Robustness assessment of the Cooperation Under Resource Pressure model (CURP): Insights on resource availability and sharing practices among hunter-gatherers

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Abstract

A well-known challenge in archaeological research is the exploration of the social mechanisms that hunter-gatherers may have implemented throughout history to deal with changes in resource availability. The agent-based model (ABM) Cooperation Under Resource Pressure (CURP) was conceived to explore food stress episodes in societies lacking a food preservation technology. It was particularly aimed at understanding how cooperative behaviours in the form of food sharing practices emerge, increase and may become the prevailing strategy in relation to changes in resource availability and expectancy of reciprocity. CURP's main outcome is the identification of three regimes of behaviour depending on the stress level. In this work, the model's robustness to the original selection mechanism (random tournament) is assessed, as different dynamics can lead to different persistent regimes. For that purpose, other three selection mechanisms are implemented and evaluated, to identify the prevailing states of the system. Results show that the three regimes are robust irrespective of the analysed dynamics. We consequently examine more in detail the long-term archaeological implications that these results may have.

1. Introduction

Natural resources and their distribution are paramount for understanding life at different scales. Regarding the human species, the role played by resources is even more significant, as resource availability is also the material basis upon which any social behaviour or strategy emerges and evolves over time. The resource exploitation strategies implemented by human societies constitute a transversal topic of interest for many research fields. In particular, the paradigm known as Human Behavioural Ecology-HBE (Nettle *et al.*, 2013) addresses in the form of archaeological studies not only functional explanations linked to carrying capacities, resource exploitation, productive aspects including technology and consumption or mobility and reproductive strategies, but also historical ones, related to the origins of agriculture, intensification and colonization processes, among others (see a review in Bird and O'Connell (2006)).

Within the most common archaeological discourse, it is often assumed that whenever resources become scarce for the existing population, human societies tend to modulate this unbalance between population and resources through changes in the production/consumption sphere. These changes might include different strategies ranging from risk minimization (Smith, 1972; Minc and Smith, 1989; White *et al.*, 2011; Zeder, 2012; Ryan and Rosen, 2016) to changes in demographic dynamics (Speth, 2004; Williams *et al.*, 2015). However, due to the intrinsic nature of Archaeology, which deals mainly with material remains, it is not straightforward to reconstruct the social domain and the food distribution patterns through them (Enloe, 2003). Consequently, several archaeological studies have focused on very specific examples such as the study of the development of trade and interchange systems (Dyke, 1999; Chapman, 2008) or the study of (communal) storage structures or technologies (see a review in (Angourakis *et al.*, 2015)).

Leaving aside the archaeological limitations due to its materiality, we know from Ethnography, Ethnoarchaeology, and Ethnohistory that hunter-gatherer (HG) societies use not only specific technologies but also social organizational measures to deal with the different scenarios produced by the heterogeneous temporal and spatial distribution of resources. Good examples of social organisational measures among HG are mobility, aggregation, and fission dynamics, which are included in Binford's packing model (Binford, no date). Another particularly relevant social measure is sharing, a complex phenomenon around which several debates regarding its economic and social function continue to exist. Sharing appears in diverse contexts where it can be explained in pursuit of different objectives ranging from showing the own reproductive potential to sheer survival. In the present study, we focus on the facet of food sharing that allows dealing with future possible subsistence instability through indirect reciprocity; the surplus is shared with other community members in the hope that they will do the same in the future ((Winterhalder, 1986; Bird, 1997; Borgerhoff Mulder and Schacht, 2012) among others).

From all the above, it appears clear that to understand the complexity of social dynamics beyond material remains and ethnographic narratives, simulation tools such as Agent-Based Modelling (ABM) provide a good framework for the exploration and analysis of social contexts.

ABM allows expanding our frames of reference for several issues that range from the very empirical to theoretical matters, as it offers the possibility to move from the micro to the macro scale studying emergent properties. In this sense, modelling becomes a theory building tool (Verhagen and Whitley, 2012; Whitley, 2016) in which, when going back to reality, it is extremely important to extend the conclusions of the model in accordance with the aim for which it was developed, as different models can be built for different purposes: generating theory, prediction, classification, etc., and its conclusions should not be extrapolated elsewhere.

ABM models work towards improving the Social Sciences in general engendering debates about new paradigms within the framework of what has been called *generative social science* (Epstein, 1999).

When linked together with Ethnography and Ethnoarchaeology, ABM models based on ethnographical knowledge allow exploring how societies behave in relation to resources (if they are shared and how) once they have been acquired. It is worth noting that the variety of variables necessary to understand social mechanisms makes computer simulation particularly suitable for their analysis, as modelling allows generating multiple environmental scenarios on variable spatial and temporal scales (Rautman, 1993; Morrison and Addison, 2008), see (Lake, 2014) for a review of social simulation in archaeological studies.

Even though social simulation is not yet considered a mainstream approach in Archaeology (Whitley, 2016), its application is increasing exponentially (Wurzer, Kowarik and Reschreiter, 2015), and there already exist good examples of the use of ABM to address not only resource management (see Freeman and Anderies (2012) and references therein) but also other social phenomena such as cooperation.

Previous research on cooperation and HG societies has dealt with specific topics like cooperative breeding (Smaldino *et al.*, 2013) or cooperative strategies for the sake of production, being cooperative hunting the most relevant example (Henrich *et al.*, 2001; Alvard and Nolin, 2002; Hill, 2002; Stiner, Barkai and Gopher, 2009).

Other research pieces in the field have focused on specific ethnographic case studies, such as those devoted to the Ache (Janssen and Hill, 2014) and the Maasai (Aktipis, Cronk and de Aguiar, 2011), or on sharing phenomena of other resources aside from food, such as territories (Freeman and Anderies, 2012).

The model of cooperation and punishment by Bowles and Gintis (2004) is also aimed at explaining collective phenomena such as food sharing and defense. Particularly, it suggests that cooperative behaviours may well be sustained thanks to strong reciprocity since even if it is an individual behaviour that coexists with other distinct behavioural patterns, it produces a social dynamic and has benefits at the social level.

In the light of the above, we aim to explore how social mechanisms regarding food sharing practices (reciprocity) change in relation to variation in resource availability (subsistence stability and instability). Specifically, we are interested in the conditions allowing the emergence of sharing and its maintenance, as well as in the scenarios that would promote its disappearance.

For this reason, we designed the CURP model, an ABM specifically conceived to offer some insights into how HG societies lacking food preservation technologies may face changing resource availability through social mechanisms of resource redistribution (Pereda, Santos and Galán, 2017). As it has already been stated, both cooperation and sharing are complex phenomena which can be analysed from different perspectives. However, both in CURP and in this paper, cooperation is modelled just as food sharing.

Agent-based simulation models have been argued to work as theoretical experiments (Edmonds and Hales, 2005) which can help to formally illustrate the implications of a particular set of assumptions in a specific context under study (for instance, in the context of the social phenomena). Although a simulation result can be understood as a valid sufficiency theorem (Axtell, 2000), it is not easy to infer from just a set of simulations if the results are a consequence of the model core set of assumptions or if they are caused by accessory aspects (Galán *et al.*, 2009, 2013). This is particularly important when simulation is used as a tool for the analysis and interpretation of social phenomena, since the ABM used is just a particular instance of a more abstract conceptual model, which could be implemented in different equivalent ways, all of them valid in principle, but whose different dynamics can lead to different stable regimes of the system (Galán and Izquierdo, 2005). Therefore, in this work, we delve further into the CURP model and check the robustness of its results to the evolutionary mechanisms (how individuals share resources and with whom). Similarly to previous social simulation research (Edmonds and Hales, 2005; Galán and Izquierdo, 2005), we use several evolutionary selection mechanisms -all of them compatible with the original conceptual idea- to better understand how wide is the range of applicability of the conclusions of the CURP model, and to try to identify which aspects are consequence of the particular dynamic and which results are robust to the specific adaptive mechanism (persistent regimes of the system). Hence, the aim is to find the prevailing stable areas of the system (once the transient period is over and the initial dynamics do not influence the dynamics anymore), in order to conduct a detailed interpretation of the results in the context of HG, based on those persistent regimes found and not on the specific dynamics to reach them.

2. The CURP agent-based model

2.1 Description of the model

The CURP model was built in NetLogo (Wilensky, 1999) under the framework of evolutionary game theory and inspired by the hypothesis that a decrease in resources would promote cooperation in terms of food sharing whenever reciprocity is possible, but once resource scarcity reaches a given threshold and reciprocity is less probable, cooperation may become a non-satisfactory strategy. The EGT framework used in this paper not only can be interpreted by natural selection models but also other decision models driven by a gradual change, in which the strategies that are more successful at a given moment are more likely to persist in the future (Sandholm, 2010; Izquierdo, Izquierdo and Vega-Redondo, 2012).

