Multilevel processes and cultural adaptation

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ABSTRACT

The last two decades have seen a proliferation of research frameworks that emphasise the importance of understanding adaptive processes that happen at different levels. We contribute to this growing body of literature by exploring how cultural (mal)adaptive dynamics relate to multilevel social-ecological processes occurring at different scales, where the lower levels combine into new units with new organizations, functions, and emergent properties or collective behaviours. After a brief review of the concept of “cultural adaptation” from the perspective of cultural evolutionary theory, the core of the paper is constructed around the exploration of multilevel processes occurring at the temporal, spatial, social and political scales. We do so by using insights from cultural evolutionary theory and by examining small-scale societies as case studies. In each section, we discuss the importance of the selected scale for understanding cultural adaptation and then present an example that illustrates how multilevel processes in the selected scale help explain observed patterns in the cultural adaptive process. The last section of the paper discusses the potential of modelling and computer simulation for studying multilevel processes in cultural adaptation. We conclude by highlighting how elements from cultural evolutionary theory might enrich the multilevel process discussion in resilience theory.

Key words: cultural adaptation; cultural evolution; multilevel selection; resilience
INTRODUCTION

The last two decades have seen a proliferation of research frameworks that emphasise the importance of understanding adaptive processes that happen at different levels. The common argument in multilevel approaches, borrowed from complexity theory, is that the combination of lower-level units often results in new higher-level units with new organizations, functions, and emergent properties or collective behaviours that do not necessarily equal the sum of attributes observed at lower-level units. As a consequence, only a multilevel approach would allow us to understand the dynamics of the non-linear interactions between the components of these systems.

Arguments for the importance of multilevel processes have been made at different scales of analysis. For example, drawing on insights from research on biological adaptation (Fischer et al., 2009), researchers have argued that cultural adaptation cannot be fully explained at a single unit of analysis (e.g., individuals), but that we need to pay attention to the interactions of different levels of social units (e.g., individuals within a group) (Waring et al., 2015). In that vein, researchers have proposed that cultural ‘group selection’ is a powerful adaptive mechanism that helps explain the spread of complex social dynamics such as cooperation. Traits promoting cooperative behaviour can be individually costly, but they could be selected at a group level if they generate large benefits within between-group competition (Richerson et al., 2015, Henrich, 2004).

A similar argument has been made in the field of ecology, with researchers arguing that biological processes may be controlled by the scale of dominant physical processes. Thus, one needs to consider the complexity of the landscape's structure to understand (and manage) biological processes at fine spatial levels (Meentemeyer and Box, 1987). Considerations of the multilevel spatial processes have been applied, for example, to understand the effectiveness of protected areas: the growing spatial isolation of areas devoted to conservation - which have become unconnected species' refuge surrounded by habitats with other land-uses- has reduced their conservation effectiveness, as processes that take place at large scales have been neglected. Such findings have led researchers to argue that the ability of protected areas to maintain species richness and their ecological functions depends on how well they are integrated within the land use dynamics of broad-scale landscapes (DeFries et al., 2005, Laurance et al., 2012).

Political scientists have also discussed how a multilevel governance system including political actors situated at different governance levels and enmeshed in an overarching policy network can contribute to natural resource governance (Cash et al., 2006, Mwangi and Wardell, 2012). Multilevel
governance moves away from the debates about opposites - centralised versus decentralised, top-down
versus bottom-up - to argue that effective governance needs attributes of political actors at
different levels (Ostrom, 2010). Ostrom defined a polycentric order as one 'where many elements are
able of making mutual adjustments for ordering their relationships with one another within a
general system of rules where each element acts with independence of other elements' (Ostrom, 1999:
57). Bali's complex irrigation system articulated around a nested hierarchy of temples (rice terrace
level temples, which depend on village temples, which depend on regional temples, which in turn
depend on the "Head of the Rice Terraces" temple) provides an example of adaptive multilevel
governance system of a common pool resource (Lansing, 2006).

In this article, we contribute to this growing body of literature by exploring how cultural adaptive
dynamics relate to multilevel social-ecological processes occurring at different scales. Following
Gibson et al. (2000) we define "scales" as the analytical dimensions used to measure and study any
phenomenon and "levels" as the units of analysis that are located at different positions on a scale.
Our contribution focuses on explaining cultural adaptation from cultural evolutionary theory
perspective. We concentrate on small-scale societies to keep the level of complexity within bearable
analytical limits (as opposed to large scale and hyper-connected societies which we deem too complex
for our exploration). The overall argument of the paper is that the understanding of cultural
adaptation depends on our capacity to identify and describe relations between higher and lower
level-units at several scales.

