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Ecology, culture and leadership: Theoretical integration and review

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ABSTRACT

Cultural and evolutionary explanations are often seen as rivals in the social sciences. It is therefore not surprising that these perspectives have also communicated little in leadership research so far. Yet, these two fields have many overlooked complementarities, which can be appreciated when examining the role of ecological factors in shaping variations in cultural leadership prototypes (CLPs) – that is, societally shared ideal attributes and behaviors that followers expect from their leaders. In this paper, we integrate and review multidisciplinary research that clarifies these complementarities. First, we discuss how different CLPs might emerge as responses to the specific threats and opportunities provided by the ecology where human groups live. Second, we review research on the link between CLPs, related cultural patterns, and specific ecological factors, ranging from more physical (e.g., climate, diseases) to more social factors (e.g., population density, warfare). Third, we highlight how CLPs might not only be evoked by current ecological conditions but are also culturally transmitted, resulting in potential mismatches between CLPs and present ecologies. Our review shows that a deeper integration of cultural and evolutionary approaches to leadership is needed to understand why variations in CLPs can emerge, and why they persist or change over time.

Introduction

Leadership is a human universal found in virtually all societies (Garfield et al., 2019; Lewis, 1974; Van Vugt et al., 2008). Yet, there is no single best way to lead around the world. For instance, followers in East-Asian countries tend to describe their ideal leaders as more authoritarian, face-saving, and compassionate than in many Western nations (Dorfman et al., 2012). In Egypt, more than 80% believe that men make better political leaders than women, but in Sweden, fewer than 6% do (EVS/WVS, 2022). Different leadership ideals exist even within the same nation. Compared to French-speaking Swiss, German-speaking Swiss hold a stronger preference for managers with a participative leadership style (House et al., 2004). Prototypical leader characteristics do not only vary in large, industrialized societies (Aycan et al., 2013; Gerstner & Day, 1994; Resick et al., 2006) but also between small-scale, pre-industrial ones (Garfield et al., 2020).

The substantial variation in cultural leadership prototypes (CLPs)[1]—that is, the societally-shared ideal behaviors, attributes, and traits that followers expect from their leaders—begs a deceptively simple question: Why do people describe ideal leaders differently across continents, countries, and sub-national regions? The prevailing answer in the leadership literature is culture, commonly defined as the "shared motives, values, beliefs, identities, and interpretations or meanings of significant events that result from common experiences of members of collectives and are transmitted across age generations" (p. 5, House et al., 2002). That is, CLPs are mainly seen as socially learned preferences stemming from pre-existing societal conditions, norms, and practices, resulting especially from repeated exposure to and interactions with individuals in authority positions (e.g., parents, teachers, business leaders, Dorfman et al., 2012). Yet, this explanation does not fully answer our question. It tells us *where* specific CLPs might be found around the world and *how* they are acquired, but it does not tell us *why*

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[1] We prefer introducing the umbrella term "cultural leadership prototypes" rather than relying on more specific terms used in leadership research (e.g., implicit leadership theories; culturally endorsed leadership theories) because these terms often refer also to specific taxonomies and/or scales of leader attributes (e.g., Dorfman et al., 2012; Epitropaki & Martin, 2004). We, thus, prefer a more generic term to clearly differentiate our broad construct of interest (i.e., the shared leadership prototypes in a given society or group) from its measurement. Also, the term "prototype" relates to cognitive approaches to leadership, which are the backbone of much literature on cross-cultural leadership (see section "Cross-cultural approaches").

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different CLPs emerge in the first place.

Motivated by this ultimate question, this paper reviews theories and evidence suggesting that CLPs might be viewed as cognitive adaptations to the threats and opportunities of particular environments that human groups inhabit – ecology, in short. While similar ideas can be traced back to the writings of philosophers like Montesquieu, here we account for the variation in CLPs by integrating cross-cultural (e.g., House et al., 2004) and evolutionary perspectives on leadership (e.g., Bastardoz & Van Vugt, 2019; Garfield et al., 2019). Following the blueprint of recent work in cross-cultural psychology (Sng et al., 2018), we review key concepts and results at the intersection of cultural and evolutionary disciplines, touching upon ideas from evolutionary psychology (Tooby & Cosmides, 1992), behavioral ecology (Nettle et al., 2013), and cultural evolution (Richerson & Boyd, 2008). We ultimately highlight how this integration can help to explain not only where different CLPs might originate from, but also when they persist over time and how they can change.

Our review and theoretical integration paper offers several new insights for leadership studies. First, we highlight how culture and evolution are not—as it is sometimes believed—rival explanations, but are complementary. Second, we review a preliminary list of potential ecological factors that might influence the emergence of heterogenous CLPs. Third, we discuss evolutionarily motivated mechanisms through which ecology might influence different CLPs, introducing the distinction between "evoked culture" and "transmitted culture" (Tooby & Cosmides, 1992) to the field of leadership. Fourth, we discuss how integrating cultural and evolutionary perspectives can help our understanding of why CLPs might sometimes be "culturally mismatched" to current ecological conditions. Finally, we propose new research ideas for research on leadership, culture, and ecology at different levels of analysis (e.g., countries, regions, work organizations, age groups), while acknowledging some conceptual and methodological challenges for future research.

Cross-cultural and evolutionary approaches to leadership: Bridging the gap

Cross-cultural approaches

Cross-cultural leadership research flourished at the end of the 20th century, fueled by the growing globalization of work and travel. Building on the foundational work on societal and organizational culture of Hofstede and other scholars (e.g., Hofstede, 1980), leadership researchers began to wonder about the universality of their theories and empirical findings. As most research was coming from the United States and a handful of other Western countries, researchers started to ask a simple question: Are the leadership styles found to be effective in these societies similarly appreciated around the globe (e.g., Bass, 1997)?

The pioneering work of Bryman (1987) and Gerstner and Day (1994) began to answer this question, which was later tackled by the largest project focusing on cross-cultural leadership to this date, GLOBE (House et al., 2013; House et al., 2004). These and other empirical studies (e.g., Aycan et al., 2013) resulted in a cross-cultural map of the ideal leadership attributes endorsed by individuals in many different societies. More than three decades after the first studies, evidence for societal variation in what followers desire from their leaders is bountiful, especially in organizational contexts (for a review, see Hanges et al., 2016). Yet, leadership universals also exist, according to GLOBE. For instance, "irritable" or "noncooperative" are widely regarded as negative descriptors of leaders, whereas "intelligent" and "decisive" are unanimously seen positively. Still, many globally appreciated attributes are best seen as *variform* universals, that is, leader descriptors mirroring general principles that are viewed similarly across the world but are enacted and interpreted differently across societies (e.g., visionary leadership is universally appreciated, but it is usually enacted with colorful and assertive oratory in the West and with quiet and non-aggressive rhetoric in the East, see Den Hartog & Dickson, 2017).

Explanations for these societal differences usually revolve around two notions: Leadership prototypes and societal culture. Leadership prototypes are relatively abstract desirable/typical leader attributes that individuals hold in their memory systems. These attributes reflect especially frequent and exemplary leaders that individuals encounter during their lifetime, like parents, teachers, supervisors, and political or business leaders (see Lord et al., 2020). Leadership prototypes, thus, vary between individuals, yet they also tend to exhibit a certain homogeneity within a society, as individuals' firsthand experiences with leader figures are relatively similar (Hanges et al., 2000; Shaw, 1990). These societally shared ideal leader attributes—what we referred to as cultural leadership prototypes (CLPs) in the introduction (see also Dorfman et al., 2004)—are usually interpreted as the result of pre-existing values, norms, and beliefs that are transmitted intergenerationally in a given society (Dorfman et al., 2012). Confirming this idea, specific CLPs correlate with *omnibus* measures of societal culture (e.g., collectivism, power distance) and are clustered into different geo-linguistic groups (e.g., Germanic Europe and Latin Europe).

Mirroring the somewhat fragmented landscape of leadership styles and behaviors (cf. Banks et al., 2018; Fischer & Sitkin, 2022), the exact content and labeling of CLPs vary across studies. However, the most popular taxonomy of CLPs is perhaps derived from the GLOBE project (House et al., 2004), which measured individuals' endorsement of 128 attributes of leadership and aggregated them into six global CLPs: (i) autonomous leadership (individualistic, independent, and unique); (ii) charismatic leadership (visionary, inspirational, as well as honest and self-sacrificial); (iii) humane-oriented leadership (modest, generous, and consideration for followers); (iv) participative leadership (non-autocratic, non-dictatorial, involving followers in decision-making); (v) self-protective leadership (face-saving, formal, status-conscious); and (vi) team-oriented leadership (generous, team-builder, and administratively competent). It is important to note that some of these CLPs have substantial empirical overlaps (see Dickson et al., 2003). At the societal level, charismatic and team-oriented GLOBE's CLPs correlate positively at about $\rho = .83$, whereas participative and self-protective CLPs correlate negatively at about $\rho = -.79$.[2] In light of these similarities, recent empirical work (Stephan & Pathak, 2016; Van de Vliert & Einarsen, 2008) has also pointed at two "*meta*-prototypes," a more leader-centric template (i.e., *non*-participative, autonomous, and self-protective leadership) and a more follower-centric template (i.e., charismatic, humane-oriented, and team-oriented leadership).

Evolutionary approaches

As research on culture and leadership reached its maturity at the turn of the 21st century, scholars coming from evolutionary backgrounds started to think about leadership more deeply. A central question motivated their efforts: Are leadership and followership evolved, universal features of human psychology and evolutionary history? To answer this question, these scholars began to build on Darwin's theory of natural selection and data from small-scale human and non-human societies, studying leadership at two different levels of explanation – proximate and ultimate (Scott-Phillips et al., 2011; Tinbergen, 1963). Ultimate explanations concern "why" questions (e.g., *why* is leadership adaptive and *why* did it evolve?), thus addressing the evolutionary function of leadership and followership. This explanatory level illuminates why leadership and followership exist to begin with, clarifying the specific problems that they solve in a particular species or a particular environment (i.e., adaptive value), as well as their evolutionary history among humans and across other species (i.e., phylogeny). Proximate

[2] Own calculations, based on data available at https://globe.bus.sfu.ca/study_2004_2007?page_id=data#data ($N = 62$).

explanations revolve around "how" questions (e.g., *how* do leadership and followership achieve their functionality?), addressing the behavioral, cognitive, emotional, and physiological mechanisms explaining how leadership and followership operate (i.e., mechanisms) and how they develop throughout individuals' lives (i.e., ontogeny, see Spisak, 2020).

