The pandemic exposes human nature: 10 evolutionary insights

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Humans and viruses have been coevolving for millennia. Severe acute respiratory syndrome coronavirus 2 (SARS-CoV-2, the virus that causes COVID-19) has been particularly successful in evading our evolved defenses. The outcome has been tragic—across the globe, millions have been sickened and hundreds of thousands have died. Moreover, the quarantine has radically changed the structure of our lives, with devastating social and economic consequences that are likely to unfold for years. An evolutionary perspective can help us understand the progression and consequences of the pandemic. Here, a diverse group of scientists, with expertise from evolutionary medicine to cultural evolution, provide insights about the pandemic and its aftermath. At the most granular level, we consider how viruses might affect social behavior, and how quarantine, ironically, could make us susceptible to other maladies, due to a lack of microbial exposure. At the psychological level, we describe the ways in which the pandemic can affect mating behavior, cooperation (or the lack thereof), and gender norms, and how we can use disgust to better activate native "behavioral immunity" to combat disease spread. At the cultural level, we describe shifting cultural norms and how we might harness them to better combat disease and the negative social consequences of the pandemic. These insights can be used to craft solutions to problems produced by the pandemic and to lay the groundwork for a scientific agenda to capture and understand what has become, in effect, a worldwide social experiment.

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"Nothing in biology makes sense except in the light of evolution" (1), and nothing about the human response to COVID-19 will either. The evolutionary arms race between humans and viruses has existed for millennia. Our bodies, packed with nutrients and the machinery of cellular reproduction, are irresistible targets for exploitation by smaller and faster-evolving organisms (2). Whereas viruses benefit from rapid replication rate and mutation potential, allowing them to quickly adapt to exploit their hosts, humans are not left defenseless. Natural selection has endowed us with a complex physiological immune system (3) that targets viruses at a cellular level and a behavioral immune system (4) that modulates human behavior to reduce the risk of contagion. Moreover, our ability to communicate and develop vast repositories of information, paired with intelligence and innate curiosity, allowed us to engineer extraordinary tools such as modern medicine. And, we have developed cultural systems of coordination that can allow us to erect walls for limiting the spread of disease.

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An evolutionary perspective can help us understand the nature of the virus, our own nature in responding to its threats, and the interactions between these. Of course, no one theory can entirely make sense of the complexity of the COVID-19 pandemic—a cascade of global events characterized by confusion as much as by illness and death. But an evolutionary approach to the pandemic provides a lens through which we can see which strategies a virus might use, which strategies we possess, and which strategies we need to acquire. The insights and research questions produced by this evolutionary approach could provide essential knowledge that could allow us to better cope with the ongoing pandemic and its downstream consequences.

For instance, as we describe below, severe acute respiratory syndrome coronavirus 2 (SARS-CoV-2) may be under evolutionary pressures to alter human behavior by increasing our extraverted tendencies—thereby creating a conduit for viral transmission from one person to another. In this respect, our own social strategies, the features that define much of what it is to be human, make us a prime target for viral exploitation. Beyond the virus–host dynamics, understanding how evolution has shaped our social minds gives us clues about how well-intentioned policies asking us to isolate and distance will profoundly affect our families, work lives, relationships, and gender roles. Finally, evolutionary principles can be applied to understand how the spread and severity of COVID-19 intersects with nationwide compassion (or lack thereof) and societal norms.

We asked 10 evolutionary scientists, including evolutionary medicine researchers, theoretical evolutionary biologists, and evolutionary psychologists, to share their insights about the evolutionary pressures on the virus, our human response to the pandemic, and how an evolutionary approach can help us cope with COVID-19. The sections that follow do not necessarily represent a consensus of all of the authors but rather a set of novel perspectives and potential approaches—from neuron to nation—that we believe should be on the forefront of the scientific agenda.

Insight 1: The Virus Might Alter Host Sociability

All agents of infection are under evolutionary pressure to manipulate host physiology and behavior in ways that enhance their survival and transmission to the next host. Physiologically, it is clear that SARS-CoV-2 affects the human body in ways that enhance the evolutionary success of the virus, by hijacking cells to create copies of itself. But, as we move from the physiological to the behavioral, it becomes less clear whether SARS-CoV-2 hijacks the neural machinery of hosts for its own ends, or whether its effects on host behavior and psychology might simply be by-products of the viral infection or immune response. The approach we take in this section is uniquely evolutionary in that the fitness interests of the virus take center stage in deriving hypotheses about the influence of SARS-CoV-2 on human physiology and behavior.