ON CULTURAL ADAPTATION
Definitions of adaptation vary across disciplines, but they all capture the idea of adjustments in a
system's behaviour and characteristics in order to cope with stress or change, leading to an
increased probability of reproduction or persistence (Smit and Wandel, 2006, Nelson et al., 2007).
Coined in evolutionary biology, the term broadly refers to the evolution of genetic or behavioural
outcomes that enable organisms or systems to cope with externally and internally driven changes in
order to survive and reproduce (Kitano, 2002, Michod and Herron, 2006). Adaptation refers to both
the current state of being adapted and to the dynamic evolutionary processes leading to adaptation.
Adaptation enhances the fitness and survival of the evolving entities.

In their analysis of the adaptive process, natural scientists have focused on biological responses
to physical changes (e.g. environment, climate) and relations with other organisms (e.g. adaptations
for competition over resources or mates or host-parasite coevolution). Social scientists have
extended the analysis of adaptation to the study of cultural responses to disturbance and change
across social groups and levels of organization (e.g. individuals, communities, countries or regions) (Adger, 2005, Waring et al., 2015, Richerson et al., 2015). There are differences in these processes: for example, cultural responses often have a degree of foresight or agency that is absent in the relatively blind process of genetic adaptation (although this difference is not absolute and cultural adaptation may also be quite myopic: see below and Mesoudi 2008). Despite these differences, the substantial similarities between the two approaches justify their comparison and integration within a common framework. Just as biological adaptation enhances the fitness and persistence of organisms and possibly of ecological communities, cultural adaptation can potentially enhance the fitness and persistence of individuals, households, communities or larger societies (Berkes et al., 2003, Boyd et al., 2011, Adger, 2005).

Over the last thirty years, two different theories have highlighted the importance of multilevel interplay in social-ecological systems adaptation: resilience theory (Gunderson and Holling, 2002) and cultural evolutionary theory (Cavalli-Sforza and Feldman, 1981, Boyd and Richerson, 1985, 2005). Resilience theory, or more recently the heuristic conceptual framework of Panarchy, has largely advanced our understanding of the complex dynamics of multilevel processes affecting different scales, with numerous articles on the topic appearing in this journal (e.g., Holdschlag and Ratter, 2013, Gunderson and Holling, 2002). Panarchy's conceptual framework focuses on the adaptive nature of complex social-ecological systems, defined as social-ecological systems with multiple interconnected elements with the capacity to change and learn from experience. It considers that understanding the interactions of the different elements of the system at various spatial and temporal levels is needed to account for the dual, and seemingly contradictory, characteristics of stability and change. One of the most important insights of resilience theory is that adaptive behaviours observed at a given scale affect the system on other scales (Gunderson and Holling, 2002, Folke, 2006, Walker et al., 2006). Indeed, major failures in conservation and natural resource management (e.g., fisheries depletion, pollution, deforestation, or global warming) can be interpreted as a consequence of the inability to take into account multilevel processes and cross-scale dynamics embedded in the management of social-ecological systems (Cash et al., 2006, Gunderson and Holling, 2002, Reid et al., 2006).

Cultural evolutionary theory has drawn inspiration and methods from the biological study of evolution and adaptation, emphasizing that the two systems of information transmission - genes and culture - are the intertwined components of a common evolutionary process (Boyd and Richerson, 1985, Cavalli-Sforza and Feldman, 1981). Just as genetic variation is passed from generation to generation with changes resulting from processes such as selection, mutation, migration and drift, cultural evolutionary theory conceptualises cultural change as a process of 'descent with modification': cultural variation is transmitted via social learning from one generation to the next (via vertical
or oblique cultural transmission) as well as within generations (via horizontal cultural
transmission), with changes resulting from processes such as (cultural) selection, mutation (or
innovation), drift and migration. Much attention has focused on transmission biases such as
conformity or prestige bias, which have no clear parallel in genetic evolution. A major innovation
of cultural evolutionary theory is in linking individual-level and population-level processes using
formal mathematical models, lab experiments, field studies and 'cultural phylogenetics' studies to
understand the population-level dynamics generated by the aggregation of individual-based processes
of social learning (Boyd and Richerson, 1985).

