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Foundational principles of an applied cultural evolutionary science for natural resource management and conservation

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Culture, as the filter through which people view the world and a key determinant of human behaviour, is central to the practice of natural resource management and conservation. Conservation is intended to moderate the impacts of human cultural modification of the environment, exists as an endeavour because it is culturally valued, and acts largely through policies to encourage or discourage targeted human behaviours. However, culture is not static; as organisms and ecologies evolve, so too does culture exist as a dynamic, interconnected, coevolving element

of the social–ecological systems in which management action is situated and implemented. Cultural evolution (CE) offers a valuable theoretical contribution to the scientific understanding of culture, cultural diversity and culture change and has the potential to be harnessed in the applied research and practice of conservation social science. We illustrate the essential principles necessary to grow an applied science of CE for natural resource management and conservation, and identify opportunities for CE to provide valuable information for science-based decision making and help conservation institutions and organizations adapt to the ongoing challenges posed by culture change. This transdisciplinary integration can contribute to improved outcomes across conservation objectives and build more resilient, sustainable social–ecological systems.

This article is part of the theme issue 'Transforming cultural evolution research and its application to global futures'.

1. Introduction

Culture is a universal aspect of human learning, perspective, experience and behaviour. In short, culture is 'the way we do things around here' [1], a descriptive and prescriptive framework for how we interact with the world and with each other. Many useful definitions of culture exist but, for the present discussion, we consider culture to be *information, acquired in whole or in part from other individuals, that is capable of affecting individual behaviour and structuring group-level patterns of behaviour* [2,3]; in short, culture is socially transmitted information. All societies have devised cultural solutions for interacting with and surviving in their local environment, and these very often include cultural practices that actively shape and manage landscapes and ecological communities [4,5]. Many societies have established formal organizations or government agencies for the purpose of managing the environment, and all extant societies engage in stewardship practices that sustain their subsistence needs and livelihoods [6–9], from local backyard horticulture to multinational agricultural and silvicultural planning. Therefore, though the examples we present in this article predominantly feature regions in which the authors hold lived and working experience in conservation, the general principles we describe apply to the diversity of conservation practices globally. Throughout, we use the term 'conservation' as shorthand to refer to the full array of knowledges and practices from natural resource management, environmental management, subfields (such as wildlife management, rangeland management and land stewardship) and local traditions that actively engage in management of the natural world for sustainable human use.

This article synthesizes knowledge sourced from a broad array of disciplines related to conservation and the study of culture and behaviour, particularly those that deal with the applied realities of managing both the environment and human–nature interactions, such as the human dimensions of natural resources [10], conservation psychology [11], social–ecological systems [12], biocultural conservation [13] and others collectively included in the conservation social sciences [14]. To this, we add a temporal and evolutionary perspective on the historical foundations of conservation practices and the modern cultural forces affecting changes in values, institutions and policies from the field of cultural evolution.

Cultural evolution (CE) is an integrative interdisciplinary field of scientific research, drawing from evolutionary biology, population genetics, biological anthropology, cognitive linguistics, behavioural ecology and others [15], that seeks to understand and describe the processes by which culture changes over time [16,17]. This understanding extends to the cultural values that reflect people's perceptions of the environment, the institutions that govern how people interact with local ecologies and economies and the diversity of practices by which they do so across differing contexts, as well as the coevolutionary consequences of these elements of culture within social and ecological systems. To date, cultural evolutionary science has seen limited application to critical global issues such as climate adaptation, biodiversity loss or sustainable energy development, though opportunities have begun to emerge [18–20].

We illustrate a series of foundational principles core to the scientific understanding of culture and culture change in the context of applied conservation and management, and in doing so, aim to build a shared understanding to support future applied research in this transdisciplinary interface. Further, we provide specific areas in which CE can (i) provide valuable scientific evidence to inform conservation decisions using a structured decision-making (SDM) framework; (ii) reframe conservation problems in terms of systems-level impacts and interactions between cultures, ecologies and economies that can yield improved outcomes across multiple objectives; and (iii) produce tools to allow conservation organizations and agencies to adapt to the urgent challenges posed by rapid cultural shifts and the loss of public support and relevancy. The integration of a CE perspective into conservation practice can enhance the material and immaterial benefits that people and ecosystems derive from the responsible management of our shared world.

2. Conservation is culture

(a) Conservation is built on cultural worldviews and values

Conservation is a cultural practice. A society's cultural worldviews shape human perceptions of and relationships with the natural world, which underpin the development of shared values and institutions, including norms and rules of behaviour [7,21,22]. Knowledge about natural systems, developed through repeated observations and interactions, is codified and transmitted, giving people the means to shape the environment in which they live [7,23]. Rooted in these culturally specific worldviews, values, institutions and knowledges—in combination with varied ecological and climatic conditions—conservation practices have been born in many distinct forms across the world's roughly 7000 present ethnolinguistic groups [24–26].

As conservation practices endure, the prioritization of different practices within a society and the allocation of resources towards those efforts are heavily influenced by cultural values [27,28]. These include both held values—deeply internalized guiding principles, developed early in life, that guide perceptions of and interactions with the world [29,30]—and assigned values—which reflect the perceived importance of particular entities like places and wildlife species [31]. Assigned values draw on held values, but are also influenced by socioeconomic conditions and prevailing cultural norms and biases [31]. They reflect the intrinsic (i.e. inherent), instrumental (i.e. utilitarian) or relational (i.e. kinship- and reciprocity-based) dimensions of importance ascribed to aspects of the environment [32,33]. These differences can manifest in, for example, valuing an old-growth tree for its own sake, or for the quality of its lumber, or as a member of the community. Within and between societies, and even within individuals, differing and sometimes incommensurable values can coexist. This state of values pluralism can engender conflict over dominant conservation practices and lead to institutional change [34,35]. Thus, recognizing that all conservation practices are rooted in culture and that a diversity of cultural valuations of nature exists is crucial for the design and implementation of effective, lasting conservation strategies that are compatible with local cultural contexts [36–38].

The values-based prioritization of conservation efforts has important ramifications for life on Earth. Cultural domestication and land use practices have shaped the existence, abundance and distribution of species for millennia [5]. Today, the ability of other species to continue to live and thrive is increasingly dependent upon human tolerance and support for their presence, with great variation in these attitudes and actions across systems [30,39,40]. Conservation institutions that originated in Western cultures and have been spread through colonialism are predominantly driven by intrinsic and instrumental values. Consequently, conservation efforts in these contexts have disproportionately prioritized charismatic and economically beneficial taxa, while taxa perceived as pests or threats to human interests (such as insects, large carnivores and introduced species) are actively pushed back or eradicated [32,40–43]. Labelling plants, animals, water, minerals and other materials as 'resources', 'commodities' or 'assets' reflects relationships rooted in human consumption and exceptionalism [44,45]. Conversely, many Indigenous and local conservation institutions centred on relational values emphasize the care of holistic systems rather than individual elements, as well as place- and kinship-based reciprocal relationships with nature [46–53]. From an understanding grounded in cultural relativism, all worldviews and values are valid and can only be properly understood within their own cultural contexts, while offering diverse adaptive solutions to the challenges of living in and managing ecosystems [54].

(b) Conservation is about managing people

The root causes of environmental degradation and biodiversity loss globally are almost exclusively owing to human behaviour [55–59]. Further, the success or failure of many key conservation interventions (e.g. policy and regulations; public communication and education; habitat acquisition and restoration; and species introductions, translocations or removals) is entirely dependent upon the effectiveness by which they can encourage or discourage specific human behaviours within local cultural contexts [60,61]. Owing to the centrality of human behaviour in achieving reliable, sustained conservation outcomes, applied research that can provide insights on the cultural determinants of human environmental behaviour and the processes by which human behaviours are linked with broader system function, or that can build tools for enacting cultural and behavioural change, is vitally important for modern conservation planning and implementation [60,62].

Critically, conservation actions have effects that ripple across entire social–ecological systems and always include consequences for humans and society. Although conservation frameworks are often premised on a conceptual separation of humans and nature, it is not possible to extricate people from the cultural, social and ecological context that drives their behaviour or from the complex webs of connections in which they are situated, nor is it possible to manage wildlife and other ecosystem components in the absence of human influence and valuation [12]. Human interactions with nature are influenced by and modify the state of the ecosystem and the state of the sociocultural system. These changes propagate to influence their future choices and interactions as well as those of others [63,64]. Social–ecological systems are highly complex and have many interacting layers and emergent, nonlinear properties [65,66]. The primary challenges in representing these systems are (i) to develop informed representations of human behaviour and decision making; and (ii) to characterize the complex, dynamic networks of human behavioural interactions with each other and with various elements of the environment; both of which can be usefully informed by integrating the essential role of culture [67–69].

(c) Conservation is done by people and organizations

Formal conservation governance structures operationalize a set of cultural values and institutions related to humans and the environment and can shape those institutions in turn [22,48]. One well-documented example comes from the set of fundamental principles for managing wildlife in North America, which has come to be known as the North American Model of Wildlife Conservation (70,71; hereafter 'the North American Model'). These principles developed during a time in which there was a pronounced cultural emphasis on the sustained exploitation of the shrinking bounty of resources available across the continent, with a focus on the management of game species to maximize the opportunity and yield of recreational harvest [72–76]. The North American Model makes specific cultural values-based prescriptions about people's relationships with wildlife—for example, that wildlife are resources owned by the public, held in trust by the government and allocated for individual use, primarily through harvest—as well as proscriptions against alternative values: for instance, any worldviews that conflict with the idea that wildlife can be owned [71].

Arising from the North American Model, state conservation agencies in the United States (US) have been supported by user-pay funding through the sale of hunting and fishing licenses and by federal taxes on firearms, ammunition, and fishing

and boating equipment [77]. This funding scheme created an incentive structure for agencies that gives priority to the cultural values and perspectives of extractive resource users in the interest of acquiring funding for conservation, which is then favourably allocated to the conservation of desired game species and the provision of harvest opportunities [78,79]. Similar feedback loops founded in instrumental values exist for other avenues of conservation funding and practice, such as in the sale of timber by forestry agencies and the leasing of public land for grazing and energy development by land management agencies [80–84].

The strong tradition of instrumental values embodied by Western conservation agencies, shaped by colonial and capitalist influences, has led to the prioritization of partners, research and policy aligned with those values, which provide disproportional benefits to extractive users [47,79]. These traditional values, alongside the internal cultural norms and incentive structures of agencies, encourage the recruitment and retention of employees that share those values and the exclusion of those with different values and worldviews [85,86]. Like-minded employees then serve to reinforce and perpetuate the embodied values of the organization and its traditional focus. This plays out through influences on policy and research priorities, partner engagement, the maintenance of institutions and the individual, values-based contributions of people to decision making on conservation issues [48,79].

3. Culture evolves

Change in social–ecological systems is dominated by uncertainty; the only certainty is that change itself is inevitable [87,88]. As the ecological components of social–ecological systems undergo changes according to an array of endogenous and exogenous processes, so too do the social and cultural components. Culture itself changes over time in ways that parallel biological evolutionary processes as it co-evolves with them. The study of these processes has coalesced under the banner of CE, an integrative interdisciplinary field of scientific research that seeks to understand the ways in which cultural diversity is generated and maintained [16,17].

Cultural information exhibits the same properties necessary for evolution by way of selection as detailed by Darwin for biological information: culture exhibits variation, competition exists between cultural variants, and cultural variants are heritable [89,90]. The existence of cultural variation is readily apparent: societies have developed diverse modes of communication and expression, diverse technologies and solutions to ecological challenges, and diverse perspectives on how people relate to the natural world [24,91,92]. Competition between cultural variants occurs at multiple levels, from the cognitive capacity and functional cost of maintaining multiple different solutions to the same problem within an individual mind, to group-level popularity and congruence with other cultural beliefs and practices, along with differences between variants in complexity, efficiency, practical requirements and attractiveness, among other factors [93–97]. Competition can also occur through the differential consequences of cultural variants on biological (or group-level) fitness that encourage the survival of particular variants, or through hitchhiking effects as part of a bundle of coupled traits [98,99]. Cultural information is inherited through cultural transmission, the core learning process that underlies CE [100]. Information undergoing cultural transmission is subject to selective forces and to cognitive and cultural filters referred to as transmission biases (or 'social learning strategies'). These act at multiple stages of the process and are based upon characteristics of the learner, the model, the information itself, the state of the system and the context in which transmission takes place [95,101,102].

Beyond broad strokes, there are important differences between the processes by which cultures evolve and those by which species evolve, and these differences can be critical to accurately representing cultural dynamics [103,104]. Notably, cultural transmission differs from genetic transmission in its potential modes: largely limited to vertical (parent-to-child) in the genetic case, but for culture commonly includes the addition of horizontal (peer-to-peer), oblique (non-parental-adult-to-child), group (multiple reinforcing sources) and even inverted (child-to-adult) pathways [100,105–107]. Cultural transmission also exhibits distinct mechanisms, ranging from learning indirectly from another individual's cultural products ('enhancement'), to copying through imitation (a focus on form) or emulation (a focus on outcome), to facilitated teaching [108]. Through the capacity of individuals to influence many unrelated learners along with the added effects of cognitive transmission biases, the success of a particular cultural practice is not limited to one-off transmission events and can instead be highly dependent upon the frequency of that practice among others (conformity bias [109]), the reputation and standing of a cultural model (prestige, dominance and success biases; [95,110]) and the framing and composition of the messaging (content biases [94,95]) . These factors present opportunities for the detailed design of behavioural interventions [111,112]. Cultural variation can be generated through the modification of existing variants—intentional or not—during the transmission process or in the course of everyday use [97,113], or through the innovation of novel variants [114,115].

As culture is transmitted within and between generations and grants the capacity to adapt to and shape diverse environments and the selective pressures they present, culture coevolves with natural systems [116,117]. In CE, these relationships are referred to as gene-culture coevolution [118], or as cultural niche construction at the broader systems level [119]. Because cultural transmission can happen repeatedly and frequently within a single generation, cultural changes can accumulate on a rapid timescale relative to typical rates of biological or ecological change [119,120]. As a theoretical lens, CE enables us to understand the complex pathways through which human culture and social–ecological systems shape each other through time and how relationships between people and their environments arise and are sustained [121,122].

4. Conservation evolves

Many conservation agencies and other organizations are currently facing a crisis of maintaining their relevancy in modern societies, with a loss of public and political support, trust, capacity and resources that impedes successful conservation implementation [123,124]. This loss of relevancy stems in large part from the widening gap between the traditional instrumental values embodied by organizations and those held by the general public where, for example, in many US state wildlife agencies, fewer than 10% of employees share the value orientation of the majority public [86,125]. These differing cultural perspectives can lead to conflict around the appropriate role of conservation organizations in society, whose needs they should serve and which types of policy are acceptable [79,126–128]. In some cases, public values and perspectives can shift on rapid timescales in response to cultural influences [129], while the self-reinforcing institutional values of conservation agencies have built up inertia and legal and regulatory bulwarks that typically make institutional change a slow, difficult and incremental process, contributing to the widening values gap [79,130]. However, major changes in priorities owing to administrative turnover or external shocks (as exemplified by the COVID-19 pandemic) can force organizations to make sweeping changes in a short period of time, leading to punctuated or saltatory patterns of institutional change [131–133].

Conservation institutions, organizations and agencies—as cultural products—are subject to cultural evolutionary forces and processes; understanding and characterizing the history of these dynamics can help in anticipating their future trajectories and how they can be navigated or intentionally shaped to desired forms [48,134–137]. Mounting criticisms of the North American Model, particularly from Indigenous perspectives and other groups that have been historically marginalized in conservation [44,49,76,138–142], are evidence of a pronounced change in the cultural adaptive landscape and a need for organizations in this space to adapt in order to survive, or risk being displaced from their niche by a different set of foundational cultural values or more culturally successful institutions [79,143–145]. Indeed, a recent review of the North American Model acknowledges that its future depends 'on its adaptability and application of its principles to contemporary wildlife conservation needs… as a dynamic set of principles that can grow and evolve' [146]. Evolutionary language is already common in the description of conservation institutions (e.g. [25,147–149]), demonstrating a need to formalize the vocabulary and models used to describe these processes of change.

Beyond the North American Model, the consequences of culture change and conflicts between cultural value systems are evident throughout the realm of conservation. Globally, the spread of colonial 'fortress' conservation practices that attempt to physically isolate ecosystems from the peoples who have lived within them, disrupting and erasing their cultural and historical ties to the environment—while normalizing a different set of human cultural interactions (e.g. tourism) that can further disturb the system—has led to situations in which the values embodied by conservation institutions and organizations are at odds with those of local cultures [150–153]. Asymmetries in power, capital, colonial histories and other factors have substantially shaped the emergence, spread and persistence of cultural values and norms globally, with consequences for conservation [47,48,154]. This point is particularly relevant for understanding how dominant conservation institutions have been established and contested over time [155,156]. Analyses of conservation policy have documented how place-based cultural systems of ecological knowledge and care are transformed, marginalized and co-opted by economic development and conflicting value systems [157,158]. These constitute significant drivers of culture change that could be integrated into a CE framework to account for interactions between cultural transmission dynamics and structural forces.

Frameworks developed in part to address these issues can both inform and be informed by a scientific understanding of culture change. Shifts towards community-based conservation, co-management and other frameworks focused on empowering local communities have seen success [159,160], but are still often framed from the standpoint of Western values and objectives and fail to be responsive to the complexity and dynamic nature of local cultural values, perspectives and knowledge [47,161–164]. Biocultural approaches have attempted to explicitly incorporate the dynamic nature of culture by recognizing the importance of intergenerational planning and institutions, enabling pathways for cultural transmission and making use of multi-level nested systems of adaptive management and governance [13,36,165–167].

In the vein of Muthukrishna *et al.* [168], conservation science is a historical science. The current diversity of conservation practices arose from a series of historical evolutionary processes, acting upon existing variation and innovating new solutions, replicating and changing through repeated transmission and has yielded both adaptive and maladaptive institutions on the selective landscapes of people living within social–ecological systems and of ideas living within collectives of cultural minds. The fact that these cultural practices and institutions are subject to intentional change through deliberate human action, a process known in CE as guided variation [102], presents the opportunity to direct the evolution of conservation institutions, organizations and agencies to be more suited to the changing social–ecological landscape and more successful in confronting the complexity of modern conservation challenges [169].

5. Applications of cultural evolutionary science to decision making in natural resource management and conservation

(a) Understanding evolving cultural influences on behaviour

For any scientific field to have applied use in conservation practice, it must provide benefits to decision making and implementation for conservation problems [170]. SDM, or decision analysis, offers frameworks to decompose a decision into sequential steps that serve to standardize the process and increase clarity and efficiency, and each step can be communicated to others to make the decision process more transparent and accountable [171–174]. The design of an SDM process, as well as many of the

tools developed to facilitate it, is partly intended to mitigate the effects of a multitude of cognitive biases that can sway human decision making towards suboptimal or irrational choices [175,176]. The literature from cognitive psychology and behavioural economics that contributed to the development of SDM, such as pioneering work by Tversky & Kahneman [177], has also been influential in understanding the heuristics and biases that shape cultural transmission processes and thus offers a bridge between these fields [96,178–182].

One common framework for SDM is referred to as the 'PrOACT' cycle, after its series of five steps: problem framing, objectives, alternatives, consequences and trade-offs (figure 1; for a detailed overview, see [183–185]). Within this cycle, the points that present the greatest opportunity for science to inform decision making have been identified as: (i) predicting the consequences of proposed alternative courses of action (step 4 in figure 1), largely through building predictive models, eliciting parameter estimates from subject-matter experts and gathering evidence to reduce epistemic uncertainty (i.e. lack of knowledge about the system); and (ii) developing alternatives (step 3 in figure 1) through the research and development of novel solutions [184]. At these points, particularly in providing tools to predict the potential consequences of conservation actions, CE can provide novel scientific contributions to improve the rigour and outcomes of conservation decision-making because of the central role of culture and culturally motivated behaviour.

Theory and prior modelling work from CE could be applied through the development of causally-based, context-specific tools capable of reducing uncertainty and predicting the potential outcomes of conservation decisions. For instance, a long tradition of cultural transmission experiments in laboratory and naturalistic environments—based upon mathematical models drawn from population genetics and epidemiology [100]—has led to a detailed understanding of the influence of various factors on how humans and other animals receive, learn and spread information, and how that information contributes to different patterns of behaviour [95,187–193]. These models have informed, and been informed by, research into the dynamics of human cooperation, the circumstances under which people tend to cooperate or come into conflict and the conditions that contribute to the relative success of cooperative groups [102,194–199]. Further work has emphasized the multilevel nature of human social and cultural structures and their layered influences on human behaviour, and has been translated into multilevel models in which these interactions are formalized [200–204]. Examples of ways in which research in these and other domains of CE could contribute to this aspect of decision making are given in table 1.

Though decision making can incorporate scientific evidence to better understand social–ecological systems and reduce uncertainty around the estimated effects of interventions upon the system, it is a process inherently driven by human cultural values [184]. Given that decision processes are always nested within a cultural context that embodies a particular worldview and a set of values and institutions, the influence of culture—along with its temporal and evolutionary dynamics—applies not only to information needs; rather, it suffuses all elements of decision making (electronic supplementary material, table S1).

We call special emphasis to the cultural context of the decision (step 0 in figure 1; electronic supplementary material, table S1) as an essential, but rarely interrogated, component of the process, as it delineates the bounds of the space in which every element of decision making takes place. Insufficient consideration of the cultural context of decision making can lead to misalignment and unanticipated outcomes if the context of the decision differs from the local context in which the actions are to be implemented [241–245]. One example of this comes from a community forest management programme in Zanzibar, Tanzania, that has continued to expand in part because it has served as a means for establishing local control over governance, even though it has not received intended carbon payments and has had mixed success for conservation outcomes [246]. For every decision, the cultural context provides the bedrock for dialogue in a process that formalizes a specific worldview and a set of values and institutions. In practice, the initial step of establishing the cultural context of the decision is typically invisible; decision makers and participants enter with a pre-existing notion of the dominant cultural perspective underlying the decision process [247]. Yet, taking the time to explicitly acknowledge and examine the cultural context in which the decision takes place can encourage critical reflexivity on the culturally embedded nature of the process and enable procedural changes that accommodate a more pluralistic understanding and more culturally appropriate and effective solutions [47,248,249].

Prominent concepts from CE can play a significant role in other steps of the decision cycle. Cultural transmission, as the core process by which information is learned and spread, is involved in nearly every stage, from how a problem is perceived and defined to implementing strategies for conserving cultural traditions themselves (electronic supplementary material, table S1). Cognitive biases and facets of culture affect the transmission process, determining who and what types of information are influential in decision making and under what contexts. The relative speed and frequency of culture change can lead to sudden shifts in the perspectives held and represented by decision makers, stakeholders and the public, which then impact how the decision is framed, discussed, analysed and implemented.

A thriving area of CE research is investigating the evolution of the capacity for culture and the cumulative modification of culture in humans and in other animals [113,228,250,251]. The existence of cultural traditions with potential fitness consequences in structured populations of non-human animals has implications for the planning and implementation of conservation actions targeting those species and their habitats, particularly if those cultural traits and associated behaviours delineate distinct subpopulations or have cultural value to people (electronic supplementary material, table S1; [227,234,252–254]).

(b) Framing culture as part of evolving natural systems

When social or cultural dimensions are considered in the course of conservation decision making, they are typically treated as static, generalized, subjective constructs that are more of an obstacle to achieving conservation outcomes than an avenue towards successful outcomes [255]. An applied CE perspective recognizes not only that the cultural context delineates the decision space and that cultural values, institutions, knowledges and perspectives are important determinants throughout the decision cycle (electronic supplementary material, table S1), but that all of these cultural elements evolve over time in concert

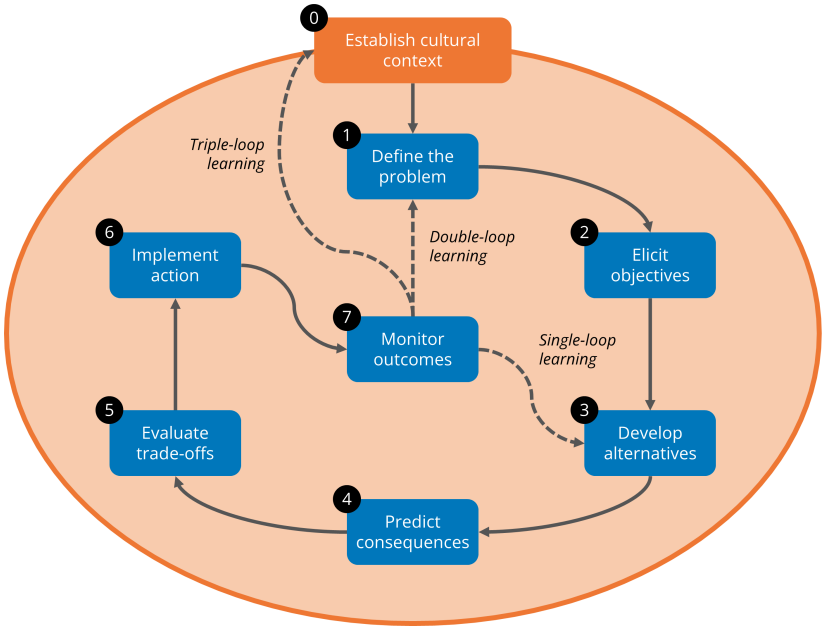

Figure 1. Depiction of a SDM cycle using the PrOACT framework (steps 1–5), with additions to represent the implementation and monitoring necessary to support adaptive management (steps 6 and 7) and the broader cultural context, including institutions and governance structures, that circumscribe the bounds of the decision space (step 0). Single-loop learning (from 7 to 3), as an integral component of adaptive management, allows incremental refinement of alternative sets of actions based upon assessment of the new system state and the impacts of management action. Double-loop learning (from 7 to 1) can occur when evaluation suggests that the problem needs to be reframed to question previous assumptions about the system, reassess fundamental objectives or consider alternatives that were previously out of scope, while remaining within the bounds of current practices, norms and policies. Triple-loop learning (from 7 to 0) involves transformation of the institutions and governance structures responsible for the decision-making process, changing the cultural context of the decision and establishing a different frame of reference for how the problem is perceived, defined and addressed. Adapted from Hammond *et al*. [183], Runge *et al.* [184] and Hemming *et al.* [185], with concepts from Pahl-Wostl [186] and the present work.

with natural systems. As such, any decision is inherently state- and time-dependent, in that the conditions and relationships that characterize the social–ecological system are constantly changing, and so the optimal solution is contingent upon the present and future states of the system and the timing of the decision.

Using theory from CE to map the causal interactions and dynamics of culture as part of an integrated social–ecological systems model allows for a more complete representation of the system, more accurate prediction of the potential effects of future systems change and targeted interventions [19]. In particular, frameworks that draw from theory on cultural niche construction and cultural multi-level selection enable the analysis of dynamic social–ecological systems at multiple scales [20,137,201,202,204,210]. Parallel, co-evolving inheritance systems of human genetics, cultures and ecologies lead to complex networks of interactions and feedbacks [119], while the effects of environmental pressures at different scales of human society lead to differing selective forces for individuals, groups, organizations and nations [202]. As an area of applied research, systems modelling has shown to be a productive avenue across many areas of conservation [256,257], and can account for the co-evolution of species with their ecologies [258] and with human social structures and processes [259,260].

Modelling work that builds on theory from CE has been productively used in case studies on topics of conservation concern, such as land use, water use and cooperative resource governance [261,262], sustainable forestry [246,263], regulation of fisheries [264] and climate adaptation [18,265]. However, models that integrate CE and can provide predictions of future system states remain scarce, exposing a gap for decision support tools that can reduce critical uncertainties about the impacts of conservation action ('value of information': [266,267]). At a higher level, a CE framework can help with understanding the institutional, economic and political factors that may cause decision-making processes to fail or produce suboptimal outcomes even when all of the necessary science is available and used appropriately.

(c) Building adaptive institutions and decision-making processes

Thinking about conservation practice and process in evolutionary terms is already embodied in adaptive management, a common framework for conservation under uncertainty [268–272], though one that is often misunderstood and misapplied [273,274]. Adaptive management can be seen as an extension of the SDM cycle for recurrent decisions, under which a decision is implemented (step 6 in figure 1; electronic supplementary material, table S1) and a monitoring programme established to gather data and assess its performance in light of alternative hypotheses about system dynamics and the effects of the decision (step 7 in figure 1; electronic supplementary material, table S1), after which the cycle begins again. Single-loop learning is the standard route for the continuation of the decision cycle under adaptive management, in which information from monitoring is used to update expectations (e.g. via Bayes' theorem [275]) and corresponding adjustments can be made to the alternatives, consequences and trade-offs that could change the optimal choice (from step 7 to 3 in figure 1; electronic supplementary material, table S1 [276,277]). Double-loop learning, an alternative route, goes a step beyond by questioning the core assumptions

Table 1. Potential applications of cultural evolutionary concepts to predicting the consequences of natural resource management and conservation decisions. Represents only step 4 (*predict consequences*) of the decision cycle shown in figure 1; a full table including all steps is presented in the electronic supplementary material, table S1. References with asterisks specifically discuss CE in the context of applied issues in natural resource management and conservation. References are provided as examples and do not constitute an exhaustive list for a particular topic.

cultural dimensions	temporal and evolutionary components	relevant concepts in cultural evolution	references to cultural evolutionary theory
management action takes place within a social–ecological system, where cultural processes can drive or mediate outcomes and be affected by those outcomes	models need to include spatiotemporal dynamics of culture and cultural evolution to predict impacts of management interventions on system	mathematical modelling of cultural evolutionary dynamics; cultural transmission; cultural niche construction; cultural multilevel selection	[9*,19*,187,201*,204*, 205–209,210*,211*]
decision frameworks allow certain types of information to be used as data or evidence	degree to which different knowledges, scientific disciplines, traditions and ideas are considered in decision making is subject to cultural forces and changes over time	evolution of science and policy; cultural transmission; cultural transmission biases	[182,212,213]
expert elicitation of information depends upon cultural definition of what types of expertise are relevant	cultural definitions of domains of expertise and cross-domain applicability can change over time, influence the transmission of information	evolution of domain specificity; cultural transmission biases	[214–216]
success of actions intended to conserve cultural knowledge and traditions depends upon availability and use of cultural transmission pathways and processes	cultural transmission pathways are dynamic and co-evolve over time with environmental change	cultural transmission; cultural transmission biases; cultural transmission pathways	[217*,218*,219*,220*, 221]
success of actions intended to induce behaviour change depends upon cultural context and compatibility of interventions and messaging with existing cultural beliefs and practices	cultural values, preferences and norms vary and change over time	evolution of pro-environmental behaviour; cultural transmission biases; evolution of norms	[95,112*,222*,223*,224]
success of actions intended to conserve non-human animal culture depends upon impacts to cultural transmission pathways and processes, along with demography and ecology	culture and other socially learnt information can affect animal behavioural and social dynamics, interactions with the environment and humans, relative fitness	evolution and function of culture in non-human animals; predictive models of cultural responses of non-human animals	[225*,226*,227*,228*,229*, 230*,231*, 232*]
	unique cultural traditions can be associated with population structure, leaving some traditions at higher risk of extinction	cultural transmission dynamics and pathways in non-human animals	[227*, 233*,234*, 235*]
cultural responses to and relationships with particular species, materials, places and ecosystems are conditional upon a history of accumulated interactions	outcomes of management actions—successful or unsuccessful—can lead to differences in species abundance, contact rates or context of interactions (including conflict) that shift the typical or normative cultural baseline of future interactions	evolution and cultural transmission of human–nature relationships	[236*, 237*]
interpretation and understanding of decision consequences are filtered through cultural perspective	cultural values, preferences and norms vary and change over time	cultural transmission biases; science communication as cultural transmission	[112*, 238]
	cultural information can change as a result of different understanding during transmission, causing unintended outcomes and affecting future transmission and cultural dynamics	cultural diffusion; copying fidelity; salience of cultural variants	[95,188,190,239,240]

made in framing the problem, which could result in a different set of objectives and alternatives in light of the knowledge that they need to address the problem in a new way (from step 7 to 1 in figure 1; electronic supplementary material, table S1 [186,278]). Finally, triple-loop learning represents sweeping transformational change of the institutions, governance structures and processes within which the decision takes place [186], which we interpret as an intentional re-envisioning of the cultural context of the decision because it seeks to actively examine and build from the plurality of cultural values and perspectives present (from step 7 to 0 in figure 1; electronic supplementary material, table S1 [249,279]). In essence, single-loop learning asks, 'are we doing things right?', double-loop learning asks, 'are we doing the right things?' and triple-loop learning asks, 'why do we think this is right?' and 'who has the rights?' [280,281].

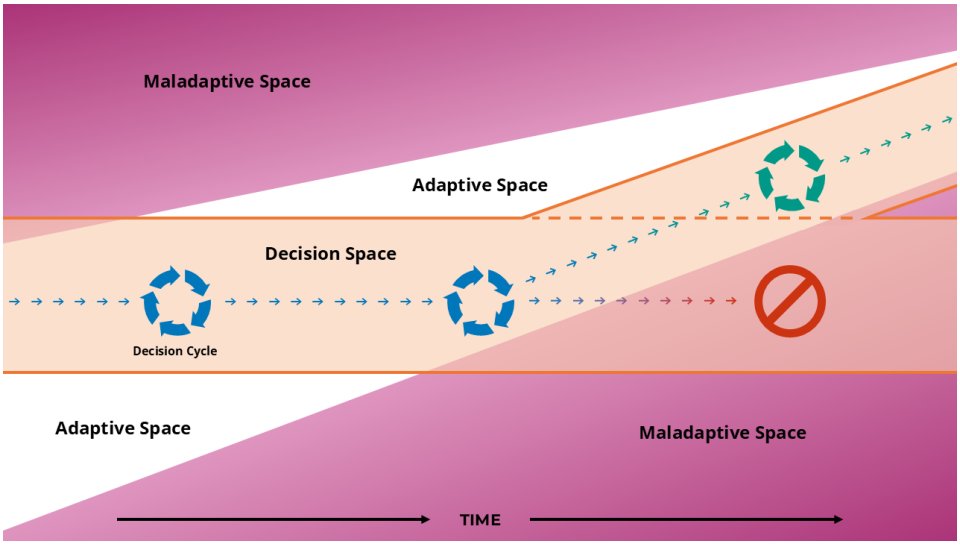

Figure 2. Conceptual diagram of an iterative decision process, taking place within a decision space determined by cultural context, as it navigates the adaptive landscape of a dynamic social–ecological system. The existing decision process (in blue), bounded (in orange) by a static set of cultural values, institutional norms, traditions and governance structures, is unable to adapt to changing social and ecological conditions (blue to red pathway), resulting in a loss of relevancy and the ultimate failure of the process to fulfil its intended purpose (in red). Alternatively, a transformational triple-loop learning process (blue to teal pathway) results in fundamental changes to the cultural context of the decision, shifting the bounds of the decision space and re-evaluating the problem in light of the changing system state, thereby enabling the transformed process (in teal) to continue to survive and adapt. Patterned after Wise *et al.* [284].