Concerning the ultimate level of explanation, evolutionary work theorizes that leader–follower relationships emerged early in human evolution—hominids are about 2–2.5 million years old—when our ancestors lived a hunter-gatherer lifestyle (Van Vugt et al., 2008). According to this perspective, leadership and followership reflect a suite of evolved (genetic) adaptations for dealing with coordination and collective action challenges that ancestral human groups probably encountered regularly. These problems are related to interpersonal dynamics within and between groups, like collective movement, group hunting, group defense, and conflict management. All these group challenges necessitate group members to reach a unified decision to stay together and function effectively, and allowing one individual—the leader—to influence the decision-making process is in principle one way to do so (Glowacki & von Rueden, 2015; Van Vugt & Smith, 2019). Literature reviews have found several similarities between leadership in small-scale human societies (which are good models of ancestral group life, von Rueden & Van Vugt, 2015) and leadership in nonhuman societies (e.g., elephant, hyena, dolphin, zebra), suggesting that leadership is indeed a universal, evolutionarily conserved mechanism (King et al., 2009; Smith et al., 2016).

A particular branch of evolutionary approaches—evolutionary leadership theory (Van Vugt, 2006; Van Vugt et al., 2008)—proposes that natural selection has endowed humans with various domain-specific psychological adaptations that enable them to choose the "right" leader in the "right" context. Building on the core principles of evolutionary psychology (see, e.g., Lewis et al., 2017), evolutionary leadership theory posits that followers' needs and preferences for leadership are activated by specific environmental cues. That is, followers rely on if-then mental heuristics enabling them to select leaders allowing the realization of coordination benefits under various environmental conditions indicating either a threat or an opportunity (Bastardoz & Van Vugt, 2019; Laustsen, 2021). Examples of adaptive follower heuristics are "when in danger, follow physically strong leaders because they can protect me" or "when in unknown territory, follow experienced leaders because they know where to go."

Regarding the proximate question, evolutionary leadership theory suggests that when a particular follower's need is salient in a particular context, it activates a mental representation of what makes for a good leader for the given situation, that is, a context-sensitive leader prototype. For instance, when voters elect a political leader in wartime they shift their preferences towards a more dominant, masculine-looking candidate (Laustsen & Petersen, 2017; Spisak et al., 2012). In times of rapid economic change, they want a younger-looking leader, presumably because young age is perceived as being linked to creativity and innovation (Spisak et al., 2014). Note however that this perspective does not suggest that context-sensitive prototypes are necessarily innate. Rather, developmental processes can shape people's leadership ideals throughout their lifetime, and maybe especially early in people's lives (Safra et al., 2017).

As in the cross-cultural literature, there is no definitive taxonomy of the qualities of leaders studied by evolutionary approaches. Yet, prototypical attributes of leaders often include dominance, trustworthiness, competence, and attractiveness (Van Vugt & Grabo, 2015), as well as charisma (Grabo et al., 2017). Evolutionary researchers have also indicated that leadership attributes might coalesce around the concepts of prestige and dominance (Cheng et al., 2013; Van Vugt & Smith, 2019) – a distinction that bears some similarities to the follower-centric (prestige) versus leader-centric (dominance) templates sometimes discussed by cross-cultural leadership scholars. Indeed, prestige is correlated with attributes such as competence, generosity, and friendliness, whereas dominance relates to qualities such as assertiveness, power, and force (Henrich & Gil-White, 2001). The overarching assumption is that there are trade-offs between these different leader templates, to the extent that the same leader characteristic might be ideal in some cases but undesirable in others. For instance, a powerful, forceful leader can be functional during a crisis or a conflict, yet, it might expose followers to risks of exploitation and coercion in less turbulent times.

Understanding cultural differences through ecology: An integration

At first glance, cultural and evolutionary approaches to leadership seem to have little in common. For starters, they build on different intellectual traditions and rely on different literature streams. Moreover, evolutionary approaches—and evolutionary leadership theory, in particular—focus especially on finding universal functions of leadership, whereas cross-cultural work highlights societal differences in leader ideals. These two approaches have also different research objectives. While evolutionarily informed work is mostly motivated by ultimate questions, cross-cultural studies usually focus on descriptive patterns and proximate mechanisms underlying different CLPs (e.g., *what* followers want from their leaders across societies? *How* are these prototypes learned and transmitted?). Yet, despite these clear differences, cross-cultural and evolutionary approaches have multiple similarities.

First, both perspectives view leadership perceptions and, ultimately, selection as guided by mental heuristics operating in a relatively intuitive and implicit manner (e.g., Bastardoz & Van Vugt, 2019; Lord et al., 2001; Lord & Maher, 1993). Second, there is an overlap in the leadership prototypes they distinguish. Attributes related to charisma, generosity, and participative or autocratic decision-making are found in both subfields and so is the notion that ideal leadership attributes converge either around a more follower-centric (e.g., charisma, participation, competence, prestige) or leader-centric template (e.g., hierarchy, self-protection, authoritarianism, dominance). Third, while evolutionary leadership theory has often focused on universals, evolutionary approaches do not deny the existence of societal variation in leadership behaviors and ideals (Garfield et al., 2019; Lonati, 2020). Rather, evolutionary logic can provide ultimate explanations for the proximate patterns documented by cross-culturalists. Cultural and evolutionary approaches are, thus, not at odds but have some key complementarities that can be better understood by considering the influence of different socio-environmental conditions—ecology, in short—in shaping leadership prototypes.

To illustrate the important unifying role of ecology, consider an analogy from the animal world (taken from Nettle, 2009a). Some grasshopper species develop either a dark or green skin color depending on their local environment. In a dark environment (e.g., a forest), the grasshopper develops a dark-colored phenotype, whereas in a light environment (e.g., grasslands) it develops a green-colored phenotype. This adaptation protects individual grasshoppers against the threat of predation, and it generates stable differences between groups of grasshoppers growing up in different ecologies. Note that skin color variation between the groups is not the result of genetic differences. The grasshoppers are from the same species and do not genetically transmit their skin color to their offspring. The between-group variation is not a cultural adaptation either. That is, the grasshopper has not learned from others what skin color is most suitable. On the contrary, each grasshopper uses a genetically evolved mechanism that allows it to switch to either a dark or light phenotype based on local ecological conditions.

The grasshopper example illustrates what is known in biology as adaptive phenotypic plasticity, that is, the biological capacity enabling members of the same species to respond adaptively to local features of the environment (DeWitt et al., 1998; West-Eberhard, 1989). The notion of plasticity has been recently discussed in cross-cultural psychology (Sng et al., 2018), leading to growing empirical interest in the origins of psychological differences between human societies (see Varnum & Grossmann, 2021). When applied to leadership, this idea offers a

conceptual bridge between evolutionary and cross-cultural approaches. If humans have been exposed to different ecologies in evolutionary history and have an evolved capacity to respond flexibly to such conditions (i.e., the if-then follower heuristics posited by evolutionary leadership theory), then the leadership attributes, behaviors, and traits they value might reflect the different ecological conditions they experience. That is, the different CLPs found by cross-cultural leadership researchers might emerge because different societies face different ecological threats and opportunities, in the present or past. This way, heterogenous CLPs could emerge among groups of people that share the same genes and have no pre-existing cultural differences but are brought up in different environments (cf. Nettle, 2009a).

Ecology, culture, and leadership: An organizing framework

The notion of plasticity puts ecology at the nexus between evolutionary and cross-cultural approaches to leadership. But which specific ecological factors matter when it comes to leadership and followership? In this section, we examine a variety of ecological conditions that have been associated in earlier research with the emergence of different CLPs or that, based on theory, should activate different leadership prototypes (see Table 1 for some salient case studies we review). For each ecological variable, we try to answer essentially two questions. First, which leadership traits, behaviors, and attributes would be functional within this particular ecology? Second, what do previous studies find about the link between ecology, leadership, and followership preferences across societies? When defining "ecology", we broadly rely on the definitions and taxonomies proposed by recent work in cross-cultural psychology (see Lu et al., 2023; Oishi, 2014; Sng et al., 2018; Talhelm & Oishi, 2019), which, in turn, has been lately informed also by theory and evidence in (human) behavioral ecology (see, e.g., Davies et al., 2012; Nettle, 2009b). Thus, we refer to ecology as any aspect of the physical (e.g., climate) or social environment (e.g., population density) that creates a potential challenge for humans and that could be plausibly tackled by following leaders with a particular constellation of (ideal) traits and behaviors.

Following an evolutionarily informed logic, we are especially interested in ecological factors that are likely to have been already present in ancestral human environments, because the adaptive plasticity argument requires enough time for humans to have evolved the context-sensitive followership psychology producing different CLPs. This is not necessarily a narrow set of ecological factors, though. Ancestral humans plausibly experienced rather heterogeneous environmental conditions, for instance, in terms of both seasonal and long-term variation in temperature and rainfall (e.g., Hofreiter & Stewart, 2009). Our ancestors plausibly also experienced variation in social ecology, living mainly in small, mobile, and egalitarian bands, but interacting also in bigger social networks and more unequal societies (Boyd & Richerson, 2022; Singh & Glowacki, 2022). Moreover, focusing on evolutionarily relevant ecologies does not imply that evolutionarily novel ecological threats (e.g., economic recession) are necessarily processed by human minds in a completely different way compared to the ancestral version of the same threat (e.g., a food shortage).

Also, note that we are interested in explaining variations in CLPs, and not leader behavior proper. As such, we do not review whether leaders who fit a particular prototype are currently more effective or if there is a match between actual leaders' behaviors and CLPs within each society. Moreover, we focus largely on leadership prototypes held in large, industrialized societies, as many of the reviewed studies have been conducted in these settings. However, we also review anthropological evidence related to ecology, culture, and leadership if it is available. Research in small-scale societies is particularly interesting because it offers first-hand evidence of how variation in leader prototypes may have come about in response to the ecological conditions operating in

Table 1
Some salient examples from our review: Ecological predictors and relationships with leadership.

Type of predictor	Ecological predictor	Potential relation to leadership	Evoked response	Main finding of representative study reference	Reference
Physical ecology	Natural disaster	Autonomous (+), charismatic (-), team-oriented (-)	Immediate collective action is key to survival	Natural disasters are linked to cultural tightness, which in turn predicts several CLPs measured across countries by the GLOBE project	Gelfand et al. (2011) Aktas et al. (2016)
	Infectious disease	Authoritarianism (+)	Need for strict social rules to avoid infection	Pathogen prevalence predicts authoritarian political governance across traditional societies and also individual authoritarianism across countries	Murray et al. (2013)
	Climatic demands *(interacted with country's wealth)*	Participative (+), self-protective (-), team-oriented (+), charismatic (+)	Preoccupation with survival or self-expression goals	Interaction between climatic demands and country's wealth, which predicts some CLPs measured by the GLOBE project	Van de Vliert and Einarsen (2008)
	Resources: Availability and predictability	Preference for dominant leader (+)	Preoccupation with survival goals/reduction of uncertainty	Evidence for a preference for stronger, more dominant leaders during economic uncertainty/downturn	Kakkar and Sivanathan (2017)
	Resources: Unequal distribution	Tyrannical/coercive leadership (+)	Reduce risk of being excluded from concentrated resource	If leaders monopolize valuable resources, followers accept more tyrannical/coercive tendencies	Mattison et al. (2016)
Social ecology	Population density	Autonomous (+), charismatic (-), team-oriented (-)	Reduce risk of conflicts and coordination failures	Population density is linked to cultural tightness, which in turn predicts several CLPs measured across countries by the GLOBE project	Gelfand et al. (2011) Aktas et al. (2016)
	Genetic relatedness and lack of diversity	Paternalistic (+)[a], humane-oriented leadership (+)[a]	Help individuals close by	(Perceived) kinship relates to prosocial tendencies toward those who live nearby	Prediction derived from inclusive fitness theory (Hamilton, 1964)
	Sex ratio *(male-biased)*	Participative (-), preference for dominant leader (+)	Reduce risk of conflicts	Male-biased sex ratio predicts preferences for stronger leaders (in the laboratory) and for non-participative CLPs measured across countries by the GLOBE project	Sheng et al. (2023)
	War and conflict	Preference for dominant leader (+)	Need for coordination in the face of an intergroup conflict	Nations that reserve a larger portion of their GDP for military spending endorse dominant leadership more	Laustsen et al. (2023)

Note: CLP = Cultural Leadership Prototype. For each ecological predictor, we summarize one/two exemplary references justifying the ecology-leadership reviewed link. More evidence and relationships between ecology and CLPs are discussed in the Section "Ecology, culture, and leadership: An organizing framework". The symbols (+) and (-) refer to either a positive or a negative potential relationship between an ecological predictor and leadership.