Within cultural evolutionary theory, 'adaptation' has broadly the same meaning as in biology,
describing the process(es) by which a cultural system becomes better fit to its environment thereby
enhancing survival and persistence. The relationship between biological and cultural adaptation can
be a subtle one: the human cultural system as a whole can be seen as a biological adaptation, one
that was selected as a way to deal with environments where change is too fast to be handled by pure
biological evolution through natural selection of the genotype. Consequently, cultural adaptations
are likely to be biologically adaptive most of the time, but not always, due to the two evolutionary
systems being partially decoupled. It is also important to note that, just as biological evolution
does not always result in biological adaptation, cultural evolution does not inevitably result in
cultural adaptation. Many studies have examined how several cultural traits without an impact on
fitness (i.e. neutral traits) exhibit variation due to non-selective stochastic processes (e.g. baby
names and pottery decorations, see Bentley et al. 2014). In other cases, cultural traits may be
functional but cultural adaptation fails to occur due to extrinsic factors, such as a reduction in
population size (the 'Tasmanian effect': Henrich 2004) or myopic psychological biases (see below).

In what follows, we use insights from cultural evolutionary theory and examples driven from
small-scale societies, to discuss the importance of multilevel processes at temporal, spatial,
social, and political scales for understanding cultural adaptation.

THE TEMPORAL SCALE
The analysis of the tempo of cultural change has provided important insights in our understanding of
cultural adaptation. First, culture is an inheritance system because it allows individuals to
transmit knowledge, skills, and other learned information, but -unlike genes- culture can
potentially be acquired from anyone in a person's social network. Cultural evolutionary scientists
have devoted much effort to the analysis of social learning, concluding that different transmission
pathways (an individual level-dynamic) impact differently the rate of cultural change (a population
level-process), and therefore the adaptive process (Henrich and Boyd, 1998). For example, all else equal, transmission among peers leads to more rapid cultural change-and potentially to cultural adaptation-than transmission from parents to offspring (Cavalli-Sforza and Feldman, 1981, Herrmann et al., 2013). Results from agent-based simulations also suggest that interaction of cultural copying rates, innovation rates, and resource variance can lead to maladaptive outcomes (Lake and Crema, 2012, Whitehead and Richerson, 2009). In sum, cultural evolutionary theory suggests that the pathway chosen to transmit information between individuals is linked to the tempo of cultural adaptation of the group.

A second insight of the tempo of cultural adaptation focuses on psychological biases that occurring at the short time scales, like a generation, have consequences at multigeneration time scales. As befits a basically adaptive evolutionary system, unsystematic micro decisions might result in long-term highly adaptive practices (Smith and Winterhalder, 1992) or prevent optimal long-term adaptation. For example, prestige bias related to consumerism, temporal discounting biases - where people prefer small, immediate payoffs to larger, delayed payoffs -, or the planning fallacy - where people unrealistically focus on positive outcomes of their actions -, can all result in maladaptive evolution (Mesoudi, 2008, Smith and Winterhalder, 1992) precisely because there is a misfit between the results of the individual short-term adaptive process and the group long-term adaptive process. The idea that rather myopic short-time scale adaptive processes may not generate long-term adaptation is well exemplified by the dynamical models of historical cultural change presented by Turchin (2003). Turchin modelled the rise and fall of agrarian empires as a consequence of changing levels of within-group cooperation and between-group conflict. In young relatively small-scale empires skilled elite classes may be beneficial to the society due to their leadership or expertise. As empires grow, elite overproduction and exploitation creates a burden within the society, reducing within-group social cohesiveness and cooperation. Neighbouring rival groups with smaller or no elite classes, and thus greater within-group cooperation, can then successfully invade and conquer the larger but internally-divided empire. The new empire then forms an elite class, which grows, followed by invasion by a new less-internally-corrupt small-scale neighbour, and the cycle continues. At play in this example are psychological biases such as the lack of elite's foresight or planning, and runaway prestige hierarchies causing elite overproduction.

Third, the investigation of the tempo of cultural evolution also points to cases of complex evolutionary dynamics in which non-linear processes cause path dependency, cycling and chaotic variation. Such dynamic is exemplified in Bettinger's (2015) study of subsistence intensification in aboriginal Western North America. In the late Holocene, the intensified use of labour intensive plant resources and fisheries substantially raised population densities and - with it - the potential for conflict. Through time, the political system evolved in what Bettinger calls "orderly
anarchy," a system characterized by the existence of a series of institutions (i.e., customary law, shell bead money, and shunning) that kept violence to a minimum and allowed individuals to cooperate in trade, fish weir construction, and other enterprises. The complex system of institutions was an alternate end point solution to the paradox that an increase on population density simultaneously generated a) increased returns from cooperative enterprises (e.g. trade) and b) higher between-groups conflictivity. As Bettinger remarks, the initial points in the organization of this system were pre-existing patrilineal kinship systems to organize defence and other forms of cooperation. So, the organization of this complex system shows, in fact, the importance of path dependency.

In sum, cultural evolutionary theory not only allows us to understand why our complex, cumulative culture evolved in the Pleistocene (Richerson and Boyd, 2013, Perreault, 2012) and compare the rates of cultural change to biological change (Henrich, 2001); such theory also equips us with insights to understand the possible tradeoffs between rather myopic short-time scale adaptive processes and long term adaptation.

THE SPATIAL SCALE

Societies being geographically constrained, the spatial dimension of cultural adaptation is closely related to the environment within which they are embedded (Meentemeyer and Box, 1987). It is worth noticing, the spatial structure of any given society is neither uniform nor random, being affected by factors such as the uneven distribution of natural resources and by variations in phenomena that operate at more than one spatial level and that are responsible for energy inputs and external disturbances (Markofsky et al., 2016). Spatial occupation is also patterned by multiscalar interactions within and between social groups, such as competition, cooperation, or exploitation (Carballo et al., 2014). Therefore, the identification of spatial patterns in social phenomena can help us explain the cultural adaptive process as related to and interactions that occur at different spatial level (Cumming et al., 2006), an undertaking eased by emerging techniques from spatial statistics (Fotheringham et al., 2010, Parker et al., 2003).

The case of the diffusion of agriculture (Neolithisation) to Europe highlights the importance of looking at the multilevel spatial dimension of cultural adaptation. The Neolithisation process represents one of the most recent cultural evolutionary shifts in human history, leading to the virtually global transition from foraging to farming economies observed over the Holocene (Skoglund et al., 2012, Mazoyer and Roudart, 2006). Since there is no evidence for a global organisation leading such transition, understanding the processes resulting on the Neolithic transformation
depends on our capacity to connect and compare different spatial dimensions of analysis.

At the coarser geographic (and temporal) scale and within the climatic framework of the Holocene, a general overview suggests the Neolithisation process was a steady global phenomenon of cultural adaptation associated with an increase in human fertility (Bocquet-Appel, 2011). However, a finer-grained analysis at the continental and local scales suggests that Neolithisation was far from "smooth". For example, the transition to agriculture in Europe seems to have been characterised by boom-and-bust population patterns, possibly constrained by environmental and climate-related dynamics or induced by endogenous factors such as rapid population growth and unsustainable farming (Shennan et al., 2013). Furthermore, there is evidence of different Neolithic traditions, or strategies adapted to specific environmental and climatic settings. For example, two traditions are associated to the main routes for the spread of the Neolithic from South-West Asia into Europe: the continental tradition is associated with a settlement and land-use strategy primarily based on agriculture, whereas the Mediterranean tradition is associated with mixed strategies largely based on nomadic and semi-nomadic pastoralism (Angelucci et al., 2009). Moreover, within these broad core areas, a multiplicity of genetic, cultural and social-ecological groupings have been recognised and described at the local levels, differences mediated by specific climatic, environmental, social and cultural settings (Barker, 2006).

In spite of, and perhaps thanks to, the multiple continental, regional and local expressions of the Neolithisation process, domestication and agriculture became a global phenomena over a relatively short period of time. A key feature of early Neolithic small-scale societies that may help explain the success of this adaptive strategy is the strong coupling between the emergence of agriculture and that of increasingly complex exchange and trade networks (Ibañez et al., 2015). Overlooked in the literature when compared to the study of agricultural developments in the domestication process, trade and exchange networks have contributed to the overall cohesion of myriads of different small-scale societies across extended regions. Through trade and exchange, local social-ecological systems and solutions, farming-based and not, were embedded within the broader Neolithic context. By increasing interaction, denser linkages contributed to raising the circulation of social and cultural-technological solutions. Such geographical connectedness has now grown beyond geographical and physical boundaries, imposing new challenges for the management of different resources, and for the integration of small-scale societies embedded through multi-level processes.
THE SOCIAL SCALE

Humans are adapted to social life in groups following a variety of organizational forms (Gowdy and Krall, 2013). Social structures operate at many levels (e.g., families, neighbourhoods, villages, clans, ethnic groups, nations, etc.). Moreover, social organization levels display a large diversity in terms of structure, social norms, and interaction. In addition, these varying layers of social interaction are often nested (Coultas, 2004).

Cultural evolutionary theory has studied how groups and organizations change as they solve collective action problems (Boyd and Richerson, 2009, Choi and Bowles, 2007). One of the more important insights of this theory has been that innovations can spread in a metapopulation despite being individually costly if the resulting new behaviour increases the fitness of the group, including adaptations to environmental or other conditions (Bowles et al., 2003, Richerson et al., 2015). Thus, groups can evolve to solve social dilemmas through the creation of sanctioning norms and punishment of non-cooperative individuals (Fehr and Gachter, 2002). The same process could operate at a different scale, with metagroups punishing non-cooperative groups, which implies that phenomena occurring at any one social level are affected by mechanisms occurring at lower and higher levels, with lower level phenomena potentially reacting to higher-level phenomena and acting to change them (Waring et al., 2015).

To explore the importance of looking at multilevel social processes when dealing with cultural adaptation, we examine the case of traditional knowledge systems. Traditional knowledge systems are defined as "a cumulative body of knowledge, practice and belief evolving by adaptive processes and handed down through generations by cultural transmission, about the relationship of living beings (including humans) with one another and with their environment " (Berkes et al., 2000: p. 1252).

Researchers have argued that some of the adaptations that explain the expansion of our species are at least partially - cultural, in other words cumulative and transmitted by social learning (Boyd and Richerson, 1985, Henrich and Boyd, 1998). Groups create and transmit a set of behavioural strategies and knowledge that allows them to solve adaptive problems such as producing food, mating, investing in offspring, or managing social interactions (Quave and Pieroni, 2015, McDade et al., 2007). Furthermore, it has been argued that such knowledge systems contribute to mediate people's capacity to cope with social-ecological change and guide decision-making regarding natural resource-management and biodiversity-conservation practices (Colding et al., 2003, Berkes et al., 2007).

The study of traditional ecological knowledge systems and how they affect cultural adaptation requires a multilevel approach. Several characteristics of traditional knowledge systems should be considered at the group-level. For example, processes such as the creation, transmission, storage,
or maintenance of knowledge rely on social efforts over time (Richerson and Boyd, 2005, Smith et al., 2008). Furthermore, as other types of knowledge, traditional knowledge is a public good, or a shared resource from which every member of a group may benefit, regardless of whether or not they personally contribute to its provision (Olson, 1965). But, because of its level of sophistication, traditional knowledge is costly to acquire (Gurven et al., 2006) and to transmit (Demps et al., 2012). For example, research suggests that hunter-gatherers' acquisition of adult-level hunting competence is not only limited by the constraints of physical capital or body size, but also because the costly investment required for proficient hunting might take many years to develop after achieving adult body size. Understanding the individual costs associated with the acquisition of knowledge is important because it means that, given the choice between several knowledge systems, people might make selective decisions in terms of the type of knowledge they want to accumulate (Sternberg et al., 2001). Such individual decisions, however affect higher levels, which might explain the current trend in the loss of traditional knowledge that many small-scale societies are experiencing (Reyes-García et al., 2013).

The analysis of multilevel social interactions also reveals patterns how social knowledge dynamics relate to cultural adaptations. If there were no multilevel interactions, and individuals acted only to optimize their survival strategies, one would expect that individual levels of traditional ecological knowledge would correlate with individual fitness. However, under a multilevel framework one should expect to see social behaviour evolve when selection operates at social levels higher than the individual: behaviours that bring benefits to the group are favoured by group selection, even when they are costly for the individual (Gintis, 2000, Fehr et al., 2002). This intuition is put forward from results of recent research among three forager societies. In such research, Reyes-García et al. (in press) found that variations at individual levels of traditional knowledge relate to individual hunting productivity and self-reported health, but not to nutritional status (a general proxy for individual adaptive success). The authors interpret the finding in the context of the pervasiveness of sharing in such societies: by sharing resources and knowledge, individuals who achieve higher returns to their knowledge transfer material and non-material resources to the rest of the group. Thus, the use of a multilevel framework allows interpreting sharing as an adaptive mechanism that increases group fitness through the redistribution of resources (see Fischer et al., 2009 for a similar argument in biology).

THE POLITICAL SCALE

Individuals engage in a wide diversity of activities in their daily lives, with a series of informal and formal institutions affecting their decisions at any point of time. Governance refers to the set
of rules that specifies who can make decisions in a given context, what aggregation rule will be used in making decisions, and how information and payoffs will be distributed in these processes (Bache and Flinders, 2004). As different decision agents (i.e., local, national and international organizations, or regional and national governments) focus on different spatial and temporal scales and as different actors can be aggregated at various levels - typically related to territoriality-governance should also be analysed from a multilevel perspective. Multilevel governance pays attention to the relations (i.e., power, contestation, learning) among political actors at different levels and how the linkages between higher and lower levels of governance institutions negatively or positively affect the decisions of political actors at different levels (Armitage, 2008, Brondizio et al., 2009).

The concept of multilevel governance emphasizes the dispersion of decision making away from a central authority upwards to the supranational level, downwards to subnational jurisdictions, and sideways to public/private networks (Bache and Flinders, 2004). The concept, originally proposed in relation to international policy, has been used to the complex politics of scale of environmental issues as local systems of biodiversity use and management usually consist of informal or customary institutions embedded in larger formal regulatory frameworks that go from the local to the international scales (Mwangi and Wardell, 2012). As an example of multilevel governance in natural resource management we discuss here the case of the governance of a protected areas overlapping with an indigenous territory, where national formal regulatory frameworks for the management of natural resources interact with informal or customary institutions.

The Tsimane' are an indigenous semi-autarkic society in the Bolivian Amazon (Huanca, 2008). Like other small-scale societies (Berkes et al., 2000, Dietz et al., 2003), the Tsimane' seem to rely on a series of flexible informal institutions (i.e., strong norms of sharing and cooperation) to deal with environmental uncertainty and unpredictable resource availability (Fernández-Llamazares et al., 2016). Such informal rules have allowed them to sustaining their livelihoods and maintain the forest with no centralized governmental control. However, since the 1970s, the Bolivian government followed international trends aiming to conserve biodiversity and established several Protected Areas in the Tsimane' ancestral territories. The government imposition of a strong regulatory framework, enforcement mechanisms, and sanctions triggered -during the 1990s- a series of protests by indigenous peoples which resulted in a more inclusive national conservation policy (Reyes-García et al., 2014). Such is the origin of the Pilón Lajas Biosphere Reserve and Indigenous Territory, where in 1992 a co-management arrangement was instituted to involve customary institutions in the protected area decision-making (Bottazzi and Dao, 2013). The novelty of the co-management approach was that it instituted the sharing of responsibility in resource management between government agencies and local communities. At a short-term scale, such an
approach promoted the coordination of activities (i.e., cocoa development projects, community-based monitoring) to deal with immediate threats such as illegal logging and colonists’ encroachment. The success of some strategies, however, has been undermined by the weakening of indigenous collective action. For example, to increase the effectiveness of local monitoring and to improve forest management, the government has granted a concession for timber extraction to one of the communities in the protected area. Although the government envisioned optimistic outcomes and increased community cooperation, the concession led to an increase in deforestation by individual indigenous peoples acting in self-interest as peer sanctioned had been eroded (Ruiz-Mallén et al., 2015).

Two important points derive from the example above. First, the analysis of multilevel governance allows spotting feedback loops between political actors operating at different levels. Thus, national policies have a clear impact on local institutions, but those -in turn- can also mobilize to affect national policies. Second, the analysis of interactions between political actors operating at different scales highlights how adaptive management strategies are challenged by interest, decision-making, and power between institutions at different levels. In our example, the two main political actors involved (i.e., the indigenous communities and the state) operate at different temporal and spatial scales, which results in different motivations. Indigenous peoples might feel their rights to land and resources are threatened, which explains their myopic behaviour in resource extraction. The government, in turn, might act under a longer-term perspective, often pushed by international conservation norms.