Here we succinctly depict the core dynamics of the model and detail the assessment of the model’s robustness to the evolutionary mechanisms, which is one of the main contributions of the present work. For further details on the singularities of CURP, please refer to Pereda et al (2017) or directly to the model, (available at openABM; https://www.openabm.org/model/5287/).

In CURP, resource pressure is modelled stochastically using two different parameters: (i) *prob-resource* (the probability of acquiring resources) and (ii) *min-energy* (the minimal proportion of the resource unit each agent needs to survive).

The model was designed as an artificial society of *N* agents, each one of them defined by three state variables: *given-energy*, *correlation*, and *fitness*, being *given-energy* and *correlation* the variables that define the agent's strategy.

Given-energy is the proportion of the resource unit that the agent under consideration wills to share. *Correlation* establishes the probability of choosing a donee among the set of possible donees, an agent with *correlation* 1 will choose the most previously cooperative individual and one with *correlation* -1 the least cooperative.

Fitness is defined as the number of time periods in which the energy obtained by the agent was greater than *min-energy*, since the conventional definition of fitness intending to maximize the expected resources may not be the most suitable for HG without food preservation techniques. This particular definition of fitness, which dissociates the resources obtained by the agents from the payoffs (and implicitly assumes diminishing marginal returns), makes the CURP model and its conclusions only applicable to societies without food preservation technologies.

Each simulation scenario is defined by the study parameters (see Table 1), which are exogenous variables established by the user that remain constant in each run.

[TABLE 1]

The procedure is the following: in each time period, each agent draws resources and gets a unit of energy with a probability equal to *prob-resource*. Then, each agent that succeeded and obtained resources shares them in two steps. First, it selects a donee from a set of the population of size *sharing-tournament-size*, constituted by agents who did not get resources (by themselves or from other donors). The selection of a donee from this set is done according to the value of the agent's *correlation*. Second, she gives the selected donee a *given-energy* proportion of the unit of energy she has. It is important to note that the proportion of energy shared by a donor (*given-energy*) is not conditioned by the *min-energy* survival threshold, which implies that the donor can end up with less energy than the minimum necessary for her own survival.

No donee will receive any more energy from other donors if she gets more energy than the survival threshold established by *min-energy*.

Finally, at the end of each time period, each agent's *fitness*, i.e., the number of non-starving periods, is updated. The *fitness* value increases by a unit if the agent has more energy than the *min-energy* survival threshold.

This process of acquiring and sharing resources with the subsequent update of *fitness* is repeated *rounds-per-generation* time periods. Once the model has run *rounds-per-generation* times, each agent updates her strategy by changing the values of her *correlation* and *given-energy* variables as follows: first she samples *strategy-tournament-size* people agents of the population and then she imitates the strategy with the highest *fitness* if it is greater than hers, unless it is affected by the *prob-mutation* probability, in which case she randomly chooses a strategy from the strategy space.

Pereda et al (2017) proved using statistical learning analysis that the results of the model depend mainly on two parameters: prob-resource and min-energy, the two variables which define resource pressure. Consequently, to understand the system dynamics and to study the emergence of cooperation and indirect reciprocity via simulation, the two-study parameters *prob-resource* and *min-energy* were evenly sampled over the range [0.2, 0.8] in steps of 0.1, to fully map the outcome space of the model (the details of the parametrisation can be found in Pereda et al (2017)). Again, each parametrisation was run 5×10^3 generations, being replicated 100 times.

2.2 CURP Previous results

Hunter-gatherer societies implement a wide variety of strategies that change according to the different socio-ecological contexts they face. In the CURP model, the different settings are characterized by distinct population volumes and by specific distributions and concentrations of resources, the latter being reproduced through the parametrization of both the probability of finding resources as well as the need of a specific amount of energy for survival. Therefore, the model sheds light on the social realm, enlightening the underlying patterns behind the emergence of two particular social behaviours: cooperation in terms of food sharing and indirect reciprocity.

In HG societies, food sharing is a specific form of cooperation which, when implemented, helps to deal with mid-stress scenarios, where it constitutes a mechanism both to face future risks of food scarcity and to manage food surplus. At the same time, cooperative strategies enhance the emergence of social links that reinforce both sharing practices and other communal behaviours (Briz i Godino *et al.*, 2014).

The first study of CURP showed that after the initial transitory dynamics, three different persistent regimes could be identified: low-stress regime, intermediate-stress regime and high-stress regime. Along these regimes, the emergence and disappearance of cooperative behaviours is the most relevant trend, which shows how cooperation (food sharing) depends both on changes on the possibility to survive (changes in *N-people* and *min-energy*) as well as on the expectancy of reciprocity (*correlation* and *given-energy*).

The three persistent regimes identified by Pereda et al. are:

1. Low-stress regime (low values of *min-energy* and high values of *prob-resource*): Under these circumstances, different strategies produce

maximum fitness. Survival is therefore very likely. Consequently, changes in the strategy space are driven by random drift. Strategy selection is not important and the average strategic behaviour of the population remains at almost constant values.

2. High-stress regime (high values of *min-energy* and low values of *prob-resource*): Very unstable behaviour is the main characteristic of this regime. The high threshold of *min-energy* and the scarcity of resources promote the emergence of low-given strategies. At the same time, new strategies to ensure survival are permanently explored by the agents, mainly because no situation is satisfactory enough.
3. Intermediate-stress regime: In this regime, cooperation and indirect reciprocity emerge. Strategies characterise by retaining the resources strictly necessary for survival and giving the rest to the population in a structured manner, since strategies of positive correlation are favoured (the agents that gave more are the ones that receive the most). Consequently, it can be asserted that the population self-organises in an indirect-reciprocity system in which the norm is to share what is not necessary for survival, with the expectancy that the rest of the population will do the same in the future (indirect reciprocity implies that one cooperates with individuals who did cooperate with other members of the population in previous stages, and whose reputation is therefore positive). Thanks to cooperation sustained through indirect reciprocity, the probability of communal survival is significantly increased at a population scale and the probability of being behind the threshold is collectively reduced.

3. Methodology

3.1 Evaluation of the robustness of the model to the selection mechanism

In some models it can be difficult to faithfully represent the real dynamics of the system under consideration, since the dynamics can be unknown, unobservable, or simply different to the ones we are considering. This motivates the use of plausible hypothesized mechanisms that could have been at work to analyse the stability areas of the system (and not so the transient dynamics), since the system could reach different persistent regimes depending on the particular dynamics imposed (Galán and Izquierdo, 2005).

To test the conclusions obtained from the CURP model and to gain confidence in the robustness of the three regimes initially identified, here we explore the impact on the results of different selection mechanisms. More specifically, the selection mechanism used in the original paper, i.e., random tournament, is compared to other three mechanisms: roulette wheel (due its popularity (Mitchell, 1996)), and two truncation and threshold selection algorithms (Lynch and Walsh, 1998): standard deviation and average selection; this last two mechanisms have been used in some of the most influential works in game theoretic social simulation about cooperation (Axelrod, 1986; Takahashi, 2000), and it has been proved that they can lead to different persistent regimes in comparison to other evolutionary mechanisms (Galán and Izquierdo, 2005). The aim of this comparison is to check if the three regimes appear irrespective of the selection mechanism i.e., that the system tends to them regardless of the internal dynamics imposed.

The selection of strategies happens every *rounds-per-generation* time periods. In the original model (Pereda *et al.*, 2017), the strategy selection process follows a random tournament: each agent chooses a random sample of other agents and imitates the best strategy, i.e., the strategy of the agent with the highest *fitness* in the sample; at the same time, she randomly chooses a strategy between the strategy space with a probability equal to a mutation parameter. One of the reasons for this approach is that both selection and mutation can be easily interpreted as social imitation and individual exploration, i.e. people usually tend to imitate the best behaviour, although they occasionally explore new alternatives.

In the present work, the three new selection mechanisms, i.e. roulette wheel, standard deviation and average selection have been implemented without changing the mutation process with respect to the original design. In the new mechanisms, just after *rounds-per-generation* time periods, the old generation of agents is replaced by a new one composed by replications of some of the old agents, chosen according to the specific selection mechanisms.

In the roulette wheel mechanism, agents are given a replication probability directly proportional to their *fitness* in the current population. Then, to replace the old generation, *n-people* agents are sampled stochastically to constitute the new generation. In the standard deviation mechanism there are two reference values: population average and population average plus standard deviation. Agents with *fitness* greater than, or equal to the population average are replicated once, while agents with *fitness* equal to or greater than population average plus a standard deviation are replicated twice. Finally, the average selection mechanism is similar to the mechanism of standard deviation. In this case, all agents with *fitness* equal to or greater than the population average are replicated twice. In order to keep the population size constant, in the standard deviation and average selection mechanism, we randomly eliminate or replicate agents of the new generation.

