The ecological approach to culture

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Abstract:

The prevailing view in the literature treats cultural dynamics as fundamentally distinct from other ecological processes—governed by a second system of inheritance and requiring a separate set of theoretical foundations. Yet at its core, culture is simply an emergent outcome of interactions among individuals and with their shared environment—the very kind of phenomenon ecologists routinely study. In fact, in many ecosystems not considered cultural, such interactions do produce stable population differences, rapid innovations, informational changes, or even cumulative dynamics. These phenomena are more pronounced in cultural ecosystems, but they are not different in kind. Accordingly, we argue that cultural ecosystems should be studied through the same mechanisms as other ecosystems—ecological modifications, phenotypic responses, legacy effects, and ecological cascades. Different ecosystems may require specific methods or concepts, but not fundamentally different theoretical frameworks. The main strength of this deflationary view of culture lies in its parsimony. If culture is not fundamentally special, we can rely on the same robust and well-tested framework—namely, inclusive fitness theory—to understand human behavior in cultural ecosystems, just as we do for animal behavior more generally. Inclusive fitness theory, in turn, can help explain both (i) individual behavior in culturally rich ecosystems and (ii) how the interaction of such behaviors gives rise to the large-scale ecological patterns we call culture.

1. Introduction

The field of evolutionary social sciences is founded on the principle that evolutionary biology provides valuable tools for understanding and explaining social phenomena in humans. While this framework has traditionally been applied to biological traits and behaviors, culture was long considered outside the purview of evolutionary explanations, often seen as too complex or dynamic to be analyzed within the same framework. However, the past decades have witnessed a transformative shift with the emergence and growth of cultural evolution as a scientific field withing evolutionary sciences (Barrett, 2014; Boyd & Richerson, 1985; Boyer, 2018; Brown et al., 2011; Claidière et al., 2014; Henrich, 2015; Mesoudi et al., 2006; Nettle, 2009; Tooby & Cosmides, 1992). This integration has allowed researchers to examine cultural phenomena such as religion, technology, and social norms not as an anomaly but as an extension of evolutionary processes.

So far, the field of cultural evolution has mostly conceptualized cultural phenomena as a second system of inheritance, analogous to (and in many ways different from) genetic inheritance (Boyd & Richerson, 1985; Brown et al., 2011; Campbell, 1965; Cavalli-Sforza & Feldman, 1981; Dawkins, 1976; Durham, 1991; Henrich, 2015; Laland & Brown, 2011; Lumsden & Wilson, 2005; Mesoudi et al., 2006). Behaviors, practices, and ideas are transmitted across generations through processes such as observation, imitation, teaching, and other forms of social learning. This replicatory dynamic gives rise to a substantially autonomous process of cultural selection that explains the features of cultural phenomena such as their persistence, their creativity and their functionality.

While this approach, often called Dual Inheritance Theory (DIT), has been pivotal in integrating cultural phenomena into evolutionary science, it increasingly relies on concepts and theories that diverge from those of standard evolutionary biology (Claidière et al., 2014; Claidière & André, 2012; Cronk, 1995; Daly, 1982; Micheletti et al., 2022, 2023; Nettle, 2020; T. C. Scott-Phillips et al., 2011, 2011, 2014; Tooby & Cosmides, 1990; West et al., 2011). Many proponents of DIT have even called for an 'extended evolutionary synthesis' moving away from the core principles of inclusive fitness theory (Laland et al., 2015).

We believe this is an unnecessarily high cost to pay for the study of culture. Evolutionary biology offers a powerful way of thinking which compels researchers to explain phenomena using a concise set of mechanisms rooted in inclusive fitness theory (Williams, 1996). Here, we argue that we don't need to pay such a cost. We propose an alternative approach to cultural phenomena that eliminates the need for a separate system of inheritance or distinct principles. Instead, we argue that the same evolutionary framework that explains biological traits can also account for cultural phenomena effectively and cohesively.

Our approach begins with the observation that while cultural phenomena are often defined by their persistence and continuity across generations, they are equally marked by innovation and change. In some cases, individual behaviors display little variations across generations, yet in others, each generation diverges significantly from the one before, and these behaviors are primarily driven by individual adaptive goals. What defines cultural phenomena is not merely their persistence and continuity, but the broader dynamic in which the behaviors of earlier generations leave a lasting impact on the behaviors of subsequent generations. This intergenerational influence creates both continuity and change.

While this intergenerational influence is often seen as unique to culture, it is not. All organisms modify their environment—a process known as 'ecosystem engineering' (Hastings et al., 2007; Jones et al., 1994). Examples include: beavers building dams; earthworms aerating soil; coral reefs forming underwater structures used by other species; elephants modifying savanna landscapes by

uprooting trees; prairie dogs digging burrow systems that will be reused by other species; kelp altering underwater currents and light availability; fungi decomposing organic matter and changing soil composition; mangroves shaping coastal landforms and sedimentation patterns; and many other phenomena. These environmental modifications persist creating 'ecological legacies' that affect subsequent generations (Cuddington, 2011; Frauendorf et al., 2021; Hastings et al., 2007; Jordan et al., 2011; Nuttle et al., 2011; D. A. Perry et al., 2008). Organisms then adapt plastically to these altered conditions, —a process often called 'ecological response' (Sheridan & Bickford, 2011; Turner et al., 2003). This, in turn, may create 'ecological cascades'. For instance, beaver dams modify water flow, sedimentation, and nutrient distribution in streams (Carpenter et al., 1985; Estes & Palmisano, 1974; Ripple & Beschta, 2012). Altered water flow then creates wetlands, to which some species respond well (e.g., waterfowl). These changes ripple through trophic levels, influencing predators, prey, and even surrounding terrestrial systems.

Importantly, not all responses to ecological modifications are genetic adaptations; many are phenotypic adjustments driven by adaptive plasticity. When an organism encounters a modified environment—whether due to beaver dam construction or changes in vegetation—it can often adjust its physiology, behavior, or developmental trajectory to cope with these new conditions without requiring genetic change. Many non-human animals plastically modulate their behaviors to exploit the novel ecological niches created by human-induced rapid environmental change (Sih, 2013; Sol et al., 2008; Tuomainen & Candolin, 2011; T. F. Wright et al., 2010). For instance, raccoons have learned to open garbage cans, forage in dumpsters, and navigate human structures to find food.

These ecological processes are not limited to between species interactions. They also occur within individuals of the same species, just like cultural phenomena. For example, bowerbirds reuse materials like colorful stones from bowers built by other bowerbirds (Madden, 2008). Similarly, new termite colonies often occupy mounds left by their predecessors (Laidre, 2021a). Lemon ants inhabit "devil's gardens" in the Amazonian rainforest—monocultures of certain tree species that they have engineered and maintained over multiple generations, often persisting for centuries (Frederickson et al., 2005). Moreover, these legacies impact the behaviors of subsequent generations. For instance, the architectural decision of one generation of bees (helicoidal or flat stacked combs) can constrain the architectural decisions of subsequent generations, leading to some architectural traditions (Di Pietro et al., 2024). Similarly, terrestrial hermit crabs architecturally remodel shells. These modified shelters are reused by subsequent generations long after the original architect's death, and their presence or absence alter the life history of the populations (Laidre, 2019).

In these examples, the behavior of past generations affects the behavior of younger generations through ecological modifications and phenotypic ecological responses. Our point is that human cultures are no different. Humans constantly produce ecological modifications to fulfill their own adaptive goals: roads, houses, tools, jokes, words, novels, songs, religious beliefs (**Figure 1**). These cultural artifacts change the material, social, and informational ecology of others, altering the conditions in which future generations survive and develop. In response, new generations plastically respond to these modified environments, using them to pursue their own adaptive goals. Over time, these interactions generate cascading effects, mirroring ecological cascades observed in non-human ecosystems.

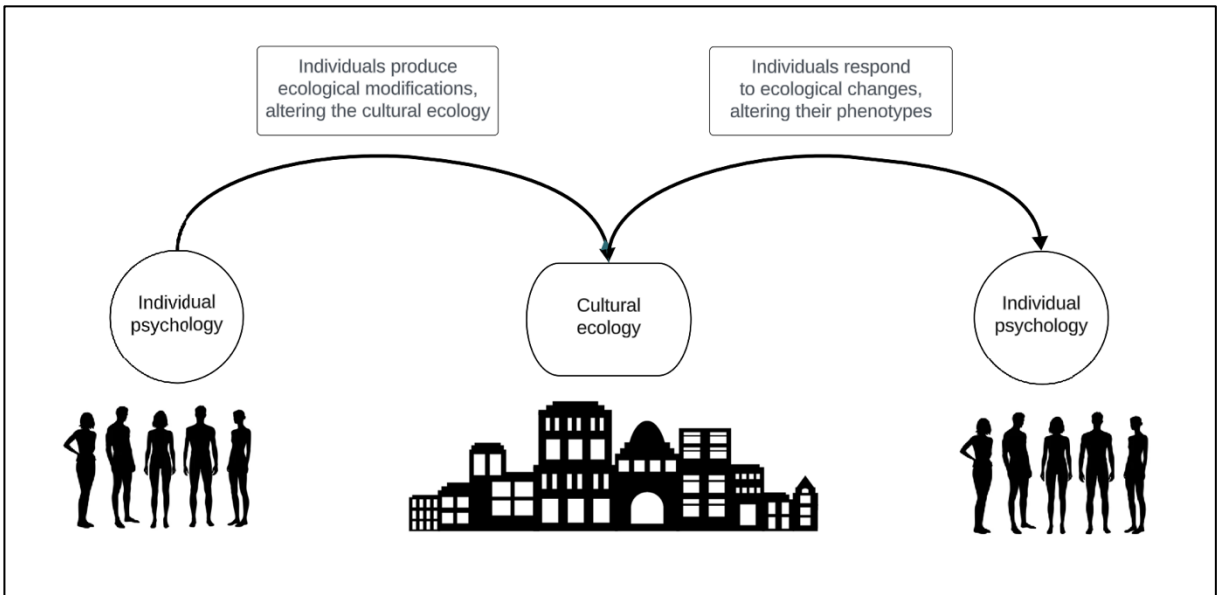

Figure 1: Ecological processes can explain why the behavior of past generations affects the behavior of younger generations. 1. Individuals from past generations produce ecological modifications; 2. These ecological modifications shape the environment of younger generations; 3. Individuals of younger generations respond to these ecological changes through phenotypic plasticity.

Importantly for the purpose of explaining cultural phenomena, individuals usually do not aim at replicating or imitating the ecological legacies that they find in their environments. Elephants do not try to imitate or replicate existing paths. They are just using what is most useful in their environment to achieve their adaptive goals (e.g. moving from one point to another in the most efficient way). Because elephants are behaviorally flexible, they have the option of ignoring existing paths (Gómez et al., 2023; Pfennig et al., 2010). If they choose to use these paths, it's because they have advantages: they're optimally laid out, and they've been maintained (branches spread apart, etc.). But individuals can nonetheless choose other paths or transform old paths (Blake & Inkamba-Nkulu, 2004; Shepard et al., 2013). Similarly, hermit crabs do not have to imitate others and use the shells they left in the environment. On the contrary, each individual crab chooses whether or not to use the shells produced by other individuals (Laidre, 2019).

The consequence of this ecological process is that individuals are most often not interested in faithfully imitating others. They are interested in acquiring food, helping their family, attracting cooperation partners, gaining status, manipulating others, avoiding pathogens, signaling their mate-value; and they can recycle, tweak, and selectively retain part of the phenotypic legacies of other individuals to fulfill these adaptive goals. The result of this process is a constant mix of re-cycling, up-cycling, down-cycling, innovation and accumulation of ecosystem modifications from one individual to the next. In other words, ecological processes do not constitute a system of inheritance.

Similarly, humans are not passive recipients of ecological modifications. They actively engage with, modify, and adapt to the cultural contexts they inhabit (Gweon, 2021; Micheletti et al., 2023; Morin, 2016; T. C. Scott-Phillips, 2022; Sperber, 1996; Sterelny, 2024; Sterelny & Hiscock, 2024). For instance, individuals innovate tools, reinterpret traditions, or negotiate social norms to suit their goals or solve local problems. Yet, sometimes, individuals preserve or recreate the legacies produced by past generations because, in some cases, such as communication systems (e.g. languages) or conventions (e.g. driving on the right), what is best for one generation is also best for a later one. As a result, individuals end up using the same items as earlier individuals—leading

to what could be conceptualized as an inheritance process. But most of the time, humans do not use exactly the same items, leading to cultural change (Claidière et al., 2018; Garland & McGregor, 2020; Karjus et al., 2020; Kirby et al., 2008, 2008; Osiurak et al., 2022; Zwirner & Thornton, 2015). Words are abandoned, syntax changes, fashions fade, technologies are replaced, novels are no longer read, cooler music emerges (Morin, 2016). A classic novel that was once a source of pleasurable entertainment is now used by the new generations as an instrument of social signaling (Bourdieu, 1984; Goffman, 1956). In essence, culture encompasses the ecological modifications individuals produce, their effects on others, and the adaptive responses they trigger.

Ecological processes do not instantly produce the rich diversity and complexity of cultural phenomena we observe today, as well as the key features that interest cultural evolution scientists such as tradition, innovation, cumulativity (Boyd & Richerson, 1985; Henrich, 2015; Mesoudi et al., 2006). Instead, these phenomena unfold over many cycles of ecological modifications, ecological legacies and ecological responses. It is the repetition of these cycles that eventually gives rise to cultural evolution.