MODELING MULTILEVEL PROCESSES IN CULTURAL ADAPTATION

The examples presented above provide an account of the complexity of processes that operate in different aspects of cultural (mal)adaptation across scales and within levels. Within cultural evolutionary theory such multilevel processes have been explored using formal modelling including a diversity of techniques, such as game theory (Gintis, 2000), analytical models (Cavalli-Sforza and Feldman, 1981, Boyd and Richerson, 1985) and computer simulations (Kohler and Gummerman, 2001). Some of these models are purely theoretical (e.g. exploring a particular mechanism, such as conformity (Henrich and Boyd, 1998)), while others use real data to explore the plausibility of a particular model against evidence (e.g. Bentley et al., 2014). Modelling techniques for past small-scale societies have been explored by Lake and Costopoulos, 2010; Lake, 2014; Wurzer, 2015.

The study of multilevel processes in cultural adaptation presents important challenges which differ from those found when exploring the same question at a single level. For example, the study of
multilevel processes forces to combine bottom-up and top-down perspectives (Lansing, 2003) and to explore potential feedback loops (Liu et al., 2007). This type of dynamics might generate nonlinear behaviour, a property of Complex Adaptive Systems (CAS, see Holland, 1992). New and old formal methods used to explore CAS are well suited to explore multilevel processes in cultural adaptation. For example, classical integrodifferential and difference equations allow for the exploration of scenarios for studying population dynamics, or it can also be used to test theory against evidence with numerical methods (e.g., Kandler et al., 2010). The low dimensionality of such models is useful when fitting historical and archaeological data which are seldom rich enough to fit complex models. Game theoretical approaches have been traditionally used for studying adaptive processes when strategic interactions are important (Smith, 1982), and can be also potentially be adapted to explore multilevel dynamics (Fletcher and Zwick, 2007). Statistical and stochastic models are increasingly popular ways to introduce heterogeneity into a population-based system. Using techniques such as Monte-Carlo methods allows the researcher to link stochastic models of individual behaviour to population-level patterns (Traulsen and Nowak, 2006). Finally, Agent-Based Models (ABMs) are well suited for exploring the emergence of macro-dynamics from micro-behaviour in spatially explicit heterogeneous environments. The flexibility provided by this technique allows modelling any type of interaction inside social-ecological systems, breaking the walls of multilevel analysis and correlation between different levels of adaptations.

Given the diversity of tools, researchers should carefully consider their different requirements when making a choice. For example, while equations solved with analytical approaches are better able to explain the dynamics of the system, their application to spatially structured data is difficult to achieve. On their side, ABMs are particularly difficult to understand, analyse and replicate. Finally, the exploration of multilevel processes in cultural adaptation ultimately needs to test theoretical models against evidence using statistical data analysis. In this context, the field would benefit from applying recent developments on model selection frameworks able to quantify the quality of competing models, both in terms of goodness-of-fit and complexity.

CONCLUSION

As resilience theory, cultural evolutionary theory highlights that a number of processes may drive cultural change and that a full understanding of this cultural change requires a proper consideration of multi-level interactions. Given this overlap, we argue that insights from cultural evolutionary theory about how multilevel processes operate might contribute to resilience theory so to strengthen its exploration of social-environmental changes. For example, the concept of 'social-ecological systems' could be enriched with considerations of culture as a cumulative and
collective inheritance system, as understanding the functioning of this system seems to relate to social adaptation, as show in our discussions on how psychological biases occurring at one specific time frame may potentially prevent optimal long-term decision-making. Similarly, understanding culture as a non-linear process showing boom-and-burst adaptive patterns due to external forcing (in the Neolithic but also in present-day marked-based economies) as well as unsustainable (maladaptive) decisions could help untangle ‘persistence and change’ in social-ecological systems. Moreover, as the example of the Neolithic suggest, understanding how cultural transmission operates and its relation to the spread of adaptive and maladaptive processes (time-wise and space-wise) can also help explain global -or large scale- transitions. At a methodological level, the large experience of cultural evolutionary theory with modelling and simulations could also contribute to the formal modelling of social-ecological resilience. While this paper is just an initial effort to bring insights from cultural evolutionary theory to resilience theory, we see much scope for integration and cross-fertilisation of research findings.

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