[a] For this ecological predictor, there is no direct evidence for an ecology-CLPs link.

settings that are plausibly closer to ancestral environments (cf. Marlowe, 2005).

Finally, in organizing our review we take a "prospector" viewpoint (Breslin & Gatrell, 2023) and present a narrative, emergent, and multi-disciplinary literature review (Baumeister & Leary, 1997). That is, we discuss some notable examples and case studies relevant to relating CLPs to ecological predictors, with the objective of building an initial framework to organize existing evidence and guide future empirical work. When direct evidence for an ecology-CLP relation is lacking, we highlight this limitation and discuss potential proxies of CLPs, like national cultural indices and societal norms (e.g., societal tightness, collectivism). Leaders represent the archetype, the "cultural hero" of any given society (Hofstede, 2001), and correlations between CLPs and various *omnibus* indices of societal culture are well documented (for a review, see Hanges et al., 2016), thus justifying informed guesses about some specific ecology-CLP associations.

Physical ecology indicators

Natural disasters

Uncontrollable natural disasters (e.g., floods, wildfires, earthquakes) have likely been a recurrent threat in human evolutionary history, causing major risks to human safety and prosperity (Buss, 2009; Frankopan, 2023). When they strike, these natural threats often require immediate collective action. It is, thus, reasonable to hypothesize that humans have evolved a psychology that enabled them to deal with the aftermath of such events, including what leaders to follow in such crises.

A particularly popular line of reasoning suggests that natural disasters (or their probability) give rise to societal tightness, that is, societal norms that advocate strict rule-following and sanctions on those who deviate from these rules (Gelfand, 2021; Gelfand et al., 2011). In ecologies that are relatively safe from natural disasters, there may be little need for social coordination and punishment of rule breakers. In contrast, in disaster-prone ecologies, immediate collective action is key to survival and societal tightness can help to enforce social coordination and cooperation. Evidence for the evolutionary plausibility of this dynamic exists. At the individual level, the computational model of Roos et al. (2015) shows that tightness can evolve as a response to group-level threats, while the neuroscientific evidence of Mu et al. (2017) shows that people synchronize their neural activity with others in response to an ecological threat, thus supporting social coordination. At a more aggregate level, cross-societal evidence for the disaster-tightness link has been obtained both within and across modern countries (Gelfand et al., 2011; Harrington & Gelfand, 2014), but not in a large sample of small-scale societies (Jackson et al., 2020). Note, however, that this null finding might be explained by the specific ethnographic measure of natural hazards used (i.e., the occurrence of food-destroying natural hazards rather than the impact of the hazards).

Societal tightness in response to natural disasters may have important implications for the activation of particular leadership prototypes, echoing the notion that "crises" call for specific leader attributes (see the recent reviews of Collins et al., 2022). In a crisis, an immediate response is required and effective leadership involves more centralization of authority and less consultation and participation of stakeholders (especially if the group has some familiarity with the crisis, see Post et al., 2022). As group coordination becomes vital, authoritarian decision-making can be more efficient than consensus-decision-making, reducing the time to act (for formal models supporting this logic, see Dessein, 2007; Gavrilets et al., 2016). Thus, we can reasonably hypothesize that if tight societies are often faced with natural disasters, people in these societies might develop a non-participative, authoritarian leadership prototype. Supporting this idea, Aktas et al. (2016) have studied the relationship between CLPs and an index of societal tightness-looseness in 29 different societies using GLOBE data. They find substantial correlations between tightness and both non-participative and self-protective CLPs, even if these relationships become smaller and non-significant when controlling for other measures of societal culture (e.g., power distance). Also, tight societies tend to have less charismatic and less team-oriented CLPs and more autonomous CLPs than loose societies. These results are no evidence of a direct link between natural disasters and CLPs, yet they suggest a contrast between a more leader-centric prototype (e.g., an autocratic leader making autonomous decisions) versus a more follower-centric prototype (e.g., an inspirational leader who consults followers) depending on the intensity of the societal threat. Supporting the link between tightness and autocratic leadership, note that Gelfand et al. (2011, see supporting online material) found that societal tightness correlates with cultural preferences for non-democratic political systems and that Jackson et al. (2020) found a relationship between societal tightness and presence of powerful leaders in small-scale societies. Specifically, community-level leaders in small-scale societies characterized by stronger social norms (e.g., the existence of punishment for norm violators) have fewer checks and balances on their execution of power.

Infectious disease

Humans—as well as prehumans—have likely been exposed to infectious diseases for several million years (Nunn & Altizer, 2006; Wolfe et al., 2007). Given the dangers of contracting an infectious disease through exposure to pathogens over human evolution (e.g., Van Blerkom, 2003), the human physiological immunological system has evolved to minimize such harm. Humans also likely have a *behavioral* immune system (Schaller & Park, 2011), that is, a set of psychological mechanisms to protect them against infection. Examples include the ability to recognize sick people from subtle cues and behavioral reactions to avoid people carrying an infection risk (e.g., Axelsson et al., 2018; Tybur et al., 2013). Disease avoidance has also been linked to several societal-level factors that are presumably protective against diseases, like the relative frequency of people with personality traits such as introversion and low openness to experience, as well as societal norms of conformity, obedience, collectivism, and xenophobia (e.g., Aarøe et al., 2017; Fincher et al., 2008; Gorodnichenko & Roland, 2017; Schaller & Murray, 2008).

Relevant to CLPs, the hypothesis is that when societies are regularly confronted with infectious disease threats—in the form of epidemics or even pandemics—people will be more willing to conform to rules and obey leaders who can protect them against such threats. This should increase preferences for dominant, authoritarian leaders who can ensure that people conform to the rules regarding social interactions (e.g., social distancing), punish whoever violates these norms, and bear the cost of excluding from the group individuals that carry an infection.

There is some correlational evidence to support this general idea. Murray et al. (2011) showed that a measure of historical pathogen prevalence (i.e., the risk of dying from infectious diseases like typhus) correlates with the probability that respondents in 83 countries see "obedience" as a quality "that children can be encouraged to learn at home", even after controlling for some potential confounders (e.g., GDP per capita). A related study (Murray et al., 2013) showed that historical pathogen prevalence correlates positively with measures of authoritarian governance at the country level (e.g., civil liberties' restrictions) and with country-averaged responses to the authoritarian personality scale of Adorno and colleagues in 31 countries (Meloen, 1996). This scale represents a measure of endorsement of authoritarian leadership (Harms et al., 2018) and, thus, has a clear negative link with the participative CLPs reported by GLOBE (cf. House et al., 2004), as well as a conceptual relationship with the dominant leadership style discussed in evolutionary approaches (Van Vugt & Smith, 2019). Murray et al. (2013) also conducted a similar analysis using data from pre-industrial societies, showing a relationship between parasite prevalence and authoritarian forms of political leadership among up to 90 small-scale societies. Relatedly, recent cross-national research during the COVID-19 pandemic also shows a link between the severity of the pandemic and the tightness of the cultural norms in a society, suggesting that

countries fared better during the crisis when they had stricter norms and punishments for deviance (Gelfand et al., 2021).

This evidence at the society level is, at least partly, counteracted by some negative results (for a discussion, see also Sng et al., 2018). With respect to leadership, Laustsen and Olsen (2022) find that priming experimental subjects to think about the COVID-19 pandemic (i.e., a major disease threat) does *not* increase how the subjects rate the importance of "dominance" as a leader trait. Note however that this experiment was run during the actual COVID-19 pandemic and, as such, participants in the control group (i.e., subjects *not* primed to think about COVID-19) might have also been thinking about COVID-19, thus diluting the estimated treatment effect. Yet, this result suggests that more research is needed to probe the pathogens-CLP link at the individual level (see also the negative results of Van Leeuwen et al., 2023).

Finally, a link has been found between exposure to infectious disease threats and preferences for healthy-looking leaders, a prototypical leader quality sometimes discussed in evolutionary leadership literature (Van Vugt & Grabo, 2015). For example, White et al. (2013) found in both real and mock election studies that when people are concerned about/exposed to infectious diseases they are more likely to vote for a physically attractive candidate as their leader. The argument is that physical attractiveness is used as a cue to infer a leader's physical health and that it pays to elect a particularly healthy leader when dealing with a contagious disease threat. A recent replication of this research during COVID-19 found, however, that people only preferred healthy-looking leaders when they were in direct contact with them (workplace supervisors) but not when thinking about distant political leaders (Laustsen & Olsen, 2022, though the caveats we discussed in the previous paragraph still apply).

Climatic demands

An immediate problem that humans probably faced throughout evolutionary history is represented by different thermo-climatic demands (cf. Parsons, 2014). Summers that are too hot or winters that are too cold pose a survival threat, to which humans adapt also culturally, for example, by wearing warm clothes, heating their houses, and planning their work activities to align with the seasons (Van de Vliert, 2013). Climatic stressors may also affect preferences for leadership – a prospect explored by a series of articles by Van de Vliert and colleagues (e.g., Van de Vliert, 2006a, 2006b; Van de Vliert et al., 2010).

Broadly speaking, the climate-CLP link posited in these articles follows the blueprint of Van de Vliert (2013)'s climato-economic theory. This theory hypothesizes that climatic conditions interact with the availability of monetary resources in society to explain various cultural orientations, and distinguishes between two opposing types of ecologies: Threatening (i.e., harsh climate *and* low resources) and challenging ecologies (i.e., harsh climate *and* high resources). Threatening ecologies should promote a general preoccupation with survival goals, thus pushing for ingroup agency and steep hierarchies (i.e., an argument in line with the one we discussed in the section about natural disasters). On the contrary, in challenging ecologies, the climatic threats are buffered by the availability of resources, thus encouraging more personal growth goals, individual agency, and flat hierarchies (Van de Vliert, 2013).

