J Archaeol Method Theory (2014) 21:385–404
DOI 10.1007/s10816-013-9185-4

A Simulation Model of Fission–Fusion Dynamics and Long-Term Settlement Change

Enrico R. Crema

Abstract Archaeological analyses often detect abrupt changes over time in the hierarchy of settlement sizes and the spatial distribution of residential units. These transformations have been explained looking at a variety of possible causes, from climatic changes to the sudden release of slowly cumulating political tensions. While many of these models offer plausible explanations for specific historical contexts, a broad-breadth model is desirable if cross-cultural analysis is sought. This paper tackles this problem by starting from the theoretical proposition that human groups are characterised by a non-linear relationship between size and per-capita fitness. Increasing group size has beneficial effects, but once a certain threshold is exceeded, negative frequency dependence will start to predominate leading to a decline in the per-capita fitness. Such a relationship can potentially have long-term implications in the spatial structure of human settlements if individuals have the possibility to modify their fitness through group fission–fusion dynamics. I will illustrate the equilibrium properties of these dynamics by means of an abstract agent-based simulation and discuss its implication for understanding long-term changes in human settlement pattern. Results suggest that changes in settlement pattern can originate from internal dynamics alone if the system is highly integrated and interconnected.

Keywords Settlement pattern · Fission–fusion · Agent-based model · Rank–size analysis

Introduction

Settlement patterns are one of the most tangible footprints of human culture on our planet. Vast regions of the world are covered by intricate patterns of residential features, emerging from aggregate, historical, and in many cases unintended outcomes of individual

---

Electronic supplementary material The online version of this article (doi:10.1007/s10816-013-9185-4) contains supplementary material, which is available to authorized users.

E. R. Crema (✉)
Institute of Archaeology, UCL, 31-34 Gordon Square, WC1H 0PY London, UK
e-mail: e.crema@ucl.ac.uk

decision-making. These patterns change continuously, driven by forces originating from within the system and disturbance processes from outside.

Archaeologists have a unique perspective of these episodes of settlement change. We see patterns unfolding, spatial configurations emerging in the landscape, and then vanishing over time. Yet, this vision is partially impaired by a relatively poor empirical record, a series of deteriorated and blurry snapshots (Dewar and McBride 1992), which we often need to interpolate with narratives drawn from ethnographic analogies and modern geography. Computer simulation provides a robust and quantitative alternative for conducting this exercise. We can infer possible underlying processes deductively, combining assumptions drawn from the anthropological and ecological literature and formally linking individual behaviour to its aggregate outcomes.

This paper seeks to contribute to this overarching research agenda by focusing on the long-term fluctuations of settlement rank–size distribution. Several authors have identified multiple hypotheses behind different shapes in empirically observed rank–size patterns. For example, a relatively uniform distribution of settlement sizes have often been associated with central place theory or assumed to be the consequence of territorial isolation with low levels of system integration; on the other hand, highly hierarchical patterns have been explained with the concentration of key resources or low-cost labor in few core locations (Johnson 1980; Savage 1997). Evidence of shifts between these two extremes have been identified amongst pre-Columbian sites in Peru (Drennan and Peterson 2004), Mesoamerican early complex polities (Carballo and Pluckhahn 2007; Griffin 2011), early farming villages in Southwestern Colorado (Kohler and Varien 2010) and prehistoric complex hunter–gatherers in Japan (Crema, 2013c). Although the cultural, political and economic context differ substantially between these case studies, they all share some similarities in their historical trajectories, with structurally akin settlement pattern and hierarchy often remerging multiple times. The settlement history of Jomon hunter–gatherers of Japan is perhaps the most striking example, with an almost regular cycle of alternation between periods of strong nucleation and dispersion (Crema, 2013c).

These archaeological evidence lead us to ask whether the re-emergence of similar spatial configurations in the long-term is the result of similar external forces reoccurring multiple times (*e.g.* climatic changes to Bond cycles; Bond *et al.* 1997), or is rather result from forces accumulating internally in the system itself, and emerging as periodic episodes of self-reorganisation and settlement change.

I will address this question via an abstract model that transcends from the details of any specific cultural context. This choice allows the development of a simple heuristic model where universal assumptions inspired from the ecological literature are combined *in silico*, without the risk of generating *ad hoc* complex models that can be hardly explored exhaustively. The primary goal is to establish whether radical shifts in the settlement pattern can occur without the aid of external perturbations to the system and identify conditions that might promote such events.

Spatial Dependency and Group Formation

A useful conceptual framework for investigating any spatial pattern is the distinction between *induced* and *inherent spatial dependencies* (Fortin and Dale 2005). The former refers to spatial distributions that are conditional to variables external to the system of interest (*e.g.* variations in population density as a consequence of different levels of resource availability), while the latter refers to intrinsic properties of the generative process that can be manifest in forms of repulsive (*e.g.* territorial spacing between settlements) and attractive forces (*e.g.* clusters of households committed to cooperative tasks).

The distinction is clear only in theory, and any real world patterning is a mixture of different forms of spatial dependencies acting at different spatial scales. Nonetheless, much of the modern statistics dedicated to point process modelling departs from this dichotomy in developing tools for assessing empirical spatial distributions (Illian *et al.* 2008; Bevan *et al.* 2013).

We can adopt the same heuristic distinction and question the distribution of settlement patterns from the perspective of their individual constituents. Induced and inherent spatial dependencies will affect the decision-making of each individual (a household, or any other aggregation of individuals sharing the same destiny after a decision) and the consequent location of individual residential units. The aggregate effect of these dependencies will ultimately result in a variety of spatial patterns, between dispersion and nucleation (Roberts 1996). This anthropic landscape can be examined by measuring the spacing between individual residential units (Crema *et al.* 2010), the spatial aggregation and segregation of the clusters (*i.e.* settlements) they form (Bevan and Connolly 2006) and the size distribution of the settlements (Drennan and Peterson 2004).

Ecological, anthropological and archaeological theory on group formation have implicitly emphasised the importance of one form of spatial dependence over another. Some authors consider the presence of residential clusters as the result of individuals being "pushed" together, while seeking to be closer to optimal locations in the landscape, attracted, for example, by a higher density of resources (Horn 1968; Jochim 1976; Cashdan 1992); others focus on the beneficial effect of the grouping itself, hence theorising that individuals are "pulled" by the presence of other individuals (Clark and Mangel 1986; Halstead and O'Shea 1989; Hawkes 1992).

