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Synthesis

A multilevel evolutionary framework for sustainability analysis

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ABSTRACT. Sustainability theory can help achieve desirable social-ecological states by generalizing lessons across contexts and improving the design of sustainability interventions. To accomplish these goals, we argue that theory in sustainability science must (1) explain the emergence and persistence of social-ecological states, (2) account for endogenous cultural change, (3) incorporate cooperation dynamics, and (4) address the complexities of multilevel social-ecological interactions. We suggest that cultural evolutionary theory broadly, and cultural multilevel selection in particular, can improve on these fronts. We outline a multilevel evolutionary framework for describing social-ecological change and detail how multilevel cooperative dynamics can determine outcomes in environmental dilemmas. We show how this framework complements existing sustainability frameworks with a description of the emergence and persistence of sustainable institutions and behavior, a means to generalize causal patterns across social-ecological contexts, and a heuristic for designing and evaluating effective sustainability interventions. We support these assertions with case examples from developed and developing countries in which we track cooperative change at multiple levels of social organization as they impact social-ecological outcomes. Finally, we make suggestions for further theoretical development, empirical testing, and application.

Key Words: *cooperation; cultural evolution; multilevel selection; sustainability; theory*

INTRODUCTION

To tackle the global sustainability crisis, societies need reliable and generalizable knowledge about the functioning and management of social-ecological systems (SESs). The immediacy of this need raises both the stakes and the uncertainty of that scientific project (Funtowicz and Ravetz 1994). Correspondingly, sustainability science blends the normative goal of achieving both environmental protection and human well-being with positive methods (sensu Stern 1993) for understanding human-environment interactions to help achieve that goal (Kates et al. 2001).

However, our current ability to generalize about SES dynamics is inadequate. As Levin and Clark (2010:109) suggest, "we need to understand at a more generalizable level which features of coupled human-environment systems enhance and which constrain their adaptability." Also, although the positive science of sustainability is rich in empirical case studies, generalization also requires general theory. Therefore, we need a general sustainability theory, particularly with regard to social systems. We offer a contribution to that end by outlining a general framework for social-ecological dynamics, demonstrating its application in specific cases, and exploring its potential to assist in intervention design.

Sustainability scientists and practitioners currently use a variety of conceptual and analytical frameworks (Binder et al. 2013), including resilience (Folke et al. 2002), vulnerability (Turner et al. 2003), coupled human and natural systems (CHANs; Liu et al. 2007), and SESs (Ostrom 2009). These frameworks help to characterize the internal causal structure that determines system states such as CHANs and SESs, and the adaptive characteristics of alternative system states such as resilience and vulnerability. These frameworks all build on a model of human-environmental systems as complex adaptive systems (Levin et al. 2013), seek to guide interventions and systemic change, and improve the discovery of the factors that determine the resiliency or vulnerability of individual systems. However, applying a complex adaptive system perspective is challenging, and generalization suffers from heterogeneity among frameworks and disciplinary approaches. We propose a set of needs that sustainability theory should address to help connect these approaches.

The term "sustainability" has two connotations in the context of an SES (Pezzey 1992:45). First, sustainability is a goal state that includes the maintenance of the environment and human well-being. Second, sustainability also means the durability of a given state over time, i.e., its resilience to perturbation. However, not all resilient states are desirable, nor are all desirable states resilient. Therefore, we must distinguish between characteristics of system states and transition dynamics between states. Human values must determine the desired state (normative component), whereas science must determine the process to achieve and maintain that state (positive component). To this end, sustainability theory should help explain the emergence and persistence of social-ecological states.

System states and transitions often depend on the development and transmission of behaviors, values, norms, and institutions, i.e., on culture. Cultural evolution, meaning change in culture over time, is generally more rapid than environmental change or genetic evolution (Perreault 2012). Cultural change such as innovation in resource exploitation often drives social-ecological outcomes, which helps to explain why human factors now

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dominate the global biosphere (Vitousek 1997, Steffen et al. 2007). Thus, sustainability theory must also include a causal model of endogenous cultural processes.

Patterns of cooperation heavily influence social-ecological outcomes. The most pernicious sustainability challenges, such as carbon emissions or biodiversity loss, contain multiple cooperation dilemmas. Because environmental conservation can be costly for some, but yields benefits to others, it often conforms to the game theoretic definition of cooperative behavior. Therefore, sustainability science could benefit from insights on the evolution of cooperation, and sustainability theory should model the evolution of environmental cooperation.

Current multilevel frameworks such as Ostrom's polycentric approach (Ostrom 2010*a*, 2010*b*), panarchy (Gunderson and Holling 2001), multilevel governance (Marks 1992, Marks et al. 1996), and others (Cash et al. 2006, Pahl-Wostl 2009) do not contain general mechanisms of causation across levels of organization, or guidance for designing policy in multilevel contexts. For example, Ostrom (2010*b*) contends that polycentric systems tend to increase cooperation, equity, and sustainability, but does not explain the mechanisms by which a polycentric arrangement facilitates these qualities. The panarchy model includes multiple hierarchical levels, but the lack of specific social processes makes panarchy difficult to apply. This is troubling for those seeking to design effective interventions, because many sustainability challenges are multilevel in nature. Therefore, sustainability theory should help explain multilevel interactions.

We present an evolutionary framework for sustainability research designed to explain the emergence and persistence of sustainable social-ecological states by focusing on the dynamics of culture and cooperation. Our framework constitutes a toolkit for elucidating interactions across multiple levels of organization, which serves to improve generalizability and inform the design of interventions in the field.

CULTURAL EVOLUTION AND SUSTAINABILITY

Sustainability researchers have already begun to embrace evolutionary explanations of human behavior to aid in understanding and addressing the sustainability crisis (Penn 2003, Beddoe et al. 2009, Ehrlich 2009, Kinzig et al. 2013, van Vugt et al. 2014). Cultural evolution is particularly useful in describing human-driven social-ecological change, such as the cultural innovations by which humans exploit their environments (Boyd et al. 2011) and the social adaptations (behaviors, beliefs, language, values, norms and institutions) that constitute society in human populations (Richerson and Boyd 2004, Mesoudi et al. 2006). Cultural evolution has found support from research in anthropology (Tehrani and Collard 2002, Borgerhoff Mulder et al. 2006), psychology (Mesoudi 2009, Livingstone et al. 2011), economics (Bergstrom 2002, Bowles 2004), and political science (Axelrod 1985, Ostrom 1990) and highlights their complementarities (Mesoudi et al. 2006).

A cultural evolutionary approach to sustainability research helps to meet the four needs articulated above. First, construing culture and behavior as an evolving system facilitates the study of the emergence and persistence of social-ecological states. Mathematical models of cultural evolution (Boyd and Richerson 1985, Turchin 2003, McElreath and Boyd 2007) and evolutionary game theory (Maynard Smith 1974, Harms 2011) can assess the stability of trait combinations in a population, reveal societal equilibria, and provide insight into transitions between states. Second, this theoretical work also provides mathematical tools for understanding endogenous cultural phenomena, including cumulative cultural adaptation (Enquist et al. 2011), ethnic marking (McElreath et al. 2003), social stratification (Henrich and Boyd 2008), organizational evolution (Cordes et al. 2008), and institutions such as private property (Bowles and Choi 2013), each of which has implications for sustainability. Third, cultural evolutionary theory is closely tied to theory on the evolution of cooperation. Many of the general factors that facilitate the evolution of cooperation, such as reciprocity and group structure (Nowak 2006), are further bolstered when cooperation can evolve culturally (Bell et al. 2009) and when conformism, social identity, reputation, and punishment are involved (Henrich 2004). Fourth, evolutionary research on multilevel selection (Okasha 2006, Field 2008) provides a foundation determining when and how cooperation can emerge because of competition between groups (Gürerk et al. 2006, Puurtinen and Mappes 2009). Because the sustainable use of resources often requires cooperation and collective action, findings from the literature on cultural evolution are of particular importance for sustainability research. We do not attempt to explain whether or how culture evolves, because others have done so sufficiently (Richerson and Boyd 2004, Mesoudi 2011). Instead, our conceptual framework builds on a few foundational considerations from this literature.

Foundational considerations

A complete model of individual behavior, group dynamics, or multilevel interactions is beyond the scope of this paper. Here we summarize some fundamental and widely acknowledged factors that drive the evolution of culture: self-interest, cultural transmission, cooperation, and the role of groups.

Self-interest

Self-interest is a central force in social, economic, and environmental change. Humans often act in their own self-interest, with a psychology guided by the forces of natural selection to maximize evolutionary fitness (Cosmides and Tooby 1994). Utility maximization models have been very successful in predicting proximate behavior based on self-interest alone. However, self-interested behavior varies both within and between populations (Henrich et al. 2010), in part because we learn about behavioral options and inherit our preferences from others through cultural transmission.

Cultural transmission

Humans learn cultural traits, e.g. behaviors, beliefs, language, values, norms and institutions, from each other using sophisticated learning strategies (Bandura 1971) that have been incorporated into mathematical models of cultural evolution. Some cultural traits are copied more than others, resulting in selection for traits that fit a niche defined by social, economic, psychological, and environmental factors. Cultural transmission helps to explain human behavioral diversity (Gelfand et al. 2011, Smith 2011). Over generations, transmission processes accumulate cultural adaptations too complex for a single individual to invent in one lifetime (Kirby et al. 2008, Lewis and Laland 2012).

Cooperation

Humans actively help one another, often at a personal cost and even when there is no chance of reciprocation (Richerson and Boyd 1998, Sober and Wilson 1999). Cooperation and prosocial behavior are necessary for the existence of large-scale cooperative systems including markets, nation states, and religions (Henrich et al. 2010). Social systems are supported by human behavioral adaptations such as reputation (Van Vugt et al. 2005), gossip (Sommerfeld et al. 2007), and punishment (Boyd et al. 2003, 2010) that stabilize cooperation in groups.