The view developed here naturally converges with the adaptive perspective of human behavioral ecology and evolutionary psychology (André et al., 2023; Borgerhoff Mulder, 1991; Boyer, 2018; Cronk et al., 2000; Micheletti et al., 2023; Nettle, 2009; Tooby & Cosmides, 1992). In essence, the ecological approach to culture continues the inclusive fitness revolution. The inclusive fitness revolution has been about understanding biological phenomena from the point of view of the genes (Ågren, 2021; Dawkins, 1976; Hamilton, 1964; Rodrigues & Gardner, 2022; Trivers, 1971, 1974; Wilson, 1975). Over the past 50 years, inclusive fitness reasoning been successfully applied to all kinds of phenotypic traits: organs, brains, diseases, sexuality, parenting, eusociality, cooperation. It has expanded from physiological traits (i.e., evolutionary biology) to behavioral traits (i.e., behavioral ecology) to psychological mechanisms (i.e., evolutionary psychology). In this paper, we propose to further expand the inclusive fitness framework to cultural products (i.e. cultural evolution).

The paper is structured as follows. In Section 2, we establish the parallels between cultural and ecological processes, demonstrating that key cultural features—such as persistence, innovation, and cumulative change—arise from standard ecological mechanisms rather than a distinct system of inheritance. This section also examines how cultural dynamics operate through the same fundamental principles as other ecosystems, highlighting the role of ecological modifications, phenotypic responses, and ecological cascades in shaping cultural evolution. Section 3 bridges the gap between inclusive fitness theory and culture, explaining how cultural phenomena emerge from individuals pursuing adaptive goals in response to environmental modifications, without requiring a separate transmission system. Section 4 discusses the broader implications of this ecological approach, emphasizing the immense benefits of reclaiming inclusive fitness theory for the study of cultural evolution. Finally, in Section 5, we examine the implications of this framework for defining culture itself, proposing a revised definition that integrates cultural phenomena within the broader framework of ecology and evolution.

2. Cultural dynamics operate through the same fundamental mechanisms as the dynamics of other ecosystems

Ecological dynamics result from the interactions of many individuals, within a shared environment they can modify, and to which they can respond. While these dynamics can be complex and difficult to predict from individual actions alone, this complexity does not require departing from standard

evolutionary analysis (Ricklefs et al., 2014). Individual actions within an ecosystem should be understood through the lens of inclusive fitness theory, as all behavior must be, and the emergent properties of the ecosystem understood as arising from these actions.

The central claim of this paper is that cultural phenomena are simply a specific instance of ecological phenomena. Culture arises from the dynamics of particular ecosystems where some individuals have exceptionally high capacities to modify their environment and to respond to others' modifications in a flexible and open-ended manner. In such ecosystems, ecological dynamics drive profound and striking changes in both the shared environment and individual behavior. The magnitude of these effects may create the illusion that cultural phenomena are qualitatively distinct from standard ecological processes. Yet the underlying mechanisms are the same. Cultural ecosystems are, fundamentally, ecosystems, and the theoretical frameworks required to understand them—particularly inclusive fitness theory—are no different from those applied to other ecosystems.

To substantiate this claim, we will systematically examine key features frequently considered unique to cultural phenomena and demonstrate that they are not qualitatively distinct (see **Table 1**). Instead, they are well-documented in standard ecological contexts.

Our approach follows a structured framework:

1. We introduce a feature commonly regarded as specific to cultural ecosystems.
2. We show that this feature also exists in standard ecological processes, highlighting its continuity across cultural and non-human ecosystems.
3. When relevant, we analyze why this feature appears qualitatively distinct in cultural ecosystems, demonstrating that its perceived uniqueness stems from its greater magnitude rather than any fundamental difference.

For clarity, we use the term 'standard ecosystems' to refer to non-human ecosystems, while 'cultural ecosystems' designate human ecosystems whose dynamics—including information flow—produce particularly pronounced effects. This terminological distinction is purely practical, akin to differentiating between marine and terrestrial ecosystems; it does not imply a fundamental qualitative divide.

Typical properties of cultural ecosystems	**Similar instances of such properties in standard ecosystems**
Produce changes at a timescale faster than biological evolution (see section 2.1)	Many animals, such as migratory birds, adjust their migration timing based on seasonal shifts without requiring genetic evolution (Charmantier et al., 2008). Similarly, urban raccoons and pigeons adapt their foraging and nesting behaviors in response to human environments (Sih, 2013; Sol et al., 2008).(Dickemann, 1979; Paige & Paige, 2023; Strassmann et al., 2012)
Produce persistence and stability (see section 2.2)	Elephants create long-lasting paths that guide the movements of future generations (Blake & Inkamba-Nkulu, 2004). Bird colonies return annually to the same sites (Danchin & Wagner, 1997). Meerkats adopt the same behavioral convention as others.(Aarts et al., 2001; Burch, 2019)
Involve informational processes (see section 2.3)	Elephants' trails not only modify the landscape but also provide visible navigational information to others (Fishlock et al., 2016). Similarly, migratory birds follow established routes, learning from previous generations (Whitehead & Rendell, 2004).
Produces innovation and creativity (see section 2.4)	Crows craft hook-shaped tools to extract food (Hunt & Gray, 2004), and chimpanzees modify sticks to fish for termites (Bandini et al., 2020), showing creative problem-solving through individual innovation.

Change individual phenotype (see section 2.4)	Early-life stress in mammals affects long-term behavior and physiology, mirroring human responses to early hardship (Snell-Rood & Snell-Rood, 2020).
Are cumulative (see section 2.5)	Coral reefs accumulate layer by layer, forming massive structures over time, just as oak forests require multiple plant generations to reach maturity (Connell & Slatyer, 1977)
Produce complex and functional innovation	Bowerbirds construct intricate courtship structures, adapting them with new materials over time (Madden, 2008).
Produce emergent properties	Starling murmurations result in coordinated movement patterns that no single bird controls. Similarly, cooperative hunting in wolves and dolphins produces complex group behaviors that increase hunting efficiency (Packer & Ruttan, 1988).
Constrain individual behavior	(Alvard, 2004; Chagnon, 1988; Cronk et al., 2019; Cronk & Gerkey, 2007; Quinlan & Flinn, 2005)Many species, such as seabirds, return to the same breeding sites, not by genetic encoding but because previous generations' choices shape their ecological options (Danchin & Wagner, 1997).
Produce contingency and path dependence	The architectural decision of one generation of bees (helicoidal or flat stacked combs) can constrain the architectural decisions of subsequent generations, leading to some architectural traditions (Di Pietro et al., 2024). Many species, such as seabirds, return to the same breeding sites (Danchin & Wagner, 1997).

Table 1. Typical properties of cultural ecosystems and their analogs in standard ecosystems. Due to space constraints, the last four properties are not discussed in the text.

2.1. Standard ecological dynamics produce changes at a timescale faster than biological evolution

One of the most striking properties of culture—arguably central to its definition—is that it consists of determinants of individuals' phenotype that are not genetic in origin and can therefore change at a timescale faster than evolution by natural selection. Yet, this property is not unique to culture. Standard ecological dynamics also lead, systematically and on a large scale, to modifications of both individual phenotypes and their environment at timescales far shorter than those of natural selection. These modifications rely on a fundamental and widespread biological mechanism: phenotypic plasticity. Cultural effects are nothing but one specific instance of this broader phenomenon.

All organisms adjust their behavior and physiology without genetic alterations, relying on specialized evolved mechanisms (Charmantier et al., 2008; Miner et al., 2005; Vinton et al., 2022). Such phenotypic ecological responses allow organisms to respond flexibly to immediate environmental challenges. For instance, many bird species have adjusted their migration timing to align with shifting seasonal patterns, such as warmer winters or changes in food availability, helping them synchronize their movements with resource distribution.

All cultural phenomena, including major shifts in societal attitudes and preferences, are ultimately instances of phenotypic plasticity. For instance, Americans and Europeans hold contrasting views on the welfare state (Alesina & Glaeser, 2004). In Europe, redistributive policies enjoy broad support, whereas in the United States, support is much lower. Experimental evidence sheds light on the psychological mechanisms behind these differences. When placed in identical situations with the same information, Danes and Americans exhibit strikingly similar cooperative behaviors (Aarøe & Petersen, 2014). Both follow a cooperative psychology: they are willing to cooperate if others do the same but tend to defect when they perceive others as defecting. The key difference lies in the ecological information available in each region. This variation in attitudes is a clear

example of psychological phenotypic plasticity—individuals adjust their behaviors and preferences in response to the informational cues provided by their local environment.

What gives human ecosystems the appearance of requiring a distinct theoretical framework boils down to two key quantitative factors:

1. *The scale of human ecological modifications to the environment and the cascading consequences of shifts in human attitudes and preferences*. Unlike other species, humans do not simply adjust their cooperative tendencies, risk-taking behaviors, or social structures in response to environmental cues. They construct institutions, belief systems, religions, literature, and art that encode and amplify their psychological states, resulting in far-reaching and highly conspicuous effects of phenotypic plasticity. These cultural outputs act as environmental modifications that, in turn, influence individual behavior, further magnifying the impact of phenotypic plasticity.

2. The breadth of phenotypic traits subject to plasticity and the precision with which environmental factors shape behavior. In species with extensive plastic responses and large-scale learning capacities, the range of potential phenotypic modifications is vast. A defining feature of human plasticity is the ability to adjust behavior based on fine-grained environmental information. This is not a unique process but rather an extension of phenotypic plasticity, albeit with particularly far-reaching consequences—manifesting in the diversity of languages, technologies, and cumulative cultural productions. Even here, the distinction is one of scale, not mechanism. Just as non-human species adaptively respond to environmental cues—using them when beneficial, ignoring them when irrelevant, and refining them when effort is worthwhile—humans respond to informational environments, adjusting their behaviors accordingly.

Thus, human ecosystems are not qualitatively distinct from other ecosystems. They are merely an extreme case of ecological dynamics, where plasticity operates on a vast scale and where environmental modifications—including informational environments—become self-reinforcing, producing cumulative and transformative effects.

2.2. Standard ecological dynamics produce persistence and stability

Another key characteristic of culture is its ability to create stable differences across populations and environments that persist across generations. Artifacts such as books, buildings, and paintings endure long after their creators are gone, while social structures like patrilineal systems and religious beliefs continue to shape societies despite the passing of individual adherents. This persistence is often regarded as a defining feature of culture—one that is frequently cited as justification for the notion of a separate system of inheritance operating alongside genetics.

Yet, the same persistence is widespread in other ecosystems, where it is not seen in the scientific literature as warranting a distinct system of inheritance. Burrows, termite mounds, or coral reefs can endure for generations after their original builders have died, continuing to shape the environment and influence the behavior of future generations (Cuddington, 2011; Frauendorf et al., 2021; Hastings et al., 2007; Jordan et al., 2011; Nuttle et al., 2011; D. A. Perry et al., 2008). Social legacies also arise naturally. Bird colonies, for instance, return annually to the same sites, creating stable social structures as new generations benefit from established breeding, feeding, and nesting grounds.

Even conventions can persist over time. As observed in meerkats, neighboring groups develop consistent differences in their activity patterns, such as the time of day they emerge from their

burrows (Thornton et al., 2010). These differences persist over multiple years, even as group members change entirely due to mortality and migration, indicating that past behaviors create expectations and shape future interactions. Similarly, among chimpanzees, specific local forms of hand-clasping during grooming become ingrained through repeated interactions (S. Perry et al., 2003). Once established, these conventions persist because individuals adjust their behavior based on past interactions and learned expectations (Formaux et al., 2022; Goldsborough et al., 2023; Van Leeuwen, 2021).

In humans, the same principle applies. Anything left in the environment by previous generations can be used by future generations and shape their behavior and preferences. A church, a road, the availability of a novel in a library, the existence of computers, or books on calculus are all instances of such legacies with sufficient durability to influence generations long after their original creators have disappeared. Here too, what sets humans apart is only the sheer quantity of stable legacies and the scale of their effects. The same properties that amplify the impact of ecological dynamics beyond genetic influences in humans also make it possible for large, finely detailed, and persistent non-genetic differences to emerge. Yet, this is not evidence of an independent system of inheritance but simply the inevitable outcome of interactions among organisms with high phenotypic plasticity and a strong capacity to modify their environment.

2.3. Standard ecological dynamics produce informational changes

One might think that standard, non-cultural ecological dynamics are solely about material effects, while culture is distinct because it involves informational dynamics. This distinction, however, is not warranted. Ecological dynamics can also be informational. For instance, when an elephant creates a path through a forest, it not only alters the material landscape but also provides visible information about the best way to navigate a difficult area (Blake & Inkamba-Nkulu, 2004; Fishlock et al., 2016). Similarly, a bird using a migratory route makes the itinerary more salient, effectively enriching the informational environment for others (Whitehead & Rendell, 2004). Another example comes from bowerbirds: when an individual discovers that colorful stones enhance its courtship display, it changes the informational landscape for others by making this resource more noticeable and relevant for mating success (Madden, 2008). More broadly, an animal can use ecological modifications for all kind of purposes such as finding the right nesting or the best foraging site, auditory pattern that others individuals have invented (Aplin, 2019), and "games" invented by others (S. Perry et al., 2003; Robbins et al., 2016; van Leeuwen et al., 2020).

