Want Climate-Change Adaptation? Evolutionary Theory Can Help *

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The idea of adaptation, in which an organism or population becomes better suited to its environment, is used in a variety of disciplines. Originating in evolutionary biology, adaptation has been a central theme in biological anthropology and human ecology. More recently, the study of adaptation in the context of climate change has become an important topic of research in the social sciences. While there are clearly commonalities in the different uses of the concept of adaptation in these fields, there are also substantial differences. We describe these differences and suggest that the study of climate-change adaptation could benefit from a re-integration with biological and evolutionary conceptions of human adaptation. This integration would allow us to employ the substantial theoretical tools of evolutionary biology and anthropology to understand what promotes or impedes adaptation. The evolutionary perspective on adaptation focuses on diversity because diversity drives adaptive evolution. Population structures are also critical in facilitating or preventing adaptation to local environmental conditions. This suggests that climate-change adaptation should focus on the sources of innovation and social structures that nurture innovations and allow them to spread. Truly innovative ideas are likely to arise on the periphery of cohesive social groups and spread inward. The evolutionary perspective also suggests that we pay careful attention to correlated traits which can distort adaptive trajectories, as well as to the importance of risk management in adaptations to variable or uncertain environments. Finally, we suggest that climate-change adaptation could benefit from a broader study of how local groups adapt to their dynamic environments, a process we call “autochthonous adaptation.”

Keywords: adaptation, climate change, anthropology, human biology

Introduction

Anthropology has a long tradition of studying adaptation. A first coherent program was laid out by Julian Steward and the subsequent development of cultural ecology endeavored to document and understand the varieties of human cultural adaptation to diverse ecologies and subsistence regimes ([Steward, 1955](#)). As interest in cultural ecology waned during the latter part of the twentieth century, the adaptation thread was picked up by more explicitly evolutionary scholars studying both the evolutionary ecology of humans embedded within ecosystems ([Winterhalder, 1980](#)) and the biological adaptations that enable culture ([Henrich and McElreath, 2003](#)). This increasing focus on adaptation in evolutionary anthropology happened in parallel with a growing interest in another process called ‘adaptation’ by other disciplines: the responses of human socio-ecological systems to the threats posed by climate change. While these uses of the term ‘adaptation’ are clearly related, there are also substantive differences between them. We will suggest that in order

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to achieve the goals of climate-change adaptation—that is, to cultivate and support responses that help individuals and communities cope with the downsides of climate change—it is necessary to understand what ‘adaptation’ actually means (Thornton and Manasfi, 2011). Furthermore, we will argue that climate-change adaptation can be improved by taking an explicitly evolutionary perspective on the subject of adaptation.

We will begin by defining how the concept of adaptation is used in evolutionary biology. We then move on to discussing the usage of adaptation in anthropology, noting a peculiar fixation with homeostasis that characterized thinking on adaptation during the heyday of cultural ecology in the mid-twentieth century. We then turn our attention to the resurgent interest in adaptation in the context of climate change. We will see that there are substantial ways that the many notions of adaptation in the climate-change literature differ from its canonical usage in evolutionary biology. The idea as used in the climate-change literature also retains an implicit focus on the maintenance of homeostasis, which is less emphasized in contemporary evolutionary theory.

After reviewing the various perspectives on the study of adaptation, we will provide a brief overview of some relevant evolutionary theory. We will then suggest that adopting an evolutionary perspective on contemporary debates about adaptation focuses our attention on several important features. At its heart, evolutionary adaptation is a story of variance: the greater the variance in a trait, the greater opportunity for adaptation and the faster adaptation will take place. For climate-change adaptation, this suggests that we should focus on the sources of innovation and risk (i.e., where variance in traits and in the environment come from), how linked traits can constrain adaptive trajectories, and how population structure can facilitate the spread of innovations or provide risk buffering. We suggest that climate-change adaptation should be conceived more broadly, as a subset of more general adaptive processes. Thinking about climate-change adaptation as an element of the human capacity to adapt then suggests that there is great utility in studying what we call *autochthonous* adaptations in local populations.

What Is Adaptation?

The notion of adaptation ultimately stems from biology. In explaining the diversity of life, Darwin recognized that he had to explain not just how new species arose but why there are so many species in the first place. The theory that species are created by a process of descent-with-modification “even if well founded, would be unsatisfactory, until it could be shown how the innumerable species inhabiting this world have been modified, so as to acquire that perfection of structure and coadaptation which most justly excites our admiration” (Darwin, 1859, 3). The idea of adaptation is thus central to Darwin’s reasoning about the origin of species. In his classic essay, Lewontin (1978, 213) writes that adaptation “is the process of evolutionary change by which the organism provides a better and better ‘solution’ to the ‘problem’ and the end result is the state of being adapted.” Futuyma (2013, 296) adds a counterfactual element, defining an adaptation as “a characteristic that enhances the survival or reproduction of organisms that bear it, relative to alternative character states (especially the ancestral condition in the population in which the adaptation evolved).” Lasker suggests simply that “adaptation is the change by which organisms surmount the challenges to life” (Lasker, 1969, 1481).

Most authors actually distinguish two forms of biological adaptation that differ in their characteristic time scale. The first is adaptation through natural selection or what is often called (especially by social-science writers) “genetic adaptation.” Adaptation through natural selection is a process that typically requires many generations. The second notion of biological adaptation takes place on the scale of an individual organism’s lifespan and is typically referred to as “physiological adaptation,” “facultative adaptation,” or “plasticity.” Physiological adaptation involves

changes in phenotype in response to environmental input within the lifetime of an individual organism (Stinson et al., 2012). This latter notion of adaptation has been extremely influential on the application of the adaptation concept to culture and social systems.

In the most generic sense, adaptation is the process by which the phenotype is shaped by feedback from the environment. This leads to a fundamental truth about contemporary notions of adaptation in biology, namely, that adaptation is dynamic because the environment is always changing. Adaptations arise because certain phenotypic variants have higher fitness in a particular environment, not because of some guiding teleology of ever-increasing complexity. For this reason, adaptation is specific to local (and historically-situated) environmental conditions, and what was once adaptive can become *maladaptive* if it no longer promotes fitness in the changed environment (Brady et al., 2019). There is little sense in saying that some organism or population is “more evolved” or “better adapted” in some absolute sense independent of the particulars of the environments in which they are embedded. This idea has its genesis in Van Valen’s *Red Queen Hypothesis* (Van Valen, 1973). In Lewis Carroll’s, *Through the Looking Glass*, the Red Queen, suggesting to Alice that she must come from a very slow place, explains “Now, here, you see, it takes all the running you can do, to keep in the same place.” In a changing environment, organisms need to continue to adapt if they want to maintain the same level of fitness.

