

Published in final edited form as:

Ecol Soc. ; 21(4): . doi:10.5751/ES-08561-210402.

Multilevel processes and cultural adaptation: Examples from past and present small-scale societies

V. Reyes-García^{1,2}, A. L. Balbo³, E. Gomez-Baggethun^{4,5}, M. Gueze², A. Mesoudi⁶, P. Richerson⁷, X. Rubio-Campillo⁸, I. Ruiz-Mallén^{2,9}, and S. Shennan¹⁰

¹Institució Catalana de Recerca i Estudis Avançats

²Institut of Environmental Science and Technology, Universitat Autònoma de Barcelona, 08193, Cerdanyola del Valles, Barcelona, Spain

³Complexity and Socio-Ecological Dynamics, Institució Mila i Fontanals, Spanish National Research Council, Barcelona, Spain

⁴Department of International Environment and Development Studies (Noragric), Norwegian University of Life Sciences, Ås, Norway

⁵Norwegian Institute for Nature Research, Oslo, Norway

⁶University of Exeter, UK

⁷University of California, Davis, USA

⁸Barcelona Supercomputing Center, Barcelona, Spain

⁹Internet Interdisciplinary Institute, Universitat Oberta de Catalunya, Spain

¹⁰Institute of Archaeology, University College London, UK

Abstract

Cultural adaptation has become central in the context of accelerated global change with authors increasingly acknowledging the importance of understanding multilevel processes that operate as adaptation takes place. We explore the importance of multilevel processes in explaining cultural adaptation by describing how processes leading to cultural (mis)adaptation are linked through a complex nested hierarchy, 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 and resilience 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 examining small-scale societies’ 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. We end the paper discussing the potential of modelling and computer simulation for studying multilevel processes in cultural adaptation.

Keywords

cultural adaptation; cultural evolution; multilevel selection; resilience

Introduction

The last two decades have seen a proliferation of frameworks underscoring the importance of understanding processes that happen at different levels. The main common argument in these different frameworks being 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 to the sum of attributes observed at lower-level units.

The argument of the importance of focusing on multilevel processes has been posited regarding 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 by focusing on the analysis of social units at one level (i.e., individual), but that we need to pay attention to the interactions of different level social units (i.e., individuals within communities) (Waring et al., 2015). In that vein, researchers have proposed that ‘group selection’ is a powerful evolutionary mechanism that can help explain some adaptive process such as the spread of cooperative behaviours: when there are multiple clearly defined groups that vary in a key trait that affects their success, group selection can potentially act to favour groups with a cooperative trait, even if this trait is individually costly (Richerson et al., 2015, Henrich, 2004).

A similar argument has been done in the field of ecology, with researchers arguing that because biological processes may be controlled by the scale of dominant physical processes, to understand (and manage) biological processes at fine spatial levels, one needs to consider the complexity of the landscape’s structure, which plays an essential role in the dynamics of complex biological systems (Meentemeyer and Box, 1987). Considerations on the importance of 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 where other land-uses prevail- has reduced their effectiveness in biodiversity conservation, as the focus on a single species might neglect its dependence on processes that take place at larger scales. Such finding has lead 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, DeFries et al., 2007).

Political scientists have also discussed how a multilevel governance system, which includes 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 – arguing that effective governance needs attributes of political actors at different levels (Ostrom, 2010). Ostrom defined a polycentric order a one ‘where many elements are capable 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 (small temples at the rice terrace level, which depend on village temples, which depend on regional temples, which depend on the "Head of the Rice Terraces" temple) provides an example of successful multilevel governance system of a common pool resource (Lansing, 2006).

In this article, we contribute to this growing body of literature by exploring how multilevel processes occurring at different scales relate to the cultural adaptive processes. We focus on cultural adaption because its growing relevance in the context of accelerated global change (Smit and Wandel, 2006, Nelson et al., 2007). We focus 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 deemed too complex for our exploration). 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. The overall argument of the paper is that the understanding of cultural adaptation depends on our capacity to intercept and describe feedbacks 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, Gallopin, 2006). 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 response to physical changes (e.g. environment, climate). Social scientists have extended the analysis of adaptation to the study of cultural response to disturbance and change across social groups and levels of organization (e.g. individuals, communities, countries or regions) (Adger, 2003, Waring et al., 2015, Richerson et al., 2015). In spite of significant differences between drivers of biological and cultural adaptation, substantial similarities exist between these two approaches: just as biological adaptation enhances the fitness and persistence of organisms and possibly of ecological communities, cultural adaptation is often seen to enhance the fitness and persistence of individual people, households, communities or larger societies (Berkes et al., 2003, Boyd et al., 2011, Adger, 2003).