3.2 Results

In the present contribution, we have defined a set of experiments that correspond to a subset of the different scenarios of resource pressure studied in the original paper. In particular, (see Table 2) we have chosen three cases of the intermediate-stress regime, one of the high-stress regime and one of the low-stress regime. The parameterization of the model corresponds to the one defined in the original work (Pereda *et al.*, 2017). Each experiment was run 5×10^3 generations (to be sure that the stationary was reached) and replicated 100 times.

[TABLE 2]

Figure 1 shows the average values of *correlation* and *given-energy* obtained for each scenario after 100 runs. The results do not vary significantly with respect to the ones obtained in the original work. It is only in the low-stress scenario that the new experiments show greater variability. The reason behind this change is the fact that with the new selection mechanisms the probability of changing the strategy is greater in comparison to the random tournament, where the probability of change was mainly driven by mutation. The new selection mechanisms implemented, aside from the mutation probability, in the case of equal payoffs, mix and shuffle the population strategies more intensively than the random tournament, allowing to move more in the average population strategy space at each run. In any case, the average results of *correlation* and *given-energy* are equivalent to the original ones for the three regimes identified, which means that the conclusions obtained by Pereda et al. are robust in all the identified regimes, i.e., that the three regimes are stability points of the system under consideration, since they are not affected by the different dynamics which can be imposed to the system.

[FIGURE 1]

As a consequence of all the above, the present work shows that the patterns found about the stable regimes are resilient and robust to the different types of dynamics. This suggests that even though the evolutionary dynamics of the real system may be different from the dynamics implemented, the behavioural mechanism of the population, in the absence of other processes, exhibits a strong tendency towards the patterns explained in CURP.

4. Discussion

Once the robustness of the results of the CURP model has been assessed and given that after considering a comprehensive set of dynamics, the confidence on them has been strengthened, it makes sense to contextualise and analyse in depth their implications from an archaeological and anthropological point of view.

According to the model, in low-stress regimes, given the abundance of resources, no adaptive pressure pushes the dominance of a sharing strategy over the others, and the co-existence of different dynamic practices may emerge. Cooperative behaviour (a norm for food sharing) becomes predominant in the intermediate-stress regime and turns to be unstable in the high-stress regime, where no strategy seems to be stable, and many individual strategies change in an attempt to innovate for survival.

4.1 Low-stress regime

Within the model, the low-stress regime represents a positive balance between population and resources where survival is highly probable. This sort of low-stress scenarios is often transitory and barely found in reality, since most environmental settings do not provide homogeneous resources (neither spatially nor temporally), and, as we know from biology and anthropology, most species/societies tend to increase population size with respect to the carrying capacity of that socioecological context, stabilizing by absorbing minor fluctuations due to density-independent factors that affect productivity (Hayden, 1972, 1986). It is a fact that population growth can be either brief (lasting a short time) or protracted; in any case, low-stress regimes are not the prevailing scenario in nature.

The transience of low-stress scenarios may be illustrated as the occupation of new areas or as a result of managing new resources. This conjuncture can be better exemplified as that of population processes, in which moderate population densities face new contexts. In such situations, available resources guarantee group survival until the society reaches a packed landscape (see Theler and Boszhardt (2006)), which can be attained either by demographic growth or simply by depletion of resources (which would produce “game sinks”, as defined in (Martin and Szuter, 1999; Lyman and Wolverton, 2002)). This makes the relationship with resources to change, being human populations in some cases responsible for extinction events (Faith and Surovell, 2009). Even though other causes such as forest clearance have been used to explain these extinction phenomena, it has been argued that overkill caused by humans may be the most plausible explanation (see reviews in Erlandson and Rick (2008) or Meltzer (2015). The extinction events may be extreme, but they exemplify how human agency effects on resource availability can make it move from low-stress to intermediate-stress regime, where new mechanisms and strategies are required to survive.

In accordance with all the above, in the CURP model, low-stress scenarios correspond to contexts where no environmental or endogenous elements push towards the selection of a particular strategy since all strategies are equally likely to succeed in terms of survival. Therefore, in low-stress contexts, the agents behave selecting their strategy indistinctly from the pool of possible behaviours, or maybe just according to previous social behavioural patterns. Besides this, and because of the absence of forces driving the development of specific strategies, these contexts, although somewhat transitory, may promote some slow transitions led by random drift mechanisms (Millstein, 2002; Bentley, Hahn and Shennan, 2004). Some pieces of research have stated that random drift and stochastic processes seem to play an important role when population sizes are small (Doebeli, Blarer and Ackermann, 1997; Pérez-Losada and Fort, 2011). Eventually, it has also been claimed that in areas with dense and predictable resources such as low-stress scenarios, competitive strategies may be favoured to maintain exclusive access to resources (Field, 2008).

4.2 Intermediate-stress regime

The different scenarios tagged as intermediate-stress regime correspond to contexts characterized by the discontinued appearance of resources of intermediate energy. Within the model, the agents’ target is to maximize their individual fitness. In the intermediate-stress regime, the prevailing behaviour of the agents is to share resources after their individual needs for survival are met; this cooperative strategy is a mechanism to deal with the future risk of scarcity, which leads to both the maximization of individual fitness as well as to the reinforcement of collective survival. The key concept here is that food sharing and indirect reciprocity emerge as a consequence of individual fitness maximization, since retaining an additional unit of resource diminishes the probability of receiving resources from other agents.

Although there are few exceptions in which HG societies store surpluses, this mostly happens when the seasonal fluctuation of specific resources is well-known and can be expected (Testart *et al.*, 1982; Whelan *et al.*, 2013), such as in the case of Northwest American complex HG or Australian aboriginal groups (Ames, 1994; Lourandos, 1997). Nevertheless, most HG societies usually face unpredictability of resources through different types of mobility and sharing (Smith, 2003; Hamilton *et al.*, 2009). In those scenarios, reciprocity is a mechanism to cope with the risk derived from environmental variability and unpredictability of resource distribution.

Regarding concepts such as stress or risk, even though they are frequently used in archaeological research, some authors claim the need for a proper definition (see a discussion in Larson et al (1996)). Several definitions of risk have been presented, in which the unpredictability over the possible outcome of a situation plays a major role (Winterhalder, 1990), while others focus on the idea of vulnerability or on surpassing a given threshold, such as that of starvation. Moreover, it can also be distinguished between those risky situations in which the possible results are known, but their probabilities are not, and situations of incomplete knowledge, in which the range of possible outcomes is unknown (Bamforth and Bleed, 2008). In both cases, unpredictability regarding resource variability forces to change the range of social decisions, sometimes with unknown or even unpredictable consequences (Rautman, 1993).

In HG contexts and in connection with risk minimization it is unavoidable to talk about the tolerated theft hypothesis (Blurton Jones, 1987), which claims that when someone is not capable of controlling a resource, she will allow access to the resource to other members of the community, as long as the cost of controlling it is much greater than the value of the resource itself (Bliege Bird and Bird, 1997; Kägi, 2001; Gurven, 2004). This hypothesis, a clear risk minimization strategy, has been considered as the origin of food transfer dynamics, as it would provide the necessary conditions for the other types of food sharing to emerge (Winterhalder, 1996).

In anthropological literature, reciprocity is used to understand how cooperation could evolve between unrelated individuals. It is also defined as the mechanism that explains how individuals make optimal decisions contingent on what others do, as the same individual acts as receptor and actor (Alvard, 2001).

In the intermediate-stress context, the heterogeneous distribution of resources happens to be a selective force that promotes the emergence and development of specific resource re-distribution mechanisms within the social domain. Reciprocal behaviour can be evolutionarily stable when individuals alternate their roles as actor and recipient so that at mid-term, investments reach all group members after some interactions (Melis and Semmann, 2010). In the case of HG, those social mechanisms for resource redistribution may be identified with the different sorts of food sharing practices, which are, in most cases, related with high-density foods and, more particularly, with meat.

These findings regarding the emergence of food sharing in intermediate-stress contexts may also assist to understand the phenomenon of the peopling of the planet. While the main part of human evolution took place in tropical areas, demographic growth, the occupation of new zones with lower or more disperse plant productivity (such as the arid areas in Africa) and the growing seasonality and heterogeneity of resources that extends towards higher latitudes, may have lead humans to adjust to major variations in food availability through social mechanisms such as food sharing (Barham and P., 2008).

For example, in the Arctic, where resources appear widely scattered, social units are highly dispersed too, so that technological innovation, as well as dynamic social organization, may have been paramount for survival (Hoffecker, 2005). Thus, it is in these mid-stress contexts where the social networks established through cooperation for survival play an essential role in all aspects of social life (Whallon, 1989). Until the 50s of the past century, most of the studies focusing on the social and economic changes faced by the Inuit communities of the North American Circumpolar regions, considered traditional food sharing bound to extinction in the face of acculturation. However, sharing as an institutionalized practice has survived and contemporary literature confirms its persistence. Even if changes appear in their material and social expression, sharing continues to be one of the organizational principles of Inuit societies and one of its most important identity traits (Lévesque *et al.*, 2000).

