



# Multilevel cultural evolution: From new theory to practical applications

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Evolutionary science has led to many practical applications of genetic evolution but few practical uses of cultural evolution. This is because the entire study of evolution was gene centric for most of the 20th century, relegating the study and application of human cultural change to other disciplines. The formal study of human cultural evolution began in the 1970s and has matured to the point of deriving practical applications. We provide an overview of these developments and examples for the topic areas of complex systems science and engineering, economics and business, mental health and well-being, and global change efforts.

cultural evolution | multilevel selection | systems engineering | economics | mental health

Darwin's theory of evolution is celebrated for its explanatory scope, prompting the geneticist Theodosius Dobzhansky to declare in 1973 that "nothing in biology makes sense except in the light of evolution" (1). However, what became the "modern synthesis" can also be called the "great constriction." The study of evolution was confined almost entirely to genetic evolution, relegating the study of human cultural change to other disciplines.

It was not until the 1970s that evolutionary thinkers started to go back to basics by defining natural selection as Darwin did—any process that combines the triad of variation, selection, and replication—irrespective of the proximate mechanisms (2). The first mathematical models of cultural evolution were based on population genetics models developed 50 y earlier (3–4).

Today, the study of cultural evolution in humans and other species is in full swing (5–12)—and these advances in basic scientific knowledge have practical applications (13–19). In this article, we will first review major developments in our basic understanding of human cultural evolution. Then, we will show how they can be applied to a diversity of positive change efforts, no matter what the scale (e.g., from the individual person to global governance) or topic domain. We elaborate for the topics of complex systems science and engineering, economics and business, mental health and well-being, and global change efforts.

## Why We Are Such a Cultural Species

The history of thinking about humans in relation to other animals is replete with claims of uniqueness that proved to be mistaken. Nevertheless, we are clearly highly distinctive in our ability to transmit learned information across generations in a cumulative fashion and to manipulate our physical and

social environments. These abilities enabled our ancestors to adapt to their environments much faster than by genetic evolution. No other species has spread over the globe, occupied dozens of ecological niches, and expanded into cooperative societies that number in the millions and even billions of genetically unrelated individuals (12, 19).

Although much remains to be learned, researchers have identified three interacting factors that account for our exceptional capacity for cultural evolution: prosociality, social control, and symbolic thought. These same factors are highly relevant for practical applications.

## Prosociality

Prosociality can be defined as any behavior oriented toward the welfare of others or one's group as a whole (14). It is a broader term than altruism or cooperation and includes everything that is required for a group to function as an adaptive unit. The premier example of an adaptive unit is a single organism, whose cells work almost entirely for the benefit of the whole, with important exceptions that will be detailed below.

Some animal societies are so prosocial that they invite comparison to a single organism and are described with terms such as "superorganism", "eusocial", and "ultrasocial" (20). The most famous examples are the eusocial insects—wasps, bees, ants, and termites—which have been compared to single organisms for millennia. More recently discovered examples include crustaceans and vertebrates (21).

Most animal societies do not invite comparison to a single organism. Members of groups cooperate to a degree and in

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specific contexts, but they also compete disruptively against each other. Even cooperation often takes the form of alliances that compete against other alliances within the same group. For comparison, imagine a highly despotic human society, where most members are exploited by elites and the elites compete endlessly with each other for power. Many animal societies are like that after millions of years of genetic evolution. They are not evolving toward a more prosocial state. Despotism is their evolutionary equilibrium.

Likewise, some multispecies ecosystems function as mutualistic assemblages, which survive and reproduce as collectives, but in many other ecosystems, the species have evolved to pursue their own adaptive strategies at cross-purposes with each other (22). Beaver ecosystems, for example, are best understood as the manipulation of the environment by members of a single keystone species for their own benefit. The impact of beavers on biodiversity and ecosystem processes such as nutrient cycling are collateral by-products (23).

Against this background, the genus *Homo* and its last surviving species, *Homo sapiens*, qualify as highly prosocial compared to our closest living relatives (chimpanzees and bonobos) and most other primate species (19, 24). Something happened in our lineage that shifted our evolutionary equilibrium and invites a comparison with other ultrasocial species rather than our phylogenetic relatives (25).

To proceed further with this line of inquiry, we need a theoretical framework that can explain the presence and absence of prosociality in all species. In his 1966 landmark book *Adaptation and Natural Selection*, George C. Williams stressed that when judged by the metric of relative fitness, most prosocial behaviors have an inherent disadvantage compared to more self-oriented behaviors expressed within the same group (26). This can be called the fundamental problem of social life in all species. Examples include cancer cells within multicellular organisms; free riders, bullies, and cheats within single-species social groups; and species that disrupt multispecies ecosystems for their own gain.