One of the most popular examples of the "push" argument is the *Ideal Free Distribution* (IFD; Fretwell and Lucas 1970; for archaeological applications, see Kennett *et al.* 2006; Winterhalder *et al.* 2010). Although different variants of the model have been proposed (*e.g.* Ideal Despotic Distribution, Møller 1995), the basic principle of the IFD suggests that, given full knowledge of the resource productivity and no constraints in the movement, the distribution of individuals will match the spatial structure of the resource density. In this equilibrium condition, all individuals will receive the same payoff, and the relocation of any individual will be detrimental to someone else. The assumption behind this outcome derives from the commonsensical notion that given a finite amount of resources, an increase in population density will lead to a decline in the *per capita* intake. This negative frequency dependence of individual fitness will lead to a decline in the attractiveness of locations with high population density.

The standard version of the IFD model does not include any beneficial role for increase in population density, as individuals will be only "pushed" to locations with higher resource density. This assumption can be relaxed and integrated with the notion that individuals might also be attracted by the presence of other individuals (the "pull" argument). Both theoretical and empirical studies support the idea that an increase in group-size provides both positive and negative effects. Examples of the former include mutual protection and defensibility (Gould and Yellen 1987), risk-sharing (Hawkes 1992), efficiency derived from labour division (Bonner 2004; Jeanson *et al.* 2007), increase in information acquisition (Clark and Mangel 1984) and higher rates of cultural evolution (Henrich 2004; Shennan 2001; but see below). However, the beneficial effects of these are scale-dependent and, in most cases, destined to decline in oversized groups. For example, the positive effect of population density to the cumulative rates of cultural evolution can be expected only for comparatively small-sized population (Vaesen 2012) while cognitive studies suggest that there are intrinsic limits in the number of human interactions that our brain can cope with (Dunbar 1993), which, when exceeded, can lead to psychological stress derived from crowding (Hill and Hawkes 1987). Other detrimental effects of large groups can include episodes of interference in subsistence activities (Sutherland 1983), reduced availability of resources (Hamilton *et al.* 2007), decreased effectiveness of intra-group communication means (Fletcher 1995) and the cost of maintaining larger territories (Cashdan 1992).

The studies listed above share the fundamental notion that variations in the individual fitness will be partly a function of group size. We can formalise this idea introducing a theoretical *per capita* fitness function $\phi(g)$, where g is the group size. While the exact shape of $\phi(g)$ will be unknown in most empirical cases, we can still infer its fundamental properties by defining critical group sizes that are expected in most scenarios. We might, therefore, define the existence of the smallest possible group size m (*e.g.* a single individual, a household, etc.) and an optimal group size g^* where $\phi(g)$ is maximised. Thus, in the basic version of the IFD model, g^* will be equal to m (the optimal group size is the smallest possible, as fitness will decline with increasing population density), while if we presume that there is a permanent positive frequency dependence we will have $g^*=\infty$. In our case we assume that: (1) both positive and negative frequency dependencies are likely to exist; (2) positive frequency dependence declines as group size increases; and (3) negative frequency dependence are likely to be the dominant force in large groups. Several studies in behavioural ecology suggest that a unimodal curve for $\phi(g)$, with a single peak at $\phi(g^*)$ can satisfy these three assumptions (Sibly 1983; Clark and Mangel 1986; Giraldeau and Caraco 1993), commonly known as *Allee* effect (Allee 1951; Greene and Stamps 2001).

The unimodal version of $\phi(g)$ has interesting properties, especially when there is a group size $\dot{g}$ with an expected fitness equivalent to the one with the smallest group size m (*i.e.* $\phi(m)=\phi(\dot{g})$). Clark and Mangel (1986: 48) label $\dot{g}$ as the "equilibrium group size", providing the following thought experiment. Consider a group with size $g<g^*$ and $g>m$. Any individual m will be prone to join such a group, since $\phi(m)<\phi(g)$, and the incumbent members of the group will allow this as long as $\phi(g+m)\geq\phi(g)$. From the perspective of the external individual, joining the group remains advantageous even when the target group is over the optimal size g^* and the fitness starts to be smaller than the theoretical maximum (this will lead to a decline in fitness to the incumbent group members, and a conflict of interests; cf. Boone 1992). However, once the size of the target group becomes $\dot{g}$, aggregation no longer offers any benefit (as $\phi(m)=\phi(\dot{g})$, see Fig. 1).

The IFD and the fitness function discussed above are undoubtedly useful heuristic models, but if we seek to understand long-term settlement dynamics, we should also consider the effects of: (1) reproduction and death as a function of fitness; (2) group fission–fusion as a response strategy for modifying fitness; and (3) possible constraints

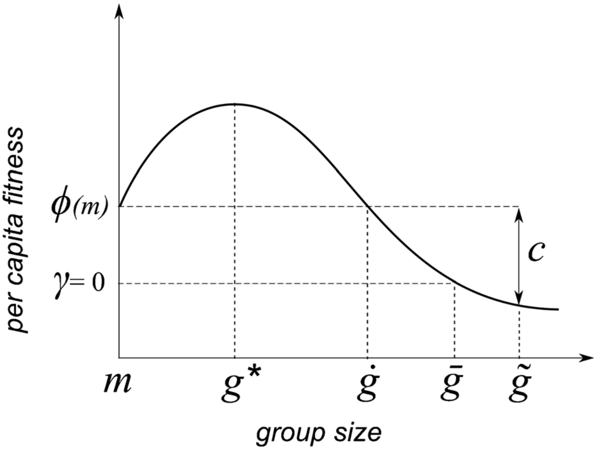

Fig. 1 Single humped fitness curve model with critical group sizes

for such movements. We can easily predict that all these three elements can strongly affect the system. A group might reach a size $g > \dot{g}$ by internal growth. At this point, being "alone" is better than being a member of a group of size g ($\phi(m) > \phi(g)$). This might lead to a fission process and potentially a subsequent fusion to another group with a higher expected fitness. However, such a dynamic will be constrained by knowledge (the individual might not be aware of a group which would provide him/her an increase in fitness) and space (fission might not be possible if space is not available within a short distance). To understand these dynamics, we need to construct a model in a flexible environment where we can easily incorporate these assumptions, without losing the simple, yet elegant underpinning principles offered by IFD and fitness curve models.

An Abstract Model of Fission and Fusion

Detailed descriptions and computer code of the simulation model can be found on the Electronic supplementary materials. This section will present an overview of the general properties of the model, its parameters and variables (see also Table 1).