The application of climato-economic theory to leadership is perhaps most clearly discussed and jointly presented by Van de Vliert and Einarsen (2008). In this article, the authors use the GLOBE data to document that autocratic and self-protective CLPs tend to be more endorsed in nations with more threatening ecologies, whereas countries that face a challenging ecology endorse a more charismatic and team-oriented CLP, conceivably because these latter ecologies represent a potential opportunity more than a threat, thus encouraging the presence of leaders focusing on long-term growth, innovation, cooperation, and individual agency (Van de Vliert, 2013). Importantly, the authors show that their result is not likely driven by outliers or major potential confounders (e.g., latitude, precipitation, political freedom), even though their design and analysis allow for no clear causal conclusion.

Note, however, that climato-economic theory suffers from some conceptual shortcomings (see the comments to the article of Van de Vliert, 2013). Especially relevant for our paper, the functionality of the relationship posited by the authors does not stem from an explicit evolutionary logic, a coherent body of ethnographic records, or behavioral ecological evidence. Moreover, the theory is based on individual-level processes, but the cited evidence comes from analyses at a more aggregated level. Overall, this casts some doubts on the evolutionary origin of the climate-by-wealth interaction effect.

Resources: Availability, distribution and predictability

Some of the ecological conditions we reviewed could be seen as specific instances of a more generic ecological factor, that is, the availability of resources that humans need to survive and thrive (like food, water, or safe sleeping sites). For instance, natural disasters often imply a sudden loss of resources, whereas the climato-economic theory sees wealth as a type of resource enabling societies to cope with harsh climatic conditions. Drawing a parallel between evolutionary relevant resources (e.g., food) and the available resources in modern societies (e.g., money, jobs) is far from obvious (Sng et al., 2018). Yet the idea that scarce and unpredictable resources might shape leadership preferences is also suggested by recent results. When there is an economic recession, people tend to prefer more authoritarian leaders (Kakkar & Sivanathan, 2017). Similarly, after the global economic crisis in 2008, researchers have observed a trend toward a more directive leadership style among workplace managers (Stoker et al., 2019).

An ecological perspective suggests that not only the availability but also the distribution of resources might be important for leadership. Resources can be relatively equally distributed within a particular space or concentrated in specific areas. In animal societies, this concentration can foster the emergence of steep societal gradients wherein a few individuals can monopolize resources or deny others access to them with force (i.e., a dominance hierarchy, Sterck et al., 1997). A somewhat similar dynamic can emerge among humans and is discussed in the evolutionary anthropology literature as contributing to hierarchy and power differences between individuals (see, e.g., Kaplan et al., 2009; Smith & Choi, 2007; Smith & Codding, 2021; Wilson & Codding, 2020). For instance, sea fish move around a large territory and therefore cannot be easily monopolized as a food resource by humans, as opposed to river fish like salmon, which are concentrated in rivers at specific times of the year. In the latter case, the resource is significantly more easily defensible, explaining why people would accept and defer to the authority of whoever controls this resource (Mattison et al., 2016). Note how such a dynamic between resource-poor and resource-rich individuals points to a tension between functionality and coercion when it comes to leadership and followership (Lonati, 2020; von Rueden, 2022). While deferring to powerful—and possibly tyrannical—individuals might not be functional *per se*, leaving a resource-rich area dominated by such individuals might be even more disadvantageous in an evolutionary sense than remaining under their rule (for a formal model, see Powers & Lehmann, 2014). In turn, this patron-client logic could explain the acceptance of more autocratic and dominant leaders (Smith & Choi, 2007).

In large-scale societies, unequal resource distributions—operationalized in terms of the Gini coefficient of a nation—have been linked to a preference for strong, dominant leaders (Sprong et al., 2019). The functional logic of this argument is, however, not so apparent, as Sprong and colleagues explain these results through a purely proximate lens (e.g., people tend to distrust democratic institutions as inequalities grow). A suggestive—though merely speculative—explanation is that unequal resource distribution might cause both relatively poor individuals and relatively rich individuals to develop a preference for strongmen, but for different reasons. Resource-poor individuals might want a forceful leader to overturn the *status quo*, while wealthier individuals might prefer a strong leader to protect their material possessions. Future research on the impact of resource

inequalities on leadership preferences could try to tease apart these two motivations, which correspond to the difference between promotion-focus (change) and prevention-focus (stability), respectively (Higgins, 1998).

Social ecological indicators

Population density

Population density refers to the number of individuals in a given space (Talhelm & Oishi, 2019). Animal behavior studies commonly find that density increases aggression due to stronger competition for resources (though this relation might not be linear, for a review and discussion, see Sng et al., 2018). When we apply this logic to humans, population density can be related to more potential for conflict among individuals, more need for mediation of disputes, and more complex coordination and collective action problems in general (see Glowacki & von Rueden, 2015; von Rueden, 2022). Thus, population density might have implications for the kind of leadership that might be in demand in society.

Building also on this intuition, formal evolutionary models on the so-called "managerial mutualism" dynamic suggest that leaders have an indispensable organizational function in larger groups (see Hooper et al., 2010; Perret et al., 2020; Powers & Lehmann, 2014; Smith & Choi, 2007). According to this view, followers will accept a steeper hierarchical differentiation—and might even pay a "fee" to some leaders to ensure their continued services (Price & Van Vugt, 2014)—when conflicts are rife (but see the recent negative result of Smith & Codding, 2021). As societies grow in size and density, people will be increasingly interacting with genetic strangers, which further intensifies the potential for coordination failure and conflict escalation and, thus, the demand for leadership. This should activate a more directive, dominant, and leader-centric prototype (to restore order), as well as an arguably more follower-centric, prestige-based prototype related to administrative competence and diplomacy (to mediate conflict). These two attributes might seem at loggerheads, yet evolutionary anthropology suggests that they can co-occur in small-scale societies. Dominant and assertive individuals can be particularly efficient at deterring in-group conflicts, yet they are trusted and followed only when they also exhibit domain-specific knowledge and fairness, if not full-blown generosity (see von Rueden et al., 2014).

A direct link between population density and CLPs in large-scale societies is, to the best of our knowledge, absent. However, some studies in cross-cultural psychology have focused on cultural variables that can be seen as proxies of these CLPs. A positive correlation between population density (both measured in 2000 and historically) and societal tightness has been documented across countries (Gelfand et al., 2011) and different regions in China (Chua et al., 2019), even though within-country evidence for the density-tightness link was not found in the US (Harrington & Gelfand, 2014). A positive link between population pressure (i.e., a concept tightly related to density) and societal tightness has been also found in pre-industrial societies (Jackson et al., 2020). The argument is that societal tightness—characterized by stricter social norms and intolerance for deviance—might be a cultural adaptation to manage the potential for conflict in highly dense environments (Gelfand, 2021), resulting also in a preference for more dominant and authoritarian leadership able to enforce norms (see our discussion on natural disasters).

A contrasting view is that a higher population density in society might result in more follower-oriented CLPs. This idea is based on insights from the evolutionary theory of life history, which suggests that high population density promotes a long-term mating strategy in humans (e.g., getting fewer children, delaying the age of first marriage, see Ellis et al., 2009). To the extent that population pressure cues intensified social competition, this could lead to preferences for leaders that stimulate individuals to delay gratification, plan ahead, and invest in the future. This logic is significantly more speculative than the managerial mutualism one, yet is backed up by some initial aggregated data. Sng et al. (2017) correlate future orientation practices (retrieved from the GLOBE data, House et al., 2004) with current population density in 55 countries. Their results highlight a positive relationship between density and future orientation, which, in turn, is suggestive of a positive association with the more follower-centric CLPs found by GLOBE, that is, charismatic, team-oriented, and humane-oriented leadership (Hanges et al., 2016). Note, however, that Sng et al. (2017) use GLOBE's future orientation *practice* (i.e., how a society is) as a predictor, while the original GLOBE project documents a correlation between CLPs and future orientation *values* (i.e., how a society should be); as a result, the mapping between GLOBE's and Sng et al. (2017)'s findings is not clear-cut. Thus, more research on the link between population density, future orientation, and CLPs is needed before making more conclusive claims about their relationships.

Genetic relatedness and diversity

Genetic relatedness refers to the presence of genetic relatives in someone's immediate environment and is an important factor in organizing animal and human societies. The argument from inclusive fitness theory (Hamilton, 1964) is that, when individuals are surrounded by their kin (with whom they share genes), there will be less conflict over resources, and individuals will generally be more helpful and generous towards each other. Kinship might have been a particularly important factor in ancestral humans. Our ancestors plausibly lived surrounded by close kin, but they probably interacted also in larger groups and in social networks containing more distant relatives, as well as complete in-group and out-group strangers (see Bird et al., 2019; Boyd & Richerson, 2022; Singh & Glowacki, 2022). Especially in these diverse social environments, the exact degree of kinship may have been difficult to assess at times. This is perhaps why humans also infer kinship from cues such as co-residence (e.g., did we grow up together?) and physical similarity (e.g., do we look alike?), resulting in more prosocial behaviors toward those that live near them or look like them (see Hackman et al., 2017; Mateo, 2015; Sng et al., 2018).

A functional link between genetic relatedness and the kind of leadership that people desire may not be immediately obvious, but it would be interesting to explore this further. First, the relatedness-generosity link suggests that high (perceived) genetic relatedness could trigger a preference for supportive leaders with considerable concern for and generosity toward followers (i.e., humane-oriented CLPs, see House et al., 2004). Similarly, one might hypothesize that genetic relatedness could be associated with paternalistic leadership – the prototype of leaders who take a personal interest in the wellbeing of followers, yet are also highly controlling and demand deference (Aycan et al., 2013). Evidence suggests that paternalistic CLPs are often observed in collectivistic societies, such as East-Asian countries like South Korea and China (see Mansur et al., 2017). Yet, in these countries, people tend to also live close to their relatives (see Yasuda et al., 2011), pointing to a potential relationship between leadership, shared genetic interest, and collectivistic orientation (for a discussion, see Sng et al., 2018) that future research could examine more in depth.

Flipping the role of genetic relatedness on its head, individuals might also react to cues of genetic dissimilarity, like the degree of ethnic diversity within a society. Ethnic diversity is often seen as a factor that hinders—or at least does not help— collective action and well-functioning institutions in society (Alesina et al., 2003; Ruttan, 2006). This raises a particularly interesting—though still speculative—possibility for leadership perceptions (Lonati et al., in press). Individuals from countries with higher historical immigration inflows (e.g., the US, Australia) have been shown to be particularly emotionally expressive in their social interactions (Rychlowska et al., 2015). According to this result, emotional expressiveness could be functional, to the extent that it could help communication in a society in which people speak different languages, display different behaviors, or follow different norms. In turn, one could speculate that the need for emotional

expressivity caused by high levels of immigration might influence the ideal communication style followers expect from their leaders across societies, resulting in heterogenous prototypes related to verbal and non-verbal leader communication – a set of attributes related to charismatic CLPs (see Lonati & Bastardoz, 2022). Whether this line of reasoning is correct and evolutionarily sensible is an open question, yet societal differences in leader communication style have been discussed in cross-cultural leadership research (Den Hartog & Verburg, 1997; Ernst et al., 2022). Research on the speeches of politicians and business leaders could, for instance, look for societal differences in the appreciation of so-called "charismatic leadership tactics" (Antonakis et al., 2022) and link these with historical migration patterns, exploring whether the colorful leader communication style typically seen as a Western specificity is less endorsed in historically more homogenous societies (e.g., Japan).