Fortunately, relative fitness differences also exist at the scale of between-group interactions, giving prosocial behaviors an inherent advantage. Groups whose members work together for the common good robustly outcompete groups whose members cannot cohere. This two-level dynamic (using the word altruism instead of prosocial) has been summarized as “Selfishness beats altruism within groups. Altruistic groups beat selfish groups. Everything else is commentary” (27, p. 345).

The need for group-level selection to explain group-level adaptations was stated by Williams in no uncertain terms: “Only by a theory of between-group selection could we achieve a scientific explanation of group-related adaptations (26, p 93).” At the time, Williams argued that between-group selection is invariably weak compared to within-group selection, so that adaptations “for the good of the group” do not exist. This empirical assessment began to change almost immediately, as detailed in the first supplementary section of this article. Not only have many examples of group-level adaptations been documented, but there are cases where social groups become so cooperative that they qualify as organisms in their own right—a major evolutionary transition (MET) [(28, 29); see ref. 30 for a recent appraisal]. Every entity that we call an organism,

such as bacterial cells, nucleated cells, multicellular organisms, and ultrasocial animal societies—even the origin of life as highly cooperative molecular reactions—is a product of higher-level selection.

The logic of two-level selection can be extended to multiple tiers of a nested hierarchy of units, such as from genes to ecosystems in biological systems and from small groups to global governance in human social systems. Generalizing the strong language of G.C. Williams: Adaptation at any given level of a multitier hierarchy requires a process of selection at that level and tends to be undermined by selection at lower levels.

This brief review of the evolution of prosociality in all species sets the stage for explaining the quantum jump in prosociality that took place in our own lineage.

## Social Control

Many factors influence the balance between levels of selection in any given species and context, including genetic relatedness, assortative interactions, and environmental challenges that require collective responses. For example, the challenges of life on the Savannah probably called for more collective responses than life in the forest (31). In addition, an especially important factor in the evolution of prosociality in our species was social control (32, 33).

Social control involves the punishment of individuals who fail to act prosocially within groups. Enforcing prosocial behaviors makes them selectively advantageous within groups but is itself a prosocial behavior (called a second-order public good) compared to nonpunishers within the same group (see ref. 20, p. 142–149, for an extended discussion; also, ref. 34). What is distinctive about punishment is that the within-group cost for the punisher is often small compared to the group-level benefits shared by the punisher along with everyone else. Based on its favorable benefit/cost ratio, a second-order public good can evolve under circumstances where the first-order public good, by itself, could not.

Punishment behaviors are found throughout the animal world. Even eusocial insect colonies, whose members are highly genetically related, also rely on policing mechanisms to enforce prosocial behaviors (35). Cellular mechanisms that prevent cancer in multicellular organisms can be seen a form of punishing mutant “cheater” cells (36).

Social control goes a long way toward explaining the differences between our species and our two most closely related living species, chimpanzees and bonobos. Bullies often get their way in chimpanzee communities, with naked aggression over 100 times more frequent than in small-scale human communities. Bonobos are more prosocial than chimpanzees but only because females are capable of collectively opposing male aggression (33).

In small-scale human societies, social control has been raised to the level of a fine art. There are strong norms governing acceptable behavior, and the actual behaviors of members are closely monitored. Good behavior is rewarded with high status and the material benefits that come with it. Bad behavior is discouraged, at first in a mild fashion such as with gossip and humor, but in extreme cases escalating to exclusion from the group and execution.

According to the anthropologist Christopher Boehm (32), this kind of “reverse dominance” extended very deeply into our ancestral past. Recently, the evolution of human prosociality is being described as a process of self-domestication similar to the selection for docile traits in our companion animals. This comparison has an intriguing implication: Selecting for docile behavior in domestic animals also selects for a suite of physiological, life history, and anatomical traits called the domestication syndrome. Since the domestication syndrome includes anatomical traits, the fossil record of *H. sapiens* and the genus *Homo* can be used as a source of evidence for the history of self-domestication, supporting Boehm’s conjecture (33, 37).

To summarize our progress so far, we are a highly prosocial species, thanks largely to our capacity for social control. This line of reasoning dovetails with the literature on other major evolutionary transitions in functional organization during the history of life, which also required the suppression of disruptive lower-level selection so that higher-level selection became the primary evolutionary force (38–42).

## Symbolic Thought

Prosociality evolves not only in the context of physical activities but also in the context of mental activities. What we notice, remember, and decide to do are all fundamentally social activities that take place among trusted others. To be truly alone or surrounded by uncaring others is to be mentally incapacitated (43).

The greatest group-level mental adaptation of all is our capacity for symbolic thought (19, 40, 44–47). Other animals have communication systems and cultural traditions, but humans are highly distinctive—to the point of being unique—in our ability to maintain a flexible inventory of symbols with shared meaning. Unlike associative learning, which results in mental associations that are tightly coupled with contiguous environmental associations, object-symbol relations in symbolic thought can be arbitrary, bidirectional, readily combined into networks and, once learned, become permanently established (48).