The spatial environment of the simulation is defined by a series of discrete patches displaced in a toroidal lattice space. Each patch has a single state variable K, representing a fixed amount of available resources. Agents represent households (or any other minimum aggregate unit) and form *groups* with all agents located in the same patch. The size g of each group determines the fitness ϕ of its members through the following two equations.

$$\xi_i = N\left(\mu_i + (g-1)^b, \varepsilon\right) \tag{1}$$

$$\phi = \begin{cases} \dfrac{\sum_i^g \xi_i}{g} & if \ \sum_i^g \xi_i < K \\ \dfrac{K}{g} & if \ \sum_i^g \xi_i \geq K \end{cases} \tag{2}$$

Table 1 Model parameters, symbols, description and sweep values

Symbol	Description	Constant and sweep values
$n_{t=0}$	Number of agents at time-step 0	10
T	Total number of time-steps	500
P	Total number of patches	100
μ	Basic individual payoff	10
ε	Payoff variance	1
b	Cooperation benefit	0.3, 0.5 and 0.8
K	Resource Input	200
ρ	Basic reproduction rate	0.05
ω_1	Death parameter 1	0.8, 1.0, 1.2 and 1.4
ω_2	Death parameter 2	5
h	Spatial interaction range	1 and 100
z	Frequency of decision making	0.1, 0.5 and 1
c	Threshold of evidence	3
k	Sample proportion of observed agents	10^{-7}, 0.5 and 1

Equation 1 computes the foraging contribution ξ_i of each agent i. This is obtained as a random draw from a Gaussian probability distribution with mean $\mu_i + (g-1)^b$ and a standard deviation ε. The assumption here is that the average contribution of each agent increases as a function of g, with the parameter b defining the rate of increase. High values of b (representing the benefit derived from cooperation) will determine higher rates of increase in ξ_i while ε will add stochasticity in the model. Equation 2 models the effects of negative frequency dependence and the benefits derived from sharing. If the total sum of all contributions is smaller than the resource input K, individual fitness φ will be the average contribution of the group (which will minimise the effect of ε with larger values of g). If the total sum is equal or greater than K, ϕ will be the ratio between the resource input size and g (all available resources will be equally shared among agents in the same patch). The combination of these two equations will create a relationship between group size and fitness with both positive and negative frequency dependencies, with a single optimal group size g^*, and an equilibrium group size $\dot{g}$.

The fitness of the agents is the key state variable driving the growth rate of individual groups (through reproduction and death) and the onset of fission and fusion events. The former is modelled by translating ϕ into probabilities of death (d) and reproduction (r) with the following two equations:

$$r = \rho \frac{\phi}{\mu} \tag{3}$$

$$d = \frac{1}{1 + e^{\phi\omega_1 - \omega_2}} \tag{4}$$

Where ρ is the basic reproductive rate (*i.e.* the reproductive rate when the agent is alone) and ω_1 and ω_2 are shape parameters of the death rate. Equation 3 determines a linear increase in the probability of reproduction with increasing fitness, while Eq. 4 determines an exponential increase of mortality rate for low fitness.

All agents have the possibility to improve their condition by means of spatial relocation (*i.e.* fission–fusion event). This will occur with a probability z and will be based on a three-stage process, where each agent *observes*, *evaluates* and possibly *imitates* other agents (Kennedy 1998). The first step will involve the choice of a *model-agent*, that is, the agent w with the highest fitness among a random sample of proportion k within a grid-distance h from the focal agent (see Fig. 2). Notice that, since fitness is equal among all members of a group, this process will mimic the selection bias towards larger, more “visible” groups with higher average fitness. The second step will be the comparison between the focal agent’s fitness (ϕ_i) the model agent’s fitness (ϕ_w) and the expected fitness for individual foraging (μ). This will be calibrated by a “threshold of evidence” of c (cf. Henrich 2001:994), so that the agent will regard the alternative strategy superior only if the difference with its own fitness is larger than this value. As a result of this comparison the focal agent might: (1) fission and leave the current group and become an individual forager; (2) migrate to another group; (3) create a new group through a fusion with another individual forager; or (4) do nothing (see Fig. 3).

The simulation proceeds in discrete time-steps t=1,2,3…T, and its initialized with the creation of $n_{t=0}$ agents randomly scattered in the spatial environment, with agents located on the same patch forming the first groups. At each time-step, the model will proceed by: (1) calculating the fitness of the agents (Eqs. 1 and 2); (2) reproducing (Eq. 3) and eliminating (Eq. 4) the agents based on fitness values; (3) moving agents into different patches if certain conditions are met (Figs. 2 and 3); and (4) recording relevant statistics about the metapopulation structure.

Rank–size Analysis, Model Implementation and Experiment Design

We can investigate the simulation output by applying the same set of methods that are conventionally used for the analysis of empirically observed settlement pattern. In the specific case, we seek to identify the shape of the rank–size distribution and its evolution over time. We first distinguish between *primate* and *convex* settlement patterns (Johnson 1980; Falconer and Savage 1995; Savage 1997; Drennan and Peterson 2004). The former can be loosely defined as a highly hierarchical system where the majority of residential units are concentrated in one or few extremely large-

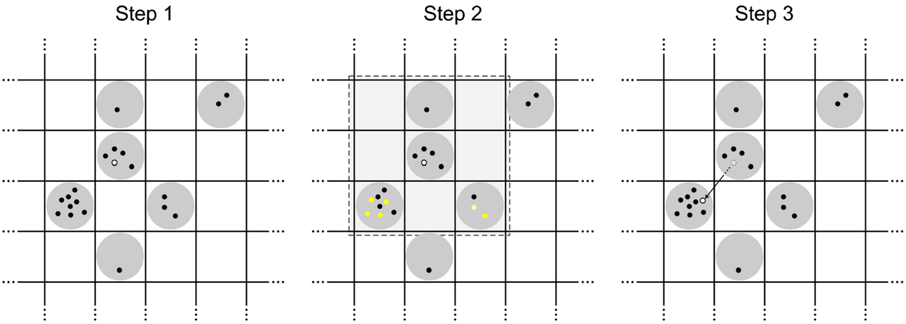

Fig. 2 Agent relocation process. Step 1: a focal agent (*white dot*) is chosen. Step 2: the focal agent samples a proportion k of agents within a grid distance h. Step 3: after comparing its own fitness with the fitness of the best agent among those sampled, the focal agent relocates (see also Fig. 3)

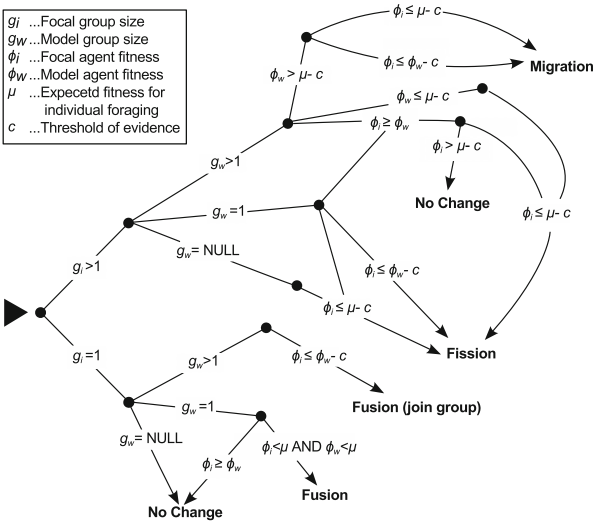

Fig. 3 Decision tree of agent relocation. At each node (starting from *left*) state variables are compared, and the outcome leading to a movement to a subsequent node, until the tips with the final decision is reached

sized settlements. In contrast, a convex settlement pattern is characterised by high levels of dispersion and a uniform distribution of settlement sizes. Formal distinction between the two systems can be based on a statistical comparison with the theoretical Zipf's law distribution (Zipf 1949): Primate system will have a rank–size plot with a steeper slope compared with such a null model, while convex systems system will exhibit the opposite pattern (see Fig. 4).