There are two possibilities for how SARS-CoV-2 might be altering human behavior. First, it may be suppressing feelings of sickness during times of peak transmissibility. SARS-CoV-2 is characterized by a high rate of viral shedding, and the peak of viral shedding—and therefore transmissibility—occurs 1 d to 2 d before the onset of symptoms (5). It is possible that SARS-CoV-2 has been particularly successful because it is highly infectious before symptoms appear. Suppressing sickness-related behavior of hosts is one way that viruses can increase their fitness. Hosts that are infected but do not feel sick are more likely to go about their usual activities, which allows them to come in contact with others whom they might infect. If they do not display symptoms of infection, the human behavioral immune system fails to activate in others (see *Insight 3: Activating Disgust Can Help Combat Disease Spread*), silently spreading to new hosts.

The second possibility of how SARS-CoV-2 could affect host behavior is by contributing to mood disorders, such as mania, that could increase activity levels and decrease feelings of sickness, at least temporarily, during times of peak transmissibility. This could potentially lead to a "tug-of-war" over host behavior, with the virus "pulling for" greater host activity and sociability and the host fighting against this to reduce activity and instead prioritize healing. If sometimes the virus is winning and other times the host immune system is able to regain control, this could manifest as a mood disorder with periods of high activity/sociability and depression/fatigue, respectively. There is a long history of case reports of mood disorders following infection with common respiratory viruses, and research suggests that people with a history of influenza and infection by previous strains of coronavirus are more likely to have mood disorders (6). Other viruses have been associated with mood disorders, including HIV (7), the 1918 influenza virus (8), and Borna disease virus (9), although causality is impossible to establish with this evidence. One study administered the influenza vaccine as a proxy for infection and found a significant change in social behavior—for the 48 h after receiving the vaccine (during the time of peak transmissibility), people interacted with others more (from 51 to 101 people) and in larger groups (from 2.4 to 5.5) than in the 48 h before receiving it (10). This study suggests exposure to viral antigens can have effects on host social behavior and is consistent with what would be expected if viruses alter host behavior to enhance viral transmission.

Viruses, in general, and SARS viruses, in particular, are known to interfere with the normal host immune response, which includes disrupting interferon (IFN) signaling (11). IFNs are molecules that help coordinate many aspects of the host's response to infection. Administration of IFN alpha (e.g., during treatment for chronic hepatitis C) is associated with depressed mood and social withdrawal (12), suggesting that inhibiting IFN signaling could be a mechanism by which SARS-CoV-2 might alter social behavior. It is also possible that SARS-CoV-2 might indirectly reduce IFN levels through exhausting CD8 T cells (13) which typically manufacture IFN gamma. However, viral effects on the sociality of the host could simply be a by-product of the virus interfering with host antiviral immunity, rather than a viral adaptation to alter host sociality.

No studies have yet looked at changes in social behavior with exposure to SARS-CoV-2. However, there is ample evidence that SARS-CoV-2 has neurological effects (14). SARS-CoV-2 seems to have a predilection for infecting neural tissue and causing neurological symptoms, found in up to 36% of patients in initial reports (15). SARS-CoV-2 has been recovered in the spinal fluid of COVID-19 patients (16), suggesting that the virus can directly invade the brain and nervous system.

SARS-CoV-2's neural effects may be a result of evolutionary adaptations of the virus itself, by-products of other effects of the virus, or the host's counterresponse to the virus. Possibly, the host's immune response to SARS-CoV-2 creates neuroinflammation that then influences host cognition and behavior in ways that have nothing to do with enhancing the fitness of the virus. However, if SARS-CoV-2 is manipulating host behavior for its own benefit, this affects how we treat and manage it. Similarly, if

SARS-CoV-2 is affecting host social behavior, this would also affect epidemiological models, because contact rates change over the course of disease progression (10). By understanding how SARS-CoV-2 is evolving and having behavioral and psychological effects on us that enhance its transmission, we will be better able to shape its evolutionary trajectory so it becomes less harmful and less lethal.

Scientific Agenda. Along with physiological symptoms, catalog neurological, psychological, and behavioral symptoms of COVID-19, and create a repository of associated biological samples. Identify whether certain suites of symptoms are associated with particular genetic variants of SARS-CoV-2, and whether natural selection is favoring variants that are associated with more neurological symptoms.

Insight 2: "Generation Quarantine" May Lack Critical Microbial Exposures

The pandemic has focused the world's attention on microbial influences on human life. Whereas the emphasis has been on the SARS-CoV-2 virus, quarantine has temporarily halted the regular exposure to novel pathogens that is characteristic of human social interaction. An evolutionary perspective reminds us we must consider the potential trade-offs of this intervention. Children and adolescents whose immune systems and brains are actively shaped by microbial exposures may be most impacted by this change. For some, decreased exposure to novel microbes will be beneficial. Viruses, including SARS-CoV-2, that cross the blood–brain barrier can cause neuroinflammation (17) or encephalitis (18); pathogenic exposures during critical neurodevelopmental windows have been linked to neurological impairment and disorders, including schizophrenia (19) and autism spectrum disorder (20).