War and conflict

Intergroup conflict has been a significant force in human evolutionary history, shaping social and political systems around the world (Bowles, 2009). These events had probably a profound impact on leadership preferences. One of the most significant ways in which warfare has influenced leadership is through the development of military leadership (Johnson, 2015). Military leaders need to make quick decisions, inspire their troops, and take calculated risks. During wars, leaders must be able to make quick and effective decisions to ensure the survival of their troops and their society. This requirement has led to the preference for leaders who demonstrate strength, dominance, and aggression, in other words, a more authoritarian leadership prototype during conflict (Fog, 2017).

Preferences for dominant and "strong" leaders have been found to increase in studies in which participants were primed with a situation involving an international conflict or a terrorist attack in their country (Laustsen & Petersen, 2020; Merolla & Zechmeister, 2009). A variety of different cues have been used to demonstrate the connection between intergroup conflict and dominant leadership ideals, including the preference for a leader with a male (versus female) name, a masculinized face, a low voice pitch, and the possession of traits such as dominance, strength, and decisiveness (Tigue et al., 2012; Van Vugt & Spisak, 2008). Indirect evidence comes from studies on individual differences and leadership preferences. Individuals who perceive the world as more conflict-ridden—with relatively high scores on social dominance orientation—have also been found to prefer more dominant leaders (Laustsen & Petersen, 2017). Anthropological studies also find that leadership in conflicts between small-scale societies is granted to relatively younger, physically stronger, and more aggressive leaders (see the review of Price & Van Vugt, 2014). Finally, even in non-human societies (such as meerkats and capuchin monkeys), leadership during intergroup conflicts is heavily male-biased (Smith et al., 2022).

So why should followers want a more dominant leader during an intergroup conflict, when there is a risk that these leaders might abuse their power position? The argument is that a conflict situation requires an aggressive response and a strong, forceful individual who had—at least ancestrally—a greater ability to inflict costs on outgroup members could ensure such a reaction (Little et al., 2007). Such leaders may also be more effective in coordinating within-group responses to external threats by punishing free riders within their society (Chen et al., 2021). Whether for reasons of aggression or defense against rival groups, the evidence suggests that the endorsement of a dominant leader increases with intergroup conflict across societies. A recent large, unpublished cross-cultural vignette study among participants in 25 nations from all six inhabited continents (e.g., Colombia, Kenya, Pakistan, Hungary, Canada, and Australia) confirmed this result (Laustsen et al., 2023). Leaders with dominant, authoritarian traits were preferred more in situations of intergroup conflict and this effect was found in no fewer than 23 out of 25 nations. Furthermore, the presence of an intergroup conflict decreased the desirability of a warmer and more competent leader prototype. Note also that having a dominant, leader-centric CLP also correlated with an ecological variable indicating a current potential war threat. Specifically, preferences for dominant leadership were substantially higher in countries that are currently spending a greater portion of their GDP on the military (e.g., China, Columbia). Finally, societal tightness—a proxy of leader-centric prototypes we already discussed—was found to correlate with the frequency of warfare in small-scale societies and with the number of territorial threats experienced by large-scale ones (Gelfand et al., 2011; Jackson et al., 2020), providing additional indirect evidence for the warfare-CLP link.

Sex ratio

A final socio-ecological factor that might shape leadership ideals is related to the demographic composition of a society, especially the sex ratio. The sex ratio is the proportion of males to females (of reproductive age) – a factor that has been found to significantly shape social systems in various group-living animals (Sng et al., 2018). Some human societies have a male-biased sex ratio, whereas others are female-biased. Extreme examples are Saudi Arabia where, for every 100 adult women, almost 136 are men. The reverse is true in Nepal where there are roughly 92 men per 100 women (United Nations, 2022). According to evolutionary theories about sexual selection, an unbalanced sex ratio in society intensifies the sexual competition among members of the more abundant sex (Buss & Schmitt, 1993). When there are relatively more men than women in society, the competition between the men intensifies, and this has been sometimes found to lead to more conflict, aggression, and violence, even though this relationship is not uncontentious (see Pollet et al., 2017; Schacht et al., 2014).

To the best of our knowledge, the influence of sex ratios on CLPs has not been studied in the leadership literature, so no strong conclusions can be made here. However, it may be that an unbalanced sex ratio constitutes a potential threat to the social fabric of society as it intensifies sexual competition and that a more authoritarian leader is needed to manage this social threat. In recent unpublished work, Sheng et al. (2023) tested this idea. They conducted various vignette studies where they manipulated the sex ratios within a fictitious country and measured people's preferences for national leaders in a mock presidential election. The results showed that a male-biased (but not female-biased) sex ratio increased the preference for more dominant, authoritarian leadership. Their analyses suggested that voters—men and women—were particularly concerned about their physical safety in a society with a male-biased sex ratio and, therefore, they opted for a strong leader. They backed this up with archival results using the GLOBE dataset, showing that participative CLPs are less prevalent in nations with a male-biased sex ratio.

Critical assessment

Our multidisciplinary review connects a set of key physical and social ecological factors to different CLPs. The evidence comes from fields as diverse as management, psychology, economics, anthropology, and biology, and it ranges from well-studied empirical relationships to much more speculative ones. Yet, despite this heterogeneity, a critical assessment of the evidence leads to some preliminary conclusions.

First, the clearest link between ecology and leadership centers around some specific CLPs. Echoing classic results in organizational behavior (i.e., threat-rigidity model, Staw et al., 1981) and more recent work in cross-cultural psychology (Gelfand, 2021), when people live in ecologies that create more pressing or complex coordination and collective action problems (e.g., natural disasters, wars, epidemics, high conflict due to population density), more directive and authoritarian leaders will be preferred or, at least, accepted more readily. As these ecologies evoke a prevention orientation and survival preoccupations, such prototypes might be functional, allowing groups to stay together and reach coordinated decisions quickly in the face of stressful situations. However, in ecologies in which coordination needs are relatively

weak, this picture changes. Leader-centric prototypes now yield few benefits for followers and rather expose them to the risks of exploitation. Thus, in low-threat ecologies (e.g., benign climate, no disease threats, peaceful conditions), followers will prefer more prestige-based, follower-centric CLPs related to egalitarianism, persuasion, competence, and (calculated) generosity; in other words, more participative, charismatic, team- and humane-oriented CLPs (cf. de Waal-Andrews & Van Vugt, 2020; Fog, 2023). The evolutionary plausibility of these ecology-CLP connections is bolstered by evidence from both small-scale societies and non-human ones (Smith et al., 2016). Especially in traditional human societies, egalitarianism and informal leadership are usually the name of the game, but more hierarchical, institutionalized, and authoritarian forms of leadership can be found among societies that face survival threats, pressing collective action problems, or that have unequally distributed and defensible resources (Glowacki & von Rueden, 2015; Jackson et al., 2020; Kelly, 2013; von Rueden, 2022). Moreover, as ancestral human groups probably faced rather diverse ecologies over a long period of time (Singh & Glowacki, 2022), it seems also plausible that there would have been enough time for the evolution of the psychological machinery needed to detect environmental threats and opportunities and organize groups effectively around leaders and followers (Van Vugt, 2006).

Second, the relationships between some ecological factors and other CLPs are more tentative. Some of the relationships we reviewed are based on proxies of CLPs (i.e., cultural dimensions). Some links are merely informed guesses stemming from evolutionary logic (e.g., genetic relatedness) or are based on some initial, unpublished empirical evidence (e.g., sex ratio). Furthermore, some of the ecology-CLP research we reviewed lacks evolutionary logic and/or anthropological support. For instance, climato-economic theory (e.g., Van de Vliert & Einarsen, 2008) is still more of an *ad hoc* explanation for societal differences in leadership than a solid theory. Similarly, the potential links between CLPs and genetic relatedness or sex ratios lack clear-cut anthropological evidence. As such, there is much need for conceptual clarification and empirical verification of these ecology-culture-leadership relationships.

Third, many of the studies we reviewed are correlational, preventing strong causal claims about the ecology-CLPs links (see Nettle, 2009b; Talhelm & Oishi, 2019). Consider the case of pathogens. While infectious disease prevalence at the country level might correlate with a specific CLP, ruling out all omitted variables that might bias this relationship is hardly possible (e.g., alternative ecological factors, unobserved institutional or economic conditions). Different societies might even have "sorted themselves" into ecologies with more or less pathogens based on their *past* CLPs or *past* prevailing cultural norms, leading to a complex reverse causality pattern (cf. Talhelm et al., 2014). All these factors might confound the disease-CLP relationship, as well as the other relationships we reviewed. Indeed, some authors suggested that the predictive power of infectious disease stress in cross-country data might have been overstated by the omission of some common causes, thus hampering the validity of the pathogen prevalence hypothesis (e.g., Currie & Mace, 2012; Hackman & Hruschka, 2013; Hruschka & Hackman, 2014). Similarly, the role of the climate-by-wealth predictor is not uncontroversial (see Kusano & Kemmelmeier, 2018).

Fourth, while our review covers some key ecological factors informed mainly by theory and research in the biological and social sciences, it does not provide an exhaustive list of ecological factors discussed across all disciplines. For instance, we focused on several sources of *extrinsic* mortality risk (wars, natural disasters), but we did not discuss *intrinsic* mortality risks (i.e., causes of death that can be largely avoided by the individual, such as their lifestyles or their age, see Gibson & Lawson, 2015), because we see these threats more as factors internal to the individual rather than an ecological variable proper (see also Sng et al., 2018). Similarly, we did not discuss residential mobility (i.e., how frequently people move), both because this factor is mainly discussed in socio-ecological psychological studies (Oishi, 2014) and because we see it more as a cultural outcome of ecology rather than an actual ecological predictor. Moreover, we did not review interactions between different ecological conditions, such as the well-known frontier ecology, a combination of dangerous and sparsely populated ecologies, like the Wild West in the US (Kitayama et al., 2010). Finally, although we touched upon the impact of various economic and political conditions (like economic inequality), we did not review them systematically because they do not necessarily represent evolutionarily relevant factors. Moreover, a stream of literature (especially in political economics, see e.g., Acemoglu et al., 2001; Gorodnichenko & Roland, 2017), sees economic development and political institutions as the outcomes of certain ecologies rather than ecological factors proper.