Consistently with all the above, it can be asserted that the cooperative enterprise which we find in many small-scale societies is the result of a long-term evolution related to limited and fluctuating resources (Handwerker, 1983). Several ethnographic pieces of evidence point to sharing as a form of cooperation on resource consumption that allows lowering the risk of shortages (see Bhanu (2014) and references therein). During seasons of scarcity these practices are reinforced so as to maintain the wellbeing of the whole group, and especially of those members who are not capable of obtaining food through their own efforts, such as children or sick and elderly people, as it has been documented among the Pumé from Venezuela (Kramer and Greaves, 2011), the Copper Inuit (Damas, 1996) or the Yámana (Gusinde, 1937) among others. In fact, the habits of consumption can change if the situation requires it, through strategies such as rationing of daily intake (Hamilton *et al.*, 2009).

The existence of social norms that promote sharing demonstrates the relevance of this cooperative strategy for the sustenance of the group (Witherspoon, 1975). The members that obtain resources distribute them to the rest, or put them into circulation within the group, in response to a socially established obligation (Kishigami, 2004). These prosocial interactions result not only in the provision of critical resources for group survival but are also encouraged as ethical and social obligations (Collings, Wenzel and Condon, 1998; Fortier, 2001). These interactions are maintained through the development of different social institutions, mainly normative (Horne and Cutlip, 2002; Kameda, Takezawa and Hastie, 2005; Ziker, 2014), that may include different types of sanctions (Horne, 2009). Through the reinforcement of social norms, sharing becomes one of the main cultural features of HG societies. Cheater detection mechanisms, as well as control mechanisms such as punishment, parcelling, partner switching, ostracism, etc. provide solutions that allow reciprocity be evolutionarily stable (Melis and Semmann, 2010). Accordingly, food distribution is identified as an identity and solidarity symbol, and it is enormously antisocial to consume food without sharing it (Witherspoon, 1975). This solidarity affects all members of the group as the obligation reaches anyone who has more resources than those that can be immediately consumed (Fortier, 2001).

In addition, the communication channels and social networks established thanks to food sharing, provide the means around which other cooperative behaviours belonging to different life spheres may be sustained, such as the establishment of marriages (Kaplan *et al.*, 1985; Hawkes, 1991) or political alliances among others (see a review in Patton (2005)). Moreover, it has also been argued that sharing accomplishes a signal function (Gurven *et al.*, 2000; Briz i Godino *et al.*, 2014) that reinforces the set of cooperative behaviours that accompany it.

4.3 High-stress regime

Within the regime of high-stress, the balance between population and resources is modified. Resources become scarcer and surpluses disappear, which translates into a growing difficulty to reach the survival threshold. Very unstable behaviours characterise the mainstream trend in such cases. The agents are continuously searching for survival strategies because no strategy is sustainable or efficient enough; innovation is therefore continuously present under high-stress conditions and this scenario might be useful to understand transitional periods.

From an anthropological point of view, in contexts of high-stress such as crisis, human societies tend to apply a wide range of responses to cope with the new conditions; when the population surpasses the carrying capacity, several mechanisms rebalance the situation so that the cycle may start again.

As we asserted in the introduction, in Archaeology, it is the production domain that is mostly used to explain how societies managed these unbalances. According to this, in crisis contexts, the mechanisms implemented can be directed towards two solutions; on the one hand, towards bringing the population back down through strategies such as migration (group fission), infanticide or decline in fertility. On the other hand, other strategies can be aimed at increasing the carrying capacity (increasing the productivity through changes in extraction procedures); good examples of these strategies are specialization (the exploitation of just a narrow range of resources (Byers and Ugan (2005)) whose on-encounter return rates are greater than those of other resources), diversification (increasing the productivity of a given territory through an increase in the variety of the resources consumed including famine foods or other resources (see Bicho and Haws (2008)), and intensification of resource exploitation (an increase in the productive output per unit of land or labour (see a discussion in Morrison (1994))).

These economic shifts have been identified in different archaeological periods. At the end of the Upper Palaeolithic, both physical indicators of activity levels and archaeological remains indicate an intensification and diversification of resource exploitation (Villotte *et al.*, 2010). Intensification has been extensively used to explain large socioeconomic shifts such as the transition to agriculture, which was preceded by a well-documented intensification of plant gathering (Wohlgemuth, 1996; Weiss *et al.*, 2004; Zeder, 2008) and animal management (Munro 2004). Besides, economic intensification has been considered a promotor of different social and organizational changes, including increasing social complexity (Johnson, 1982; Schurr and Schoeninger, 1995; Fitzhugh, 2003).

It is interesting to note, that beyond the production sphere and the social mechanisms that can be implemented to cope with unbalances, other phenomena such as social learning, may speed up innovation rates particularly in scenarios with high-density populations (Marquet *et al.*, 2012). Therefore, in high-stress contexts related to an increase in population, a plausible explanation for the wide exploration of strategies could be that the bigger the population, the higher the probability of knowledge and information transmission. This fact, together with a higher probability of random drift due to bigger population size, may explain the emergence of innovation in such contexts.

According to the adaptive cycle, which is one of the earliest metaphors from resilience thinkers that would latter give rise to resilience theory, extended periods of growth in which relationships change from loosely to tightly connected, are followed by release and reorganization processes (Nelson *et al.*, 2006; Lancelotti *et al.*, 2016). Therefore, in the context of resource crisis, organisational change is becoming an area of interest per se, as it provides a wider perspective of how human beings face resource unbalances, beyond the economic strategies mentioned.

These ideas of organisational change are perfectly coherent with the results of the CURP model since they show how under high-stress regime social agents try different alternatives, even though none of them stands out and becomes predominant. According to previous research, cooperation best emerges in contexts of stability (Nowak *et al.*, 2004), while in high-stress regimes, instability appears together with a decrease in cooperation. Whereas the promotion of cooperation reduces intraspecific competition (Hamilton *et al.*, 2009), high-stress contexts would promote changes in organizational strategies and the subsequent competitiveness.

When cooperative behaviours are not the primary strategy anymore, direct competition for resources may appear even among groups with different economic strategies (Bukach, 2004), leading to possible scenarios of conflict. In circumscribed contexts in which the carrying capacity has been reached, both environmental degradation and/or population stress have been commonly understood as primary sources of conflict (Theler and Boszhardt, 2006; Field, 2008).

It could be asserted that in intermediate-stress regimes societies reach a fluctuating equilibrium that enables the predominance of cooperation as a viable coordinated survival strategy. However, high-stress regimes can also emerge due to exogenous reasons that may lower resource richness with independence of the socio-ecological setting and the population size variations. Such could be the case of the Western Colonization and the Ecological Imperialism processes, in which an overexploitation of resources may have lead indigenous societies in a first instance to reinforce their cooperative strategies as a way to cope with the new situation, and in other cases to cross the boundary separating cooperative behaviour from other strategies that leave aside reciprocity. This shift from intermediate-stress to high-stress regime may enlighten the social breakdown of indigenous populations that induced the disappearance of their traditional lifestyles, forcing them to change to survive.

5. Conclusions

CURP analyses how individuals in environments with changing resource availability interact with other individuals either through cooperative (food sharing) or selfish strategies, producing as result an aggregate social behaviour. The model gives insights on how human societies may have faced changes in resource availability due to the occupation of new territories, socio-ecological changes or demographic growth among others.

We have assessed the robustness of the CURP model to some of the most popular selection and learning mechanisms. Our analysis confirms that the model leads to the same persistent regimes –low-stress, intermediate-stress and high-stress– regardless of the dynamics imposed. The particular regime reached by the population is determined by the resource pressure.

Once confirmed the robustness of the model, which strengthens our confidence in the results obtained, a detailed archaeological and anthropological contextualization of CURP results has been provided, indicating how societies may implement, increase or lower food sharing strategies when facing stress of different magnitudes. This helps to hypothesize and better understand possible past behaviours and how resource crisis were overcome in the context of hunter-gatherer societies. In particular, our results highlight the role of indirect reciprocity as a population coordination mechanism that promotes cooperation in the form of food sharing.

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References

Aktipis, C. A., Cronk, L. and de Aguiar, R. (2011) ‘Risk-Pooling and Herd Survival: An Agent-Based Model of a Maasai Gift-Giving System’, *Human Ecology*, 39(2), pp. 131–140. doi: 10.1007/s10745-010-9364-9.