Although reduced exposure to neuropathic viruses during quarantine may protect some, normal brain development requires adequate and diverse microbial exposure. During development, communication between the gut microbiota of a young animal and the microglial brain cells that shape networks through myelinization and selective synaptic pruning influence its future cognitive, motor, and affective characteristics (17). Young animals experimentally deprived of normal microbiota develop into adults with altered cognition and anxiety (21), and an irregular host microbiome is implicated in developing some neurodegenerative diseases (22).

The adaptive benefits of microbe exposures on developing brains and immune systems may include enhanced coordination between protective behaviors and immunologic responses. Adolescence prepares animals for a range of dangers they may encounter in adulthood, including exposure to new pathogens. Predispersal exposures to microbes prime developing immune systems for anticipated novel microbial threats. This is why adolescents leaving for college receive vaccinations to prime their immune systems for pathogens they may encounter for the first time. Similarly, the immune systems of adolescent animals are primed by low-level exposures to microbes from the outside world through brief forays, *practice dispersals*, into the outside world, including play with conspecifics and other social activities (23, 24). But the risk-taking, neophilia, and drive to be sexual and socialize that characterize adolescence and promote dispersal are influenced by microbiota now fundamentally altered for many millions of adolescents around the world. COVID-19 has temporarily ended practice dispersals, physical peer-to-peer play, sexual activity, and other activities which would otherwise bring millions of adolescents into contact with novel microbes.

Although there may be fewer cases of virally induced neuropathology, such policies will also result in a generation whose neurodevelopment will have been influenced disproportionally more by the microbial environment of their natal family in quarantine than by the outside world. The impact that reduced exposure to the microbial outside world will have on "generation quarantine" will likely vary based on duration of quarantine and an individual's developmental stage—but is otherwise unknown. Following the neurodevelopmental consequences of quarantine will add to our understanding of how microbial environments shape young individuals into the adults they ultimately become.

Scientific Agenda. Conduct comparative analyses of gut microbiota of quarantined and postquarantined infants, children, and adolescents from a range of countries with variation in duration of mandatory quarantine. Assess the impact of microbiota on measures of neurodevelopment, cognition, and affective states.

Insight 3: Activating Disgust Can Help Combat Disease Spread

Disgust is a physical and social protective system that is a product of, and sheds light on, our evolutionary past. Disgust protects across three domains, all of which relate to pathogen exposure (25, 26). First, disgust is part of our food psychology and motivates avoidance of foods harboring, for instance, signs of toxins and microorganisms. Second, disgust is part of our sexual psychology and motivates avoidance of sexual partners (e.g., family members) judged to potentially risk the immunocompetence and, hence, health and viability of offspring. Last, and most pertinent, disgust is part of our physical contact psychology and motivates avoidance of individuals displaying signs of infection, surfaces revealing microbial infestation, and the skin, mouth, anus, and bodily fluids of unknown others. Together, consumption, coitus, and contact are all behaviors regulated by disgust and—because of the link to disease—all associated with one or more historical foodborne, sexually transmitted, or contact-facilitated pandemics.

Motivations to physically distance and to cleanse after contact with potentially contaminated surfaces are native to the contact disgust system but are strongest when there are clear signs of disease—blood, guts, bodily fluids, yellow eyes, pale skin, lesions, or a runny nose. In the COVID-19 pandemic, this is not what most people see. Family, friends, coworkers, and strangers look healthy—as they can be asymptomatic for days, not knowing they are infected (27). Without ecologically valid cues to infection, the contact avoidance function of disgust remains idle, posing an acute challenge to lawmakers enacting rules enforcing distancing. Given that valued relationships are often marked by gentle physical contact (e.g., hugs, handshakes, kisses), it is difficult to dissuade people from reaffirming their "close relationships," especially during a time when such relationships are sorely needed. Disgust might therefore be important, although sometimes less potent than other emotions, such as empathy, to persuade people to distance.

One way to improve the public's response to the next pandemic would be to appeal to several emotions and include information successful in triggering our ancient psychology of disease avoidance. In addition to statistics and the fear and anxiety they might evoke, images of individuals who are ill and display signs of sickness or images that clearly show pathogens on common surfaces might activate the disgust system and further motivate adherence to mitigation guidelines (28). There are drawbacks to this approach too; vile disease images could be potentially traumatic, and personal disgust can influence moral sentiments in nefarious ways (26). Ultimately, the decision to distance will reside with the individual, so the more tactics we can use to motivate this behavior, the better, and disgust—along with fear and empathy—is an important emotion in this effort.

Scientific Agenda. Compare efficacy of disgust-eliciting messaging versus non−disgust-eliciting messaging on public health behaviors, such as handwashing, wearing masks, and maintaining safe distances. Gauge public opinion on the acceptability of using disgust-eliciting messaging directed at children versus adults.

