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.

Keywords: cooperation; cultural evolution; multilevel selection; sustainability science; theory
1. Introduction

To tackle the global sustainability crisis, societies need generalizable knowledge about the functioning and management of social-ecological systems, based on empirical research. Sustainability science is grounded in strong and diverse empirical case studies, but it lacks a theoretical framework for integrating insights across case studies, particularly with regard to social systems. Here we outline such a framework, demonstrate its application in specific cases and explore its potential to assist in theory development and intervention design.

Sustainability scientists and practitioners currently employ 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 social-ecological systems (SES) (Ostrom 2009). These frameworks help to characterize the internal causal structure that determines system states (CHANS, SES), and the adaptive characteristics of alternative system states (resilience, vulnerability). These frameworks all build on a model of human-environmental systems as complex adaptive systems (CAS) (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 CAS 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 a social-ecological system (Pezzey 1992). First, ‘sustainability’ is a goal state that includes the maintenance of the environment and human wellbeing. Second, ‘sustainability’ also means the durability of a given state over time—its resilience to perturbation. But not all resilient states are desirable, nor are all desirable states resilient. So, we must distinguish between characteristics of system states and transition dynamics between states. 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 – that is, on culture. Cultural evolution – 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 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. Since 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 2010b; Ostrom 2010a), panarchy (Gunderson 2001), multilevel governance (Marks et al. 1996; Marks 1992), and others (Pahl-Wostl 2009; Cash et al. 2006) do not contain general mechanisms of causation across levels of organization, or guidance for designing policy in multilevel contexts. For example, Ostrom contends that
polycentric systems tend to increase cooperation, equity, and sustainability (Ostrom 2010b), but does not explain the mechanisms by which a polycentric arrangement facilitates these qualities. The panarchy model includes multiple hierarchical levels, but a lack of specific social processes make it 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.

Here 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.

2. 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 (Beddoe et al. 2009; Ehrlich 2009; Penn 2003; 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) which constitute society in human populations (Mesoudi et al. 2006; Richerson & Boyd 2005). Cultural evolution has found support from research in anthropology (Borgerhoff Mulder et al. 2006; Tehrani & Collard 2002), psychology (Mesoudi 2009; Livingstone et al. 2011), and economics (Bowles 2004; Bergstrom 2002), 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 & Richerson 1985; Turchin 2003; McElreath & 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 & Boyd 2008), organizational evolution (Cordes et al. 2008), and institutions such as private property (Bowles & 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 where conformism, social identity, reputation, 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 due to competition between groups (Gürerk et al. 2006; Puurtinen & Mappes 2009). Because the sustainable use of resources often requires cooperation and collective action, findings from the literature on cultural evolution is of particular importance for sustainability research. Our conceptual framework builds on a few foundational considerations from this literature.
3. 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 & Tooby 1994). Utility maximization models have been very successful in predicting proximate behavior based on self-interest alone. But 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 & Laland 2012).

Cooperation. Humans actively help one another, often at a personal cost and even when there is no chance of reciprocation (Sober & Wilson 1999; Richerson & Boyd 1998). Cooperation and prosocial behavior is 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. 2010; Boyd et al. 2003) that stabilize cooperation in groups.

Groups. Humans are adapted to group life (Richerson & Boyd 2005). We live in uniquely structured social groups (Gowdy & Krall 2013), signify group membership with cultural markers (Efferson et al. 2008), and conform to group social norms (Coulta 2004). Social groups facilitate cooperation by allowing cooperators cluster (Wilson & Dugatkin 1997; Fletcher & 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 (Boyd & Richerson 2009; Choi & Bowles 2007). Through this process, known as cultural group selection (Henrich 2004; Boyd & 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 in press) and group-level adaptations to environmental conditions (Ostrom 2008; Ostrom 1990).

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 & 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.

4. Cultural multilevel selection

Multilevel environmental governance remains an intransigent problem, due to the overwhelming complexity of untangling causality and recommending intervention. Gupta (2007) found “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. Multilevel selection is particularly useful for social dilemmas, in which the interests of the group are at odds with those of individuals. A cooperative individual in a social dilemma benefits group members at a cost to themselves, decreasing their relative fitness while increasing the average fitness of the group. As a result, 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 (Figure 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.

The principles of multilevel selection 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).

Cultural multilevel selection (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.

![Levels of selection conflict in social dilemmas](image)

**Figure 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.

5. **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 & 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 (Figure 2).

Group selection will tend to be stronger than individual selection when (a) a greater fraction of total trait variation occurs between groups than between individuals, (b) the relative benefits to the group are greater, and (c) the costs to altruistic individuals are lesser (Wilson et al. 2013). Conflicts between levels of selection may exist without becoming outright human conflicts, and 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.

Figure 2. The CMLS framework provides a comparative heuristic for determining cooperative outcomes in an environmental dilemma. The relationship between the dominant level of selection (→) and the social scale of an environmental dilemma (↑) determines the spread of a cooperative environmental trait (○). (A) When the dominant level of selection is below that of the dilemma, selection on individuals favors individualistic strategies, non-cooperation (●), 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 (○) and a resolution to the dilemma.