Within the last three decades, two different theories have highlighted the importance of multilevel interplay in social-ecological systems adaptation: cultural evolutionary theory (Waring et al. 2015; Richerson et al. 2015) and resilience theory (Gunderson and Holling, 2002). Cultural evolutionary theory has broadly adopted the biological definition, emphasizing that two co-evolving systems of inheritance, genes and culture, shape human behaviour (Boyd and Richerson, 1985, Cavalli-Sforza and Feldman, 1981). As for genes, we

inherit cultural traits from the population we belong to. Cultural evolutionary theory has led the field in linking individual-level and population- or society-level processes, mainly trying to understand the population-level consequences of the individual-level processes of social learning (Boyd and Richerson, 1985). Because of differences in the cultural and genetic evolutionary processes, cultural adaptations do not necessarily correspond exactly to genetic ones. In particular, human societies usually involve substantial cooperation between non-relatives, something that is uncommon and limited in extent in other species.

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 (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). According to resilience theory, major failures in conservation and natural resource management (e.g., fisheries depletion, pollution, deforestation, or global warming) are a consequence of the inability to take into account multilevel processes and cross-scale dynamics embedded in the management of social-ecological systems (Millennium Assessment, 2005, Cash et al., 2006, Gunderson and Holling, 2002, Reid et al., 2006).

We draw on insights from both intellectual traditions to discuss the importance of multilevel interplay in cultural adaptation.

The Temporal Scale

The analysis of tempo of cultural change has provided important insights to understand cultural evolution. First, culture is dynamic because it constitutes an inheritance system, with knowledge, skills, and other learned information transmitted from generation to generation. Unlike genes, culture can be acquired from anyone in a person's social network, leading to the "viral" rates of change observed with the advent of mass and social media. Cultural evolutionary scientists have devoted much effort to the analysis of social learning concluding that different transmission pathways (an individual level-process) 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, horizontal transmission among peers leads to more rapid cultural change than vertical transmission from parents to offspring (Cavalli-Sforza and Feldman, 1981). So, innovations would spread slowly in a society where transmission of knowledge is done mainly through vertical transmission, whereas horizontal transmission could allow for rapid evolution (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). For example, in (Whitehead and Richerson, 2009)'s

simulation, long runs of low variance environments favoured excessive reliance on cultural copying at the expense of innovation, so when large environmental excursions occurred, they tended to result in extinctions.

A second insight of the analysis of the tempo of cultural evolution 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 (Mesoudi, 2008), can all result in maladaptive evolution.

Third, the investigation of the tempo of cultural evolution often points to cases of complex evolutionary dynamics in which non-linear processes cause path dependency, cycling and chaotic variation. Using a combination of high resolution archaeological record and ethnographic data from aboriginal Western North America, Bettinger (2015) reconstructed the region's history of subsistence intensification. In the late Holocene, the intensified use of labour intensive plant resources and fisheries substantially raised population densities and potential for conflict. 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 problems of increased conflict and increased returns to cooperative enterprises resulting from increasing population density, like trade. Interestingly, Bettinger remarks that the initial points in the organization of this system were pre-existing patrilineal kinship systems to organize defence and other forms of cooperation, thus providing evidence of the importance of path dependency.

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). Drawing on the work of Ibn Khaldun on the coastal city-states of North Africa and their tribal hinterlands, Turchin modelled the rise and fall of agrarian empires throughout history 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. Using dynamic evolutionary models, Turchin (2003) showed that this cycle of elite overproduction and empire collapse fits well with historical dynamics of actual empires across Europe and Asia. At play in this example are many of the psychological biases previously mentioned, such as the lack of foresight or planning on the part of elites, and runaway prestige hierarchies causing elite overproduction. Are small-scale societies

likely to be subject to similar dynamics? Perhaps so. Edmund Leach (Leach, 1954) observed two different forms of social organization among the Kachin peoples of Highland Burma: Chiefdoms ruled by hereditary elites and egalitarian villages. Leach presented evidence that these systems tended to evolve into one another over time in a way that is reminiscent of Turchin's model.

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 detect cases in which rather myopic short-time scale adaptive processes may not generate long term adaptation.

The Spatial Scale

Landscape ecologists explore interaction across spatial scales based on the argument that fine biological processes often react to dominant physical processes at a larger scale (Meentemeyer and Box, 1987). Similarly, societies being geographically constrained, the spatial dimension of cultural adaptation is closely related to the environment within which the society is embedded. The resilience of any given socio-ecological system is affected, among others, by scale matching (and mismatching) between social and ecological dynamic processes and interactions that occur at the spatial scale (Cumming et al., 2006). However, the spatial distribution of any given society is neither uniform nor random, being affected, among others, by 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.). Spatial occupation is also patterned by multiscale interactions within and between social groups, such as competition, cooperation, or exploitation (Carballo et al., 2014). Therefore, the analysis of spatial patterns can help explain the cultural adaptive process, a undertaking eased by emerging techniques from spatial statistics (Fotheringham et al., 2010, Parker et al., 2003).