Communication, in particular, is a great instrument of informational ecological modification, aimed at altering a specific aspect of one's environment—namely, the mental states of others (Davies et al., 2012). In courtship, for instance, communication aims to persuade a potential mate to accept the sender as a reproductive partner, ensuring reproductive success. In competitive interactions, aggressive signals are used to deter rivals or assert dominance, influencing the receiver's behavior to avoid costly conflicts. Parent-offspring communication, such as begging calls, induces parents to deliver food, enhancing offspring survival. Similarly, territorial marking conveys dominance and ownership, reducing the likelihood of direct confrontations.

Here too, what sets cultural ecosystems apart is the scale of the phenomenon, not its nature. Human information dynamics operate on a much larger scale (T. C. Scott-Phillips, 2022). We continuously introduce new information into the environment—new ideas, words, technologies—reshaping the informational landscape for others. Yet, the nature of these dynamics is not qualitatively different from other ecological information processes. While human communication is enriched and made more flexible by social cognition—the ability to understand, predict, and influence others' mental states—the basic nature of the process remains the same: the sender of

the signal aims to achieve an effect in the receiver's mind, while the receiver interprets and uses the signal in a way that aligns with their own interests (T. Scott-Phillips, 2014).

Importantly, while standard ecological dynamics involves information processes, not just material processes, conversely, cultural dynamics are not solely about information. Cultural ecosystems, like any other ecosystems, also change through material and structural transformations. Just as beaver dams or coral reefs alter water flow and reshape the physical environment, influencing the behavior and life histories of individuals within them, human-driven material changes shape social structures and individual behaviors— and this, too, is culture. For instance, agricultural practices such as irrigation and deforestation leave lasting legacies. In Mesopotamia, extensive irrigation gradually increased soil salinity, reducing agricultural productivity and contributing to progressive aridification, which in turn weakened early civilizations (Shahid et al., 2018). In ancient Greece, large-scale tree cutting for land clearance and shipbuilding led to soil erosion and deforestation, ultimately depleting agricultural capacity and undermining economic stability (Harper, 2017). These cases illustrate how human modifications to the material environment create enduring legacies that shape behavior and cultural evolution for generations (Boivin et al., 2016). More broadly, agricultural practices—through their effects on technological and economic development, natural ecosystems, and pathogen transmission—can explain key patterns of cultural evolution and the persistence of cultural differences (Diamond, 1997). In the end, there is no difference between standard ecological dynamics and cultural dynamics: both involve material and informational processes.

2.4. Standard ecological dynamics produce innovation and creativity

Another striking feature of cultural dynamics is their creativity and open-endedness, leading to behavioral changes that seem to go far beyond what was originally "planned" by the biology of our species. This, too, is an intuitive reason why culture is often thought to require a theoretical foundation distinct from standard biology and ecology. Yet, even here, this distinction is unwarranted. It is true that classic examples of ecological dynamics, such as beaver dams or coral reefs, largely result from rigid genetic programming in individual behaviors or physiology. However, standard ecological dynamics can also be creative and innovative, driven by specialized mechanisms of adaptive plasticity.

In recent years, a wealth of studies has shown that non-human animals (especially birds, cetaceans and primates) constantly create and invent new behaviors and new tools, thanks to their specialized cognitive capacities (Kolodny et al., 2015). For example, juvenile New Caledonian crows spontaneously manufacture and use tools without prior human demonstration. Similarly, naive chimpanzees spontaneously started using sticks to scoop floating bread from a container of water (Bandini et al., 2020). Moreover, non-human animals excel at creatively repurposing resources within their environments (Lehtonen et al., 2023; Van Casteren et al., 2012). Bowerbirds, for instance, incorporate plastic chips, coins, nails, rifle shells, or pieces of glass into their bowers to attract mates (Madden, 2008). Similarly, apes reuse cotton sheets, and shredded newspaper to build nests that help them sleeping comfortably (Anderson et al., 2021). These examples show that ecological dynamics, just like cultural dynamics, can produce flexible and innovative responses to environmental challenges.

Here too, what sets cultural ecosystems apart is the quantitative scale of their innovation and open-endedness, not a qualitative difference. Humans possess more generative dispositions, more capacities for cognitive control, social cognition, inferential learning and so on (see below **section 3.2**) (Osiurak & Reynaud, 2020; T. C. Scott-Phillips, 2022; Tomasello, 2022). These capacities allow them to achieve goals, shaped by natural selection, with extraordinary flexibility—adapting their

strategies based on circumstances, available tools, environmental resources, informational cues, and the actions of others around them. This open-ended nature of human cognition leads to particularly rich and complex cultural dynamics. Yet, once again, a quantitative difference does not justify the need for a separate theoretical framework.

2.5. Standard ecological processes change individuals' phenotype, not only their environment

Another striking aspect of cultural dynamics is that they do not merely change our environment—they change us. We are not the same as past generations, and we are not the same depending on where we are born and where we live. These effects can be physiological, influencing traits such as height, longevity, or life history, or cognitive, shaping our mentalities, preferences, beliefs, and knowledge. Yet, this is not unique to cultural dynamics—it is found in all ecological dynamics. Ecologically driven phenotypic modifications occur whenever individuals alter the environment in ways that change the biological or cognitive states of others. A classic example is the milk-bottle-piercing behavior observed in England, where some birds learned to access cream by puncturing bottle tops (Sherry & Galef, 1984). This innovation not only allowed them to exploit a new resource but also altered the behavior of observing birds, creating lasting cognitive legacies. Another example is social competition and social inequalities. Inequalities in resource access, social status, and inherited wealth shape individual phenotypes by influencing the costs and benefits of different behavioral strategies through developmental plasticity (Ilany & Akcay, 2016; Mousseau & Fox, 1998; Murray et al., 2008; Snell-Rood & Snell-Rood, 2020; Strauss & Shizuka, 2022). Lower-ranking individuals often experience chronic stress due to resource scarcity and social competition, leading to elevated cortisol levels, which in turn increase vigilance, reduce exploration, and alter social engagement. In contrast, dominant individuals with stable resources tend to have lower stress levels, greater risk tolerance, and more proactive social and resource-acquisition strategies.

In humans, embodied legacies will often manifest as lasting behavioral or physiological adaptations resulting from early-life experiences. A classic example is seen in individuals who experience significant early stress, such as a lack of parental support or insufficient energetic intake. These conditions can trigger developmental adjustments, leading to reduced physical growth and the adoption of stress-responsive strategies aimed at enhancing resilience and survival in challenging environments (Belsky et al., 1991; Ellis et al., 2009; Frankenhuis et al., 2016). These adaptive strategies, while beneficial in harsh conditions, can persist throughout an individual's life, influencing behavior, health, and social interactions (Petersen & Aarøe, 2015). At the population level, such embodied legacies can have far-reaching effects. For instance, during and after World War II, the severe famine in Germany profoundly impacted the development of children. These children exhibited lower levels of health as adults, reflecting the long-term physiological consequences of early malnutrition. Additionally, they exhibited reduced levels of social trust that were detectable decades later, and probably impacted the societal dynamics of post-war Germany (Kesternich et al., 2020).

2.6. Standard ecological dynamics are cumulative

Cumulative culture is often presented as a species-specific trait that defines what makes humans unique and places us in a distinct evolutionary dynamic. Yet, here too, cumulative effects are also found in other ecological dynamics. In standard ecology, cultural accumulation simply goes by another name—it is called 'ecological succession' (Ricklefs et al., 2014). After the emergence of a new land the structure of an ecological community change over time, with microorganisms and plants (lichens and mosses) first, and then grassy stage, smaller shrubs, and trees when more resources have accumulated in the environment (Connell & Slatyer, 1977; Emery, 2010). Coral reef

formation is another example: coral polyps build calcium carbonate structures over generations, resulting in massive reef systems. Similarly, earthworm activity over generations leads to soil aeration and nutrient cycling, cumulatively enhancing soil fertility and influencing plant growth.

In the same way, human cultures build on the accumulation of the legacies produced by other individuals (on wealth legacies see Borgerhoff Mulder et al., 2009; on technological legacies see Diamond, 1997; Mokyr, 1992). These legacies can be seen as a capital of resources, knowledge and social relationships that individuals can use to modulate their strategies (André & Baumard, 2020). This process is an instance of ecological succession in the sense that some individuals have modified the environment, which now contains intellectual as well as social, physical capital that was not present before, enabling other individuals to perform actions that were not possible before (just as before lichens modified rock, it was not possible for mosses to establish themselves). Just as oak forests require a large number of preliminary stages involving hundreds of generations of different plants that modify the environment and enrich it, so sophisticated kayaks, writing and printing require a large number of preliminary stages involving hundreds of generations of different individuals that modify the environment and enrich the informational environment of humans (Diamond, 1997; Mokyr, 1992).

2.7. Conclusion: cultural ecosystems are one type of ecosystem among others

Taken together, the above discussions show that the properties often claimed to be unique to culture are, in fact, widely found in the dynamics of virtually any ecosystem. Like cultural dynamics, ecological dynamics can drive rapid and profound changes in individual phenotypes, create lasting non-genetic differences, accumulate over time, involve information exchange and behavioral innovations, and give rise to emergent properties.

The central argument of this article is that this resemblance is not merely a superficial similarity or an intellectually appealing metaphor. The reason every characteristic of cultural phenomena has an equivalent in standard ecological phenomena is that cultural ecosystems are, quite simply, ecosystems. Human beings are an integral part of their ecosystem, actively modifying it and responding to it with adaptive phenotypic plasticity. And nothing in these interactions—whether between humans themselves or between humans and other components of their ecosystem—is fundamentally different from interactions in other ecosystems (see **Table 1**). Human ecology, and therefore human culture, obeys the same fundamental theoretical principles as ecology in general, and uses the same concepts.

Concept	Definition	Examples in standard ecosystems	Examples in cultural ecosystems
Adaptive plasticity	The ability of an organism to modify its physiology, behavior, or development in response to environmental conditions, enhancing survival and reproduction.	Bird species adjusting migration timing in response to climate shifts, as warmer winters lead to earlier breeding seasons and altered flight routes (Charmantier et al., 2008)	Changes in risk-taking behavior in response to socioeconomic conditions. Individuals in resource-scarce environments tend to prioritize short-term gains, while those in stable, affluent environments exhibit greater long-term planning and investment in education and relationships (Pepper & Nettle, 2017).
Ecological modification	A change an organism induces in its environment—whether physical, social, or informational—that alters	Elephants modifying savanna landscapes by uprooting trees, which changes vegetation composition, affecting biodiversity and the distribution	In ancient Greece, large-scale tree cutting for land clearance and shipbuilding led to soil erosion and deforestation, ultimately depleting agricultural capacity, undermining

	conditions for itself or others.(Aarts et al., 2001; Burch, 2019)	of herbivores and predators (Blake & Inkamba-Nkulu, 2004).	economic stability and changing Greek culture (Harper, 2017).
Ecological response	The behavioral, physiological, or developmental adjustments organisms make in reaction to ecological modifications, either through genetic or phenotypic change.	Urban pigeons and raccoons adapting their foraging behavior to human environments by using artificial structures for nesting and scavenging food from human waste, rather than relying on natural food sources (Sih, 2013; Sol et al., 2008).	The adoption of new agricultural practices in response to climate change, such as shifts from rain-fed to irrigation-based farming, affecting settlement patterns and economic structures (Diamond, 1997)
Legacy effects	The long-term influence of past ecological modifications that persist beyond the original modifier and continue to affect future generations or populations, either through genetic or phenotypic change.	In meerkat populations, neighboring groups develop stable differences in their foraging schedules, with some groups consistently emerging from their burrows later than others (Thornton et al., 2010). These patterns persist across generations, even as individual group members are replaced.	The persistence of legal institutions over generations, shaping social structures and individual behaviors long after their original architects have disappeared (Ostrom, 1990).
Ecological cascade	A chain reaction of ecological changes triggered by an initial modification, where successive responses ripple through the ecosystem, either through genetic or phenotypic change.	The big-headed ants disrupted the mutualistic relationship between native ants and the dominant whistling-thorn trees, leaving the trees vulnerable to elephant browsing. This increased browsing led to more open landscapes with higher visibility, which, in turn, reduced the hunting efficiency of lions on their primary prey, the plains zebras (Gaynor, 2024; Kamaru et al., 2024).	The introduction of cattle domestication in Africa led to shifts from matrilineal to patrilineal descent systems, altering inheritance rules, gender roles, and societal structures (Holden & Mace, 2003; H. Kaplan et al., 2000)

Table 2. Key ecological processes common to both biological and cultural evolution

There is hence no justification for creating a separate theory to study cultural phenomena, any more than a special theory is needed to study lake ecosystems or boreal ecosystems. While specific methods and concepts may be necessary for different types of ecosystems, this does not imply the existence of multiple ecologies or fundamentally different theories.

3. Understanding cultural ecosystems through the lens of inclusive fitness theory

The dynamics of an ecosystem, cultural or otherwise, emerge from the combined actions of the individuals within it—both their interactions with the abiotic environment and their interactions with one another. To analyze any focal feature of an ecosystem, three key steps are required:

1. Identify the individuals whose actions shape this feature, influencing its fine-grained properties.
2. Characterize the logic of their actions through the lens of inclusive fitness theory—that is, identify the adaptive goals individuals are pursuing when they act in ways that shape this feature.

3. Understand how these individual actions interact with one another and with the abiotic environment to produce the feature.

Consider for instance the case of a beaver dam and the meadow it creates (Johnston, 2015; J. P. Wright et al., 2002). The function of dam construction is not to shape wetlands or benefit the broader ecosystem; rather, each individual is pursuing its own adaptive goal—creating a stable aquatic environment that provides protection from predators and access to food. By constructing dams, beavers raise water levels, flooding surrounding areas to create deeper ponds where they can build lodges and navigate safely. However, while this behavior benefits beavers, it also introduces conflicts of interest with other species. For instance, fish that require fast-moving streams may struggle to survive in the newly created still waters, while terrestrial plants and animals may experience habitat loss due to flooding.