Insight 4: The Mating Landscape Is Changing, and There Will Be Economic Consequences from a Decrease in Birth Rates

Differential reproduction is the key to change over time. Humans have an evolved menu of mating strategies as products of successful reproduction, including long-term pair bonds, short-term casual sex, and everything in between (29). The COVID-19 pandemic is influencing these mating strategies and will have a profound impact on the global mating and economic landscape.

Short-term mating is the most obvious strategy to be affected. Novel sex partners are potential virus vectors, rendering the costs of casual sex steeper. In-person sex is being replaced, perhaps temporarily, with online versions—sexting, video cams, and virtual sex. For those who risk in-person sex, the use of condoms, although effective against many sexually transmitted infections, will not prevent contracting COVID-19, since transmission can occur through contact with an infected person's mouth, nose, skin, or breath. An evolutionary perspective predicts that those who pursue a fast life history strategy—marked by short-term mating pursuit, frequent partner switching, deceptive mating tactics, and steep future discounting (30)—are most likely to risk in-person sex during the pandemic and become potential superspreaders.

Although the pandemic-related costs of short-term mating should make a long-term pair-bonding strategy more attractive, the pandemic also temporarily shrinks the market for long-term partners. Singles in search of a commitment must settle for online preliminaries or dating at a safe social distance. Touch and scent are central to mating compatibility (31), but distance deprives individuals of this vital information. Mating at a distance exacerbates the tendency of people to interpolate positive values for qualities for which they lack reliable information, such as honesty, emotional stability, and sexual history. This overidealization creates unrealistic expectations that risk being shattered when an eventual meeting takes place in real life. Unless virus test certificates become common, romantic consummation will be delayed for all but the medically uninformed and the high risk-takers—trends that may, in turn, bias birth outcomes.

The economic recession brought on by the global pandemic could bring about dramatic changes to long-term mating opportunities and reproductive outcomes. An evolutionary perspective predicts that women will be reluctant to commit to men lacking financial stability, given the priority they place on this quality in long-term mating (32). It also predicts that men, in turn, will postpone marriage until they feel they have adequate resources to attract women of adequate or commensurate mate value (33). As marriage rates plummet and people postpone reproduction, at least for a period of time (34), some nations already on the cusp of population replacement level will fall dangerously below it as people opt to avoid bringing a baby into a virus-plagued world. Birth-rate drops, in turn, have cascading consequences for economic outcomes—job opportunities, the ability of countries to provide safety nets to an aging demographic, and a global economic contraction.

Scientific Agenda. Use data from dating apps, sexually transmitted infection rates, and surveys to understand shifts in mating behaviors as waves of outbreak, lockdowns, and economic downturns occur. Monitor birth-rate change in populations with birth rates at or below replacement level. Investigate associations between people's decisions to remain single or to delay having children with fears about the pandemic and dissatisfaction with mating options due to resource loss and other factors.

Insight 5: Gender Norms Are Backsliding, and Gender Inequality Is Increasing

With schools shut down, families have unanticipated needs for childcare. Who is picking up this slack? In April of 2020, women lost more jobs than men, in part because more women than men are employed in hospitality and service industries that lost customers. However, at that same time, women more than men felt more pressured to quit their jobs in order to manage added household responsibilities of childcare and education, and worried more that declines in their productivity during the pandemic would negatively impact their careers (35). Before the pandemic, women already felt more stressed than men by competing family and job roles (36). With children at home, that stress seems to lead women to become homemakers and makeshift teachers.

Gendered work trends have a quantitative signature in academia. In medicine and Earth sciences, a declining proportion of women posted preprints in March and April of 2020 compared with the same months in 2019 (37). In medicine, compared to submission rates in 2019, proportionately fewer women have submitted papers about COVID-19 (38). This is happening at a time when men are showing heightened productivity (37).

The default explanation in social science is to blame outdated gender stereotypes and lack of empowerment for women (39). However, women's and men's evolved preferences play an important role. One of the insights from evolutionary approaches to understanding sex differences is that women are far more limited in the number of offspring they can produce in their lifetimes than are men (40), and women, like females across primate species, have evolved to contribute a higher level of obligatory investment in each offspring through pregnancy and lactation (41). Therefore, throughout evolutionary history, a woman's reproductive fitness hinged on the success of each individual offspring to a greater extent than a man's. As a result (or in concert), women evolved stronger motivations to attend to the details of childcare and may feel pressured to accept more childcare and homemaking responsibility when others, such as teachers and childcare workers—or extended kin, who might otherwise help out—cannot.

Evolutionary reasoning predicts women will leave the workplace or sacrifice their productivity more than men will. This could result in a large-scale backslide toward "traditional" gender norms. With the loss of their own economic autonomy, many women will come to rely on male partners as breadwinners, exacerbating the structural problems underlying gender inequality. This may shift families toward traditional structures and conceptions of gender—a shift toward social conservatism, which might have consequences for attitudes about premarital and extramarital sex (42).

