



The coevolution of economic institutions and sustainable consumption via cultural group selection



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ABSTRACT

Empirical research has identified various institutions that improve resource longevity by supporting individual resource conservation. However, the mechanisms by which these institutions emerge have not been established. We speculate that economic institutions which support resource conservation, such as property regimes and systems of production, may emerge via a process of cultural group selection amongst social-ecological systems. To explore this proposition, we develop a multilevel selection model of resource management institutions with endogenous group dynamics. The endogenous design permits us to determine whether a given social adaptation is due to individual or group-level evolution. We demonstrate how resource conservation and supporting economic institutions coevolve, and reveal when cultural group selection is involved. In the model, sustainable societies emerge in only a minority of cases. Simulations reveal that property norms facilitate sustainable outcomes most, followed by social group marking, and production norms. We describe the institutional transitions which occur along the evolutionary trajectory most likely to achieve sustainability. Analysis of the model reveals that when groups compete indirectly for survival in a harsh environment cultural group selection favors institutions that support resource conservation. However, when groups compete for abundant resources institutions emerge to support overconsumption.

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1. Introduction

Sustainability entails both the preservation of natural resources and the provision of human wellbeing (Clark and Dickson, 2003). But because humans often benefit from overexploitation of resources, these goals are frequently in conflict. Institutions may solve this conflict by balancing individual and collective interests. Thus, achieving both sustainability goals requires establishing sustainable behaviors (e.g. resource conservation), and maintaining those behaviors through durable supporting institutions (e.g. property regimes).

The largest and most challenging sustainability problems such as anthropogenic climate change, regional water depletion, biodiversity loss, pollution and overfishing share a number of common features. They involve entire populations, consume renewable resources, occur over large territories and play out over periods much longer than a human lifespan. These conditions create social-environmental dilemmas in which the short-term interests of the individual require resource consumption and conflict with the long-term survival and wellbeing of the population, which requires resource conservation. Environmental conservation is therefore often hard to maintain because it requires

the cooperation of individuals at the cost of their short-term utility. In other words, achieving cooperation is a fundamental problem in many of our major sustainability challenges.

Human cooperation dynamics are well studied in game theory, economics, evolutionary biology, and psychology. This research shows that cooperative behavior can be augmented or stabilized by factors that enhance group structure or create more effective groups. For instance, reciprocity, punishment, conformity, and ethnic marking can encourage cooperation within human groups, particularly when clearly defined groups compete for resources (Boyd and Richerson, 2002, 2009; Buchan et al., 2011; Chudek and Henrich, 2011; Wilson et al., 2014). One major implication for sustainability efforts is that mechanisms that maintain group structure also tend to promote the adoption of cooperative and individually costly behaviors, such as voluntary resource conservation, and may therefore provide a promising applied tool. However, the role of group structured cultural evolution, or *cultural group selection* (Henrich, 2004; Richerson et al., 2016), in achieving and maintaining cooperative behaviors such as conservation has been largely overlooked in ecological economics and the sustainability literature. A second implication for sustainability is that human cooperation is typically directed toward group goals rather than beneficial outcomes for humanity or the environment. So, to leverage group structure and cooperative dynamics toward sustainable outcomes one must attend

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to the differences between goals and objectives at the individual, group, and population scales.

A separate strain of research details how institutions, as the formal and informal rules that govern social behavior (North, 1990), can bolster cooperation, conservation and effective resource management (Ostrom, 1990), thereby boosting chances for resource sustainability. Rustagi et al. (2010) present evidence from the management of forest commons that both cooperative conservation and the supporting institution of monitoring are key factors in sustaining the resource. However, it remains unclear how these supporting institutions could come to be well fit to their environment (Folke et al., 2007) in the first place. This leads to a conundrum. If sustainable behaviors require supporting institutions, where do supporting institutions come from? To better understand this problem, we turn to the special role of group structure in the co-evolutionary dynamics of institutions and cooperative behaviors.

We conduct a test of Waring et al.'s (2015) hypothesis that cooperative conservation practices and supporting institutions may both emerge *de novo* via cultural group selection. Our theoretical model demonstrates that supporting institutions can emerge via cultural group selection, but that cultural group selection may also favor exploitative institutions and overconsumption in certain circumstances. In this paper, we present agent-based computer simulations elaborating this hypothesis, determine how prevailing conditions determine institutional evolution and suggest avenues for further refinement.

2. Groups, culture, and evolution

Evolutionary theory has value for ecological economics and sustainability research (Beddoo et al., 2009; Rammel et al., 2007; Waring et al., 2015). If properly employed, evolutionary models can help specify the conditions required for desirable social equilibria, such as resource conservation. With an eye to this possibility, we briefly review theory concerning the evolution of cooperation in group-structured cultural populations. For a review of the empirical evidence for cultural group selection, see Richerson et al. (2016).

Culture can be described as information which can be passed between individuals, such as behaviors, beliefs, norms, technology (Richerson and Boyd, 2005), as well as organizing information such as institutional roles and rules (Smaldino, 2014). Theory on the evolution of culture utilizes dynamic models to consider the various factors that determine how behaviors or cultural traits compete and spread in a population. These models consider factors such as costs and benefits, cultural transmission, institutions, and population structure. Cooperative behavior has garnered extra attention in this tradition. One common factor in the emergence of cooperation is group structure: all known mechanisms for the evolution of cooperation foster interactions between cooperative individuals (Fletcher and Doebeli, 2009; Nowak, 2006). The essence of this insight is that when cooperators can interact preferentially with other cooperators by any means, the benefits of cooperation are concentrated within groups, and cooperative behavior can propagate. Therefore, group structure is a fundamental factor in the evolution cooperation in any context.