The capacity for symbolic thought is not necessarily computationally difficult. The main challenge from an evolutionary perspective is to explain its adaptive value (44). What good is an interior world that has become largely decoupled from the exterior world? The answer is that the interior world results in a suite of behaviors that is enacted in the exterior world. In this respect, a symbolic system becomes a cultural inheritance system, which first evolved by genetic evolution and then coevolved with it throughout our history as a species.

Like the genetic inheritance system, the cultural inheritance system has an impressive combinatorial diversity. Even a handful of interrelated symbols that vary in their meaning and connections give rise to innumerable combinations, with each “symbotype”—a term coined to stress the comparison with genotypes—also potentially resulting in a different suite of phenotypic traits for selection to operate upon (18).

The coevolution of a genetic and cultural stream of inheritance is called the dual inheritance theory (8, 49, 50). As the faster process, cultural evolution often plays the lead role. First, we adapt to our environments culturally, and then,

genetic evolution follows at a slower pace. The genetic evolution of lactose absorption in adult humans, following the cultural evolution of dairying practices, is a well-documented example (51).

Genetic and cultural evolution are so intertwined that child development cannot take place except in a cultural milieu. The Jesuit Priest and paleontologist Pierre Teilhard de Chardin was among the first to appreciate this dependency when he wrote: “a new matrix, coextensive with the whole human group, was formed about the newly born human child—a matrix out of which he cannot be wrenched without incurring mutilation in the most physical core of his biological being.” (52) Modern research substantiates this view of cultural transmission and child development in considerable detail (5, 13, 53, 54).

Human cultural evolution is a multilevel process, no less than genetic evolution. In other words, a culturally derived trait can potentially succeed by increasing the fitness of individuals relative to other individuals within a group, by increasing the fitness of groups relative to other groups in a multigroup population, and so on for multiple tiers of groups. Human history is a fossil record of multilevel cultural evolution, leading to a net increase in the scale of functionally organized societies, with many reversals along the way (9). Modern life is a tug-of-war among levels of selection at multiple scales and contexts. Positive change requires altering the balance between levels of selection to bring about functional organization where it does not currently exist.

The second supplementary section of this article provides historical context and shows how generalized Darwinism can avoid the deeply problematic application of evolutionary theory associated with Social Darwinism.

## Practical Applications

We will briefly describe how these ideas from basic science can be applied to four major policy areas.

**Complex Systems Science and Engineering.** The developments in evolutionary science that we have recounted, starting roughly in the 1970s, were paralleled by developments in complex systems science (55). With the advent of widespread computing, a Pandora’s box was opened for the study of complex systems of all sorts—physical, biological, and social. Cellular automata and agent-based models showed that very simple behaviors at the level of the agent could produce very complex behaviors at the level of the whole system. Patterns in nature could now perhaps be explained as properties of complex systems rather than as products of natural selection. Terms such as “chaos”, “the butterfly effect,” and “multiple attractors” captivated the public imagination (56).

Integrating the developments of evolutionary science and complex systems science is still a work in progress. In particular, it is important to identify two meanings of the key phrase “complex adaptive system” (CAS): A complex system that is adaptive as a system (CAS1) and a complex system composed of agents following their respective adaptive strategies (CAS2; 57). Multilevel selection theory speaks clearly about this distinction: Despite being complex, CAS2 systems do not automatically self-organize into CAS1 systems.

Instead, a process of selection at the level of the whole system is required and tends to be undermined by selection at lower levels within the system.

Most accounts of complex systems theory do not make this distinction, intermixing examples of CAS1 systems (e.g., the immune system, the brain, and social insect colonies) and CAS2 systems (e.g., ecosystems, traffic flows, and war; 58). There is little awareness that CAS2 systems can be profoundly maladaptive as whole systems. A search on the Web of Science resulted in over a thousand hits for the phrase “complex adaptive systems” and zero hits for the phrase “complex maladaptive systems” (59).

The main reason why complex systems theorists fail to make the distinction is because CAS1 and CAS2 systems alike can be highly interdependent and exhibit emergent properties, multiple basins of attraction, nonequilibrium dynamics, and so on. The properties of all complex systems cannot address the specifically evolutionary question of how a complex system can evolve into an adaptive unit.

The practical relevance of multilevel selection is therefore immense. Nearly every positive change effort is an attempt to create a system that functions well as a system (CAS1). Nearly every social pathology is a result of agents within a system acting at cross-purposes with each other (CAS2). How to convert CAS2 systems into CAS1 systems is therefore *the* policy question across all topic domains.