Groups

Humans are adapted to group life (Richerson and Boyd 2004). We live in uniquely structured social groups (Gowdy and Krall 2015), signify group membership with cultural markers (Efferson et al. 2008), and conform to group social norms (Coultas 2004). Social groups facilitate the emergence of cooperation by allowing cooperators to cluster and share the collective benefits of cooperation (Wilson and Dugatkin 1997, Fletcher and Doebeli 2009). Groups also evolve. Groups whose members cooperate and solve collective-action problems tend to grow and proliferate at the expense of groups that fail to do so (Choi and Bowles 2007, Boyd and Richerson 2009). Through this process, known as cultural group selection (Henrich 2004, Boyd and Richerson 2010), successful group behaviors spread in a population of groups despite being individually costly (Bowles et al. 2003, Richerson et al. 2015). As a result, human groups display emergent organizational behavior (Smaldino 2014) and group-level adaptations to environmental conditions (Ostrom 1990, 2014).

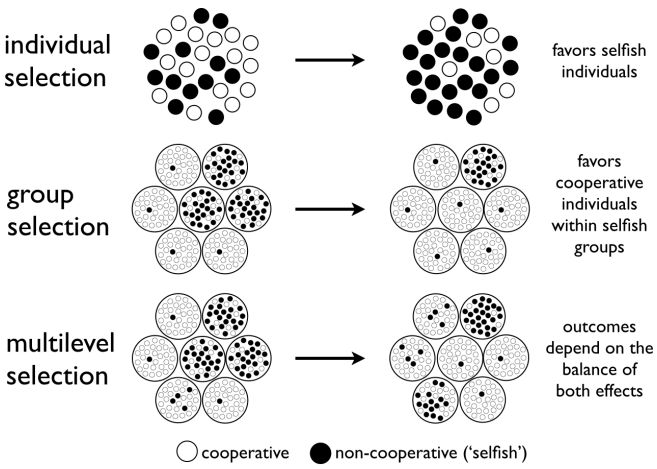
The cultural evolution of groups and organizations has direct environmental consequences. Groups exploit resources, design products, enforce environmental standards, and galvanize political change. Cultural evolution gives us an expanded framework for studying how any type of organization evolves in response to social and ecological environments. For example, competition between private enterprises (van den Bergh and Gowdy 2009) for employees, supplies, and buyers drives business and product innovation through a process of cultural evolution. This competition can also select for strategies that shift costs elsewhere by destroying natural resources or degrading social capital. When nations change the environmental behavior of industries through regulation, taxes, and labeling, they are altering the selective pressures faced by corporations (Auld et al. 2008, Gulbrandsen 2009), which respond adaptively. Human group-centric adaptations and cultural selection between groups can also give rise to organizations capable of solving environmental cooperation dilemmas (Ostrom 2000). However, there is no guarantee that cooperation will emerge in any given case because groups, like individuals, often evolve to act in their short-term interest, recapitulating a tragedy of the commons at a higher organizational level. Therefore, we must analyze the emergence of cooperation between assemblies of groups as well as between individuals. This requires a multilevel perspective.

CULTURAL MULTILEVEL SELECTION

Multilevel environmental governance remains an intransigent problem because of the overwhelming complexity of untangling causality and recommending intervention. Gupta (2007:132) found that "there is no objective way to determine the appropriate level of [policy or action on] climate change or other environmental problems" in multilevel contexts. We propose that cultural multilevel selection (CMLS) theory can be adapted to address Gupta's problem directly.

Multilevel selection (MLS) theory in biology clarifies evolutionary processes when populations are structured in groups (Okasha 2006, Simon et al. 2013). Within groups, selection is driven by differences in fitness between members, or "relative fitness." Likewise, if groups compete within a supergroup, selection of groups will depend on the relative fitness of groups. MLS states that processes at both levels matter. MLS is particularly useful for social dilemmas, in which the interests of the group are at odds with those of individuals. Cooperative individuals in a social dilemma benefit group members at a cost to themselves, decreasing their relative fitness while increasing the average fitness of the group. Consequently, the selection of cultural traits at the group and individual levels will favor conflicting outcomes, and the result is determined by the balance of selection across levels (Fig. 1). Conflicts between levels of selection are a generalizable theoretical tool, applying to any social dilemma at any level, whether between nations in Europe or between children on a sports team. The evolutionary interactions between levels have been modeled in multiple ways (Frank 1995, Simon et al. 2013), and the same formalisms can serve as a general model for cultural change (El Mouden et al. 2014). Group-beneficial outcomes are more likely to evolve when migration between groups is low, variation between groups is high, and the individual cost of altruism is relatively low. This holds true even when the cooperative individuals are at a disadvantage within their own groups.

Fig. 1. A simplified graphical model of multilevel selection. In social dilemmas, outcomes depend on the level of organization on which selection operates most strongly. To determine the dominant level of selection, the direction and magnitude of selection at the relevant levels should be estimated and compared.



The principles of MLS are already used to manage genetic evolution. In animal husbandry, individual animals kept in pens sometimes conflict aggressively with group members, reducing

health and total productive growth. In these systems, human breeders artificially increase the strength of between-group selection by breeding animals from groups with high productivity rather than choosing individuals with high productivity. This results in less aggression, more growth, and higher total productivity (Wade et al. 2010, Turner 2011).

CMLS considers the importance of group structure, relative fitness, and conflicts between levels of selection as they operate in human cultural systems. Group-level selection is enhanced in cultural systems as opposed to biological ones because of factors including conformity, ethnic marking, punishment, and cultural equilibria (Vega-Redondo 1993, Richerson et al. 2015). Probably as a result, culture displays greater variation between groups than is found in genetic populations (Bell et al. 2009), making group-level selection more common. This suggests that conflicts between levels of selection may be more common in cultural systems as well.

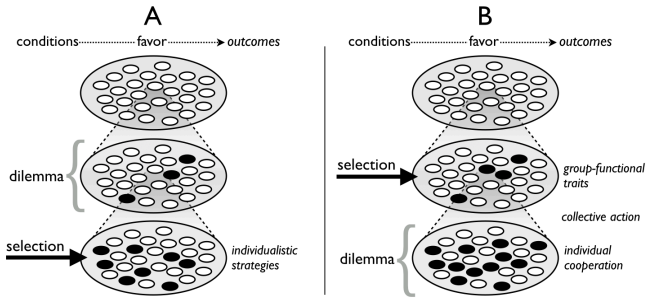
A MULTILEVEL SELECTION FRAMEWORK FOR SUSTAINABILITY ANALYSIS

The central facet of our framework is that the hierarchical levels of human social organization may operate as levels of selection in the evolution of cultural traits, organizational features, and environmental behavior. Modern human societies have many organizational levels (e.g., individual, city, nation, international body) across multiple domains (e.g., civic, enterprise, religious, educational, recreational). Any domain could be an arena for selection in a particular analysis (Wilson and Kniffin 1999, Wilson et al. 2013). By comparing the dominant level of selection with the organizational scale of the environmental dilemma, scientists can better predict cooperative evolution and social-ecological outcomes (Fig. 2). Group selection will tend to be stronger than individual selection when (1) a greater fraction of total trait variation occurs between groups than between individuals, (2) the relative benefits to the group are greater, and (3) the costs to altruistic individuals are lesser (Wilson et al. 2013). Conflicts between levels of selection may exist without becoming outright human conflicts, but may operate slowly, while driving long-term social system change. This may be the case, for example, in many of the environmental management dilemmas central to sustainability research.

The greatest environmental dilemmas are regional or global challenges, such as carbon emissions, overfishing, deforestation, pollution, and freshwater conflicts. The interactions between organizations and individuals at multiple levels make coherent analysis and effective policy advice extremely challenging. We use case studies to show that cultural multilevel selection helps us assess the strength of cultural selection for environmental behaviors on groups and individuals, and to understand why and in what context costly conservation practices can emerge. To understand and react to these challenges, we must assess the patterns of variation, benefits, and costs for entities at each level.

Our framework yields several practical advantages to this end. First, it identifies conflicts between levels of selection that drive social evolution, allowing researchers to track cascades of social change between levels. Second, the framework is a descriptive construct, with no prescription of the desired system state or assumptions about transitions between states. Third, the focus on trait frequency, benefits, costs, and behavioral transmission provides a consistent system for organizing the facts of environmental behavioral change. Finally, the CMLS approach provides a comparative heuristic (visualized in Fig. 2) to identify the appropriate level for policy intervention and a solution to the problem Gupta identified.

Fig. 2. The cultural multilevel selection (CMLS) framework provides a comparative heuristic for determining cooperative outcomes in an environmental dilemma. The relationship between the dominant level of selection (→ right arrow) and the social scale of an environmental dilemma ({ right brace) determines the spread of a cooperative environmental trait (open circle). (A) When the dominant level of selection is below that of the dilemma, selection on individuals favors individualistic strategies, noncooperation (filled circle), resulting in an unresolved dilemma. (B) When the dominant level of selection is above that of the dilemma, selection on groups favors group-functional traits, collective action, individual cooperation (open circle) and a resolution to the dilemma.



CASE NARRATIVES

The CMLS framework is designed to spur hypothesis generation and testing. Before hypothesis testing is possible, however, we must find common patterns across empirical cases. A set of guiding questions helps to organize the empirical details of social-ecological cases so that the framework may be fruitfully applied.

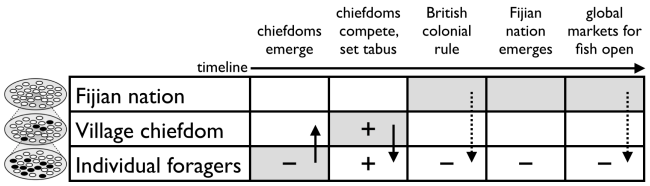
1. What is the focal trait (behavior, norm, or organizational trait)? Describe the proximate function of the trait in an environmental context, how it is transmitted, and whether it is a cooperative trait, i.e., costly to the actor, beneficial to others.
2. What is the organizational environment for that trait? Describe the types of organizations involved, the organizational niche and survival requirements of each type, and how they interact within and across levels of organization.
3. What are the levels of selection for that trait? Describe how trait selection operates through the influence of competition, migration, imitation, and demographic change at each organizational level. Identify the dominant level of selection.
4. What is the history of the trait? Describe any documented change in trait distributions, individual and organizational populations, and selection regimes. Identify changes in the dominant level of selection over time.