Drennan and Peterson (2004) provide a useful index for distinguishing primate and convex systems. Their A-coefficient analysis returns a single index A as a standardised measure of deviation from the theoretical Zip's law distribution. Positive values suggest convex patterns, with a maximum of 1, reached when all settlements have the same size. Negative values will indicate primate patterns, although, in this case, the minimum can be theoretically smaller than −1. Notice that A has been calculated only when the observed numbers of groups were equal or higher than five, an arbitrarily chosen threshold necessary to observe the most commonly found shapes of rank–size curves (cf. Figure 1 in Savage 1997).

We can obtain time-series of A from the simulation outputs, which will describe the equilibrium properties of the system for each parameter combination. This will allow us to answer the first research question (*i.e.* Can transitions between primate and convex patterns occur in the absence of external disturbance processes?) by determining whether rank–size distributions are at stable equilibria (*i.e.* a *point attractor*) or are instead characterised by shifts between primate and convex shapes. In the latter case, we want to determine whether these transitions occur in a periodic or quasi-periodic fashion (*i.e.* a *limit-cycle attractor* or a *toroidal attractor*), or behave chaotically, with a complete absence of repeated sequences of A (*i.e.* a *strange attractor*; see McGlade 1995 for discussions on the notion of attractors and its archaeological relevance). Figure 5 shows four examples of attractors with their respective time-series and scatter plots of A_t against A_{t+1}.

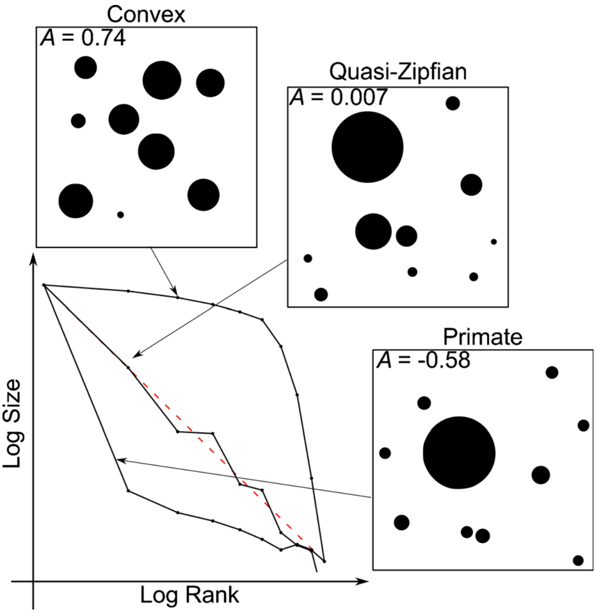

Fig. 4 Convex, quasi-Zipfian, and Primate patterns, with corresponding rank–size plots and *A* coefficients

The choice of the model parameters is perhaps one of the biggest burdens in ABMs. Variables with bounded ranges (*e.g.* between 0 and 1; *z*, *k,* and *h* in this case) can be easily explored by systematic sweeps with predefined interval bins. Variables with unbounded ranges are harder to choose, and educated guesses are commonly adopted on the basis of expert knowledge (*e.g.* Dean *et al.* 2000; Smith and Choi 2007). When these are not available or not applicable, we need to define parameter values on the basis of known relationship to other key variables. If we conceptualise a

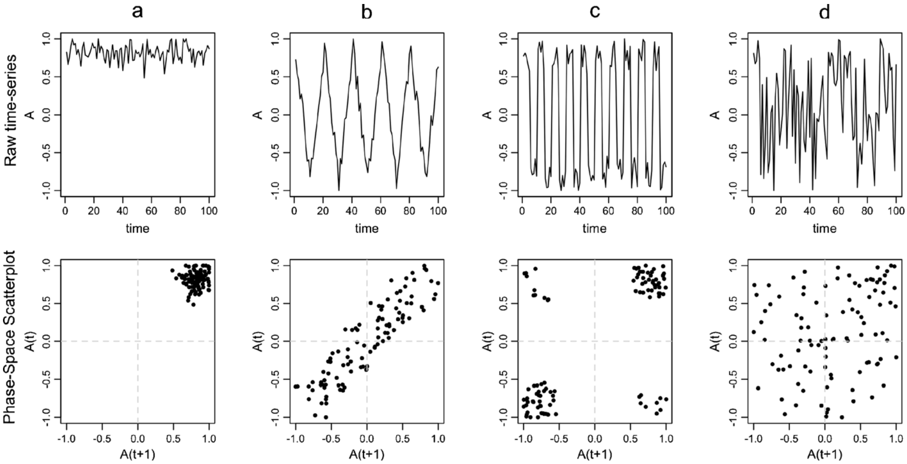

Fig. 5 Time-series and phase-space scatterplot for different types of attractors: **a** point attractor with small fluctuations at high values of *A*; **b** limit cycle attractor with gradual change between primate and convex patterns; **c** limit cycle attractor with sudden shifts between primate and convex patterns; **d** strange attractor with chaotic oscillations of *A*

p-dimensional parameter space, where p is the number of parameters, we can expect that certain patterns are likely to be reoccurring despite different numeric combinations of the parameters. Thus, an ideal exploration strategy is to exploit this structure, trying to minimize the input information (choice of parameter values), maximising at the same time the output information (identification of boundaries between different types of equilibria in the parameter space).

In practical terms, we need to formally define the expected relationship between parameters and different behaviours of the system. Here, I concentrate on parameters relevant to the internal growth of each group (reproduction and death) and the fission–fusion dynamics. We first derive the intrinsic growth rate γ as the difference between r and d defined in Eqs. 3 and 4. With other things being equal, a group is expected to increase its size with positive values of γ and decrease its size with negative ones. Since γ is a function of g, we can define $\overline{g}$ as the group size when $\gamma=0$ (*i.e.* the zero-growth group size). We can also derive a fission group size $\widetilde{g}$, as the one satisfying the condition $\phi(\widetilde{g}) = \phi(\dot{g}) - c$. Once we have established these two and additional critical group sizes (see Fig. 2), we can envisage four distinct scenarios: (1) the intrinsic growth rate reaches zero at the equilibrium group size $(\widetilde{g}=\dot{g})$; (2) the intrinsic growth rate reaches zero between the equilibrium group size, and the expected fission size $(\dot{g} < \overline{g} < \widetilde{g})$; (3) the intrinsic growth rate reaches zero at the fission group size $(\overline{g}=\widetilde{g})$; and (4) the intrinsic growth rate reaches zero above the fission group size $(\overline{g}>\widetilde{g})$. We can achieve these four scenarios by sweeping only one of the parameters of Eq. 4 (ω_1), holding the others (c,ρ,ω_2) constant.