So, what are adaptations? In short, adaptations are solutions to persistent problems presented by the environment, broadly construed (Pisor & Jones, this issue). These solutions are selected from a range of possible alternative solutions. As such, there is always an implicit optimization problem lurking under the surface of an adaptation, that is, “which of the available solutions offers the greatest increase in fitness relative to others in the population?” This underlying optimization leads to the popular—but occasionally problematic—approach to understanding adaptation by reverse engineering phenotypes, as advocated by Williams (1966) and discussed by Lewontin (1978). This approach involves observing a trait and seeking to determine what function it could have had in past environments, such that natural selection acted upon it. Natural selection thus yields organismal “design without a designer” (Ayala, 2007).

From the outset of the serious evolutionary analysis of adaptation, biologists have marveled at the beauty and complexity of adaptations. Darwin (1859, 490) famously waxed “There is grandeur in this view of life, with its several powers, having been originally breathed into a few forms or into one; and that, whilst this planet has gone cycling on according to the fixed law of gravity, from so simple a beginning endless forms most beautiful and most wonderful have been, and are being, evolved.” This, then, is a central theme to the study of evolutionary adaptation. The idea of an adaptation carries a positive valence: scientists who study biological adaptations marvel at their beauty and elegance and generally see adaptation as a positive force. An adaptation is a trait that solves a problem because its bearers differentially prospered. We will see that this positive valence is not shared by all definitions of adaptation.

Anthropological Usage of Adaptation

While the broad biological meaning of adaptation—providing a solution to a problem—generally holds in anthropology, one particular perspective on physiological adaptation has dominated the human ecology, human biology, and biological anthropology literatures. This perspective is most easily seen in the way that human biologists explored the adaptations that allow people to survive and thrive in the face of environmental challenges such as heat or cold stress, high altitude, and water stress (Baker, 1969; Lasker, 1969; Stinson et al., 2012). The theme that arises from this tradition relates physiological adaptation as maintenance of homeostasis and the literal physiological approach of human biologists informed a more metaphorical application of the concept to human

behavior, institutions, and social structures (Alland, 1975).

Definitions of adaptation built around the maintenance of homeostasis dominated most work in anthropology in the middle and latter parts of the twentieth century. The homeostatic metaphor was extended from individuals to societies, as can be seen in the cybernetic approach of Gregory Bateson (summarized in his later work, Bateson, 1972) and carried on through the work of cultural ecologists such as Vayda, Netting, Rappaport, and others. Because the maintenance of homeostasis requires feedback mechanisms, this work specifically emphasized adaptation in terms of feedback (Collins, 1965) that “[keeps] or [restores] some property or variable of a system within a certain range of states or values” (Vayda, 1968, 102). Perhaps the best-known of the cybernetic human ecologists, Rappaport similarly defined adaptation as “the processes by which organisms or groups of organisms, through responsive changes in their own states, structures, or compositions, maintain homeostasis in and among themselves in the face of both short term environment fluctuations and long term changes in the composition or structure of their environments” (Rappaport, 1971, 60).

Despite working at approximately the same time as the classic homeostatic cultural ecologists, Sahlins saw adaptation as “maximizing the social life chances” (Sahlins, 1964, 136). He also emphasized that this maximization is done with respect to the constraints placed upon those adapting by not only the environment, but both “the internal structure of culture and the external pressure of environment.” Sahlins’s perspective echoed that of human biologist Morris Goodman, who noted that organic systems face constraints in two directions—that is, they must be internally and externally adapted (Goodman, 1963). Adaptations must obviously provide an advantage with respect to the external environment, but they must also be compatible with other elements of the organism’s phenotype. At a cultural level, this suggests that a solution to some external problem must also be compatible with the constellation of norms and practices that make up the culture.

While working very much within the homeostatic tradition, Vayda and McCay (1975) provided an important innovation for thinking about human adaptation. They were “particularly concerned with problems that carry the risk of morbidity or mortality, the risk of losing an ‘existential game’ in which success consists simply in staying in the game” (1975, 293). In this way, they align with the notion of Slobodkin (1964) that the process of evolution can be viewed as an existential game between the organism and nature. Vayda and McKay’s approach is also mirrored in the germinal work of Holling (1973), which has had a profound influence on the development of thought about climate-change adaptation. Consistent with Vayda and McKay’s focus on risk management, we see adaptation as encompassing Holling’s original conception of resilience, which he motivated by suggesting persistence is a more salient outcome than equilibrium. This mode of thought on adaptation benefits “by viewing the behavior of ecological systems in terms of the probability of extinction of their elements, and by shifting emphasis from the equilibrium states to the conditions for persistence” (Holling, 1973, 2). We highlight Holling’s original meaning both because it has been so influential for subsequent work on climate-change adaptation, but also because there has been considerable slippage in the implications of resilience. While Holling (1973) was explicitly trying to move away from homeostatic, equilibrium concepts, the idea of resilience has increasingly come to mean resistance to change (Olsson et al., 2015), a distinctly homeostatic notion.

Risk management is particularly salient to understanding the human adaptive complex (Jones, 2011). Humans life histories are highly unusual and suggest that the management of risk must be an important component of their selective history. While variance in a trait at the population level may be good for adaptation, variance in fitness and its components is generally bad for individuals and lineages because of the multiplicative nature of fitness (e.g., Gillespie, 1974). Jones (2011) suggested that the extremely unusual combination of very late age at first reproduction and relatively

high fertility indicates that human life-histories are best interpreted as bet-hedging—adaptations that trade-off the mean to reduce variance. The avoidance of extinction through reproductive bet-hedging suggests that environmental variability and risk management have been fundamental elements of the human evolutionary experience (Pisor & Jones, this issue). As recently noted by Price and Jones (2020), many of the psychological quirks people show with regard to risk, uncertainty, and time preference may be attributable to selection on fitness-promoting behavior in highly variable environments. Here we suggest that any notion of adaptation is incomplete if it fails to consider the risk environmental and demographic variability pose for fitness.