While this insight is lacking from general complex systems theory and other theoretical frameworks such as neoclassical economics (see below), it is not entirely new. In fact, many practical change efforts that are driven by experience, rather than by theory, converge upon system-level selection because it is the only thing that works. In the engineering profession, for example, it is common knowledge that systems quickly reach a point where they cannot be modeled with analytical equations, calling for a more experimental approach that includes physical prototypes, computer simulations, and digital twins. The whole system cannot be optimized by separately optimizing the parts. Instead, the whole-system consequences of interactions among the parts must be included in the analysis. This amounts to a process of system-level cultural evolution in which all three ingredients—the target of selection, variation oriented around the target, and replication of best outcomes—are carefully managed.

A similar story can be told for every major policy domain, such as national governance, the smart cities movement, rural and international development efforts, the manufacturing industry, and efforts to create entrepreneurial ecosystems (60). In all cases, efforts that rely excessively on the pursuit of lower-level interests (*laissez faire*) result in problematic CAS2 systems. Efforts that rely excessively on centralized planning fail because the systems are too complex to be comprehended by any group of experts. Experience pushes pragmatic change efforts into the zone of system-level cultural evolution.

An example from the manufacturing industry is the continuous improvement cycle pioneered by Sakichi Toyoda, first in the automatic loom industry and then in the fledgling automobile industry (61; discussed from a cultural evolutionary perspective in ref. 11, ch. 9). Workers at a Toyota assembly plant are expected to signal any dysfunction, resulting in a

swarm of activity to fix the problem. Candidate solutions are implemented experimentally, and the consequences for the whole assembly plant are monitored to take cascading effects and unforeseen consequences into account. This is clearly a variation–selection–replication process with the performance of the whole system as the explicit target of selection, even if the inventors of the process never used the word “evolution”.

Similar examples across policy domains not only provide much to learn from but also illustrate a problem: Each domain is a world unto itself, described in its own special language, and largely unknown beyond its borders. In evolutionary terms, they are examples of convergent cultural evolution similar to turtles, snails, and armadillos independently evolving hard shells.

Multilevel cultural evolutionary theory provides a more general description and rationale for the necessity of system-level selection, enabling previously isolated examples to be compared with each other and the development of a domain-general set of practical tools for going about it (14). This is the same kind of explanatory scope that is customary for the study of genetic evolution but only now starting to take place for the study of human cultural evolution.

**Economics and Business.** The economic metaphor of the invisible hand suggests that the lower-level pursuit of self-interest robustly benefits the higher-level common good. This is the exact opposite of multilevel selection theory, which suggests that lower-level selection tends to undermine the higher-level common good.

Adam Smith invoked the metaphor of the invisible hand only three times. The full corpus of his writing, including his *Theory of Moral Sentiments* in addition to his *Wealth of Nations*, is much more nuanced (62; see ref. 63 for a discussion of Smith’s *Moral Sentiments* informed by evolution). The same can be said for many schools of economic thought, but the dominant school—known as neoclassical economic theory—comes close to an elaborate justification of “greed is good”, which started to invade the business world in the 1970s with Milton Friedman’s famous dictum that the only social responsibility of a business is to increase profits for its shareholders (64; see ref. 65 for the harmful effects of this legacy).

The “greed is good” ethos of economics and business does not lack critics—but it does lack a principled alternative paradigm. That is what multilevel cultural evolutionary theory is in a position to provide. A key figure in this paradigm shift is the political scientist Elinor Ostrom, who studied groups that attempt to manage common-pool resources such as forests, pastures, fisheries, and the groundwater (66, 67). Orthodox economic wisdom held that the overexploitation of these resources (the famous “tragedy of the commons”; 68) can be avoided only by privatizing the resource or by top-down regulation. Ostrom’s research proved otherwise: Groups can self-manage common-pool resources if they implement eight core design principles (CDPs).

Despite the fame of winning the 2009 Nobel in economics, Ostrom’s work represents another example of a great idea trapped inside disciplinary boundaries. She was unknown to most economists when she won “their” prize, and her approach remains best known in the context of common-pool resource management (69). Fig. 1 presents a version of the

1 Clear group <b>identity</b> and shared sense of <b>purpose</b>
2 <b>Equitable</b> distribution of benefits and resources
3 <b>Inclusive</b> decision-making
4 <b>Transparency</b> of behavior
5 Graduated <b>responding</b> to helpful and unhelpful behavior
6 Fast and fair <b>conflict resolution</b>
7 <b>Autonomy and authority</b> to implement CDP1-CDP6
8 Appropriate <b>relations with other groups</b> (consistent with CDP1-CDP7)

Fig. 1. “Core design principles” for successful cooperation.