Fission–fusion dynamics are triggered primarily by a "meliorising" principle (Mithen 1990: 31–32): Agents decide to move when an alternative choice (in most cases adopted by the model agent) is "significantly" better (*i.e.* the difference is larger than the threshold of significance c). A key parameter in this case is b, the benefit derived from aggregation. Recall that increasing values of b will lead to higher rates of fitness increase as a function of group size, while smaller values will determine only a marginal improvement compared to individual foraging. Since the difference in fitness between the focal and model agent and the threshold of evidence c are ultimately driving the movement of the agents, we can predict the outcome of different combinations of these two parameters when everything else is held constant. Figure 6 shows the probability that the difference between the focal agent and model agent fitness is lower than c for different group sizes and parameter combinations of b and c. The level plots depict in most cases two areas with high probability, one where the focal group is oversized (high values of g_i) and hence attracted to smaller-sized group closer to the optimal size (dashed line), and another where the focal group is sub-optimal and attracted to larger groups closer to the optimal size. This is true for all parameter combinations, although when the threshold of evidence c is higher, the probability of small focal groups moving to the model group is high only when b is also high. Figure 6 suggests that holding c constant to high values and sweeping the benefit of cooperation b allows us to explore a more diverse range of combinations, in some where migration comes almost exclusively from oversized-groups (*e.g.* $b=0.3$ and $c=3$ in Fig. 6) and others where members of small-sized suboptimal groups migrate as well (*e.g.* $b=0.8$ and $c=3$ in Fig. 6).

Table 1 summarises the parameter values used for the experiments. The resulting parameter space is defined by 5 dimensions and 216 unique points (3 sweeps for z, b, and k, 2 for h, and 4 for ω_1). Each combination has been explored computing 100 runs

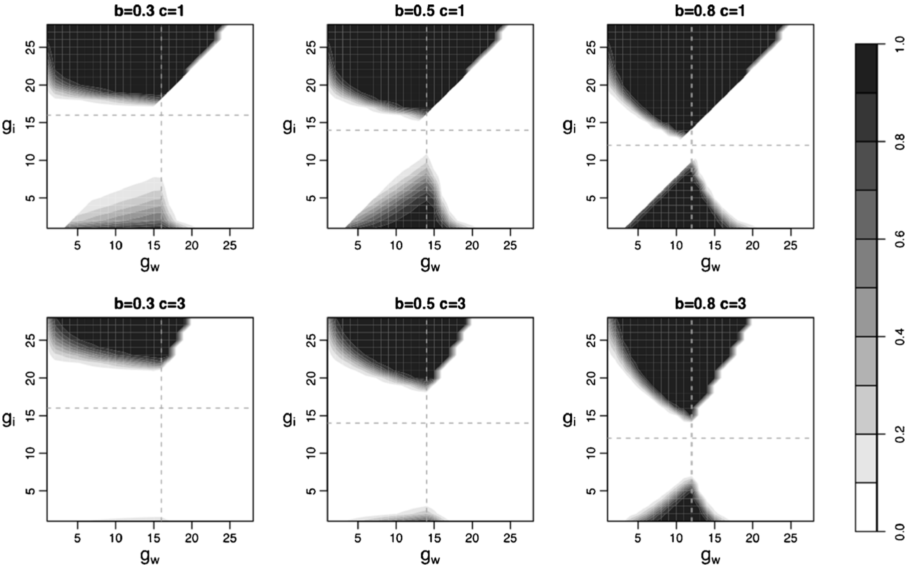

Fig. 6 Probability of migration for different parameter combinations of *b* and *c* at different combinations of the focal (g_i) and model agent's (g_w) group sizes

of the model, recoding for each A_t, the A-coefficient value at each time-step *t*, up to $t=500$. The result has been plotted in pairs of four-dimensional plots, showing the combined time-series of all runs and scatter-plots of A_t against A_{t+1}. In all cases, the

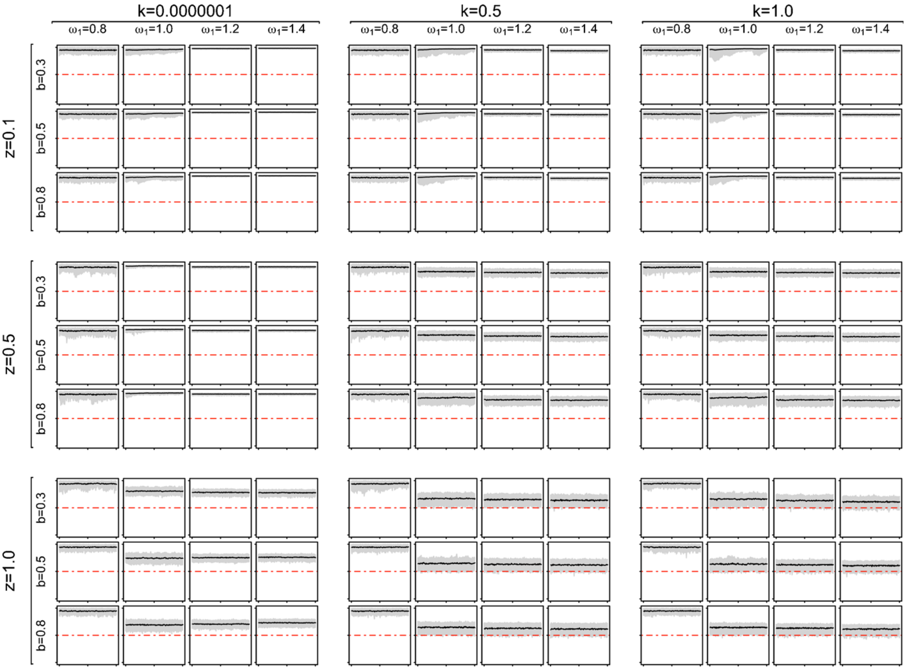

Fig. 7 Time-series parameter space of *A* with $h=1$. The *grey-shaded* area is the 95 % envelope of simulation runs; the *solid line* is the average *A* value among the runs, and the *red point and dash line* indicates $A=0$. The *y*-axes (*A*) range between −1 and 1, while the *x*-axes range from $t=300$ to $t=500$

first 300 time-steps have been discarded. This was necessary to remove the “burn-in” phase where the system moved from its initial conditions to its equilibrium state.