To illustrate the advantages of a multilevel evolutionary approach, we have organized the details of existing SESs according to the framework. The objective of this effort is to apply a structured and consistent accounting of change to uncover patterns and generate hypotheses. Each narrative lays out a coarse history of change at multiple organizational levels following a simple rubric and attempts to answer the guiding questions outlined above. We present four short narratives spanning a range of timespans, social scales, resource types, organizational forms, and degrees of economic development as examples of how to use guiding questions in a post hoc analysis.

Marine tenure institutions in Fiji

Traditional marine tenure systems in Fiji appear to have emerged under conditions of strong community-level selection. These systems collapsed after colonization and globalization resulted in strong competition for fish resources at both the national and individual levels (see Fig. 3).

Fig. 3. Traditional fishing restrictions in Fiji may have lessened because of a change in the dominant level of selection. Before colonial rule, traditional chiefly fishing bans may have been supported by competition between groups. Following colonization, village level organization weakened, and Fiji began to compete as a nation in global fish markets. Individual competition for fish resources is higher, and village competition for income also drives fishing efforts. Unrestrained harvest (–), harvest restraint or limits (+), collective action (↑ up arrow), group reinforces harvest restraint (↓ down arrow), group weakens harvest restraint (dotted down arrow). Shaded cells represent dominant level of selection.



Focal trait

Traditional fisheries regulations include exclusive clan ownership of certain reefs, clan-specific prohibitions (*tabu*) on particular marine resources, and temporary reef closures. These systems are recognized for their value in conservation (Berkes et al. 2000) and have been incorporated into modern ecological conservation programs (Johannes 2002, Drew 2005), even as the sociocultural norms that keep them in place are changing (Kuster et al. 2005).

Organizational context

Fijian society includes a social hierarchy in which households (*vuvale*) are nested in extended households (*itokatoka*), one or more of which comprise a clan (*mataqali*). Multiple clans constitute a *yavusa,* the highest order kin group (sometimes an entire village). Typically, villages have local chiefs, and clusters of villages may have a paramount chief. Here we focus on three levels of organization: (1) individual marine foragers, (2) village chiefdoms, and (3) the nation-state of Fiji.

Levels of selection

Prior to British colonization, Fijians engaged in subsistence harvesting, while village chiefdoms managed marine resources with traditional rules and competed through warfare. At the individual level, we make the simplifying assumption that foragers minimize effort to meet subsistence needs. This is consistent with what present-day Fijians report (Golden et al. 2014). At the village chiefdom level, each village has exclusive marine foraging rights to bounded territories, so could benefit from sustainable harvesting. Some village- and clan-level marine tenure systems in the Pacific may serve this function through closing certain reef or deep-sea fishing areas (Hviding and Ruddle 1991, Veitayaki 1998). Under ecological stressors such as cyclones or droughts, villages without norms to regulate harvesting may be more likely to suffer a resource collapse. This situation would favor groups with more conservative sustainable strategies. Prior to colonization, villages also competed through warfare and politicking for access to resources such as arable land, fresh water, and fishing grounds. Warfare is resource intensive, and historical evidence indicates that villages were easier to defend than to invade (Derrick 1946). This suggests that between-village conflict would favor the persistence and even the expansion of villages that enforced more sustainable strategies for resource consumption.

History

Colonization precipitated two major changes that reduced the primacy of the village level in all matters: the rise of commercial fishing and the suppression of intervillage warfare. Local and regional trade existed in Fiji prior to globalization, but Fiji's natural resources are now open to a vastly larger source of demand. Thus, it appears the cultural evolutionary forces that selected for traditional marine tenure practices in Fiji have changed. At the village level, colonial rule has weakened chiefly powers and duties, and marine tenure decisions now often depend on general consensus. This makes decisions susceptible to individual interests because they may require community consensus. Rather than competing via warfare, villages now compete for income and modern conveniences by selling local resources, e.g., fish and crops, or by courting tourist traffic. At the individual level, many contemporary Fijians forage for subsistence, but also exchange resources for cash. Individuals can accumulate wealth in this manner, even harvesting species that are not eaten locally (Golden et al. 2014; M. A. Kline, *unpublished data*). Villagers can now "vote with their feet" and move to villages that are more market integrated or leave village life altogether (Scheyvens 2008). Competition between villages may now favor more exploitative foraging strategies that create greater market integration.

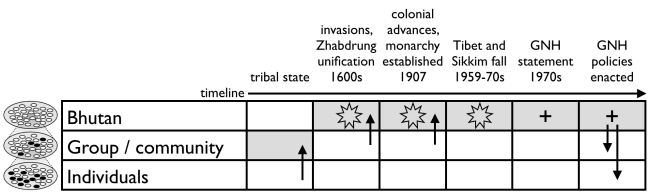
Summary

Our narrative suggests that in Fiji, strong individual selection for unrestrained harvesting was initially held in check by selection for marine foraging restrictions within clans and villages, spurred by local resource competition and warfare. British colonization of Fiji and continued integration with the global market altered the dominant level of selection, strengthening the nation-state and weakening the power of traditional village chiefs (White and Lindstrom 1997).

National environmental policy in Bhutan

The coincidence of Bhutan's conservation policy and Gross National Happiness (GNH) development framework, and their articulation with a Buddhist national identity, reveal how persistent external threats influenced policy selection at the national level for sovereignty and resource protection (see Fig. 4).

Fig. 4. Bhutan's environmental policy, which emerged as part of a process to craft a national identity and may have been influenced by the threat of annexation. From the 1600s through the 1970s, Bhutan has experienced a series of external threats, including the fall of peer societies to larger powers. These pressures appear to have caused an attempt to fortify Bhutanese sovereignty through cultural and religious consolidation. The king of Bhutan declared the importance of Gross National Happiness (GNH) in 1972 (Karma et al. 2012). GNH became a set of development objectives and indicators, including environmental status. Cooperative conservation policies (+), collective action (e.g. political unification; ↑ up arrow), group reinforces conservation behavior (↓ down arrow), competition or threat (open star). Shaded cells represent dominant level of selection.



Focal trait

Bhutan's sustainable development approach aims to maximize GNH and undergirds policies that have ensured high levels of habitat protection (MAF 2010), decentralized natural resource management (Brooks and Tshering 2010), constrained individual-level resource use (Rinzin 2006, Brooks 2010, RGB 2010), and limited the environmental impact of commercial ventures such as hydropower (NEC 2008), agriculture (Vidal and Kelly 2013), and tourism. These polices constitute a social dilemma in that they require individuals and groups to forgo economic opportunities and wealth.

Organizational context

Bhutan contains four primary ethnic groups, each with distinct clan lineages. These groups have been unified under the national government, though not without conflict (Schappi 2005). Until recently the king held dictatorial power in the country, eliminating political competition and disagreement over policy. Bhutan contends with other nations as well, including both small peer nations (Himalayan Buddhist kingdoms) and large predatory nations (Britain, China, India), which have annexed the peer nations.

History

Historically, the geographically isolated communities of Bhutan were culturally and linguistically diverse, but characterized by high levels of internal conformity and cooperation (van Driem 1999, Ura 2004). Invasions in the 17th century lead to unification under a theocratic ruler (Rose 1977), and 19th-century British colonial advances contributed to the formation of a hereditary monarchy in 1907 (Rose 1977, Ura 2004). More recent perceived threats to Bhutan's sovereignty included the annexation of neighboring Buddhist Himalayan societies by China, which occupied Tibet in 1959; and India, which annexed Sikkim in the 1970s; and the influx of Nepali immigrants in the 1980s and 1990s (Priesner 1998, Brunet et al. 2001, Ura 2004). These threats, along with diffuse forces of globalization (Ura 2004), were perceived as jeopardizing Bhutan's resources and autonomy. In response, the Bhutanese government sought to foster a national cultural and religious identity to protect the country's sovereignty and security (Planning Commission Secretariat 1999, Ura 2004). Buddhist philosophy and practice influence most aspects of social, cultural, and political life in Bhutan (Aris 1979) and serve as the bedrock for Bhutan's national identity (Priesner 1998, Ura 2004). The GNH approach is also derived from aspects of Buddhist belief and practice, especially the concept of the "middle path" (Planning Commission Secretariat 1999). Thus, the emergence of Bhutan's sustainable development approach may be closely related to the development of a Buddhist-based national identity and may be a product of external existential threats to the country.

Levels of selection

Competition between ethnic communities and villages fueled warfare (Vas 1986) that likely led to resource extraction. Persistent external threats at the national level selected for efforts to protect Bhutan by unifying distinct communities, aligning individual and community interests, and inculcating a shared national identity. However, consolidation comes with individual and community costs. The alignment of the national benefits of sustainable development and strengthened sovereignty with individual and community benefits of greater well-being is evident in policies that are guided by the GNH approach. As an example of the cost of conservation, Bhutan's forest policies limit household access to timber to preserve 60% forest cover in perpetuity (MAF 2010). However, Bhutan's environmental policies are founded on Buddhist beliefs, ethics, and cultural traditions, which may have offset the costs to individuals and communities that result from strict conservation policies. Additionally, Bhutan's unique national tourism policy places the high costs of reduced environmental impact on visitors. Now Bhutan's strategy may be spreading via cultural transmission (RGB 2012) because several countries, e.g. Germany, Canada, France, and China, have begun to integrate measures of well-being to direct their own development efforts (United Nations General Assembly 2011, Brooks 2013).

Summary

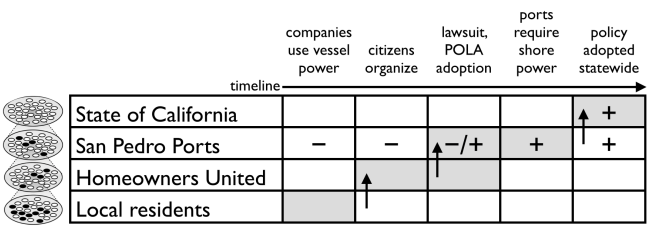
The Bhutanese case suggests that competition at the level of the nation accelerated political unification and efforts to establish a shared national identity (Schappi 2005), promote social cohesion (within-group cooperation), and protect the nation's cultural and environmental sovereignty. These changes were also facilitated by the centralized power of a hereditary monarchy. Bhutan's policies put in place constraints on individual and community-level resource use. The associated costs of these restrictions appear to have been offset by a focus on well-being and happiness and the acceptance of those costs seems to have been eased by the strong sense of national identity. The CMLS framework also leads us to consider the possibility that Bhutan's recent transition from a hereditary monarchy to a parliamentary democracy is likely to

increase competition between political parties, which may change the selection regime and ultimately weaken the environmental components of the GNH approach.