The case of the diffusion of agriculture (Neolithization) to Europe highlights the importance of looking at the spatial dimension of social-ecological adaptation from a multi-level perspective. 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, Hornborg and Crumley, 2006). Since there is no evidence for a global organisation leading such transition, understanding the processes leading to 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, Goudie, 1993). 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 locally 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, defined as strategies adapted to specific environmental and climatic settings. At the sub-continental level, for example, two traditions are associated to the main routes for the spread of the Neolithic from the Near East (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 to mixed strategies largely based on nomadic and semi-nomadic pastoralism (Angelucci et al., 2009). Within these broad core areas of European Neolithisation, a multiplicity of genetic, cultural and socio-ecological groupings have been recognised and described at the regional and 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 phenomenon 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 (Ibanez 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 socio-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 and multi-scalar processes.

The Social Scale

Humans are social beings adapted to group life (Richerson and Boyd, 2005). We live in uniquely structured social groups which can take many organizational forms (Gowdy and Krall, 2013) and we conform to social norms and conventions (Coultras, 2004). Social organization operates at many levels (e.g., families, neighbourhoods, villages, clans, ethnic groups, nations, etc.). Moreover, social organization levels display a large variability in terms of structure (who belongs to each group) and interaction, with levels often being nested.

Cultural evolutionary theory has studied how groups and organizations evolve as they solve collective action problems (Boyd and Richerson, 2009, Choi and Bowles, 2007) suggesting that successful group behaviours can spread in a metapopulation despite being individually costly (Bowles et al., 2003, Richerson et al., 2015). Such process might result in group-level adaptations to environmental or other conditions (Ostrom, 2008). Thus, it has been argued that groups can evolve to solve environmental cooperation dilemmas, for example through the creation of sanctioning norms and punishment to non-cooperative individuals (Fehr and

Gachter, 2002). The same process could operate at a different scale, with metagroups punishing non-cooperative groups. This implies that phenomena occurring at any one social level are affected by mechanisms occurring at the same level, but also at lower and higher levels. Lower level phenomena react to higher-level phenomena, and then may act to change it (Waring et al., 2015).

To explore the importance of looking at multilevel social processes when dealing with cultural adaptation, we examine here the case of traditional knowledge systems, 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 adaptive 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 help in human adaptive strategy 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 traditional knowledge rely on social efforts, or in the additive contributions of many individuals over time (Richerson and Boyd, 2005, Smith et al., 2008, Nazarea, 2006). 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 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 to 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). At a higher social level, the phenomena might explain the current trend in the loss of traditional knowledge that many small-scale societies are experiencing (Reyes-García et al., 2013)

Furthermore, 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 if they are costly for the individual (Gintis, 2000, Fehr et al., 2002). This intuition is supported by 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 argue that this can be explained due to 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. In a multilevel framework, sharing can be seen as an adaptive mechanism that increases group fitness through the redistribution of resources (see (Fischer et al., 2009, Michod and Herron, 2006) for a similar argument in the biological sciences).

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. The set of operational rules that provides structure for day-to-day decisions within any given group are typically the result of decisions made in a collective-choice arena. Governance refers to the set of rules that specifies who can make decisions in such contexts, what aggregation rule will be used in making these decisions, and how information and payoffs will be distributed in these processes (Bache and Flinders, 2004). As different decision agents (local organizations, regional governments, national governments, and international organizations) tend to focus on different spatial and temporal scales in their respective interest, and as various levels of governing bodies can be aggregated at various levels typically related to territoriality, governance should also be analysed from a multilevel perspective.

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 was originally proposed in relation to international policy, but has later been adapted to the complex politics of scale of environmental issues (Mwangi and Wardell, 2012). Thus, local systems of biodiversity conservation, use, and management, usually consisting of informal or customary institutions embedded in larger formal regulatory frameworks that go from the local to the international scales. In such context, local decision-making is challenged since formal institutions' interests typically prevail over informal or customary institutions' needs. Thus multilevel governance pays attention to the relations (i.e., power, contestation, learning) among political actors at different levels (Folke et al., 2005, Armitage, 2008, Brondizio et al., 2009), and how the linkages between higher and lower levels of governance institutions negatively or positively affect the decisions of political actors at different levels.

We discuss here an example focusing on multilevel governance in natural resource management. Many current local systems of biodiversity conservation, use, and management are based on informal or customary institutions. But such systems are also embedded in broader formal regulatory frameworks, from the local to the international scales, which in

turn are shaped by cultural norms and conventions. Protected areas overlapping with indigenous territories allow for the exploration of the interactions between actors involved in natural resource management at multiple scales. We discuss here the interaction of actors at different scales and the effects of such interactions in adaptive management.