The dynamics of cultural systems are increasingly studied in the framework of cultural evolution, a rapidly growing field that sits at the intersection of evolutionary biology, anthropology, and psychology. Earliest formalization came from the work of Cavalli-Sforza and Feldman (e.g., Cavalli-Sforza and Feldman, 1973; Feldman and Cavalli-Sforza, 1975; Cavalli-Sforza and Feldman, 1981) and Durham’s (e.g., Durham, 1979, 1992) gene-culture co-evolution theory. However, the early work that has had perhaps the most influence on the development of the field, largely as a result of the authors training the next generation of scholars, is that of Boyd and Richerson (1985). Importantly, their approach does not require any connection between cultural and genetic evolution. Cultural evolutionary studies generally focus on the different processes through which cultural traits can be transmitted and the consequences of these transmission processes for the dynamics of cultural systems, often with particular attention to the role of demography (Mesoudi, 2016; Derex and Mesoudi, 2020).

In contrast to the classic evolutionary view of adaptation occurring through natural selection on genes, cultural evolutionary models often incorporate processes that at least implicitly allow for intent to become part of the process of adaptation. Models of “guided variation” assume that individuals choose which cultural traits to adopt based on their own experimentation or social learning about the payoffs of different traits (Boyd and Richerson, 1985). An important insight from this literature is that the dynamics of these systems are complex, and there are many factors that can limit the discovery or spread of adaptive cultural traits. Particularly important variables include the cost of individual versus social learning (Rogers, 1988), errors in the learning process (Henrich, 2004), and spatial or temporal heterogeneity in the environment (Derex and Boyd, 2016). Cultural evolutionary studies therefore allow us some insight into the conditions that can make it difficult for adaptive cultural traits to emerge and take root, even when agents have an ability to anticipate the consequences of their decisions. The state of being adapted, therefore, still emerges after the fact, as a consequence of population dynamics and selective processes.

Adaptation and Climate Change

While interest in studying adaptation faded from the research agendas of non-evolutionary anthropologists toward the end of the 20th century, the idea was taken up with vigor over the past three decades by interdisciplinary scientists concerned with the negative effects of climate change on human livelihoods and well-being. Despite the long history of studies of adaptation within anthropology, this new notion of adaptation as *climate-change adaptation* has become dominant in literature on human-environment interactions. What do scholars concerned with the consequences of climate change for human populations mean when they use the term ‘adaptation’? How is this distinct from more conventional evolutionary and anthropological conceptions of the term?

First, *adaptation* is typically contrasted with *mitigation* (Pelling, 2010). This contrast seems important for understanding the ways that climate-change adaptation differs in its usage from more traditional definitions of adaptation. Mitigation consists of actions meant to reduce or limit

climate change. On the other hand, the term *adaptation* often carries a negative valence in the climate-change literature: adaptations are necessary because mitigation has failed (Ford, 2008). Al Gore was famously anti-adaptation, writing that “Believing that we can adapt to just about anything is ultimately a kind of laziness, an arrogant faith in our ability to react in time to save our skins” (Gore, 1993, 240). From the standpoint of evolutionary scientists, conditioned to think of adaptation as an optimal solution to a persistent problem, this negative framing of adaptation is puzzling. However, there is still visible overlap between the way both communities of scholars use the term. The Intergovernmental Panel on Climate Change (IPCC) defines adaptation as “the process of adjustment to climate effects to moderate the negative impacts and/or enhance the positive impacts of climate change” (Field et al., 2012). Pielke (1998) suggests that adaptation is “adjustments in individual groups and institutional behavior in order to reduce society’s vulnerability to climate” (p. 159), while Brooks (2003) defines adaptations as “adjustments in a system’s behavior and characteristics that enhance its ability to cope with external stress” (p. 8). All these definitions suggest managing the increasing downsides of environmental variability, but narrow the focus of adaptation down from a general process to one specific to the variability that arises from climate change.

Carter (1996) defines adaptation “as any adjustment—passive, reactive, or anticipatory—that can respond to anticipated or actual consequences associated with climate change.” This idea of anticipatory adaptation is present in the works of numerous authors (Smit et al., 2000; Smit and Wandel, 2006; Massetti and Mendelsohn, 2018). For example, Smithers and Smit (1997, 133) suggest that “while the responses of biological systems to perturbations are entirely reactive, the responses of human systems are both reactive and proactive, incorporating environmental perception and risk evaluation as important elements of adaptation strategies.” While there are parallels between anticipatory adaptation, as used in the climate-change context, and the guided variation of cultural evolution, the emphasis on anticipatory adaptation seems bizarre. As noted earlier, though some degree of anticipation of the consequences of a decision is a part of some evolutionary models, actual adaptation emerges through the interaction of these decisions and the environment. There is no adaptation without feedback. Furthermore, given the dynamism of (evolutionary) adaptation, it is perhaps difficult for evolutionary scientists not to see it as an ongoing dialogue between organism (or population) and environment.

The definition of adaptation in the climate change literature also has clear echoes of the homeostatic adaptation of cybernetic cultural ecology. Nelson and colleagues (2007, 397) define adaptation “as the decision-making process and the set of actions undertaken to maintain the capacity to deal with future change or perturbations to a social-ecological system without undergoing significant changes in function, structural identity, or feedbacks of that system while maintaining the option to develop.” Climate change perturbs populations away from their status quo; adaptation brings them back. However, despite the implicit reliance on homeostatic logic, unlike early cybernetic cultural ecology, the climate change literature frequently fails to explicitly consider feedback processes. The endpoint of analyses is often the identification of possible (but usually untested) ‘adaptations’ for avoiding negative consequences of climate change, leaving possible feedbacks resulting from the adoption of these ‘adaptations’ beyond the scope of the research. For instance, “eating more store food” is sometimes suggested as an adaptive strategy for Inuit coping with reduced access to country food as a result of climate change (e.g., Pearce et al., 2010). Such an ‘adaptation’ may be an adequate way to remedy hunger in the short term, but any substantial increase in reliance on store foods would undoubtedly have complex (but negative) impacts on Inuit health and well-being in the long-term (Searles, 2002; Egeland et al., 2011, see also Pontzer, this issue). Magnan et al. (2016) describe a number of short-term climate-change adaptation efforts that have in fact led to ‘maladaptation’ in the long-term (defined as a reduced ability to cope

with climate change), partly because too little is known about the properties of the socio-ecological systems on which interventions have been enacted.