Air quality policy in California

An investigation of air quality policy in California shipping ports displays a cooperative cascade across levels of public government, which resulted in successful regulatory solutions (see Fig. 5).

Fig. 5. Clean air regulations at California shipping ports may have been adopted in part because of between-port competition. Poor air quality from shipping ports drove citizens to form a collective unit to change policy. The resulting lawsuit required cleaner shore power at one port, which then pushed for identical regulations for a neighboring port. Shore power was then adopted all California ports. Allowing vessel power (–), requiring costly shore power (+), collective action, e.g., citizen political organization (↑ up arrow). Shaded cells represent dominant level of selection.



Focal trait

Ocean-going vessels account for the majority of port-related emissions of particulate matter, NO_x and SO_2 (POLA 2005). When berthed, ocean-going vessels require power for ancillary ship systems. We focus on the corporate use of shore-based electrical power as an alternative to running ship engines when berthed. Shore power requires investments by both port authorities and shipping companies, whereas the benefits of the technology are bestowed primarily upon local residents in the form of reduced noxious emissions. Shore power adoption therefore constitutes a social dilemma.

Organizational environment

Shipping companies compete for profit, and implementing low-emission shore power systems is costly. The Port of Los Angeles (POLA) and the Port of Long Beach (POLB) are publically owned ports in adjacent cities on San Pedro Bay, and they compete for shipping traffic. The economic benefits of the shipping ports accrue at the local, state, and national levels through tax revenue and domestic jobs (BST Associates 2007). Local residents bear disproportionate costs in terms higher rates of asthma (LBACA 2008), cardiovascular disease, and cancer (Barringer 2005) than those of the nation.

Levels of selection

At the corporate level, competition between shipping companies favors the use of vessel-based power in port, because the health costs are externalized to individual residents. The neighboring ports compete for shipping traffic, such that either port would lose business by adopting air quality restrictions that increase the cost to corporations. As a result, selection at the level of the port also favors vessel power. Similarly, tax revenue from ports selects for industry-friendly policies at the level of the state. At the level of individual local residents, evidence of negative health effects selects against supporting vessel power, although residents have no direct recourse on the trait.

History

In 2001, local residents concerned with the health effects of emissions joined to oppose the construction of a new container terminal at POLA. Despite this opposition, the city approved construction of the terminal. Homeowner groups then joined forces, forming San Pedro and Peninsula Homeowners United, and enlisted the help of the Natural Resources Defense Council. Together, they sued the City of Los Angeles and the Army Corps of Engineers for violations of the California Environmental Quality Act, and won (NRDC 2012). Three years later the new POLA terminal opened as the first shore power container facility in the world. With the ports so close together, POLA could hardly be penalized for emissions it might not be causing. Pressure on POLB to operate with equivalent regulations mounted. Two years later POLA and POLB joined to create the San Pedro Bay Ports Clean Air Action Plan, which precludes attempts to undercut each other in terms of environmental regulation rigor. Components of the San Pedro Bay Ports Clean Air Action Plan were later imitated at the state level, and now shore power is required at all major California ports.

Summary

This example illustrates how a collective action among individuals in response to a local environmental dilemma can initiate a cooperative cascade in the domain of public government, resulting in successful regulatory solutions. This result appears to have been aided by the strength of California environmental laws, public ownership of commercial ports, and strong competition between neighboring ports. It may also have been assisted by weak selection on corporations to oppose the regulations either through low relative costs of implementing shore power or strong competition between shipping companies for California business.

Litter in the United States

The history of littering and litter regulations in the United States demonstrates the importance of examining competitive interactions between governmental and corporate organizational domains in determining environmental outcomes (Melosi 2005; see Fig. 6).

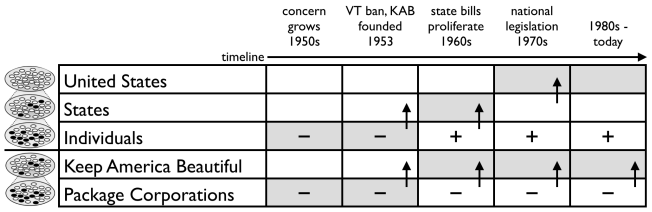
Focal trait

We define individual littering behavior as the act of leaving nonbiodegradable packaging and disposable waste in the open. Litter production is the manufacture of materials that eventually become litter. Littering and litter production together pose a social dilemma in that all individuals and groups benefit from a reduction in litter and litter production, but no individual or group benefits by bearing the cost of reducing litter or litter production, or enforcing bans or regulations to stop it.

Organizational environment

Democratic governments at the city, state, and national levels represent their citizens and help solve collective-action problems and cooperation dilemmas, often by passing legislation, including banning certain individual or corporate actions or products. Private corporations in the fast food, soft drink, cigarette, and

Fig. 6. Corporations appear to have formed a cooperative supergroup to avoid the costs of solving the litter problem. In the 1950s litter was a growing problem. Litter regulations began to spread, putting costs on litter-producing corporations. In response, corporations formed a cooperative public advocacy group with the goal of casting the responsibility for litter cleanup on individuals. State regulations halted the spread of these litter regulations, and today litter is broadly considered an individual responsibility. Littering and litter production (–), litter cleanup and reduced production (+), cooperation and collective action (↑ up arrow). Shaded cells represent dominant level of selection in both corporate and governmental domains.



packaging industries benefit by selling goods to consumers and producing disposable packaging to deliver them efficiently.

Levels of selection

Litter accumulation negatively influences the health and environment of individuals and municipalities. Because the individual benefit of littering is immediate and tangible, whereas the costs of litter are indirect and accumulate over time, individual selection favors littering. At the levels of the city and state, governments gain the benefits of better hygiene, better living conditions, and increased property values from reduced litter accumulation. The costs of enforcing antilittering policy vary from cheap (producer bans) to expensive (public waste management systems). These conditions select for cheap antilittering policy at the group level in government. Like governments, corporations could opt to prevent littering with biodegradable or reduced packaging or collection systems at a cost to their financial welfare. Corporations that bear such costs when other corporations do not will be selected against in a market economy. Both corporations and governments themselves can form collections of groups, or "supergroups." However, these supergroups are without peers or face no pressure beyond satisfying in the interests of their constituents.

History

In the early 20th century, discarded waste became a public problem because individuals and businesses discarded waste in public spaces, streets, and rivers. In the 1950s it was unclear whether the costs of the litter problem would be born by governments through waste management systems or corporations through extended producer responsibility. In 1953, Vermont passed the first law to ban nonrefillable bottles. Other states followed suit. In the 1960s and 1970s, major national environmental legislation proliferated, and nine more states adopted bottle deposit laws in the 1970s and 1980s (CRI 2009). Following the Vermont bill, an association of corporations from the beverage, packaging, and tobacco industries founded the industrial advocacy group Keep America Beautiful (KAB; CRI 2009, KAB 2013) with a mission to "engage individuals in responsibility for improving their community environments" (IRS 2013). KAB's campaigns downplay legislative solutions that extend producer responsibility and promote individually focused antilittering campaigns and community cleanup drives (Melosi 2005, Royte 2007). One KAB campaign proclaimed: "People Start Pollution, People Can Stop It." KAB remains active and well funded today (IRS 2013, KAB 2014), and has successfully influenced cultural norms about where the responsibility for litter lies.

Summary

The history of litter in the United States reveals a core environmental dilemma that triggered cooperative cascades in both the corporate and governmental domains. First, individuals cooperated through public government to solve the problem, producing regulations that cascaded and grew through the levels of governmental hierarchy. Federal and state regulation imposed a selection pressure on corporations, who then cooperated to produce a supergroup to solve their collective problem by making litter a public rather than a corporate responsibility. The success of corporate supergroup KAB reveals that organizations at the same level in different domains, e.g., government and corporate, may often compete regarding environmental dilemmas, resolving the original cooperation dilemma (littering) only to recapitulate it at a higher level (hidden costs of landfills).

ROUTES FOR INTERVENTIONS

We believe that as the CMLS perspective matures it will be able contribute to the design and evaluation of sustainability policy. Previous frameworks, including polycentricity and panarchy, suggest social-ecological solutions constitute a "fit" to a particular local context and can be discovered through experimentation. The evolutionary aspect of the framework naturally leads to experimentation as well, but cultural evolution additionally provides a map of the process by which solutions come to be fit in the first place. For example, adaptive capacity is a potent but vague concept in the sustainability literature. An evolutionary approach clarifies the mechanisms of adaptation and offers the possibility of developing measurements of adaptive capacity. We show how the CMLS framework reveals the evolutionary mechanisms that underlie current environmental conservation policies and point toward new ideas for interventions.

Target the appropriate level of selection

We must first discover how CMLS bears on current policies. For interventions, one major insight is that the dominant level of selection will vary between systems that may otherwise seem similar. Take, for example, residential energy conservation efforts. Research has shown that in residential neighborhoods conservation policies targeting individual behavior have been effective (Ayres et al. 2013), whereas in college dormitories policies that target group behavior have proven successful (Petersen et al. 2007). This may be because the dominant level of selection for electricity consumption behavior differs between residential neighborhoods, i.e., households, and college dormitories, i.e., coresident social groups. Therefore, identifying the dominant level of selection in a given system may help guide future policy efforts.

