

LETTER

The co-evolution of social institutions, demography, and large-scale human cooperation

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Abstract

Human cooperation is typically coordinated by institutions, which determine the outcome structure of the social interactions individuals engage in. Explaining the Neolithic transition from small- to large-scale societies involves understanding how these institutions co-evolve with demography. We study this using a demographically explicit model of institution formation in a patch-structured population. Each patch supports both social and asocial niches. Social individuals create an institution, at a cost to themselves, by negotiating how much of the costly public good provided by cooperators is invested into sanctioning defectors. The remainder of their public good is invested in technology that increases carrying capacity, such as irrigation systems. We show that social individuals can invade a population of asocials, and form institutions that support high levels of cooperation. We then demonstrate conditions where the co-evolution of cooperation, institutions, and demographic carrying capacity creates a transition from small- to large-scale social groups.

Keywords

Agriculture, cooperation, institutions, irrigation, large-scale societies, Neolithic Demographic Transition, punishment, tragedy of the commons.

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INTRODUCTION

Understanding the origin of large-scale human societies is of interest to both the social and biological sciences. For many millennia humans lived in small-scale hunter-gatherer societies, engaging in localised cooperative interactions such as hunting and food sharing (Boehm 1999; Kaplan *et al.* 2009; Whiten & Erdal 2012). Much work has addressed how cooperation could evolve under natural selection in such small-scale societies. Mechanisms for this include kin discrimination (Hamilton 1975; Dawkins 1976), direct and indirect reciprocity (Trivers 1971; Nowak & Sigmund 2005), punishment of defectors (Oliver 1980; Boyd & Richerson 1992), and cultural group selection (Boyd & Richerson 1990; Turchin 2010).

Models of these mechanisms, however, usually assume that the choice of actions by group members are uncoordinated. That is, each individual decides in isolation whether to cooperate or not, whether and who to punish, etc. While the extent to which hunter-gatherer groups meet the assumption of entirely uncoordinated social decisions has been questioned (Boyd *et al.* 2010; Whiten & Erdal 2012; Guala 2012), this assumption becomes even more problematic when attempting to explain the origin of large-scale societies. This is because post-hunter-gatherer groups engage in social behaviours that affect a large number of individuals, and which require some degree of coordination and planning; clear examples include the construction of irrigation channels, trade links, and fortifications. In particular, human groups typically have various institutions that help to coordinate social interactions and diffuse social dilemmas (Ostrom 1990; North 1990; Hurwicz 1996; Turchin 2003; Guala 2012). A key question is then: how can cooperation-promoting institutions co-evolve with demography to create a transition from small- to large-scale social groups? Addressing this provides an understanding of the role of social evolution in the Neolithic Demographic Transition and the origin of agricultural societies.

We study this here using a model of the cultural co-evolution of social institutions and demography. By ‘institution’, we follow the game theoretic definition in which an institution represents a set of game forms (Hurwicz 1996). That is, an institution is a set of alternative rules (‘rules of the game’) that determines the outcomes of the social interactions individuals engage in (e.g. different possible distributions of material resources). The particular institutional rules that will be implemented are then selected from this set. Humans need not remain trapped in a prisoner’s dilemma situation, but rather they may form an institution and communicate with each other such as to agree upon rules that transform the game structure into one where cooperation may be a stable equilibrium (Ostrom 1990; Ostrom & Gardner 1993).

Real-world examples of this process are provided by the self-organised management of irrigation systems (Hunt 1988; Trawick 2001; Janssen *et al.* 2012), where rules devised and enforced by the resource users themselves can prevent a tragedy of the commons (Hardin 1968) in water usage. For example, institutional rules might specify how much water may be taken and when, as in the 600-year-old self-managed *buerta* irrigation systems in Valencia, Murcia, and Alicante (Ostrom 1990). Rules may also specify how often individuals should contribute to construction and maintenance of the system, as in the *zanjira* irrigation systems in the Philippines (Ostrom 1990). In both cases, the institutional rules are created by a peer assembly of group members, and are enforced through both peer monitoring and the creation of formal guard roles that are funded from the irrigator’s common resources. These examples illustrate that cooperation-promoting institutions do not have to be coercively imposed by a dominant leader, as has been assumed in some recent evolutionary models (e.g. Hooper *et al.* 2010; Isakov & Rand 2011; Sasaki *et al.* 2012). Moreover, as examples of the institutionalised regulation of irrigation systems, they are of direct relevance to the origin of agricultural societies (Carballo 2013).

We consider a scenario in which individuals can voluntarily choose to take part in a social activity, and create institutional rules to regulate it. These individuals compete with asocials who choose not to take part in, or benefit from, the social activity, and whose pay-offs are not affected by the institutional rules and the cost of their formation (these individuals are asocial in the sense of not joining the institution; they could still have other social interactions such as consumption of shared resources within groups). The particular case that we consider is the option to engage in the cooperative development and usage of agricultural technology, as exemplified by an irrigation system. This technology provides a benefit to those that produce it, by increasing their yield. Through the resulting increase in carrying capacity, the development of such technology is thought to have been a driver of the transition from small-scale nomadic to larger scale sedentary societies (Spencer 1993; Carballo *et al.* 2012).

We model the technology as a partly excludible good; asocial individuals who do not take part in its production are not able to benefit from it. However, amongst social individuals who choose to participate, there is the opportunity for free-riding. Social individuals then play a two-stage game. In the first stage, the institution is formed and individuals determine how much of their common resources (a fraction $1-b$) should be used to monitor and sanction free-riding defectors – this is the formation of institutional rules governing the social activity. The remainder of their common resources (b) are invested in production of the technology. We assume that all social individuals pay a cost to form the institution, which represents the time and effort spent creating the institutional rules. In the second stage of the game, after the sanctioning rules have been agreed upon, social individuals play a public goods game. Defectors are then sanctioned according to the institutional rules agreed in the first stage.

We demonstrate here that the co-evolution of institution formation, cooperation, and demography in such a setting can provide an explanation of the transition from small- to large-scale societies.

THE MODEL

Life cycle and population structure

We consider a population that is subdivided into a finite number N_p of resource patches or sites (Wright's 1931 finite island model of dispersal). The life cycle consists of discrete and non-overlapping generations, as follows. (1) Local interactions occur on each patch, with social individuals forming an institution. (2) Each individual on a patch has a Poisson distributed number of offspring who survive to adulthood, with the mean of the distribution being determined by the local social interactions and resource abundance (defined explicitly below). (3) Adults of the previous generation perish. (4) Each individual of the descendant generation either remains on its local patch (with probability $1-m$) or disperses to a randomly chosen patch (excluding the natal one).