At the same time, beaver activity generates new ecological opportunities. Muskrats frequently burrow into beaver lodges or build their own small dams, further modifying water flow. Bacteria and aquatic invertebrates break down organic material trapped by the dam, altering water chemistry and nutrient cycling. Over time, these ecological modifications extend far beyond the beavers' original goals. As abandoned ponds gradually fill with sediment, they transition into meadows, creating a new ecological landscape that persists long after the beavers have left. These legacy effects reshape the environment for future generations of beavers and support an entirely different set of species, from amphibians thriving in the remaining wetlands to grazing mammals benefiting from the newly formed meadows.

Crucially, beaver dams are not the product of a single individual but of multiples individuals. While each beaver acts independently, multiple individuals often contribute to reinforcing and maintaining the same dam over time, sometimes across successive generations. This interplay between individual adaptive behaviors, collective construction, and long-term ecological transformations illustrates how ecosystems emerge from the actions of multiple agents pursuing their own goals, often leading to complex and sometimes unintended ecological outcomes.

Since our claim is that cultural ecosystems are ecosystems like others, it follows that understanding a cultural phenomenon also requires the same steps. Consider the example of a church such as Notre Dame de Paris. The building is not the result of a singular individual but rather the product of the actions of many individuals pursuing different goals, each acting within their own adaptive strategies (Duby, 1983; Le Goff, 2009). To simplify, we can distinguish several key motivations: a large portion of the Parisian population saw the construction of the cathedral as a way to demonstrate divine power, reinforce belief in supernatural monitoring and encourage moral discipline—illustrated, for example, by the tympanum depicting the Last Judgment. The deacon of Paris, Maurice de Sully, and the clergy sought to assert the Church's influence, while the King of France, Louis VII, and later Philippe Auguste, supported the project to reinforce Paris's status as a political and religious center of the kingdom (Bruzelius, 1987). Also, for the monarchy, Notre Dame was not just a religious symbol but also a political statement, demonstrating the wealth of the crown, the king's Christian virtues, and his role in upholding divine order. The prévôt des marchands and the wealthy bourgeoisie saw Notre Dame as an opportunity to increase the prestige of Paris, which in turn boosted commerce and civic pride. Pilgrims and ordinary believers provided a significant share of the funding through alms, donations, and special collections in exchange to special interactions with supernatural powers (through the relics) and an increase in moral reputation (through the indulgences). Each of these actors contributed to the cathedral's construction, but building Notre Dame itself was not their goal—each individual was pursuing their own fitness-related interests, whether in status, cooperation, power, or religious devotion.

Beyond its original purpose, Notre Dame created new ecological opportunities. Guilds of artisans and craftsmen viewed the cathedral's construction as an economic and social opportunity, securing employment, prestige, and professional recognition through their craftsmanship in stonework, stained glass, and sculpture. The cathedral also became a focal point for civic life (markets, public meetings, royal ceremonies).

The construction of Notre Dame de Paris took place within a specific cultural ecology, shaped by the ecological modifications produced by earlier generations. For instance, the cathedral's design reflects legacies from earlier periods, such as the cruciform ground plan, modeled after Roman basilicas, and the belief in punishment in the afterlife, visible in the tympanum. However, these ecological innovations were not passively accepted. They also evolved in response to technological and economic changes in the ecology. One major transformation was the architectural revolution enabled by technological innovations such as ribbed vaulting, pointed arches, and flying buttresses, which allowed for taller, more luminous structures (Gimpel & Barnes, 1983). Another significant shift—also facilitated by technological progress and rising living standards—was a change in psychological priorities, as people's concerns moved beyond material survival toward long-term moral and spiritual development (Baumard et al., 2022; Morris, 1987). This led to an increasing emphasis on personal piety, confession, and moral responsibility, culminating in the doctrinal formalization of Purgatory (Le Goff, 1986; Vauchez, 2010). This transformation is visible in the tympanum of Notre Dame, where, unlike earlier depictions that divided souls strictly between Heaven and Hell, intermediate figures appear in states of uncertainty, reflecting the growing belief in Purgatory as a transitional space for purification. The evolution of Notre Dame's architecture and iconography thus illustrates how cultural legacies persist but are continuously reshaped by new ecological conditions.

Over time, Notre Dame took on entirely new meanings and functions, detached from their initial religious intent (De Saint Pulgent, 2023). In the 19th century, architect Viollet-le-Duc led a dramatic restoration, reshaping the cathedral to align with a romanticized vision of the Middle Ages, rather than strictly preserving its historical authenticity. Around the same time, Victor Hugo's The Hunchback of Notre Dame transformed the cathedral into a literary and cultural icon, using it as the backdrop for a popular novel that revived public interest in Gothic architecture. Today, Notre Dame is no longer primarily a religious symbol but a global icon, serving as a national emblem of France, a major tourist attraction, and a site of cultural heritage (De Saint Pulgent, 2023). Most visitors are not motivated by supernatural punishment; instead, they engage with their own vision of Notre Dame, whether as an artistic and architectural wonder, a historical artifact, or a place of contemplation and spiritual inspiration. This is evident in debates over restoration choices—such as whether to reintroduce the original colors on the tympanum—where different stakeholders interpret its significance through competing perspectives.

Crucially, Notre-Dame itself is not, in any meaningful sense, an adaptation. First, it is a joint product of many individuals with diverse and sometimes conflicting goals, rather than a singular adaptive strategy. Second, what is adaptive is not the cathedral itself, but the motivational and cognitive systems that led to its creation—such as the need to enhance status (the Archdeacon), moral reputation (the King), cooperative interaction (the people), or economic gain (the craftsmen). Notre Dame is only a joint phenotypic expression of these adaptations.

As visible in these examples and in the three steps above, adaptationist thinking and inclusive fitness theory is just as central to understanding cultural phenomena as it is to explaining any animal behavior—and, more broadly, any biological process. However, this does not mean that the properties of culture can be directly deduced from a simplistic application of inclusive fitness theory. The causal link between inclusive fitness principles and the properties of an ecosystem,

cultural or otherwise, is almost always subtle and indirect (André et al., 2023; Baumard, Fitouchi, et al., 2023). Yet, this causal link does exist, and recognizing it provides a coherent framework for interpreting ecological phenomena.

In the following sub-sections, we will explore the subtleties of this causal link in the specific case of cultural ecosystems. We will introduce six key principles that characterize how the logic of biological adaptation—rooted in inclusive fitness—operates within cultural ecosystems and ultimately shapes cultural phenomena. This will allow us to see that, however subtle and indirect this link may be, the insight provided by adaptationist reasoning remains just as illuminating and essential for understanding culture as it is in the rest of biology.

3.1. Cultural phenomena are not produced directly by natural selection, but by proximate adaptive mechanisms designed to achieve intermediate fitness goals

The evolutionary approach to animal behavior, whether in a cultural or a standard ecosystem, does not claim that individuals directly seek to maximize their inclusive fitness when making decisions. Instead, it argues that individuals rely on proximate mechanisms—physiological and cognitive systems—that have been shaped by natural selection to produce behaviors that enhanced inclusive fitness in ancestral environments (see **Figure 2**).

This distinction between ultimate (evolutionary) explanations and proximate (psychological) mechanisms is crucial. Ultimate explanations describe why a trait or behavior evolved—its function in promoting survival and reproduction—while proximate explanations describe how the behavior is generated in real-time by an organism's cognitive and physiological systems (Al-Shawaf, 2024; Cosmides & Tooby, 1987; T. C. Scott-Phillips et al., 2011). Animals do not seek to pass on their genes; rather, they experience hunger, fear, sexual attraction, or parental attachment—proximate mechanisms that guide behaviors in ways that increase inclusive fitness. This distinction is especially relevant to cultural evolution. Individuals do not design institutions, technologies, or traditions with the proximate goal of maximizing fitness.

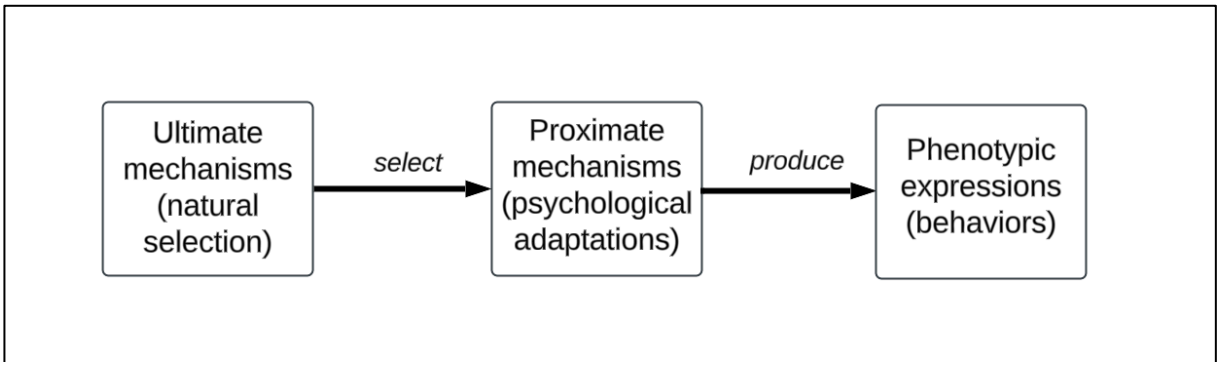

Figure 2: Individuals rely on proximate mechanisms—physiological and cognitive systems—that have been shaped by natural selection to produce behaviors that enhanced inclusive fitness in ancestral environments

3.2. Cultural phenomena are often produced by adaptive biological mechanisms that are flexible and generative, rather than rigid and stereotyped

A key challenge in applying the inclusive fitness framework to cultural evolution is that cultural phenomena exhibit significant variability—they differ across societies, change over time, and are shaped by environmental and historical contingencies. This variability might seem difficult to reconcile with traditional evolutionary explanations, which often focus on fixed, heritable traits.

One crucial distinction in evolutionary theory is between an adaptation and its phenotypic expression. This distinction is especially important in the case of plastic adaptations, where a single evolved mechanism can produce a wide range of phenotypic outcomes depending on environmental conditions (see **Figure 3**). An adaptation refers to an evolved trait—whetherphysiological, cognitive, or behavioral—that was shaped by natural selection because it conferred a fitness advantage in ancestral environments. However, this adaptation does not produce a fixed outcome. Instead, it operates as a developmental or psychological mechanism that generates context-dependent phenotypic expressions. For example, the human cooperative system is a universal adaptation, but its phenotypic expression varies—one person might cooperate a lot, another slightly less, and another not at all, depending on individual differences and environmental factors.

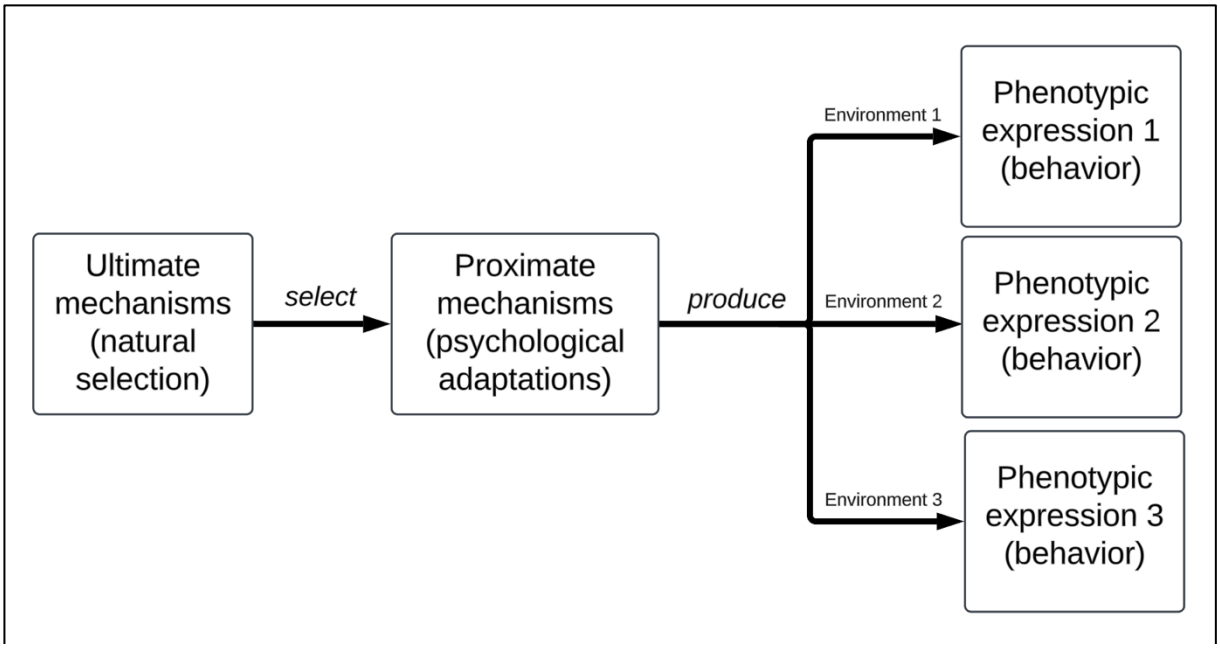

Figure 3: A single evolved mechanism can produce a wide range of phenotypic outcomes depending on environmental conditions

Moreover, not all adaptations produce rigid, pre-determined outputs. Many function as generative adaptations, meaning they achieve adaptive goals not by specifying a single fixed response, but by generating variable, context-dependent solutions to recurring challenges. A clear example of this is the adaptive immune system, which does not encode a predetermined defense against specific pathogens but instead creates novel immune responses tailored to the particular threats an individual encounters. Each response is unique, yet the underlying system is an adaptation shaped by natural selection.