Women and men in traditional families prefer norms that activate moral judgments that can insulate those family structures, including negative attitudes about promiscuity (43). A consequence of the pandemic, therefore, could be a reduction in tolerance across a range of issues, including nonmonogamous mating arrangements, legal abortion, and rights for sexual minorities—who violate traditional gender roles and are also stereotyped as promiscuous (44).

The looming recession will increase competition among women for access to desirable mates (see *Insight 4: The Mating Landscape Is Changing, and There Will Be Economic Consequences from a Decrease in Birth Rates*). There will also be greater competition among men as they strive to secure increasingly rare positions of status and wealth. These changes could contribute to gender norms that emphasize attractiveness for women and status competition for men. For instance, in cities and nations with greater economic inequality, women self-sexualize more in social media posts (45). For men, economic inequality at both the cross-cultural level and neighborhood level is associated with increased rates of male-on-male homicide, which seems to be driven by men's concerns with social status rather than a purely instrumental need to survive (46). Participants in a US online survey completed in January 2020 (prior to the US outbreak) and then later in March/April 2020 showed modest shifts upward in traditional gender stereotypes and endorsement of traditional gender roles (47), consistent with gender norms changing in response to COVID-19.

Collectively, these forces produced by the pandemic are likely to lead to a backslide in economic independence for women. Nonetheless, it is possible that the pandemic might have some positive effects on gender equality. The acceptability of remote work could allow women to continue working when previously they would have left the workforce to care for young children. Moreover, if more mothers and fathers are at home during work hours, uneven housework could become more obvious and fixable. Whether the pandemic is beneficial or harmful for men and women remains unknown—but evolutionary thinking provides important insight into where to look and what questions to ask.

Scientific Agenda. Track and compare shifts in women's and men's workforce participation and their link to increased childcare pressure. Examine whether changes in income inequality increase gendered tactics of competition that reinforce traditional gender roles, which further predict reductions in women's workforce participation. Investigate how support for new childcare needs could lessen gendered productivity declines and endorsement of traditional gender norms.

Insight 6: An Increase in Empathy and Compassion Is Not Guaranteed

There is anecdotal evidence that, in previous crises, such as hurricanes, earthquakes, and terrorist attacks, the common reaction—contrary to popular belief—is not a descent into savagery. Rather, in cases such as Hurricane Katrina and the London Blitz, there is an outpouring of solidarity and mutual aid (48). Barriers of class and race are temporarily suspended, and the benefit of the collective becomes priority (49).

With respect to the current crisis, some psychologists are optimistic (e.g., ref. 50), seeing an outburst of prosocial and altruistic behavior—"catastrophe compassion," as one scholar puts it (51). Among other considerations, the adoption of social distancing practices by billions of individuals is interpreted as "perhaps the most populous act of cooperation in history" (51). This interpretation is said to be supported by recent studies suggesting that the motivation to engage in these practices is increased by appeals to public health, more so than appeals to personal health (52), and increased, as well, by empathy inductions (53).

This is all consistent with a Rousseauian perspective: Human nature is fundamentally kind, and, stripped of the constraints of civilization, we are more equal, more generous, and mentally healthier. But there are also reasons to favor a less rosy view. Research on the behavioral immune system suggests that disease threat makes people intolerant and punitive toward outgroups (54). Nations with a history of high levels of infectious disease have lower rates of extraversion (55), and experimentally inducing disease threat spurs social withdrawal (56).

Moreover, it's unclear whether behaviors such as social distancing actually do reflect cooperative motives, as opposed to concerns about oneself, concerns about close family members, and worries about social shaming and legal sanctions. None of the studies cited as supporting altruistic motives look at actual social distancing; instead (for obvious practical reasons), they look at people's expressed willingness to engage in social distancing, and hence the findings can be readily explained by a social desirability bias.

In fact, there is no evidence, to our knowledge, for any overall increase in kindness, empathy, and compassion right now relative to nonpandemic times. One study, specifically designed to explore this issue, does find that people claim to experience more interdependence with neighbors and humanity now than in prepandemic times—but also finds that they are less likely to agree that helping someone in need "is the right thing to do" (57). Furthermore, at least in the United States—although less so in countries such as Canada—this pandemic is not bringing people together; rather, responses reflect the partisan divide that so characterizes recent times, with conservatives and liberals having different views about wearing masks, the wisdom of a continuing lockdown, and much else.

Finally, the analogy with previous disasters might not be apt. We are not sifting through rubble to rescue those trapped in fallen buildings; we are not crammed into the London underground at midnight, tending the injured while the Luftwaffe drops bombs from above. We are in isolation. Quarantine exerts a serious psychological cost (58), and, as social animals, the benefits of shared experience and mutual suffering may not hold when we are, for the most part, alone. Or perhaps this is too grim an assessment; perhaps Zoom and social media are sufficient to evoke in us feelings of warmth and solidarity. The most prudent conclusion here, given the lack of consistent evidence, is to admit that we don't yet know—but we should find out.