Results

Figures 7 and 8 depict the time-series of A for the spatially local ($h=1$) and global ($h=100$) variants of the model. In all cases, the local model exhibits a stable equilibrium with a uniform distribution of group sizes (convex pattern). When the frequency of decision-making (z) and the proportion of observed agents (k) are both high, and when $\overline{g}>\dot{g}$ (zero-growth size larger than the equilibrium group size; *i.e.* when $\omega_1 \geq 1.0$), the equilibrium value of A is slightly lower, suggesting small levels of settlement hierarchy. Nonetheless, the pattern can still be regarded as convex, with A_t being always positive.

When the range of interaction is global (Fig. 8), the parameter space looks rather different. Stable convex patterns can be now observed only when k and z are set to their smallest values (with exceptions when $\omega_1=0.8$, *i.e.* when the population size is smaller due to higher mortality rate at smaller group sizes; see Eq. 4, also Crema 2013b). When k and/or z are set to higher values, the 95 % simulation envelope covers both positive and negative values of A, suggesting potential transitions between primate and convex patterns.

The scatter-plots of A_t against A_{t+1} can illustrate the nature of these dynamics (Figures 9 and 10). The high concentration of points in the top-right corner for the

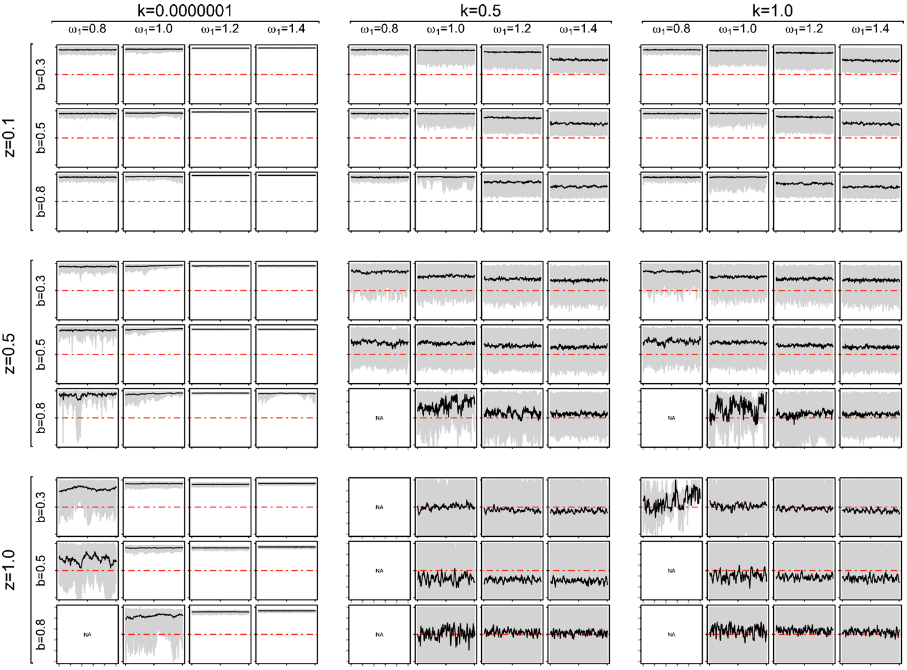

Fig. 8 Time-series parameter space of A with $h=100$. The *grey-shaded area* is the 95 % envelope of simulation runs; the *solid line* is the average A value among the runs, and the *red point and dash line* indicates $A=0$. The y-axes (A) range between −1 and 1, while the x-axes range from $t=300$ to $t=500$. Notice that some parameter combinations with low intrinsic growth-rate did not produce a sufficient number of groups (5) to produce reliable estimates of A and hence has been excluded from analysis

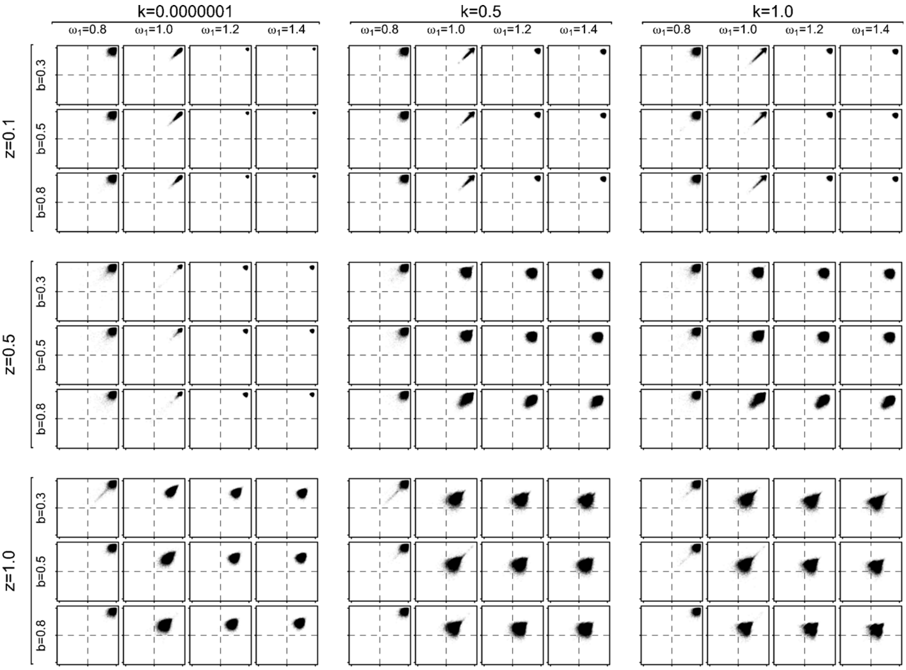

Fig. 9 Phase-space scatterplot parameter space of A with $h=1$. The y-axes and X-axes range between −1 and 1; the *dashed lines* are drawn at $A_t=0$ and $A_{t+1}=0$. The point depicts A coefficients in the interval between $t=300$ and $t=500$

spatially local version of the model ($h=1$) confirms a stable system at high values of A. With $k\geq 0.5$, $z=1$, and $\omega_1\geq 1.0$ the points are slightly more dispersed and closer to the centre of the plot (suggesting fluctuations between different settlement systems exhibiting higher hierarchy), but the overall behaviour of the system appears to be the same throughout the parameter space.

Once again, in the spatially global version of the model (Fig. 10), we can observe a radically different picture. When k is set to its smallest value, we still observe a high density of points in the top-right corner, but a diagonal trend suggests that smaller values of A are occasionally observed. A careful look at individual time-series suggests that these are associated with sporadic transitions to more hierarchical systems, always followed by a return to the original equilibrium state with high values of A. These patterns can be observed when the intrinsic growth rate is comparatively low ($\omega_1=0.8$). In these regions of the parameter space, groups are more likely to suffer an increased mortality after immigration events, and consequently, a higher diversity in the group size distribution is occasionally expected after fission–fusion dynamics.