The centrality of feedback to adaptive processes creates a problem for the adaptation-mitigation binary, which [Head \(2010\)](#) notes is actually relatively new. As mitigation is an action taken by an individual (or collectively by a group of individuals) to improve their condition in the face of an environmental stressor, then mitigation would itself be considered adaptation in an evolutionary framework. More importantly, however, thinking about adaptation and mitigation as parts of a common process is consistent with recent thinking in evolutionary biology surrounding *niche construction* ([Odling-Smee et al., 2003](#); [Laland et al., 2016](#)). As noted by [Lewontin \(1983\)](#), traditional views of adaptation see the organism as passively adapting to a largely autonomous environment. Lewontin suggested that, in fact, organisms take an active role in shaping their environments. This insight was then formalized into the framework we now recognize as niche construction ([Odling-Smee et al., 2003](#)). Humans are clearly modifying our environment ([Field et al., 2012](#)) and our actions to ameliorate any negative consequences to our livelihoods and welfare, whether these actions are considered adaptation or mitigation, will have consequences for the environment to which we will further need to respond.

Finally, in the climate change literature the unit of analysis—what it is that actually “adapts”—is often taken to be the “socio-ecological system,” a vaguely-defined concept that is applied at multiple scales and using different ecological, political, or social and cultural criteria. A specific human settlement and its local resource catchment area are often taken as the specific object of study. However, decades of research in anthropology point out the dangers and difficulties of considering human settlements or groups at any scale as isolated systems whose members have convergent interests ([Vayda and McCay, 1975](#); [Moran and Lees, 2019](#)). ‘Adaptations’ suggested in the climate change literature are often behaviors to be adopted by individuals, with limited consideration of collective action problems or barriers to uptake, such as different costs and benefits to people of varying socioeconomic status. In contrast, both evolutionary biology and evolutionary anthropology primarily conceive of adaptation at the individual level, though they recognize there are specific conditions under which selection can act at the group level ([Sober and Wilson, 1998](#); [Boyd and Richerson, 2002](#)). This is because natural selection will favor traits that improve the relative fitness of an individual within a population and not those that favor the survival of a group ([Williams, 1966](#)). The idea that individuals will adopt behaviors for the purpose of improving the resilience of the “socio-ecological system” or the “community” is therefore one that is potentially highly problematic from an evolutionary perspective and also potentially highly consequential to the effectiveness of interventions. In particular, the assumption that cultural practices promote resilience because they are intended to “benefit the group” (itself a holdover from cybernetic cultural ecology) can mask inequalities that would likely constrain the resilience of the poorest members of the population ([Moritz, 2013](#); [Ready, 2018](#)). While there are arguments for capitalizing on the structure of competing groups to achieve environmental ends ([Waring et al., 2015](#)), we think it is unlikely that the rather stringent conditions that favor group-level adaptation, in which the within-group costs are lowered relative to the between-group benefits ([Zefferman, 2018](#)), are likely to apply in most cases of contemporary climate-change adaptation.

We can summarize what we see as the common differences between evolutionary adaptation and the development of the concept in the climate-change literature. These differences can be encapsulated by four contrasts:

1. **Positive vs. negative valence:** in climate-focused definitions, adaptation is often framed with a negative valence, apparently because there is a normative value placed on homeostasis. Adaptation consists to efforts to control the negative impacts of exogenous sources of

change. In contrast, adaptation is generally seen as the positive result of a selective process in evolutionary approaches. We note that these positive/negative valences are distinct from how we might evaluate the consequences of an adaptation.

2. **Reactive vs. anticipatory:** adaptation in the classic evolutionary context is necessarily reactive, while the term often connotes change anticipating future climate variability in the climate-change community. There is an implied teleology in many of these ideas. While cultural evolutionary processes can accommodate anticipatory behavior, the long-term outcomes of anticipated changes cannot be known until trade-offs are actually realized and feedbacks accounted for; in short, until selection has acted on them. We only know whether something is actually adaptive in retrospect.
3. **Adaptation as general process vs. adaptation as climate-change specific:** nearly all of the definitions used by the climate community see adaptation as something that pertains specifically to climate change and its attendant consequences. They do not envision the broader process of adaptation that is more commonplace in the evolutionary sciences, and that in evolutionary anthropology, incorporates the social and cultural environment more fully. Removing climate-change adaptation from broader adaptive processes contributes to the implicitly homeostatic framing of systems in the climate change literature.
4. **Individual vs. group-level adaptation:** The climate change literature often takes the “socio-ecological system” or “the community” as a unit of analysis, even though these are composed of heterogeneous groups and individuals. Evolutionary theory in contrast generally focuses on individuals. Though group-selection processes are often considered in evolutionary studies, these are carefully grounded in analyses of within-group dynamics that can potentially derail adaptive trajectories (Frank, 1997).

Are these differences between climate science and evolutionary science in how the concept of “adaptation” is used important? We argue that yes, they are. Given the confusion in how the term is used in climate science, and the urgency of the challenges posed by climate change, and the importance of predicting how communities may respond now and in the future to anthropogenic climate change, evolutionary theory can help us better establish how climate-change adaptation is most likely to work—and accordingly, how climate scientists, development partners, and policymakers can foster adaptations that are locally appropriate and lasting.

Reuniting Evolutionary Theory and Climate-Change Adaptation

What does evolutionary theory have to offer climate-change adaptation? In this section, we will discuss (1) the central role of variance in traits for determining the rate of adaptation, and (2) the implications of indirect selection that can arise from selection on covarying traits. One fundamental point that will emerge from this is the importance of generating diversity from which selective processes can then shape adaptations. This mandate for diversity leads us to think about the origin and spread of innovations which, in turn, leads to another key point of evolutionary theory, namely, (3) how selection operates in heterogeneous populations. We further discuss these ideas in light of the apparent importance of risk-management in many aspects of human adaptation. From this review, we will summarize the lessons from evolutionary theory for climate-change adaptation. We emphasize that our focus is purely on “cultural” (i.e., non-genetic) adaptation; we think of traits here as being things like technologies, behaviors, beliefs, or institutions that have the potential to be transmitted via social learning. While they may be cultural, they are nonetheless subject to evolutionary forces (Henrich et al., 2008). We should note, however, that the topics enumerated above have generally not yet been fully incorporated into the theory of cultural evolu-

tion, but we see great promise for future synthesis, particularly around the idea of adaptive culture change in response to pervasive environmental stressors. The applicability of cultural evolution to problems in sustainability has enjoyed some recent attention (e.g., [Waring et al., 2015](#); [Waring and Tremblay, 2016](#); [Brooks et al., 2018](#); [Kline et al., 2018](#); [Zefferman, 2018](#)).