This principle applies not only to immune responses but also to cognitive and behavioral traits. Many evolved systems do not specify a single fixed behavior but rather provide the capacity to generate variable solutions to recurring adaptive problems. For example, a spider's ability to build a web is an adaptation, but each web is different, shaped by local conditions such as the arrangement of branches, rocks, and wind exposure. The mechanisms guiding web construction remain products of natural selection, even though the specific web structure is variable. In the same way the construction of elaborate bowers by male bowerbirds is an adaptive behavior shaped by sexual selection. However, each individual bowerbird creates uniquely designed bowers based on locally available resources—materials such as colored objects, berries, feathers, and stones—as well as environmental constraints like predator presence and competition from rivals.

It is worth emphasizing that these flexible and innovative responses are fundamentally rooted in evolved proximate mechanisms (Tomasello, 2022). What natural selection does is to set fitness-goal (implemented as preferences), leaving the individual some freedom to select the best way to meet these objectives, using the cognitive tools at its disposal (Fawcett et al., 2013; Nettle & Scott-Phillips, 2023; Osiurak & Reynaud, 2020; Singh, 2022; Taborsky & Oliveira, 2012; Tooby & Cosmides, 1992). To describe the capacities involved in these innovative behaviors, cognitive psychologists use the terms 'goal-oriented behaviors' or 'agentic behavior' (Tomasello, 2022): genes do not code for specific behaviors, but for higher-level adaptive goals (e.g., food, status, partners, information) and for specialized cognitive capacities (e.g., mental rotation, motor cognition) whose function is to enable individuals to achieve their goals flexibly (Sterelny, 2001; Tomasello, 2022) (see **Figure 4**).

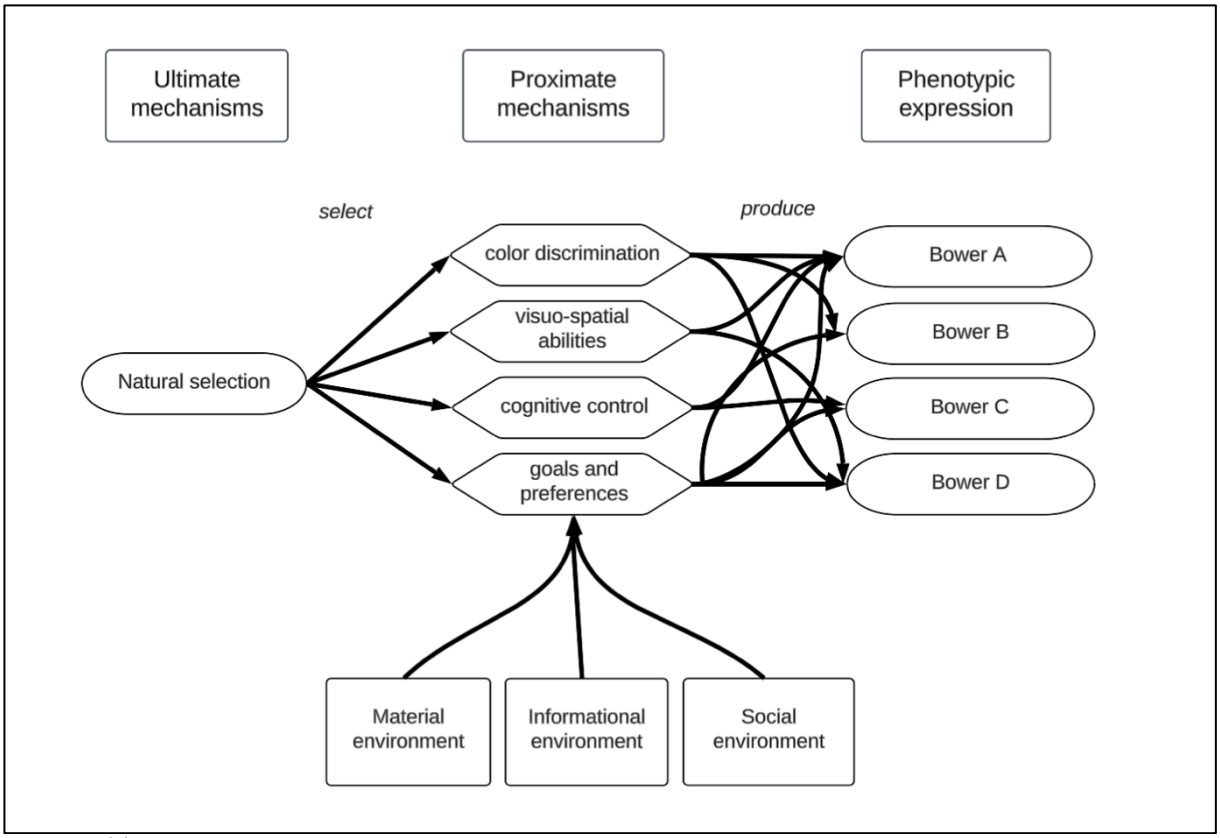

Figure 4: The evolutionary origins of flexible ecological modifications. Bowerbirds construct elaborate bowers to attract mates. Natural selection sets objectives (e.g., increasing mating success) as goals or preferences, while allowing individuals to creatively achieve them using evolved cognitive tools such as color discrimination, visuo-spatial abilities, and cognitive control. These mechanisms enable bowerbirds to tailor their displays to local environments and available resources.

Generative cognitive functions explain a great deal of the variability of cultural phenomena. A hunter in the Arctic and a hunter in the African savanna both need tools to hunt, yet their solutions differ—one may develop a harpoon, the other a bow and arrow. Despite these differences, both tools are tokens of the same generative function—a complex interplay of causal cognition, motor skills, executive function, and the motivation to acquire food—which has enabled humans to thrive in the skill-intensive foraging ecological niche (Kaplan et al., 2009; Sperber, 1996; Tooby & DeVore, 1987). The specific form of a tool depends on available materials, ecological constraints, and cultural legacies left by previous generations, but the underlying mechanisms that guide this process remain cognitive adaptations (see **Figure 5**).

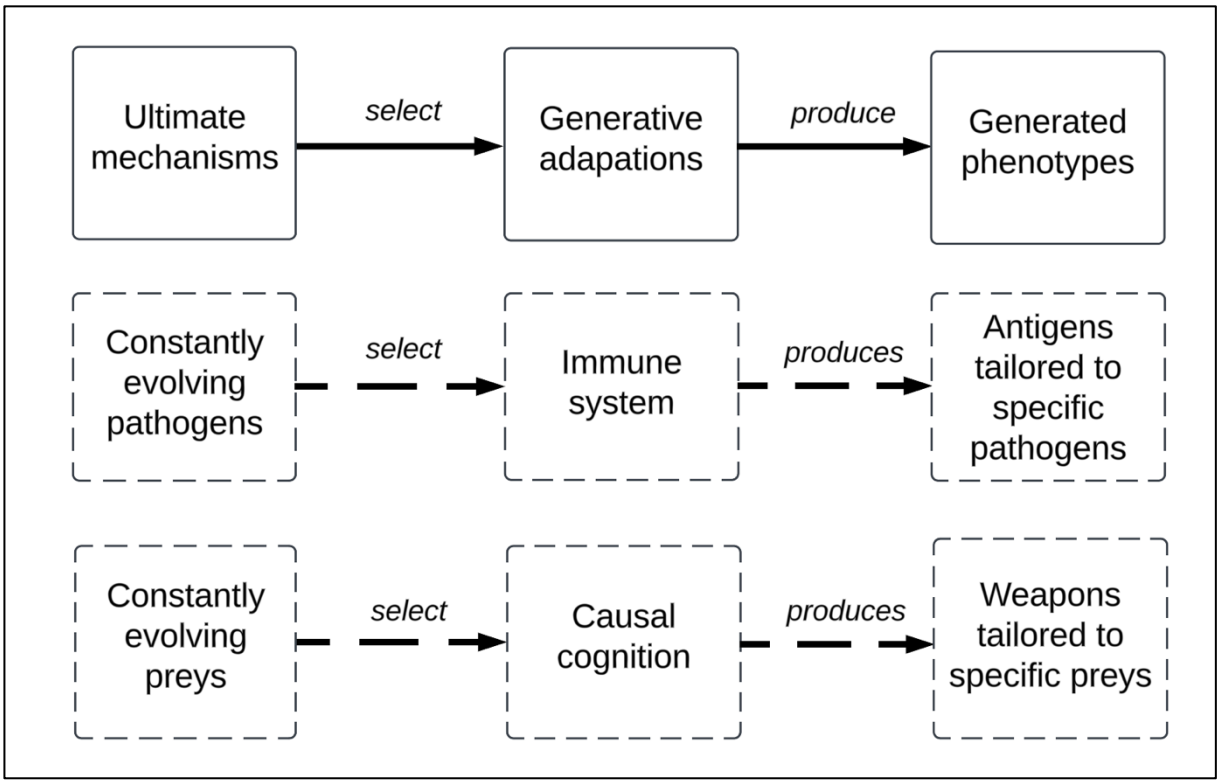

Figure 5: Generative functions and generated phenotypes.

Generated cultural products—such as spears, words, or clothing—are not adaptations, they are phenotypic expressions generated by cognitive adaptations to achieve fitness-enhancing goals. Just as a spider's web is not itself an adaptation but a phenotypic expression of the evolved mechanisms for web-building.

3.3. Cultural phenomena often result from the joint actions of multiple individuals with potentially divergent inclusive fitness interests

Another challenge in cultural evolution is that many cultural products—houses, boats, roads, and institutions—are not produced by a single individual but emerge from the collective actions of multiple individuals. This seems to complicate the application of inclusive fitness theory, which typically analyzes traits in terms of individual genetic interests. However, this issue can be understood through the concept of joint phenotypes, which explains how a single phenotype can result from the interaction of multiple genotypes, sometimes with overlapping but also conflicting evolutionary interests (O'Brien et al., 2021; Queller, 2014).

The notion of joint phenotype is key to understanding the form and structure of cultural products, because it allows us to understand why the form and structure of a particular individual's phenotype may not correspond to that individual's fitness interests. A joint phenotype is simply a phenotype that result from more than one genome. The human body is a prime example of a joint phenotype, particularly when considering the interaction between the human genome and the genomes of the microorganisms that make up the microbiome (Figueiredo & Kramer, 2020). Similarly, the body of a pregnant woman is another example of a joint phenotype, as it reflects the genetic contributions and the interest of both the mother and the fetus. For instance, the fetus, carrying half of its genes from the father, may demand more resources from the mother than what is optimal for the mother's health. This is because the fetus's evolutionary interest is to maximize its own growth and chances of survival, potentially at the expense of the mother's well-being (Haig, 1993).

Extended phenotypes can be joint phenotypes (Laidre, 2021b; Phillips, 2009). For instance, among jackdaw pairs, both partners contribute to building the nest which, therefore, is the product of two individuals with different genotype, and partly overlapping but also partly conflicting interests (Hahn et al., 2021). Similarly, a bower in a joint phenotype. It results from the interaction between the genome of the builder and the genomes of the competitors. The builder's genes influence the creation and initial decoration of the bower, while the competitors' genes can alter its final state by removing decorations or causing damage (Madden, 2008).

Likewise, cultural phenomena can be understood as the joint extended phenotypes of many genotypes whose interests are not fully aligned, with some conflictual interactions and some cooperative or mutualistic (André et al., 2023; Cosmides & Tooby, 1987; Tooby & Cosmides, 1990). A house, for example, is the extended phenotype of its inhabitants, just as birds' nests, beavers' dams and rodents' burrows are. The design of the house, its size, construction materials and organization are the result of a compromise between the objectives of the inhabitants and the constraints of the environment. The notion of joint phenotypes is a way of thinking about conflicts of interest. Not all residents have exactly the same interests. Some prioritize comfort (for their children's health, or their own health), others external appearance (to signal specific traits, such as wealth or taste), still others social spaces (to build and maintain their social capital). Depending on the balance of power and the degree to which individual interests overlap, the shape of the house will therefore vary from one household to another.

For instance, many cultural behaviors that seem puzzling from an inclusive fitness standpoint—such as engaging with strangers on social media, mastering a musical instrument, or writing a novel—persist despite their apparent lack of direct survival or reproductive benefits, because they function as costly signals, allowing individuals to display desirable qualities like intelligence, creativity, expertise, strength, or social commitment through hard-to-fake artifacts and behaviors. Elaborate storytelling, literary skills, or musical mastery can signal intelligence and dedication, just as excelling in extreme sports can demonstrate coordination and resilience. Even witty social media posts or participation in niche communities can act as signals of social intelligence, trend awareness, or coalition membership.

Signaling plays a particularly crucial role in human communication. While it is often assumed that people communicate primarily to transmit accurate facts, much of human communication serves social and strategic functions. For example, research has shown that many individuals endorse or share fake news not necessarily because they believe it to be true, but because doing so signals certain personal qualities—such as independence, loyalty to a group, or assertiveness. In this case, the act of communication itself functions as a costly signal (Altay et al., 2022; Crockett, 2017; Osmundsen et al., 2021; Petersen et al., 2023).