Single- and double-loop learning are technical and procedural steps that enable the core functioning of adaptive management [269]. Monitoring is meant to enable the decision process to adapt to changes in the system and typically includes ecological, geophysical and climatic variables indicative of the state of the system, its relationships and management objectives [282,283]. However, a CE perspective suggests that, for an integrated social–ecological system, a robust monitoring programme would need to include relevant indicators of the social and cultural elements of the system, as they constitute critical elements of the system state, are subject to change over time, and can have substantial impacts on the choice and performance of a particular course of action (electronic supplementary material, table S1 [277]). Moreover, failing to account for the position of the decision process and its underlying governance structures and institutions within the space of a dynamic social–ecological system risk the process becoming decoupled from and misaligned with trends of sociocultural change. In an evolutionary sense, the decision-making apparatus navigates through a social–ecological adaptive landscape, and failing to detect and adapt to components of systems change—cultural or otherwise—can cause the decision process to become maladapted to its current environment. Then, any alternatives considered under the existing context, no matter how novel, will be unable to 'right the ship' because they remain limited within the maladaptive bounds of the decision space (figure 2).

Only through triple-loop learning, equivalent to a transformational change process at an organizational or institutional level, can the cultural context of the decision process have the opportunity to adapt (figure 2; [47,48,79,186,249,285]). Though the concept of adaptive governance has been variously defined, understood and implemented [166,286], under this integrative CE framing, adaptive governance is simply an extension of adaptive management that formalizes regular double- and triple-loop learning cycles, in the way that adaptive management is an extension of SDM that includes single-loop learning [186]. This is what Fisk *et al.* [48] refer to as 'steering the ship with intention'—a deliberate process of continual learning and responsiveness to the changing conditions of the social–ecological system to direct an organization and its decision-making processes, through mutable governance and power structures, that enables continued survival, improved outcomes and greater relevancy, representation and support.

The concept of guided variation from CE emphasizes the ability of humans to select desired cultural variants and guide our own evolution in a way that is distinct from the limitations posed by typical routes of biological adaptation [102,169,287,288]. Further, literature from CE on the evolutionary basis, function and dynamics of cultural institutions, particularly those related to conservation, can provide valuable insights into the past, present and potential future states of conservation institutions and organizations and the processes by which they change [135,136,289]. If developed into accessible tools, CE science could aid conservation agencies engaging in transformational change and triple-loop learning processes by providing support for responding to social–ecological systems change, dealing with challenges such as overcoming internal and external resistance to change, restoring broad-based cultural relevancy and building networks of partners and stakeholders to expand capacity, engagement and the impacts and benefits from responsible conservation practice [79,290].

6. Conclusion

The integration of CE with natural resource management and conservation is still nascent, but initial explorations into this applied scientific interface are already underway [19,20,182,201,202,265,291]. We argue that this novel transdisciplinary domain of conservation social science has the potential to provide significant benefits by way of (i) a rigorous science on culture, culture

change and their effects on behaviour, to inform robust and effective conservation decision making; (ii) a novel framework by which human culture and its evolutionary processes are understood as central to the dynamic, coevolving nature of social–ecological systems and our ability to predict their future dynamics; and (iii) tools to enable conservation organizations and agencies to intentionally shape their own evolution and maintain the ability to survive, adapt and provide maximal benefits for people and for ecosystems under global change. CE also has the capability to fill urgent needs in conservation practice, including applied tools for behaviour change to solve present and emerging crises.

The need to develop CE into an applied science for conservation poses challenges. Brooks *et al.* [292] detail a number of difficulties communicated by practitioners across different domains looking to apply CE to their work, including the relative impenetrability of the language and theory used in CE to people unfamiliar with the field and the lack of focus by CE researchers thus far on demonstrating applied benefit and value from the adoption of a CE framework when established alternatives exist. These speak to the need for CE researchers to engage directly with decision makers and applied scientists across different fields to develop an understanding of domain-specific issues that could benefit from CE theory and develop tools fitted to those contexts, ideally as part of a co-creative process that involves both parties at all stages from problem framing to implementation and beyond. Further, given the focus of decision support tools on predicting the future impacts of a variety of potential interventions on a system, it will be important for CE researchers to be able to pivot from developing descriptive models of past or present evolutionary dynamics to ones that can project future and counterfactual scenarios given sets of alternative parameters or conditions [62,184,255].

Concurrently, we hope this work encourages conservation social scientists to engage more with the burgeoning CE literature and partner with CE researchers to build applied tools for conservation decision making. CE calls attention to critical factors arising from the dynamic evolutionary processes underlying cultural and behavioural change, including the evolved context of group-level cooperation and management of public goods, the cognitive biases involved in dictating the transmission of information through and between social networks and the selection of information for decisions, and the webs of ever-changing relationships connecting ecologies to human social, economic and political systems, including conservation practice itself. These can provide for a level of critical reflexivity within the field of conservation on the foundations of its present institutions in a particular set of cultural values and provide the basis and the means for engaging in intentional adaptive change [47,48]. Crucially, CE can provide value for conservation in that it fills a critical need for a rigorous science of culture change in a time in which rapid shifts in cultural values, norms and institutions are creating urgent challenges for conservation organizations and agencies across the globe [293,294]. Conservation is culture, culture evolves, and so too can the science and practice of conservation continue to adapt to best steward and sustain the systems that support present and future generations.

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Data accessibility. This article has no additional data.

Supplementary material is available online [295].

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

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