Alvard, M. S. (2001) ‘Mutualistic hunting’, in Stanford, C. and Bunn, H. (eds) *he early human diet: The role of meat*. Oxford: Oxford University Press, pp. 261–278.

Alvard, M. S. and Nolin, D. A. (2002) ‘Rousseau’s Whale Hunt?’, *Current Anthropology*, 43(4), pp. 533–559. doi: 10.1086/341653.

Ames, K. M. (1994) ‘The Northwest Coast: Complex Hunter-Gatherers, Ecology, and Social Evolution’, *Annual Review of Anthropology*, 23, pp. 209–229. Available at: http://links.jstor.org/sici?sici=0084-6570%281994%292%3A23%3C209%3ATNCCHE%3E2.0.CO%3B2-G.

Angourakis, A., Santos, J. I., Galán, J. M. and Balbo, A. L. (2015) ‘Food for all: An agent-based model to explore the emergence and implications of cooperation for food storage’, *Environmental Archaeology*. Maney Publishing, 20(4), pp. 349–363. doi: 10.1179/1749631414Y.0000000041.

Axelrod, R. (1986) ‘An Evolutionary Approach to Norms’, *American Political Science Review*, 80(04), pp. 1095–1111. doi: 10.2307/1960858.

Axtell, R. (2000) ‘Why agents?: on the varied motivations for agent computing in the social sciences’, in Macal, C. M. and Sallach, D. (eds) *Proceedings of the Workshop on Agent Simulation: Applications, Models, and Tools*. Argonne, IL, pp. 3–24. doi: 10.1016/j.cep.2007.02.029.

Bamforth, D. B. and Bleed, P. (2008) ‘Technology, Flaked Stone Technology, and Risk’, *Archeological Papers of the American Anthropological Association*, 7(1), pp. 109–139. doi: 10.1525/ap3a.1997.7.1.109.

Barham, L. and P., M. (2008) *The first Africans: African archaeology from the earliest toolmakers to most recent foragers*. Cambridge: Cambridge University Press.

Bentley, R. A., Hahn, M. W. and Shennan, S. J. (2004) ‘Random drift and culture change’, *Proceedings of the Royal Society B: Biological Sciences*, 271(1547), pp. 1443–1450. doi: 10.1098/rspb.2004.2746.

Bhanu, B. A. (2014) ‘Food sharing and distribution of resources among hunter-gatherers: a conceptual clarification’, *The Eastern Anthropologist*, 67(3–4), pp. 325–343.

Bicho, N. and Haws, J. (2008) ‘At the land’s end: Marine resources and the importance of fluctuations in the coastline in the prehistoric hunter–gatherer economy of Portugal’, *Quaternary Science Reviews*, 27(23–24), pp. 2166–2175. doi: 10.1016/j.quascirev.2008.08.011.

Binford, L. R. (no date) *Constructing frames of reference: an analytical method for archaeological theory building using ethnographic and environmental data sets*. Berkeley and Los Angeles, CA: University of California Press.

Bird, D. W. (1997) ‘Delayed Reciprocity and Tolerated Theft: The Behavioral Ecology of Food-Sharing Strategies’, *Current Anthropology*, 38(1), pp. 49–78. doi: 10.1086/204581.

Bird, D. W. and O’Connell, J. F. (2006) ‘Behavioral Ecology and Archaeology’, *Journal of Archaeological Research*, 14(2), pp. 143–188. doi: 10.1007/s10814-006-9003-6.

Bliege Bird, R. and Bird, D. W. (1997) ‘Delayed Reciprocity and Tolerated Theft: The Behavioral Ecology of Food-Sharing Strategies’, *Current Anthropology*, 38(1), pp. 49–78. doi: 10.1086/204581.

Blurton Jones, N. G. (1987) ‘Tolerated theft, suggestions about the ecology and evolution of sharing, hoarding and scrounging’, *Social Science Information*, 26(1), pp. 31–54. doi: 10.1177/053901887026001002.

Borgerhoff Mulder, M. and Schacht, R. (2012) ‘Human Behavioural Ecology’, in *Encyclopedia of Life Sciences*. Chichester, UK: John Wiley & Sons, Ltd. doi: 10.1002/9780470015902.a0003671.pub2.

Bowles, S. and Gintis, H. (2004) ‘The evolution of strong reciprocity: cooperation in heterogeneous populations’, *Theoretical Population Biology*, 65(1), pp. 17–28. doi: 10.1016/j.tpb.2003.07.001.

Briz i Godino, I., Santos, J. I., Galán, J. M., Caro, J., Álvarez, M. and Zurro, D. (2014) ‘Social Cooperation and Resource Management Dynamics Among Late Hunter-Fisher-Gatherer Societies in Tierra del Fuego (South America)’, *Journal of Archaeological Method and Theory*, 21(2), pp. 343–363. doi: 10.1007/s10816-013-9194-3.

Bukach, D. (2004) ‘The Mesolithic-Neolithic Transition on the Channel Islands: Adopting Agriculture in an Emerging Island Landscape’, *Environmental Archaeology*, 9(2), pp. 155–162. doi: 10.1179/env.2004.9.2.155.

Byers, D. A. and Ugan, A. (2005) ‘Should we expect large game specialization in the late Pleistocene? An optimal foraging perspective on early Paleoindian prey choice’, *Journal of Archaeological Science*. doi: 10.1016/j.jas.2005.05.003.

Chapman, J. (2008) ‘Approaches to trade and exchange in earlier prehistory (Late Mesolithic–Early Bronze Age).’, in *Prehistoric Europe: theory and practice,* p. 333–355.

Collings, P., Wenzel, G. and Condon, R. (1998) ‘Modern food sharing networks and community integration in the central Canadian Arctic’, *Artic*, 51(4), pp. 301–314.

Damas, D. (1996) ‘Culture Summary: Copper Inuit’, in. New Haven, Conn.: HRAF Publication Information: New Haven, Conn.: HRAF, 1996. Computer File.

Doebeli, M., Blarer, A. and Ackermann, M. (1997) ‘Population dynamics, demographic stochasticity, and the evolution of cooperation.’, *Proceedings of the National Academy of Sciences of the United States of America*, 94(10), pp. 5167–71. Available at: http://www.ncbi.nlm.nih.gov/pubmed/9144209.

Dyke, R. M. Van (1999) ‘The Chaco Connection: Evaluating Bonito-Style Architecture in Outlier Communities’, *Journal of Anthropological Archaeology,* 18(4), p. 471–506. Available at: file:///Users/DZ/Documents/Mendeley Desktop/Dyke - 1999 - The Chaco Connection Evaluating Bonito-Style Architecture in Outlier Communities.pdf.

Edmonds, B. and Hales, D. (2005) ‘Computational simulation as theoretical experiment’, *Journal of Mathematical Sociology*, 29(February 2015), pp. 209–232. doi: 10.1080/00222500590921283.

Enloe, J. (2003) ‘Food sharing past and present’, *Before Farming*, 2003(1), pp. 1–23. doi: 10.3828/bfarm.2003.1.1.

Epstein, J. M. (1999) ‘Agent-based computational models and generative social science’, *Complexity*, 4(5), pp. 41–60. doi: 10.1002/(SICI)1099-0526(199905/06)4:5<41::AID-CPLX9>3.0.CO;2-F.

Erlandson, J. and Rick, T. (2008) ‘Archaeology, Marine Ecology, and Human Impacts on Marine Environments’, in Erlandson, J. and Rick, T. C. (eds) *Human impacts on ancient marine ecosystems: a global perspective*. London: University of California Press, pp. 1–20.