Variance, Covariance, and Indirect Selection

[Fisher \(1958\)](#) first emphasized the importance of variance for adaptation. The response of a trait to selection depends upon both the intensity of selection and the variance in the trait ([Falconer and Mackay, 1996](#)). A trait under more intense selection pressure has a greater response. Similarly, a trait with more variability (i.e., additive genetic variance, the basis of narrow-sense heritability) will respond more to selection. When the phenotype is composed of multiple, covarying traits, we need to consider covariance between traits as well as the variance within a trait. The multivariate breeders' equation ([Lande, 1979, 1982](#)) tells us how a vector phenotype changes as a result of selection. The change in the multivariate phenotype of k traits that can be represented by a multivariate Gaussian distribution is the product of the additive genetic covariance matrix (the so-called **G**-matrix) and the selective gradient on the multivariate phenotype:

$$\Delta \mathbf{z} = \mathbf{G} \mathbf{s},$$

where $\Delta \mathbf{z}$ is a $k \times 1$ vector of the change in the mean phenotype $\mathbf{z}$, $\mathbf{G}$ is the $k \times k$ additive genetic variance-covariance matrix, and $\mathbf{s}$ is the fitness gradient evaluated at $\mathbf{z}$. That is, $\mathbf{s}$ is a vector of partial derivatives of fitness, w , with respect to the different elements of $\mathbf{z}$, scaled by mean fitness, $\bar{w}$: $s_j = \partial w / \partial z_j \cdot \bar{w}^{-1} = \partial \log w / \partial z_j$. In the case of cultural evolution, the **G**-matrix would measure the covariance of different cultural elements with each other, while fitness would refer to the rate of increase of the suite of cultural elements.

To the best of our knowledge, the multivariate breeders' equation has not been used in cultural evolutionary studies; however, we suggest it is nonetheless informative about cultural-evolutionary processes, particularly given its deep connections to the Price equation ([Day and Bonduriansky, 2011](#); [Bijma, 2020](#)), which is a fundamental tool for studying cultural evolution ([McElreath and Boyd, 2006](#)). When cultural assemblages come as a package, how does selection on one component affect the outcome? Geometrically, the selection gradient is a vector defining a point in k -dimensional space. It is the direction in which selection is pushing the phenotype. The **G**-matrix transforms the vector depending on the magnitude of the variances (i.e., the diagonal elements) and the pattern of the covariances. These covariances account for *indirect selection*, where strong selection on high-variance traits that covary with other traits can distort the response to selection away from the expected optimum as defined by the selection gradient. This is the key: indirect effects in traits that come as a package can alter the selective process in ways that can be surprising if such indirect effects are not accounted for (see plots in Supplementary Material). In other words, the multivariate breeder's equation provides a way to model how changes in one cultural trait may produce the more complex indirect feedback processes briefly mentioned earlier, and which have generally not been considered in most cultural evolutionary work or in the climate change approach to adaptation.

Thinking about indirect selection and, more generally, multi-trait cultural evolution is still in its infancy. [Brown and Feldman \(2009\)](#) provided an important idea of *cultural epistasis*, wherein the expression of a trait depends on its cultural background; however, Brown and Feldman do not link it directly to formal models of cultural evolution or adaptation. [Yeh et al. \(2019\)](#) have provided some interesting results, most notably that "cultural-hitchhiking" can be common when there are

frequent linkages (that is, covariance) between cultural elements and that, at intermediate levels of cultural linkage, the adaptiveness of cultural elements can be reduced.

Diversity (or heterogeneity) is clearly fundamental for adaptation in biological systems. In social systems, its role in improving the performance of teams and institutions has received increasing attention ([Hong and Page, 2004](#); [Phillips, 2014](#); [Page et al., 2019](#)). As with biological adaptation, a diversity of ideas and potential solutions means that adaptive responses have more material on which to draw. However, perhaps equally important is the finding that diverse teams lead to the questioning of assumptions about how ideas naturally fit together ([Phillips, 2014](#)). The existence of diverse ideas in an organization, and the debate these ideas entail, can break strong covariances between ideas and foster adaptive solutions. While there is no obvious direct analogy to this process in traditional quantitative genetics, it is reminiscent of the observation in the evolution-of-complexity literature that epistatic variance—the interactive, or multiplicative, relationships between traits—can be converted to additive variance following population bottlenecks because the epistatic interactions become weakened through drift ([Hansen, 2006](#)). When these linkages are weakened (in other words, when the covariance between traits is reduced), selection can foster adaptation more quickly. We suggest that diversity in groups helps play the same role in cultural evolutionary processes. By challenging assumptions that might simply be accepted by more homogeneous groups, diverse social groups break up excessive covariance between traits that can impede movement toward adaptive attractors.

Selection in Heterogeneous Populations

Variance in traits is the key to adaptation, but that variance is reduced by the process of adaptation itself as the adaptive solution comes to dominate the population. Population structure is essential for the maintenance of diversity. With what is perhaps surprising coherence, both evolutionary and social theory provide insights into how structure promotes diversity and what kinds of structures are most effective in doing so ([Houston and McNamara, 1992](#); [Kawecki and Stearns, 1993](#); [Centola, 2018](#)). A metapopulation is a population comprised of subpopulations connected through dispersal ([Hanski and Gilpin, 1997](#)). When some populations have positive (intrinsic) growth rates and others have negative growth rates, the metapopulation is characterized by source-sink dynamics. Positive-growth subpopulations are sources, while negative-growth subpopulations are population sinks. [Kawecki and Stearns \(1993\)](#) noted that typically subpopulations become sinks because the organisms comprising them are not well-adapted to their local conditions, potentially because of local environmental change. Intuitively, we would imagine that the force of selection would be particularly strong on subpopulations that are not well adapted to local conditions. However, because of the connectivity among subpopulations, selection is entrained to the mean of the overall metapopulation. This mean, in turn, will be dominated by the sources. The adaptation of the demographically dominant subpopulation inhibits the adaptation of the smaller subpopulations: the mean trait will reflect the conditions experienced by the source subpopulations, not the sinks. In short, strongly-connected metapopulations lead to the loss of adaptive local environmental tracking. This is also a problem noted by [Whitehead and Richerson \(2009\)](#) in the context of over-reliance on social learning. Connectivity hampers adaptive innovation through regression to the mean.