CDPs that can be applied to all groups whose members are trying to cooperate to achieve common goals (70, 71). The first CDP defines the group and its purpose. CDP2-6 coordinate interactions within the group and suppress disruptive self-serving behaviors. In evolutionary terms, a group that strongly implements CDP2-6 accomplishes a miniature MET for its internal governance. CDP7-8 extend the same principles to between-group interactions. It is highly noteworthy that the CDPs are scale independent—as relevant to interactions among nations in the global village as interactions among individuals in real villages. We will return to this point in the final section.

Generalizing the CDPs, across both contexts and scales, leads to a bold prediction: Virtually all functionally oriented groups can benefit from implementing the CDPs, no matter what their specific purpose. A second prediction is that business groups, on average, will be deficient in all of the CDPs due to the blinding influence of neoclassical economics and the shareholder value model.

Both predictions are supported by a survey study that asked participants to provide information about CDP implementation and group performance outcomes in two groups that they knew well: a workplace group and any other group of their choice (72). Implementation of the CDPs correlated strongly with performance outcomes in all kinds of groups, and business groups, on average, were deficient in all eight CDPs. The largest deficits were in decision-making (CDP3), sense of identity and purpose (CDP1), and local autonomy (CDP7). In other words, many people surveyed in this study felt that in their workplaces they do not take part in the decisions that impact them, do not find much meaning in their work, and are not allowed to do their jobs as they see fit.

These are averages. Some businesses do a great job implementing the CDPs and thrive as a result. Other kinds of groups sometimes fail to implement the CDPs and break down as a result. Moreover, in addition to this survey study, evidence for the efficacy of the CDPs in the business and management literature is overwhelming, once one knows what to look for (73).

The existence of abundant evidence, which somehow gets ignored, returns us to the concept of symbolic systems as cultural genomes or “symbotypes.” Nothing “makes sense” all by

itself—only against the background of the symbolic meaning systems inside our heads. When the symbotype is neoclassical economics and the shareholder value model, certain actions make sense, such as maximizing quarterly earnings, ranking employees and firing the lowest 10% every year, and so on. The elites often benefit from these practices and have what seems like an authoritative theory to argue for its societal benefits. Against this background, contrary evidence becomes invisible or easy to ignore as anomalous. For example, many corporations continue to engage in “rank and yank” firing practices despite compelling evidence against its efficacy (74).

When the symbotype is multilevel cultural evolutionary theory, the “best practices” of the shareholder value model appear pathological, evidence for the efficacy of the CDPs is in plain sight and confirm theoretical expectations rather than appearing anomalous. As Einstein put it: The theory decides what can be observed (75).

Before the advent of the shareholder value model, it seemed like common sense for corporations to act as solid citizens and to see their own welfare as part of the welfare of a larger whole. In opposition to the shareholder value model, a number of movements have arisen within the business world, including Triple Bottom Line (76), B-Corporations (77), Regenerative Economics (78), Conscious Capitalism (79), and more recently, ESG (Environmental, Social, and Governance) investing. Along with the positive change efforts described in the section on complex systems science and engineering, these are examples of convergent cultural evolution, which are important as far as they go but can go farther by fitting within a more general theoretical framework.

**Mental Health and Well-Being.** Clinical psychology seeks positive change at the level of the individual, sometimes extending to couples and families. Training in clinical psychology includes a strong biological component, such as neuroscience, endocrinology, and epigenetics, but—as with other topic areas—evolution is construed in narrowly genetic terms. A recent special issue of the journal *Clinical Psychology Review* broadens the view along the lines of this article (80). Here, we will focus on two key factors: treating the individual as an evolving unit and multiple levels of treatment.

**Treating the individual as an evolving unit.** The Darwinian triad of variation, selection, and replication can be an intragenerational process in addition to an intergenerational process. The best-known example is the vertebrate immune system, which includes an innate and adaptive component. The innate component is an elaborate system of defenses that evolved by genetic evolution and does not change during the lifetime of the organism. The adaptive component involves the creation of tens of millions of antibodies and the selection of those that successfully bind to antigens. These two components are not separate but coordinate intimately with each other to defend the organism against infectious agents and rogue elements (e.g., cancers).

The human behavioral system can be regarded as much like the immune system. In this case, the innate component is a modular architecture highlighted by the discipline of evolutionary psychology (81), which evolved by genetic evolution and does not change during the lifetime of the organism. The adaptive component is the capacity for open-ended

behavioral change highlighted by behaviorism—what B.F. Skinner called “selection by consequences” (82, 83). The fact that these two schools of thought within psychology can be integrated with each other is itself a new development (18, 84). So is the extension of traditional behaviorism beyond the kind of operant conditioning found in many species to include the distinctively human capacity for symbolic thought, as briefly described above (40, 48).