When $k\geq 0.5$, we can identify three different scenarios that can be distinguished on the basis of the frequency of decision-making. When this has its lowest values ($z=0.1$), the point cloud is located exclusively in the top-right quadrant, indicating a convex pattern (see also Fig. 11a), with fluctuations positively correlated with ω_1. When $z=0.5$, the scatter plot occupies all four quadrants, but the highest density is still in the top-right corner. This suggests a stable equilibrium with occasional "escapes" from the main basin of attraction (see also Fig. 11b). In other words, the system is in most cases convex, but with episodes of sudden shifts from convex to

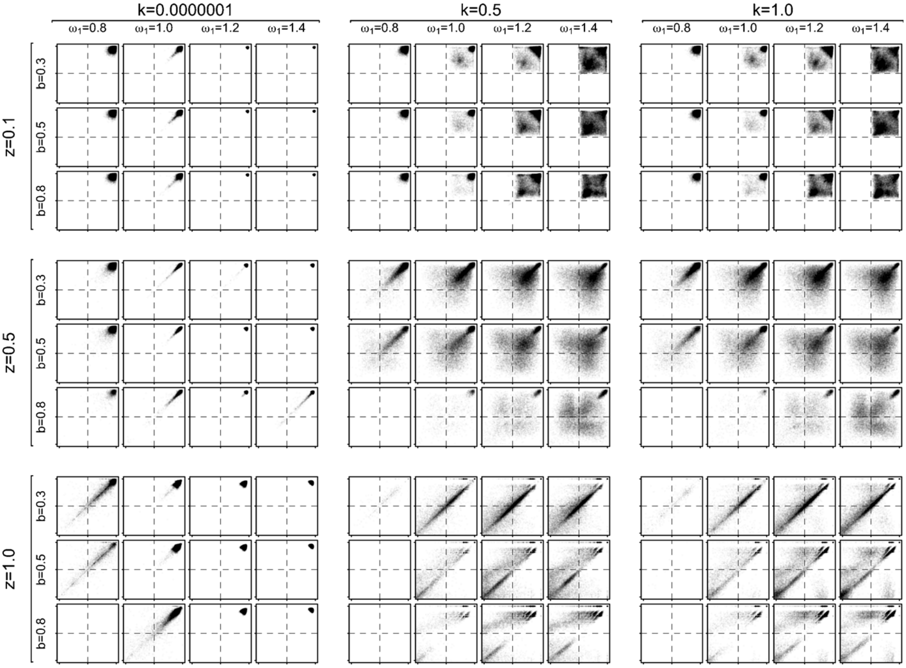

Fig. 10 Phase-space scatterplot parameter space of A with h=100. The y-axes and X-axes range between −1 and 1; the *dashed lines* are drawn at A_t=0 and A_{t+1}=0. The point depicts A coefficients in the interval between t=300 and t=500. Notice that some parameter combinations with low intrinsic growth-rate did not produce a sufficient number of groups (5) to produce reliable estimates of A and hence has been excluded from analysis

primate and from primate to convex patterns. Finally, when z=1.0, the scatter plots exhibit a strong diagonal pattern surrounded by lower-density points. This (see also Fig. 11c and d) suggests the presence of a system fluctuating around different metapopulation structures, with occasional sudden shifts between primate and convex patterns. Instances where the diagonal lines are uninterrupted (*e.g.* when b=0.3) are indicative of a relative gradual transition between the two systems (Fig 11c; cf. Fig. 5b), although the transition from primate to convex is always faster than the opposite. When $b \geq 0.5$, the diagonal is “broken” (cf. Fig. 5c), indicating more sudden transitions between high and low values of A (Fig. 11d).

Discussion: Dynamics of Metapopulation Change

The exploration of the parameter space allowed us to identify several properties of the model given the assumptions defined by its parameters. First, stable equilibria are always convex settlement patterns, a result conforming to the expectations of the ideal free distribution models. Given a uniform distribution of resources, full knowledge and freedom of movement, the metapopulation structure will be ultimately characterised by a homogenous size distribution “matching” the resource input, hence a convex rank–size pattern.

Relaxing the assumption of a uniform resource distribution might potentially lead to different equilibria, although this will be heavily dependent on the spatial structure

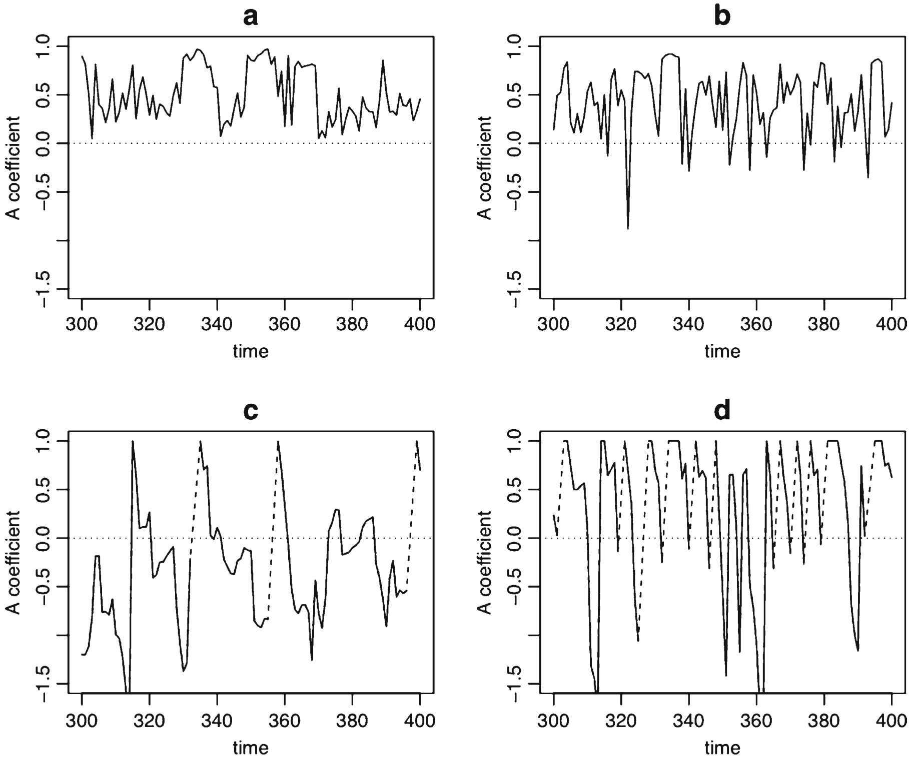

Fig. 11 Time-series of A for single runs of the simulation: **a** $h=100$, $k=1$, $z=0.1$, $b=0.5$, and $\omega_1=1.4$; **b** $h=100$, $k=1$, $z=0.5$, $b=0.3$, and $\omega_1=1.4$; **c** $h=100$, $k=0.5$, $z=1$, $b=0.3$, and $\omega_1=1.2$; **d** $h=100$, $k=1$, $z=1$, $b=0.8$, and $\omega_1=1.2$. Missing values of A have been linearly interpolated and shown as *dashed lines*

of resources. Experiment runs where the resource input of the patches were randomly drawn from a Gaussian distribution show that convex stable equilibria would still emerge (Crema 2013a). In these scenarios, fission–fusion events lead groups to reach patches with the highest resource input within their neighbourhood, and as long as these local optima have similar absolute values of K, the rank–size distribution is expected to be convex. Strongly skewed resource distribution or a high overall population density might instead lead to the emergence of primate systems. In the former case, local optima are more likely to have different resources in different parts of the landscape, while in the latter case suboptimal patches are more likely to be colonised. The number of these alternative scenarios is too high to be discussed here, but the basic model proposed in this paper could easily integrate these and provide predictions of long-term settlement equilibria for specific spatial distribution of resources.