Conditions that Favor Innovation

The discussion of the last section showed that local adaptation can be inhibited by regression to the mean when metapopulations are strongly connected. A similar insight has been made in

Figure 1: Metapopulation with source-sink structure. Vertices (populations) are drawn in relative proportion to their size, while the arrows indicate the direction of dispersal and are proportional to its rate.

the study of innovation in both cultural evolution and sociology. Innovation is stifled by excessive connectivity, particularly to dominant cultural groups, and is cultivated by particular social structures that promote diversity. In this section, we discuss these social structures and relate the mechanisms by which they promote innovation back to the theory of selection in heterogeneous environments.

Henrich (2010, 117) emphasizes population connectedness as a predicate for innovation: “a highly interconnected population can have high innovativeness even when it has relatively low inventiveness.” Thus, the degree of innovation in a population can be high, even if it is not creative, as long as it is strongly connected. While the dissemination of adaptive solutions to persistent problems certainly depends on the connectivity of a population, as with adaptation in metapopulations, the spread of innovations in social networks can actually be hampered by strong connectivity (Centola, 2018). The problem with connectedness is that it’s a two-way street. Yes, information about novel ideas can be disseminated as a result of connectedness. However, connectedness also leads to regression to the mean through peer pressure and social sanction. These are central ideas from Coleman’s (1988) conception of *social capital* as embodied in social closure. What matters more for innovation than uniform connectedness is heterogeneity.

The development of innovation is fostered by heterogeneous *structure*. There needs to be some clustering of the network (implying cohesion) but clusters still need to be relatively distinct. As with the metapopulation model of Kawecki and Stearns (1993), too much connectivity between clusters swamps out local responsiveness. This is a fundamental point made in the cultural evolution literature by Derex and Boyd (2016) and Derex et al. (2018), who note that population fragmentation maximizes cultural accumulation. Homogeneously-connected populations allow innovations to spread, but do not possess sufficient diversity to generate innovations. Local dispersal maintains clusters and thus maintains diversity, whereas long-distance dispersal reduces diversity by breaking up clusters (Kerr et al., 2002). These observations are consistent with the seemingly paradoxical finding that innovations spread from the less-connected periphery of populations to the core, rather than the other way around (Centola, 2019).

Consider the densely-connected network in figure 2. While an innovation could spread rapidly to all parts of the graph if it were to appear in the light blue region (i.e., the core), the sort of social sanction described by Coleman (1988) is likely to prevent such innovative ideas from taking hold in the first place: “Effective norms in an area can reduce innovativeness in an area, not only

Figure 2: Dense network with stongly-connected peripheral group (purple) where innovations can potentially be cultivated.

deviant actions that harm others but also deviant actions that can benefit everyone” (Coleman, 1988, S105). In contrast, innovations developed in the strongly-internally-connected, but peripheral subpopulation (indicated in purple) have a greater chance of growing to a critical mass; once they do, these innovations can begin to take foothold in the larger population through the process of complex contagion described by Dodds and Watts (2005) and Centola (2018). While the purple subpopulation is strongly connected—and, therefore, susceptible to the innovation-stifling effects of social sanction like the broader network—it is essentially a closed clique (technically it’s a 4-core) and it is small. A group of 10 individuals from the core of this broader network would be similarly connected overall, but their connections are embedded within a larger, more cohesive community (Centola, 2015). More cohesiveness leads to more social sanction and less innovative-ness (Coleman, 1988; Steinert-Threlkeld, 2017).

Further, unlike the genetic systems on which many cultural-evolutionary models are based, the generation of cultural variants is neither completely random nor is it rare (Fogarty et al., 2015). Cultural innovation arises, in part, from attempts to solve problems, so we should expect that repeated innovation should be common, and this has implications for dynamics (Fogarty et al., 2015). The perspective from research on complex contagions suggested by Centola (2018) fits well into this. Just as cultural innovation is not rare, complex behaviors are not based on a single, brief exposure. Repeated exposure is likely to happen in cohesive communities that are nonetheless freed from the potentially overwhelming social sanction and pressure to conform from a larger population. The quality that should really make innovation happen is analogous to the concept of beta diversity in ecology and conservation biology (Whittaker, 1960)—that is, a high degree of turnover in norms, practices, or institutions across communities in a landscape should be conducive to the generation of innovation and therefore, ultimately, adaptation.

Social learning greatly increases the potential rate of adaptive cultural evolution. Even when individual learning is costless, social learning can dominate in large measure because the behavior of others has already been subject to some selection. Social learning induces efficiencies because of this filtering phenomenon (Rendell et al., 2010). This efficiency, however, comes at a potential cost. First, social learning can dominate cultural dynamics even if, in the absence of sufficient variance in exposure to novel ideas, it reduces mean fitness (Rendell et al., 2010). Second, extensive reliance on social learning can lead populations to stop adaptively tracking their environments. Whitehead

and Richerson (2009) show how this phenomenon can lead to catastrophic consequences and emphasize how promoting individual learning and innovation may be the only way to avoid such catastrophes. When represented as a cultural-transmission network, very strong social learning suggests a strongly-connected population and leads to the perverse selective dynamics described by Kawecki and Stearns (1993) and discussed above, while fostering individual learning generates structure. One mechanism to dampen this maladaptive effect is to ensure and maintain population substructure (Bunce and McElreath, 2018).

Summarizing the innovations literature, once again, the key outcome that facilitates innovation is diversity. This time, however, the diversity is structural rather than phenotypic. Connectivity is important for dissemination of innovations, but as in the case of evolution in heterogeneous landscapes, can impede responsiveness to local conditions. In the case of social networks, this results from innovations being squashed by regression to the mean, due to conformist bias and social sanction. As noted by Derex and Boyd (2016) and Derex et al. (2018), the optimal social structure for the spread of innovations will be characterized by intermediate connectivity. Moreover, innovations are likely to flow from peripheral communities, where the social sanction of network closure is reduced (Coleman, 1988), into the core of larger groups (Centola, 2018, 2019).