Group selection is simply the process of natural selection across groups (Okasha, 2004), as often occurs through direct or indirect group competition. Just as natural selection on individuals favors individual adaptations, group selection facilitates the accumulation of group-level adaptations (Wilson and Wilson, 2007). For group selection to be a prevailing evolutionary process, three elements are required: group structure, trait variation between groups, and trait-driven differences in group fate. Group selection is rare in natural genetic systems (but see Pruitt and Goodnight, 2014 for an example), but animal breeders, who can tightly control social groupings, regularly employ group selection to breed cooperative, docile and productive animal strains (Wade et al., 2010). In real-world systems, group selection is difficult to detect because behavioral selection can occur on many levels simultaneously, and in conflicting directions. *Multilevel selection* provides

a framework to account for these countervailing pressures statistically (Okasha, 2004).

Human groups are a special case. Unlike most animals, human group membership can be signaled with culturally transmitted symbols, or social markers. Human group boundaries are therefore free to evolve along with the rest of culture (Boyd and Richerson, 1987; McElreath et al., 2003). Also unlike other animals, human social groupings are often strong enough to determine individual survival yet transcend biological relatedness (Nowak and Highfield, 2011). Well-marked social groups facilitate cooperation and solving collective action problems such as resource procurement and inter-group conflict (Boyd and Richerson, 2009). Empirical demonstrations have also shown that when initially meaningless social markers are culturally inherited, they rapidly evolve to demarcate groups, assisting the emergence of cooperation (Efferson et al., 2008). Moffett (2013) even argues that societies cannot persist without stable cultural group markers.

The fact that social marking facilitates the development of cooperative groups is one reason that group selection is stronger in human culture than other systems (Bell et al., 2009; Durham, 1992; Richerson et al., 2016). Moreover, differential learning and imitation between groups can facilitate the spread of group-level adaptations. Differential between-group imitation, or *imitative group selection*, is one of three mechanisms of cultural group selection, along with differential between-group proliferation and migration (Henrich, 2004). For example, some villages (groups) might store seasonal rainfall in a reservoir while others do not (group-level trait variation). If villages that store their water have better health outcomes (differential fate), or are imitated more frequently (differential imitation), then cultural group selection can occur on village water management behaviors, and the frequency of reservoirs should increase across the population of villages. And, as long as water storage is imitated enough between villages, the group-level adaptation could spread even if it came at a net cost to individuals.

We surmise that both cooperation and supporting institutions are necessary to achieve long-term sustainable environmental resource use, and that social groupings are fundamentally related to both factors. Cultural group selection has been mostly employed to explain the rise and spread of cooperative behaviors (Richerson and Boyd, 2005). But some have argued that group-structured cultural evolution can also explain the evolution of complex institutions (Bowles et al., 2003; Richerson and Henrich, 2012; van den Bergh and Gowdy, 2009).

3. Institutional evolution

Institutions can be considered as a kind of group-level cultural trait, composed of the coordinated actions of individuals in specialized roles, producing outcomes that cannot be replicated by any individual (Smaldino, 2014). Institutional scholars often describe institutional change as a process of social evolution. For instance, Ostrom's (1990) institutional design principles are among the clearest examples of group-level adaptations in human cultures because they appear to be generally advantageous to common pool resource management groups (Ostrom, 1990), social-ecological governance groups (Anderies et al., 2004), and perhaps any human group (Wilson et al., 2013, 2014). Although Ostrom argued that institutions for collective action, such as her design principles, emerge through a process of cultural evolution (Ostrom, 2008), she did not specify *which* evolutionary mechanisms might be involved. This leaves an important explanatory gap: how do institutions that foster collective action emerge and spread?

Ecological economists have proposed that various economic institutions might evolve by cultural group selection (Safarzynska and van den Bergh, 2010; van den Bergh and Gowdy, 2009). Wilson et al. (2013) have suggested that Ostrom's design principles, in particular, evolved via cultural group selection. To give flesh to these hypotheses, consider the impact of Ostrom's institutional principles on group success in evolutionary terms: if the principles sustain resources, they may also

contribute to group longevity, wealth, growth and imitation by other groups. Thus, if sufficiently advantageous to the group, an institution might proliferate by one of the mechanisms of cultural group selection. We focus on two fundamental economic institutions with direct connection to environmental status: property and production.

Property, the exclusive rights to resource use, is a fundamental economic institution (Rousseau, 1755/1984). Ostrom's first principle describes a property regime as being composed of clearly defined resource use boundaries. Property boundaries limit resource benefits in such a way as theory suggests should promote the evolution of cooperative behaviors (e.g. conservation) through group competition. However, property boundaries must be maintained, often at individual cost, and property institutions do not arise spontaneously, but must emerge through the action of individual behaviors and norms.

Production is the process by which value is created in an economic system. Production systems are especially important when they produce value beyond what any individual can create. In such cases, production systems can be considered group-level traits, requiring the coordinated action of multiple individuals. Institutions of production that facilitate the creation of surplus resources also help mitigate the risk of stochasticity and uncertainty (Bowles et al., 2003; Winterhalder, 1986), prolong resource supplies, and provide social stability. Thus, institutions of economic production might impact the incentives for, and evolution of, sustainable practices.

To recap, Wilson et al.'s (2013) hypothesis that Ostrom's principles evolved via cultural group selection is a special case of Waring et al.'s (2015) hypothesis that cooperative conservation practices and their supporting institutions both emerged via the same process. Both hypotheses are firmly based in well-supported evolutionary theories, but neither has been explicitly tested. Our intent in this paper is to examine both hypotheses in concert, and to demonstrate the role of group-structured cultural evolution in both. We first briefly review the relevant evolutionary modeling work to date.

4. Evolutionary models of conservation behavior

Ecological economists have been vexed by the question of how sustainable consumption might evolve. For example, the individual-level evolutionary model of Buenstorf and Cordes (2008) found that sustainable consumption could not persist due to the greater benefits of freeriding. Other evolutionary models of conservation face related problems. See Safarzyńska et al. (2012) for an extensive review. Multilevel selection models are models of behavioral evolution and group structure. Those which also include a social dilemma over resource use are often too complex to fully analyze mathematically, and simulation is used to characterize the full model dynamics. This literature explores how conservation behavior might become viable through the action of supporting factors even when individually costly (e.g. Pepper and Smuts, 2001; Safarzyńska, 2013). For example, Noailly et al. (2007, 2009) recover Boyd and Richerson's (1992) classic finding that punishment can maintain cooperation and extend it to a common-pool resource scenario. Sigmund et al. (2010) demonstrate that imitative learning can promote institutions for governing the commons. Pérez and Janssen (2014) find that agent mobility interacts with resource dynamics to determine the likelihood of sustainability. These models of conservation behavior often recapitulate the finding that factors that strengthen group structure also promote cooperation (Boyd and Richerson, 2002; Bernhard et al., 2006; Choi and Bowles, 2007; Hammond and Axelrod, 2006), underscoring the need for multilevel analysis.

Multilevel selection models can be categorized by how they implement group structure or group-level processes. In most models, group-level processes are exogenous. For example, Bowles et al. (2003) use a fixed group warfare process in which groups with greater mean fitness are duplicated and replace loosing groups. Bowles and Choi (2013) use a similar group-structured imitation process. Fixed group reproduction mechanisms are also common. In such models, groups fission when

they reach a certain size, with the daughter group replacing another group selected at random (García and van den Bergh, 2011; Traulsen and Nowak, 2006). Safarzyńska (2013) also employs fixed group population size and replaces collapsed groups with a duplicate of a surviving group. However, because the exogenous approach entails unrealistic assumptions about the formation and destruction of groups, models that employ exogenous group processes cannot render strong conclusions about the role group-level processes in social evolution.

By contrast, an endogenous approach to modeling multilevel selection allows groups and group interactions to emerge from individual characteristics and processes. Evolutionary models that allow group structure to emerge in this way have yielded insights into the evolution of social behaviors (Epstein, 1999; Pepper and Smuts, 2001; Smaldino et al., 2013). For example, Pepper and Smuts (2001) build an endogenous multilevel selection model of costly resource conservation behavior. Instead of building group selection directly into the model, Pepper and Smuts measure selection statistically. This allows the authors to detect the strength of selection at any organizational level. Pepper and Smuts find that grouping of agents around resources can drive the evolution of conservation behaviors through a type of spatial group selection. More recently, Schank et al. (2015) showed that fair behavior can evolve in a scenario with no apparent advantage to fairness if individuals could aggregate into emergent social groups.

We developed an endogenous multilevel selection model to investigate the coevolution of conservation preferences and the supporting institutions of property and production. We focus on the role of socially marked groups, and allow social markers themselves to evolve. Thus, both group structure, and the factors that maintain it emerge endogenously in our model. The endogenous design creates naturalistic causal patterns whereby individual interactions lead to group differentiation and institutional diversity, and institutional diversity influences group-level outcomes, which in turn feedback to determine the diffusion of individual behaviors.

This approach also allows us to ask novel theoretical questions. First, how does group structure and supporting institutions interact in the evolution of resource conservation regimes? Second, insofar as they assist the emergence of conservation behavior, under what conditions do supporting institutions of property and production themselves arise and persist? Finally, what causal factors characterize the evolutionary pathway that results in the most readily durable, sustainable institutions?

5. Materials and methods

5.1. Model overview

We develop an endogenous multilevel selection model in which consumption behavior evolves in a population exploiting a shared common-pool resource. Consistent with prior literature, our model involves a resource-use dilemma and the transmission of individual traits. Unlike other models, group structure emerges endogenously through the evolution of social markers. This section provides a conceptual overview. The model is detailed exhaustively in the appendix, and NetLogo source code is available on the OpenABM repository at <http://www.openabm.org/model/4627>.

The environment is modeled as a large square grid of resource patches. Each patch contains a renewable stationary stock such as a forest or grassland. Agents occupy patches singly, and must consume resources to survive and reproduce. Patch extraction is the only source of raw resources, so to achieve population persistence, aggregate resource use must be below maximum sustainable yield. However, individuals benefit from larger harvests. Resource use therefore constitutes a common pool resource dilemma. Individuals assume one of two fixed harvest or consumption preferences, which are calibrated to be above (H) and below (L) the maximum sustainable yield (MSY) for a patch. Agents may also harvest resources from a local commons, shared with eight neighboring locations, which may also be occupied (Fig. 1A).

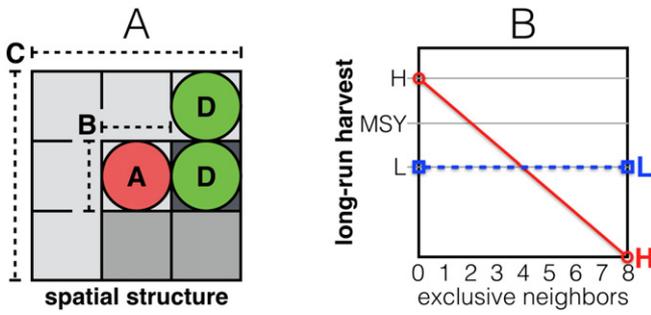


Fig. 1. Model spatial structure and simplified harvest payoff function. Spatial structure (A): Agents (circles) occupy resource patches individually. Resource stock (shades of grey) is contained within patches. A focal agent (A) harvests from its local patch (B), and its local commons (C), which also contains the eight neighboring patches. Only neighboring agents (D) may interact with the focal agent directly. Agent colors denote social markers. Long-run harvest (B): Assuming an agent excludes neighbors from its focal patch, it's access to the local commons decreases with the number of neighbors holding exclusive property norms such that with 8 neighbors, high consumption (H) depletes focal patch, but low consumption (L) is sustainable.

Harvested resources are consumed or stored. Agents may also create *processed resources* by engaging in a cooperative production process with another agent. The two resources are stored and consumed separately, and processed resources are always consumed first.

Agents are not assigned to groups, but hold symbolic group makers. This allows them to differentiate their behavior with others based on markers. Social markers are costless, and are inherited, imitated, or very rarely changed at random (i.e. behavioral mutation). The groups that form in this way are naturalistic because they do not define individual behavior, do not determine group interactions, have complex spatial extent and varying levels of social participation. As we shall see, correlations between group makers and other behavioral traits emerge endogenously. Socially marked groups may grow, shrink, split, merge or expire.

Agents are capable of two simple institutional behaviors, involving interactions with other agents. These are *property defense* and *cooperative production*. In property defense, agents pay a cost to defend their local patch from neighbors who would otherwise harvest from it. In

cooperative production, agents pool harvested resources with a neighbor to create and split additional resources. This takes the form of a two-player public goods game in which raw resources are transformed into processed resources. Both types of institutional behavior have *social scope*, so that agent behavior is a function of the social markers of the agent and its neighbor. For example, an agent with a 'group property' norm shares its local patch only with agents with the same social marker. Meanwhile, other agents with the same marker may instead consider their local patch to be private property. There are three social scopes: inclusive (I - all agents), exclusive (E - same marker) and antisocial (A - no agents) (see Fig. 2). Each agent holds two institutional norms with social scope (e.g. private property, open production) which determine behavior contingent upon the markers of the agents with which it interacts, and thereby influence outcomes. For example, antisocial property norms allow an agent to completely control resources on her local patch, but at high property defense costs, whereas inclusive property norms incur no direct costs of property defense, but subject the individuals local patch to exploitation by neighbors.

Individual behaviors evolve. Agent behavioral traits are transmitted through both reproduction and imitation. When an agent gains sufficient resources to reproduce, the offspring agent inherits the same resource consumption behavior and cultural traits. Agents also imitate agents in their local area with more stored resources. Behavioral innovation (or mutation) also occurs. As a result, behavioral traits are spread differentially based on how they influence resource accumulation.

Agents die as an increasing function of age, or when they have insufficient resource to pay the cost of living. Reproduction is asexual and occurs when an agent has accumulated sufficient resources and resides near an empty patch. Offspring inherit the traits of their parents with small chance of mutation. Faithful inheritance of traits does not necessarily reflect a role of genetics, but merely the vertical transmission of norms, as through teaching. Agents may also migrate to a neighboring patch, if it contains more resources than their current patch, with a small probability. Migration and reproduction together cause the network structure of social interactions to evolve along with individual behaviors.

Simulations were initialized with nine groups of twelve spatially clustered agents. Each group is assigned a unique social marker and one of the nine unique combinations of behavioral norms, so that each

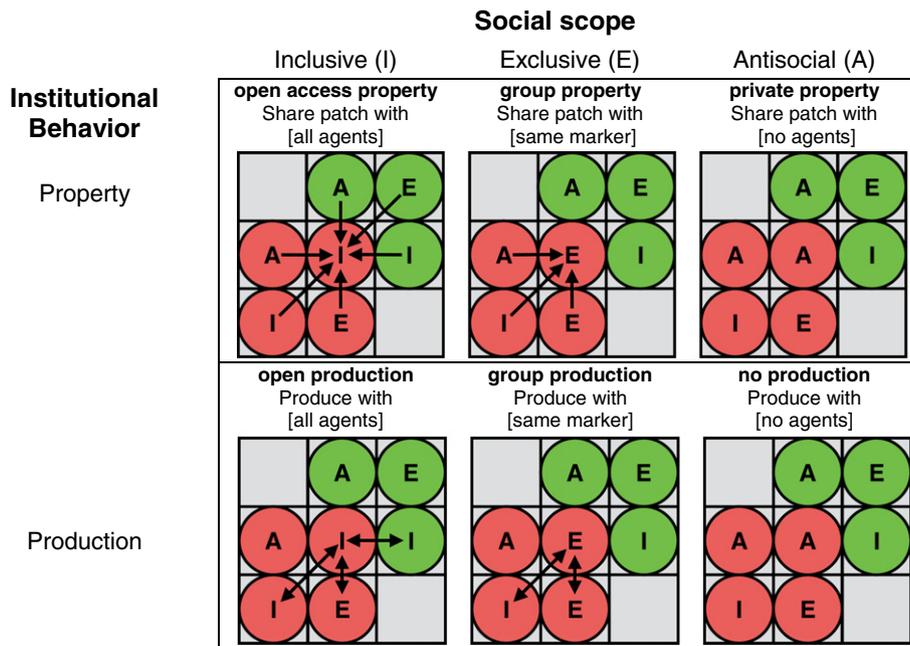


Fig. 2. Examples of institutional behaviors with each social scope. Property and production behaviors each may take any one of three social scopes (I, E, A), for three possible institutional norms. Given any institutional norm, the resulting agent behavior depends upon the other agents it interacts with. Each round, all property interactions occur, while an agent only conducts production with a single random partner each round. Spatial configuration is for example.

member of a group is initially identical. All agents were initialized with low (sustainable) harvesting preferences. The simulation proceeds in discrete time steps, in which each agent has the opportunity to harvest, engage in institutional interactions, and reproduce.

5.2. Measuring group selection

Endogenous group structure presents the opportunity to precisely measure the relative strengths of group selection and individual selection as they fluctuate over time. We use the Price equation (Okasha, 2004; Price, 1972) to compute the strength of individual and group selection for all harvesting, production, and property traits, following McElreath and Boyd's (2007) formulation,

$$\bar{w}\Delta\bar{z} = \underbrace{\text{cov}(w_g, z_g)}_{\text{group selection}} + E[\underbrace{\text{cov}(w_{ig}, z_{ig})}_{\text{individual selection}}] \quad (1)$$

which relates the average change in trait frequency, $\Delta\bar{z}$, normalized by the average fitness, \bar{w} , to the sum of covariances between the trait and the fitness of those possessing the trait at the group, g , and individual, i , levels. Individual fitness, w_{ig} , is defined as the number of offspring produced by individual i in group g . Group fitness, w_g , is defined as the average fitness of the individuals in group g . These two components may hold opposite signs, as with a social dilemma, or align when a trait has similar fitness effects on individuals and groups (Panchanathan, 2011). The strength and sign of individual and group selection on consumption preferences, for example, will vary based on factors such as resource availability, the number of groups, and the distribution of institutional behaviors. We compute the components of selection for all traits.

5.3. Simulation experiments

To characterize the coevolution of conservation preferences and supporting institutions, we conducted a series of simulation experiments. Experimental treatments varied both the availability of supporting institutions and the presence of social markers (Table 1).

Table 1

Simulation experiments varied the availability of institutional behaviors and social markers. In conditions with no social markers, exclusive property and production traits (E) are equivalent to the all-inclusive variants (I). An additional four treatments (2A, 2B, 4A, 4B) each make only a single institutional option available.

#	Treatment	Social markers	Institutional behaviors
1	Baseline		
2	Institutional reference		X
3	Group reference	X	
4	Unrestricted	X	X

In treatments with no social markers, all agents share a single marker and marker mutation is disabled. In treatments with no options for institutional behavior, agent norms were fixed to the simplest state for that institution: open access property (I) or no production (A). Each treatment was replicated 1000 times at benchmark parameter values.

Additional treatments also varied the two institutional behaviors independently. Sensitivity analyses were conducted for the twelve most important parameters in our simulation, in the unrestricted treatment, and 100 replications were performed at each parameter value. Since a common criticism of group selection models is that they rely on unrealistic initial conditions (West et al., 2011), we tested an alternative initialization condition in which social markers were not correlated with institutional norms. This configuration only reduced the frequency of population survival, but all other conclusions hold. Sensitivity and robustness results are reported in the Appendix.

6. Results

The model achieves one of two gross equilibria well before 1000 steps when simulations were halted. Model dynamics follow a consistent pattern. Initially, resources grow rapidly, populations expand, and over-harvesting behavior spreads through imitation and reproduction. The population then reaches carrying capacity, over-harvesting depletes resources, and the population crashes (Fig. 3). Because population survival in this model depends requires resource conservation, only those populations which develop a dominant culture of conservation behavior survive in the long term. In the majority of simulations, the population goes extinct by ~250 steps. In the best-case, unrestricted treatment, where agents of all possible institutional combinations are supplied with flexible social markers, and initialized with 100% conservation preferences, only 40% of populations survive to 1000 steps. Even fewer populations survive in more restrictive treatments.

Remnant populations may survive when low harvesting behavior and resources both persist, as observed in other models of cooperation with limited resources (Smaldino et al., 2013). In these cases, a rough equilibrium is obtained in which the population stabilizes at around 25% of carrying capacity, resources at close to 15%, and conservation preferences at nearly 90% frequency (Fig. 3). Thus, our model differs from that of Buenstorf and Cordes (2008) in that it can achieve long-term equilibrium of sustainable consumption preferences, albeit rarely.

6.1. Multilevel selection of conservation behavior

Results reveal that institutions evolve differently when socially markers are available, and that supporting institutions and groups operate synergistically to promote conservation behavior. Without supporting institutions, agent populations reliably become extinct by

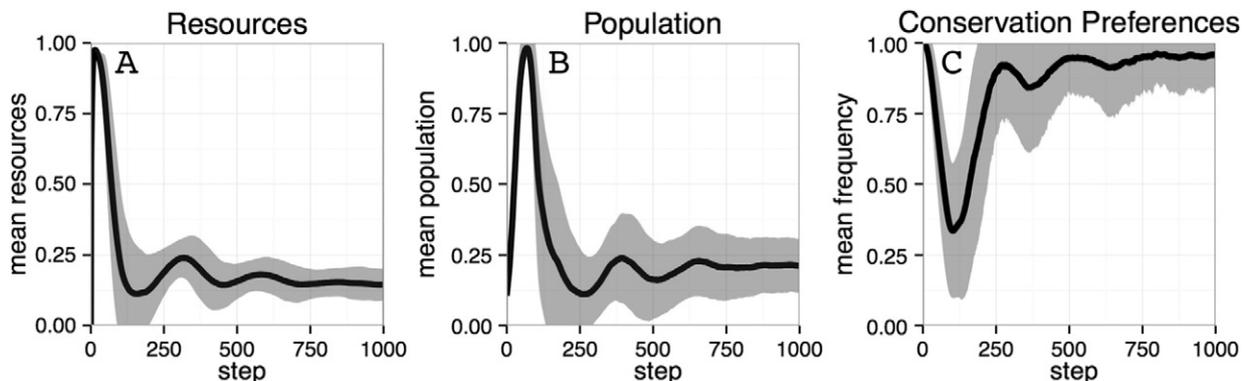


Fig. 3. Simulation results across all treatments. Means for (A) proportion of maximum resources, (B) proportion of maximum population, and (C) frequency of sustainable consumption preferences with 1 σ error ribbons.

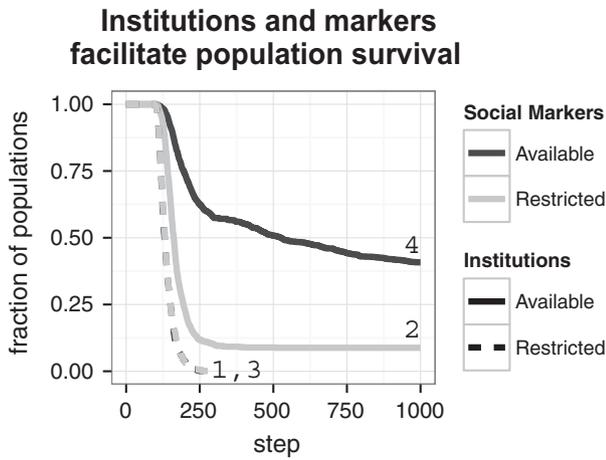


Fig. 4. Population persistence over time in treatments 1–4. Institutions are necessary for persistence, but populations with social markers are four times more likely to survive.

~250 steps, regardless of the presence of social markers, revealing that the evolution of institutions (specifically property) is necessary for the emergence of conservation in this model. This can be seen when comparing the effect of institutions and social markers on population survival (Fig. 4). Emergent supporting institutions are also sufficient to achieve widespread conservation preferences and resource sustainability, while social marked groups are not. However, institutional options alone only achieve a sustainable equilibrium 9% of the time. By contrast, when social markers and institutions coevolve, sustainable outcomes become much more common (41%). Therefore, group structure facilitates institutional evolution and the widespread adoption of conservation preferences. For the greatest chances of a sustainable equilibrium, social groups and institutions need to coevolve.

Institutions that support conservation behavior evolve most readily when social markers enable a process of cultural group selection. Decomposing selection for conservation behavior using the Price equation, we find that competition within groups selects against conservation in all treatments, but between-group selection favors conservation when institutions are available (Fig. 5). When social markers and institutions coevolve, group selection for conservation overwhelms the within-group competition selecting against conservation (Fig. 5A), starting negative then growing increasingly positive over time. This demonstrates the possibility of Waring et al.'s (2015) hypothesis that the emergence and persistence of sustainable resource use and durable supporting institutions can be enhanced by a process of cultural group selection. Thus, when institutional options are unrestricted, property

and production norms coevolve, and institutions emerge that help stabilize sustainable consumption. Next, we examine which particular property and production institutions emerge, and how they evolve.

6.2. The evolution of durable economic institutions

Since unrestricted institutional evolution results in the highest rates of population sustainability, we should like to know what property and production institutions emerge when options are unrestricted. Recall that an agent may hold one of three alternative norms, inclusive (I), exclusive (E) or antisocial (A), in both institutional domains, for nine possible combinations. Fig. 6 juxtaposes the population dynamics of agents with conservation preferences holding each combination in the unrestricted treatment. Only combinations with private property norms produced stable or growing populations in the long term (Fig. 6, right column). The temporal dynamics are important, however. While private property achieves the greatest long-term populations, private property norms only emerge late in the simulation. By contrast, the combination of group property group production (center panel), flourishes early and gradually declines in cycles ~250 steps in length. Therefore, even though private property is the most durable property norm, it develops from an initial group property regime.

Fig. 7 compares the components of selection for property and production norms in the unrestricted treatment. Individual selection remains near zero for all norms, but group selection favors group production, group property and private property norms. The strength of group-level selection for group property stalls out, while it keeps rising for private property and group production. This shows that exclusive, group-centric institutions are favored by between-group selection. However, counter to expectations, private property emerges via group selection. This outcome coincides with a spatial pattern that emerges later in the simulations, in which individuals live in small clusters and harvest from more of their local commons (see the Appendix).

In summary, we find that group-centric institutions of production and property emerge in the short run via group selection when a lucky group with both norms manages to survive the resource crash. In the long run, group property gives way to private property, which counterintuitively evolves via group selection as groups become smaller and more isolated. These results reveal an interesting set of transitions in institutional evolution.

6.3. Transitions in institutional evolution

Finally, we unpack the causes of the institutional transitions observed in the model. Our simulations show that the nature of competition between groups determines the character of the institutions

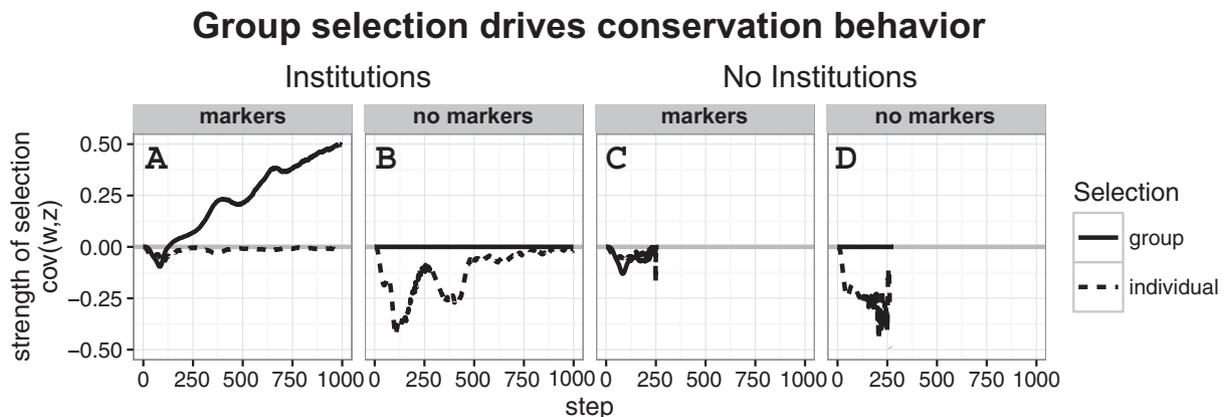


Fig. 5. The average strength of selection for conservation varies over time at individual and group levels. Panes represent treatments: A = 4, B = 2, C = 3, D = 1. Group-level processes of cultural evolution select for conservation behavior and supporting institutions, driving the sustainability transition most commonly observed in the model.

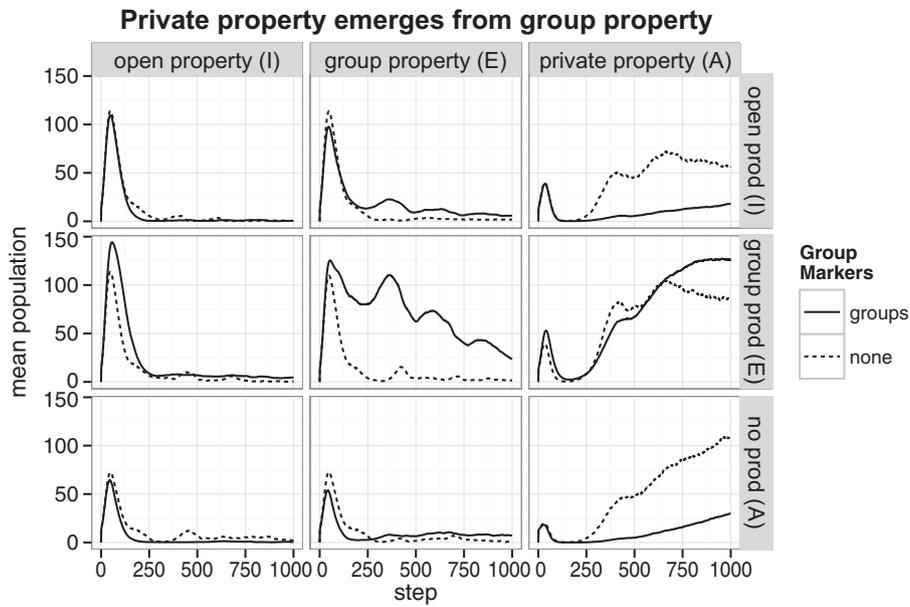


Fig. 6. Mean populations of institutional norm combinations with conservation preferences across 1000 simulations in the unrestricted treatment (4, solid line), and the institutional reference treatment (2, dashed line). Norm combinations that do not include conservation preferences do not maintain large populations.

which are selected. As we have established, the model follows a consistent pattern in which overconsumption behavior leads to a resource collapse. In this initial phase, scramble competition for resources creates strong selection at both individual and group levels for resource conservation. After the resource crash, if one large group with the right combination of norms emerges and can outlast others in the low-resource environment, the population can recover. This starts a second phase in which competition for survival and longevity in a harsh environment selects for resource conservation.

The institutional transitions concerning conservation can be seen by plotting population survival as a function of the strength of group selection for conservation preferences (Fig. 8). The plot reveals a general upward trajectory with transitions marked by reversals in the slope of the relationship. When the slope is positive, groups with more conservation preferences survive longer, increasing total population survivorship. When slope is negative, groups with more conservation preferences die off faster, causing a decrease in total population survivorship.

Three hairpin bends in Fig. 8 correspond to changes in the nature of group competition as it influences resource use. Transition A (~100–250

steps) corresponds to the initial phase during which groups with low harvesting behavior are outcompeted by those which consume more, and die off (negative slope). After the crash, resources become limiting, and only groups with conservation preferences survive and proliferate (positive slope). The transitions represent a change in the nature of between-group competition caused by resource availability. Transitions B (~500 steps) and C (~750 steps) recapitulate the same process in smaller cycles corresponding to the decline of group property norms (Fig. 6, center panel) as the system approaches the private property equilibrium. Therefore, our model finds that institutional evolution follows patterns observed before (Pérez and Janssen, 2015): if groups compete for bountiful resources, overharvesting is favored, but, if groups compete for scarce resources in a harsh environment, cooperation is favored.

7. Discussion

We describe a model that combines renewable resources with socially marked groups and the endogenous evolution of property and

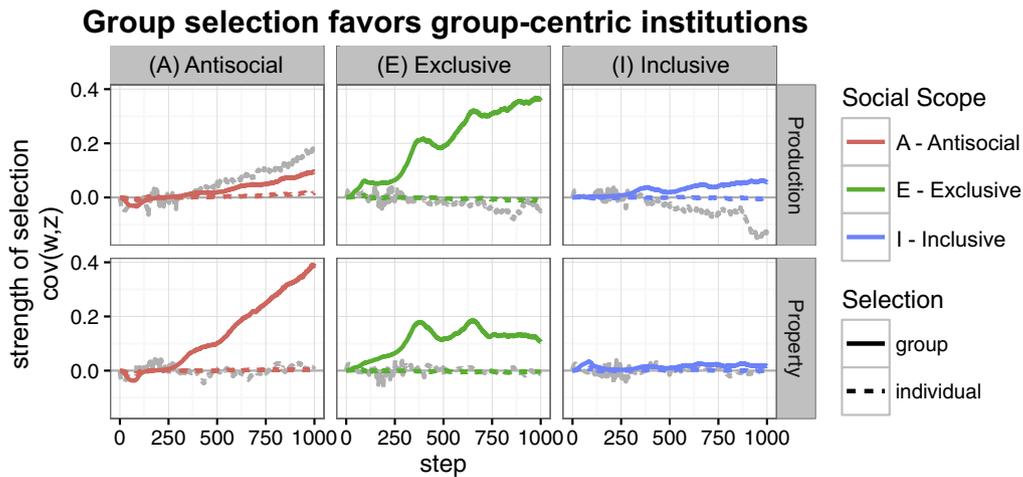


Fig. 7. Group selection for exclusive property norms is stronger than individual selection. Group selection for group property rises early and is surpassed by group selection for private property in the long term. Mean values across 1000 simulations of the unrestricted treatment 4. Grey dotted lines represent individual selection in the institutional reference treatment (2).

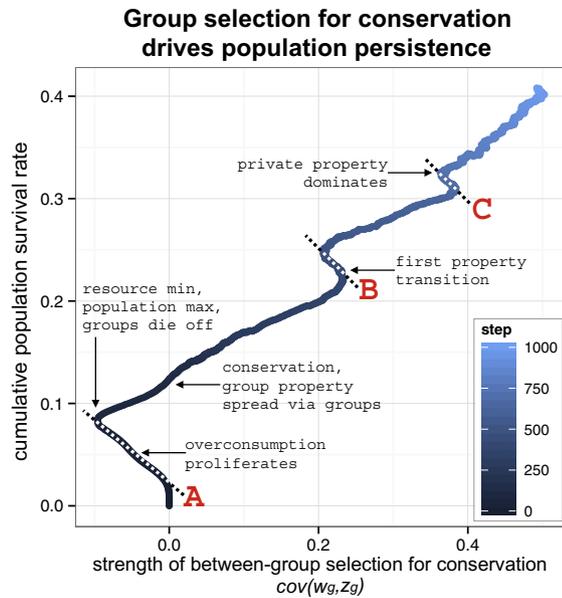


Fig. 8. Cumulative rate of population persistence as a function of the strength of group selection on conservation preferences. Transitions A, B and C correspond to periods when the mode of between group competition changes from resource acquisition to survival. Transition A drives the emergence of conservation preferences and group property. Transitions B and C serve to eliminate groups with group property norms at the benefit of groups with private property norms. Means across 1000 simulations in the unrestricted treatment.

production institutions. The model sheds some light on the relationship between cooperative resource conservation, emergent institutions and long-term sustainability. The model provides a theoretical demonstration that conservation preferences and sustainable resource use can be stabilized by the evolution of property and production institutions via cultural group selection. The chances of population survival in the model are not favorable. However, of the factors we explored property norms enhanced the likelihood of sustainable outcomes the most. Property interacted synergistically with emergent group structure, which was the second most important factor. Production norms also aided sustainable outcomes. We note also that while Ostrom listed eight design principles for sustainable collection action, our model permits only a subset of these to evolve. Our results are therefore promising; similar methods might further elucidate the paths by which more sustainable societies could evolve.

We found that the evolutionary trajectory most likely to achieve sustainable resources and population entails two institutional transitions. First, the population must achieve widespread conservation after initial overconsumption. This first transition occurs most readily with group-centric norms of property and production coevolve with consumption preferences. A second transition occurs later in which group property gives way to private property in the long term. Importantly, these institutional transitions are driven by the nature of competition between groups. When resources are plentiful, competition for resources encourages the evolution of overconsumption, but when resources become limiting, group competition for longevity selects for durable institutions that support cooperative conservation behavior.

In these simulations, sustainable consumption and supporting institutions emerge through various processes of between-group selection. This finding supports prior work showing that cultural group selection is a likely mechanism for the evolution of institutions in general, and bolsters the conclusion that exclusive property institutions enhance resource conservation. It stands to reason that the rest of Ostrom's principles may also result from and be maintained through cultural group selection – a proposition which would be tested with similar modeling

efforts. Our model helps to flesh out the mechanics of a formal theory of the emergence and persistence of sustainable behaviors and institutions called for by Waring et al. (2015).

Our methods diverge from the previous literature on institutional evolution by creating a system of endogenous group formation and dissolution. This approach allows a rigorous characterization of how levels of selection in cultural evolution determine social (and ecological) outcomes, and helps to clarify how cultural trajectories can separate alternative social-ecological states.

Countless factors influence the evolution of behaviors and institutions, many of which were not included in our model. Factors that may be worthy of future investigations include environmental factors (e.g., resource heterogeneity, resource fluctuations, and alternative resource systems such as fisheries, irrigation or pastoral systems), institutional options (e.g., alternative norms, markets, democratic rules), and social processes (e.g., enforcement, conformity, punishment). For simplicity, our model utilized a somewhat unrealistic social structure. The group sizes match some small-scale human resource management systems, but the strict resource limitation and long time scale are more appropriate for civilizations. Nevertheless, the results we derive appear well suited to explain the emergence of Ostrom's principles. We hope similar models will be built around actual social-ecological systems to answer questions about the most reliable evolutionary trajectories by which they might reach sustainable states.

8. Conclusions

To choose a sustainable future, humanity needs the ability to distinguish between evolutionary trajectories that lead to alternative future social-ecological states. Theories from the social sciences and sustainability research have not proved sufficient to this task. To select between alternative futures, we must be able to reliably simulate alternative trajectories of social change, and evaluate their likelihood. This model is a step in that direction. While Epstein (2006) quips, "if you can't grow it, you can't explain it," we worry that if we can't simulate a sustainable future, we may not be able to live one. Our theoretical model is demonstration that it is possible to grow alternative social-ecological histories that provide insight through their contrasts.

Our model suggests that a major institutional sustainability transition to widespread resource conservation would be more likely after a global resource collapse. This result is not appealing, but it might be realistic. Inter-group conflict appears to be more likely following resource collapse such as may be caused by climate change (Hsiang et al., 2013). It would be foolish to assume that a peaceful post-collapse transition is likely, and equally foolish to assume that sustainable behaviors and institutions will naturally emerge before a collapse. Instead, it is our hope that simulations such as this can help predict and avoid the group conflict likely to emerge when resources become scarce. Similar models can be used to explore factors that might mitigate the severity of a resource crash, or to find ways to accelerate a peaceful sustainability transition before more destructive types of group selection take effect.

The threat of conflict is real, and cultural group selection is no panacea. Warfare is probably the most forceful driver of group level cultural and institutional change. But warfare will not select for the cultural and institutional changes we need. Thus, we need a better understanding of the conditions and operation of each alternative mechanism of cultural group selection in order to choose between them.

A major goal of sustainability policy is to enhance the spread of sustainable behaviors and institutions. We provide a theoretical demonstration that sustainable consumption and durable institutions may emerge more reliably when groups compete for longevity. This insight has policy relevance. To encourage conservation and durable institutions, societies should incite peaceful group competition for ecological longevity and avoid the destructive scramble competition for resources. Our theoretical demonstration is a first step toward explaining the emergence of durable institutions that promote sustainable behavior.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.ecolecon.2016.09.022>.

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