Similarly, many ritual behaviors appear puzzling when analyzed from the perspective of the individuals who pay for services with unclear efficacy. They look like "by-products" or "mismatches". Yet they make perfect sense when viewed from the perspective of those who instigate and promote them (André et al., 2023). Ritual specialists—such as shamans, priests, or fortune tellers—often gain economic rewards, social prestige, or political influence, regardless of whether their services provide tangible benefits to their followers (Hong et al., 2023; Singh, 2018). A similar dynamic exists in junk food production, where consumers bear long-term health costs, yet producers profit by exploiting deep-seated human preferences for calorie-dense foods, which evolved in environments of nutritional scarcity. In both cases, the fitness interests of producers and consumers are misaligned, illustrating how cultural ecosystems, like standard ecosystems, do not involve only cooperative interactions. Cultural traits do not need to benefit everyone to remain stable and persist; they only need to benefit those who promote or control them.

Another key fitness goal playing a role in cultural evolution is the pursuit of influence and control over others, shaping their behavior in ways that serve individual or mutual interests. This can involve regulating sexuality through practices such as genital mutilation, foot binding, veiling, or menstrual huts, which impose constraints on reproductive autonomy and social mobility (Dickemann, 1979; Paige & Paige, 2023; Pazhoohi et al., 2017; Strassmann et al., 2012). It can also extend to enforcing cooperation by fostering belief in supernatural punishment, organizing large mandatory gatherings like religious ceremonies, or establishing easily monitored cooperative norms, such as wearing specific clothing (Baumard & Chevallier, 2015; Fitouchi et al., 2023; Fitouchi & Singh, 2022). Additionally, cultural mechanisms are often used to shape coalitional allegiances, as seen in the propagation of nationalist myths or the strategic dissemination of fake news to reinforce group identities and manipulate political or social landscapes (Sijilmassi et al., 2024). In all these cases, cultural practices function as tools for social control, influencing individual behavior in ways that benefit those who impose them, whether by reinforcing hierarchies, maintaining group cohesion, or securing power.

3.4. Cultural phenomena are often emergent features, that do not even exist at the individual level

Another challenge in cultural evolution is that many cultural products have an effect that is only tangible at the aggregate level, emerging from the interactions of many individuals rather than providing immediate, direct benefits to any single person. This also appears to contradict the individual-based logic of evolutionary theory, which explains behaviors in terms of their fitness consequences for the individual producing them. Furthermore, these large-scale cultural phenomena—such as institutions, road systems, or financial markets—are often conceptualized as emerging from the top down, as group-level structures resulting from some form of group selection, rather than as products of individual strategies shaped by natural selection.

However, this challenge is not unique to cultural phenomena. Many non-human species also produce large-scale collective phenomena that emerge from individual decisions yet benefit the group as a whole. Examples include flocking in birds, schooling in fish, or cooperative nest-building in social insects, all of which persist because they enhance the fitness of participating individuals by providing protection from predators, improved foraging efficiency, or environmental modification (Cantor et al., 2021; Farine et al., 2015; Jolles et al., 2017). These group-level traits can thus be understood as emergent phenotypes that arise not from a single individual, but from the coordinated actions of many individuals.

In the same way, large-scale cultural systems can be conceptualized as emergent phenotypes, where individuals participate in and shape these structures because doing so aligns with their own adaptive interests. Institutions, for instance, may seem to follow a logic beyond individual actions, much like flocking in birds or schooling in fish. Yet, in reality, institutions are not imposed top-down by an external force; rather, they emerge as the aggregate result of adaptive behaviors shaped by individual incentives and constraints (Lie-Panis & André, 2022).

For example, the creation of legal systems, financial regulations, or public goods provision can be traced back to individuals acting in their own interest—seeking to reduce risks, prevent free-riding, and ensure predictable interactions. A clear historical case is rural Japan's communal forest management, where villagers faced a cooperation dilemma: each person had an individual incentive to overuse resources, but excessive defection would lead to depletion of the shared forest. Rather than relying solely on spontaneous prosocial behavior, villagers invested time and resources to design a institution in which monitors would track compliance and enforce rules (Ostrom, 1990).

The effectiveness of this institution did not depend on an external group-level force but on the fact that monitors themselves had incentives to act fairly—otherwise, they risked damaging their own reputations and losing their role.

Thus, institutions are not separated from human evolutionary dynamics. Just as collective behaviors in animals—such as cooperative nest-building or synchronized group defense—arise from individual adaptive benefits, institutions are social technologies that are intentionally designed to harness and amplify reputation-based incentives, ensuring that cooperation remains stable even in large, complex societies. This perspective reconciles the seemingly top-down nature of institutions with the bottom-up logic of evolutionary theory, demonstrating that complex social structures emerge from individual strategies rather than requiring an external group-level force.

3.5. Cultural phenomena are the outcome of proximate psychological mechanisms selected to maximize inclusive fitness in environments that may differ from this cultural ecosystem

Lastly, another challenge is that cultural evolution occurs on timescales too rapid for natural selection to directly shape genetic traits. Human cultural practices often change within decades or even years, while genetic evolution requires much longer periods to manifest significant shifts. Therefore, the responses individuals and societies exhibit to changing environmental or social conditions are governed by evolved proximate mechanisms— such as food preferences, moral intuitions, kin-recognition systems, social emotions (e.g., guilt, shame, pride)—that were shaped by natural selection in ancestral environments (Cosmides & Tooby, 1987; Symons, 1990; Tooby & Cosmides, 1990, 1992).

This raises the possibility that cultural behaviors may not always be optimal when the ecosystem—whether cultural or otherwise—deviates significantly from the environments in which human cognitive mechanisms evolved. Things are similar when studying ecological response to rapid anthropogenic changes such as pollution. For instance, in environments polluted by plastic waste, turtles often mistake plastic bags floating in the ocean for jellyfish (Schuyler et al., 2014). This is because sea turtles have evolved to detect food, like jellyfish, by using visual cues that help them identify prey based on shape and size. In environments polluted by plastic waste, this proximate mechanism leads them to mistake plastic bags floating in the ocean for jellyfish.

However, the extent of such mismatches should not be overstated. Humans are highly flexible and plastic, capable of adapting to a wide range of conditions, and their behavior remains largely adaptive even in cultural ecosystems that differ significantly from ancestral settings (see above section 3.2). Even when mismatches occur, they are not accidents; they often persist because they serve the interests of certain individuals or groups (André et al., 2023). For instance, the modern abundance of hyper-palatable foods exploits deep-seated preferences for sugar and fat, which evolved in environments where such resources were rare and valuable. The resulting overconsumption and obesity epidemic is not a mere evolutionary mismatch—it exists because it benefits those who produce and market these products. This phenomenon mirrors standard ecological dynamics, where some organisms exploit the perceptual or cognitive biases of others for camouflage, deception, or courtship. Similarly, in cultural ecosystems, artifacts and institutions can emerge that harness or manipulate human proximate mechanisms, shaping behavior in ways that may not align with long-term fitness interests.

4. The immense benefits of reclaiming inclusive fitness

The power of inclusive fitness theory in understanding animal behavior lies in its ability to impose strict constraints on what evolution can and cannot produce. The most significant cost of

developing a separate theory for behaviors influenced by "culture," distinct from the framework applied to other behaviors—as in dual inheritance theory—is that it removes these constraints, stripping the study of culture of its predictive power.

In dual inheritance theory, cultural phenomena are seen as the product of a mix of logics—partly "biological", partly "cultural"—whose proportions can be adjusted as needed. One can, for instance, attribute a phenomenon to a combination of genetic predispositions, vertical cultural transmission, prestige bias, and/or content bias in whatever proportions best fit the case at hand. Such a high-degree-of-freedom theory is, unsurprisingly, capable of fitting—indeed, overfitting—any cultural observation. But it fails to predict or truly explain cultural phenomena.

The immense benefit of the ecological approach to culture is that, by being a parsimonious and therefore constraining framework for cultural behaviors, it restores the predictive power of adaptationist reasoning. Cultural phenomena arise like any other ecological phenomenon—from the combined actions of individuals seeking to maximize their inclusive fitness. This approach goes beyond merely describing or retroactively fitting observations; it allows for genuine understanding, and even generates testable predictions, drawing on the predictive power of adaptationist reasoning constrained by inclusive fitness theory.

One striking feature of cultural evolution is the apparent absence of any general rule. Some cultural traits remain remarkably stable for generations, while others shift abruptly. Sometimes, people faithfully adopt the behaviors of others; at other times, they discard them entirely in favor of new ones. Cultural behaviors can sometimes exhibit a clear functional logic, whether at the individual or collective level, yet in other cases, they seem entirely maladaptive at any scale. While these seemingly contradictory observations can always be accommodated within DIT models by adjusting the parameters of cultural transmission on an *ad hoc* basis, such adjustments do not explain the underlying logic that determines these parameter values in each case. In contrast, cultural ecology, which places human agents and their interests at the heart of cultural dynamics, offers a framework for explaining these apparent contradictions without relying on ad hoc assumptions.

4.1. Explaining the direction of cultural change

The direction of cultural change varies significantly across different cultures and historical periods. In some societies, romantic love gains importance, while in others it declines (Baumard et al., 2022; Zhong et al., 2023); cooperation sometimes becomes central, while at other times competition intensifies (Martins & Baumard, 2020; Safra et al., 2022). Occasionally, different cultures evolve in parallel, converging on similar social forms, whereas at other times their trajectories diverge sharply.

The ecological approach—thanks to its reliance on adaptationist reasoning—provides a framework for understanding and predicting these patterns. For instance, across diverse regions, societies often develop strikingly similar structures and social dynamics. One example is the emergence of a "warrior complex," characterized by chronic internal warfare, blood feuds, fraternal interest groups and expansionist, segmentary lineages based on male descent. But why do such patterns recur across cultures? The answer lies in how ecological conditions shape social organization through their effects on economic production, family structure, and conflict dynamics.

During the Iron Age, improvements in selective breeding, animal husbandry, and milk processing technologies transformed pastoral economies. In this new cultural ecology centered around herd management, an adult male's reproductive success became increasingly dependent on herd size rather than direct labor input (Borgerhoff Mulder et al., 2009; H. S. Kaplan et al., 2009). This shift granted greater power to parents, as inheritance of livestock became essential for marriage and

economic independence. As a result, family structures adapted. Patrilineality replaced matrilineality as families began prioritizing male heirs, whose reproductive success varied more than that of females (Holden & Mace, 2003). Polygyny became widespread, as wealthier men could accumulate larger herds and support multiple wives, with benefits extending to the broader kin group (H. Kaplan et al., 2000).

The pastoral mode of subsistence also shaped warfare and social dynamics. Unlike agricultural resources, herds are individually owned yet highly vulnerable to theft, making raiding a profitable and common strategy. Additionally, bride capture—where women from weaker groups were forcibly integrated into dominant lineages—became a key reproductive and political strategy. These pressures drove the emergence of a warrior ethos, which included: chronic internal warfare and blood feuds, as kin groups sought to protect and expand their herds, fraternal interest groups, where coalitions of brothers and male relatives defended shared family resources, expansionist, segmentary lineages, where male descent determined political and military alliances (H. S. Kaplan et al., 2009; Keeley, 1997; Lienard, 2014; White & Burton, 1988).

These patterns, shaped by the economic and reproductive incentives of pastoralism, illustrate how cultural evolution is fundamentally a response to ecological modifications. Societies facing similar ecological landscape tend to converge on comparable social structures, kinship systems, and conflict dynamics (see **Figure 6**).

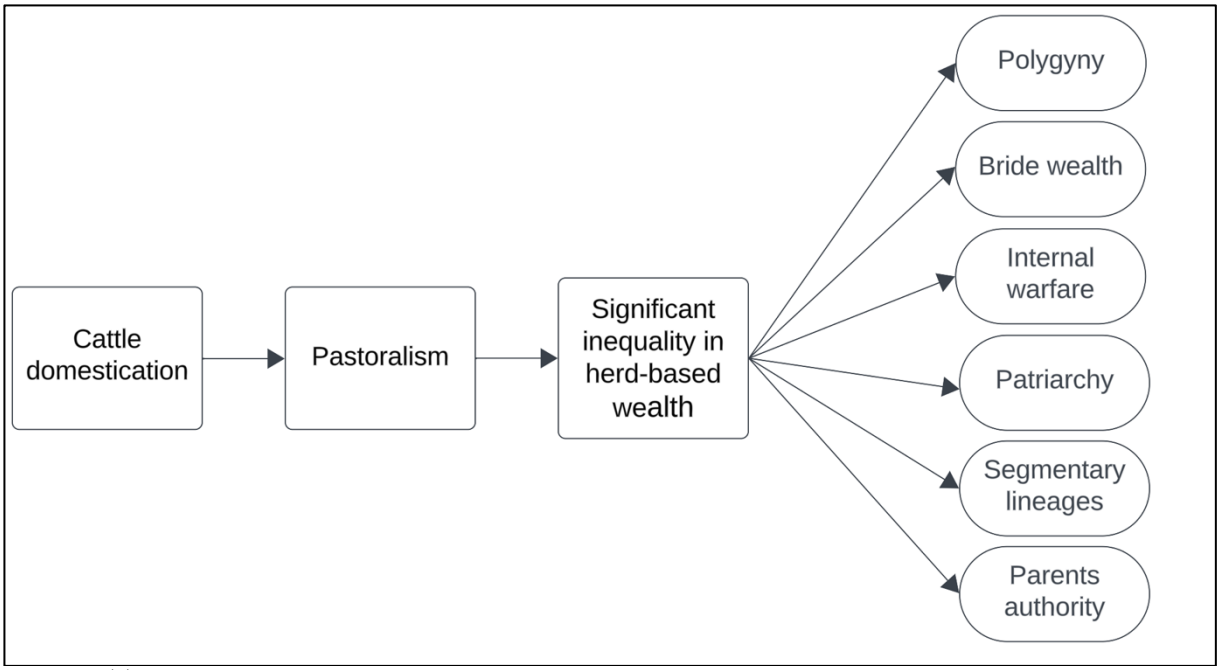

Figure 6: The cultural evolution of cattle domestication in the MENA region. The domestication of cattle in Eastern Africa during the Iron Age led to a new cultural ecology focused on herd management, which influenced family organization, male reproductive success, and social structures, resulting in increased patrilineality, high levels of polygyny and internal warfare from Kaplan et al., 2009)

Another striking trend in cultural evolution is the process of 'modernization' (Giddens, 2023; Inglehart & Welzel, 2005; Weber, 1968). Across societies, economic development leads to remarkably consistent convergence in human behavior. As resources increase, people become more future-oriented, more exploratory, and more cooperative. But why do these patterns emerge repeatedly, not only across different cultures but also within societies, when comparing individuals from higher and lower social classes? The answer lies in humans' ability to adjust their motivational priorities in response to ecological conditions. Research in socioecological psychology, behavioral ecology, and behavioral economics shows that individuals living in harsh environments, marked by

resource scarcity and unpredictability, exhibit distinct behavioral strategies. In such conditions, people are more likely to prioritize immediate survival, display lower cognitive exploration, and invest less in trust-based cooperation (Pepper & Nettle, 2017). In contrast, individuals in resource-rich environments tend to favor long-term planning, intellectual curiosity, and cooperative behaviors, as the risks of investing in the future are lower and the potential benefits are greater (Boon-Falleur et al., 2024).