Faith, J. T. and Surovell, T. A. (2009) ‘Synchronous extinction of North

America's Pleistocene mammals', *Proceedings of the National Academy of Sciences*. doi: 10.1073/pnas.0908153106.
Field, J. S. (2008) 'Explaining Fortifications in Indo-Pacific Prehistory', *Archaeology in Oceania*, 43(1), pp. 1–10. doi: 10.1002/j.1834-4453.2008.tb00025.x.
Fitzhugh, B. (2003) 'The Evolution of Complex Hunter-Gatherers', in *The Evolution of Complex Hunter-Gatherers*. Boston, MA: Springer US (Interdisciplinary Contributions to Archaeology), pp. 1–10. doi: 10.1007/978-1-4615-0137-4.
Fortier, J. (2001) 'Sharing, Hoarding, and Theft: Exchange and Resistance in Forager-Farmer Relations', *Ethnology*, 40(3), p. 193. doi: 10.2307/3773965.
Freeman, J. and Anderies, J. M. (2012) 'Intensification, Tipping Points, and Social Change in a Coupled Forager-Resource System', *Human Nature*, 23(4), pp. 419–446. doi: 10.1007/s12110-012-9154-8.
Galán, J. M. and Izquierdo, L. R. (2005) 'Appearances can be deceiving: Lessons learned re-implementing Axelrod's "Evolutionary Approach to Norms"', *Journal of Artificial Societies and Social Simulation*, 8(3). Available at: http://jasss.soc.surrey.ac.uk/8/3/2.html.
Galán, J. M., Izquierdo, L. R., Izquierdo, S. S., Santos, J. I., del Olmo, R. and López-Paredes, A. (2013) 'Checking Simulations: Detecting and Avoiding Errors and Artefacts', in Edmonds, B. and Meyer, R. (eds) *Simulating Social Complexity*. Berlin, Heidelberg: Springer Berlin Heidelberg (Understanding Complex Systems), pp. 95–116. doi: 10.1007/978-3-540-93813-2_6.
Galán, J. M., Izquierdo, L. R., Izquierdo, S. S., Santos, J. I., del Olmo, R., López-Paredes, A. and Edmonds, B. (2009) 'Errors and Artefacts in Agent-Based Modelling ', *Journal of Artificial Societies and Social Simulation*, 12(1), p. 1. Available at: http://jasss.soc.surrey.ac.uk/12/1/1.html.
Gurven, M. (2004) 'To give and to give not: The behavioral ecology of human food transfers', *Behavioral and Brain Sciences*, 27(04). doi: 10.1017/S0140525X04000123.
Gurven, M., Allen-Arave, W., Hill, K. and Hurtado, M. (2000) '"It's a Wonderful Life": signaling generosity among the Ache of Paraguay', *Evolution and Human Behavior*, 21(4), pp. 263–282. doi: 10.1016/S1090-5138(00)00032-5.
Gusinde, M. (1937) *Die Feuerlenad Indianer. Die Yamana. Vom Leben und Denken der Wassernomaden am Kap Hoorn*. Mödling: Verlag der Internationalen Zeitschrift 'Anthropos'.
Hamilton, M. J., Burger, O., DeLong, J. P., Walker, R. S., Moses, M. E. and Brown, J. H. (2009) 'Population stability, cooperation, and the invasibility of the human species', *Proceedings of the National Academy of Sciences*, 106(30), pp. 12255–12260. doi: 10.1073/pnas.0905708106.
Handwerker, W. P. (1983) 'The First Demographic Transition: An Analysis of Subsistence Choices and Reproductive Consequences', *American Anthropologist*, 85(1), pp. 5–27. doi: 10.1525/aa.1983.85.1.02a00010.
Hawkes, K. (1991) 'Showing off', *Ethology and Sociobiology*, 12(1), pp. 29–54. doi: 10.1016/0162-3095(91)90011-E.
Hayden, B. (1972) 'Population control among hunter/gatherers.', *World Archaeology*, 4(2), pp. 205–221.
Hayden, B. (1986) 'Resources, rivalry, and reproduction: the influence of basic resource characteristics on reproductive behavior', *Culture and Reproduction*. Westview Press Boulder, CO, pp. 176–195.

Henrich, J., Boyd, R., Bowles, S., Camerer, C., Fehr, E., Gintis, H. and McElreat, R. (2001) ‘In Search of Homo Economicus: Behavioral Experiments in 15 Small-Scale Societies’, *American Economic Review*, 91(2), pp. 73–78.

Hill, K. (2002) ‘Altruistic cooperation during foraging by the Ache, and the evolved human predisposition to cooperate’, *Human Nature*, 13(1), pp. 105–128. doi: 10.1007/s12110-002-1016-3.

Hoffecker, J. F. (2005) *A prehistory of the north: human settlement of the higher latitudes*. Rutgers University Press.

Horne, C. (2009) *The Rewards of Punishment: A Relational Theory of Norm Enforcement*. Palo Alto, CA: Stanford University Press.

Horne, C. and Cutlip, A. (2002) ‘Sanctioning Costs and Norm Enforcement’, *Rationality and Society*, 14(3), pp. 285–307. doi: 10.1177/1043463102014003002.

Izquierdo, L., Izquierdo, S. and Vega-Redondo, F. (2012) ‘Learning and Evolutionary Game Theory’, *Encyclopedia of the Sciences of learning*, 36(1988), pp. 1782–1788. doi: 10.1007/978-1-4419-1428-6_576.

Janssen, M. A. and Hill, K. (2014) ‘Benefits of Grouping and Cooperative Hunting Among Ache Hunter–Gatherers: Insights from an Agent-Based Foraging Model’, *Human Ecology*, 42(6), pp. 823–835. doi: 10.1007/s10745-014-9693-1.

Johnson, G. A. (1982) ‘Organizational Structure and Scalar Stress’, in C. Renfrew, M. R. and B. S. (ed.) *Theory and explanation in archaeology: the Southampton conference*. New York: Academic Press, p. 389–421.

Kägi, W. (2001) ‘The tragedy of the commons revisited: sharing as a means to avoid environmental ruin’, in *IWOE Discussion Paper 91*. Institut für Wirtschaft und Ökologie.

Kameda, T., Takezawa, M. and Hastie, R. (2005) ‘Where Do Social Norms Come From?’, *Current Directions in Psychological Science*, 14(6), pp. 331–334. doi: 10.1111/j.0963-7214.2005.00392.x.

Kaplan, H., Hill, K., Cadeliña, R. V, Hayden, B., Hyndman, D. C., Preston, R. J., Smith, E. A., Stuart, D. E. and Yesner, D. R. (1985) ‘Food Sharing Among Ache Foragers: Tests of Explanatory Hypotheses [and Comments and Reply]’, *Current Anthropology*, 26(2), pp. 223–246. doi: 10.1086/203251.

Kishigami, N. (2004) ‘A New Typology of Food-Sharing Practices among Hunter-Gatherers, with a Special Focus on Inuit Examples’, *Journal of Anthropological Research*, 60(3), pp. 341–358. doi: 10.1086/jar.60.3.3630754.

Kramer, K. L. and Greaves, R. D. (2011) ‘Postmarital Residence and Bilateral Kin Associations among Hunter-Gatherers’, *Human Nature*, 22(1–2), pp. 41–63. doi: 10.1007/s12110-011-9115-7.

Lake, M. W. (2014) ‘Trends in Archaeological Simulation’, *Journal of Archaeological Method and Theory*, 21(2), pp. 258–287. doi: 10.1007/s10816-013-9188-1.

Lancelotti, C., Zurro, D., Whitehouse, N. J., Kramer, K. L., Madella, M., García-granero, J. J. and Greaves, R. D. (2016) ‘Resilience of small-scale societies ’ livelihoods : a framework for studying the transition from food gathering to food production’, *Ecology and Society*, 21(4), p. art8. doi: 10.5751/ES-08757-210408.

Larson, D. O., Neff, H., Graybill, D. A., Michaelsen, J. and Ambos, E. (1996) ‘Risk, Climatic Variability, and the Study of Southwestern Prehistory: An Evolutionary Perspective’, *American Antiquity*, 61(02), pp. 217–241. doi:

10.2307/282419.

Lévesque, C., De Juriew, D., Lussier, C. and Trudeau, N. (2000) ‘Between abundance and scarcity: food and the institution of sharing among the inuit of the circumpolar region during the recent historical period’, in Duhaime, G. (ed.) *Sustainable food security in the Arctic: state of knowledge*. Canada: CCIPress, pp. 103–1015.

Lourandos, H. (1997) *Continent of hunter-gatherers: new perspectives in Australian prehistory*. Cambridge: Cambridge University Press.

Lyman, R. L. and Wolverton, S. (2002) ‘The Late Prehistoric-Early Historic Game Sink in the Northwestern United States’, *Conservation Biology*, 16(1), pp. 73–85. doi: 10.1046/j.1523-1739.2002.00066.x.

Lynch, M. and Walsh, B. (1998) *Genetics and analysis of quantitative traits*. Sunderland, MA: Sinauer.

Marquet, P. A., Santoro, C. M., Latorre, C., Standen, V. G., Abades, S. R., Rivadeneira, M. M., Arriaza, B. and Hochberg, M. E. (2012) ‘Emergence of social complexity among coastal hunter-gatherers in the Atacama Desert of northern Chile’, *Proceedings of the National Academy of Sciences*, 109(37), pp. 14754–14760. doi: 10.1073/pnas.1116724109.

Martin, P. S. and Szuter, C. R. (1999) ‘War Zones and Game Sinks in Lewis and Clark’s West’, *Conservation Biology*, 13(1), pp. 36–45. doi: 10.1046/j.1523-1739.1999.97417.x.

Melis, A. P. and Semmann, D. (2010) ‘How is human cooperation different?’, *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365(1553), pp. 2663–2674. doi: 10.1098/rstb.2010.0157.

Meltzer, D. J. (2015) ‘Pleistocene Overkill and North American Mammalian Extinctions*’, *Annu. Rev. Anthropol*, 44, pp. 33–53. doi: 10.1146/annurev-anthro-102214-013854.