For the practicing clinical psychologist, this means that both the need for therapy and the therapeutic process can be understood as a form of personal evolution. Darwinian evolution in all its forms does not make everything nice. In the context of personal evolution, it can lead to behaviors that are adaptive in a narrow sense, such as protecting the individual from immediate harm or controlling social partners for short-term relative gain (“surviving”) but become obstacles to the well-being of self and others in a larger sense (“thriving”). Getting from “surviving” to “thriving” requires managing the process of personal evolution, consciously choosing the target of selection, orienting the behavioral repertoire around the target, and retaining the practices that take one in the direction of valued goals. Given that thriving almost always means collaborating with others, getting from surviving to thriving also involves a shift from selection of behavior for individual protection to selection for collaboration in groups.

A class of therapeutic methods that adopt such an approach are the mindfulness-based techniques of so-called “third wave” cognitive behavioral therapy, such as acceptance and commitment therapy (ACT), dialectical behavior therapy (DBT), and mindfulness-based cognitive therapy (MBCT). These methods are effective not only for individuals who are sufficiently distressed to seek therapy for mental health problems but also to address behavioral health or social wellness and to improve performance no matter what one’s current skill level. ACT alone is supported by over 1,000 randomized control trials (85) demonstrating its efficacy for a constellation of behaviors, some associated with therapy (e.g., anxiety and depression) and others associated with training (e.g., academic, business, or sports performance).

A key construct of ACT is psychological flexibility, which in evolutionary terms maps onto the capacity to manage multilevel and multidimensional biopsychosocial adaptability. Adaptability refers to the ability to show healthy variation, selection, and retention of context-appropriate skills in the areas of emotion, cognition, attention, sense of self, motivation, and overt behavior. What are these skills? Healthy emotional openness and cognitive flexibility, instead of avoidance and self-judgment; healthy conscious attention to the now, instead of mindless rumination and worry; and healthy values clarity and commitment skills, instead of a lack of meaning, purpose, and behavioral self-efficacy.

Just as groups vary in their implementation of the core design principles, individuals vary in their adaptability. Those on the high end of the distribution roll with the punches and stay on the course of their true values without needing to be coached. A recent systematic review (86) found that across the entire world’s literature of randomized trials of psychosocial methods for mental health improvement, concepts allied to mindful adaptability accounted for well more than

half of the successful identification via mediational analysis of pathways to positive outcomes.

For those who want to become more adaptable, methods as simple as reading a book and working through its exercises, without seeing a trainer, can result in significant and long-lasting improvements (87, 88). Indeed, after successful testing in several randomized trials (e.g., ref. 89), the World Health Organization now freely distributes an ACT-based program called Self-Help Plus in 21 different languages (90) because it successfully altered adaptability and mental health outcomes in victims of war, and the WHO concluded it was helpful for “for anyone who experiences stress, wherever they live and whatever their circumstances.”

**Multiple levels of treatment.** All forms of face-to-face psychotherapy can be thought of as group processes. Even if an individual person is seen, and neither a couple or family nor a group of individuals as occurs in group therapy, psychotherapy is a social process between a therapist and a client. As we have seen, whenever a MET occurs, the group becomes the organism, and group members function in the context of a larger whole. This concept has become well established for cells within multicellular organisms and individual insects within social insect societies. It needs to be part of the conceptual system used to understand therapy itself.

Throughout our history as a species, individuals never lived alone. They always lived in the context of highly cooperative groups—even when those groups were warring with other groups. This means that social resources were always available to individuals along with their personal resources. Our brains and bodies therefore evolved by genetic evolution to integrate personal and social resources when making their myriad trade-off decisions, most of which operate beneath conscious awareness (91, 92).

Against this background, social isolation—reliance only on one’s personal resources—is interpreted by our brains and bodies as an emergency situation. The most natural, obvious, and practical solution from a multilevel perspective is the provision of social resources by helping the individual function in the context of meaningful and appropriately structured groups (i.e., by implementing the core design principles). By analogy, if an ant becomes separated from her colony, she needs to be returned to her colony—not therapy at the level of the individual ant!

A meta-analysis of treatments for adult depression demonstrates the imperative of basic social support. Correlationally, the quality of the therapeutic relationship predicts the outcomes of psychological intervention (93; discussed in ref. 92). When tested in randomized trials, however, being able to increase the quality of the therapeutic alliance differentially by intervention and as a result seeing differential changes in outcomes is rarely seen (93). This paradox is partially unpacked by considering instances when the therapeutic relationship functioned as a mediator, and psychological flexibility measures were also taken. Then, adding in the client’s increase in psychological flexibility removed the variance from the therapeutic alliance (94).