These patterns, sometimes referred to as 'behavioral constellations of deprivation' (Pepper & Nettle, 2017) or 'behavioral constellations of abundance,' (Baumard, 2019) reflect adaptive responses to local resource availability: when resources are abundant, it makes sense to delay gratification and invest in uncertain but potentially high-reward strategies; when resources are scarce, prioritizing immediate survival needs is the more optimal strategy. This aligns with Maslow's idea that basic needs must be met before individuals pursue higher-level goals (see **Figure 7**) (Boon-Falleur et al., 2024; Kenrick et al., 2010).

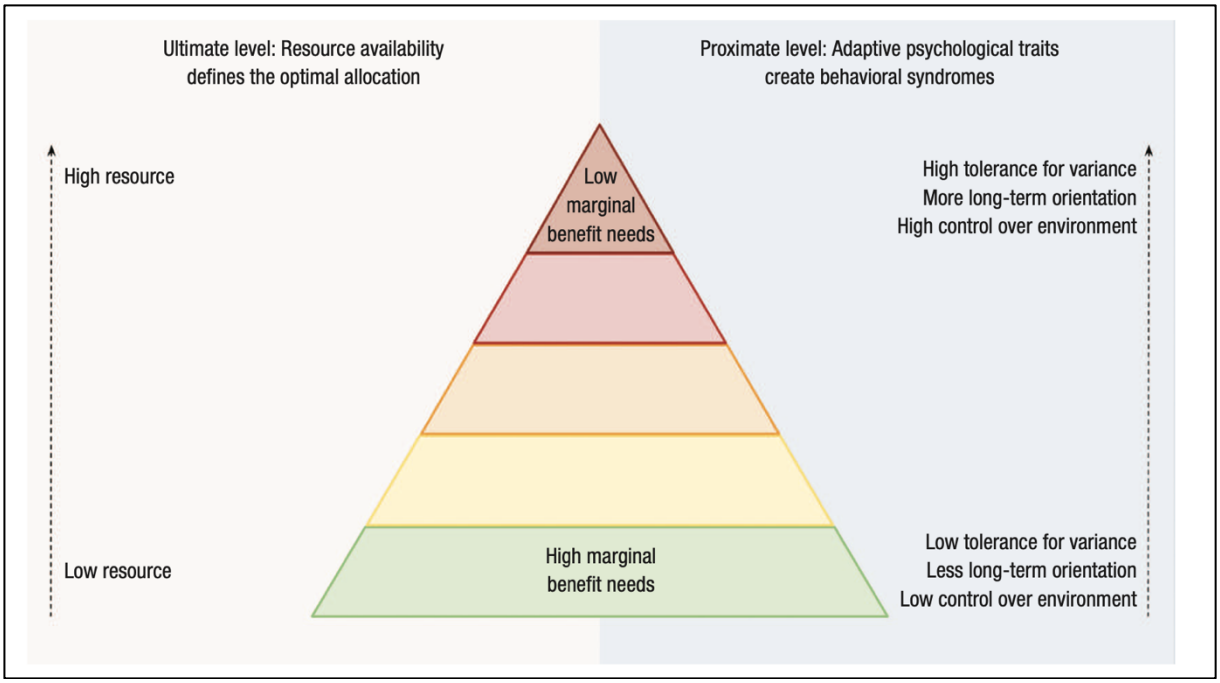

Figure 7: The pyramid of needs and its psychological consequences. Individuals should first allocate their resources to the needs with the highest marginal benefit then move to the needs with the lowest marginal benefit. This dynamic, in turn, influences a number of psychological traits. Individuals have a higher tolerance for variance in returns, a more long-term orientation, and higher control over their environment.

Such a phenomenon explains the direction of cultural change. As societies develop, they do not simply accumulate wealth; they reshape their ecological conditions, fostering environments of higher living standards, security, and opportunity (Boon-Falleur et al., 2024). These new conditions, in turn, encourage the development of traits such as independence, creativity, and long-term planning, ultimately driving cultural shifts toward individualism, innovation, and social tolerance (Baumard, 2019). Over time, these individual adaptations contribute to broader societal transformations (see **Figure 8**). As more individuals adopt cooperative strategies and prioritize long-term goals, institutions evolve to support fairness, inclusivity, and democratic governance (Guillou et al., 2023; Inglehart, 2018; Martins & Baumard, 2020; Safra et al., 2022). As cognitive exploration increases, societies produce more intellectual, artistic, and technological advancements, leading to a rise in fictional worlds, abstract reasoning, and innovation (Dubourg et al., 2021; Dubourg & Baumard, 2021; Inglehart, 2018). Thus, economic development does not arbitrarily

change cultures—it fundamentally transforms human ecological conditions, triggering predictable shifts in motivation, cognition, and social behavior.

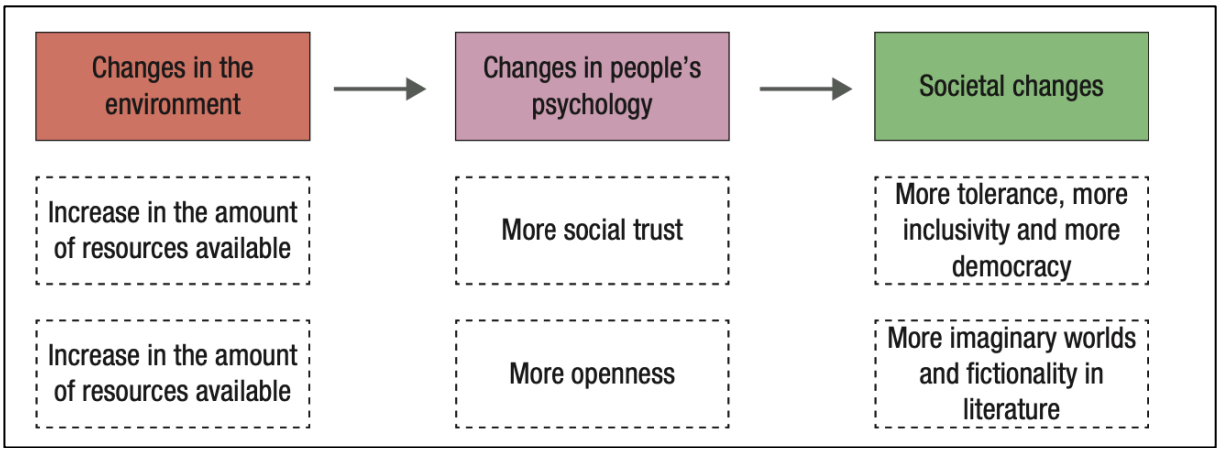

Figure 8: Changes in resource availability lead to changes in people's psychology which in turn explain cultural-level changes. When individuals face exogenous changes in the availability of resources, for example, through changes in climatic conditions or innovation, they will change the way they allocate resources between different needs. This will translate into psychological and behavioral changes at the proximate level, which will ultimately result in changes at the cultural level.

As economic development increases across generations, psychological preferences shift over time, shaping the trajectory of human societies. One striking example is the evolution of literary fiction, where material conditions influence people's literary preferences (Baumard et al., 2022; Baumard, Safra, et al., 2023; Zhong et al., 2023). During periods of economic prosperity and improved living standards—such as Classical Greece, Roman Italy, Renaissance Europe, and Ming China—literature tends to emphasize romantic and love themes, reflecting the increased value placed on emotional relationships in stable environments (Sorokowski et al., 2023). Even when authors build upon existing cultural legacies—drawing from past characters, myths, and plot structures—they adapt these narratives to contemporary ecological conditions, often by amplifying romantic themes or emphasizing individual agency in relationships (Baumard et al., 2022; Zhong et al., 2023). This pattern illustrates a fundamental principle of cultural evolution: the direction of cultural changes is ultimately explainable within the framework of inclusive fitness.

This principle can also explain cultural divergences. Consider, for instance, Western Europe's early development of individualism, tolerance, self-discipline, and romantic love—features less prominent in other regions during the same historical period. Such disparities largely stem from geographical differences in resource availability, climate, and biodiversity. Western Europe's temperate climate, fertile soils, and abundant waterways provided ideal conditions for early agricultural development, leading to stable food surpluses and accelerated technological advancement (Diamond, 1997). Similarly, the abundance of fresh, cool water sources facilitated lower disease burdens and more stable food supplies. These favorable ecological conditions thus encouraged greater investment in long-term projects, future-oriented thinking, and self-expression, explaining Europe's early cultural divergence from other regions (Welzel et al., 2021).

4.2. Explaining the pace of cultural change

Some cultural traditions persist unchanged for generations—such as driving on a particular side of the road or consistently using certain words—while others transform abruptly and dramatically. This variation can be explained by recognizing that cultural behaviors are generated by individuals with extensive cognitive flexibility, who adaptively respond to changing ecological and social conditions. Whether traditions remain stable or undergo rapid transformation depends on both

environmental and psychological factors. In some contexts, preserving existing practices is adaptive—either because the environment remains stable or because deviation from established norms is too costly (e.g. norms regulating driving or the meaning of words). In other situations, innovation becomes advantageous, either because new opportunities arise or because environmental change makes risk-taking advantageous.

The ecological approach draws on adaptationist thinking to predict when cultural stability or rapid transformation is likely. Cultural stability or change is first influenced by ecological shifts and their effects on psychology. For instance, individuals who lived through World War II developed conservative values and tight social norms shaped by scarcity and violence, whereas subsequent generations, raised in environments characterized by peace and abundance, embraced openness, risk-taking, and tolerance. Cultural change occurred gradually, initially slowed by the numerical dominance of older generations, but eventually accelerated during the cultural revolutions of the 1960s as younger generations became politically influential and demographically dominant (Inglehart, 2018). Similarly, during the Iron Age, technological advances in animal husbandry created a new cultural ecology centered on herd management. This shift increased male reproductive inequality, prompting families to prioritize male inheritance and adopt patrilineal structures. It also intensified warfare and promoted a warrior ethos, characterized by chronic internal conflict, fraternal alliances, and expansionist lineages aiming to secure herds and reproductive opportunities.

Another key driver of rapid cultural change is shifts in the balance of power between social groups. For example, many men's initiation rites and bachelor cults in traditional societies functioned primarily to benefit older males by controlling younger men's reproductive opportunities, thus enhancing older males' prospects for polygyny. However, as soon as ecological or technological changes (such as greater access to firearms or economic resources) empowered younger men, these rites rapidly declined or disappeared (Wiessner, 2002; Wiessner et al., 2024). Similarly, changes in the balance of power affect peacemaking practices: older men often favor peace due to their greater accumulated resources and higher risk exposure, whereas younger men may pursue conflict as a means of gaining reputation or wealth (Wiessner, 2002; Wiessner et al., 2024).

Cultural stability or change also depends on individuals' general preference for novelty or tradition, a preference shaped plastically by environmental conditions encountered during development. Adaptationist predictions rooted in risk management theory suggest that individuals living in affluent and stable environments can afford greater risk-taking, leading to less faithful cultural transmission, higher innovation rates, and thus more rapid cultural evolution—conditions exemplified by the Industrial Revolution in Western Europe (Baumard, 2019).

Critically, humans can adapt and innovate culturally far more rapidly than genetic evolution allows, due to their exceptional cognitive flexibility, especially in social cognition. Mindreading (theory of mind)—the ability to infer the mental states, intentions, and beliefs of others—enables humans to swiftly generate new norms and conventions in response to changing contexts (Heintz & Scott-Phillips, 2023; Sperber & Wilson, 1995). Unlike fixed animal communication systems, human communication is context-dependent and inferentially driven, allowing individuals to spontaneously establish novel cultural practices when ecological conditions demand them.