Risk-reduction vs. Innovation?

In our earlier discussion of anthropological approaches to adaptation, we also described how human life histories, which are characterized by very late ages of first reproduction, relatively high fertility, and long reproductive spans, are quite unusual. Jones (2011) has suggested they can be understood as adaptations to highly-variable environments which can induce potentially large variance in fitness—meaning partly that these adaptations may be intended to buffer the risk of “zero fitness” (i.e., death/extinction). The definition of fitness is a difficult problem in the philosophy of biology (Rosenberg and Bouchard, 2020), but it is clear that a satisfactory measure of fitness should account for both differential increase (e.g., as given by the multiplicative rate of increase) and extinction risk (Pence and Ramsey, 2013). Risk management has also long played an important role in anthropological understandings of human behavior and culture, evolutionary and otherwise (e.g., Ortiz, 1973; Halstead and O’Shea, 1989; Cashdan, 1990), including in our own work on foraging strategies (Jones et al., 2013), exchange (Ready, 2018), and in- vs. out-group social ties (Pisor and Gurven, 2016).

In an early piece on climate-change adaptation, Smithers and Smit (1997) draw a fundamental distinction between adaptations that buffer risk (and maintain the status quo) and adaptations that involve “evolution to a new state” (and are thus transformative). Again, however, we think this distinction is not productive. New strategies for buffering risk may be innovative and could be also transformative if, for instance, they lead to a redistribution of wealth within a population.

An evolutionary perspective suggests that close attention should be paid to the relationship between risk-preferences, risk-buffering strategies, and innovation. In the previous section we discussed how innovation—the production of new cultural traits—is an underlying condition for new adaptations to emerge. But, colloquially, innovation is generally understood to be a risky (though potentially high reward) endeavor. Certainly, if the payoffs to adopting an innovation are themselves risky or uncertain (the latter meaning the payoff or its variance are unknown), then such innovations will be less likely to be adopted by risk-averse decision-makers. This problem has been much discussed in the anthropological and economic literature on peasant farmers (e.g., Lipton, 1968; Weeks, 1970; Shahabuddin and Mestelman, 1986), which warns us that we should carefully consider how the spread of innovations may interact with poverty and inequality.

Human risk-buffering strategies are deeply social: they involve exchange of resources, in-

formation, assistance, and bodies over different spatial and temporal scales. Theoretically, one might expect that networks produced through the actions of individuals seeking to manage their exposure to risk would reflect the spatial and temporal scales of important sources of risk (Winterhalder, 1990). For instance, buffering of environmental risk on a relatively small-scale (e.g., day-to-day variance in hunting success) might be fostered by within-group sharing. Strong sharing norms enforced by social sanctions (as described among the !Kung by Lee (1969), for example) are common among historically-known hunter-gatherers. At the same time, Wiessner (1982) depicts long-distance long-term *Hxaro* exchange partnerships among the !Kung as a strategy for buffering larger, inter-annual kinds of risk such as droughts. This combination of dense local clusters with some connectivity between them sounds at least superficially like the structure we have described as fostering the dissemination of innovation (see also Migliano et al., 2020). Critically, however, it is important not to conflate function with design (Ensminger, 1994): though social practices and structures may have consequences, it does not mean that they evolved for that purpose. An important and not yet fully answered set of research questions relevant for our understanding of human adaptation, both today and in the past, lie in better understanding the relationship between population size and structure, different sources and scales of risk, and cultural innovation (Henrich et al., 2016; Fogarty and Creanza, 2017). For example, under what circumstances can risk-buffering strategies produce social structures that enhance innovation, and when might they inhibit them? How did different kinds of environmental risks and risk-management practices interact with innovation in the past, and how can this history help provide insight into adaptation to climate change today?

Autochthonous Adaptation

Above we have sketched the contours of an evolutionary approach to understanding how novel cultural adaptations emerge and spread. In this final section we propose the concept of *autochthonous adaptation* as a useful lens for identifying and studying this process empirically. Rather than contributing yet another entry to a typology of adaptation, our perspective focuses on the broader adaptability of people and on adaptation as a process rather than a specific outcome.

The term “autonomous adaptation” is used for “automatic or in-built responses to climate change” (Carter, 1996, 30) as a contrast from more planned or prescriptive adaptations. We define *autochthonous adaptation* to retain the idea of a naturally-occurring response but also to emphasize that it comes from within the group undertaking the adaptation. Autochthonous adaptations are responsive to changing environments, arise from local processes and decision-making, and are dynamic, changing as the environment itself changes. Because autochthonous adaptation is rooted in a particular locality, it can lead to better tracking of the environment and greater ecological/energetic productivity (Lansing, 1991; Netting, 1993; Bird et al., 2012; Tucker, 2014). Autochthonous adaptations are a predicate for survival in many populations around the world today (Bird and Bird, this issue; Douglas & Rasolondrainy, this issue; Kramer & Hackman, this issue). The peripheral status of many of these populations with regard to larger, market-integrated societies also means they are likely to be sources of innovation. This suggests that protecting minority cultures from being overwhelmed by dominant cultural groups is an important goal for maintaining adaptive potential (Bunce and McElreath, 2018).

The study of autochthonous adaptation is what anthropologists have done historically (Bennett, 1976). Whether it is the ritual cycle of the Maring preventing land degradation (Rappaport, 1971), the *subak* system synchronizing irrigation schedules in Bali (Lansing, 1991), peasant farmers choosing the scale for cultivation that optimizes output (Netting, 1993), San hunter-gatherers managing shortfall risk through long-distance ritual sharing of *hxaro* (Wiessner, 1982), or Martu

burning for short-term foraging gain producing a more productive landscape (Bird et al., 2008), autochthonous adaptation is the fundamental object of analysis for anthropologists working in an ecological framework.