This can be said in another way. While clinical psychologists should certainly cultivate nurturing relationships with their clients, these relationships cannot last forever. It is critical to

help clients establish other nurturing relationships in their lives, which can continue after the therapeutic relationship ends, and to internalize the benefits of good social support in ways that self-amplify. When the therapist models psychological flexibility and mindful adaptability skills, good therapeutic alliances form and people change (86). These effects will tend to last if the client then internalizes those same skills and applies them in their own personal and social life, leading to better and more satisfying relationships and creating a self-amplifying system of adaptability and social support (95–97).

Embedding individuals in meaningful and appropriately structured groups produces a double benefit: Individuals thrive, and the groups are much more efficacious than individuals can be on their own. A bridge is also created between topic areas (such as clinical psychology, business, and economics) that previously were largely isolated from each other. Furthermore, small groups need to be embedded within larger groups, as we will show in the next section.

**Global Change.** The basic principles of multilevel selection are scale independent, equally relevant to within-group and between-group interactions, all the way up to interactions among nations and giant corporations within the global village. The larger the scale of governance, the more difficult the challenges. We are not naive about the difficulty of global change efforts. Nevertheless, realizing that global change efforts are not different in kind from smaller-scale efforts is an important conceptual simplification. What we must work toward is relatively straightforward from a multilevel evolutionary perspective, even if it might be very difficult.

**The earth system as the ultimate unit of selection.** We have seen that multilevel selection is like a perverse alchemist who turns gold into lead. Self-preservation—a good thing—becomes disruptive selfishness. Helping kith and kin—a good thing—becomes cronyism and nepotism. The welfare of my nation—a good thing—leads to international conflicts. Thriving economies—a good thing—leads to overheating the earth. Nearly everything that is pathological at higher scales can be traced to behaviors that are prosocial at smaller scales.

The only solution to this problem is for policies to be formulated with welfare of the whole-earth system in mind. This is not sufficient by itself, as we will elaborate below, but the basic logic of multilevel selection reveals that it is necessary. There is no invisible hand to permute lower-level interests into higher-level welfare other than our own conscious efforts.

Superficially, it might seem that selection at the planetary scale is impossible because our planet is not competing with any other planets. What makes planet-level selection possible is a decision-making process that makes planetary welfare the target of selection, orients variation around the target, and identifies and replicates better practices, realizing they will be sensitive to context. This is how conscious cultural evolution takes place at smaller scales, as described in the previous sections, and can also take place at the global scale.

The concept of the whole earth as a cooperative system and the primary social identity of an individual was beyond the imagination only a few centuries ago. Nevertheless, when it comes to cultural evolution, the past does not predict the future. Given the myriad forms of globalization that have taken

place during the last century, it is difficult not to consider the whole earth as a single system that must transition from CAS2 (“survive”) to CAS1 (“thrive”). Human social groups are nearly always socially constructed. To say “I am first and foremost a human being and citizen of the earth” is no more difficult than to say “I am an American” or “I am a Christian.” (98)

Many people have already adopted a whole-earth ethic, which does manifest as action to a degree—but they do not have a common and authoritative theoretical framework to invoke and from which to derive effective policies. This is in contrast to neoclassical economics and its elaborate mathematical justification of the invisible hand metaphor. Multilevel selection reveals the invisible hand metaphor to be profoundly untrue. It is simply not the case, in economics or any other policy domain, that the lower-level pursuit of self-interest robustly benefits the common good. However, multilevel selection does lead to another, more legitimate conception of the invisible hand metaphor (99). We must act in two capacities: as designers of whole systems and as participants in the systems that we design. As designers, we must have the welfare of the whole system in mind, which is the opposite of the invisible hand metaphor. As participants, we can indeed respond to our local concerns without having the whole system in mind. Put another way, selection at the level of whole systems *is* the hand, which winnows the small set of lower-level behaviors that benefit the common good from the much larger set of lower-level behaviors that undermine the common good.

**Small groups as the cells of multicellular societies.** One of the most radical implications of multilevel cultural evolution is to identify not the individual but the small, functionally oriented, and appropriately structured group as the fundamental unit of human society (92). This was the only scale of human society at the origin of our species and needs to remain the “cells” of larger-scale societies today.

It might seem that humans should be genetically programmed to adopt the core design principles or more generally the social organization that suppresses disruptive self-serving behaviors within groups, so that the group becomes the primary unit of selection. This is probably true to a degree. Our moral psychology, for example, can be interpreted as part of the innate component of our behavioral system. It is an empirical fact, however, demonstrated by Ostrom for common-pool resource groups and likely to hold for all types of groups that they *vary* in their implementation of the core design principles. Only some achieve a high degree of implementation on their own.

Part of this variation is due to symbolic systems that downplay the importance of groups and portray the self-interested individual as the fundamental unit of society. Remember that our behaviors as humans are governed at least as much by our symbotypes as by our genotypes. Hence, sociologists such as Robert Putnam have documented the erosion of small groups during the second half of the 20th century up to the present (100). While this is regrettable, the trend is reversible. Once we adopt a theory that properly showcases the importance of small and appropriately structured groups, for both individual thriving and efficacious action at larger scales, then we can proceed to rebuild the cellular fabric of large-scale society across all social contexts.