Alter the level of selection

We suspect that some common intervention strategies may be successful because they do alter the level of selection. Economic incentives such as subsidies and taxes are common and effective environmental policy tools. When a tax or subsidy is applied to a social dilemma, its application may alter the dominant level of selection. Therefore, these financial instruments might be applied more precisely by considering their influence on the balance of selective forces between levels as the focal outcome. Third-party certification systems may also change the dominant level of selection. The emergence of collective action as a result of Marine Stewardship Council certification may be one such case. Foley and McCay (2014) suggest the availability of a lucrative new "sustainable" fish market spurs collective action among fishing groups within a fishery because access to that market depends on certification. Because certification is tied to an independent fishery assessment, no fishing group can achieve certification alone. This forces fishers to cooperate and form a larger group to maintain certification and the market it provides. Thus, the Marine Stewardship Council process enhances participation in part by changing the dominant level of selection from fishers to the fishery. Altering the level of selection may not always be possible or advisable, but the possibility provides an additional lens to evaluate and select effective policy options.

Shift trait variation across levels

Trait variation provides the raw material for selective processes that drive behavioral and institutional adaptation. Current research on cultural trait variation tends to focus on the influence of variation within groups or populations. For instance, evidence suggests that at a variety of scales, greater ethnic variation is associated with reduced social cohesion and cooperative outcomes (Alesina et al. 1999, Ruttan 2006, Waring and Bell 2013). Meanwhile, individual variation, ethnic and otherwise, appears to increase creativity in small groups (McLeod et al. 1996, Paulus and Nijstad 2003). What the present research misses, however, is the way in which variation is distributed within versus between groups, and how that distribution might be managed productively. Because selection is roughly proportional to available trait variation, policies that increase trait diversity at a given level may often enhance selection at that level. Variation can be shifted between levels by policies that encourage or discourage sorting of individuals. Specifically, encouraging individuals to join groups that are homogenous for the relevant trait should increase between-group selection for the trait, whereas sorting individuals into diverse groups is likely to shift the balance of selection toward the individual level. For example, educational research has measured the influence of sorting students into homogenous learning groups on student learning outcomes (Beebe-Frankenberger et al. 2004, Collins and Gan 2013). Likewise, sustainability interventions that manage the distribution of the sustainability-relevant cultural traits across levels may help facilitate stronger selection on the desired level. Other policy levers on trait variation include migration, communication, and social learning, as well as direct approaches to incentivize or discourage innovation.

Leverage the evolution of cooperation

The evolution of cooperation can also be leveraged to achieve sustainability goals. We've argued that humans are skilled at forming cooperative groups to overcome adaptive challenges and that sustainability is itself a multipronged adaptive challenge. Although we cannot provide a blueprint for such policy solutions, the factors that tend to enhance the evolution of cooperation are well known and include smaller group size, repeat interactions, punishment mechanisms, and reputation effects. Thus, as Ostrom (2010*b*) argued, the process of cooperative self-organization, utilized loosely in private enterprise, might be a powerful policy tool for the evolution of cooperative conservation of the commons. Wilson and colleagues (2014) argue that the determinants of group success are sufficiently understood to merit their application to improving group outcomes today (Evolution Institute, Prosocial groups http://www.prosocialgroups.org/).

Avoid ethnocentric solutions

One concern, however, is in the strength of ethnocentric institutions. Humans have group-level adaptations that make the emergence of groupcentric, ethnocentric, nationalistic, and racist institutions common. Ethnocentric institutions tend to emerge when social identity (religious, ethnic, racial) comes to correlate with group membership. When they do arise, ethnocentric institutions draw on parochial altruism and social identity psychology, and can become stronger than equivalent egalitarian institutions. Ethnocentric institutions should be avoided for obvious humanitarian reasons. The CMLS perspective gives us a means to explain their emergence and persistence, and to strategically avoid situations that could lead to their emergence.

DIRECTIONS FOR FUTURE RESEARCH

Our framework represents a first step toward an evolutionary and applied theory of sustainability, but much remains to be done. First, the framework should be tested and expanded by applying it to established bodies of research that systematically explore the emergence of sustainable practices. For instance, research on voluntary environmental governance (Prakash and Potoski 2006, Potoski and Prakash 2009) is organized around the economic concept of clubs and club goods that closely parallels the evolutionary model of adaptive groups. Likewise, psychologists studying hierarchical organizations have developed a body of research on multilevel interactions, concerned with emergence of organizational traits and the role of trait variation (Kozlowski and Klein 2000) within an implicitly evolutionary framework. These connections provide excellent opportunities for theoretical cross-fertilization and empirical development.

Additionally, the CMLS framework could enable a reinterpretation of classic studies. We can hypothesize that the emergence of coordination in Subak irrigation networks in Bali (Lansing and Kremer 1993) may have resulted from stronger selection at the level of the water collective than the level of the farmer. In Maine, where the practice of marking female breeding lobsters for conservation has been studied with a cultural evolutionary model (Acheson and Gardner 2011), we could ask whether competition and strong selection at the level of the harbor gang might have driven the emergence of the trait.

The framework should also be of immediate use to those presently studying multiscale system dynamics (Holdschlag and Ratter 2013) and multilevel governance of ecological systems (Cash et al. 2006), and in cases where data have been collected at multiple levels over time. For these sorts of studies, applying the framework

would be a matter of organizing the facts into a rubric as we have demonstrated and using the resulting patterns to generate testable hypotheses. To move from generating to testing hypotheses, however, will require both theoretical and methodological development.

Theoretical development is needed to refine our expectations about how social and ecological factors jointly influence the evolution of environmental cooperation. For this we need to develop consistent methods for modeling CMLS phenomena and to merge CMLS models with detailed biophysical models. We need to address numerous theoretical questions as well. When can it be said that there is no dominant level of selection? How does group-level selection influence environmental traits that are not embedded in social dilemmas? When does the sociopolitical landscape determine selection pressures for environmental behavior, and when not? Theoretical work can also help improve our understanding of how to analyze CMLS phenomena most accurately. Finally, we hope that the CMLS framework will be integrated with extant frameworks for SES change.

Methodological development is needed even more, starting with an expanded and detailed rubric for developing a CMLS-based empirical investigation. This should include decision factors that help determine when a full CMLS approach is not necessary. Scholars would also benefit from guidance on how to determine the existence of an environmental dilemma, which organizational levels to include, and how to draw their boundaries, as well as a precise method for linking traits across organizational levels. CMLS investigations will surely rely on the same methods that environmental social science uses today, but will also require the development of new methods for measuring benefits and costs, trait occurrence, and inheritance, and for quantifying behavioral selection at different levels of organization. We think these improvements will accrue, along with the true value of the framework, from empirical studies and careful interventions designed around the guiding questions and insights laid out here.

CONCLUSION

Sustainability science and policy need theoretical tools that address the emergence and persistence of sustainable SESs, but complement current theory and research. A fundamental insight of our framework is that in environmental dilemmas cultural group selection on cooperation provides an excellent candidate mechanism for the emergence of cooperative environmental behavior and stable social function. In a nutshell: if the strength of selection on groups for resource conservation outweighs the strength of selection on individuals for greater consumption, costly conservation practices and group-beneficial policies can emerge.

Responses to this article can be read online at:
http://www.ecologyandsociety.org/issues/responses.php/7634

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LITERATURE CITED

Acheson, J., and R. Gardner. 2011. The evolution of the Maine lobster V-notch practice: cooperation in a prisoner's dilemma game. *Ecology and Society* 16(1): 41. [online] URL: http://www.ecologyandsociety.org/vol16/iss1/art41/

Alesina, A., R. Baqir, and W. Easterly. 1999. Public goods and ethnic divisions. *Quarterly Journal of Economics* 114 (4):1243-1284. http://dx.doi.org/10.1162/003355399556269

Aris, M. 1979. *Bhutan, the early history of a Himalayan Kingdom*. Aris & Phillips, Warminster, UK.

Auld, G., L. H. Gulbrandsen, and C. L. McDermott. 2008. Certification schemes and the impacts on forests and forestry. *Annual Review of Environment and Resources* 33(1):187-211. http://dx.doi.org/10.1146/annurev.environ.33.013007.103754

Axelrod, R. 1985. *Evolution of cooperation*. HarperCollins Canada, Toronto, Ontario, Canada.

Ayres, I., S. Raseman, and A. Shih. 2013. Evidence from two large field experiments that peer comparison feedback can reduce residential energy usage. *Journal of Law, Economics, & Organization* 29(5):992-1022. http://dx.doi.org/10.1093/jleo/ews020

Bandura, A. 1971. *Social learning theory*. General Learning, New York, New York, USA.

Barringer, F. 2005. California air is cleaner, but troubles remain. *The New York Times*, 3 August.

Beddoe, R., R. Costanza, J. Farley, E. Garza, J. Kent, I. Kubiszewski, L. Martinez, T. McCowen, K. Murphy, N. Myers, et al. 2009. Overcoming systemic roadblocks to sustainability: the evolutionary redesign of worldviews, institutions, and technologies. *Proceedings of the National Academy of Sciences of the United States of America* 106(8):2483-2489. http://dx.doi.org/10.1073/pnas.0812570106

Beebe-Frankenberger, M., K. M. Bocian, D. L. MacMillan, and F. M. Gresham. 2004. Sorting second-grade students: differentiating those retained from those promoted. *Journal of Educational Psychology* 96(2):204-215. http://dx.doi.org/10.1037/0022-0663.96.2.204

Bell, A. V., P. J. Richerson, and R. McElreath. 2009. Culture rather than genes provides greater scope for the evolution of large-scale human prosociality. *Proceedings of the National Academy of Sciences of the United States of America* 106(42):17671-17674. http://dx.doi.org/10.1073/pnas.0903232106

Bergstrom, T. C. 2002. Evolution of social behavior: individual and group selection. *Journal of Economic Perspectives* 16 (2):67-88. http://dx.doi.org/10.1257/0895330027265

Berkes, F., J. Colding, and C. Folke. 2000. Rediscovery of traditional ecological knowledge as adaptive management. *Ecological Applications* 10(5):1251-1262. http://dx.doi.org/10.1890/1051-0761(2000)010[1251:roteka]2.0.co;2

Binder, C. R., J. Hinkel, P. W. G. Bots, and C. Pahl-Wostl. 2013. Comparison of frameworks for analyzing social-ecological systems. *Ecology and Society* 18(4): 26. http://dx.doi.org/10.5751/ES-05551-180426

Borgerhoff Mulder, M., C. L. Nunn, and M. C. Towner. 2006. Cultural macroevolution and the transmission of traits. *Evolutionary Anthropology* 15:52-64. http://dx.doi.org/10.1002/evan.20088

Bowles, S. 2004. *Microeconomics: behavior, institutions, and evolution*. Princeton University Press, Princeton, New Jersey, USA.