Scientific Agenda. Track changes in prosociality, empathy, and xenophobia over the course of the pandemic and how they interact with perceived disease threat. Compare these attitudes to before the pandemic and to past nondisease tragedies. Document and investigate cross-country variability in these patterns (see *Insight 9: Cultural Evolutionary Forces Impact COVID-19 Severity*).

Insight 7: We Have Not Evolved to Seek the Truth

Humans evolved in small groups under threat of starvation, predation, and exploitation by outsiders—and generally lived brief lives, favoring short-term strategies for consuming resources that could support successful reproduction (59). We have not evolved to think clearly about long-term threats like pandemics—which are statistically abstract and global. And yet, for at least a century, we've understood that the threat of a deadly pandemic is real and ever present (60). How should we have responded to this knowledge?

We should have prepared for the next pandemic in advance. But, to do this, we would have had to feel the need to prepare—and been willing to incur actual costs in the face of what could have seemed, in the absence of dead and dying people, like nothing more than morbid speculation.

Unfortunately, most of us are terrible at weighing risks presented as abstract probabilities (61). We also heavily discount the well-being of our future selves (62), along with that of distant strangers (63) and future generations (64), and in ways that are both psychologically strange and, in a modern environment, ethically indefensible. We're highly susceptible to conspiracy thinking (65), and display an impressive capacity to deceive ourselves, before doing the hard work of deceiving others (66). These predispositions likely endowed our ancestors with advantages (67, 68), but they also suggest that our species is not wired for seeking a precise understanding of the world as it actually is.

Thus, our conversation about most things tends to be a tissue of false certainties and unhedged bets. We look for evidence to support our current beliefs, while ignoring the rest (69). When we encounter friends or family in thrall to some fresh piece of misinformation, we often lack the courage to correct them. Meanwhile, behind a screen of anonymity, we eagerly confront the views of complete strangers online. Paradoxically, the former circumstance presents an opportunity to actually change opinion, while the latter is more likely to further entrench people in their misinformed views (70). Although these predispositions did not cause SARS-CoV-2 to first enter the human population, they are, at least in part, responsible for the pandemic that ensued.

Scientific Agenda. Evaluate methods to combat shortcomings in reasoning due to mismatches between the demands of the ancestral past and the present, conspiracy thinking, and the spread of misinformation, both in face-to-face communication and on social networks, particularly as they relate to the pandemic and health-relevant information.

Insight 8: Combating the Pandemic Requires Its Own Evolutionary Process

Some of the insights above point to flaws in our human nature that contributed to the pandemic and may make navigating it more difficult. But humans are paradoxical creatures. On one hand, we are products of genetic evolution in ancestral environments that bear little resemblance to modern environments. These "evolutionary mismatches" are likely responsible for our frequent lack of alarm in response to the pandemic. On the other hand, we constructed those modern environments, so our capacity for rapid cultural evolution—via behaviors, values, and technologies—must be acknowledged along with our genetic human natures.

This duality is captured by the label *dual inheritance theory*, which posits both a genetic stream and a cultural stream of inheritance that have been coevolving with each other for as long as we have been a species (71). The slower process of genetic evolution often follows where the faster process of cultural evolution leads, as we know from classic examples such as lactose tolerance in adults (a genetic adaptation) in cultures that keep livestock (a cultural adaptation) (72).

How can we use our knowledge of dual inheritance theory to make cultural evolution take place faster and at a larger scale than ever before—even so fast that it can keep pace with the genetic evolution of the virus? One way is to focus on the three ingredients that define a Darwinian process—selection, variation, and replication—and manage them at a systemic scale. In other words, we must identify a systemic target of selection (such as reducing transmission of the virus), orient variation around the target (including monitoring unplanned variation and controlled experiments), and identify and replicate best practices. Cultivating cultural evolution in this manner must be done realizing that such practices are likely to be sensitive to context, requiring adaptive adjustments at a finer scale (73), and that measuring efficacy will be difficult and not entirely objective.

Cultural evolution must be well monitored; otherwise, it will still take place but will result in outcomes that contribute to problems rather than solutions (e.g., conspiracy thinking and distrust of health experts). A key insight of evolutionary thinking is that—in contrast to the metaphor of the invisible hand—the pursuit of lower-level interests, such as short-term individual, corporate, partisan, or nationalistic interests, is far more likely to undermine than contribute to the global common good (74). Human cooperation in all its forms requires identifying the most relevant group, establishing norms that define the welfare of the group, and establishing mechanisms that reward good behavior and punish bad behavior. For the first time in history, we have the technological means to function as a global village of nations, but this requires scaling up the same mechanisms that make cooperation possible at all levels. The challenges of scaling up might be daunting, but the first step is to establish the theoretical necessity of doing so.