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. Here 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 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 Figure 2) to identify the appropriate level for policy intervention, and a solution to the problem Gupta identified.

6. 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 social-ecological systems according to the framework. The objective of this effort is to apply a structured and consistent accounting of change in order 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 employ 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, and which collapsed after colonization and globalization resulted in strong competition for fish resources at both the national and individual levels.

**Focal trait.** Here we explain the emergence and change of marine tenure systems in Fiji. Traditional fisheries regulations include exclusive clan ownership of certain reefs, clan-specific prohibitions (*tabus*) 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 (Drew 2005; Johannes 2002) 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 (*vuvali*) 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: (a) individual marine foragers, (b) village chiefdoms, and (c) 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 (Veitayaki 1998; Hviding & Ruddle 1991). Under ecological stressors such as cyclones or droughts, villages without norms to regulate harvesting may be more likely to suffer a resource collapse. This 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.

![Figure 3. Traditional fishing restrictions in Fiji may have lessened due to a change in the dominant level of selection.](image)

**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 inter-village 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, and also exchange resources for cash. Individuals can accumulate wealth in this manner, even harvesting species that are not eaten locally (Kline 2010; Golden et al. 2014). 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 & 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.

Focal trait. Bhutan’s sustainable development approach aims to maximize Gross National Happiness (GNH), and undergirds policies that have ensured high levels of habitat protection (MAF 2013), decentralized natural resource management (Brooks & 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 & 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 predator 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 between communities (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 (occupying Tibet in 1959) and India (annexing 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 (RGOB & Planning Commission Secretariat 1999; Ura 2004). Buddhist philosophy and practice influences most aspects of social, cultural, and political life in Bhutan (Aris 1979) and serves 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” (RGOB & 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 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 wellbeing is evident in policies that guided by the
GNH approach. As an example of the cost of conservation, Bhutan’s forest policies limit household access to timber in order to preserve 60% forest cover in perpetuity (MAF 2013). 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) as several countries (e.g. Germany, Canada, France, and China) have begun to integrate measures of wellbeing to direct their own development efforts (UN 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. Acceptance of the associated costs appears to have been eased by the strong sense of national identity and offset a focus on wellbeing and happiness. 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 resulting in successful regulatory solutions.

**Focal trait.** Ocean-going vessels (OGVs) account for the majority of port-related emissions of particulate matter, NO\textsubscript{x} and SO\textsubscript{2} (Anon 2005). When berthed, OGVs require power for ancillary ship systems. Here 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, while
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 compete for shipping traffic. The economic benefits of the shipping ports accrue at the level of the state, through tax revenue, and the nation, through the provision of domestic jobs (Anon 2007). Local residents bear disproportionate costs in terms higher rates of asthma (Anon n.d.), cardiovascular disease, and cancer (Barringer 2005) than those of nation.

**Levels of selection.** At the corporate level, competition between shipping companies favors the use of vessel-based power in port, since 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 (SPPHU), and enlisted the help of the Natural Resources Defense Council (NRDC). Together, they sued the City of Los Angeles and the Army Corps of Engineers for violations of the California Environmental Quality Act (CEQA), 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 (CAAP), which precludes attempts to undercut each other in terms of environmental regulation rigor. Components of CAAP were later imitated at the state level, and now shore power is required at all major California ports.

![Figure 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 (†). Shaded cells represent dominant level of selection.](image-url)
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, 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 CA 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).

Focal trait. We define individual littering behavior as the act of leaving non-biodegradable 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, 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 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, while 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 anti-littering policy vary from cheap (producer bans) to expensive (public waste management systems). These conditions select for cheap anti-littering 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 the interests of their constituents.

History. In the early 20th century, discarded waste became a public problem as individuals and businesses discarded waste in public spaces, streets and rivers. In the 1950’s 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 non-refillable bottles. Other states followed suit. In the 60’s and 70’s, major national environmental legislation proliferated, and nine more states adopted bottle deposit laws in the 70’s and 80’s (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, Inc., KAB (KAB 2013; CRI 2009) 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 anti-littering campaigns and community cleanup drives (Royte 2007; Melosi 2005). One KAB campaign proclaimed: “People Start Pollution, People Can Stop It.” KAB remains active and well funded today (KAB 2014; IRS 2013), and has successfully influenced cultural norms about where the responsibility for litter lies.

Figure 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 of litter clean up to individuals. State regulations halted their spread, and today litter is broadly considered an individual responsibility. Littering and litter production (−), litter clean up and reduced production (+), cooperation and collective action (†). Shaded cells represent dominant level of selection in both corporate and governmental domains.

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 public rather than corporate responsibility. The success of corporate supergroup KAB reveals that organizations at the same level in different domains (government and corporate) may often compete in environmental dilemmas, resolving the original cooperation dilemma (littering) only to recapitulate it at a higher level (hidden costs of landfills).

7. Routes for interventions

This CMLS framework contributes to the design and evaluation of sustainability policy by focusing on the factors that can be used to encourage behavioral selection for sustainable practices at the level above that of the relevant environmental dilemma. We offer a few additional ideas for interventions.

Alter the dominant level of selection. The appropriate level of selection will vary by context. For example, to reduce electricity consumption, policies that target individual behavior have been effective in residential neighborhoods (Ayres et al. 2013), while in the more collective social setting of college dormitories, policies that target group behavior have proven successful (Petersen et al. 2007).
Hypothetically, this is because the dominant level of selection for electricity consumption behavior differs between residential neighborhoods (households) and college dormitories (co-resident social groups).

**Alter the number of organizational levels.** One simple way to alter the levels of selection is by managing organizational populations or creating and removing levels of social organization. For instance, marine policy might limit the population of fishing enterprises by issuing a limited number of licenses, or mandate the existence of a fishing council to manage a certain zone in the fishery. Likewise, adding a level above the current top level can shelter the entities at that level from the effects of within-group competition, and make between-group fitness more important. This can facilitate the evolution of cooperative strategies with groups.

**Alter the costs and benefits.** Economic incentives and taxes are common and effective environmental policy tools. However, when a tax or incentive is applied to a social dilemma, its application may alter the dominant level of selection. Therefore, these financial instruments should be applied considering their influence on the balance of selective forces between levels as the focal outcome. In addition, policies should make use of social costs and benefits by heeding the influence of reputation, shaming, status competition and related social mechanisms that stabilize cooperation. These costs and benefits may often be both more effective and cheaper to implement.

**Alter the partitioning of variance.** Behavioral and institutional evolution responds to costs and benefits, but also to more subtle factors such as patterns in trait variation. Policy makers or advocacy groups might choose policies designed to increase or decrease behavioral variation in the relevant trait at the individual or group level. Increasing variance in the behavior between groups, and reducing it within groups should usually have the effect of making groups matter more, and thereby may encourage individual-level cooperative behaviors. In order to alter variance partitioning, policies might target processes such as migration, communication and social learning, as well as direct approaches to incentivize or discourage innovation.

**Leverage the evolution of cooperation.** One factor that is rarely employed in policy design is the evolution of cooperation. Humans are skilled at forming cooperative groups to overcome adaptive challenges, and sustainability is itself a multi-pronged adaptive challenge. The emergent process of self-organization might be our most powerful policy tool. Cooperative self-organization is utilized in commercial enterprise, but could be better understood and applied in guiding the evolution of cooperative environmental management. Indeed, this is what Ostrom has argued for so persuasively (Ostrom 2010b).

**Avoid ethnocentric solutions.** One concern, however, is in the strength of ethnocentric institutions. Humans have group-level adaptations that make the emergence of group-centric, ethnocentric, nationalistic, and racist institutions common. Ethnocentric institutions tend to emerge in cases where social identity (i.e. religious, ethnic, racial) correlates with group membership. When ethnocentric institutions do arise, they will tend to be stronger than equivalent institutions that do not draw on parochial altruism and social identity psychology, and tend to favor the interests of their ethnic constituency. 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.
8. Directions for future research

Our framework represents a first step toward greater integration of sustainability and cultural evolution research, theory development and application. The framework should be of immediate use to those studying multi-scale system dynamics (Holdschlag & Ratter 2013) and multilevel governance of ecological systems (Cash et al. 2006), and where data has 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.

One area ripe for such analysis is the domain of non-government, third-party certification systems, such as the Marine Stewardship Council, the Forest Stewardship Council, which exist explicitly to increase conservation and environmental protection in various natural resource industries. For instance, Foley and McCay analyze the emergence of collective action in Marine Stewardship Council (MSC) certification (Foley & McCay 2014). Their analysis suggests that the lucrative ‘sustainable’ fish market at spurs collective action among fishing groups within a fishery because access to that market depends on certification, and because certification is tied to a regional fishery assessment, no group can achieve certification alone. This forces groups to cooperate to maintain certification and the valuable market it provides. In this way, the MSC process appears to enhance conservation behavior through an intentional change in the dominant level of selection. However, for true fishery sustainability, the MSC certification process must accurately assess environmental impact, which it may not always achieve (Jacquet et al. 2010; Christian et al. 2013).

The framework also allows researchers to ask new questions of classic studies. For example, in Lansing and Kremer’s work on the emergence of coordination in Balinese irrigation networks (Lansing & Kremer 1993), we can hypothesize the dominant level of selection that allowed successful networks to form. Or, in Maine, where the practice of marking female breeding lobsters has been studied with a cultural evolutionary model (Acheson & Gardner 2011), we could ask whether strong selection at the level of the harbor gang might have driven the emergence of this conservation trait.

Next, the framework needs to be combined with rich and detailed biophysical models, and integrated with extant empirical frameworks for social-ecological systems change. We view our case studies as illustrative efforts in this direction, but we think the true value of this framework will result from studies and interventions designed around the guiding questions and insights laid out here.

9. Conclusion

Sustainability science and policy would benefit from theoretical tools that address the emergence and persistence of sustainable social-ecological systems. Our conceptual framework complements current research and is based on cultural multilevel selection, a fundamental insight of which is that 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.
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