Last, we did not systematically review the psycho-social mechanisms through which ecology affects leadership prototypes (e.g., based on individual experience, learning from others). Part of the reason is that the reviewed studies are not always explicit on these mechanisms and seem to sometimes point to conceptually distinct mechanisms. For instance, some studies in our review focused on ecological factors that are relatively time-invariant (e.g., climate), whereas others focus on ecological variables that can vary substantially even within one generation (e.g., population density, sex ratio). Some studies focus on ecological predictors measured around the same time as the studied CLPs (e.g., Van de Vliert, 2006a), whereas others focus on historical ecological predictors from decades ago (in the XX Century, Murray & Schaller, 2010). These findings suggest that some relationships between ecology and leadership preferences are enduring, whereas others may be more transient, indicating different ways in which people learn about and adapt to their local ecology.

Pathways from ecology to CLPs: Evoked and transmitted culture

To motivate this paper, we asked: Why do people describe ideal leaders differently in different parts of the world? The review we conducted so far provides some first answers to this question. If different ecological factors—which represent evolutionarily relevant, recurring challenges for humans—activate different leadership prototypes and if different societies face distinct ecological conditions, then heterogenous CLPs might just be the result of individuals reacting in a similar way to their societies' ecology. Taken at face value, this mechanism suggests that there may be variation in CLPs that does not require any history, tradition, or learning from others, that is, the factors that social scientists usually associate with the term "culture". So, does this mean that only ecology matters and that "culture" plays absolutely no role in prototype formation? Clearly not. On the contrary, CLPs are *also* developed through social learning dynamics, wherein individuals in each society acquire leadership prototypes by observing peers, family members, teachers, religious institutions, or the media. But then, how can we reconcile the role of social learning with the one of ecology?

Answering this question requires discussing the different mechanisms that can in principle give rise to any given ecology-CLP link. A particularly intuitive way to do so—we believe—traces back to the distinction between "evoked culture" and "transmitted culture" proposed in evolutionary psychology (Gangestad et al., 2006; Tooby & Cosmides, 1992). Evoked culture refers to patterns of behaviors and preferences that are not directly transmitted and learned, but are caused by the same innate psychology responding adaptively to different ecological conditions. Evoked culture is, thus, aligned with the key tenets of evolutionary leadership theory (Van Vugt et al., 2008) and suggests that leadership prototypes can stem from the interaction between ecology and evolved human nature. However, leadership prototypes can be also acquired through the observation and imitation of others within the same society, that is, through social learning dynamics that are often invoked in cross-cultural leadership studies (Dorfman et al., 2012). These shared ideas and beliefs about leadership that are transmitted within and across generations can be referred to as "transmitted culture" (a topic studied by another branch of evolutionary

disciplines, the cultural evolution or gene-culture coevolution, Richerson & Boyd, 2008).

To further clarify the difference and the links between evoked and transmitted culture, let us consider the variation between societies when it comes to authoritarian CLPs. The evoked culture mechanism suggests that existing ecological conditions—such as wars or pathogen threats—might require political leaders to quickly mobilize society in the face of these hazards, thus explaining why people in some societies might prefer a more authoritarian type of leadership *right now* (note: evoked culture does not suggest that genetic differences directly cause some societies to be more authoritarian, but rather that our innate psychology has evolved to accept more authoritarian leaders when certain ecological cues are present). Yet, the transmitted culture mechanism suggests that a societal preference for more authoritarian leaders may not necessarily reflect current ecological conditions. Instead, this prototype could echo *past* events or conditions, including what people have learned from relevant others in their society about how a particular ecological threat was handled (e.g., World War II or the 1918 flu pandemic). Past ecological conditions can, thus, generate path-dependency, wherein parents, peers, media, teachers, or religious institutions can transmit certain CLPs inter-generationally (e.g., "our country always had strong leaders") even if the initial conditions that gave rise to such cultural prototype are no longer present (see Fig. 1 for a schematic representation of both the evoked and the transmitted culture mechanisms).

Evoked and transmitted culture can both explain societal differences and, from an evolutionary viewpoint, they can be seen as two functionally equivalent ways through which adaptive plasticity to the ecology can be deployed (Nettle et al., 2013). However, these two mechanisms rely on completely different assumptions and make sharply different predictions regarding *how* different CLPs come about, *how* CLPs might change over time, and *how* CLPs might be—at least temporarily—mismatched to the ecological conditions. Specifically, evoked culture suggests that, if CLPs represent a functional response to the ecology, then an ecological change that bears some resemblance to ancestral ones should be matched by a quick adaptive change in CLPs, too (cf. Varnum & Grossmann, 2017). For instance, people's preferences for leadership may quickly shift after a war ends, when peaceful relations must be again built with neighboring countries – think of Winston Churchill, a great wartime leader who lost the British elections immediately after World War II, arguably because he did not fit the prototype of a peace-transitioning leader. The evoked culture argument can, thus, be seen as an evolutionary justification for individual responses that could be described as "ecologically rational".

Conversely, transmitted culture allows for some temporal persistence in CLPs. Intuitively, if individuals in a society tend to copy each other's preferences without devoting much attention to the environment, CLPs might "stagnate" when ecological conditions shift. This might be especially the case when an ecology does not change rapidly over time and, thus, what one learns from previous generations remains somewhat informative about the new ecological conditions (see Chang et al., 2011; Giuliano & Nunn, 2021; McElreath et al., 2005; Nettle, 2009a; Rogers, 1988). Notable examples of cultural persistence include subsistence theories (Nisbett et al., 2001), which suggest that contemporary psychological differences between societies are explained by traditional modes of subsistence that existed several generations ago (e.g., hunting, herding, farming, or fishing; for empirical evidence, see Buggle, 2020; Talhelm et al., 2014). For instance, more individualistic and independent societal norms are found in societies that have traditionally adopted a pastoral, nomadic lifestyle in which families moved with their cattle, whereas more collectivistic and interdependent orientations are found in societies that have traditionally adopted farming and agriculture (i.e., ecologies characterized by higher population density, risk of pathogens, and more unequal resource distribution). Other examples include the already-mentioned historical settlements in frontier ecologies. This ecology is believed to have fostered a strong ethos of independence (e.g., "rugged individualism", "frontier spirit") and a culture-of-honor ethos in which families have to fend for themselves in the absence of strong institutions, something that persists to this day in some regions of the world, like the Deep South in the US or Hokkaido in Japan (Bazzi et al., 2020; Kitayama et al., 2010; Kitayama et al., 2006).

Cultural persistence in CLPs has been documented by Lonati (2020), who shows that the distribution of non-participative CLPs around the world is explained by geo-climatic conditions that historically favored intensive agricultural practices (e.g., irrigation). This subsistence type is believed to have generated a high population density, thus favoring the emergence of more authoritarian governments with directive leaders able to organize collective action and solve coordination problems related to agricultural production, the storage and redistribution of food, and the conflicts that could easily emerge among growing agrarian groups. Moreover, the patchy distribution of productive land and agricultural yield that could be easily monopolized by a handful of individuals likely favored the acceptance of high power and economic differentials between leaders and followers. Such shifts in CLPs were plausibly triggered by a functional reaction to the change in subsistence (which, in turn, can be thought of as a change in a constellation of ecological factors) and were then transmitted intergenerationally, even though these prototypes may have little value in contemporary societies that transitioned from agriculture to (post-)industrialization.

The transmitted culture mechanism also suggests that some CLPs might even come about through recent historical events and might have, at an extreme, no functional underpinning. For instance, Grosjean and Khattar (2019) show that the massively male-biased sex ratio experienced in some Australian regions during the 19th century, caused by English convicts being shipped there, triggered long-term negative effects on gender equality, resulting in negative attitudes towards women working and hampering women participation in high-rank occupations. In line with the transmitted culture mechanism, people in such areas still perceive men to be more suitable leaders than women today (see also Alesina et al., 2013).

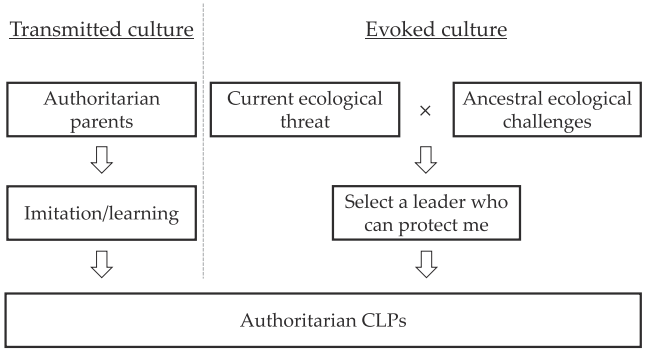

Fig. 1. Evoked and transmitted culture: An example.

Constraints on evoked and transmitted culture

So far, we implicitly assumed that individuals could develop their leadership prototypes more or less "freely" and "flexibly" when faced with different ecological conditions, relying either on the evoked or transmitted culture mechanisms. This assumption simplified considerably our exposition, yet it might not always be credible. Rather, there are at least two constraints that might limit both functional and socially learned responses to ecological conditions: Formal institutions and developmental experiences.

Formal institutions

By formal institutions, we mean laws and formal rules that human groups devise to structure social interactions (North, 1991; Powers et al., 2016). These rules might be powerful means through which CLPs are

maintained, in line with the coercive pressure argument often discussed in organizational theory (DiMaggio & Powell, 1983). Consider an extreme—though illustrative—example. In a political autocracy, dissent against the tyrant is usually prohibited by law and enforced by the police. Thus, while people might very well dislike the tyrant and obtain no benefit at all from living in a dictatorship, they might still be rarely exposed to explicit critique against him. This constraint might cause individuals to internalize a rather authoritarian leadership prototype, not because this prototype is functional, but rather because individuals only experience, learn, and transmit authoritarian prototypes in the media, during their education, and at work.

Such interplays between institutional factors and cultural transmission proper might be particularly important in the case of CLPs because formal institutions are likely directly influenced by political and business leaders – that is, those holding important power positions (Singh et al., 2017). Consider again Lonati (2020)'s example of the persistent changes brought about by historical agriculture. The initial emergence of directive leaders was perhaps functional in the first agricultural communities. Over time, however, more coercive changes probably emerged, too. It seems reasonable to believe that powerful individuals able to monopolize agricultural resources took advantage of the situation, setting up explicit and implicit institutions enabling them to preserve their power, favor their own interests, and reinforce their legitimacy (non-democratic institutions, military, see, e.g., Bentzen et al., 2017), but also to shape the cultural transmission of CLPs. In turn, the combination of transmitted culture and institutional forces might explain strong forms of cultural persistence that each mechanism, in isolation, could not rationalize (cf. Alesina & Giuliano, 2015). For instance, cultural transmission alone is unlikely to sustain the intergenerational persistence of extremely disadvantageous behaviors, beliefs, and preferences in the face of major ecological changes (see, e.g., Giavazzi et al., 2019; Henrich & McElreath, 2003). However, formal institutions might augment the effect of cultural transmission, "locking in" entire societies to suboptimal CLPs. Note also that the possibility that some societies might conquer other ones, thereby spreading their own norms, values, and institutions by force, complicates matters further, representing yet another constraint through which CLPs might come or not come about (cf. Turchin, 2016).