Individuals in this population carry two cultural traits that are transmitted vertically from parents to offspring – an important mode of cultural transmission in extant hunter-gatherer groups (Hewlett *et al.* 2011), and one which parallels genetic transmission (Cavalli-Sforza & Feldman 1981). The first trait determines the social behaviour of individuals. Specifically, whether the individual joins an institution and contributes to the public good (is a cooperator), joins an institution but does not contribute (is a defector) or remains outside

of an institution and hence receives no public good or sanctioning (is asocial). A mutation (or innovation) on this trait changes the value to one of the other two variants chosen at random. The second trait is a continuous number b varying between 0 and 1, which is interpreted phenotypically as the proportion of public good that the bearer would like its group to invest in helping as opposed to sanctioning. Asocials carry this trait but do not express it, as they do not participate in institution formation. A mutation on this trait changes the value according to a truncated normally distributed random variable (with variance σ), centred around the current trait value. The probability that an offspring undergoes a mutation is μ , in which case one of the two traits sampled at random is mutated.

How the institution affects reproduction

Fitness

The expected number $w_{\tau j}(t)$ of offspring who survives to adulthood (fitness) produced by an individual of type $\tau \in \{a, c, d\}$ (asocial, cooperator, and defector respectively) in patch j at time t is assumed to follow a Beverton–Holt model (e.g. Chow & Hsieh 2013) with two niches. Specifically, cooperators and defectors (socials) on a patch occupy a social niche in which they can improve their environment through cooperative investment in technology. Asocials do not take part in or benefit from this activity, and hence occupy a different ecological niche. An example would be a horticultural rather than agricultural mode of subsistence (Kaplan *et al.* 2009). The degree of competition between these niches is set by two parameters, α_{as} and α_{sa} , which give the per capita effect of socials on asocials' fitness and asocials on socials' fitness respectively. According to these assumptions, we write the fitnesses of the three types on patch j at time t as

$$\begin{aligned} w_{aj}(t) &= \frac{r_a}{1 + n_{aj}(t)/K_a + \alpha_{as}[n_{cj}(t) + n_{dj}(t)]} \\ w_{cj}(t) &= \frac{r_c}{1 + [n_{cj}(t) + n_{dj}(t)]/K_{sj}(t) + \alpha_{sa}n_{aj}(t)} \\ w_{dj}(t) &= \frac{r_{dj}(t)}{1 + [n_{cj}(t) + n_{dj}(t)]/K_{sj}(t) + \alpha_{sa}n_{aj}(t)}, \end{aligned} \quad (1)$$

where $n_{\tau j}(t)$ is the number of individuals of type τ on patch j at time t . The numerator in each expression can be thought of as the maximal growth rate of an individual of the corresponding type, whereas the denominator as the intensity of density-dependent competition faced by that individual. We now detail the parameters in these expressions.

Growth rate and sanctioning

First, $r_a (\geq 0)$ is the maximal growth rate of an asocial type. Namely its growth rate in the absence of density dependence, which occurs when the denominator of $w_{aj}(t)$ is equal to one. The maximal growth rate of a cooperator is assumed to be given by

$$r_c = r_a - I - C, \quad (2)$$

where $I (\geq 0)$ is the cost of participating in institution formation, whereas $C (\geq 0)$ is the individual cost of producing an amount B of public good. This entails that an amount $n_{cj}(t)B$ of public good is created on patch j by cooperators, which can be devoted to resource enhancement or sanctioning. Social defectors participate in institution formation but do not contribute to the public good, and

can be sanctioned for this. We assume that the maximal growth rate of a defector is

$$r_{dj}(t) = r_a - I - \frac{[1 - b_j(t)]n_{cj}(t)B}{n_{dj}(t)}, \quad (3)$$

where $1 - b_j(t)$ is the proportion of the public good produced on patch j devoted to sanctioning. We assume that this fraction of the public good is used for two purposes: first, to fund a monitoring and sanctioning system, and second, to incentivise monitoring behaviour by providing direct benefits to individuals who actively monitor. We provide empirical examples of such a set-up in the *Discussion* section, but we do not explicitly model at the micro-level the monitoring and sanctioning actions that take place after an institution has been formed (see Weissing & Ostrom 2000 for such a model). Instead, our focus is on the selection pressures that population structure and demography exert on institutional forms.

Given these assumptions, $[1 - b_j(t)]n_{cj}B/n_{dj}(t)$ represents the per capita cost of being sanctioned for defecting. The value of $b_j(t)$ in our model is set by an aggregation rule, as is standard in social choice theory (Conradt & List 2009). This is a function that transforms a collection of individual preferences into a group's decision, and represents a functional abstraction of the communication and negotiation process between social individuals on a patch. This type of functional abstraction is often used in models of decision making in animal social groups (Conradt & Roper 2003; Conradt & List 2009), where the effects of the outcome of the decision-making process on fitness are of more evolutionary interest than the proximate behavioural mechanisms underlying it. We first consider the case where $b_j(t)$ is set by the mean preference of social individuals on patch j :

$$b_j(t) = \frac{1}{n_{cj}(t) + n_{dj}(t)} \sum_{i=1}^{n_j(t)} s_{ij}(t) b_{ij}(t), \quad (4)$$

where $s_{ij}(t) = 1$ if individual i on patch j is a cooperator or defector (i.e. a 'social'), $s_{ij}(t) = 0$ otherwise, $b_{ij}(t)$ is the preference of individual i on patch j at time t and $n_j(t) = n_{cj}(t) + n_{dj}(t) + n_{aj}(t)$ is the total number of individuals on patch j . This type of decision making is well documented empirically in animal social groups (Conradt & Roper 2003), as well as in humans from hunter-gatherers to industrial societies (Hastie & Kameda 2005).

Carrying capacity enhancement

The parameter $K_a (\geq 0)$ in eqn 1 can be thought of as the 'carrying capacity' of asocial individuals, which is the base carrying capacity in the absence of social interactions. This interpretation follows from the fact that in the absence of cooperators and defectors, and assuming deterministic growth, the equilibrium number of asocials on a patch is $(r_a - 1)K_a$. Throughout this article we fix $r_a = 2$ (without loss of generality), so that K_a can be regarded as the intrinsic carrying capacity of a patch in the absence of social interactions.

A key element of our model is that the institution, by facilitating coordinated cooperation, allows the possibility of increasing the carrying capacity $K_{sj}(t)$ of social individuals. This is a dynamic variable depending on the remainder of the public good not used for sanctioning: $b_j(t)n_{cj}(t)B$. This good is invested into increasing the carrying capacity of cooperators and defectors on the patch, for which we assume the functional form

$$K_{sj}(t) = K_a + \beta \{1 - \exp[-\gamma b_j(t)n_{cj}(t)B]\}, \quad (5)$$

which is a positive concave function of the number of cooperators. The benefits of increased public good eventually become saturated, with a maximal possible increase in carrying capacity of β . The parameter γ sets the gradient of the increase in carrying capacity with respect to investment in cooperation.