Bowles, S., and J.-K. Choi. 2013. Coevolution of farming and private property during the early Holocene. *Proceedings of the National Academy of Sciences of the United States of America* 110(22):8830-8835. http://dx.doi.org/10.1073/pnas.1212149110

Bowles, S., J.-K. Choi, and A. Hopfensitz. 2003. The co-evolution of individual behaviors and social institutions. *Journal of Theoretical Biology* 223(2):135-147. http://dx.doi.org/10.1016/s0022-5193(03)00060-2

Boyd, R., H. Gintis, and S. Bowles. 2010. Coordinated punishment of defectors sustains cooperation and can proliferate when rare. *Science* 328(5978):617-620. http://dx.doi.org/10.1126/science.1183665

Boyd, R., H. Gintis, S. Bowles, and P. J. Richerson. 2003. The evolution of altruistic punishment. *Proceedings of the National Academy of Sciences of the United States of America* 100 (6):3531-3535. http://dx.doi.org/10.1073/pnas.0630443100

Boyd, R., and P. J. Richerson. 1985. *Culture and the evolutionary process*. University of Chicago Press, Chicago, Illinois, USA.

Boyd, R., and P. J. Richerson. 2009. Culture and the evolution of human cooperation. *Philosophical Transactions of the Royal Society B: Biological Sciences* 364(1533):3281-3288. http://dx.doi.org/10.1098/rstb.2009.0134

Boyd, R., and P. J. Richerson. 2010. Transmission coupling mechanisms: cultural group selection. *Philosophical Transactions of the Royal Society B: Biological Sciences* 365(1559):3787-3795. http://dx.doi.org/10.1098/rstb.2010.0046

Boyd, R., P. J. Richerson, and J. Henrich. 2011. The cultural niche: why social learning is essential for human adaptation. *Proceedings of the National Academy of Sciences of the United States of America* 108(Suppl 2):10918-10925. http://dx.doi.org/10.1073/pnas.1100290108

Brooks, J. S. 2010. Economic and social dimensions of environmental behavior: balancing conservation and development in Bhutan. *Conservation Biology* 24:1499-1509. http://dx.doi.org/10.1111/j.1523-1739.2010.01512.x

Brooks, J. S. 2013. Avoiding the limits to growth: gross national happiness in Bhutan as a model for sustainable development. *Sustainability* 5:3640-3664. http://dx.doi.org/10.3390/su5093640

Brooks, J. S., and D. Tshering. 2010. A respected central government and other obstacles to community-based management of the matsutake mushroom in Bhutan. *Environmental Conservation* 37(3):336-346. http://dx.doi.org/10.1017/s0376892910000573

Brunet, S., J. Bauer, T. De Lacy, and K. Tshering. 2001. Tourism development in Bhutan: tensions between tradition and modernity. *Journal of Sustainable Tourism* 9:242-263. http://dx.doi.org/10.1080/09669580108667401

BST Associates. 2007. Pages 1-65 *in Trade impact study*. Final Report. BST Associates, Bothell, Washington, USA.

Cash, D. W., W. Adger, F. Berkes, P. Garden, L. Lebel, P. Olsson, L. Pritchard, and O. Young. 2006. Scale and cross-scale dynamics: governance and information in a multilevel world. *Ecology and Society* 11(2): 8. [online] URL: http://www.ecologyandsociety.org/vol11/iss2/art8/

Choi, J.-K., and S. Bowles. 2007. The coevolution of parochial altruism and war. *Science* 318:636-640. http://dx.doi.org/10.1126/science.1144237

Collins, C. A., and L. Gan. 2013. *Does sorting students improve scores? An analysis of class composition*. NBER Working Paper No. 18848. National Bureau of Economic Research, Cambridge, Massachusetts, USA. http://dx.doi.org/10.3386/w18848

Cordes, C., P. J. Richerson, R. McElreath, and P. Strimling. 2008. A naturalistic approach to the theory of the firm: the role of cooperation and cultural evolution. *Journal of Economic Behavior & Organization* 68(1):125-139. http://dx.doi.org/10.1016/j.jebo.2008.03.008

Cosmides, L., and J. Tooby. 1994. Better than rational: evolutionary psychology and the invisible hand. *American Economic Review* 84(2):327-332.

Coultas, J. C. 2004. When in Rome ... an evolutionary perspective on conformity. *Group Processes & Intergroup Relations* 7 (4):317-331. http://dx.doi.org/10.1177/1368430204046141

Container Recycling Institute (CRI). 2009. Keep America beautiful: a history. CRI, Culver City, California, USA. http://toolkit.bottlebill.org/opposition/KABhistory.htm.

Derrick, R. A. 1946. *A history of Fiji*. The Colony of Fiji, Government Press, Suva, Fiji.

Drew, J. A. 2005. Use of traditional ecological knowledge in marine conservation. *Conservation Biology* 19(4):1286-1293. http://dx.doi.org/10.1111/j.1523-1739.2005.00158.x

Efferson, C., R. Lalive, and E. Fehr. 2008. The coevolution of cultural groups and ingroup favoritism. *Science* 321 (5897):1844-1849. http://dx.doi.org/10.1126/science.1155805

Ehrlich, P. R. 2009. Cultural evolution and the human predicament. *Trends in Ecology & Evolution* 24(8):409-412. http://dx.doi.org/10.1016/j.tree.2009.03.015

El Mouden, C., J.-B. André, O. Morin, and D. Nettle. 2014. Cultural transmission and the evolution of human behaviour: a general approach based on the Price equation. *Journal of Evolutionary Biology* 27(2):231-241. http://dx.doi.org/10.1111/jeb.12296

Enquist, M., S. Ghirlanda, and K. Eriksson. 2011. Modelling the evolution and diversity of cumulative culture. *Philosophical Transactions of the Royal Society B: Biological Sciences* 366 (1563):412-423. http://dx.doi.org/10.1098/rstb.2010.0132

Field, A. J. 2008. Why multilevel selection matters. *Journal of Bioeconomics* 10(3):203-238. http://dx.doi.org/10.1007/s10818-007-9018-1

Fletcher, J. A., and M. Doebeli. 2009. A simple and general explanation for the evolution of altruism. *Proceedings of the Royal Society B: Biological Sciences* 276(1654):13-19. http://dx.doi.org/10.1098/rspb.2008.0829

Foley, P., and B. McCay. 2014. Certifying the commons: eco-certification, privatization, and collective action. *Ecology and Society* 19(2): 28. http://dx.doi.org/10.5751/ES-06459-190228

Folke, C., S. Carpenter, T. Elmqvist, L. Gunderson, C. S. Holling, and B. Walker. 2002. Resilience and sustainable development: building adaptive capacity in a world of transformations. *AMBIO* 31(5):437-440.

Frank, S. A. 1995. George Price's contributions to evolutionary genetics. *Journal of Theoretical Biology* 175(3):373-388. http://dx.doi.org/10.1006/jtbi.1995.0148

Funtowicz, S. O., and J. R. Ravetz. 1994. The worth of a songbird: ecological economics as a post-normal science. *Ecological Economics* 10(3):197-207. http://dx.doi.org/10.1016/0921-8009(94)90108-2

Gelfand, M. J., J. L. Raver, L. Nishii, L. M. Leslie, J. Lun, B. C. Lim, L. Duan, A. Almaliach, S. Ang, J. Arnadottir, et al. 2011. Differences between tight and loose cultures: a 33-nation study. *Science* 332(6033):1100-1104. http://dx.doi.org/10.1126/science.1197754

Golden, A. S., W. Naisilsisili, I. Ligairi, and J. A. Drew. 2014. Combining natural history collections with fisher knowledge for community-based conservation in Fiji. *PLoS ONE* 9(5):e98036. http://dx.doi.org/10.1371/journal.pone.0098036

Gowdy, J., and L. Krall. 2015. The economic origins of ultrasociality. *Brain and Behavioral Sciences, in press*. http://dx.doi.org/10.1017/s0140525x1500059x

Gulbrandsen, L. H. 2009. The emergence and effectiveness of the Marine Stewardship Council. *Marine Policy* 33(4):654-660. http://dx.doi.org/10.1016/j.marpol.2009.01.002

Gunderson, L. H., and C. S. Holling, editors. 2001. *Panarchy: understanding transformations in human and natural systems*. Island Press, Washington, D.C., USA.

Gupta, J. 2007. The multi-level governance challenge of climate change. *Environmental Sciences* 4(3):131-137. http://dx.doi.org/10.1080/15693430701742669

Gürerk, Ö., B. Irlenbusch, and B. Rockenbach. 2006. The competitive advantage of sanctioning institutions. *Science* 312 (5770):108-111. http://dx.doi.org/10.1126/science.1123633

Harms, W. 2011. Evolutionary games and the modeling of complex systems. Pages 163-176 *in* C. A. Hooker, editor. *Philosophy of complex systems*. North-Holland, Amsterdam, The Netherlands. http://dx.doi.org/10.1016/b978-0-444-52076-0.50005-5

Henrich, J. 2004. Cultural group selection, coevolutionary processes and large-scale cooperation. *Journal of Economic Behavior & Organization* 53(1):3-35. http://dx.doi.org/10.1016/s0167-2681(03)00094-5

Henrich, J., and R. Boyd. 2008. Division of labor, economic specialization, and the evolution of social stratification. *Current Anthropology* 49(4):715-724. http://dx.doi.org/10.1086/587889

Henrich, J., J. Ensminger, R. McElreath, A. Barr, C. Barrett, A. Bolyanatz, J. C. Cardenas, M. Gurven, E. Gwako, N. Henrich, et al. 2010. Markets, religion, community size and the evolution of fairness and punishment. *Science* 327:1480-1484. http://dx.doi.org/10.1126/science.1182238

Holdschlag, A., and B. M. W. Ratter. 2013. Multiscale system dynamics of humans and nature in The Bahamas: perturbation, knowledge, panarchy and resilience. *Sustainability Science* 8 (3):407-421. http://dx.doi.org/10.1007/s11625-013-0216-6

Hviding, E., and K. Ruddle. 1991. A regional assessment of the potential role of customary marine tenure (CMT) systems in contemporary fisheries management in the South Pacific. *FFA Report* 91:71.

