pattern, with SS genotypes detecting smile disappearance slower than the other genotypes. It is argued that the SS genotype may be linked to greater susceptibility to environmental input, and in this case, leads to sensitization to culturally emphasized social cues (i.e., smiling).

The basic premise of the gene-culture interaction approach—that the same genotype can lead to different outcomes in different environments—parallels the concept of phenotypic plasticity proposed here. Again, the current framework provides a theoretical foundation for why such sensitivities to the environment would exist in the first place—because different psychologies would be adaptive in different ecologies. Work on gene-culture interactions therefore sheds insight on the specific genetic mechanisms that may underlie phenotypic plasticity, and itself demonstrates the utility of an approach that considers cultural variation in terms of outcomes of ecologically sensitive genes.

Another relevant approach is intersubjective culture (Chiu et al., 2010). In contrast to other perspectives to culture, which tend to focus on the influence of personal beliefs and values, the intersubjective approach emphasizes the influence of perceptions of what others believe and value (see also institutional theory of culture; Yamagishi & Suzuki, 2009). Intersubjective perceptions can sometimes play an even more critical role than personal beliefs. For instance, intersubjective perceptions of collectivism (e.g., “Koreans tend to sacrifice their own interest for the group”) predict the perceived harm of norm violations where personal collectivism does not (e.g., “I tend to sacrifice my own interest for the group”; Shteynberg, Gelfand, & Kim, 2009). Similarly, intersubjective perceptions, and not self ratings, of conscientiousness at the nation level predict actual indicators of conscientiousness (e.g., clock accuracy; Heine, Buchtel, & Norenzayan, 2008).

A behavioral ecological concept relevant to the intersubjective approach is frequency dependent selection, which draws from game theoretic principles (Maynard Smith, 1982). The classic example is the “hawk-dove” game, in which individuals can adopt either of the two strategies within a population of other hawks and doves. The ideal strategy depends on the existing proportion of hawks and doves. For instance, in a population of predominantly doves (which share resources when encountering other doves, and concede resources when encountering challenges from hawks), adopting a hawk strategy leads to greater benefits. But when the population is predominantly hawks (which take resources from doves but fight over resources with other hawks and often get injured), adopting a dove strategy can sometimes be more adaptive. More broadly, the adaptive strategy to adopt depends on the prevalence of other strategies in the population. As a form of plasticity, frequency-dependent strategy switching has been used to understand behavioral variation in a wide variety of species (e.g., foraging behavior: Mottley & Giraldeau, 2000; Wilson, 1998; mating strategies: Gross, 1991a; mimicry: Borer, Van Noort, Rahier, & Naisbit, 2010).

Just as intersubjective culture emphasizes the perceptions of others' beliefs and values in driving behavior, frequency dependent selection prioritizes the likely strategies of others as a critical factor. Frequency dependent thinking has yet to be broadly applied to understanding cultural psychological variation, and may yield novel insights.¹⁰ For instance, individuals' life history strategies may be influenced by the (perceived) life history strategies of others. If a fast strategy is associated with an orientation toward

short-term mating relationships, an environment with many fast strategists might mean an ecology with intense competition for short-term mates. For an individual entering such an environment, adopting a slow, *long-term* mating oriented strategy may instead be more adaptive, as that may help avoid competition (also see Gangestad & Simpson, 1990).

We note, though, that both frequency dependent selection and intersubjective culture face the same problem of lacking ultimate explanations, as also highlighted above with socioecological psychology. This is because the two approaches require others to first adopt a certain strategy, or hold certain beliefs, which then leads again to the same origins question: where did *their* strategies, beliefs, or values come from? The answer may trace back to the current ecological framework—that, for example, others' fast life history strategies resulted from the high mortality ecologies in which they live. Nonetheless, both frequency dependent selection and intersubjective culture share an emphasis on the importance of the behaviors, beliefs, and values of others as a critical, yet often overlooked factor. The intersection between the two represents a place where future work is likely to be highly productive.

Finally, the current framework has important overlap with the notion of “evoked culture” (Tooby & Cosmides, 1992). The idea of evoked culture stems from the premise that evolution has selected for domain-specific sensitivities to environmental inputs. The analogy often used is that of a jukebox; a jukebox itself does not change across time and space, but the songs it plays vary according to its patron's preferences. In relation to the mind, the proposal is that everyone has the same jukebox (i.e., evolved sensitivities), but the psychology that each individual adopts, or their “song,” may vary as a result of different environmental inputs (see also Kenrick, Li, & Butner, 2003). For instance, how much physical attractiveness is valued in a potential mate varies across cultures. One factor that influences mate preferences for attractiveness is parasite prevalence, with individuals in societies having higher levels of parasite prevalence also exhibiting stronger preferences for physical attractiveness (Gangestad et al., 2006). This reflects an evolved sensitivity to pathogen prevalence, with physical attractiveness being prioritized more under high parasite stress as it may reflect a potential mate's ability to resist and withstand diseases.

Evoked culture shares conceptual roots with the current framework and has inspired important discoveries. Existing empirical work has, however, focused predominantly on the ecological dimension of pathogen prevalence (e.g., Fincher & Thornhill, 2012; Schaller & Murray, 2008), as reviewed earlier, and has yet to be extended to the full range of ecological dimensions outlined here. The current framework also explicitly pushes for the consideration of the interaction of ecological dimensions, and more broadly, the characterization of cultural groups in terms of ecological profiles. Finally, the current framework, as outlined earlier, also serves an integrative function, drawing upon and uniting important bodies of work that have accumulated in cultural psychology, and providing a common foundation from which to also think of multiple levels of culture and cultural change.

¹⁰ We note that some existing cultural psychological work has drawn upon the same fundamental game theoretic principles (e.g., Cohen, 2001), although without explicit links to frequency dependent selection and phenotypic plasticity.

In sum, the current framework is conceptually linked and complementary to multiple existing perspectives, but is nonetheless unique in its theoretical contributions, empirical predictions, and application scope.

In Closing

The attempt to identify and explain cultural psychological variation is currently one of the most vibrant areas of work in psychology. The importance of examining psychological variation across cultures cannot be understated, and has profound implications for many long-held assumptions of our discipline (Henrich, Heine, & Norenzayan, 2010). As highlighted earlier, this endeavor has led to a large number of novel theoretical and empirical contributions.

Our aim has been to further this endeavor by advancing a framework that draws upon thinking in behavioral ecology. We have conceptualized psychological variation across societies as resulting from adaptive phenotypic plasticity—from the environmentally sensitive psychological and behavioral flexibilities that have evolved in response to the varying ecological conditions our species has encountered throughout its ancestral history. The implications of this framework are both broad and deep. It highlights novel ecological factors for future study, the psychologies that these ecologies elicit, and their implications for human cultural variation. It provides more nuanced conceptions of certain ecological factors, enabling a number of fine-grained predictions about cultural variation. It integrates bodies of work within cultural psychology and provides an ultimate logic for existing explanations. It provides a way of thinking about multiple levels of culture and cultural change. And it begins to provide an initial taxonomy of cultural groups—by characterizing them in terms of their critical ecological dimensions. Our hope is that this approach will both synthesize existing thinking and advance it, ultimately moving toward a richer understanding of the origins and current states of human psychological diversity.

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