While it is new to describe it in formal evolutionary terms, managed cultural evolution with systemic goals in mind has taken place at subglobal scales throughout history and in the present, providing many positive examples to learn from. For instance, some of the best change methods in the corporate world employ rapid cycles of variation, selection, and replication with various production goals in mind (75). The same methods can be applied to a global pandemic and other global challenges by becoming more expansive about the production goals.

Scientific Agenda. Treat differences in nation/state responses to COVID-19 as natural experiments in evolutionary processes by documenting different phylogenies of responses, measuring the efficacy of each, and then replicating successful approaches in necessary areas and future pandemics.

Insight 9: Cultural Evolutionary Forces Impact COVID-19 Severity

Evolutionary principles can be applied to understand cultural adaptations during the COVID-19 pandemic. Human groups under collective threat experience evolutionary pressures to tighten social norms and punish people who deviate from norms. Accordingly, we can predict that societies worldwide will tighten in response to the pandemic. From an evolutionary perspective, strict norms and punishments that deter free riders are essential to helping groups coordinate their social action to survive, and thus would be adaptive in times of threat. Consistent with this reasoning, nations with histories of ecological and human-made threats (e.g., natural disasters, disease prevalence, resource scarcity, and invasions) tend to be tight (i.e., have stricter norms and little tolerance for deviance), whereas groups with less threat tend to be loose (i.e., have weaker norms and more permissiveness) (76). Variation in tightness in nonindustrial societies is also related to collective threats such as pathogen prevalence, population pressure, scarcity, and warfare (77).

Evolutionary game-theoretic (EGT) models also confirm that differences in normative tightness evolve as a cultural adaptation to threat. These models of cultural dynamics are useful for understanding how human behaviors evolve over time, with the aim of illuminating evolutionary stable states. With respect to culture, a stable state represents the behavioral norms that are adaptive and can be expected to remain in the population under certain conditions. EGT models show that, as societal threats increase, agents who abided by cooperative norms and punished others for deviating thrived and had an advantage over agents that did not adhere to and enforce norms (78). Technically speaking, as threat increases, agents operate in a space of lower payoffs, which increases the selection pressure they face to engage in coordinated and cooperative interactions. Accordingly, groups require stronger norms and punishment of deviance to survive under high threat (78). Indeed, experimentally priming humans with collective threat leads to an increase in desired tightness—either from God or government (79, 80).

While tightening is an evolutionary adaptation to threat, potential "evolutionary mismatches" may interfere with this evolved response, with tragic consequences, as we have seen in the spread of COVID-19 in certain nations. For instance, because environmental changes like COVID-19 can occur very rapidly—but evolution is a gradual process—there are, inevitably, periods when populations need to "catch up," often with deleterious consequences.

The varying reactions of nations around the world to early stages of the pandemic reveal potential evolutionary mismatches, wherein some loose societies have had a delayed and often conflicted reaction to tightening norms. Countries that are tight (e.g., South Korea, Japan, China) have been highly effective at limiting COVID-19 cases and deaths (81). By contrast, loose cultures (e.g., Spain, Brazil, and the United States) have had an explosion of cases and deaths in early stages. EGT models also illustrate that loose cultures take far longer to cooperate when under threat than tight cultures (82). Because people in loose cultures have generally experienced fewer ecological threats, they may be more likely to underestimate the risk of COVID-19 than those in tight cultures. Likewise, because loose cultures prioritize freedom over rules, they may experience psychological reactance when tightening is required. The situation is compounded when governmental leaders minimize threat signals. Thus artificially diminishing the intensity of the threat can reduce the tightening response, which reinforces the evolutionary mismatch. Research is sorely needed on how to prevent such mismatches and increase norm-abiding behaviors during future waves of the pandemic and future collective threats.

Tight–loose theory also makes predictions about other societal dynamics that may occur as a result of the COVID-19 pandemic. Research has shown that, as groups tighten to deal with coordination needs, they also experience a number of trade-offs associated with order versus openness. Tightness is associated with more monitoring, synchrony, and self-control, which is critical for coordinating in the face of threat (83). Yet tightness is also associated with higher ethnocentrism and lower tolerance of people from stigmatized groups (80), as well as lower creativity (84). Finding ways to maximize both openness and order—that is, to be "culturally ambidextrous"—is a key challenge for human societies now and in the future.

Scientific Agenda. Assess changes in nation/community tightness–looseness before and after pandemic as a function of disease severity. Determine how cultures can quickly (and possibly temporarily) adopt tight norms in the face of fast-acting threats and avoid potential mismatches that occur in the absence of sufficiently strong cues of disease (see *Insight 3: Activating Disgust Can Help Combat Disease Spread*).

Insight 10: Human Progress Continues

Evolutionary reasoning makes several predictions about the future humans will face in the wake of the pandemic—from shifts away from economic independence for women to birth rates dipping below thresholds needed to maintain some human populations. These are some depressing possibilities that invite a conclusion that humanity is spiraling downward to a new low point. Those who deny the possibility of social progress might feel vindicated by the COVID-19 pandemic of 2020, because it shows that life has gotten worse rather than better. But has it?

Many people have trouble reconciling the demonstrable fact of human progress—that, over time, we have become healthier, better fed, richer, safer, and better educated—with the constraints of human biology. Some fear that, if the mind has evolved as a complex structure, then progress would be impossible, because "you can't change human nature." Therefore, either there cannot be such a thing as progress or there cannot be such a thing as human nature.

But these are confusions which arise from misconceptions of human nature and of human progress (85, 86). Among the adaptations making up human nature is the triad of faculties that adapt us to the "cognitive niche" (87): know-how, which allows us to understand the physical world and try out new ways to manipulate it to our advantage; language, which allows us to share and recombine these ideas; and sociality, which gives us the motive to coordinate ideas and actions with our fellows for mutual benefit. Among the brainchildren of these faculties are inventions that magnify their own power, including the printed and electronic word and institutions of science and governance, which allow knowledge to accumulate over generations. When people deploy knowledge to improve their lives, retaining and combining the innovations that work and discarding those that don't, progress can take place.

That's all that progress consists of. It is not, contrary to conceptions of Herbert Spencer and other Victorians (88, 89), a mystical evolutionary force that propels us ever upward. On the contrary, the forces of nature tend to grind us down, including the inexorable increase in physical disorder and the evolutionary conflicts between parasites and hosts, predators and prey, and conspecifics and one another. It's only the application of hard-won knowledge that allows us to eke out local and provisional advances against the constant challenges to our well-being.

Among these challenges are outbreaks of infectious disease. Bouts of outbreak over millennia were the selective pressure that led to the evolution of our innate, adaptive, and behavioral immune systems.

Yet it was our cognitive adaptations that led to the recent conquest of the infectious diseases that felled our ancestors in great numbers. They allowed us to discover vaccination, sanitation, antisepsis, antibiotics, antivirals, and other advances in public health and medicine that have dramatically extended life expectancy.

So it should come as no surprise, and is no refutation of the fact or the possibility of progress, that another infectious pathogen has launched an offensive against us; that is in the very nature of life. Yet the biology of *Homo sapiens* gives us good reasons to expect that the disease will be subdued in its turn—not as an inevitable step in some march of progress, but if (and only if) we redouble the commitment, which human evolution enables but does not guarantee, to the development and application of scientific knowledge to improve human well-being.

Scientific Agenda. Identify the social norms, common beliefs, reigning ideologies, and sociological and political institutions across countries and historical periods that foster the discovery and application of scientific knowledge to solve perennial human problems.

Conclusion

COVID-19 has brought radical change, through deaths, stress of extended quarantine, confusion that slowed adequate responding, social unrest at a massive scale, and a long and uncertain social and economic aftermath. This radical change is global—no human, anywhere, is unaffected by COVID-19.

To understand the virus and our response to it, we need to understand how viruses and humans evolve. We know that there is a long history of the coevolution of viruses and humans. Viruses evolve to exploit their hosts to encourage their own replication, but they also depend on hosts to survive. Humans can tolerate some manipulation by viruses, but we have also evolved to combat them. This delicate coevolutionary dance is why we often seem to be running as fast as we can, just to stay in the same place (90).

However, humans also possess the tool of scientific insight that gives us a broader view than what the virus can see. Perhaps this can help us stay one step ahead. By understanding the nature of viral strategies, we can better anticipate the spread of COVID-19 and try to block it. Likewise, by understanding human nature, we can try to activate evolved motivational systems that will help fight the virus, such as providing cues that trigger our behavioral immune system. Understanding human nature will also enhance our ability to address the aftermath of COVID-19, as it has disrupted so many of our fundamental human activities, such as mating, parenting, and simply maintaining social contact.

Herein, we have described 10 insights offered by a broad range of evolutionary thinkers, with expertise ranging from evolutionary medicine to broadscale cultural evolution. These insights offer possibilities for guiding science to address the spread of COVID-19 and its inevitable aftermath. However, these insights represent only a limited snapshot of this historic moment, and a selection of topics, although important, that an evolutionary perspective on the pandemic can provide.

The objective in providing these insights is to help make sense of the vast confusion that mars this pandemic and to illuminate paths for research. In addition to insights that can produce immediate action, the pandemic has provided us with unique opportunities to witness human nature as it unfolds, from changes in patterns of reproduction, shifting social norms, and curiosities of cognition that can warp our recognition of threat. This paper is a call to action in science—both in the application of existing knowledge about viral and human nature and also as an opportunity to make discoveries that would not be possible except when a global social experiment is underway.

Data Availability.

There are no data underlying this work.

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