Our model defines a stochastic process for the state variables ($n_{aj}(t)$, $n_{cj}(t)$, $n_{dj}(t)$, $b_j(t)$) in each patch j of the spatially structured population. These variables allow us to evaluate the average frequency of each type, and the average b -value in the population. Due to the strong nonlinearity of our model, we analyse the stochastic process by means of individual-based simulations. The baseline parameters used for the simulations, unless otherwise specified, are given in Table 1.

RESULTS

Before proceeding to the analysis of the full model, we first present results for a population where social interactions are well-mixed (single patch), to aid intuition of the model dynamics.

Evolution under well-mixed social interactions

Neither cooperators, defectors, or asocials are stable when interactions are well-mixed (Fig. 1a). Cooperators may invade a population of asocials once their frequency rises above a threshold by stochastic means. But cooperators are stable against defectors only when the cost of cooperating is less than the cost of being sanctioned $\{C < [1 - b(t)]n_c(t)B/n_d(t)\}$. This depends on the b -value of the institution and, in turn, on the b -preferences of the social individuals (eqn 4). However, under well-mixed social interactions there is no selection pressure on individual b -preferences. This is because the only way that an individual's b -preference affects its fitness is through its contribution to forming the b -value of its patch (eqn 4), the effects of which are felt by all social individuals on the patch equally (eqns 3 and 5). As a consequence, the b -value of the institution changes entirely as a result of mutations to individual b -preferences (Fig. 1b).

Because of these mutations, the institutional b -value may increase over time. However, as it becomes close to one then cooperation can no longer be maintained in the face of mutant defectors. This is because too little of the public good of social individuals is invested into sanctioning defectors, and so the cost of cooperating becomes greater than the cost of being sanctioned. Consequently, defectors replace cooperators. Defectors, in turn, are then replaced by asocials. This is due to the loss of cooperative investment in technology, which means that the carrying capacity of social individ-

Table 1. Baseline parameter settings

Parameter	Value
Cost of cooperating, C	0.1
Base growth rate, r_a	2
Per capita effect of asocial individuals upon socials, α_{sa}	0.05
Per capita effect of social individual upon asocials, α_{as}	0.05
Maximum increase in carrying capacity due to cooperation, β	300
Mutation rate, μ	0.01
Variance of normal distribution used for mutations on b , σ	0.1
Number of patches, N_p	50

uals is no longer enhanced relative to asocials (eqn 5 and Fig. 1c). However, defectors still pay the cost, I , of forming an institution. This means that in the absence of cooperators they are less fit than asocials, and so the social niche is no longer viable.

The end result is that under well-mixed social interactions, cooperation cannot be maintained as a stable equilibrium. Even though

institutions can sometimes be successfully formed, there is no selection pressure towards those that support cooperation. However, as the next section shows, institutional evolution is very different in a spatially structured population.

Evolution in a spatially structured population

Dynamics of institutional evolution

We first consider a structured population with the following ecological and demographic parameter values: $K_a = 20$, $B = 0.9$, $I = 0.1$, $\gamma = 0.0075$. In such a population, cooperators are able to invade asocials when rare (Fig. 2a, all simulations were started from an initial condition in which asocials are fixed within every patch, and the b -preference of each individual set randomly from a uniform distribution). Investment in public good can then remain stable even in the presence of recurrent defector and asocial mutations (Fig. 2d), and in the presence of recurrent mutations to individual b -preferences (Fig. 2e).

Crucially, once cooperation has invaded, it is maintained even as the number of social individuals subsequently increases to a very large size. In particular, although the base patch carrying capacity needs to be relatively small at the start of invasion (for instance 20 individuals in Fig. 2) to guarantee direct or indirect benefits, after invasion it substantially increases (by tenfold in Fig. 2f) due to the benefits of public good invested in environmental improvement. The individual b -preferences typically evolve to large values, but not to unity (approximately in the range 0.8–0.9; Figs. 2b and e). An institutional b -value in this range provides sufficient sanctioning for cooperators to remain stable against defectors, while allowing a large increase in the carrying capacity of socials (Fig. 2f). This increase in the carrying capacity of social individuals makes them evolutionarily stable against invasion by asocials, who may reoccur on the patch by mutation or migration.

Why do the individual b -preferences stabilise when social interactions are structured? In a structured population, there is variation in institutional b -values. Individuals under different institutions will then have different expected numbers of offspring, depending on the b -value on their patch (eqns 1 and 5). Individuals benefit from institutions with a b -value that decreases density-dependent competition, as they produce more offspring. This in turn increases patch size. Crucially, patches whose institutions sustain a larger number of individuals also export a larger absolute number of migrants. Because migrants carry their b -preferences to their new patch, they cause the institution in their new patch to become more like the one in their natal patch. Thus, institutions with an b -value that causes the number of social individuals to grow to a larger size will export more migrants, and hence their members will spread their institution form to other patches.

In this way, the variance in b -values between patches creates a selection pressure favouring larger individual b -preferences, and hence the creation of institutions that invest more public good into increasing carrying capacity. On the other hand, too large an institutional b -value causes defectors to increase in frequency, and hence the amount of public good produced to decline. This in turn causes a decrease in the carrying capacity of individuals under such institutions, which then means that they export absolutely fewer migrants per generation. Thus, institutions with too large an b -value also spread their institution form at a slower rate. As a result, migration between patches favours an evolutionarily stable type of institution