Internal Revenue Service (IRS). 2013. Keep American Beautiful, Inc. federal tax filing. Internal Revenue Service, Washington, D. C., USA.

Johannes, R. E. 2002. The renaissance of community-based marine resource management in Oceania. *Annual Review of Ecology and Systematics* 33(1):317-340. http://dx.doi.org/10.1146/annurev.ecolsys.33.010802.150524

Kates, R. W., W. C. Clark, R. Corell, J. M. Hall, C. C. Jaeger, I. Lowe, J. J. McCarthy, H. J. Schellnhuber, B. Bolin, N. M. Dickson, et al. 2001. Sustainability science. *Science* 292(5517):641-642.

Keep America Beautiful (KAB). 2013. *KAB: a beautiful history*. KAB, Washington, D.C., USA. http://www.kab.org/site/PageServer?pagename=about_history

Keep America Beautiful (KAB). 2014. *Programs and initiatives overview*. KAB, Washington, D.C., USA. http://www.kab.org/site/PageServer?pagename=programs_home

Kinzig, A. P., P. R. Ehrlich, L. J. Alston, K. Arrow, S. Barrett, T. G. Buchman, G. C. Daily, B. Levin, S. Levin, M. Oppenheimer, et al. 2013. Social norms and global environmental challenges: the complex interaction of behaviors, values, and policy. *BioScience* 63(3):164-175. http://dx.doi.org/10.1525/bio.2013.63.3.5

Kirby, S., H. Cornish, and K. Smith. 2008. Cumulative cultural evolution in the laboratory: an experimental approach to the origins of structure in human language. *Proceedings of the National Academy of Sciences of the United States of America* 105(31):10681-10686. http://dx.doi.org/10.1073/pnas.0707835105

Kozlowski, S. W. J., and K. J. Klein. 2000. A multilevel approach to theory and research in organizations: contextual, temporal, and emergent processes. Pages 3-90 *in* K. J. Klein and S. W. J. Kozlowski, editors. *Multilevel theory, research, and methods in organizations: foundations, extensions, and new directions*. Jossey-Bass, San Francisco, California, USA.

Kuster, C., V. C. Vuki, and L. P. Zann. 2005. Long-term trends in subsistence fishing patterns and coral reef fisheries yield from a remote Fijian island. *Fisheries Research* 76(2):221-228. http://dx.doi.org/10.1016/j.fishres.2005.06.011

Lansing, J. S., and J. N. Kremer. 1993. Emergent properties of Balinese water temple networks: coadaptation on a rugged fitness landscape. *American Anthropologist* 95(1):97-114. http://dx.doi.org/10.1525/aa.1993.95.1.02a00050

Levin, S., T. Xepapadeas, A.-S. Crépin, J. Norberg, A. de Zeeuw, C. Folke, T. Hughes, K. Arrow, S. Barrett, G. Daily, et al. 2013. Social-ecological systems as complex adaptive systems: modeling and policy implications. *Environment and Development Economics* 18(2):111-132. http://dx.doi.org/10.1017/s1355770x12000460

Levin, S. A., and W. C. Clark. 2010. *Toward a science of sustainability*. The National Science Foundation, Airlie Center, Warrenton, Virginia, USA.

Lewis, H. M., and K. N. Laland. 2012. Transmission fidelity is the key to the build-up of cumulative culture. *Philosophical Transactions of the Royal Society B: Biological Sciences* 367 (1599):2171-2180. http://dx.doi.org/10.1098/rstb.2012.0119

Liu, J., T. Dietz, S. R. Carpenter, M. Alberti, C. Folke, E. Moran, A. N. Pell, P. Deadman, T. Kratz, J. Lubchenco, et al. 2007. Complexity of coupled human and natural systems. *Science* 317 (5844):1513-1516. http://dx.doi.org/10.1126/science.1144004

Livingstone, A. G., R. Spears, A. S. R. Manstead, and M. Bruder. 2011. The more, the merrier? Numerical strength versus subgroup distinctiveness in minority groups. *Journal of Experimental Social Psychology* 47(4):786-793. http://dx.doi.org/10.1016/j.jesp.2011.03.012

Long Beach Alliance for Children with Asthma (LBACA). 2008. *Report to the community on asthma*. LBACA, Long Beach, California, USA.

Marks, G. 1992. Structural policy in the European Community. *in* A. M. Sbragia, editor. *Euro-politics: institutions and policymaking in the new European community*. Brookings Institution Press, Washington, D.C., USA.

Marks, G., L. Hooghe, and K. Blank. 1996. European integration from the 1980s: state-centric v. multi-level governance. *JCMS: Journal of Common Market Studies* 34(3):341-378. http://dx.doi.org/10.1111/j.1468-5965.1996.tb00577.x

Maynard Smith, J. 1974. The theory of games and the evolution of animal conflicts. *Journal of Theoretical Biology* 47(1):209-221. http://dx.doi.org/10.1016/0022-5193(74)90110-6

McElreath, R., and R. Boyd. 2007. *Mathematical models of social evolution: a guide for the perplexed*. New edition. University Of Chicago Press, Chicago, Illinois, USA. http://dx.doi.org/10.7208/chicago/9780226558288.001.0001

McElreath, R., R. Boyd, and P. J. Richerson. 2003. Shared norms and the evolution of ethnic markers. *Current Anthropology* 44 (1):122-129. http://dx.doi.org/10.1086/345689

McLeod, P. L., S. A. Lobel, and T. H. Cox, Jr. 1996. Ethnic diversity and creativity in small groups. *Small Group Research* 27 (2):248-264. http://dx.doi.org/10.1177/1046496496272003

Melosi, M. V. 2005. *Garbage in the cities: refuse, reform, and the environment*. University of Pittsburgh Press, Pittsburgh, Pennsylvania, USA.

Mesoudi, A. 2009. How cultural evolutionary theory can inform social psychology and vice versa. *Psychological Review* 116 (4):929-952. http://dx.doi.org/10.1037/a0017062

Mesoudi, A. 2011. *Cultural evolution: how Darwinian theory can explain human culture and synthesize the social sciences*. University of Chicago Press, Chicago, Illinois, USA. http://dx.doi.org/10.7208/chicago/9780226520452.001.0001

Mesoudi, A., A. Whiten, and K. N. Laland. 2006. Towards a unified science of cultural evolution. *Behavioral and Brain Sciences* 29(4):329-347. http://dx.doi.org/10.1017/s0140525x06009083

Ministry of Agriculture and Forests (MAF). 2010. *National forest policy of Bhutan 2010*. Royal Government of Bhutan. Thimphu, Bhuta.

National Environment Commission (NEC). 2008. *Bhutan environment outlook*. National Environment Commission Secretariat, Royal Government of Bhutan, Thimphu, Bhutan.

National Resources Defense Council (NRDC). 2012. Cleaning up southern California's air: NRDC's work at southern California's ports. NRDC, New York, New York, USA. http://www.nrdc.org/air/diesel-exhaust/california-air-quality.asp

Nowak, M. A. 2006. Five rules for the evolution of cooperation. *Science* 314(5805):1560-1563. http://dx.doi.org/10.1126/science.1133755

Okasha, S. 2006. *Evolution and the levels of selection*. Clarendon Press, Oxford, UK. http://dx.doi.org/10.1093/acprof:oso/9780199267972.001.0001

Ostrom, E. 1990. *Governing the commons: the evolution of institutions for collective action*. Cambridge University Press, Cambridge, UK. http://dx.doi.org/10.1017/cbo9780511807763

Ostrom, E. 2000. Collective action and the evolution of social norms. *Journal of Economic Perspectives* 14(3):137-158. http://dx.doi.org/10.1257/jep.14.3.137

Ostrom, E. 2009. A general framework for analyzing sustainability of social-ecological systems. *Science* 325 (5939):419-422. http://dx.doi.org/10.1126/science.1172133

Ostrom, E. 2010*a*. Beyond markets and states: polycentric governance of complex economic systems. *American Economic Review* 100(3):641-672. http://dx.doi.org/10.1257/aer.100.3.641

Ostrom, E. 2010*b*. Polycentric systems for coping with collective action and global environmental change. *Global Environmental Change* 20(4):550-557. http://dx.doi.org/10.1016/j.gloenvcha.2010.07.004

Ostrom, E. 2014. Do institutions for collective action evolve? *Journal of Bioeconomics* 16(1):3-30. http://dx.doi.org/10.1007/s10818-013-9154-8

Pahl-Wostl, C. 2009. A conceptual framework for analysing adaptive capacity and multi-level learning processes in resource governance regimes. *Global Environmental Change* 19(3):354-365. http://dx.doi.org/10.1016/j.gloenvcha.2009.06.001

Paulus, P., and B. Nijstad, editors. 2003. *Group creativity: innovation through collaboration*. Oxford University Press, Oxford, UK. http://dx.doi.org/10.1093/acprof:oso/9780195147308.001.0001

Penn, D. J. 2003. The evolutionary roots of our environmental problems: toward a Darwinian ecology. *Quarterly Review of Biology* 78(3):275-301. http://dx.doi.org/10.1086/377051

Perreault, C. 2012. The pace of cultural evolution. *PLoS ONE* 7 (9):e45150. http://dx.doi.org/10.1371/journal.pone.0045150

Petersen, J. E., V. Shunturov, K. Janda, G. Platt, and K. Weinberger. 2007. Dormitory residents reduce electricity consumption when exposed to real-time visual feedback and incentives. *International Journal of Sustainability in Higher Education* 8(1):16-33. http://dx.doi.org/10.1108/14676370710717562

Pezzey, J. 1992. *Sustainable development concepts: an economic analysis*. The World Bank, Washington, D.C., USA. http://dx.doi.org/10.1596/0-8213-2278-8

Planning Commission Secretariat. 1999. *Bhutan 2020: a vision for peace, prosperity, and happiness*. Royal Government of Bhutan, Thimphu, Bhutan.