### Importance of social control and mesoscale social identities.

So far, we have emphasized the importance of a global social identity and the importance of small, appropriately structured groups. There remains a veritable tropical rainforest of mesoscale social identities, such as a person's nationality, ethnicity, gender, religion, political affiliation, and the multilevel institutional structure of any large-scale society (101, 102). These identities are part of our cultural evolutionary past and the starting point for future cultural evolution. We cannot make them go away, any more than we can make our personal histories go away. In many cases, they deserve to remain strong as long as they are coordinated—and policed—with the global good in mind.

To begin, it is important to grasp the radical implications of dual inheritance theory for understanding the nature of human cultural diversity. Gene-centric views of human evolution, including the field of evolutionary psychology during its early days (81), imagined a universal human nature that evolved by genetic evolution. Cultural variation was regarded as a thin veneer caused as much by the triggering of genetically evolved modules as by open-ended cultural evolution.

Social constructivists from sociology and cultural anthropology have always opposed this view (e.g., refs. 103 and 104), and dual inheritance theory is validating their critique to a considerable degree. Differences between societies can run very deep, reflecting separate cultural evolutionary histories. Much previously regarded as universal human nature is actually quite peculiar and restricted to cultures that are WEIRD: Western, Educated, Industrialized, Rich, and Democratic (6).

Once we view human societies as products of cultural evolution, we can interpret their differences in the same way that biologists interpret differences among species due to a combination of isolation and response to different selection pressures (105, 106). This is an advance over social constructivism in sociology and cultural anthropology, which, while properly critical of genetic determinism, did not adopt an evolutionary perspective to explain cultural diversity.

It is here that the concept of mismatch becomes central for the study of cultural evolution, no less than genetic evolution (107, 108). In both cases, adaptations to past environments can become maladaptive in new environments. The human impact on the planet, which is so massive that it has been labeled the Anthropocene, has created genetic mismatches for nearly every species on earth—and cultural mismatches for nearly every human society on earth. What worked in the past can tragically misfire in the present. Only ongoing cultural evolution can solve this problem, and unless it is mindfully directed, it will result in pathological CAS2 systems rather than coordinated CAS1 systems.

An especially important axis of cultural variation in this regard is from “tight” to “loose” (109). Societies vary in their need for immediate collective action based on environmental contexts such as natural disasters, disease pandemics, warfare, and intensive agriculture. Cultures that adapt to these contexts have strong social norms and little tolerance for deviant behavior (“tight”).

Cultures inhabiting relatively safe environments, with little need for immediate collective action, evolve to become “loose”, with norms of tolerance for individual differences. There are still protections against antisocial behaviors, and the variation can be adaptive at the group level by exploring new evolutionary pathways in ways that are prohibited by the need for immediate collective action. Most cultures are capable of varying their degree of tightness and looseness depending on the context. For example, airport check-in procedures around the world are tight, no matter how tight or loose a society in other respects.

The COVID pandemic provided a natural experiment in cultural evolutionary mismatch. Collective action was called for in all nations, but some were better adapted than others based on their past histories. An analysis of fifty-seven nations concluded that those on the loose end of the continuum had five times the cases and eight times the deaths as nations on the tight end of the continuum (110). Loose nations were mismatched to the pandemic environment as far as their immediate attempt at collective action was concerned.

In general, every meso-scale social identity calls for an understanding of its cultural evolutionary history leading up to the present and how it can further evolve to function in the context of the global common good. This process is a collective version of the therapeutic and training methods described in the previous section. Therapy and training at meso-scales might be more difficult than at the individual level, but it is not different in kind. Likewise, social control might be harder to implement at a global scale, but it is not different in kind.

### Completing the Darwinian Revolution

Dobzhansky's dictum that nothing in biology makes sense except in the light of evolution has been repeated so often that it is easy to become numb to its meaning. It is extraordinary that evolutionary biologists can routinely change the organisms they study and research questions they ask, seamlessly integrating functional, historical, developmental, and mechanistic perspectives (11).

This article illustrates how the study of human cultural evolution can achieve a similar explanatory scope. At the level of basic scientific knowledge, we can address the “big questions” such as human origins, the nature of cultural diversity, and the net increase in the scale of human society over the course of human history—with many reversals along the way and no guarantee for the future unless we structure our social environments appropriately.

At the level of practical applications, we have sampled four very different topic domains. The two common denominators for all positive change efforts are the need to cooperate and the need to be adaptable in multiple contexts and at multiple scales. Once this is comprehended in all its generality, we can look forward to a surge of effective policies that consciously evolve a world that works for all.

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