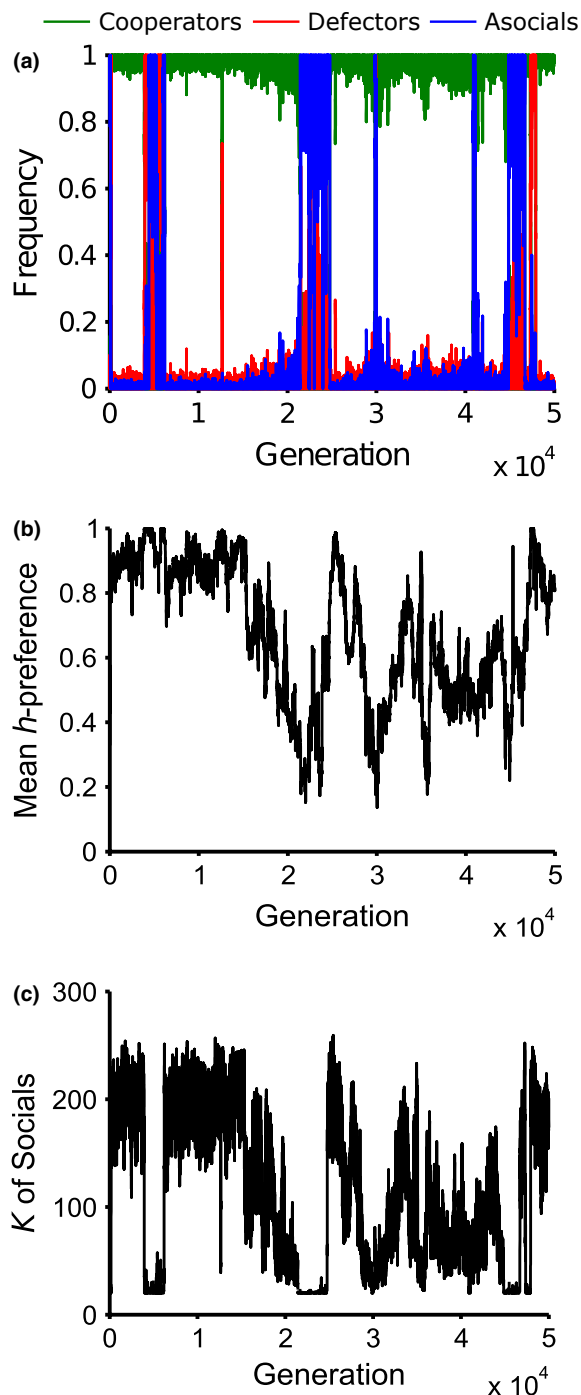


Figure 1 Cooperation-promoting institutions are not stable in a single well-mixed interaction group. (a) Frequency of cooperators, defectors, and asocials. (b) Mean individual b -preference (arithmetic average across all individuals in the population) as a function of time. (c) Carrying capacity of social individuals as a function of time. Parameters: $K_a = 20$, $B = 0.9$, $I = 0.1$, $\gamma = 0.0075$.

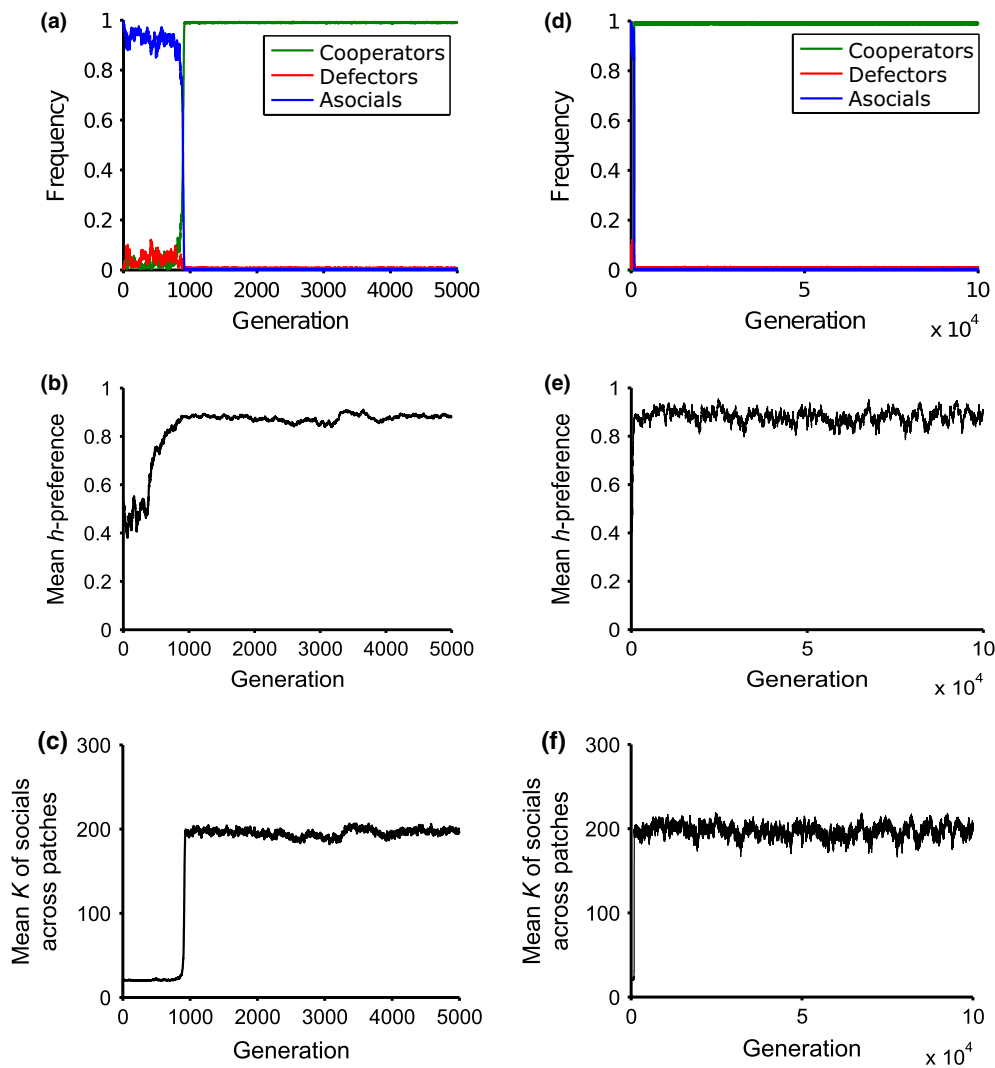


Figure 2 In a spatially structured population, institutions that support cooperation evolve and are stable. (a) Frequency of cooperators, defectors, and asocials over 5000 generations. (b) Mean b -preference (arithmetic average across all individuals in the population) over 5000 generations. (c) Mean carrying capacity of social individuals (mean $K_{sj}(t)$) over 5000 generations, averaged across patches. (d) Frequency of cooperators, defectors, and asocials over 10^5 generations. (e) Mean b -preference over 10^5 generations. (f) Mean carrying capacity of social individuals over 10^5 generations, averaged across patches. Parameters: $K_a = 20$, $B = 0.9$, $I = 0.1$, $\gamma = 0.0075$.

that invests most, but not all, of the public good into increasing carrying capacity.

By creating competition among institutions, population structure and migration generate a selection pressure on individual institutional preferences. Successful institutions sanction – but not too hard.