Focusing on autochthonous adaptation—that is, the specific adaptive problems faced by people and the dynamic process of solving these problems—also brings into focus other problematic aspects of the adaptation concept in the climate change literature. Existing studies of autochthonous adaptation frequently highlight that broader social, economic, and political factors constrain the ability of many populations to adapt to climate change more than a lack of local knowledge or innovation (e.g., Wenzel, 2009, Bird and Bird, this issue), as do theoretical critiques of the climate-change adaptation literature (Cameron, 2012; Veland et al., 2013). These critiques highlight that the homeostatic perspective on adaptation is problematic because it assumes that the state of the system is something that *should* be returned to. Homeostasis becomes rather less than adaptive when the existing state of the system is already not well suited for the environment. When not viewed as a process that maintains homeostasis, then adaptation means change. Though the long-term impacts of centuries of colonialism clearly show the potentially negative effects of rapid, exogenously-imposed culture change, the climate-change literature generally has not considered how processes of adaptation may be traumatic or erosive to cultural identity. Studies in cultural evolution have only begun to touch on such questions, but Bunce and McElreath (2018) find that establishing boundaries that minority groups can cross but which restrict the crossing of the more powerful population allows the persistence of the cultural norms of minority communities.

Discussion

The concept of *adaptation* means quite different things to different scholarly communities. While the idea has its ultimate roots in evolutionary biology, it has been a central theme in anthropological investigations into the human condition. In many respects, anthropological usage of the concept has largely mirrored the biological sense, but the cultural ecology of the mid 20th century focused excessively on adaptation as the maintenance of a frequently poorly-specified homeostasis. Much current research specifically addressing the concept of adaptation focuses on the important topic of human adaptation to climate change. While the concept of climate-change adaptation is clearly deeply related to broader evolutionary conceptions, it nonetheless departs from biological adaptation in important respects as well. Key differences relate to the extent to which adaptation can be proactive, what entities are adapting, and whether adaptation is treated as a dynamic or homeostatic process. In this sense, discourse on climate-change adaptation has largely adopted the homeostatic perspective of mid-20th-century social science, despite the fact that research today is primarily framed using the concept of resilience, a non-equilibrium idea.

An evolutionary perspective suggests a particular concreteness to adaptation. While many of the definitions of climate-change adaptation emphasize that an adaptation can be anticipatory, this means that the proposed adaptations have not been field tested, as it were. For a behavior-change to be an adaptation, surely it has to work on the ground. This is why anticipatory adaptation is so problematic. It isn't until ideas are field tested that all the trade-offs and any unanticipated consequences are known. Climate-change adaptation policies can have unexpected negative consequences, among other things, for reducing future adaptive capacity (Hiers et al., 2016; Magnan et al., 2016). We suggest that for a change to be called an “adaptation,” a behavior needs to have experienced at least one generation of reproduction, whether that is biological or, much more likely in the context of climate-change adaptation, cultural reproduction. This perspective is actually aligned with early definitions of adaptation within the climate literature (e.g., Glantz, 1992;

Burton et al., 1993). Such reproduction allows for at least some of the trade-offs and unintended consequences to be played out so that a putative adaptation can be evaluated as to whether it is actually adaptive. We reiterate, however, that organisms and their environments are coevolving systems, as suggested by niche construction theory (Odling-Smee et al., 2003). Adaptation is a continuous process, and always relative to the other variants (e.g., ways of doing things) present in the population. Long live the Red Queen!

The more dynamic evolutionary understanding of adaptation fundamentally emphasizes the need to pay attention to variance. In this paper, we have discussed three distinct ways that variance matters for adaptation. First, variance (or diversity) in potential solutions to environmental problems represents the raw material from which selection shapes adaptation. Intuitively, the more possible solutions there are to choose from, the more likely that a better solution will be found. This suggests that we should think more about how to foster sources of variability for solutions to problems induced by climate change. Second, through analogy with the multivariate breeders' equation and the developing theory of cultural epistasis (Brown and Feldman, 2009; Yeh et al., 2019), covariance between linked traits can inhibit the adaptive response of a multi-trait phenotype even to strong selection. Consistent with findings that diverse teams tend to question implicit cultural assumptions and produce more innovative solutions to problems (Phillips, 2014; Page et al., 2019), we have suggested that behavioral and cultural diversity may play an essential role in weakening unnecessary linkages between cultural traits that may inhibit movement toward adaptive solutions. This cultural process is reminiscent of the increase in additive variance following population bottlenecks (Hansen, 2006). Third, variance in social structure is essential for permitting local adaptation, for ensuring the spread of cultural innovations, and for increasing the net benefit of cumulative culture for the population more generally (Whitehead and Richerson, 2009; Derex and Boyd, 2016; Steinert-Threlkeld, 2017; Centola, 2019).

These three roles for variance are all related to the processes through which adaptations are shaped. The fourth way that variance is essential for an evolutionary perspective on adaptation is for understanding the nature of adaptation itself and the willingness of individuals and communities to take up innovations that might prove adaptive. We have suggested that adaptation is ultimately a matter of management of environmental risk, a gambit to avoid Mayr's "non-random elimination" (Mayr, 1997, Pisor & Jones, this issue). While variance at the population level increases the potential adaptive response of the population, variance at the individual level (e.g., in access to resources) can be catastrophic. Reducing variance by accepting a trade-off with the mean is the essence of risk management. The very networks through which innovations diffuse are also essential components of risk-management portfolios of people in subsistence populations. We need to be aware of the functionalist trap (Ensminger, 1994) of equating current utility for design. While the social structures of subsistence populations may resemble the sorts of structures that promote the diffusion of innovations (e.g., Migliano et al., 2020; Derex and Boyd, 2016), this doesn't mean that this structure was selected for this purpose. There are multiple potential forces shaping social structure and the transmission of cultural traits. Central among these are asymmetries in population size or power across groups. In general, understanding the forces that shape the social structures, institutions, and behaviors we observe will aid us in predicting how these features will respond to changing environments.

The world is complex and there are many possible solutions to problems presented by the environment. Understanding the processes of culture change (e.g., where ideas/innovations come from, what their dynamics are once they enter a population) and selection, and having knowledge of what adaptations have emerged with respect to past problems (including social, political and economic aspects of environments), provides a powerful framework for evaluating the efficacy and viability of the planned "adaptations" policymakers wish to foster. This indicates an urgency

to the study of autochthonous adaptation in diverse settings: from remote subsistence groups to mega-cities, in the past and in the present. This includes the process of adapting to new policy environments, such as carbon emission caps, and exploring how and why such policies may be unstable. Documenting and understanding these adaptations, especially understanding how the adaptations feed back on the environment and induce trade-offs, should be a foundational feature of any attempts by policymakers or development partners to manage the deleterious effects of climate change. This perspective necessitates some humility on the part of planners and governments, as it acknowledges the fact that we still have much to learn about the dynamics of socio-ecological systems.

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