Millstein, R. L. (2002) ‘Are Random Drift and Natural Selection Conceptually Distinct?’, *Biology & Philosophy*, 17(1), pp. 33–53. doi: 10.1023/A:1012990800358.

Minc, L. D. and Smith, K. P. (1989) ‘The spirit of survival: cultural responses to resource variability in North Alaska’, in Halstead, P. and O’Shea, J. (eds) *Bad Year Economics: Cultural Responses to Risk and Uncertainty*. Cambridge: Cambridge University Press, pp. 8–39.

Mitchell, M. (1996) *An Introduction to Genetic Algorithms*. Cambridge, MA: MIT Press.

Morrison, A. E. and Addison, D. J. (2008) ‘Assessing the role of climate change and human predation on marine resources at the Fatu-ma-Futi site, Tutuila Island, American Samoa: an agent based model’, *Archaeology in Oceania*, 43(1), pp. 22–34. doi: 10.1002/j.1834-4453.2008.tb00027.x.

Morrison, K. D. (1994) ‘The intensification of production: Archaeological approaches’, *Journal of Archaeological Method and Theory*, 1(2), pp. 111–159. doi: 10.1007/BF02231414.

Munro, N. D. (2004) ‘Zooarchaeological Measures of Hunting Pressure and Occupation Intensity in the Natufian’, *Current Anthropology*, 45(S4), pp. S5–S34. doi: 10.1086/422084.

Nelson, M. C., Hegmon, M., Kulow, S. and Schollmeyer, K. G. (2006) ‘Archaeological and Ecological Perspectives on Reorganization: A Case Study from the Mimbres Region of the U.S. Southwest’, *American Antiquity*, 71(3), p. 403. doi: 10.2307/40035359.

Nettle, D., Gibson, M. A., Lawson, D. W. and Sear, R. (2013) ‘Human behavioral ecology: Current research and future prospects’, *Behavioral Ecology*, 24(5), pp. 1031–1040. doi: 10.1093/beheco/ars222.

Nowak, M. A., Sasaki, A., Taylor, C. and Fudenberg, D. (2004) ‘Emergence of cooperation and evolutionary stability in finite populations’, *Nature*, 428(6983), pp. 646–650. doi: 10.1038/nature02414.

Patton, J. Q. (2005) ‘Meat sharing for coalitional support’, *Evolution and Human Behavior*, 26(2), pp. 137–157. doi: 10.1016/j.evolhumbehav.2004.08.008.

Pereda, M., Santos, J. I. and Galán, J. M. (2017) ‘A Brief Introduction to the Use of Machine Learning Techniques in the Analysis of Agent-Based Models’, in Hernández, C. (ed.) *Advances in Management Engineering*. Springer, pp. 179–186. doi: 10.1007/978-3-319-55889-9_11.

Pereda, M., Zurro, D., Santos, J. I., Briz i Godino, I., Álvarez, M., Caro, J. and Galán, J. M. (2017) ‘Emergence and Evolution of Cooperation Under Resource Pressure’, *Scientific Reports*, 7, p. 45574. doi: 10.1038/srep45574.

Pérez-Losada, J. and Fort, J. (2011) ‘Spatial dimensions increase the effect of cultural drift’, *Journal of Archaeological Science*, 38(6), pp. 1294–1299. doi: 10.1016/j.jas.2011.01.004.

Rautman, A. E. (1993) ‘Resource Variability, Risk, and the Structure of Social Networks: An Example from the’, *American Antiquity*, 58(3), pp. 403–424. doi: 10.2307/282104.

Ryan, P. and Rosen, A. (2016) ‘Managing Risk through Diversification in Plant Exploitation during the Seventh Millennium BC’, in *Climate and Cultural Change in Prehistoric Europe and the Near East*, p. 117.

Sandholm, W. H. (2010) *Population Games and Evolutionary Dynamics*. Cambridge, MA: MIT Press.

Schurr, M. R. and Schoeninger, M. J. (1995) ‘Associations between Agricultural Intensification and Social Complexity: An Example from the Prehistoric Ohio Valley’, *Journal of Anthropological Archaeology*, 14(3), pp. 315–339. doi: 10.1006/jaar.1995.1016.

Smaldino, P. E., Newson, L., Schank, J. C. and Richerson, P. J. (2013) ‘Simulating the Evolution of the Human Family: Cooperative Breeding Increases in Harsh Environments’, *PLoS ONE*. Edited by A. Mesoudi, 8(11), p. e80753. doi: 10.1371/journal.pone.0080753.

Smith, C. S. (2003) ‘Hunter–gatherer mobility, storage, and houses in a marginal environment: an example from the mid-Holocene of Wyoming’, *Journal of Anthropological Archaeology*, 22(2), pp. 162–189. doi: 10.1016/S0278-4165(03)00017-5.

Smith, P. E. L. (1972) ‘Changes in population pressure in archaeological explanation’, *World Archaeology*. Routledge, 4(1), pp. 5–18. doi: 10.1080/00438243.1972.9979517.

Speth, J. D. (2004) ‘Hunting pressure, subsistence intensification, and demographic change in the Levantine Late Middle Paleolithic’, in Goren-Inbar, N. and Speth, J. D. (eds) *Human Paleoecology in the Levantine Corridor*. Oxford: Oxbow Books, pp. 149–166.

Stiner, M. C., Barkai, R. and Gopher, A. (2009) ‘Cooperative hunting and meat sharing 400-200 kya at Qesem Cave, Israel’, *Proceedings of the National Academy of Sciences*, 106(32), pp. 13207–13212. doi: 10.1073/pnas.0900564106.

Takahashi, N. (2000) ‘The Emergence of Generalized Exchange’, *American*

Journal of Sociology, 105(4), pp. 1105–1134. doi: 10.1086/210400.
Testart, A., Forbis, R. G., Hayden, B., Ingold, T., Perlman, S. M., Pokotylo, D. L., Rowley-Conwy, P. and Stuart, D. E. (1982) ‘The Significance of Food Storage Among Hunter-Gatherers: Residence Patterns, Population Densities, and Social Inequalities’, *Current Anthropology*. [University of Chicago Press, Wenner-Gren Foundation for Anthropological Research], 23(5), pp. 523–537. Available at: http://www.jstor.org/stable/2742392.
Theler, J. L. and Boszhardt, R. F. (2006) ‘Collapse of Crucial Resources and Culture Change: A Model for the Woodland to Oneota Transformation in the Upper Midwest’, *American Antiquity*, 71(03), pp. 433–472. doi: 10.1017/S0002731600039767.
Verhagen, P. and Whitley, T. G. (2012) ‘Integrating Archaeological Theory and Predictive Modeling: a Live Report from the Scene’, *Journal of Archaeological Method and Theory*, 19(1), pp. 49–100. doi: 10.1007/s10816-011-9102-7.
Villotte, S., Churchill, S. E., Dutour, O. J. and Henry-Gambier, D. (2010) ‘Subsistence activities and the sexual division of labor in the European Upper Paleolithic and Mesolithic: Evidence from upper limb enthesopathies’, *Journal of Human Evolution*, 59(1), pp. 35–43. doi: 10.1016/j.jhevol.2010.02.001.
Weiss, E., Wetterstrom, W., Nadel, D. and Bar-Yosef, O. (2004) ‘The broad spectrum revisited: Evidence from plant remains’, *Proceedings of the National Academy of Sciences*, 101(26), pp. 9551–9555. doi: 10.1073/pnas.0402362101.
Whallon, R. (1989) ‘Elements of Cultural Change in the Later Paleolithic’, in Mellars, P. and Stringer, C. (eds) *The Human Revolution*. Princeton, NJ: Princeton University Press, pp. 433–454.
Whelan, C. S., Whitaker, A. R., Rosenthal, S. J. and Wohlgemuth, E. (2013) ‘Hunter-Gatherer Storage, Settlement, and the Opportunity Costs of Women’s Foraging’, *American Antiquity*, 78(4), pp. 662–678.
White, P., Bowdler, S., Kuhn, S., McNiven, I., Shott, M., Veth, P. and White, P. (2011) ‘Forum: Backed Artefacts: Useful Socially and Operationally’, *Australian Archaeology*, 72(1), pp. 67–75. doi: 10.1080/03122417.2011.11690534.
Whitley, T. G. (2016) ‘Archaeological Simulation and the Testing Paradigm’, in Burg, M. B., Peeters, H., and Lovis, W. A. (eds) *Uncertainty and Sensitivity Analysis in Archaeological Computational Modeling*. Springer, pp. 131–156.
Wilensky, U. (1999) *NetLogo*. Evanston, IL: Center for Connected Learning and Computer-Based Modeling, Northwestern University,. Available at: http://ccl.northwestern.edu/netlogo/.
Williams, A. N., Ulm, S., Turney, C. S. M., Rohde, D. and White, G. (2015) ‘Holocene Demographic Changes and the Emergence of Complex Societies in Prehistoric Australia’, *PLOS ONE*. Edited by N. Bicho, 10(6), p. e0128661. doi: 10.1371/journal.pone.0128661.
Winterhalder, B. (1986) ‘Diet choice, risk, and food sharing in a stochastic environment’, *Journal of Anthropological Archaeology*, 5(4), pp. 369–392. doi: 10.1016/0278-4165(86)90017-6.
Winterhalder, B. (1990) ‘Open field, common pot: Harvest variability and risk avoidance in agricultural and foraging societies’, in Cashdan, E. A. (ed.) *Risk and uncertainty in tribal and peasant economies*. Boulder, CO: Westview Press, pp. 67–87.
Winterhalder, B. (1996) ‘A marginal model of tolerated theft’, *Ethology and Sociobiology*, 17(1), pp. 37–53. doi: 10.1016/0162-3095(95)00126-3.