The co-evolution of institutions and demography can produce a transition to very large-scale cooperation

The results in Fig. 2 illustrate that the co-evolution of institutions with patch carrying capacity can produce evolutionarily stable public good production in groups of 200 individuals. This is already a large number of individuals, and one for which contribution to public good would be unlikely to evolve if it were the initial patch carrying capacity, K_a (see also *Sensitivity to parameters*, below). Can this co-evolution allow for the emergence of cooperation between an even larger number of individuals? The parameter β sets an upper bound for the amount that technology can increase carrying capacity in our model. To investigate the evolution of larger scale public good pro-

duction we therefore increased β tenfold, to 3000, thus allowing for the possibility of larger groups given sufficient investment in technology. We correspondingly decreased γ by tenfold to 0.00075, to keep the gradient of the benefit function (eqn 5) proportionate. We again set the initial patch carrying capacity equal to 20. Rare cooperators again invaded asocials, and cooperation remained stable even as the number of social individuals grew from 20 to 1000 (Figs 3a and c). The population mean of individual b -preferences again remained in the region of 0.8–0.9 (Fig. 3b). This demonstrates that the co-evolution of institutions with demography can create a transition from small to very large cooperative groups.

Sensitivity to parameters

We investigated sensitivity to the model parameters (Fig. 4). For each set of parameters, we started from a structured population fixed for asocials in every patch, and ran the simulation for 50 000 generations. We recorded whether cooperators were at a global fre-

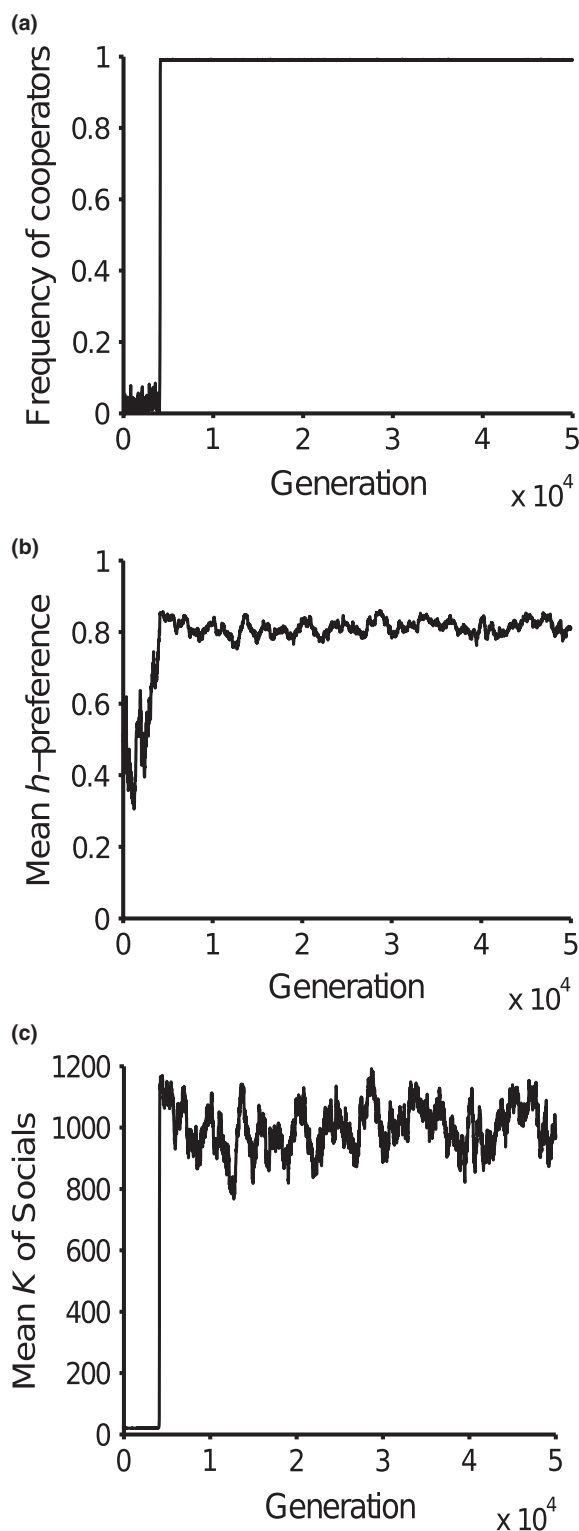


Figure 3 The co-evolution of institutions with demography can create a transition from small- to large-scale cooperative groups. (a) Cooperation invades under a smaller initial patch size and is maintained at equilibrium. (b) Individual b -preferences (arithmetic average across all individuals in the population) stabilise to create institutions that invest most public good into technological improvement, while still providing sufficient sanctioning to maintain cooperation against defectors. (c) The benefits of cooperation allow the number of social individuals to become very large. Parameters: $K_a = 20$, $B = 0.9$, $I = 0.1$, $\beta = 3000$, $\gamma = 0.00075$ (see text).

quency greater than 0.95, averaged over the last 1000 generations of the simulation run. We refer to this as the cooperative equilibrium being reached in that run (in no trial did we ever observe cooperation to decrease below 0.95 frequency, once it had exceeded this level). We repeated this process 100 times for each set of parameters, and plotted the number of runs in which the cooperative equilibrium was reached. Our analysis focused on how changing each parameter affected the largest initial patch size (K_a), under which cooperators could reliably invade within 50 000 generations and be maintained at greater than 0.95 frequency. All other parameters were kept at their base values as given in Table 1.

Decreasing the benefit of cooperation (B) decreases the largest initial patch size under which cooperators can invade and maintain an institution (Fig. 4a). In addition, when cooperation does invade, the carrying capacity of social individuals is enhanced by a lower amount for lower B (Fig. S1a). This follows from the fact that less public good is available to be invested in environmental improvement (eqn 5). Increasing the cost of creating an institution, I , also decreases the largest patch size under which cooperators can invade asocials (Fig. 4b). However, when the cost of creating an institution is set to zero, then cooperators can invade under a larger range of patch sizes. Figure 4c shows that the range of patch sizes under which cooperators can invade also increases with the gradient (γ) of the benefit function in eqn 5. Increasing the gradient also increases the equilibrium number of cooperators and hence makes the value of $K_{sj}(t)$ reached closer to the asymptotic value of eqn 5, $K_a + \beta$ (Fig. S1b). That is, cooperators increase in number when the benefit assigned to environmental improvement produced by one extra cooperator, bB , raises the carrying capacity of social individuals by at least one.

Figure 4d shows that increasing the migration rate between patches decreases the maximum patch size under which cooperators reliably invade asocials. Intuitively, this is because increased migration decreases the variance between patches (or relatedness between individuals in a patch), and so reduces the indirect fitness benefits of cooperation that accrue from helping relatives, a direct consequence of limited dispersal (Hamilton 1971). Indeed, in the limiting case of panmictic migration (given by $m = 1 - 1/N_p$), there are no indirect benefits to cooperation. However, because there are several patches there is still a variance between institutions, unlike in the case of a single patch. Thus, institutional b -values can still potentially stabilise and support cooperation. We found that under panmictic migration between patches, cooperators could reliably invade solely through direct fitness benefits if the initial patch size was below 17. Indirect fitness benefits, and hence limited dispersal, are required for cooperation to invade under patch sizes larger than this.