Primate systems could emerge, however, without the presence of a heterogeneous distribution of resources or the induction of some external disturbance. The exploration of the parameter space has in fact indicated that highly hierarchical systems can appear when the agents' movements amplify small pre-existing variations in fitness between groups (originating from its stochastic components; *e.g.* ε in Eq. 1). When these are highly interconnected (high values of h) and agents have a high probability of sharing the perceived optimal choice/destination (high values of k), a group with a slightly higher per capita fitness will be immediately invaded, leading to the emergence of a highly hierarchical primate system. When the benefit of cooperation (*b*) is high, this process is strongly stimulated (cf. Fig. 6) and determines fast fission–fusion dynamics, where dominant groups are rapidly invaded and abandoned when they become suboptimal. In other words, the absence of forces constraining the movement and the knowledge of the agents (*z*, *k* and *h*) lead to the emergence of highly unstable metapopulation structures. This pattern closely resembles the "tragedy of commons" (Hardin 1968), where the global pursuit for optimality (joining the group with the "best" size to increase fitness) leads to the emergence of sub-optimality (the "best" group becomes oversized, and fitness declines).

Conclusion

The idea that endogenous forces are capable to induce radical changes in settlement patterns is not itself new in archaeology. Previous simulation-based studies in archaeology have shown how this is possible for a variety of assumptions (Griffin 2011; Renfrew and Poston 1979). This paper shares similar conclusions by using a simpler model that can be generalised to a wider range of societies, transcending from the details specified in previous works.

The key parameters defining the largest component of the model behaviour are those related to the mobility of the agents. When agents can move everywhere, anytime and have perfect knowledge, we expect high rates of changes between primate and convex systems. Conversely, when agents are spatially constrained, move less frequently, and have imperfect knowledge we expect a convex system, as long as the resources are distributed homogenously. This dichotomy has some parallels with studies on self-organised criticality where patterns of underlying "tension" determine the frequency and magnitude of catastrophic events (Scheffer 2009). In some cases, these "tensions" might be released locally, with not effects at the global scale; in others, these might propagate through space, triggering transformations at the macro level. Similarly, it is worth highlighting that the instability of highly integrated systems bears some parallelism with recent studies on cultural evolution which suggests how high levels of knowledge (Lake and Crema 2012) and foresight (Xue *et al*. 2011; Wren *et al*. under review) are often sub-optimal. In our case, high degrees of knowledge and interconnectivity lead to a cascade of events where an initial increase in fitness is followed by a decline.

The dynamic nature of highly integrated systems leads also to suggest that a narrow focus on the dichotomy convex-primate might hinder the relationship between the generative processes and the archaeologically observed pattern. Pairing high-level integration with primate systems and low-level integration with convex systems would incorrectly assume that the expected equilibrium for a given structural properties of the system is stable and static. In the case of the model presented here, high-level integration system can be recognised only when the nature of alternation between convex and primate systems is identified. Thus, empirical patterns should always be examined taking into consideration that the temporal window of analysis might be too small to capture the full nature of the generative process behind.

It is worth reminding also that real-world systems are characterised by levels of integration that are different from some of the results portrayed by the simulation exercise. Both instances of absolute isolation or complete integration are highly unlikely, and intermediate levels should be expected. Nonetheless, the model presented here can provide the extremes of a spectrum that can be used as a template for assessing empirical data. The crucial element for validating the model proposed here is to infer the level of system integration from available archaeological and historical proxies. The spatial range of interaction between communities can be inferred from the topographic properties of the landscape and how these can isolate or promote integration based on different models of movement (McRae 2006; McRae *et al*. 2008; Bevan 2011), or identified by indirect proxies based on cultural similarity (*e.g.* by assessing stylistic features in pottery; see, for example, Shennan and Bentley 2008). A recent study by Bevan and Wilson (2013) on the settlement hierarchy of Bronze Age Crete provide some promising directions in this regard. Their model of network evolution (based on a combination of point process and entropy-maximising interaction models) could be integrated with fission–fusion dynamics, allowing to formally test the hypotheses generated in this paper using the empirical record.

Finally, it should be noted that the model proposed in this paper has enough flexibility to incorporate further assumptions on the relationship between metapopulation dynamics, frequency-dependent fitness and resource distribution. These can be linked to dynamics of cultural transmission (cf. Lake and Crema 2012) processes of positive and negative niche construction (Odling-Smee *et al*. 2003) and other evolutionary models that can widen our understanding of long-term settlement-pattern change.

Acknowledgments This paper benefited from comments and feedback from Andrew Bevan and Mark Lake, to whom I am extremely grateful. I would also like to thank Rick Schulting and James Steele for insightful comments on the agent-based model, Marco Madella and Bernardo Rondelli for inviting me to contribute to this special issue and the UK Art and Humanities Research Council funded UCL Centre for the Evolution of Cultural Diversity for granting me access to the UCL Legion High Performance Computing Facility. Finally, I would like to thank the three anonymous reviewers who offered me detailed feedbacks, comments and suggestions for improving this work. A UCL Graduate School Research Scholarship funded the project.

References

Allee, W. C. (1951). *The social life of animals*. Boston: Beacon Press.

Bevan, A. (2011). Computational models for understanding movement and territory. In V. Mayoral Herrera & S. Celestino Pérez (Eds.), *Tecnologías de Información Geográfica y Análisis Arqueológico del Territorio* (pp. 383–394). Mérida: Anejos de Archivo Español de Arqueología.

Bevan, A., & Connolly, J. (2006). Multiscalar approaches to settlement pattern analysis. In G. Lock & B. Molyneaux (Eds.), *Confronting scale in archaeology: Issues of theory and practice* (pp. 217–234). New York: Springer.

Bevan, A., Crema, E., Li, X., & Palmisano, A. (2013). Intensities, interactions and uncertainties: Some new approaches to archaeological distributions. In A. Bevan & M. Lake (Eds.), *Computational approaches to archaeological space* (pp. 27–52). Walnut Creek: Left Coast Press.

Bevan, A., & Wilson, A. (2013). