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

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Abstract

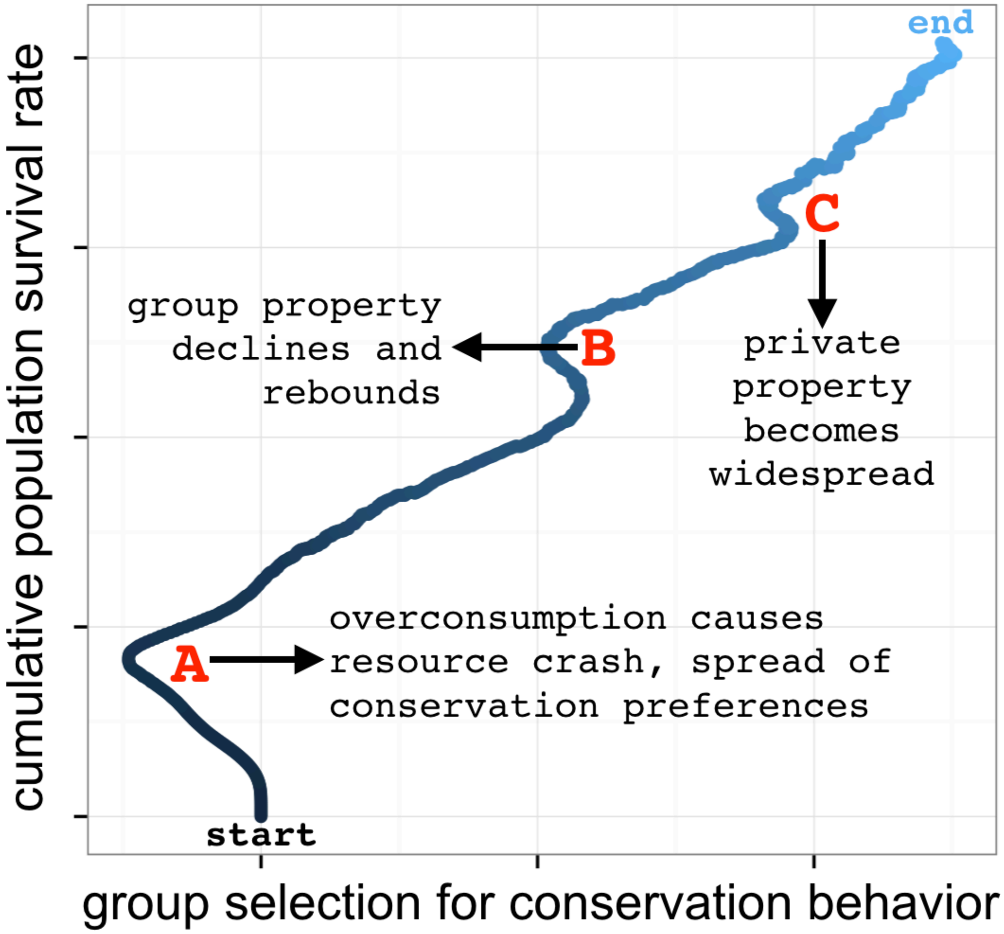
Empirical research has identified various institutions that improve resource longevity by supporting individual resource conservation. However, the mechanisms by which these institutions emerge have not been established. We speculate that economic institutions which support resource conservation, such 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.

Keywords

cultural group selection; institutions; conservation; cooperation; agent-based model

Highlights

- We create a multilevel selection model of common pool resource management to study the evolution of sustainable institutions and behaviors.
- The model allows for the endogenous formation and dissolution of groups of agents with variable property norms, production norms, consumption preferences and social markers.
- Sustainable social-ecological outcomes are rare, but conservation behavior and durable institutions arise primarily when groups compete indirectly for survival and longevity.
- Property evolution proves necessary for sustainable outcomes, but the emergence of property institutions depends heavily on group structured cultural evolution.



- A multilevel selection model was used to study the evolution of conservation behavior and supporting institutions.
- Endogenous model design facilitated measurements of the strength of cultural group selection in institutional evolution.
- Sustainable social-ecological systems arose when groups competed indirectly for survival in a harsh environment.
- Three major transitions in institutional evolution were marked by shifts in the direction of group selection for conservation behavior.

1. Introduction

Sustainability entails both the preservation of natural resources and the provision of human wellbeing (Clark & 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 (Robert Boyd & Richerson 2009; Boyd & Richerson 2002; Buchan et al. 2011; Chudek & 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 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 (Beddoe 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 & 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 & 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 & 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 & 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 & Highfield 2011). Well-marked social groups facilitate cooperation and solving collective action problems such as resource procurement and inter-group conflict (Boyd & 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 & Boyd 2005). But some have argued that group-structured cultural evolution can also explain the evolution of complex institutions (Bowles et al. 2003; Richerson & Henrich 2012; van den Bergh & 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. 2014; Wilson et al. 2013). 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 & van den Bergh 2010; van den Bergh & 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 Safarzynska 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; Safarzynska, 2013). For example, Noailly et al. (2009; 2007) recover Boyd and Richerson's (1992) classic finding that punishment can maintain cooperation and extend it to a common-pool resource scenario. Sigmund and colleagues (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 & Richerson 2002; Bernhard et al. 2006; Choi & Bowles 2007; Hammond & 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 & van den Bergh 2011; Traulsen & Nowak 2006). Safarzynska (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 & 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 of the model only. The agent-based 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 (Figure 1A). 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.

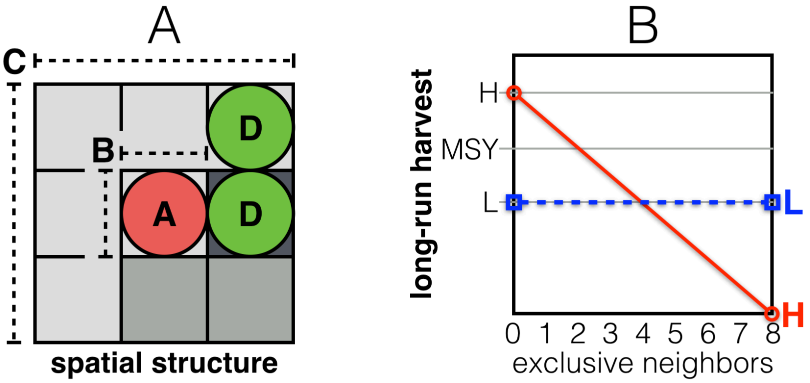


Figure 1. Model spatial structure and simplified harvest payoff function. Spatial structure (A): Agents (circles) occupy resource patches individually. Resource stock (shades of grey) is contained within patches. A focal agent (A) harvests from its local patch (B), and its local commons (C), which also contains the eight neighboring patches. Only neighboring agents (D) may interact with the focal agent directly. Agent colors denote social makers. 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.

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 Figure 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.

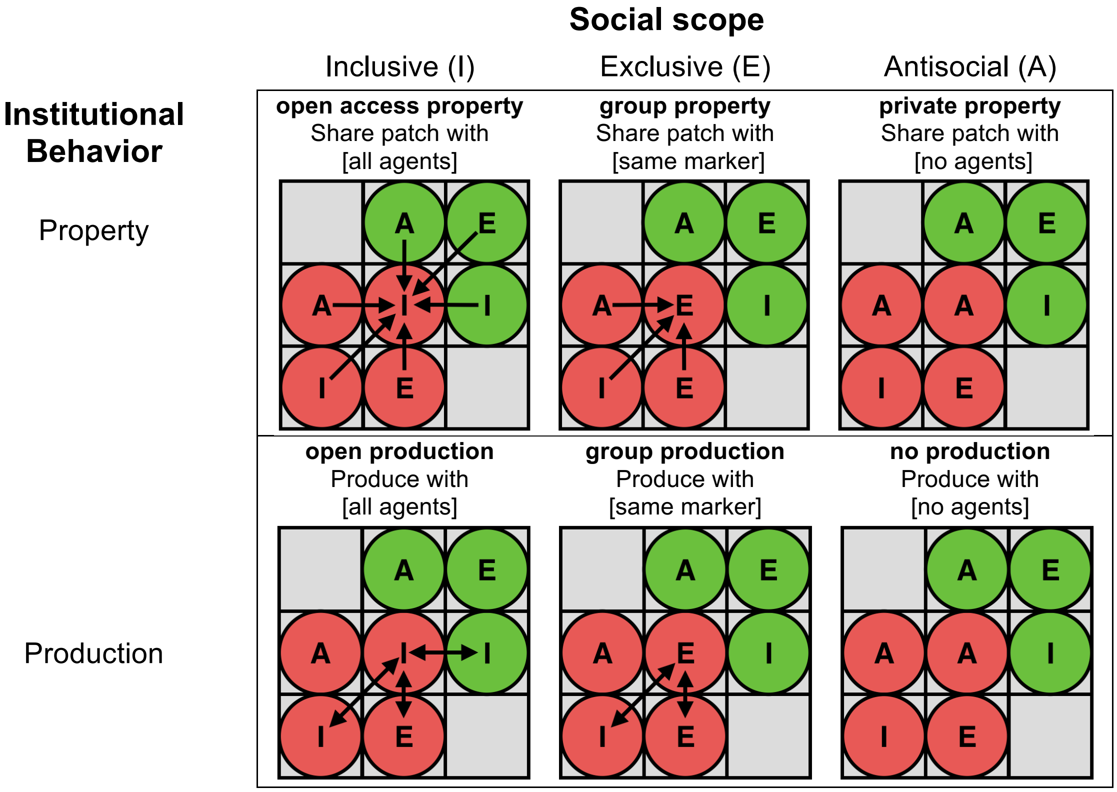


Figure 2. Examples of institutional behaviors with each social scope. Property and production behaviors each may take any one of three social scopes (I, E, A), for three possible institutional norms. Given any institutional norm, the resulting agent behavior depends upon the other agents it interacts 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.

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 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,

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

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 instructions and the presence of social markers (Table 1). 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.

#	Treatment	Social Markers	Institutional Behaviors
1	Baseline		
2	Institutional Reference		X
3	Group Reference	X	
4	Unrestricted	X	X

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) make only a single institutional option available.

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 (Figure 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.

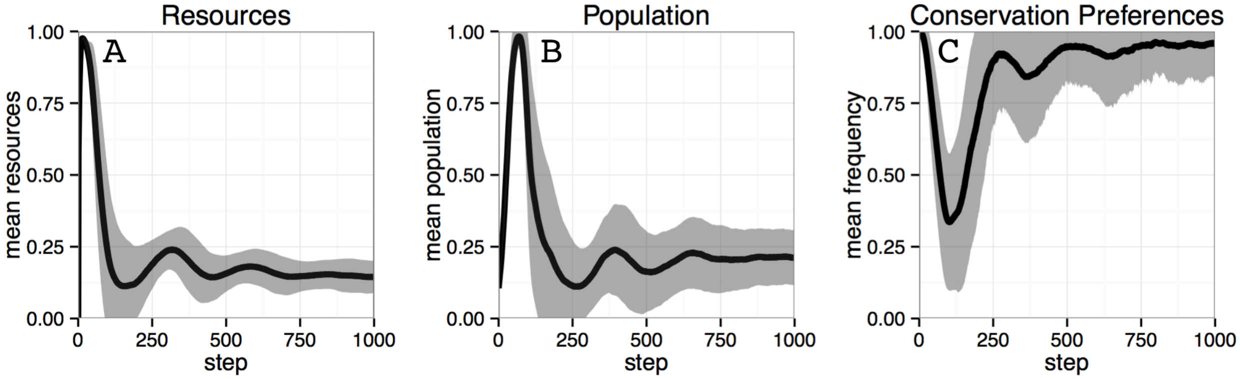


Figure 3. Simulation results across all treatments. Means for (A) proportion of maximum resources, (B) proportion of maximum population, and (C) frequency of sustainable consumption preferences with 1σ error ribbons.

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 (Figure 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 ~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 (Figure 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.

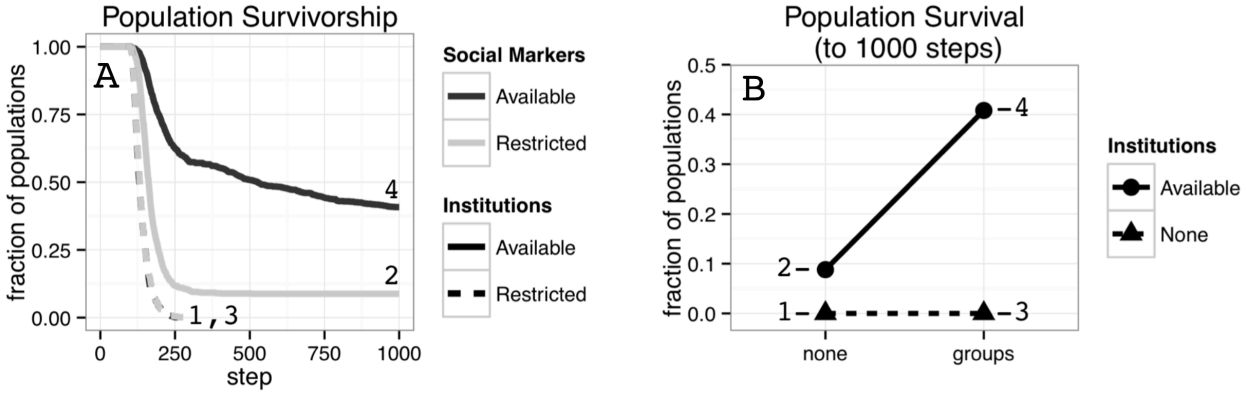


Figure 4. Population persistence over time (A) and at step 1000 (B) in treatments 1-4. Institutions prove necessary for persistence, but populations with social markers are four times more likely to survive.

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 (Figure 5). When social markers and institutions coevolve, group selection for conservation overwhelms the within-group competition selecting against conservation (Figure 5A), starting negative then growing increasingly positive over time. This demonstrates the possibility of Waring'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.

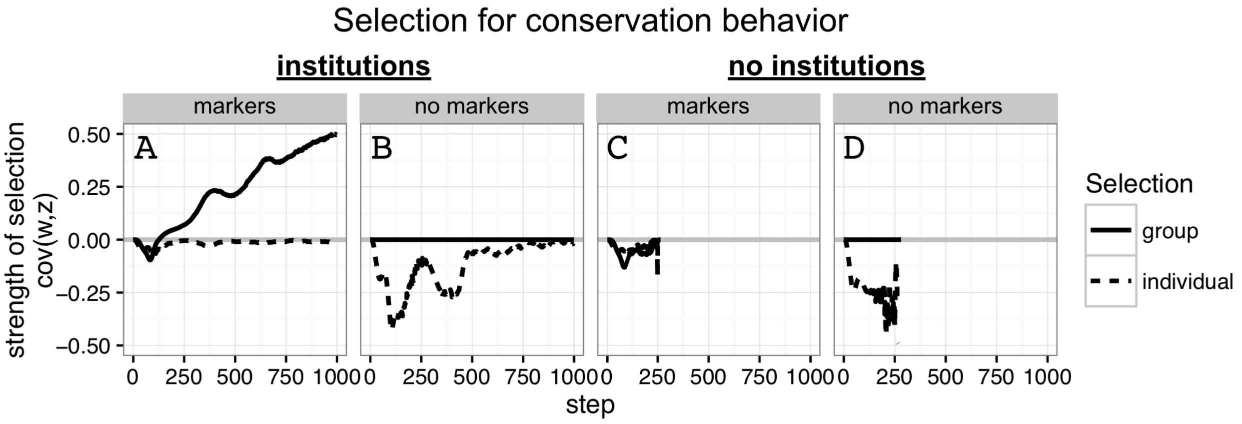


Figure 5. The average strength of selection for conservation varies over time at individual and group levels. Panes represent treatments: A=4, B=2, C=3, D=1. Group-level processes of cultural evolution select for conservation behavior and supporting institutions, driving the sustainability transition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

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. Figure 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 (Figure 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.

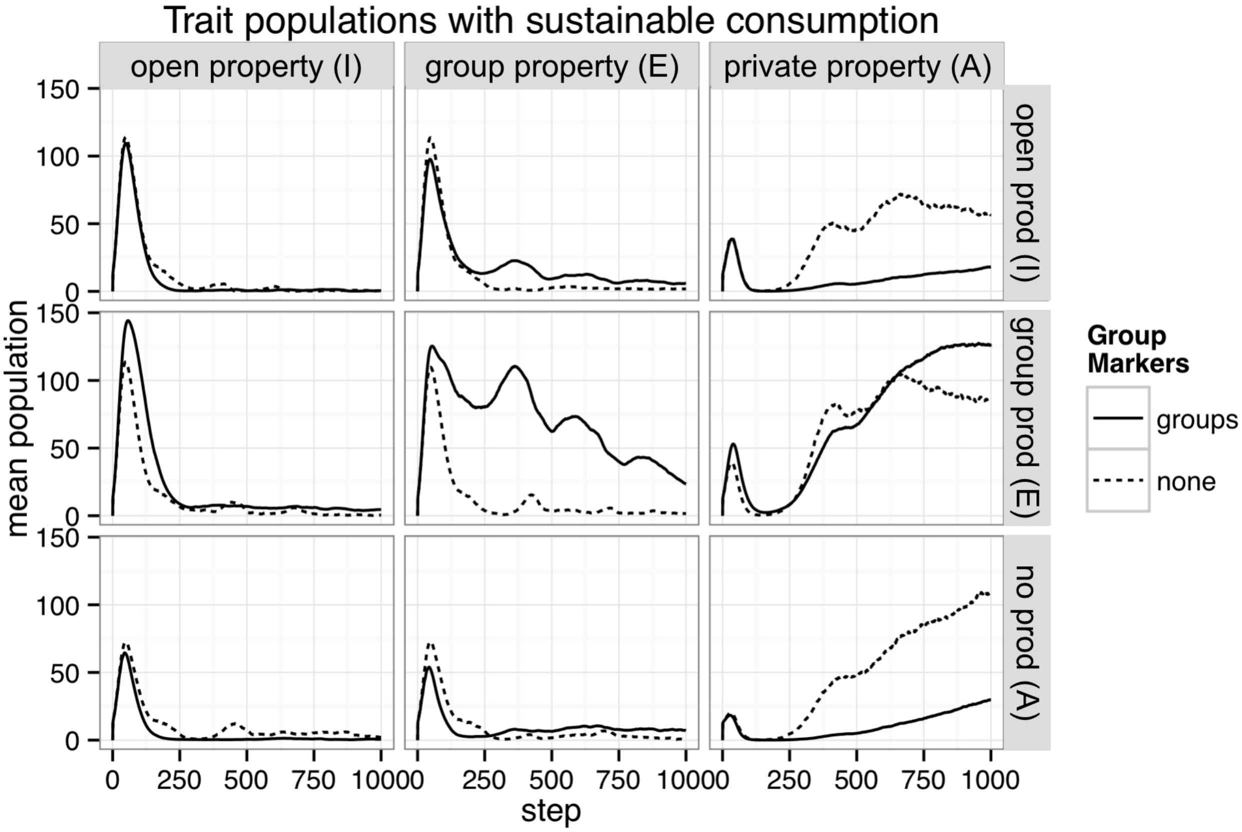


Figure 6. Mean populations of institutional norm combinations with conservation preferences across 1000 simulations in the unrestricted treatment (4, solid line), and the institutional reference treatment (2, dashed line). Norm combinations that do not include conservation preferences do not maintain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

Figure 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 be 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 appendix).

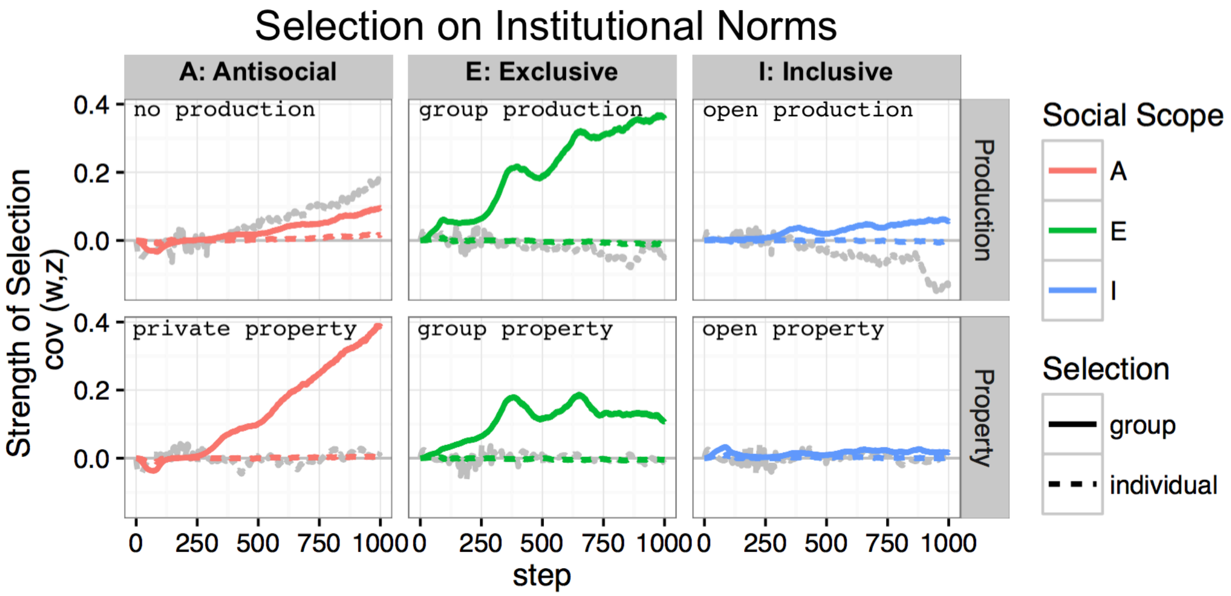


Figure 7. Group selection for exclusive property norms is stronger than individual selection. Group selection for group property rises early and is surpassed by group selection for private property in the long term. Mean values across 1000 simulations of the unrestricted treatment 4. Grey dotted lines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

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 which are selected. As we have established, the model follows a consistent pattern in which overconsumption behavior leads to a recourse collapse. In this initial phase, scramble competition for resources creates strong selection at both individual and group levels for resource consumption. 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 (Figure 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.

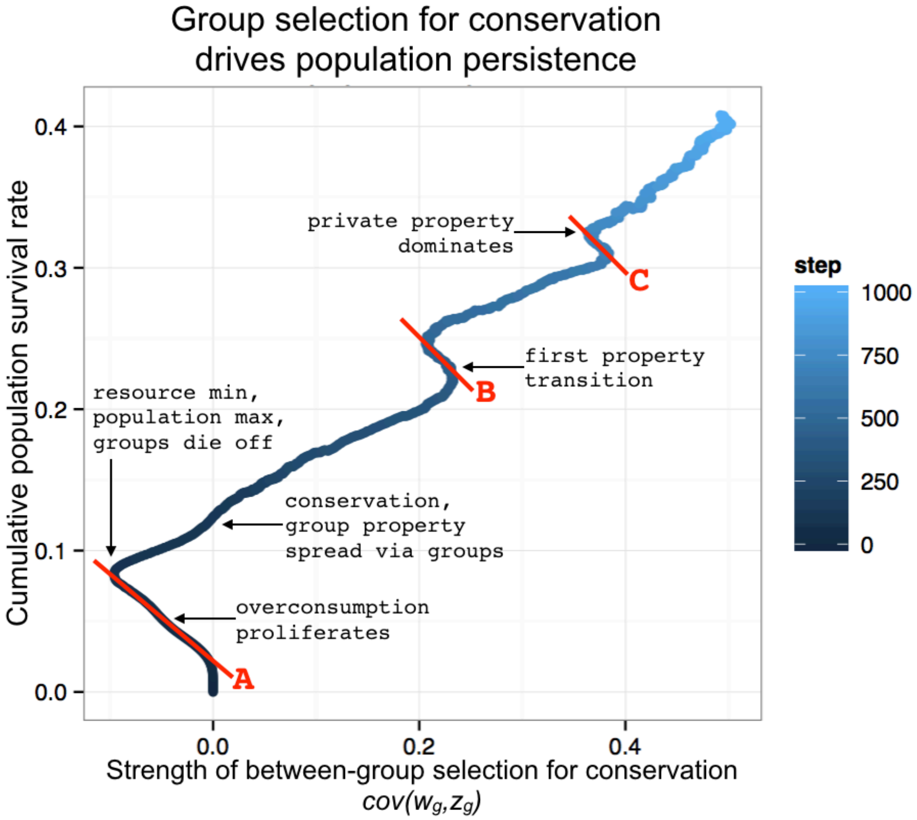


Figure 8. Cumulative rate of population persistence as a function of the strength of group selection on conservation preferences. Transitions A, B and C correspond to periods when the mode of between group competition changes from resource acquisition to survival. Transition A drives the emergence of 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.

Three hairpin bends in Figure 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 (Figure 6, center panel) as the system approaches the private property equilibrium. Therefore, our model finds that institutional evolution follows patterns observed before (Pérez & 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 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 alternative future social-ecological states and the cultural evolutionary trajectories that lead to each. 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 appear to be more likely following resource collapse or 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, although cultural group selection is a common and powerful force in human societies, but it is no panacea. Warfare may be its most forceful rapid driver. 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 over resources. Our theoretical demonstration is a first step toward explaining the emergence of durable institutions that promote sustainable behavior.

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Appendix

This appendix includes supporting documentation and analysis for the endogenous multilevel selection model of sustainable resource use institutions. This includes a robustness test of initial conditions, additional results, an extensive sensitivity analysis, and documentation in ODD format. The model is available at openabm.org/model/4627.

Table of Contents

1. Theoretical Structure

As described in the manuscript, this model presents additional layers of causation to typical social models of environmental resource use, namely social and economic feedback at the level of the group. The standard social science model suggests that environmental resources are preserved by restrained consumption, which is in turn facilitated by supporting institutions. Such a theory is incomplete as it cannot explain the existence of institutions. Evolutionary models have posited mechanisms for institutional evolution as well. The model presented here adds an additional layer to standard evolutionary models based on individual behavioral evolution, namely institutional feedback via group level economic consequences and cultural group selection (see Figure 1).

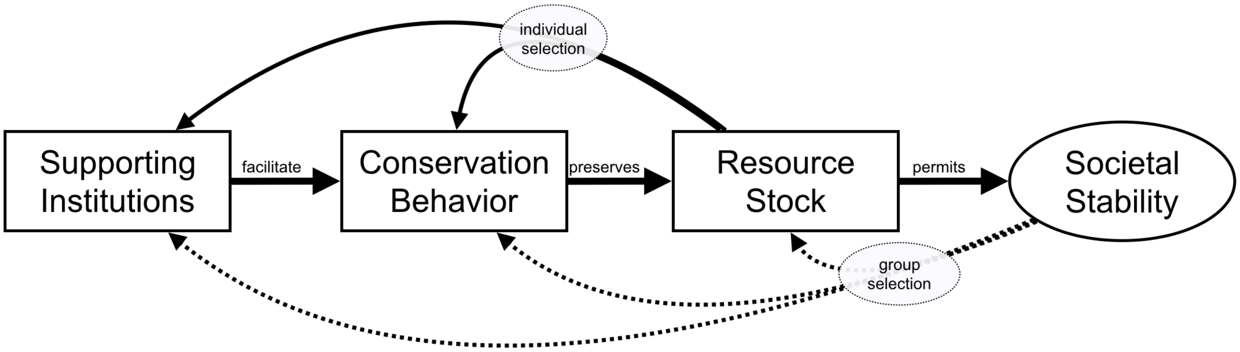


Figure 1. A conceptual model of multiple levels of social causality. Group selection may mediate the influence of societal outcomes on supporting institutions.

In addition, the majority of group selection models employ exogenous group structure, group population restrictions, or fixed group interaction mechanisms. We term this the exogenous approach to group selection models. By contrast, we employ an endogenous approach, in which groups are not represented formally in the model in any way, and can only be measured. Instead, individuals hold traits including group marker traits which allow them choose interaction partners, for instance. Social markers themselves evolve as individuals adopt them strategically from neighbors with better economic or fitness conditions. In this way our model has endogenous group formation and interactions. This method permits a measurement of the strength of selection at both individual and group levels, and reveals more information about relevant processes of institutional evolution. See Figure 2.

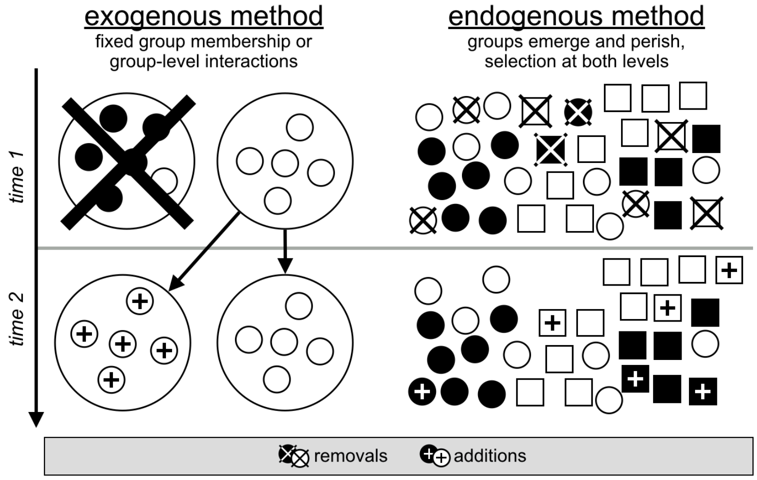


Figure 2. A graphical comparison of the endogenous and exogenous methods of modeling group selection.

Because we must measure groups to measure selection at the group level, the way in which we count groups is important. In this model, agents have spatial location and a social marker, and therefore agent groups have both social and spatial dimension, both of which change over time. As a result, groups are not perfectly definable, as you will see below. As a result, separate spatial clusters of agents may carry the same group marker, but be different in other respects. Those trait differences will matter, and may influence the survival of the individuals in each cluster. However, we use social markers to count groups, for two reasons. The first is simplicity. The second is that counting all individuals with a single social group marker is a conservative approach. Because this method undercounts the number of groups and over counts of the amount of within-group variation, it results in an overestimate of the strength of individual selection and an underestimate of the strength of group selection. Because the importance of group selection in determining outcomes is of primary theoretical interest, underestimates are more sound than overestimates.

2. Detailed Model Description

2.1. Simulation Sequence

Simulation runs proceed in discrete time steps, each of which involves the following stages. In each stage, the agent order is randomized to avoid order effects.

1. **Property.** Each agent determines how many neighbors to defend its focal patch against, according to its property norm. Costs are incurred accordingly.
2. **Harvesting.** Each agent attempts to harvest raw resources from its local commons, with its harvesting goal dictated by its harvesting norm.
3. **Production.** Each agent chooses a random neighbor. If their norms are compatible, the pair engages in cooperative production to turn their raw resources into processed resources.
4. **Survival.** Each agent incurs a resource cost for continued survival.

5. **Death.** Agents die if they have exhausted their resources or by increasing probability with age.
6. **Reproduction.** The remaining agents reproduce if they have sufficient resource stocks and if there is a vacant local patch.
7. **Migration.** Some agents move to a neighboring patch, if one is vacant.
8. **Imitation.** Some agents engage in payoff-biased imitation, copying the norms and markers of their more successful neighbors.
9. **Regrowth.** Patches replenish some of their raw resources.

2.2. Resources, Patches and Agent Traits

Interactions occur on a discrete square lattice comprised of $L \times L$ patches. Space is toroidal, so that the left and top patches border the right and bottom patches, respectively. Each patch j each contain a renewable resource, which grows according to the logistic function

$$N_{j(t+1)} = N_{j(t)} + rN_{j(t)}(1 - N_{j(t)}/\mathrm{K}) \qquad 1$$

where $N_{j(t)}$ is the resource stock on patch j, at time t, r is the maximum growth rate, and K is the patch carrying capacity. For each patch, initial resources are drawn from a random uniform distribution between 0 and K. If a patch becomes depleted (i.e., $N = 0$), it spontaneously achieves refuge-level resources, F_s with probability F_p (see Table 1). The maximum sustainable yield for a patch is therefore

$$Y^* = \frac{Kr}{4} \qquad 2$$

Patches may only be occupied by one agent at any time. Each agent i has a resource consumption preference, or harvest preference $h_i \in \{H, L\}$, where $H > Y^*$ is an unsustainable harvest preference, and $\mathrm{L} < Y^*$ is a sustainable harvest preference. As a result, the opportunity cost of a sustainable harvest preference, C_s, is the proportion of Y^* by which the high harvest preference exceeds the low harvest, such that the difference between the two harvest preferences, $H - L = C_sY^*$, and $Y^*=(H + L)/2$.

Agents may share resources with their neighbors through two types of social interaction, guided by individual behavioral norms. A property norm, p_i, determines how agents share the raw resources on the patch they occupy, and a production norm s_i, determines how they share resources they have already harvested and stored. Each norm is defined by its exclusivity, or the set of neighboring agents with whom to share: all agents (inclusive, I), group members (exclusive, E), or no agents (antisocial, A). In the case of property norms these correspond to open access (I), group property (E) and private property (A), respectively. For production, these correspond to production with anyone (I), group production (E), and no production (A), respectively. Each agent i displays its group membership via a symbolic marker trait g_i, which for convenience may take on an integer value between one and nine. Agent traits h_i, p_i, s_i, and g_i may change within an agent's lifetime through payoff-biased imitation, as well as between generations through mutation of offspring traits.

The model is initialized with groups of twelve spatially clustered agents (see Figure 4A). Each group is assigned a group marker and one of the nine possible combinations of behavioral norms, and each member of a group is initially identical. All agents are initialized with low harvesting preferences, *H*, and given stored raw resources, SR_i, chosen at random from a uniform distribution between 0 and cost of reproduction, C_R. The simulation proceeds in discrete time steps. In each step, the order in which agents are selected for action is randomized to avoid order effects.

2.3. Property, Harvest and Payoff

At the beginning of each time step agents may defend the resources in their focal patch from neighbors. Any agent in the local commons may attempt to harvest from the agent's focal patch. Agents pay a per-neighbor defense cost C_D to prevent neighbors from harvesting on their focal patch. Total defense cost is determined by the agent's property norm, p_i, indicating the set of neighbors to defend from, and the count of those neighbors in the agent's local commons. Agents then harvest from the patches in their local commons from which they have not been excluded. Note that maintaining group property, E, presents a social dilemma in two distinct ways. First, in a spatially clustered group of agents with exclusive property norms, the agents on the periphery bear the costs of defending the group property while those in the center gain the benefit defending the group resources, but pay no defense costs. Second, for an agent with total defense costs less than total harvesting potential, it will be cheaper to adopt a private property norm, stopping neighbors from harvesting on its patch, while continuing to collect from neighbor's patches. Agents harvest from patches in decreasing order of resource abundance until they meet their harvest preference, *h*, or until available resources are depleted. Agents may store raw harvested resources up to a storage limit, S_l.

Consequently, the payoff, Π_h, to harvest preference *h*, is the minimum of *h* and available resources, *R*, which is determined by the resources, R_c, in each of the 8 neighboring patches, *c*, and whether an agent on each of those patches has property norms, E_c, which exclude, $E_c=0$, or include, $E_c=1$, the focal agent. Thus, when only determined by resource access and property norms, the payoff is

$$\Pi_h = \min\left(h, R_p + \sum_{c=1}^{8} R_c E_p\right) \qquad 3$$

2.4. Production

Next, agents engage in economic production, converting harvested resources into processed resources and generating a surplus. The production process is a symmetrical dyadic public goods game. Each agent *i* chooses a random neighbor *k*. If the production norms s_i and s_k are mutually inclusive, both agents will contribute. Combinations of s_i and s_k that allow contribution are (I,I), (E,I) with same the markers, and (E,E) with the same markers. Agents contribute a fraction γ of their accumulated harvested resources to the game. If this fraction exceeds the cost of living, C_L, agents contribute their total resources minus C_L. Contributions are summed, multiplied by a factor of production, θ, and divided evenly. Note that when $1 < \theta < 2$, production constitutes a social dilemma if agents' resources are equal, but this changes when there are wealth disparities. For example, with $\theta = 1.5$, agents with contributions more than three times as large as those of their partners lose resources by participating. However, agents do not take wealth disparities into account.

2.5. Survival, death and reproduction

Next, the cost of living C_L, is deducted from each agent's resource supply. To meet the costs of living, C_L, and reproduction, C_R, agents use processed resources first and harvested resources only when their processed resources are insufficient, because consuming harvested resources directly is wasteful. Agents who are not able to pay the full cost of living die and are removed from the simulation. Agents can also die by chance with a probability of death, D_i, for an agent i increases with age, a, such that

$$\mathrm{D_i} = \frac{1}{1+e^{(80-a_i)/8}} \tag{3}$$

Next, surviving agents reproduce asexually if they have resources in excess of C_R and if there is an empty patch among their eight nearest neighboring patches (their Moore neighborhood), in which case one is chosen at random for the offspring to occupy. To ensure that high harvesting agents cannot reproduce immediately, the cost of reproduction, C_R, is equal to twice the difference between the high harvest preference and the cost of living, $2(H - C_L)$. The offspring inherits the traits of the parent each of which undergoes random mutation at rate μ.

2.6. Migration and Imitation

Agents then attempt to migrate with probability m. In this case, the agent will move to an unoccupied patch in its Moore neighborhood, assuming one exists, with the greatest current resources.

Finally, agents imitate each other. With probability λ, each agent attempts to imitate another agent with greater total resource wealth within patches with centers within radius ρ. If such an agent is found, the focal agent will copy the production and property norms, harvesting preference and marker trait of that agent, without error. If there exist more than one such agent, one will be selected at random. When $\rho = 1$, the imitation radius includes only the von Neumann neighborhood (orthogonal 4 patches), when $1<\rho<2$ the imitation radius is the Moore neighborhood (surrounding 8 patches), and when $\rho = 2$, the imitation radius includes the 12 closest patches. Complete documentation in ODD format are supplied in the appendix. The simulation was created in NetLogo (Wilensky, 2014), and is available for download and review at openabm.org/model/4627.

2.7. Benchmark Parameters

Parameter	**Description**	**Benchmark**	**Range**
Lattice size, L	Width and length of the square lattice.	32	na
Refuge size, F_s	Resource refuge level.	3	na
Refuge probability, F_p	Probability a depleted patch will regrow.	0.001	na
Initial groups, G_n	Initial number of groups.	9	na
Initial group size, G_s	Initial number of individuals in each group.	12	na
Carrying capacity, K	Maximum resources a patch can contain.	200	na
Intrinsic growth, r	Maximum resource growth rate.	0.5	[0,1]
Cost of sustainable harvest, C_s	Proportion of Y^* by which high harvest exceeds low.	1	[0,2]
Cost of living, C_L	Proportion of Y^* expended for survival every step.	0.2	[0,1]
Storage limit, S_l	Maximum resources an agent can store, applies separately to harvested and processed resources.	10^6	$[10^2, 10^6]$
Cost of defense, C_D	Per neighbor cost of defending a patch.	1	[0,10]
Production contribution, γ	Desired proportion of raw resources an agent contributes to cooperative production.	0.5	[0.1,1]
Return to production, θ	Growth rate for resources invested in cooperative production.	1.5	[1,3]
Imitation rate, λ	Per trait probability of imitation.	0.05	[0,1]
Imitation radius, ρ	Radius within which peer agents are observed for imitation.	2	[1,20]
Mutation rate, μ	Per trait probability that each trait is randomly selected during reproduction.	0.003	[0,0.1]
Migration rate, m	Probability an agent attempts to move to a neighboring patch with more resources.	0	[0,0.1]

Table 1. Benchmark parameter values used in simulation experiments, and parameter ranges tested during sensitivity analysis.

3. Robustness Tests

We also tested an alternative initialization condition. In the standard initialization procedure each of the nine groups is composed of twelve identical individuals all of whom are assigned one of the nine possible trait combinations. This condition creates strong initial between-group selection because groups are perfectly correlated with trait differences. The alternative condition is identical except that individuals are randomly mixed between groups, so that group markers were not correlated with traits. As expected, reducing initial correlation between traits and groups reduced group selection and increased the chances of population extinction. While 35% of populations survived under standard initialization, only 14% survived under randomized groups. Thus our initialization procedures favor stronger between-group selection in the early phase of the simulation. However, this result shows that group selection can occur in our model even when groups are mixed, which suggests that sustainable consumption and supporting institutions would obtain, albeit at lower frequencies. See Figure 3.

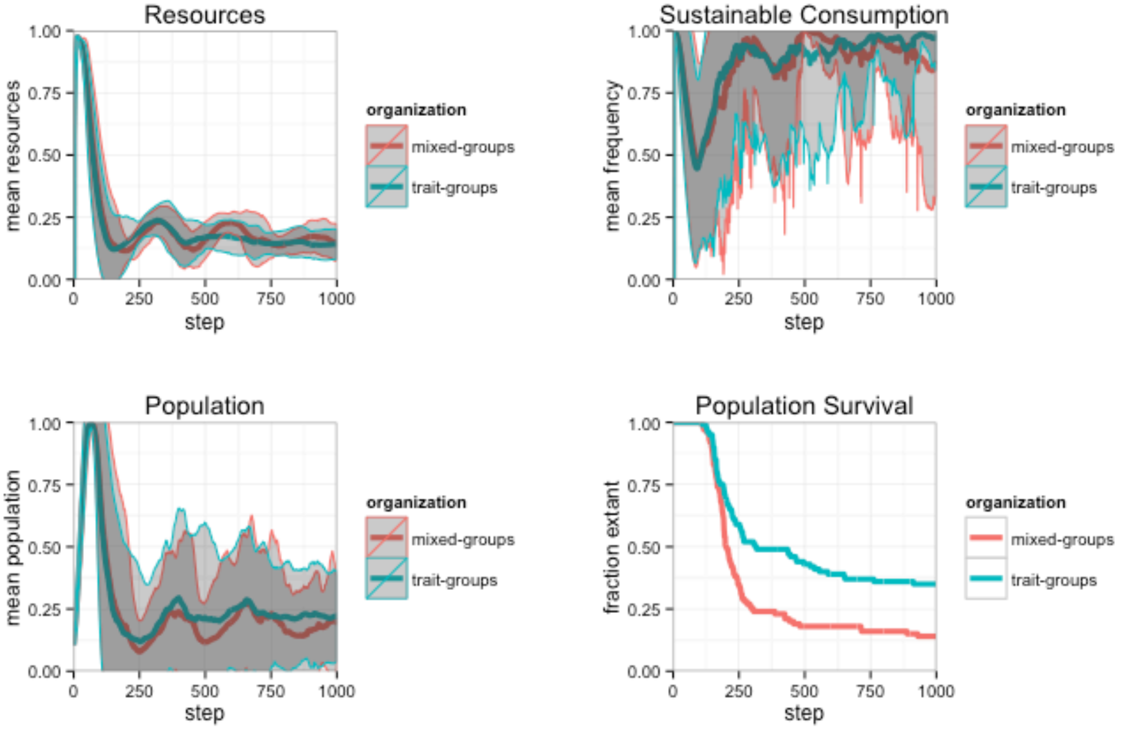
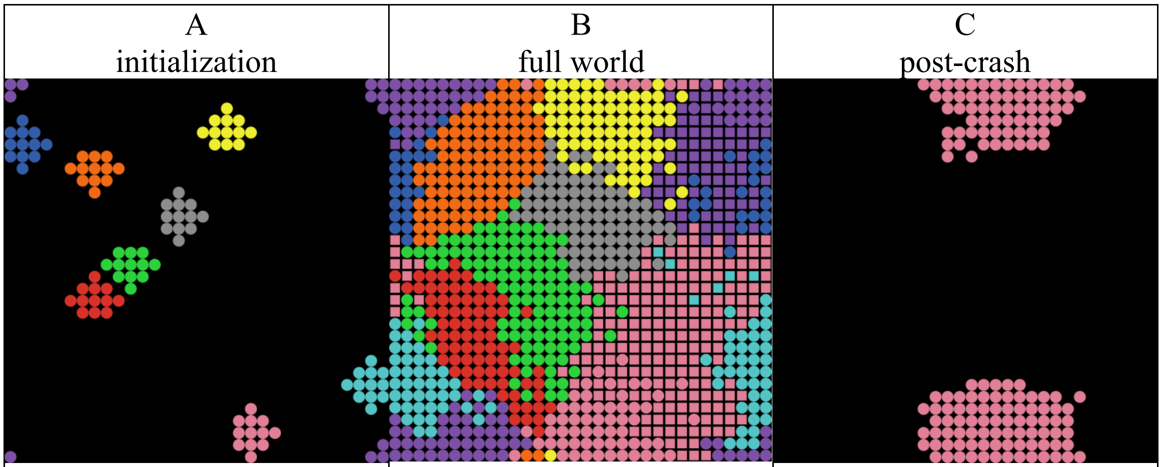


Figure 3. A robustness test reveals that our standard initialization procedure sets the stage for greater population survival than an alternative in which traits are distributed evenly among the individuals of mixed groups. In the plots the central lines represent the mean with 1σ error ribbons from 100 runs of both initialization conditions in the unrestricted treatment.

4. Additional Results

4.1. Spatial patterns

Representative spatial configurations from a run of the unrestricted treatment are supplied for reference.



A
initialization

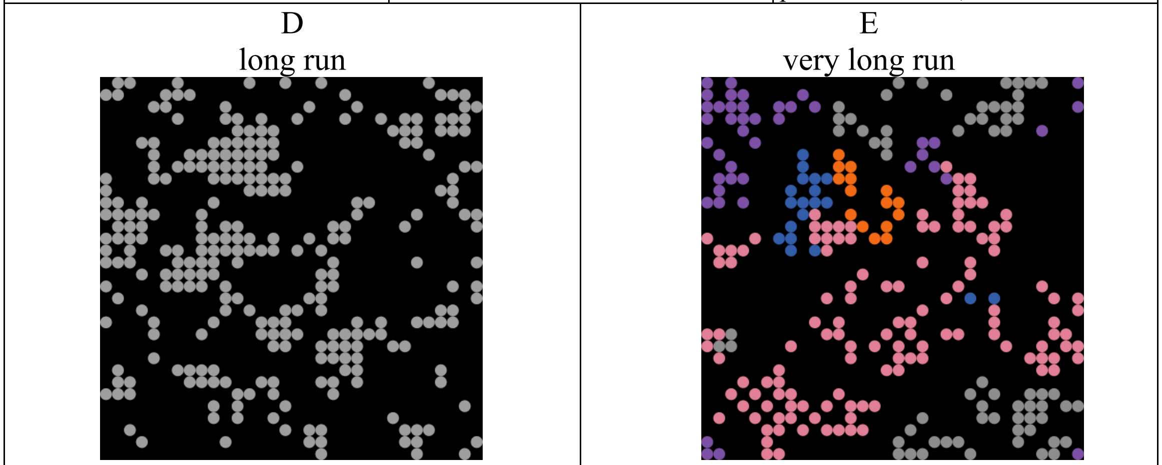
t=0, groups=9,
population=10% (108)

B
full world

t=90, groups=9,
population=100% (1024)

C
post-crash

t=158, groups=1, population=13.5%, low harvest=100%, group property=100%, group production=92%, resources = 11%



D
long run

t=1000, groups=1, population=27%, low harvest=100%, private property=100%, group production=63%, resources = 14%

E
very long run

t=10,000, groups=5, population=28%, low harvest=98.2%, private property=97.3%, no production=72%, group production=28%, resources = 16%

Figure 4. Representative spatial configurations from a run of the unrestricted treatment. Color represents group markers, dots represent individuals with sustainable harvest preferences, squares represent individuals with unsustainable harvest preferences.

4.2. Norm combinations with unsustainable preferences

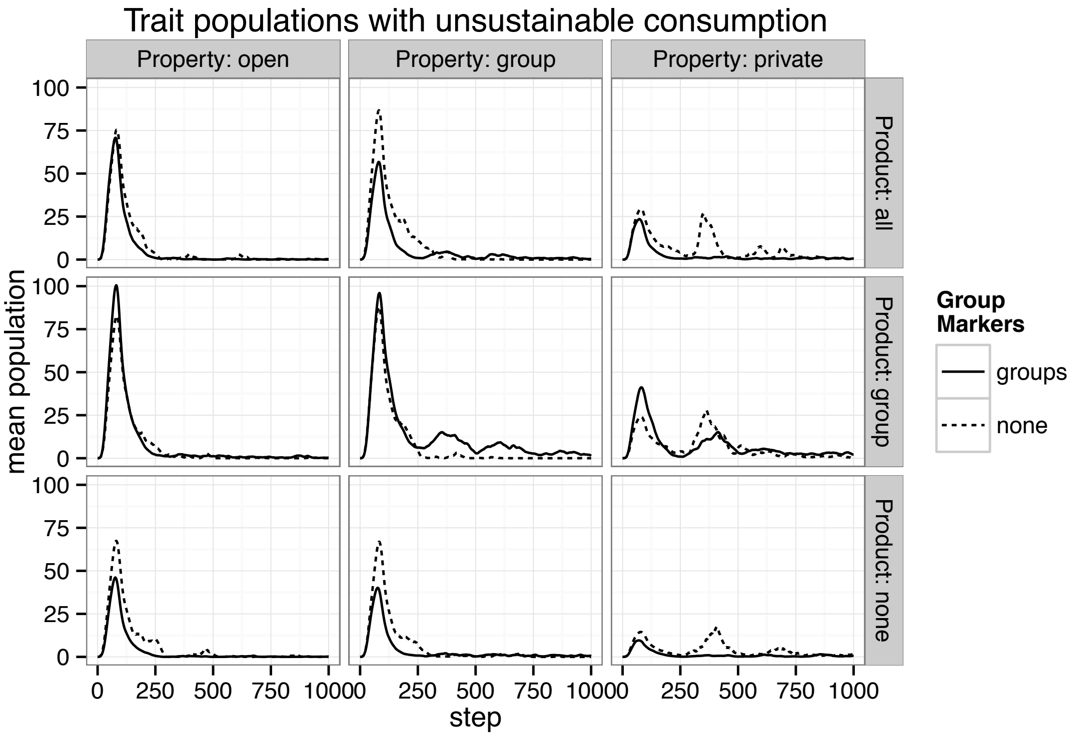


Figure 5. Mean populations of all nine possible institutional norm combinations without conservation preferences across 1000 simulations in the unrestricted treatment (4, solid line), and the institutional reference treatment (2, dashed line). Norm combinations that do not include conservation preferences do not maintain large populations.

4.3. Group selection statistics

Examining the relationship between the strength of group selection and the cumulative survival probability reveals insights about the evolutionary trajectory of each treatment.

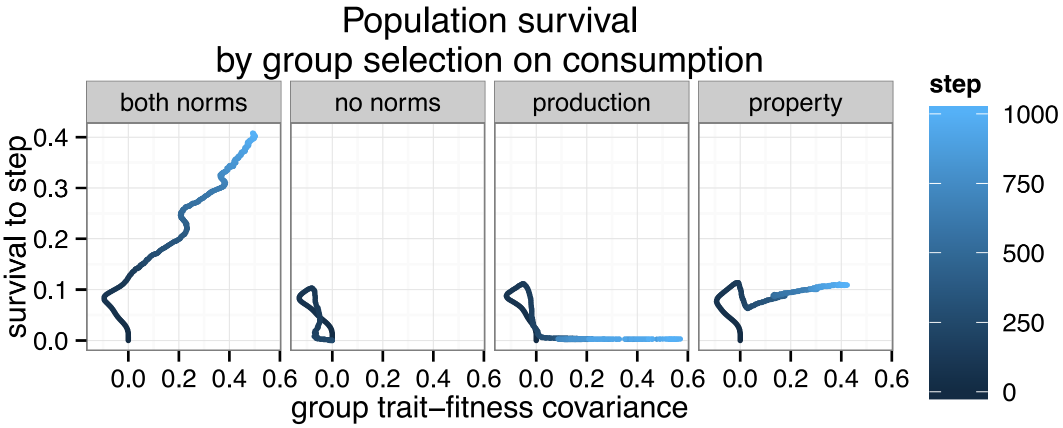


Figure 6. The treatment conditions in which the strength of group selection is correlated with cumulative survival probability are the unrestricted condition and the property condition. Lines represent the mean with of 1000 runs.

5. Sensitivity Analyses

We ran one-dimensional sensitivity analyses for eleven major parameters. These analyses test that our benchmark parameter values are reasonable when compared to their possible range. In addition, this analysis reveals what parameter changes will result in changes in the likelihood of the emergence of sustainable institutions.

We test each parameter by running 100 simulations to 1000 time steps at each of at least 10 parameter values, and examine four output currencies: resource status, sustainable consumption preferences, population size, and population persistence. We summarize these results at the end of the 1000 step simulations. Each simulation was run in the unrestricted evolution condition with the default parameter set. We plot each output indicator over the selected range of values with 95% confidence intervals except for population survival where they cannot be calculated. The vertical lines represent the default value of the parameter. We tested the eleven most influential parameters in the model. These were the parameters in Table 1 for which the Range column is specified.

For most parameters, we find that resources, population size, and sustainable consumption respond less than population survival. In essence, if a parameter influences the emergence of sustainable equilibria, it changes population persistence, but not the nature of those societies that do persist to 1000 steps. Thus, there are many opportunities to reduce the likelihood of the emergence of sustainable resource consumption and the institutions that support it. However, because we know that people can and do sometimes manage resources sustainably, we focus on the conditions that have allowed that to occur. The sensitivity analysis characterizes the larger parameter space around that explored in the paper.

5.1. Intrinsic growth, *r*

The maximum resource growth rate, *r*, is the canonical ecological growth function of a renewable resource. An *r* of 0 represents a non-renewable resource, and r=1.0 represents a doubling of the resource every step. If *r* is assumed to be a net yearly biological production of a renewable resource, then reasonable growth rates range from 0.01 to 1.

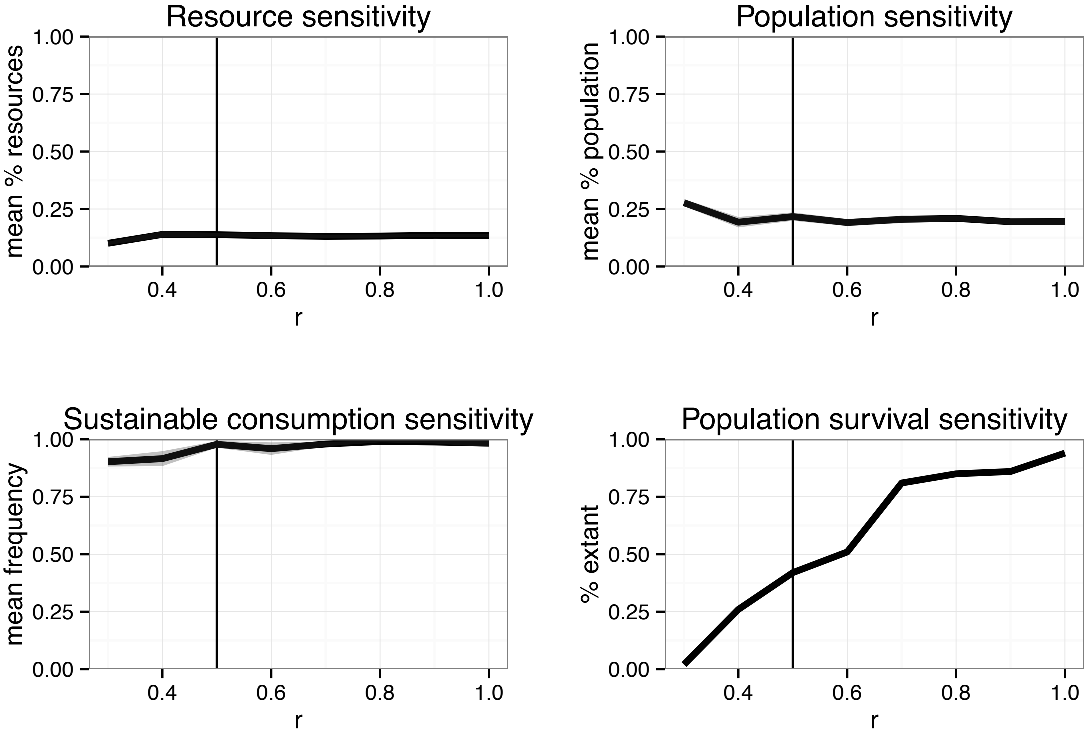


Figure 7. Model sensitivity to the intrinsic rate of resource growth. Plots of mean output currency at t=1000 with 1σ error ribbons. 100 simulations were run at each tested parameter value in the unrestricted evolution condition, using the default parameter set. Error ribbons for population survival cannot be calculated. Vertical lines represent the default value of the parameter.

Setting r=0 produces 100% responses on all variables. This is caused by a complication resulting in perfect survival rate at r=0. This unrealistic occurs because of various model parameters that are calculated based on maximum sustainable yield, *Y**. Future research interested in extremely low values of r might decouple those parameters. Here, we tested *r* from 0.3 to 1.0. Resource levels, population size and sustainable consumption were unresponsive to changes in *r*. Unsurprisingly; however, a greater growth rate allows a greater fraction of populations to persist. This occurs because even though many parameters scale with *Y**, changing *r* does not entail changing K. The benchmark value of *r* falls in the middle of the range of population survival.

5.2. Cost of sustainable harvest, C_s

The cost of sustainable harvest, C_s, is the proportion of maximum sustainable yield, *Y**, by which high harvest exceeds low, centered on *Y**. C_s ranges between 0 and 2. When C_s = 0.0 there is no difference between high and low harvesting, both types harvest *Y** exactly. A value of 2.0 corresponds to a low harvest rate of zero and a high harvest rate of 2*Y**. Both maximum and minimum values are of the parameter are not useful, so we tested the range between 0.2 and 1.4.

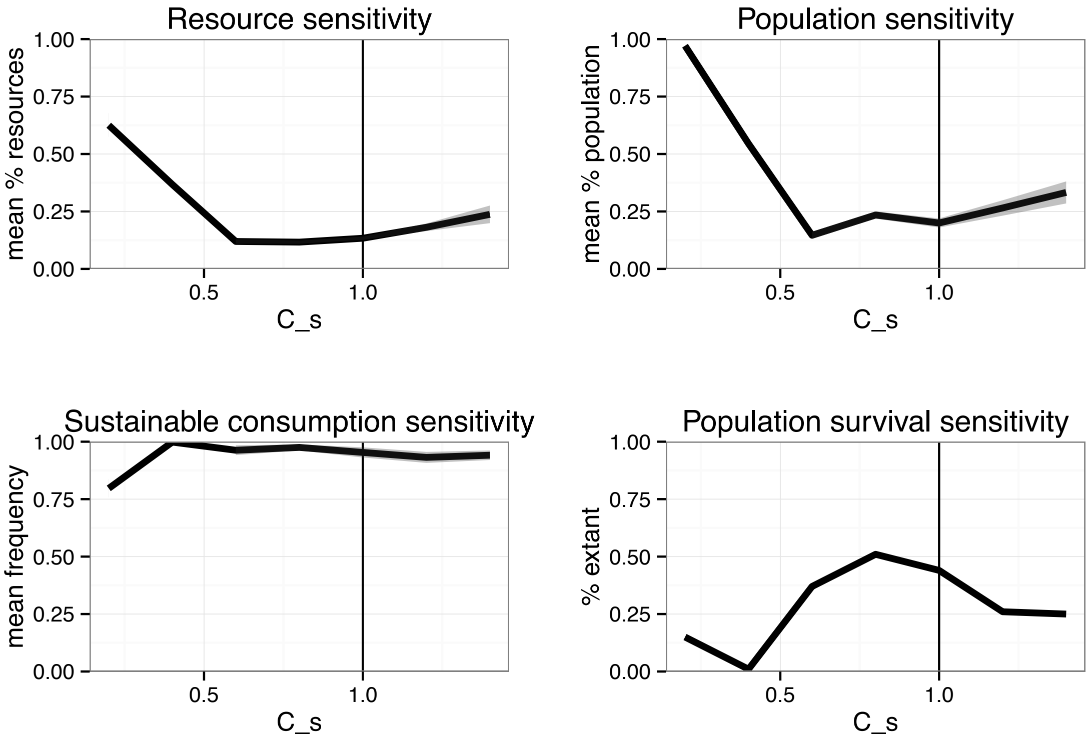


Figure 8. Model sensitivity to the cost of sustainable harvest. Plots of mean output currency at t=1000 with 1σ error ribbons. 100 simulations were run at each tested parameter value in the unrestricted evolution condition, using the default parameter set. Error ribbons for population survival cannot be calculated. Vertical lines represent the default value of the parameter.

The frequency of sustainable consumption was not sensitive to C_s. Resource levels and population size at t=1000 both declined from high values at C_s=0.2, and then increased above the benchmark value at C_s=1.0. Population survival is convex with C_s, reaching a maximum at C_s=0.8 of ~50% population survival. One explanation for this effect is that at low levels of C_s close to Y^*, the differences between the two harvest levels are small, at intermediate levels of C_s, the larger gap effectively makes high harvesters die off more rapidly aiding the emergence of sustainable outcomes, while at the levels above C_s=1, low harvests are not sufficient to sustain the agents who practice sustainable consumption.

5.3. Cost of living, C_L

The cost of living, C_L, is the proportion of Y^* an individual expends for survival every step. An C_L of 0 means that individuals can survive without any environmental consumption, while a value of 1 denotes that the entire maximum sustainable yield of a patch is required to support one individual, every time step. We tested the range between 0 and 1.

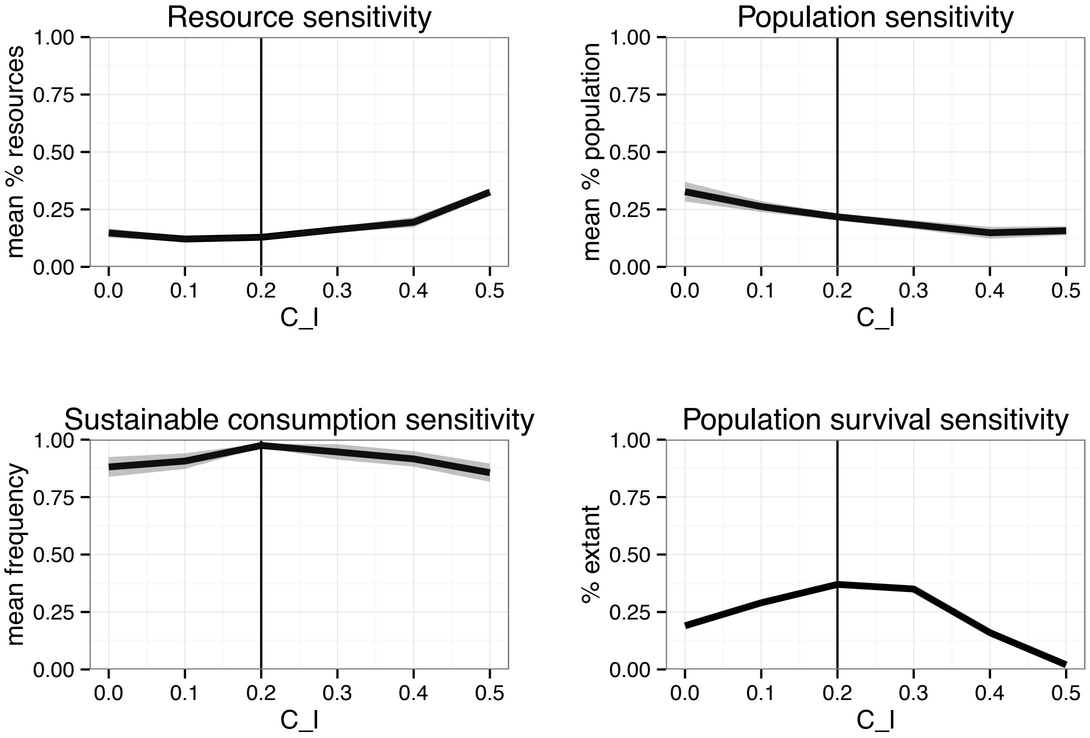


Figure 9. Model sensitivity to cost of living. Plots of mean output currency at t=1000 with 1σ error ribbons. 100 simulations were run at each tested parameter value in the unrestricted evolution condition, using the default parameter set. Error ribbons for population survival cannot be calculated. Vertical lines represent the default value of the parameter.

Although we simulated cost of living runs between 0 and 1, above $C_L = 0.5$ (cost of living = $Y^*/2$) no population survived to 1000 steps, so they are not reflected in the plots below. Interestingly, both the total population survival and the frequency of sustainable consumption were highest at our benchmark value of 0.2, although the peaks are low. These results are not surprising, however, because at a value of 0, survival is free (but consumption still continues), while at a value of 0.5, any occupied patch will be depleted in a only few steps. Thus, a concave function of population survival on cost of living is expected. Overall, an intermediate value of C_L allows higher population survival, and increasing or decreasing C_L would cause a reduction in the emergence of sustainable regimes.

5.4. Storage limit, S_l

The storage limit, S_l, is the total amount of resources an agent can hold of each of harvested and processed types. We varied S_l between 0 and 10^7, while the default value is 10^6, which allows an agent to have both 10^6 harvested resources and another 10^6 processed resource units in storage.

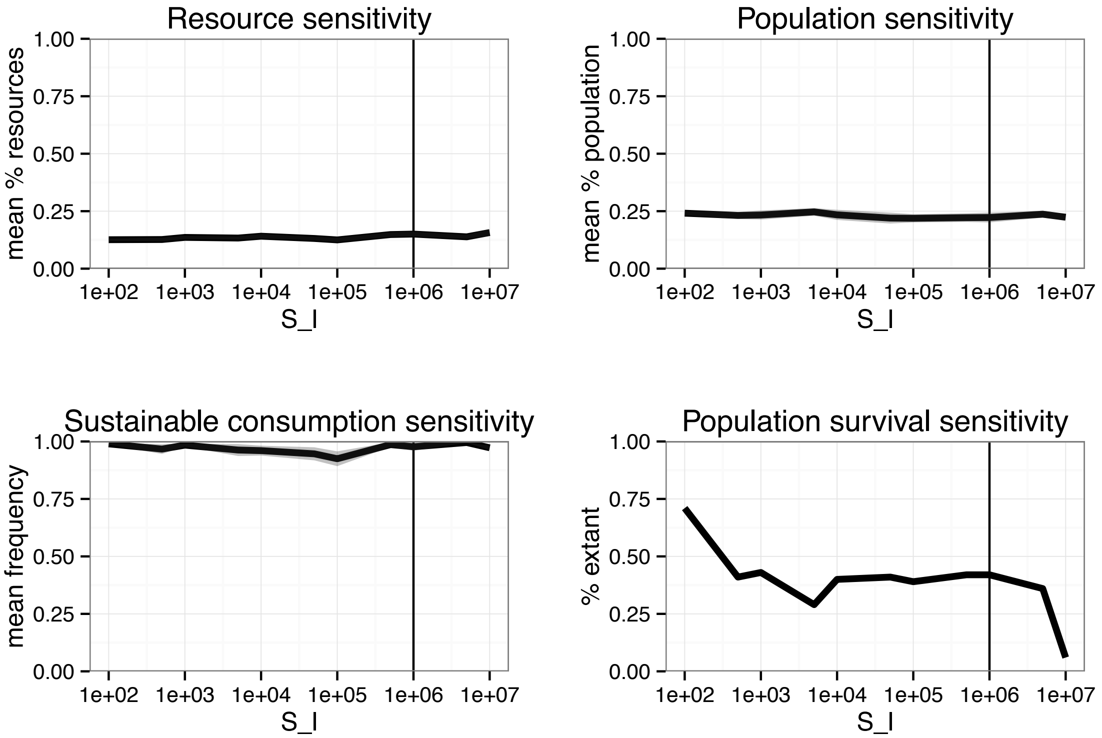


Figure 10. Model sensitivity to the storage limit. Plots of mean output currency at t=1000 with 1σ error ribbons. 100 simulations were run at each tested parameter value in the unrestricted evolution condition, using the default parameter set. Error ribbons for population survival cannot be calculated. Vertical lines represent the default value of the parameter.

The total volume of resource storage has no major impact on resources, population size, or the frequency of sustainable consumption at t=1000, but population survival declines with increasing storage capacity. Somewhat counterintuitively, sustainable populations are less likely to emerge when the individual ability to store resources is greater. This is due to the fact that greater storage levels allow individuals to survive longer without any resource input, and therefore increases the scope for unsustainable consumption. The benchmark value of $S_l=10^6$ falls within the middle of the population persistence curve.

5.5. Cost of defense, C_D

The marginal cost of defense, C_D, is the cost for an agent to prevent neighboring agents from harvesting on the patch they occupy. The total cost of defense each round will vary between 0 and $8C_D$. We varied C_D between 0 and 10.

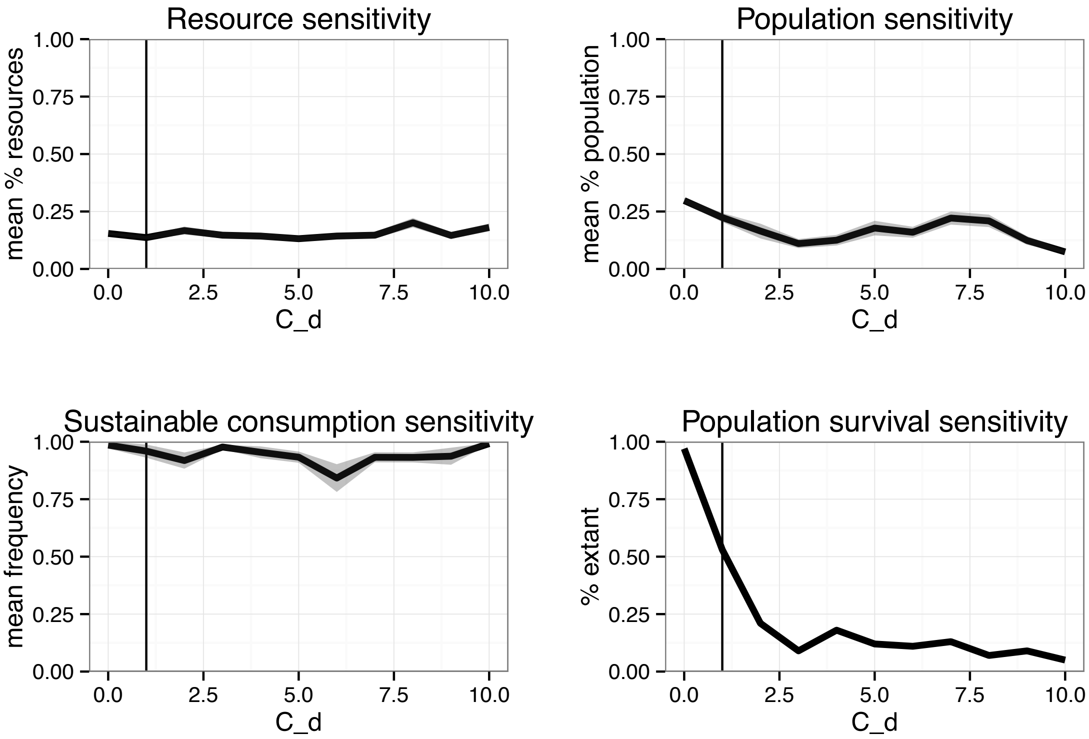


Figure 11. Model sensitivity to the cost of defense. Plots of mean output currency at $t=1000$ with 1σ error ribbons. 100 simulations were run at each tested parameter value in the unrestricted evolution condition, using the default parameter set. Error ribbons for population survival cannot be calculated. Vertical lines represent the default value of the parameter.

As with most parameters, the only outcome metric that varies substantially with the cost of defense is population persistence, which declines with increasing defense costs. This occurs because increases to defending resource productivity damage the total benefits of both group and private property regimes.

5.6. Production contribution, γ

The production contribution, γ, is the amount of harvested (unprocessed) resources an individual will attempt to contribute to cooperative production in the public goods production function. If the agent cannot contribute this amount and still have C_L left to pay for survival, then the agent pays their entire harvested resources – C_L, instead. γ can vary between 0 and 1, and the benchmark value is 0.5.

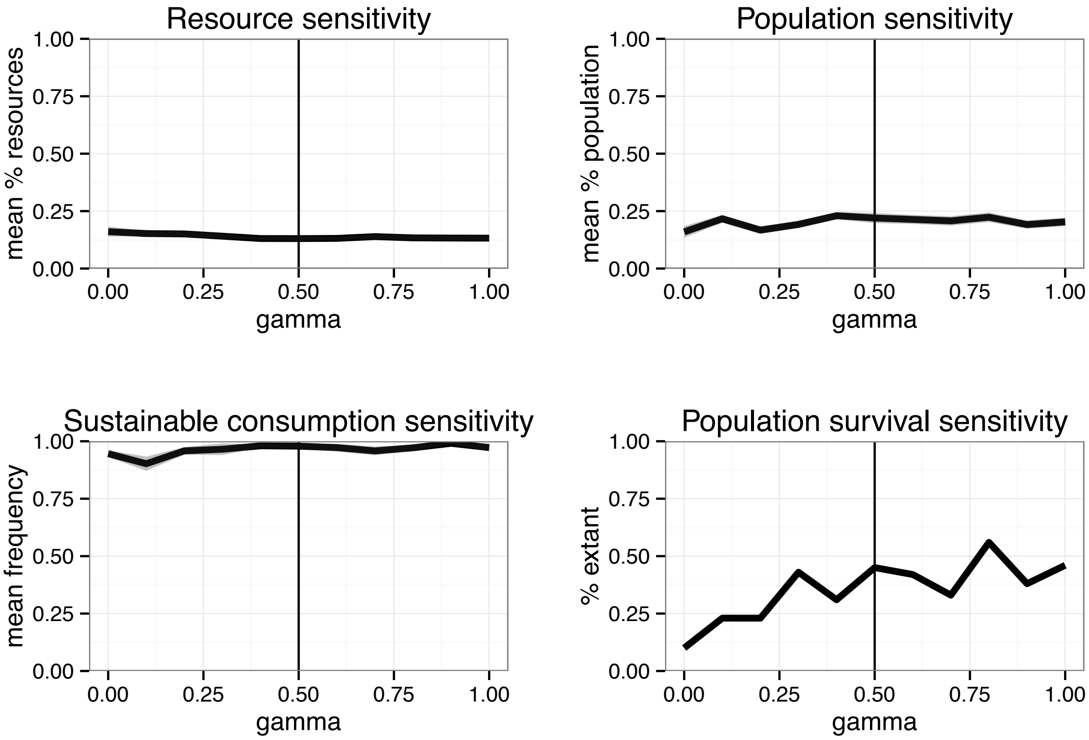


Figure 12. Model sensitivity to contribution to cooperative economic production. Plots of mean output currency at $t=1000$ with 1σ error ribbons. 100 simulations were run at each tested parameter value in the unrestricted evolution condition, using the default parameter set. Error ribbons for population survival cannot be calculated. Vertical lines represent the default value of the parameter.

Population survival increases with the sharing proportion, but other indicators do not vary much by sharing proportion.

5.7. Return to production, θ

The return to production, θ, is the return on investment in the dyadic public good interaction. We varied θ at intervals of 0.1 between 1.0 and 3.0. A θ of 1.0 represents zero return on resources invested, a value of 2.0 represents a doubling of the investment. The range of 1.0-2.0 is reasonable range of resource productivity values. We also included simulations all the way to $\theta=3.0$, which represents a tripling of invested resources.

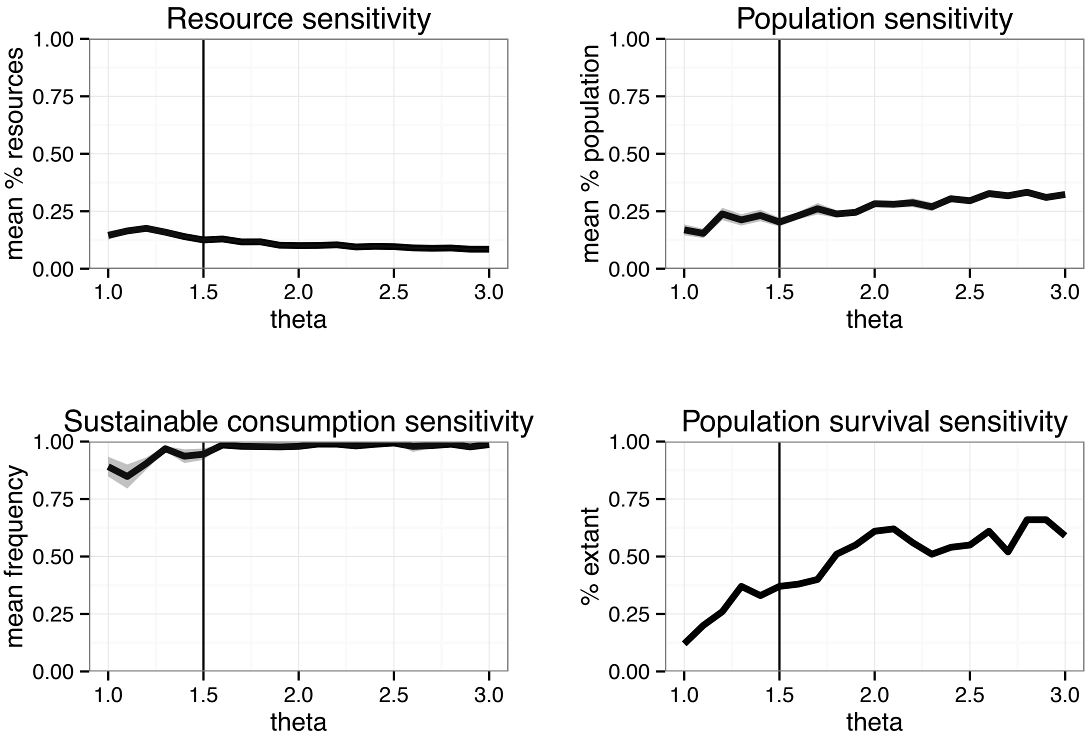


Figure 13. Model sensitivity to the return to economic production. Plots of mean output currency at t=1000 with 1σ error ribbons. 100 simulations were run at each tested parameter value in the unrestricted evolution condition, using the default parameter set. Error ribbons for population survival cannot be calculated. Vertical lines represent the default value of the parameter.

Resources, population size, and sustainable consumption do not vary dramatically with θ. Resources and sustainable consumption display almost no change over the tested parameter range, and long term population size only increases from ~20% to 30% of K. Population survival increases with θ, ranging between 15% (at θ =1) to 65% (at θ =3). Our selected value, (θ =1.5) rests in the middle of this distribution.

5.8. Imitation rate, λ

The rate of imitation, λ, is the probability that an agent will attempt to imitate a more wealthy agent within the imitation radius, ρ, per step. The imitation rate can vary naturally between 0 and 1, and the benchmark value is 0.05, and we tested the values between 0 and 0.1. The value of λ=0.1 corresponds to attempting to imitate 10% of the time.

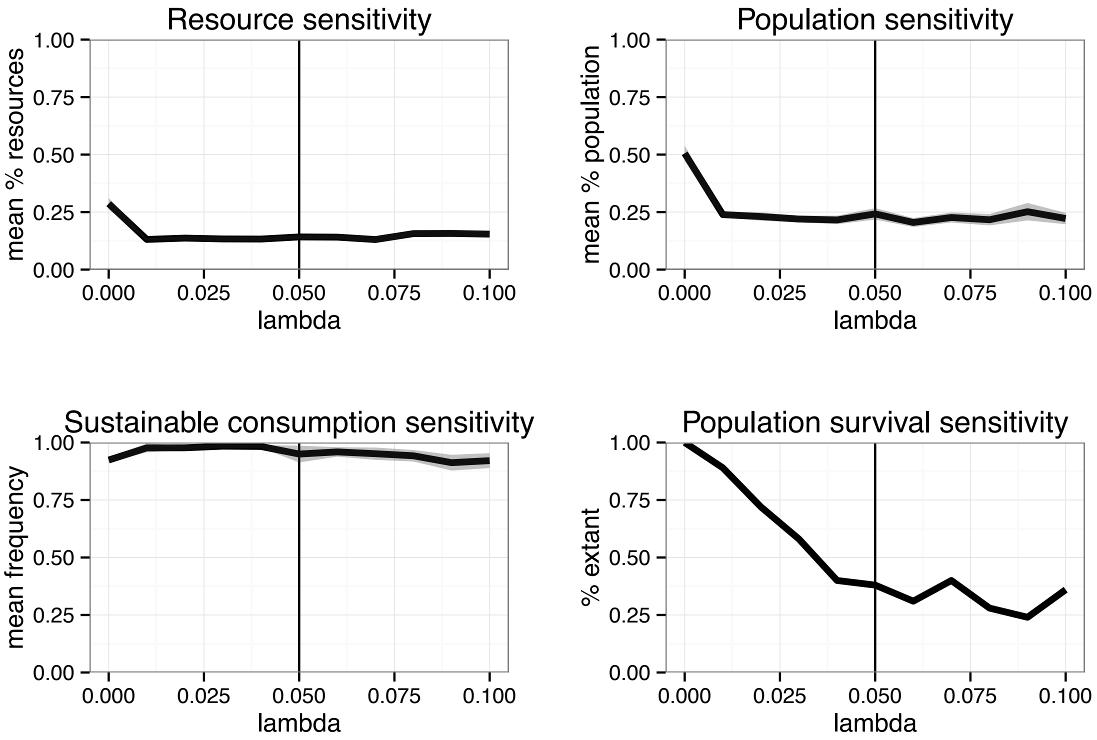


Figure 14. Model sensitivity to the imitation rate. Plots of mean output currency at t=1000 with 1σ error ribbons. 100 simulations were run at each tested parameter value in the unrestricted evolution condition, using the default parameter set. Error ribbons for population survival cannot be calculated. Vertical lines represent the default value of the parameter.

Populations survive with greater frequency as λ decreases, but the other parameters are largely unchanged over the tested range. We expect that increasing λ to 1.0 would cause a continued decline in population survival, as it would facilitate the spread of unsustainable consumption preferences that are associated with greater wealth, because the resource wealth is the cue agents use to imitate.

5.9. Imitation radius, ρ

The imitation radius, ρ, is the straight-line distance from the center of a focal agents patch to the other patches within which a patch must fall for an agent occupying that patch to be included in the population of agents that the focal agent will imitate from. This radius can vary between 0 and 24. At ρ=24, all agents can sample agents to imitate from the entire simulated world. The benchmark value of ρ = 2, which includes the agents resource commons and the next four closest patches for a total of 12 patches. The model uses payoff biased imitation, so that we should expect unsustainable consumption preferences to increase with ρ.

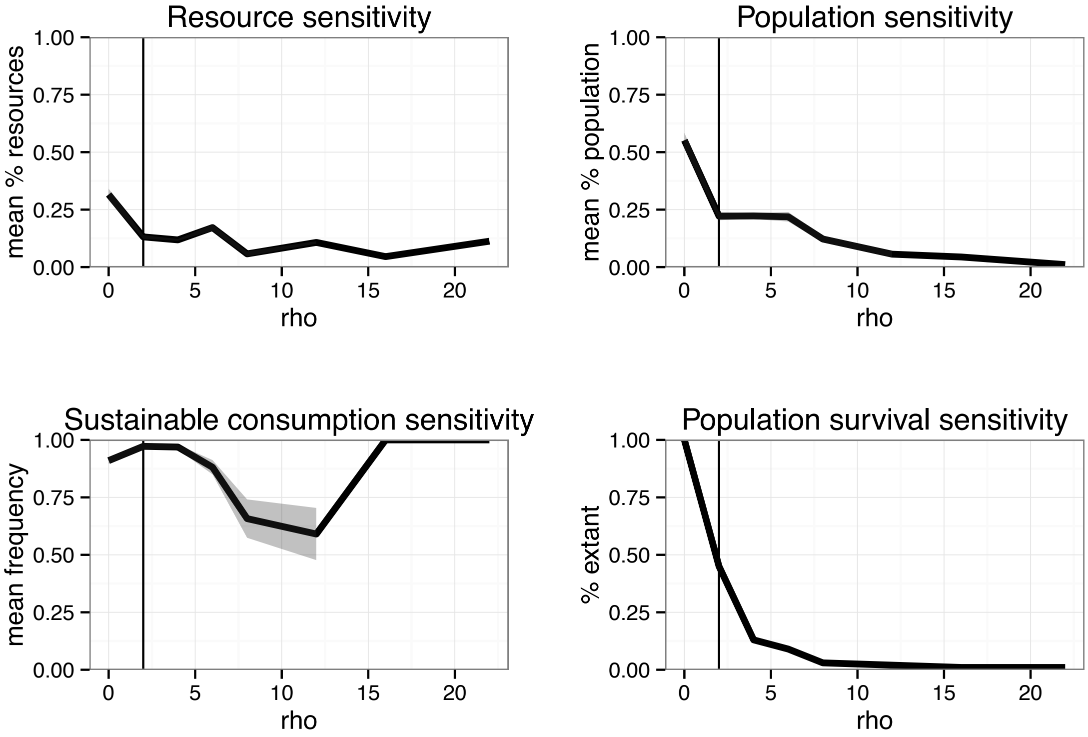


Figure 15. Model sensitivity to the imitation radius. Plots of mean output currency at t=1000 with 1σ error ribbons. 100 simulations were run at each tested parameter value in the unrestricted evolution condition, using the default parameter set. Error ribbons for population survival cannot be calculated. Vertical lines represent the default value of the parameter.

As expected, as the radius of imitation increases, resources, population size and population survival all decline. Counterintuitively, we observe a U-shaped relationship of sustainable consumption on ρ. The increase in sustainable consumption beyond ρ=12 should be taken lightly because almost no populations survive under such global imitation conditions. The benchmark value of ρ=2 creates a regime of local imitation, which suggests that local imitation is key to the group selection of sustainable resource management institutions.

5.10. Mutation rate, μ

The mutation rate, μ, is the independent rate at which each trait is mutated during reproduction. Mutation does not occur during the rest of the agent life span, while imitation does. Mutation can vary between 0 and 1, but because genetic mutation rates are low and vertical cultural transmission is more conservative, we set the benchmark mutation rate to 0.003, and tested values between μ=0 and μ=0.1.

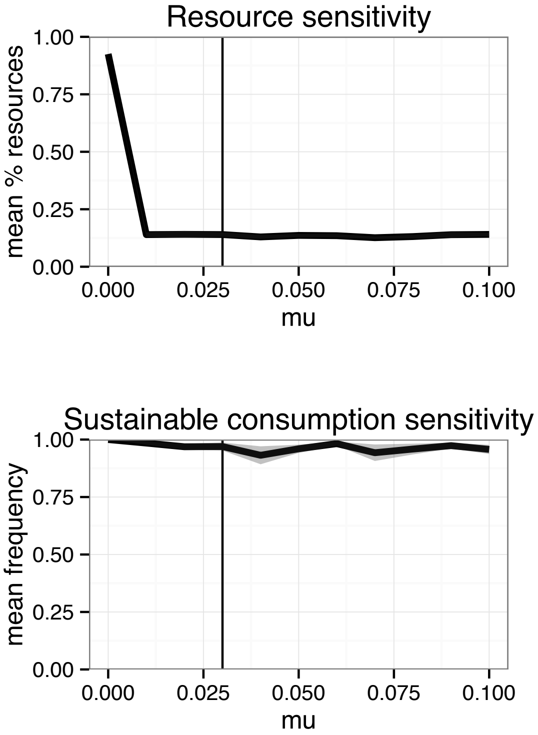


Figure 16. Model sensitivity to the mutation rate. Plots of mean output currency at t=1000 with 1σ error ribbons. 100 simulations were run at each tested parameter value in the unrestricted evolution condition, using the default parameter set. Error ribbons for population survival cannot be calculated. Vertical lines represent the default value of the parameter.

When μ=0, resources, population size and population survival all reach nearly 100%, but above that number the outcome variables decline as mutation creates a never-ending stream of resource free-riders.

5.11. Migration rate, *m*

The migration rate, *m*, is the rate at which individuals attempt to move within their local resource commons. This rate can vary between 0 and 1, and the benchmark value is 0. Sensitivity analysis shows that varying migration has no effect on any outcome parameter.

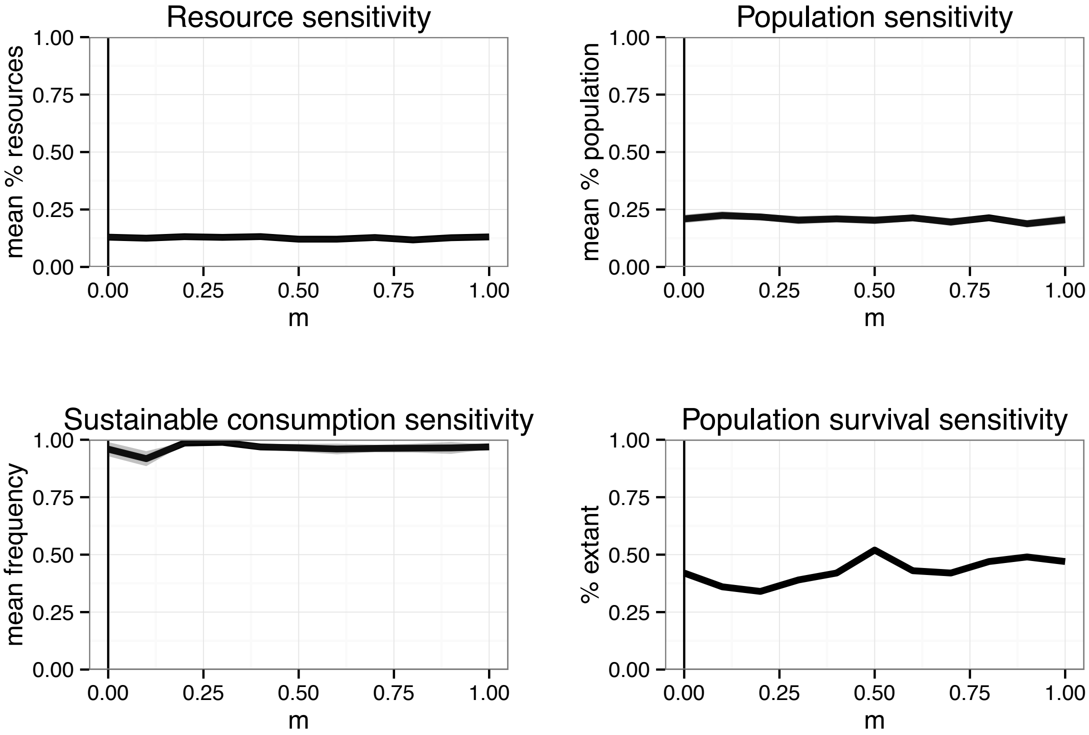


Figure 17. Model sensitivity to the migration rate. Plots of mean output currency at t=1000 with 1σ error ribbons. 100 simulations were run at each tested parameter value in the unrestricted evolution condition, using the default parameter set. Error ribbons for population survival cannot be calculated. Vertical lines represent the default value of the parameter.

6. ODD Format Documentation

6.1. Purpose

This model was constructed for the purpose of exploring the conditions under which sustainable management of a renewable and exhaustible natural resource is able to emerge within a simple society characterized by the potential for collaborative production for surplus and rudimentary group structure and mechanisms. Specifically, the model aims to simulate the emergence of key social and economic norms, including the first of Ostrom's design principles (resource use boundaries), and commonly found in successful resource management institutions. The model allows social groups and economic regimes to emerge endogenously, and proliferate when successful, and fail due to resource collapse. This evolutionary approach allows us to uncover those factors, which increase the frequency of the emergence of sustainable resource management.

6.2. Entities, state variables, and scales

Entities in the model include agents (individuals) and spatial units (patches of land). Although social groups exist, they do not act collectively, rather the agents' behavior is at times contingent upon group affiliations.

6.2.1. Agents

The agents in the model have four primary traits that govern behavior; a group maker, a harvesting preference, a property norm, and a production norm. Agents also have an identity number and a spatial location defined as the patch upon which they are standing. Agents are also characterized by their age, their lifetime reproductive success. Three resource variables are associated with agents; total resources harvested within a time step, as well as two stored-resource totals for unprocessed and processed resources. Table 1 lists the state variables and provides a brief description of each.

Agent Variable	**Description**	**Range**
Group marker, g_i	Marker that identifies agent as a member of a given social group	[1,9]
Sharing trait, s_i	Ternary trait determining agent's behavior in a pairwise sharing encounter: share with no one (A), group members (E), or all individuals (I)	A,E,I
Harvesting trait, h_i	Binary trait (*high harvesters* and *low harvesters*) determining maximum raw resources an agent attempts to harvest from its available land	H,L
Property norm, p_i	Ternary trait determining which neighboring agents an agent will defend its property (and, specifically, its harvestable resources) against: defend against no one (A), out-group members (E), or all individuals (I)	A,E,I
Agent identity, who_i	Identifier associated with the agent	positive integer
Agent location, $patch\_at_i$	Location associated with the agent as defined by the patch the agent is currently standing on	integer pair
Agent age, age_i	Number of simulation time steps the agent has survived	positive integer
Harvested amount, H_i	Running total of the amount of resource that has been harvested at a given time step	positive integer
Raw resources, r_i	Accumulated resources harvested from the land	positive integer
Processed resources, p_i	Accumulated resources produced by contributing raw resources to a cooperative process (modeled as a two-person public goods game)	positive integer
Reproductive success, rs_i	Running total of the number of offspring of an agent within its lifespan	positive integer

6.2.1. Patches

These entities have only two attributes, patch resources and patch regrowth rate. These are listed in Table 2 below along with their descriptions.

Patch Variable	**Description**	**Range**
Patch resources, $crop_j$	Amount of resource currently growing upon the patch	positive integer
Patch regrowth, pr_j	Local patch maximum intrinsic rate of growth	positive integer

6.2.2. Environment

The model has no externally varying environmental conditions.

6.2.3. Collectives

Although agents have a group identity, this group does not act as a collective. No joint decisions are made, and although social identity is shared, all actions are individual.

6.2.4. Spatial and Temporal Scales

Each grid cell or patch represents a plot of land large enough to feed a person or family. The model is a 32 x 32 torus. Each time step represents approximately one year.

6.3. Process overview and scheduling

The following provides a general version of the process overview and scheduling. For more detail regarding each of the procedures, please see the *submodels* section or the model code. At initialization, agents, patches and global variables are set up. The following process repeats every time step.

- *Patch defense*: Agents pay a cost to defend their focal patch.
- *Harvesting*: Agents harvest resources from their focal and neighboring patches.
- *Sharing*: Agents have the opportunity to produce processed resources with a neighbor.
- *Pay cost of living*: Agents lose resources in order to stay alive.
- *Death*: Agents die if their resources drop below zero or due to a random events, the probability of which increases with age.
- *Reproduction*: Agents with sufficient resources attempt to reproduce.
- *Migration*: Agents move to an empty neighboring patch.
- *Imitation*: Agents may imitate the traits of others with certain biases.
- *Patch growth*: Patch resources increase if they are below maximum.
- *Aging*: Agents grow older.
- *Cap resources*: Agents resources above a threshold are eliminated.

6.4. Design concepts

6.4.1. Basic principles

This model places a spatially-explicit ABM of the evolution of cooperation within the context of a social-ecological system. It draws upon theory regarding cooperation, commons dilemmas, group selection, and Ostrom's design principles.

6.4.2. Emergence

Spatially coherent social groups of like agents emerge endogenously. Groups that persist sometimes consist of parochial and cooperative agents who harvest at low levels.

6.4.3. Adaptation

Agents adapt at genetically and culturally. Agents have a simple 4 locus ‘behaviorome’ [harvest, group, property, production]. In the genetic portion, mutation of all these traits occurs with a given probability at reproduction. Death and differential reproduction then create selection and adaptation on these loci over time. In the cultural portion, agents adapt every round through a process of payoff-biased imitation.

6.4.4. Objective

Agents have a harvest preference that they attempt to satisfy. Beyond that, agents do not have internalized goal states, or encoded objectives.

6.4.5. Learning

There is no learning in this model.

6.4.6. Prediction

There is no prediction in this model.

6.4.7. Sensing

Agents observe the group markers, wealth, and traits of the other agents in their Moore neighborhood and within the imitation radius of their patch. Agents observe these variables perfectly, but only do during the model routine. Agents are also able to sense the amount of resource on their current patch as well as the amount of resource on neighboring patches.

6.4.8. Interaction

Agents interact with patches by harvesting resources. Agents both compete and cooperate. Agents interact with other agents through defense of their patch, engagement in cooperative production, reproduction and imitation.

6.4.9. Stochasticity

There is stochasticity in the initialization of patch resources, in the placement of the initial agents, in the assignment of traits to agents, in migration, imitation, and mutation of offspring traits, and in all probabilistic procedures.

6.4.10. Collectives

Each agent interaction for the purposes of economic production can be seen as a brief collective in that the payoff received from the public goods game is dependent upon the participation of both actors and is split between the two parties. The collective then splits at the end of the round. Alternatively socially marked groups can be seen as collectives, with common social marking, and sometimes common production or harvesting traits. However, these collectives do not perform collective behaviors *per se*.

Observation

We collected population size, frequency of low harvest norm, frequencies of each production norm, frequencies of each property norm, number of groups, mean individual conservation-fitness covariance, and group conservation-fitness covariance by timestep. Agents do not observe or sample the world.

6.5. 5. Initialization

- The model world is initialized with nine groups of 12 agents each. Groups are located randomly on the 32x32 patch grid. All individuals begin the simulations with the conservative harvesting trait.
- The global parameters, listed in Table 1, are set at model initialization. The values at which they are set within the model are detailed in section eight, Simulation experiments/model analysis.

6.6. Input data

This theoretical model does not require any input data.

6.7. Submodels

Beyond model procedures, no submodels exist in this model. See the model description for an overview of the procedures, and the model code for the procedures themselves.