Developmental experiences

When presenting the notion of plasticity with the grasshopper example, we implicitly assumed that individuals are extremely malleable in their responses to ecology. However, evolutionary literature suggests that this assumption is not always correct. Biologists distinguish between two types of adaptive plasticity: Behavioral and developmental plasticity. Behavioral plasticity is typically reversible and can emerge as an immediate reaction to the ecology. In contrast, developmental plasticity emerges in well-defined periods of one's lifetime, takes more time to develop, and is generally non-reversible (see, e.g., Chenard & Duckworth, 2021). Ideally, organisms could gain much from being flexible throughout their lifetime, so why would a more limited, developmental form of plasticity ever evolve?

The answer is given by life-history theory, which posits that organisms allocate their energy efficiently to different activities (i.e., survival, growth) to maximize their fitness in the face of different ecological conditions (for reviews, see Del Giudice et al., 2015; Ellis et al., 2009). Plasticity engenders fitness costs related to the maintenance of the sensory/cognitive machinery needed to react to the environment and/or to learn from others, as well as costs related to the production of the adaptation at hand (more complex genetic costs also exist, see DeWitt et al., 1998). Thus, it might be cheaper to monitor the ecology only during shorter critical windows rather than keeping the costly machinery going throughout one's entire life. Not surprisingly, developmental plasticity is usually highest when individuals are young. This way, environmental conditions can be monitored early on and individuals can then modulate an adaptive response that remains fixed for the rest of their lifetimes (e.g., Frankenhuis et al., 2019). Of course, the risk of this developmental strategy is that such a response might become mismatched later in life if the ecological conditions happen to change.

The role of developmental experiences has implications for the formation of leadership prototypes throughout one's lifetime. Children and adults sometimes rely on the same cues to select leaders (Antonakis & Dalgas, 2009), suggesting that leadership prototypes might be formed at a young age. Yet, events and conditions experienced early in life might have profound and long-lasting consequences on the formation of leadership prototypes. Indeed, children who experience harsh socioeconomic conditions and adolescents who live in high-conflict families tend to endorse more authoritarian forms of leadership prototypes once they grow up (Safra et al., 2017; Walker et al., 2020). This suggests that people might have developmental windows in which their leadership prototypes are particularly receptive to ecological cues and to cultural transmission (cf. Keller, 1999; Keller, 2003).

Discussion, implications, and conclusions

Ultimately, this review and theoretical integration paper shows that cross-cultural and evolutionary approaches to leadership are not only compatible but that they are complementary and can enrich each other (cf. Apicella & Barrett, 2016; Norenzayan, 2006). The main contribution of this paper is to place ecology at the nexus of these two traditions to understand where CLPs originate from, why they vary, and when and how they change over time. We thus encourage leadership scholars to take advantage of the complementarities of evolutionary and cultural approaches, which we summarize schematically in Fig. 2. In the next sections, we discuss some potential avenues for fostering such integration, as well as conceptual and methodological issues that future research will need to address.

Why do CLPs vary?

Our paper has reviewed and organized some ecological predictors that leadership researchers might want to use to test hypotheses about the functional origins of societally shared leadership prototypes. Yet, our review is not a definite taxonomy, but rather a starting point that exemplifies the generative potential of an ecological framework to study variations in CLPs. Thus, we hope that our paper will spark a suite of conceptual and empirical endeavors that will help to develop and test a complete ecological theory of leadership. Such empirical efforts could be aided by the pending publication of the new cross-national data of the GLOBE 2020 project, which will offer much sought-after cross-societal data.

We especially foresee three major axes of future research. First, as we considered only some key ecological factors coming out of earlier research, future research could focus on other ecological predictors that may be linked to leadership preferences (e.g., climate change, frontiers).

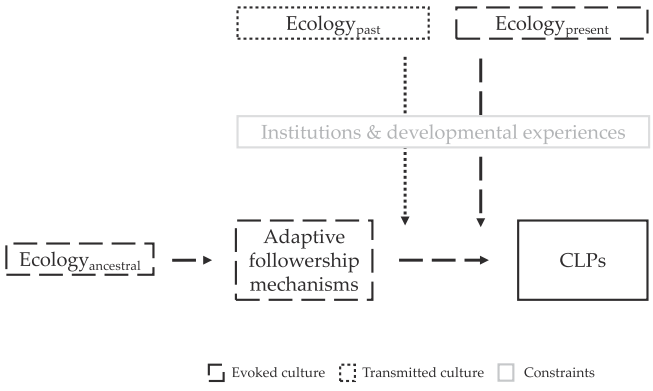

Fig. 2. Present and past ecology and cultural leadership prototypes (CLPs).

Second, the fact that different ecological conditions tend to co-vary in the real world (e.g., population density and infectious disease risks) might push leadership scholars to develop more parsimonious taxonomies. Third, future research might find it useful to elaborate on the co-occurrence of different ecological factors that could give rise to CLPs composed of leader attributes that are usually seen as competing or almost contradictory (e.g., benevolent and authoritarian leaders in societies with high genetic relatedness and high risk of disasters).

What ecologies favor more feminine CLPs?

Future research could also focus on CLPs that do not feature prominently in our review. For instance, prototypes related to leader gender are often discussed in the leadership literature, but they are studied less in cross-cultural research (e.g., neither the original GLOBE project nor its follow-ups measure a specific CLP linked to gender proper). Yet, this topic is important for theory and practice, and researchers interested in the link between ecology, gender, and leadership might find it useful to build on our review for at least two reasons.

First, CLPs related to gender coalesce, at least partly, into specific CLPs we reviewed. Specifically, more authoritarian and directive CLPs might be related to a general preference for male leaders, whereas participative and humane-oriented CLPs might mirror a preference for female leaders, in line with social role theory (i.e., agentic males vs. communal females, Eagly & Karau, 2002). Thus, one might speculate that CLPs favoring women will be activated in times of peace, in small groups, and in high genetic-relatedness ecologies (i.e., leadership in family networks, see Smith et al., 2018). Second, the evolutionary and cultural pathways we reviewed might be particularly relevant in the case of CLPs related to gender. Evolutionary literature suggests that sex differences in the opportunities and motivations to lead do exist (see Smith et al., 2021). Yet these evolved differences might interact with both ecological conditions and cultural transmission. For instance, the presence of monopolizable resources might push men to compete, possibly violently, for these resources in a winner-takes-all manner, thus reducing the chance for women to attain powerful leadership positions. This gap initially present in certain ecologies might have then been perpetuated and multiplied by a process of cultural transmission and institutional pressures. In turn, a better understanding of these dynamics might help to eliminate the gender gap in leadership, promoting gender equality in the workplace and beyond.

When do CLPs change over time?

This review provides some thoughts on why CLPs change over time (cf. Sng et al., 2018; Varnum & Grossmann, 2017). This topic has received attention from leadership scholars only recently (see the GLOBE 2020 project), yet it is of utmost importance, especially in an era of migration patterns, climate change, pandemics, and other major socio-ecological disruptions. Studying how CLPs react to sudden ecological changes could be a particularly fruitful avenue for future research. For instance, we know that individual leadership prototypes have some temporal stability in the workplace (Epitropaki & Martin, 2004), but are CLPs also stable across years or even decades when local ecologies may have changed quite substantially (cf. Offermann & Coats, 2018; Pagda et al., 2021; Ubaka et al., 2023)?

On the one hand, the evoked culture argument suggests that CLPs could shift rather quickly in the case of sudden ecological changes, such as natural disasters or pandemics (e.g., the COVID-19 crisis). This prediction has two caveats, though. First, while young individuals might be particularly reactive to the ecology, older individuals might be unable to adapt their leadership prototypes. As a result, CLPs might take an entire generation to change completely, causing temporary within-society disagreement about the most desirable leader attributes (cf. Norris & Inglehart, 2019). Second, the ability to react adaptively to a certain ecology is constrained by the fact that this ecology must have some similarity with the conditions under which humans have evolved. As a result, if the new ecological conditions are radically different from the ones that were present ancestrally (e.g., nuclear disasters, trade wars), then people could make the wrong trade-offs in selecting a leader to tackle these problems (i.e., evolutionary mismatch, Li et al., 2018).

On the other hand, explanations based on transmitted culture imply a more significant time lag in how people calibrate their leadership prototypes to novel conditions. Think for instance about a scenario where one's parents experienced harsher conditions (e.g., war, recession) compared to the ones of their children. Will children's prototypes of leadership be updated or not? Our review provides no clear answer to this question but sketches some interesting scenarios. A possibility is that CLPs might persist long after the ecology that evoked them has changed, but only if the new ecology is sufficiently similar to the new one, if the ecological change is not sudden, or if some specific institutional constraints that were present before the ecological change can sustain the initial CLP. Such new predictions might be particularly relevant for policy, helping to uncover the dynamics of CLPs that might still echo events and conditions of an ancient past, but that could harm minorities or stereotyped groups (e.g., prototypes related to traditional gender roles).

Can CLPs change over individuals' lifetimes?

Our review and theoretical integration also advances new questions about the development of leadership prototypes across people's lifespans, a timely topic according to both evolutionary (Spisak, 2020) and organizational psychology writings on leadership (Lord et al., 2020). For instance, is the individual ability to respond functionally and flexibly to the challenges and opportunities of the local ecology fully operational already when individuals are born?

Tackling this topic would ideally require longitudinal data, creative natural experiments, twin studies, or sibling-comparison designs (see Tither & Ellis, 2008). However, simpler approaches might also provide some initial answers. To test if specific ecological conditions affect the ontogenetic development of leadership prototypes, one might look at how various ecological shocks—such as the COVID-19 pandemic, sudden economic recessions, wars, and demographic transitions—have changed CLPs, checking specifically if such changes are more visible across some age groups or birth cohorts (cf. Bianchi, 2014; Cotofan et al., 2023; Winkler, 2021). For instance, the recent COVID-19 pandemic might have caused individuals to endorse more authoritarian leadership and to support stricter norms (see, e.g., Alsan et al., 2020; Amat et al., 2020). But was this shift stronger among people who were more at risk of contracting the virus (i.e., elderly cohorts) or among more plastic individuals (i.e., young cohorts)?

To what extent are CLPs culturally transmitted or evoked?

Our discussion about evoked and transmitted culture begs a natural question: Are CLPs evoked or transmitted? Answering this query is empirically daunting because these two forces usually co-exist in the field. That is, while humans certainly rely massively on cultural transmission, they probably also react to the environment (Heine & Norenzayan, 2006). Complexifying matters further, these mechanisms likely affect each other. On the one hand, cultural transmission hinges on naturally selected psychological mechanisms that have been probably shaped by past ecological conditions (Chang et al., 2011; Henrich & Boyd, 1998). On the other hand, culturally transmitted traits contribute to shaping the ecology where individuals live, affecting individuals' evoked responses and, in longer time frames, even genetic evolution (e.g., the emergence of dairy farming pushed humans to develop greater lactose tolerance, see Laland et al., 2000). Thus, rather than asking *if* CLPs are the result of evocation or transmission, leadership researchers might more profitably ask *how much* of CLPs are the result of either mechanism.