Port of Los Angeles (POLA). 2005. *Port of Los Angeles baseline air emissions inventory 2001*. Executive Summary. Starcrest Consulting Group, LLC, Houston, Texas, USA.

Potoski, M., and A. Prakash, editors. 2009. *Voluntary programs: a club theory perspective*. MIT Press, Cambridge, Massachusetts, USA. http://dx.doi.org/10.7551/mitpress/9780262162500.001.0001

Prakash, A., and M. Potoski. 2006. *The voluntary environmentalists: green clubs, ISO 14001, and voluntary environmental regulations*. Cambridge University Press, Cambridge, UK. http://dx.doi.org/10.1017/cbo9780511617683

Priesner, S. 1998. Bhutan in 1997: striving for sustainability. *Asian Survey* 38:155-160. http://dx.doi.org/10.2307/2645673

Puurtinen, M., and T. Mappes. 2009. Between-group competition and human cooperation. *Proceedings of the Royal Society B: Biological Sciences* 276(1655):355-360. http://dx.doi.org/10.1098/rspb.2008.1060

Richerson, P., R. Baldini, A. Bell, K. Demps, K. Frost, V. Hillis, S. Mathew, E. Newton, N. Narr, L. Newson, et al. 2015. Cultural group selection plays an essential role in explaining human cooperation: a sketch of the evidence. *Behavioral and Brain Sciences, in press*. http://dx.doi.org/10.1017/s0140525x1400106x

Richerson, P. J., and R. Boyd. 1998. The evolution of human ultra-sociality. Pages 71-95 *in* I. Eibl-Eibesfeldt and F. K. Salter, editors. *Indoctrinability, ideology, and warfare: evolutionary perspectives*. Berghahn, New York, New York, USA.

Richerson, P. J., and R. Boyd. 2004. *Not by genes alone: how culture transformed human evolution*. University of Chicago Press, Chicago, Illinois, USA. http://dx.doi.org/10.7208/chicago/9780226712130.001.0001

Rinzin, C. 2006. *On the middle path: the social basis for sustainable development in Bhutan*. Labor Grafimedia, Utrecht, The Netherlands.

Rose, L. 1977. *The politics of Bhutan*. Cornell University Press, Ithaca, New York, USA.

Royal Government of Bhutan (RGB). 2010. *National forest policy of Bhutan 2010*. Royal Government of Bhutan, Thimphu, Bhutan.

Royal Government of Bhutan (RGB). 2012. *The report of the high-level meeting on well-being and happiness: defining a new economic paradigm*. The Permanent Mission of the Kingdom of Bhutan to the United Nations, New York, New York, USA.

Royte, E. 2007. *Garbage land: on the secret trail of trash*. Hachette Digital, New York, New York, USA.

Ruttan, L. M. 2006. Sociocultural heterogeneity and the commons. *Current Anthropology* 47(5):843-853. http://dx.doi.org/10.1086/507185

Schappi, D. 2005. *Cultural plurality, national identity, and concensus in Bhutan*. Center for Comparative and International Studies, ETH Zurich. University of Zurich, Zurich, Switzerland.

Scheyvens, R. 2008. Fiji: an encyclopaedic atlas. *New Zealand Geographer* 64(1):80-81. http://dx.doi.org/10.1111/j.1745-7939.2008.131_2.x

Simon, B., J. A. Fletcher, and M. Doebeli. 2013. Towards a general theory of group selection. *Evolution* 67(6):1561-1572. http://dx.doi.org/10.1111/j.1558-5646.2012.01835.x

Smaldino, P. E. 2014. The cultural evolution of emergent group-level traits. *Behavioral and Brain Sciences* 37(3):243-254. http://dx.doi.org/10.1017/s0140525x13001544

Smith, E. A. 2011. Endless forms: human behavioural diversity and evolved universals. *Philosophical Transactions of the Royal Society B: Biological Sciences* 366(1563):325-332. http://dx.doi.org/10.1098/rstb.2010.0233

Sober, E., and D. S. Wilson. 1999. *Unto others: the evolution and psychology of unselfish behavior*. Harvard University Press, Boston, Massachusetts, USA.

Sommerfeld, R. D., H.-J. Krambeck, D. Semmann, and M. Milinski. 2007. Gossip as an alternative for direct observation in games of indirect reciprocity. *Proceedings of the National Academy of Sciences of the United States of America* 104 (44):17435-17440. http://dx.doi.org/10.1073/pnas.0704598104

Steffen, W., P. J. Crutzen, and J. R. McNeill. 2007. The anthropocene: are humans now overwhelming the great forces of nature. *AMBIO* 36(8):614-621. http://dx.doi.org/10.1579/0044-7447(2007)36[614:TAAHNO]2.0.CO;2

Stern, P. C. 1993. A second environmental science: human-environment interactions. *Science* 260(5116):1897-1899. http://dx.doi.org/10.1126/science.260.5116.1897

Tehrani, J., and M. Collard. 2002. Investigating cultural evolution through biological phylogenetic analyses of Turkmen textiles. *Journal of Anthropological Archaeology* 21(4):443-463. http://dx.doi.org/10.1016/s0278-4165(02)00002-8

Turchin, P. 2003. *Historical dynamics: why states rise and fall*. Princeton University Press, Princeton, New Jersey, USA.

Turner, B. L., R. E. Kasperson, P. A. Matson, J. J. McCarthy, R. W. Corell, L. Christensen, N. Eckley, J. X. Kasperson, A. Luers, M. L. Martello, et al. 2003. A framework for vulnerability analysis in sustainability science. *Proceedings of the National Academy of Sciences of the United States of America* 100(14):8074-8079. http://dx.doi.org/10.1073/pnas.1231335100

Turner, S. P. 2011. Breeding against harmful social behaviours in pigs and chickens: state of the art and the way forward. *Applied*

Animal Behaviour Science 134(1-2):1-9. http://dx.doi.org/10.1016/j.applanim.2011.06.001

United Nations General Assembly. 2011. *Resolution 65/309. Happiness: towards a holistic approach to development*. 19 July 2011. United Nations General Assembly, New York, New York, USA. [online] URL: http://www.un.org/en/ga/search/view_doc.asp?symbol=A/RES/65/309

Ura, K. 2004. *Dieties, archers, and planners in the era of decentralisation*. Karma Ura, Thimphu, Bhutan.

Van den Bergh, J. C. J. M., and J. M. Gowdy. 2009. A group selection perspective on economic behavior, institutions and organizations. *Journal of Economic Behavior & Organization* 72 (1):1-20. http://dx.doi.org/10.1016/j.jebo.2009.04.017

Van Driem, G. 1999. *Languages of the greater Himalayan region*. Research School CNW. Leiden University, Leiden, The Netherlands.

Van Vugt, M., V. Griskevicius, and P. W. Schultz. 2014. Naturally green: harnessing stone age psychological biases to foster environmental behavior. *Social Issues and Policy Review* 8(1):1-32. http://dx.doi.org/10.1111/sipr.12000

Van Vugt, M., G. Roberts, and C. Hardy. 2005. Competitive altruism: development of reputation-based cooperation in groups. Pages 531-540 *in* D. M. Buss. *The handbook of evolutionary psychology.* Wiley, Hoboken, New Jersey, USA.

Vas, E. A. 1986. *The dragon kingdom: journeys through Bhutan*. Lancer International, New Delhi, India.

Vega-Redondo, F. 1993. Competition and culture in an evolutionary process of equilibrium selection: a simple example. *Games and Economic Behavior* 5(4):618-631. http://dx.doi.org/10.1006/game.1993.1034

Veitayaki, J. 1998. Traditional and community-based marine resources management system in Fiji: an evolving integrated process. *Coastal Management* 26(1):47-60. http://dx.doi.org/10.1080/08920759809362342

Vidal, J., and A. Kelly. 2013. Bhutan set to plough lone furrow as world's first wholly organic country. Poverty Matters blog. *The Guardian,* 11 February. [online] URL: http://www.theguardian.com/global-development/poverty-matters/2013/feb/11/bhutan-first-wholly-organic-country

Vitousek, P. M. 1997. Human domination of Earth's ecosystems. *Science* 277(5325):494-499. http://dx.doi.org/10.1126/science.277.5325.494

Wade, M. J., P. Bijma, E. D. Ellen, and W. Muir. 2010. Group selection and social evolution in domesticated animals. *Evolutionary Applications* 3(5-6):453-465. http://dx.doi.org/10.1111/j.1752-4571.2010.00147.x

Waring, T. M., and A. V. Bell. 2013. Ethnic dominance damages cooperation more than ethnic diversity: results from multi-ethnic field experiments in India. *Evolution & Human Behavior* 34 (6):398-404. http://dx.doi.org/10.1016/j.evolhumbehav.2013.07.003

White, G. M., and L. Lindstrom. 1997. *Chiefs today: traditional Pacific leadership and the postcolonial state.* Standford University, Stanford, California, USA.

Wilson, D. S., and L. A. Dugatkin. 1997. Group selection and assortative interactions. *American Naturalist*:336-351. http://dx.doi.org/10.1086/285993

Wilson, D. S., S. C. Hayes, A. Biglan, and D. D. Embry. 2014. Evolving the future: toward a science of intentional change. *Behavioral and Brain Sciences* 37(4):395-416. http://dx.doi.org/10.1017/s0140525x13001593

Wilson, D. S., and K. M. Kniffin. 1999. Multilevel selection and the social transmission of behavior. *Human Nature* 10(3):291-310. http://dx.doi.org/10.1007/s12110-999-1005-x

Wilson, D. S., E. Ostrom, and M. E. Cox. 2013. Generalizing the core design principles for the efficacy of groups. *Journal of Economic Behavior & Organization* 90(Suppl):S21-S32. http://dx.doi.org/10.1016/j.jebo.2012.12.010