Witherspoon, G. (1975) *Navajo kinship and marriage*. University of Chicago Press.
Wohlgemuth, E. (1996) ‘Resource Intensification in Prehistoric Central California: Evidence from Archaeobotanical Data’, *Journal of California and Great Basin Anthropology Joumal of Califomia and Great Basin Anthropology*, 18(1), pp. 81–103. Available at: http://escholarship.org/uc/item/6qh339x2%5Cnhttp://www.escholarship.org/help_copyright.html#reuse.
Wurzer, G., Kowarik, K. and Reschreiter, H. (2015) *Agent-based modeling and simulation in archaeology*. Vienna, Austria: Springer.
Zeder, M. A. (2008) ‘Domestication and early agriculture in the Mediterranean Basin: Origins, diffusion, and impact’, *Proceedings of the National Academy of Sciences*, 105(33), pp. 11597–11604. doi: 10.1073/pnas.0801317105.
Zeder, M. A. (2012) ‘The Broad Spectrum Revolution at 40: Resource diversity, intensification, and an alternative to optimal foraging explanations’, *Journal of Anthropological Archaeology*, 31(3), pp. 241–264. doi: 10.1016/j.jaa.2012.03.003.
Ziker, J. P. (2014) ‘Sharing, Subsistence, and Social Norms in Northern Siberia’, in Ensminger, J. and Henrich, J. (eds) *Experimenting with social norms: fairness and punishment in cross-cultural perspective*. New York, NY: Russel Sage Foundation, pp. 337–356.

CAPTIONS: Illustrations and tables

Table 1. Study parameters for each simulation scenario in the CURP model.

Table 2. Experiments of selection mechanisms

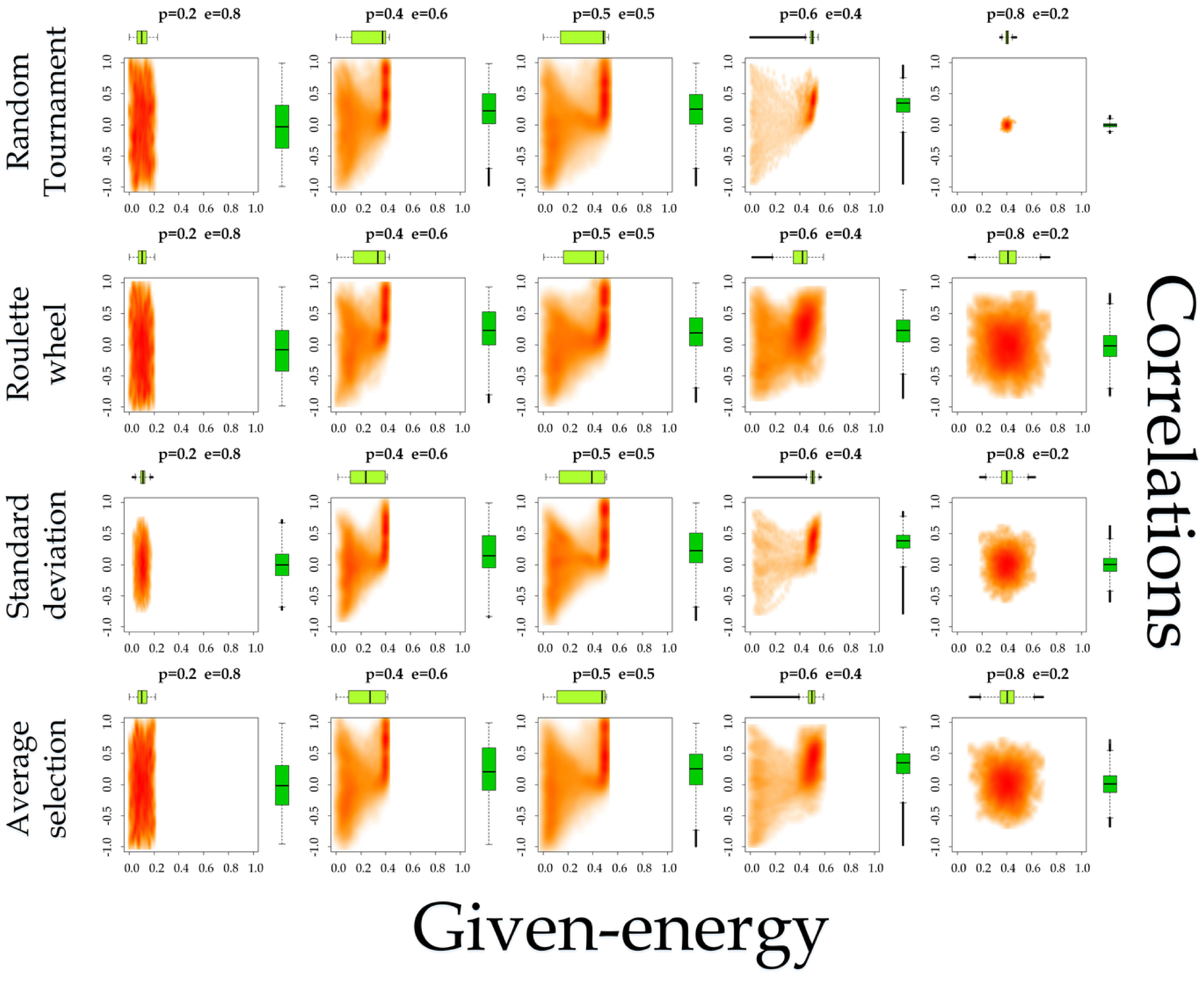
Figure 1. This figure shows the simulation results obtained for each evolutionary or learning selection mechanism analysed, five combinations of parameters have selected for each selection mechanism. Each subfigure shows the density of the simulation results of the model in the space of the averaged strategies of the population: (i) *given-energy* (horizontal axis) and (ii) *correlation* (vertical axis) and two box-plots to summarize and compare the distributions. The parameters *prob-resource* (p in titles) and *min-energy* (e in titles) correspond in the left column to a high-stress regime, in the right column to a low-stress regime, and the three central columns to mid-stress regimes. In this smoothed colour density scatterplot, darker values (red) indicate a higher probability of the simulation to be found in the corresponding averaged population states. The outcomes obtained show that the results and conclusions of the model are robust to the mechanisms analysed.

Parameter	Description
N-people	The number of agents.
Prob-resource	The probability that an agent obtains a resource unit at each time period.
Min-energy	The minimal proportion of the resource necessary for survival.
Sharing-tournament-size	percentage of agents from the population that obtained no resource at a time period and that are susceptible of being chosen by a particular donor.
Strategy-tournament-size	percentage of agents from the population that a particular agent takes into account for selecting a new strategy. The agent samples strategy-tournament-size agents from the population and then she imitates the best strategy, i.e., the strategy of the agent with the highest fitness if the corresponding fitness is greater than her own.
Prob-mutation	The probability that an agent decides to follow a new strategy randomly chosen from the strategy space.
Rounds-per-generation	Number of time periods for which the values of the parameters that define each agent's strategy remain unchanged. Agents can change their strategy every rounds-per-generation time periods.

Table 1. Study parameters for each simulation scenario in the CURP model.

Experiment	prob-resource	min-energy
Low-stress regime	0.8	0.2
Intermediate-stress regime 1	0.6	0.4
Intermediate-stress regime 2	0.5	0.5
Intermediate-stress regime 3	0.4	0.6
High-stress regime	0.2	0.8

Table 2. Experiments of selection mechanisms


p=0.2 e=0.8
p=0.4 e=0.6
p=0.5 e=0.5
p=0.6 e=0.4
p=0.8 e=0.2
Random Tournament
Roulette wheel
Standard deviation
Average selection
Correlations
Given-energy
-1.0
-0.5
0.0
0.5
1.0
0.0
0.2
0.4
0.6
0.8
1.0