Sensitivity to other model assumptions

For the results presented so far, we assumed that the institutional b -value was formed by taking the mean b -preference of social individuals on the patch (eqn 4). This is but one possible way of aggregating individual preferences. Two other possible ways are to take the modal preference, or to have one individual act as a leader and obtain the institutional b -value from his or her own b -preference. We investigated the effect of both of these cases in our model (Appendix S1). Importantly, we found the model results to be qualitatively insensitive to forming the institutional b -value in either of these ways, as opposed to taking the mean b -preference of social

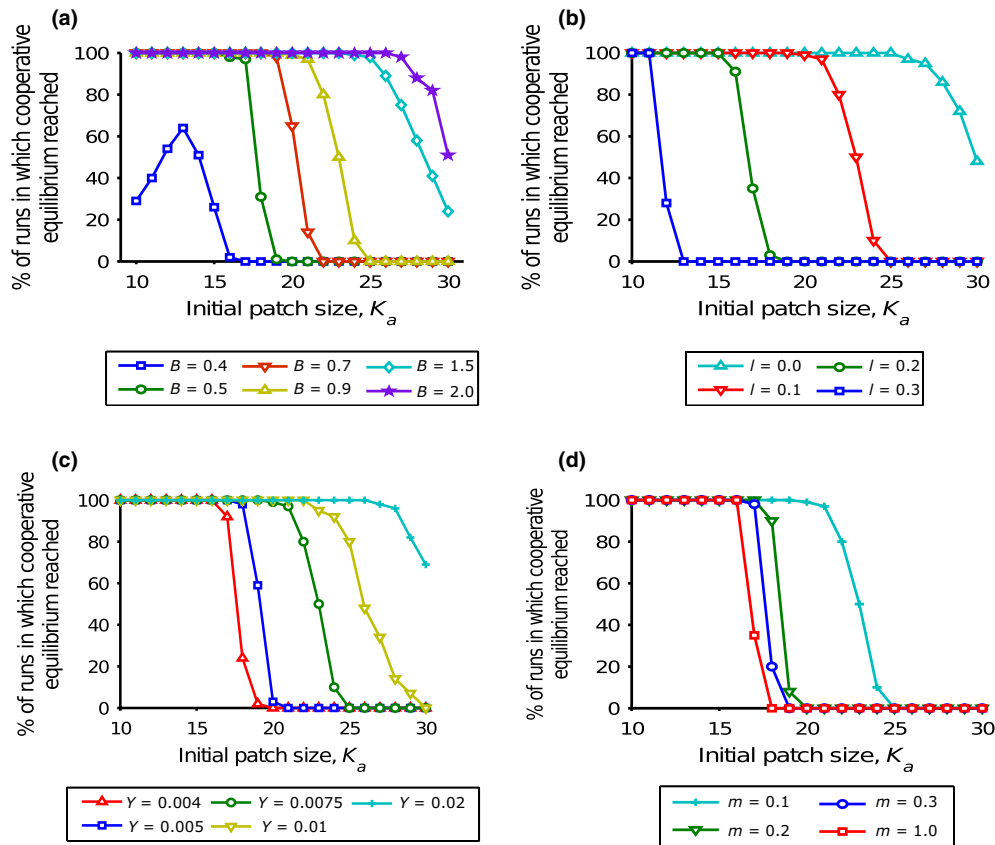


Figure 4 Sensitivity to parameters. Plots show the percentage of runs (of 100) in which the cooperative equilibrium was reached within 50 000 generations (see text). (a) Decreasing the benefit of cooperation decreases the maximum initial patch size under which cooperation reliably invades ($m = 0.1$, $I = 0.1$, $\gamma = 0.0075$). (b) Increasing the cost of institution formation decreases the maximum patch size under which cooperation reliably invades. ($m = 0.1$, $B = 0.9$, $\gamma = 0.0075$). (c) Increasing the gradient of the benefit function (γ in eqn 5) increases the range of patch sizes under which invasion occurs ($m = 0.1$, $B = 0.9$, $I = 0.1$). (d) Increasing the migration rate decreases the maximum patch size under which cooperation reliably invades ($B = 0.9$, $I = 0.1$, $\gamma = 0.0075$).

individuals on the patch. This therefore suggests that our results are quite robust to the particular mechanistic details of how the institutional b -value is aggregated from individual preferences.

We also investigated the effect of relaxing several other assumptions. We first relaxed the assumption that social individuals are always able to reach an agreement about the institutional b -value, by allowing for the failure to reach consensus if the variance in socials' b -preferences was greater than a threshold value (Appendix S2). We also relaxed the assumption that all social individuals must take part in institutional negotiations, and pay the cost I for doing so. Instead, we allowed for socials that do not pay I , and whose b -preferences are not taken into account when forming the institutional b -value (Appendix S3). We found that a small fraction of individuals pay I at equilibrium (Fig. S3), which is sufficient to maintain an institution (the selection pressure for some individuals to pay I again results from population structure and migration: demes with some individuals who do pay I are able to form an institution and grow to a larger size, and thus export more migrants). We also considered the effect of varying the efficiency of sanctioning, by multiplying the per capita cost of being sanctioned by a constant between 0 and 1 (Appendix S4). Finally, we considered a version of the model (Appendix S5) that is reminiscent of 'pool punishment' models of sanctioning (Sigmund *et al.* 2010; Perc 2012), in which mutant individuals may pay for cooperation but not

for sanctioning. We found that in all these variants, social individuals were still able to invade and maintain institutions under a wide range of parameters (Figs S2–S7).

DISCUSSION

Starting from a population consisting entirely of asocials, we determined conditions under which social individuals could invade and create institutions that support cooperation in very large groups, thereby generating a transition from small- to large-scale social groups. Unlike in related models that include asocial individuals (Sigmund *et al.* 2010; Sasaki *et al.* 2012), their presence is not necessary for the invasion of punishment. Rather, the inclusion of asocials in our model actually makes establishment of an institution more difficult, by providing outside options. Our results show that for invasion of a costly institution to occur, the patch size must initially be relatively small (Fig. 4). However, once social individuals have invaded, the institution drives a large increase in the scale of cooperation, and is maintained in the face of recurrent mutations (Fig. 3).