Both laboratory and field evidence can contribute to answering this question. To bring evidence for evoked culture, it is necessary (though not sufficient) to show that a temporarily salient ecological condition makes people endorse a certain leadership prototype. This can be typically done by varying ecological cues in the laboratory (as some experimental papers we reviewed did, see also Nettle, 2009b), or by looking at creative natural experiments. Another promising avenue for separating evoked and transmitted culture comes from a research design known as the "epidemiological approach" (Fernández, 2011). This design studies if migrants and migrants' descendants still exhibit behaviors typical of their country or region of origin once they move to a new country. Applied to leadership, this design tests a simple prediction (see Lonati, 2021). If migrants' leadership prototypes change quickly once they move to a new country (i.e., less than one generation), then it means that the flexibility caused by an evoked cultural response could be at play. Yet, if prototypes persist into the second generation, this means that transmitted culture could explain the heterogeneity in CLPs.

Some care is required when designing and interpreting such studies, though. When manipulating ecological threats in the experimental laboratory, researchers should avoid eminent demand effects (e.g., Lonati et al., 2018). When relying on the epidemiological approach, results need to be read with some caveats in mind (Fernández, 2011). Cultural evolutionary work suggests that cultural traits can be transmitted by peers (i.e., horizontal transmission), by older unrelated individuals (i.e., oblique transmission), or by parents (i.e., vertical transmission, Creanza et al., 2017). Thus, evidence for a rapid change of leadership prototypes after moving to a new country is consistent both with an evoked culture response and with a horizontal or an oblique cultural transmission mechanism. In turn, evidence for leadership prototypes stability across generations provides strong evidence for cultural transmission, but only if the researchers can ensure that the migrants do not sort into or recreate the ecologies typical of their home country in the new country of residence. For instance, this issue might emerge if immigrants and immigrants' descendants tend to systematically live, work, and interact in a neighborhood with only other immigrants. If that is the case, the stability of leadership prototypes could simply imply that old and new ecology are just too similar to evoke any meaningful change.

Can CLPs vary at different levels of analysis?

Throughout our review, we have relied on many articles discussing links between ecology, culture, and leadership at the country level. Yet, focusing on ecological predictors helps to appreciate the multilevel links between ecology and leadership. That is, if individuals develop specific leadership prototypes in the face of particular ecological threats and opportunities, then this will be sufficient to create differences in leadership prototypes at any level of analysis, be it at the country-, region-, social class-, or generation level. In turn, this notion can have a potential impact on cross-cultural leadership studies.

First, ecological differences could be used to explain differences in CLPs within the same country (cf. Sng et al., 2018). The study of within-nation differences is an overlooked topic in leadership studies (see Den Hartog & Dickson, 2017), even if organizational scholars have remarked that within-country cultural variability is often much larger than between-country one (e.g., Taras et al., 2016) and that using countries as a unit of analysis when studying culture might be conceptually problematic (Baskerville, 2003). Second, ecological differences could explain why different groups that live in a similar *physical* ecology might develop different cultural traits, as their *social* ecologies might differ substantially. For instance, individuals from lower and higher social classes may have different preferences for leaders, being exposed to different types and degrees of ecological threat (cf. Sng et al., 2018).

Last, and perhaps more speculatively, ecological differences might also be used to study different prototypes of leadership across various industries, work sectors, or even departments of the same organization. For instance, do workers in organizations with greater infection risks, such as a hospital, develop a more hierarchical, authoritarian leader prototype? Even within the same organization, people may have different leadership ideals depending upon threats in the local ecology (e.g., ER versus the HR department of a hospital). Of course, this intuition rests on the possibility that the ecological predictors we reviewed could be mapped onto contemporary contextual features of organizations. In some cases, the link is easily made (e.g., different ecologies in which the army or the arts industry operate), while it is shakier in other cases (e.g., would a business takeover be perceived as an "ecological threat" by employees?). We leave to future research the important task of discussing if, when, and how ecological factors proper can directly be translated into a taxonomy of "organizational ecologies".

Limitations and methodological considerations

Need for more evolutionary evidence

At the core of this paper is the notion that ecology and leadership might be functionally related. While this idea is backed up by significant conceptual and empirical work, our review of ecological predictors suggests that more evidence is needed to show that the ecology-CLPs are themselves evolved (cf. Schmitt & Pilcher, 2004). This is no easy task, as we will never know for sure the conditions in which our distant ancestors lived, the group activities they engaged in, or their leadership preferences. Precisely for this reason, future research interested in ecology and CLPs should devote more attention to evolutionary anthropological sources and evidence from small-scale societies. Traditional societies that exist to this day are not clones of our Pleistocene ancestors, but they are the closest available approximation of the conditions under which the psychological mechanisms related to leadership have plausibly evolved (Marlowe, 2005; von Rueden & Van Vugt, 2015). Thus, if there is evidence for a functional ecology-leadership link in these traditional, often geographically isolated societies, then there is an indication that the ecology-CLP link of interest might indeed be innate (cf. Witkower et al., 2021). Similarly, evidence from non-human societies (e.g., elephants, chimpanzees) on how ecological factors drive different leadership structures can help to establish the convergent validity of a presumed ecology-CLP connection (cf. Barsbai et al., 2021; Smith et al., 2022).

Care is, however, required when interpreting aggregated-level data coming either from small-scale or contemporary societies. The risk is to fall into the so-called "ecological fallacy", that is, erroneously attributing a characteristic or relationship that is observed at an aggregate level to the members of the aggregate units (e.g., country-level differences interpreted as individual-level differences, see Pollet et al., 2014). This conceptual slip-up is likely to emerge if the individual-level mechanisms behind any posited leadership-ecology connection are under-specified. Thus, we can only invite future research to keep in mind that any putatively functional ecology-CLP link should reflect a documented individual psychological or physiological mechanism that is based on a recurrent environmental threat in the ancestral past. Some of the ecological predictors we reviewed in this paper meet this condition more clearly, thanks to laboratory and neuroscientific evidence at the individual level. However, the individual-level processes implied by other ecological predictors are less evident (e.g., climato-economic theory, see Fischer, 2013), suggesting that much more work is needed to probe their existence and their possible evolved nature.

To make a convincing case about individual-level processes, expounding a clear logic with a verbal model is needed. Yet, formal models used by evolutionary scholars are usually more convincing, because they can clarify the conditions under which a given leadership behavior is individually advantageous in a given ecology, thus providing some indirect evidence for the plausibility of the individual reaction to the ecology. For instance, formal models confirm the basic mechanics behind the potential ecology-CLP link in the case of natural disasters (Roos et al., 2015) and in the case of managerial mutualism (Smith & Choi, 2007). Empirical evidence is then needed to provide supportive

evidence for the validity of a putative psychological mechanism. For instance, showing that group members are more likely to vote for a more dominant, authoritarian leader when inducing a particular ecological threat in a laboratory experiment suggests that a similar reaction might emerge in the field, too (cf. Van Vugt & Spisak, 2008). Neurobiological and genetic studies can finally uncover the exact mechanisms underlying individual responses to ecology. These studies are clearly ambitious at the current stage, as genetic and neuroscientific evidence is virtually absent in our review and remains a rarity in leadership studies in general (Song et al., 2022; Zhang et al., 2023). Still, showing beyond doubt that a given ecology-CLP link has an evolutionary origin will ultimately require deep knowledge of genetic architecture and neural mechanisms (cf. Owens, 2006).

Causal inference

As we already mentioned, several endogeneity problems can emerge when studying the link between ecology and CLPs, creating interpretation issues (cf. Antonakis et al., 2010; Nettle, 2009b). Thus, we invite future research on ecology and leadership to devote more attention to causal inference. At a minimum, researchers should explicitly model and discuss the role of potential confounders, showing the robustness of their main results both when including and excluding various control variables in regression or path models. Conditioning on all potentially omitted common causes is, however, virtually impossible. Moreover, an overzealous inclusion of control variables in a regression model might even backfire, leading to the potential inclusion of "bad controls", that is, variables that are outcomes of the ecological predictor of interest (see, e.g., Cinelli et al., 2022; Li, 2021). Thus, more convincing solutions to issues related to omitted common causes might include multilevel data. For instance, if the ecological factor and the CLP of interest are both measured at a sub-national level, then the researcher can include country fixed effects in estimation, to model country-level differences in economic development, institutions, and other unobserved factors (see, e.g., Alesina et al., 2013). A last possibility is to minimize most eminent endogeneity concerns thanks to specific research designs that can also be applied to the study of ecology, culture, and societal differences (e.g., instrumental variables, spatial regression discontinuity).

A related, subtler issue concerns the independence of observations in cross-societal data, like cross-country ones found in many management articles. Different countries can have a common cultural history (Mace et al., 1994). Thus, it may be problematic to consider countries like the US and UK as truly independent, due to their obvious historical linkages that might persist over time. In turn, the non-independence of different groups might invalidate some ecological explanations, like the infectious disease threat one (Currie & Mace, 2012). Solutions for these problems are non-trivial, yet revolve around so-called "phylogenetic methods"; interested readers can refer to Mesoudi (2019) for an informal discussion. At a minimum, however, running regressions on cross-national data by adding continent dummies and (or) excluding some specific groups of countries as a robustness check should be the norm, so to document if a given result holds both between and within macro-areas and if it is not driven by a small groups of culturally related countries (Currie & Mace, 2012).

Finally, note that focusing on ecological predictors does not only present methodological challenges but might also offer some interesting opportunities. Being relatively distal predictors, sudden variation in an ecological variable could be used as a natural experiment (Sieweke & Santoni, 2020). For instance, some studies we discussed use geo-climatic variables as instrumental variables for historical patterns (Lonati, 2020; Talhelm et al., 2014) or rely on plausibly exogenous shocks in ecological conditions (e.g., natural disasters, important economic downturns) as independent variables (Winkler, 2021). Such creative attempts can provide leadership researchers with some ideas on how to estimate causally cleaner relationships between ecology, culture, and leadership.

Coda

From a cross-cultural viewpoint, vast societal differences in ideal leader attributes and behaviors may at first glance be seen as evidence against an evolutionary argument for leadership. Conversely, from an evolutionary viewpoint, it might be appealing to dismiss the burgeoning evidence for societal variation in leadership prototypes and focus, instead, only on universal attributes. Yet, evolutionary logic can help cross-culturalists understand *why* societal differences in leadership prototypes exist, while cross-cultural data serve as a reminder for the evolutionists of *how* complex and persistent human cultures can be. In this paper, we reviewed theories and results from different disciplines that point to the role of ecology in connecting these two perspectives. We merely scratched the surface of many complex issues, and our theoretical integration leaves many questions unanswered. Still, we hope that leadership researchers will take advantage of this initial step, and work towards the development of a more integrative leadership science, combining both cultural and evolutionary perspectives.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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