The Tsimane', an indigenous semi-autarkic society in the Bolivian Amazon, share strong kinship and cultural values (Huanca, 2008). As 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.). They have also developed a wide range of informal rules, norms, and sanctions for common management of forest resources, which have allowed for sustaining their livelihoods across generations with no centralized governmental control. Since the late 1970s, however, the Bolivian government has established several Protected Areas in the Tsimane' ancestral territories. The strong regulatory framework, enforcement mechanisms, and sanctions imposed by the government triggered, during the 1990's, a series of protest of Bolivian lowland indigenous peoples. The result was a land tenure reform and changes in national conservation policy frameworks to include indigenous peoples in the management of natural resources (Reyes Garcia et al., 2014).

Such is the origin of the Pilon 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 such co-management approach was that it instituted the sharing of responsibility in resources management between government agencies and local communities. At a short scale, such approach has 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. But the success of some strategies has been undermined by the weakening 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 lead to an increase in deforestation (Ruiz-Mallén et al., 2015).

Why, in the example above, the involvement of local actors did not result in adaptive management? The two main political actors at stake (i.e., the indigenous communities and the state) operate at different temporal and spatial scales, which might results in different incentives. 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 and pushed by international conservation norms. The analysis of interactions between political actors operating at different scales highlights how adaptive management strategies are challenged by interest, decision-making, and issues of power between institutions at different levels. It also shows that multilevel linkages evolve and are maintained by the organisations and institutions involved in resource management to further their own interests (Adger et al., 2005).

Modeling Multilevel Processes in Cultural Adaptation

The examples presented above provide a discursive account of the complexity of processes that operate in different aspects of cultural (mis)adaptation across scales and within levels. How can we explore such complexity in a more systematic way? In the final section of this paper, we discuss the potential of modelling for understanding multilevel processes operating in cultural adaptation.

Evolutionary approaches to cultural change entail a rich tradition of developing formal models to explore questions related to the adaptiveness and dynamics of culture (Mesoudi, 2015, Boyd and Richerson, 2005). The approach includes 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. The study of multilevel processes forces the researcher to combine bottom-up and top-down perspectives (Lansing, 2003) and potential feedback loops (Liu et al., 2007). As we have seen, 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 adaptations. For example, classical *integrodifferential and difference equations* allow for the exploration of scenarios for studying population dynamics. The approach is particularly useful for gaining theoretical insights. 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 (Slobodkin and Rapoport, 1974, Smith, 1982). This type of model can potentially be adapted to explore multilevel dynamics despite the challenges that this added complexity would pose for finding analytical solutions (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 us to model any type of interaction inside socio-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 able to better 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. Classical Null Hypothesis Significance Testing (NHST) is useful to validate that the identified patterns were actually generated by non-random processes, but additional tools are needed when more than one process can explain the same dynamic. 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 (i.e. maximum likelihood combined with Akaike Information Criterion, Bayesian inference, see Burnham and Anderson 2002).

Conclusion

The process of cultural adaptation -whether our interest lies in the longer (cultural evolution) or the shorter (resilience) time frames- requires the exploration of multilevel processes. Culture is a dynamic inheritance system passed through social learning from person to person (horizontally) and from generation to generation (vertically). A number of variations may happen though time in the transmission of cultural information. For example, psychological biases occurring at one specific time frame have consequences at larger temporal scales, thus preventing optimal long-term decision-making. Likewise, different time frames in the understanding of cultural and biogeophysical phenomena may lead to poor long-term decision-making. In politics specifically, a problem of fit is often observed for institutions unable to coherently map on to the biogeophysical scale, and choices made at one temporal level may fail to anticipate consequences at another temporal level. Human relationships also rely largely on the capacity to network over large geographical areas. Networks act within (horizontally) and across (vertically) levels and scales. They affect most phenomena emerging from human interaction, from the household to society at large, from economy to politics, and from local to global organisations. Strategies generated locally in small-scale societies may spread widely through interrelated networks, thus contributing to strategy persistence while enhancing the network own complexity.

As the examples presented here show, multilevel processes might generate nonlinear behaviour, in which the aggregation of units at one level can result in large scale patterns difficult to understand with linear models. Because multilevel processes are pervasive and susceptible to identification and analysis there is a need to explore new methods that help their study. The understanding of complex feedbacks in socio-ecological systems requires a great capacity of abstraction and formalisation as well as the commitment to a reliable system of updating and verification of one's hypotheses. We argue that modeling tools can help researchers to formalize and further explore issues as the ones discussed here. Finally, although the examples presented here have focused on multilevel processes, we acknowledge that there are also important cross-scale interactions, which should also be considered in understanding the cultural adaptive process.

Acknowledgements

This paper results from the author's discussion at the ICREA Workshop "Small-Scale Societies and Environmental Transformations: Co-evolutionary Dynamics" funded by ICREA Conference Awards. Reyes-García acknowledges financial support from the European Research Council under the European Union's Seventh Framework Programme (FP7/2007-2013) / ERC grant agreement n° FP7-261971-LEK and from the CONSOLIDER SimulPast Project ("Simulating the Past to Understand Human Behaviour" CSD2010-00034). ALB has worked on this paper on contract Juan de la Cierva Programme (JCI-2011-10734, MICINN-MINECO, Spain).

Literature Cited

- Adger WN. Social capital, collective action, and adaptation to climate change. *Economic Geography*. 2003; 79:387–404.
- Adger WN, Brown K, Tompkins EL. The political economy of cross-scale networks in resource co-management. *Ecology and Society*. 2005; 10
- Angelucci DE, Boschian G, Fontanals M, Pedrotti A, Verges JM. Shepherds and karst: the use of caves and rock-shelters in the Mediterranean region during the Neolithic. *World Archaeology*. 2009; 41:191–214.
- Armitage D. Governance and the commons in a multi-level world. *International Journal of the Commons*. 2008; 2:7–32.
- Bache, I.; Flinders, M. *Multi-level Governance*. Oxford: Oxford University Press; 2004.
- Barker, G. *The Agricultural Revolution in Prehistory*. Oxford: Oxford University Press; 2006.
- Bentley RA, O'brien MJ, Brock WA. Mapping collective behavior in the big-data era. *Behavioral and Brain Sciences*. 2014; 37:63–76. [PubMed: 24572217]
- Berkes F, Berkes MK, Fast H. Collaborative integrated management in Canada's north: The role of local and traditional knowledge and community-based monitoring. *Coastal Management*. 2007; 35:143–162.
- Berkes F, Colding J, Folke C. Rediscovery of traditional ecological knowledge as adaptive management. *Ecological Applications*. 2000; 10:1251–1262.
- Berkes, F.; Colding, J.; Folke, C. *Navigating social-ecological systems: building resilience for complexity and change*. Cambridge, UK: Cambridge University Press; 2003.
- Bocquet-Appel J-P. *Science*. 2011; 333:560–561. [PubMed: 21798934]
- Bottazzi P, Dao H. On the road through the Bolivian Amazon: A multi-level land governance analysis of deforestation. *Land Use Policy*. 2013; 30:137–146.
- Bowles S, Choi JK, Hopfensitz A. The co-evolution of individual behaviors and social institutions. *Journal of Theoretical Biology*. 2003; 223:135–147. [PubMed: 12814597]
- Boyd, R.; Richerson, P. *Culture and the Evolutionary Process*. Chicago: University of Chicago Press; 1985.
- Boyd, R.; Richerson, P. *The origin and evolution of cultures*. Oxford: Oxford University Press; 2005.
- Boyd R, Richerson PJ. Culture and the evolution of human cooperation. *Philosophical Transactions of the Royal Society B-Biological Sciences*. 2009; 364:3281–3288.
- Boyd R, Richerson PJ, Henrich J. Rapid cultural adaptation can facilitate the evolution of large-scale cooperation. *Behavioral Ecology and Sociobiology*. 2011; 65:431–444. [PubMed: 21423337]
- Brondizio ES, Ostrom E, Young OR. Connectivity and the Governance of Multilevel Social-Ecological Systems: The Role of Social Capital. *Annual Review of Environment and Resources*. 2009; 34:253–278.
- Carballo DM, Roscoe P, Feinman GM. Cooperation and Collective Action in the Cultural Evolution of Complex Societies. *Journal of Archaeological Method and Theory*. 2014; 21:98–133.
- Cash DW, Adger WN, Berkes F, Garden P, Lebel L, Olsson P, Pritchard L, Young O. Scale and cross-scale dynamics: Governance and information in a multilevel world. *Ecology and Society*. 2006; 11
- Cavalli-Sforza, LL.; Feldman, MW. *Cultural Transmission and Evolution: A Quantitative Approach*. Princeton: Princeton University Press; 1981.
- Choi J-K, Bowles S. The coevolution of parochial altruism and war. *Science*. 2007; 318:636–640. [PubMed: 17962562]

- Colding, J.; Elmqvist, T.; Olsson, P. Living with disturbance: building resilience in social-ecological systems. *Navigating Social-Ecological Systems: Building Resilience for Complexity and Change*. Berkes, F.; Colding, J.; Folke, C., editors. Cambridge: Cambridge University Press; 2003.
- Coultas JC. When in Rome... An evolutionary perspective on conformity. *Group Processes & Intergroup Relations*. 2004; 7:317–331.
- Cumming GS, Cumming DHM, Redman CL. Scale mismatches in social-ecological systems: Causes, consequences, and solutions. *Ecology and Society*. 2006; 11
- Defries R, Hansen A, Newton AC, Hansen MC. Increasing isolation of protected areas in tropical forests over the past twenty years. *Ecological Applications*. 2005; 15:19–26.
- Defries R, Hansen A, Turner BK, Reid R, Liu J. Land use change around protected areas: management to balance human needs and ecological functions. *Ecological Applications*. 2007; 17:1031–1038. [PubMed: 17555216]
- Demps K, Zorondo-Rodriguez F, Garcia C, Reyes-Garcia V. Social learning across the life cycle: cultural knowledge acquisition for honey collection among the Jenu Kuruba, India. *Evolution and Human Behavior*. 2012; 33:460–470.
- Dietz T, Ostrom E, Stern PC. The struggle to govern the commons. *Science*. 2003; 302:1907–1912. [PubMed: 14671286]
- Fehr E, Fischbacher U, Gächter S. Strong reciprocity, human cooperation, and the enforcement of social norms. *Human Nature-An Interdisciplinary Biosocial Perspective*. 2002; 13:1–25.
- Fehr E, Gächter S. Altruistic punishment in humans. *Nature*. 2002; 415:137–140. [PubMed: 11805825]
- Fernández-Llamazares A, Diaz-Reviriego I, Gueze M, Cabeza M, Pyhälä A, Reyes-García V. Local perceptions as a guide for the sustainable management of natural resources: empirical evidence from a small-scale society in Bolivian Amazonia. *Ecology and Society*. under review.
- Fischer J, Peterson GD, Gardner TA, Gordon LJ, Fazey I, Elmqvist T, Felton A, Folke C, Dovers S. Integrating resilience thinking and optimisation for conservation. *Trends in Ecology & Evolution*. 2009; 24:549–554. [PubMed: 19665820]
- Fletcher JA, Zwick M. The evolution of altruism: Game theory in multilevel selection and inclusive fitness. *Journal of Theoretical Biology*. 2007; 245:26–36. [PubMed: 17087973]
- Folke C. Resilience: The emergence of a perspective for social-ecological systems analyses. *Global Environmental Change-Human and Policy Dimensions*. 2006; 16:253–267.
- Folke C, Hahn T, Olsson P, Norberg J. Adaptive governance of social-ecological systems. *Annual Review of Environmental Resources*. 2005; 30:22.
- Fotheringham, AS.; Brunson, C.; Charlton, M. *Qualitative Geography. perspectives on Spatial Data Analysis*. The Sage handbook of qualitative geography. London: SAGE; 2010.
- Gallopín GC. Linkages between vulnerability, resilience, and adaptive capacity. *Global Environmental Change*. 2006; 16:293–303.
- Gintis H. Strong Reciprocity and Human Sociality. *Journal of Theoretical Biology*. 2000; 206:169–179. [PubMed: 10966755]
- Goudie, A. *The human impact on the natural environment*. Oxford: Blackwell Publishers; 1993.
- Gowdy J, Krall L. The ultrasocial origin of the Anthropocene. *Ecological Economics*. 2013; 95:137–147.
- Gunderson, LH.; Holling, CS. *Panarchy: understanding transformations in human and natural systems*. Washington, D.C.: Island Press; 2002.
- Gurven M, Kaplan H, Gutierrez M. How long does it take to become a proficient hunter? Implications for the evolution of delayed growth. *Journal of Human Evolution*. 2006; 51
- Henrich J. Cultural Transmission and the Diffusion of Innovations: Adoption Dynamics Indicate That Biased Cultural Transmission Is the Predominate Force in Behavioral Change. *American Anthropologist*. 2001; 103:992–1013.
- Henrich J. Cultural group selection, coevolutionary processes and large-scale cooperation. *Journal of Economic Behavior & Organization*. 2004; 53:3–35.
- Henrich J, Boyd R. The Evolution of Conformist Transmission and the Emergence of Between-Group Differences. *Evolution and Human Behavior*. 1998; 19:215–241.

- Herrmann PA, Legare CH, Harris PL, Whitehouse H. Stick to the script: The effect of witnessing multiple actors on children's imitation. *Cognition*. 2013; 129:536–543. [PubMed: 24045001]
- Holdschlag A, Ratter BMW. Multiscale system dynamics of humans and nature in The Bahamas: perturbation, knowledge, panarchy and resilience. *Sustainability Science*. 2013; 8:407–421.
- Holland, JH. *Complex adaptive systems*. Daedalus; 1992.
- Hornborg, A.; Crumley, CL. *The world system and the Earth system. Global socioenvironmental change and sustainability since the Neolithic*. Walnut Creek, CA: Left Coast Press; 2006.
- Huanca, T. *Tsimane' Oral Tradition, Landscape, and Identity in Tropical Forest*. La Paz: Imprenta Wagui; 2008.
- Ibanez JJ, Ortega D, Campos D, Khalidi L, Mendez V. Testing complex networks of interaction at the onset of the Near Eastern Neolithic using modelling of obsidian exchange. *Journal of the Royal Society, Interface / the Royal Society*. 2015; 12
- Kandler A, Unger R, Steele J. Language shift, bilingualism and the future of Britain's Celtic languages. *Philosophical Transactions of the Royal Society B: Biological Sciences*. 2010; 365:3855–3864.
- Kitano H. Systems biology: A brief overview. *Science*. 2002; 295:1662–1664. [PubMed: 11872829]
- Kohler, TA.; Gummerman, GJ., editors. *Dynamics of Human and Primate Societies: Agent-Based Modeling of Social and Spatial Processes*. Oxford: Oxford University Press; 2001.
- Lake MW, Crema ER. The Cultural Evolution of Adaptive-trait Diversity when Resources are Uncertain and Finite. *Advances in Complex Systems*. 2012; 15
- Lansing JS. *Complex Adaptive Systems*. *Annual Review of Anthropology*. 2003; 32:183–204.
- Lansing, JS. *Perfect Order: Recognizing Complexity in Bali*. Princeton University Press; 2006.
- Laurance WF, Useche DC, Rendeiro J, Kalka M, Bradshaw CJA, Sloan SP, Laurance SG, Campbell M, Abernethy K, Alvarez P, Arroyo-Rodriguez V, et al. Averting biodiversity collapse in tropical forest protected areas. *Nature*. 2012; 489:290–+. [PubMed: 22832582]
- Leach, E. *Political systems of Highland Burma: A study of Kachin social structure*. Oxford: Berg Publishers; 1954.
- Liu J, Dietz T, Carpenter SR, Alberti M, Folke C, Moran E, Pell AN, Deadman P, Kratz T, Lubchenco J, Ostrom E, et al. Complexity of coupled human and natural systems. *Science*. 2007; 317:1513–1516. [PubMed: 17872436]
- Markofsky S, Ninfo A, Balbo A, Conesa FC, Madella M. An investigation of local scale human/landscape dynamics in the endorheic alluvial fan of the Murghab River, Turkmenistan. *Quaternary International*.
- Mazoyer, M.; Roudart, L. *A History of World Agriculture. From the Neolithic Age to the Current Crisis*. London Sterling: EarthScan; 2006.
- Mcdade TW, Reyes-garcia V, Blackinton P, Tanner S, Huanca T, Leonard WR. Ethnobotanical knowledge is associated with indices of child health in the Bolivian Amazon. *Proceedings of the National Academy of Sciences of the United States of America*. 2007; 104:6134–6139. [PubMed: 17389376]
- Meentemeyer, V.; Box, EO. Scale effects in landscape studies. In: Turner, MG., editor. *Landscape Heterogeneity and Disturbance*. New York: Springer-Verlag; 1987.
- Mesoudi A. Foresight in cultural evolution. *Biology and Philosophy*. 2008; 23:243–255.
- Mesoudi A. *Cultural Evolution: A Review of Theory, Findings and Controversies*. *Evolutionary Biology*. 2015
- Michod RE, Herron MD. Cooperation and conflict during evolutionary transitions in individuality. *Journal of Evolutionary Biology*. 2006; 19:1406–1409. [PubMed: 16910968]
- Millennium Assessment. *Ecosystems and Human Well-being: Synthesis*. Washington, DC: 2005.
- Mwangi E, Wardell A. Multi-level governance of forest resources. *International Journal of the Commons*. 2012; 6:79–103.
- Nazarea VD. Local knowledge and memory in biodiversity conservation. *Annual Review of Anthropology*. 2006; 35:317–335.
- Nelson DR, Adger WN, Brown K. Adaptation to environmental change: Contributions of a resilience framework. *Annual Review of Environment and Resources*. 2007; 32:395–419.

- Olson, M. The logic of collective action. Cambridge, MA: Harvard University Press; 1965.
- Ostrom E. The challenge of common-pool resources. *Environment*. 2008; 50:8–20.
- Ostrom E. Beyond markets and states: Polycentric governance of complex economic systems. *American Economic Review*. 2010; 100:641–672.
- Ostrom, V. Polycentricity. *Polycentricity and Local Public Economies: Readings from the Workshop in Political Theory and Policy Analysis*. McGinnis, M., editor. Ann Arbor: University of Michigan Press; 1999.
- Parker DC, Manson SM, Janssen MA, Hoffmann MJ, Deadman P. Multi-agent systems for the simulation of land-use and land-cover change: A review. *Annals of the Association of American Geographers*. 2003; 93:314–337.
- Perreault C. The pace of cultural evolution. *PLoS ONE*. 2012; 7:e45150. [PubMed: 23024804]
- Quave C, Pieroni A. A reservoir of ethnobotanical knowledge informs resilient food security and health strategies in the Balkans. *Nature Plants*. 2015; 1:1–6.
- Reid, WV.; Berkes, F.; Wilbanks, T.; Capistrano, C. Bridging scales and local knowledge in assessments. Washington DC: Island Press; 2006.
- Reyes-García V, Gueze M, Diaz-Reviriego I, Duda R, Fernández-Llamazares Á, Gallois S, Napitupulu L, Orta-Martínez M, Pyhälä A. The adaptive nature of culture. A cross-cultural analysis of the returns of Local Environmental Knowledge in three indigenous societies. *Current Anthropology*. in press.
- Reyes-García V, Gueze M, Luz A, Macia M, Orta-Martínez M, Paneque-Gálvez J, Pino J, Rubio-Campillo X. Evidence of traditional knowledge loss among a contemporary indigenous society. *Evolution and Human Behaviour*. 2013; 34:249–257.
- Reyes Garcia V, Paneque-Galvez J, Bottazzi ME, Luz AC, Gueze M, Macia M, Pachecho P. Indigenous land reconfiguration and fragmented institutions: A historical political ecology of the Tsimane' lands (Bolivian Amazon). *Journal of Rural Studies*. 2014; 34:282–291.
- Richerson P, Baldini R, Bell A, Demps K, Frost K, Hillis V, Mathew S, Newton E, Narr N, Newson L, Ross C, et al. Cultural Group Selection Plays an Essential Role in Explaining Human Cooperation: A Sketch of the Evidence. *Behavioral and Brain Sciences*. 2015:1–71. FirstView.
- Richerson, P.; Boyd, R. Not by genes alone: How culture transformed human evolution. Chicago: University of Chicago Press; 2005.
- Richerson, P.J.; Boyd, R. Rethinking paleoanthropology: A world queerer than we supposed. *Evolution of Mind, Brain, and Culture*. Hatfield, G.; Pittman, H., editors. Philadelphia: University of Pennsylvania Museum of Archaeology and Anthropology; 2013.
- Ruiz-Mallén I, Corbera E, Calvo-Boyero D, Reyes-Garcia V, Brown K. How do biosphere reserves influence vulnerability and adaptation? Evidence from Latin America. *Global Environmental Change*. 2015; 33:87–108.
- Shennan S, Downey SS, Timpson A, Edinborough K, Colledge S, Kerig T, Manning K, Thomas MG. Regional population collapse followed initial agriculture booms in mid-Holocene Europe. *Nature Communications*. 2013; 4
- Skoglund P, Malmstrom H, Raghavan M, Stora J, Hall P, Willerslev E, Gilbert MTP, Gotherstrom A, Jakobsson M. Origins and Genetic Legacy of Neolithic Farmers and Hunter-Gatherers in Europe. *Science*. 2012; 336:466–469. [PubMed: 22539720]
- Slobodkin LB, Rapoport A. An optimal strategy of evolution. *Quarterly Review of Biology*. 1974:181–200. [PubMed: 4411986]
- Smit B, Wandel J. Adaptation, adaptive capacity and vulnerability. *Global Environmental Change*. 2006; 16:282–292.
- Smith, EA.; Winterhalder, B. *Evolutionary Ecology and Human Behavior*. New York: Aldine De Gruyter; 1992.
- Smith, JM. *Evolution and the theory of games*. Cambridge: Cambridge University Press; 1982.
- Smith K, Kalish M, Griffiths T, Lewandowsky S. Cultural transmission and the evolution of human behaviour. *Philosophical Transactions of the Royal Society B-Biological Sciences*. 2008; 363:3469–3476.

- Sternberg R, Nokes C, Geissler P, Prince R, Okatcha F, Bundy D, Grigorenko E. The relationship between academic and practical intelligence: a case study in Kenya. *Intelligence*. 2001; 29:401–418.
- Traulsen A, Nowak M. Evolution of cooperation by multilevel selection. *Proceedings of the National Academy of Sciences of the United States of America*. 2006; 103:10952–10955. [PubMed: 16829575]
- Turchin, P. *Historical Dynamics: Why States Rise and Fall*. Princeton, NJ: Princeton University Press; 2003.
- Walker B, Gunderson L, Kinzig A, Folke C, Carpenter S, Schultz L. A handful of heuristics and some propositions for understanding resilience in social-ecological systems. *Ecology and Society*. 2006; 11
- Waring TM, Kline MA, Brooks JS, Goff SH, Gowdy J, Janssen MA, Smaldino PE, Jacquet J. A multilevel evolutionary framework for sustainability analysis. *Ecology and Society*. 2015; 20
- Whitehead H, Richerson PJ. The evolution of conformist social learning can cause population collapse in realistically variable environments. *Evolution and Human Behavior*. 2009; 30:261–273.