A structured population generates variation in institutional b -values (a group-level trait), which causes individuals with different b -preferences in different patches to produce different expected numbers of offspring. Variation between institutional b -values therefore generates a selective pressure on individual b -preferences, which is particularly

strong in our explicit demographic model owing to the fact that individuals form institutions that are likely to increase local carrying capacity. This increase in carrying capacity generally markedly raises the selection pressure on social traits causing it (Lehmann *et al.* 2006), as their carriers export a significantly larger number of successful migrant offspring than individuals living in smaller groups. Thus, individuals rapidly spread their institutional and behavioural preferences to other patches. In this way, group structure solves the problem posed by institution evolution when interactions are well-mixed. Importantly, warfare, group extinctions, or group fissioning are not required for this mechanism to work. The spread of institutions through population growth and migration is aligned with the demic diffusion hypothesis for the spread of agriculture across Neolithic Europe (Ammerman & Cavalli-Sforza 1984).

The degree to which the carrying capacity of human groups was affected by the origin of agricultural technology is an important empirical question. Data from cemeteries show a marked increase in fertility during the origin of agriculture, indicating significant population growth (Bocquet-Appel 2011). Other studies suggest that while the population density of hunter-gatherer groups is usually below 0.1 person/sq. mi., that of early dry farmers is around 4 persons/sq. mi. (Hassan & Sengel 1973). Moreover, estimates for the population density of early irrigation farming have ranged from 16 to 25 person/sq. mi. (Hassan & Sengel 1973). Thus, the density of human groups practising irrigation farming may have been up to 250 times greater than that of hunter-gatherers. Such data suggest that a relatively large value of β is plausible in our model.

Our institutional approach to sanctioning should be contrasted with typical models of peer or 'altruistic' punishment (e.g. Boyd & Richerson 1992; Boyd *et al.* 2003; Nakamaru & Iwasa 2005; Lehmann *et al.* 2007). In those models, each cooperator decides in isolation whether to punish a defector or not, and pays a unilateral cost for doing so. The main focus of such models is then to address the 'second-order free-rider' problem. That is, if acts of punishment are individually costly to the punisher, then the sanctioning system itself becomes a public good that is vulnerable to exploitation. If such altruistic punishment is to evolve, then it must be through indirect, kin-selected benefits (it is often suggested that these necessary indirect benefits arise through quite specific mechanisms, such as pairwise intergroup warfare under limited dispersal, e.g. Boyd *et al.* 2003). However, outside of artificial economic games played in the laboratory, empirical evidence for punishment acts that decrease the direct lifetime fitness of the punisher remains scant (Baumard 2010; Guala 2012). Rather, field studies have demonstrated that successful sanctioning institutions work by creating conditions that provide *direct benefits* to individuals who actively monitor and enforce institutional rules (Ostrom 1990; Baumard 2010; Guala 2012). Our model has captured these direct benefits in a simple manner, by considering the evolution of institutional rules that allow for the individual costs of monitoring and sanctioning to be paid for from the public good. A similar abstraction from the mechanistic details of day-to-day monitoring and sanctioning has also been used in recent models of pool punishment (Sigmund *et al.* 2010; Perc 2012). Nevertheless, it is insightful to consider anthropological evidence for how monitoring and sanctioning are incentivised on a mechanistic level.

Ostrom (1990) describes how the use of common land in the Hirano, Nagaïke, and Yamanoka villages in Japan was governed by a set of institutional rules that determined how much a household could harvest from the commons each year, and at what time. The

villagers then often used some of their common resources to hire monitors – individuals who specialised in patrolling the commons and reporting violations. These individuals were further incentivised to actively monitor, by allowing them to demand a supply of money and saké from any defectors whom they personally found (Ostrom 1990). Thus, sanctioning became a profitable activity for those monitors who were efficient in finding defectors (Guala 2012). Similarly, in the *buerta* irrigation systems in Spain, individual irrigators were often nominated to act as monitors by their peers, and were incentivised by being able to keep a third of the fine levied on any defector whom they found (Ostrom 1990).

Furthermore, the monitors are themselves accountable to ordinary group members in the commons institutions studied by Ostrom (1990). A monitor who is seen to under-perform can be quickly stripped of the role, causing the cost of shirking to be greater than the cost of monitoring. In all these empirical cases, institutional arrangements cover the cost of monitoring and sanctioning and so prevent a second-order free-rider problem from occurring.

Coordinated, large-scale, cooperation between individuals was likely to have become particularly important during the transition from hunter-gatherer to agricultural societies (Boone 1992; Kaplan *et al.* 2009; Hooper *et al.* 2010; Carballo *et al.* 2012). For example, there is archaeological evidence that the need to cooperatively construct irrigation systems was a driver in the evolution of social institutions in pre-Hispanic Mexico (Spencer 1993; Carballo *et al.* 2012). Construction of an irrigation system can, in turn, increase carrying capacity. Co-evolution of institution creation, cooperation, and demography could therefore be a key driver in the transition from small-scale hunter-gatherer to large-scale agricultural societies. Our model has demonstrated the logical cogency of such an explanation.

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AUTHORSHIP

STP and LL designed research; STP performed research; STP analysed data; STP and LL wrote the manuscript.

REFERENCES

- Ammerman, A.J. & Cavalli-Sforza, L.L. (1984). *The Neolithic Transition and The Genetics of Populations in Europe*. Princeton University Press, Princeton, NJ.
- Baumard, N. (2010). Has punishment played a role in the evolution of cooperation? A critical review. *Mind. Soc.*, 9, 171–192.
- Bocquet-Appel, J.P. (2011). When the world's population took off: The springboard of the Neolithic Demographic Transition. *Science*, 333, 560–561.
- Boehm, C. (1999). *Hierarchy in the Forest: The Evolution of Egalitarian Behavior*. Harvard University Press, Cambridge, MA.
- Boone, J.L. (1992). Competition, cooperation and the development of social hierarchies. In: *Evolutionary Ecology and Human Behavior* (eds. Smith, E.A. & Winterhalder, B.). Aldine de Gruyter, New York, pp. 301–337.
- Boyd, R., Gintis, H. & Bowles, S. (2010). Coordinated punishment of defectors sustains cooperation and can proliferate when rare. *Science*, 328, 617–620.
- Boyd, R., Gintis, H., Bowles, S. & Richerson, P.J. (2003). The evolution of altruistic punishment. *Proc. Natl. Acad. Sci. U. S. A.*, 100, 3531–3535.
- Boyd, R. & Richerson, P. (1992). Punishment allows the evolution of cooperation (or anything else) in sizable groups. *Ethol. Sociobiol.*, 13, 171–195.