In any case, individuals never passively absorb cultural values when they don't need it. Instead, they demonstrate epistemic vigilance, critically evaluating information's credibility and utility before adopting it (Mercier, 2020; Sperber et al., 2010). This ability is widespread in the animal kingdom—female peacocks prefer elaborate tails as reliable signals of genetic quality (Dawkins & Krebs, 1978) and vervet monkeys assess alarm calls based on the caller's reliability (Seyfarth & Cheney, 2003).

In humans, epistemic vigilance plays a crucial role in filtering misleading and manipulative information while integrating useful knowledge. People rarely believe falsehoods unless doing so serves their interests—apparent gullibility often functions as a strategic social move, allowing individuals to signal coalition membership, project confidence, or enhance their status, rather than reflecting a failure of reasoning.

4.3. Explaining the fine-grained properties of cultural products

Cultural products exhibit specific, non-random features that emerge from their interaction with human cognitive constraints. Consider the shape of letters—why do certain patterns recur across widely different writing systems, while others are nearly absent? The answer lies in the same principles that govern ecological adaptation: just as organisms evolve signals suited to their receivers' sensory systems (Davies et al., 2012), producers of cultural products must tailor their creations to the cognitive capacities of their consumers. For instance, letter shapes are not arbitrary but constrained by how the human visual system processes symbols (Changizi et al., 2006; Dehaene & Cohen, 2007; Morin, 2018). Human vision is particularly attuned to certain geometric features, such as symmetry, intersections, and simple line arrangements, because these are common in natural environments—from the contours of objects to the branching of trees and the junctions of limbs in animals. Writers attempt to minimize the cognitive costs of the receptors by designing and preferentially using writing systems that are easier to distinguish. This is why letters rarely feature highly intricate, curved, or irregular forms—such designs are harder for the brain to process efficiently. Instead, letters tend to be composed of simple strokes and intersections, aligning with the visual system's natural ability to detect contrast and patterns (Changizi et al., 2006; Dehaene & Cohen, 2007; Morin, 2018).

This principle generalizes across cultural domains: writers seek to craft fiction that captivates, priests design rituals to persuade, and artists create art forms that resonate aesthetically with human perception and cognition (Dubourg & Baumard, 2021; Hong et al., 2023; Morin, 2016; Sijilmassi et al., 2024; Singh, 2018; Sperber & Hirschfeld, 2004). Romantic narratives, for instance, frequently utilize recurring plot devices—love at first sight, tragic separations, enduring devotion, and self-sacrifice for love—that reflect core psychological features of romantic attraction and attachment (Buss, 2018; Fletcher et al., 2015). Producers of these narratives strategically exploit universal cognitive predispositions such as partner idealization, emotional bonding, long-term commitment, and the reprioritization of life around romantic relationships (Baumard et al., 2022). Thus, romantic stories operate as superstimuli, intentionally constructed to intensify and amplify humans' evolved psychological mechanisms related to pair-bonding, capturing attention and triggering profound emotional engagement (Dubourg et al., 2024; Dubourg & Baumard, 2022).

This principle also applies to religious beliefs. Across human societies, spirits, gods, and karmic forces consistently punish uncooperative behaviors such as theft, murder, adultery, and stinginess, typically inflicting disease, premature death, or eternal damnation in hell, while rewarding cooperative behaviors either in this life or the next (Boyer, 2001; Fitouchi & Singh, 2022). This pattern of moralistic supernatural punishment is especially prominent in major world religions, including Abrahamic traditions (e.g., Islam, Judaism, Christianity), karmic religions (e.g., Buddhism, Hinduism, Jainism), and East Asian folk religions (Baumard et al., 2015; Fitouchi et al., 2025). Because their inclusive fitness depends on the quality of cooperation in their society, influential individuals—such as priests and other leaders—shape beliefs that resonate with intuitions about reputation management and morality, making them more persuasive and effective at promoting prosocial behavior (Fitouchi et al., 2025). This account also explains key features of moralizing religions, such as their strong emphasis on proportionality—ensuring that supernatural rewards align with virtuous deeds and that sins are met with appropriate penance) (Baumard & Boyer, 2013)

and the centrality of puritanical morality and self-discipline (Baumard & Chevallier, 2015; Fitouchi et al., 2021).

4.4. Explaining both the functional and the dysfunctional sides of culture

Some cultural behaviors have a clear functional role, benefiting individuals and sometimes even entire societies. Modern medical practices, for instance, offer undeniable benefits to patients. Similarly, many dietary practices, including traditional ones, are likely to have physiological advantages for individuals (D. M. T. Fessler, 2002; D. Fessler & Navarrete, 2003; Flaxman & Sherman, 2000; Hagen et al., 2023; Placek et al., 2017). The same often holds true at the collective level. While far from perfect, many institutional arrangements clearly exhibit mutually beneficial properties (Hechter, 1987; Ostrom, 1990)

Yet in other cases, the opposite is true. Many cultural practices persist and even thrive despite appearing inefficient, harmful, or oppressive to individuals, or lacking any clear functionality or rationality for society as a whole. Take, for example, the men's cults in Melanesia, where older males coerce younger males through initiation rituals to maintain dominance and control over female reproductive access. These cults are often secretive, highly ritualized, and structured around intense, sometimes violent initiation rites (Wiessner, 2002; Wiessner et al., 2024).

The cultural approach provides a direct explanation of these apparent contradictions, based on the considerations of the inclusive fitness interests of the individuals involved.

1. Individually adaptive cultural practices are expected when individuals are free to choose what suits them without interference from others whose interests conflict with theirs. In such cases, individuals' goal-directed adaptive mechanisms—including flexible generative mechanisms—allows them to approach adaptive behaviors. In dietary choices, for instance, people are to some extent free of their choices. As a result, they are often in line with individual benefits (D. M. T. Fessler, 2002; D. Fessler & Navarrete, 2003; Flaxman & Sherman, 2000; Hagen et al., 2023; Placek et al., 2017). A similar logic applies to modern medical practices, where the relationship between doctors and patients is built on trust and cooperation. As a result, medical discoveries and innovations are developed and refined in the service of people's health.

2. Mutually beneficial cultural practices are expected at the collective level when individuals share common interests and/or have sufficient trust in one another to cooperate. This is the case, for instance, with institutions designed to promote cooperation, which are created, developed, and refined, provided that individuals maintain a sufficient level of trust (Hechter, 1987; Lie-Panis et al., 2023; Ostrom, 1990).

3. Dysfunctional and oppressive cultural practices are likely to emerge when individuals have conflicting interests and lack reciprocal trust, and when some are able to impose their will on others through coercion or manipulation. In the case of men's cults in Melanesia, older men benefit from monopolizing women and do not engage in cooperative trust-based relationships with younger men (Wiessner, 2002; Wiessner et al., 2024). Instead, they seek to coerce, deceive, and subject them to extreme rituals designed to enforce submission and delay their access to reproductive opportunities. In such cases, there is no reason to expect cultural practices to be adaptive for all individuals involved, let alone for society as a whole. These practices only serve those who promote and impose them, reflecting the competing interests of individuals or subgroups within a population.

5. A new definition of culture

The ecological approach leads to a new way of conceptualizing cultural phenomena. In this approach, cultural phenomena result from the way individuals change their environment (by producing ecological modifications), and the way these environmental changes affect the environment of individuals, inducing a phenotypic response in other individuals (see **Figure 9**). This continuous cycle of ecological modification and response drives cumulative cultural change, making cultural evolution a fundamentally phenotypic process, by opposition to the genetic process that characterize biological evolution. Therefore, culture should be defined as some change resulting from ecological modifications produced by others.

However, while ecological modifications in typical ecosystems are usually interspecific—scientists commonly refer to legacies such as beaver dams shaping lake communities—in cultural ecosystems, the focus is primarily on intraspecific effects. Examples include birds opening milk bottles, macaques washing potatoes, chimpanzees using lithic tools, and whales developing distinct songs.

Based on this distinction, we propose the following definition of culture: culture is *any phenotypic change resulting from intraspecific ecological modifications*.

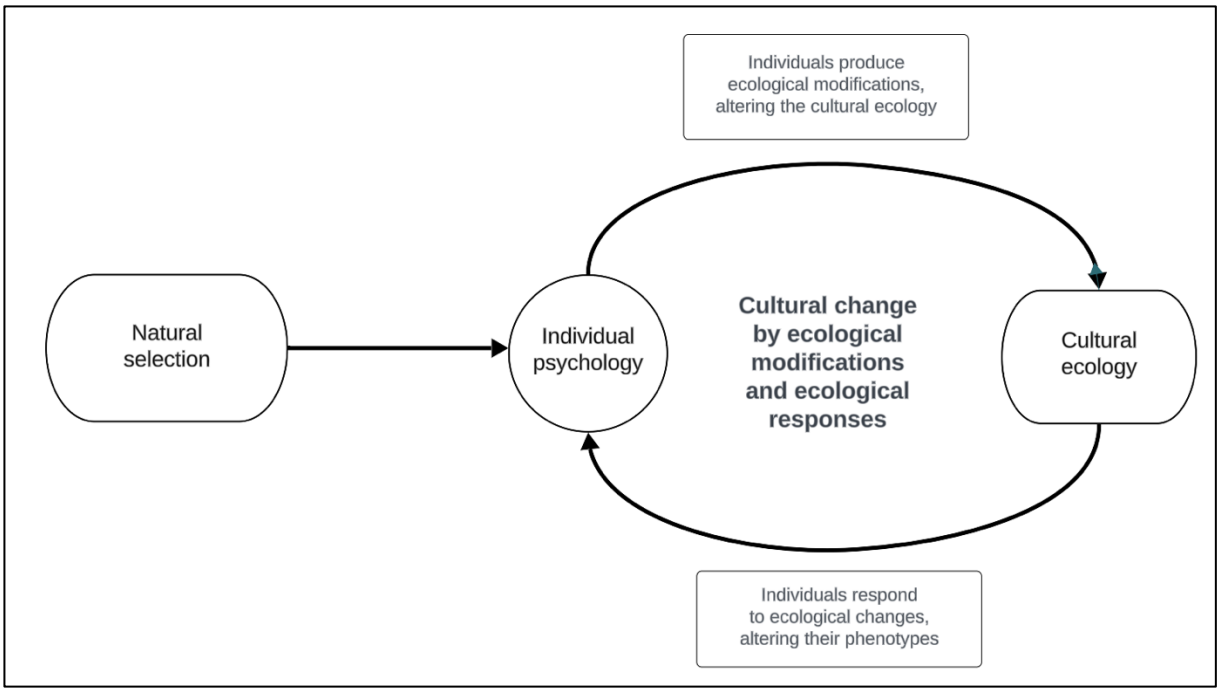

Figure 9: Evolution shapes genetic programs that code for evolved mechanisms that, in turn, (i) produce ecological modifications and (ii) allow individuals to respond to ecological modifications. Cultural phenomena emerge from the cumulative effects of ecological modifications, which alter the human environment and, in turn, generate new phenotypic changes, further altering the environment (for a similar view, see Boone & Smith, 1998).

This broad definition reconciles the notions of "evoked culture" and "transmitted culture" (Tooby & Cosmides, 1992). “Evoked culture” is used to describe cases where some variation in behavior is due to the evolved plasticity of the mind in responses to changes in the material environment (resources, pathogens, warfare), whereas “transmitted culture” is used to describe cases where some variation in behavior is due to the evolved plasticity of the mind in responses to changes in the informational environment. In both cases, the phenomenon is cultural because the ecosystem has been modified by previous generations. Individuals produce new behaviors because their behavioral strategies respond to the resources and constraints accumulated by previous

generations. They also produce new words, new tools, new knowledge because their mind responds to information accumulated (voluntarily or not) by previous generations (parents, teachers, peers). In both cases, evoked and transmitted, the new generations are different than the previous ones because of adaptive phenotypic plasticity: individuals adjust their strategy to the information and the resources available in their environment.

Note that this perspective might give the impression that we advocate abandoning the term 'cultural evolution' entirely and replacing it with cultural ecology. But this is not the case. We still need a conceptual tool to capture changes that occur over time within a cultural ecosystem. In this sense, cultural evolution remains a necessary concept within the cultural ecology toolbox, but only in its broad, common-sense meaning—as a way to refer to some change over time. This, once again, mirrors standard ecology, where terms like landscape evolution or ecosystem evolution are commonly used—not to refer specifically to Darwinian biological evolution, but simply to describe gradual transformations (Micheletti et al., 2023). Similarly, cultural evolution should be understood as a descriptive term for historical change, not a mechanism distinct from the ecological processes that drive cultural dynamics

To conclude, reframing cultural evolution as an ecological process rather than a separate system of inheritance aligns the study of culture with established evolutionary principles. This ecological perspective eliminates the need for a dual-inheritance framework while offering a more parsimonious and predictive account of cultural dynamics. It explains both the stability and variability of cultural phenomena without invoking mechanisms beyond those already observed in ecological and evolutionary systems. Just as ecological interactions shape species' behaviors and environments over time, cultural dynamics emerge from individuals modifying and responding to their surroundings in pursuit of adaptive goals. Future research should further explore how ecological cascades and phenotypic plasticity drive long-term cultural change, deepening our understanding of the feedback loops between human behavior and cultural environments. Ultimately, integrating culture within the broader framework of ecology and evolution enhances our ability to explain cultural diversity and transformation without resorting to theoretical extensions that separate cultural evolution from biological evolution.

Declaration of generative AI and AI-assisted technologies in the writing process

During the preparation of this work the authors used GPT4 in order to improve clarity and readability. After using this tool, the authors reviewed and edited the content as needed and take full responsibility for the content of the publication.

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