- Boyd, R. & Richerson, P.J. (1990). Group selection among alternative evolutionarily stable strategies. *J. Theor. Biol.*, 145, 331–342.
- Carballo, D.M., Roscoe, P. & Feinman, G.M. (2012). Cooperation and collective action in the cultural evolution of complex societies. *J. Archaeol. Method. Th.*, DOI: 10.1007/s10816-012-9147-2.
- Carballo, D.M. (2013). Cultural and evolutionary dynamics of cooperation in archaeological perspective. In: *Cooperation & Collective Action: Archaeological Perspectives* (ed. Carballo, D.M.). University Press of Colorado, Boulder, CO.
- Cavalli-Sforza, L.L. & Feldman, M.W. (1981). *Cultural Transmission and Evolution: A Quantitative Approach*. Princeton University Press, Princeton, NJ.
- Chow, Y. & Hsieh, J. (2013). On multidimensional discrete-time Beverton-Holt competition models. *J. Differ. Equ. Appl.*, 19, 491–506.
- Conradt, L. & List, C. (2009). Group decisions in humans and animals: a survey. *Philos. Trans. R. Soc. Lond. B Biol. Sci.*, 364, 719–742.
- Conradt, L. & Roper, T.J. (2003). Group decision-making in animals. *Nature*, 421, 155–158.
- Dawkins, R. (1976). *The Selfish Gene*. Oxford University Press, Oxford, UK.
- Guala, F. (2012). Reciprocity: weak or strong? What punishment experiments do (and do not) demonstrate. *Behav. Brain Sci.*, 35, 1–15.
- Hamilton, W.D. (1971). Selection of selfish and altruistic behaviour in some extreme models. In: *Man and Beast: Comparative Social Behavior* (eds. Eisenberg, J. & Dillon, W.). Smithsonian Institutions Press, Washington, DC, pp. 59–91.
- Hamilton, W.D. (1975). Innate social aptitudes in man, an approach from evolutionary genetics. In: *Biosocial Anthropology* (ed. Fox, R.). Malaby Press, London, UK, pp. 133–155.
- Hardin, G. (1968). The tragedy of the commons. *Science*, 162, 1243–1248.
- Hassan, F.A. & Sengel, R.A. (1973). On mechanisms of population growth during the neolithic. *Curr. Anthropol.*, 14, 535–542.
- Hastie, R. & Kameda, T. (2005). The robust beauty of majority rules in group decisions. *Psychol. Rev.*, 112, 494–508.
- Hewlett, B.S., Fouts, H.N., Boyette, A.H. & Hewlett, B.L. (2011). Social learning among congo basin hunter-gatherers. *Philos. Trans. R. Soc. Lond. B Biol. Sci.*, 366, 1168–1178.
- Hooper, P.L., Kaplan, H.S. & Boone, J.L. (2010). A theory of leadership in human cooperative groups. *J. Theor. Biol.*, 265, 633–646.
- Hunt, R.C. (1988). Size and the structure of authority in canal irrigation systems. *J. Anthropol. Res.*, 44, 335–355.
- Hurwicz, L. (1996). Institutions as families of game forms. *Jpn. Econ. Rev.*, 47, 113–132.
- Isakov, A. & Rand, D.G. (2011). The evolution of coercive institutional punishment. *Dyn. Games Appl.*, 2, 97–109.
- Janssen, M.A., Bousquet, F., Cardenas, J.C., Castillo, D. & Worrapimphong, K. (2012). Field experiments on irrigation dilemmas. *Agr. Syst.*, 109, 65–75.
- Kaplan, H.S., Hooper, P.L. & Gurven, M. (2009). The evolutionary and ecological roots of human social organization. *Philos. Trans. R. Soc. Lond. B Biol. Sci.*, 364, 3289–3299.
- Lehmann, L., Perrin, N. & Rousset, F. (2006). Population demography and the evolution of helping behaviors. *Evolution*, 60, 1137–1151.
- Lehmann, L., Rousset, F., Roze, D. & Keller, L. (2007). Strong reciprocity or strong ferocity? A population genetic view of the evolution of altruistic punishment. *Am. Nat.*, 170, 21–36.
- Nakamaru, M. & Iwasa, Y. (2005). The evolution of altruism by costly punishment in lattice-structured populations: score-dependent viability versus score-dependent fertility. *Evol. Ecol. Res.*, 7, 853–870.
- North, D.C. (1990). *Institutions, Institutional Change and Economic Performance (Political Economy of Institutions and Decisions)*. Cambridge University Press, Cambridge, UK.
- Nowak, M.A. & Sigmund, K. (2005). Evolution of indirect reciprocity. *Nature*, 437, 1291–1298.
- Oliver, P. (1980). Rewards and punishments as selective incentives for collective action: theoretical investigations. *Am. J. Sociol.*, 85, 1356–1375.
- Ostrom, E. (1990). *Governing the Commons: The Evolution of Institutions for Collective Action (Political Economy of Institutions and Decisions)*. Cambridge University Press, Cambridge, UK.
- Ostrom, E. & Gardner, R. (1993). Coping with asymmetries in the commons: self-governing irrigation systems can work. *J. Econ. Perspect.*, 7, 93–112.
- Perc, M. (2012). Sustainable institutionalized punishment requires elimination of second-order free-riders. *Sci. Rep.*, 2.
- Sasaki, T., Brännström, Å., Dieckmann, U. & Sigmund, K. (2012). The take-it-or-leave-it option allows small penalties to overcome social dilemmas. *Proc. Natl. Acad. Sci. U. S. A.*, 109, 1165–1169.
- Sigmund, K., De Silva, H., Traulsen, A. & Hauert, C. (2010). Social learning promotes institutions for governing the commons. *Nature*, 466, 861–863.
- Spencer, C.S. (1993). Human agency, biased transmission, and the cultural evolution of chiefly authority. *J. Anthropol. Archaeol.*, 12, 41–74.
- Trawick, P.B. (2001). Successfully governing the commons: Principles of social organization in an andean irrigation system. *Hum. Ecol.*, 29, 1–25.
- Trivers, R.L. (1971). The evolution of reciprocal altruism. *Q. Rev. Biol.*, 46, 35–57.
- Turchin, P. (2003). *Historical Dynamics*. Princeton University Press, Princeton, NJ.
- Turchin, P. (2010). Warfare and the evolution of social complexity: a multilevel-selection approach. *Structure and Dynamics*, 4, Article 2. Available at: <http://www.escholarship.org/uc/item/7j11945r>.
- Weissing, F. & Ostrom, E. (2000). Irrigation institutions and the games irrigators play: rule enforcement on government- and farmer-managed systems. In: *Polycentric Games and Institutions: Readings from the Workshop in Political Theory and Policy Analysis*. University of Michigan Press, Ann Arbor, pp. 366–398.
- Whiten, A. & Erdal, D. (2012). The human socio-cognitive niche and its evolutionary origins. *Philos. Trans. R. Soc. Lond. B Biol. Sci.*, 367, 2119–2129.
- Wright, S. (1931). Evolution in mendelian populations. *Genetics*, 16, 97–159.

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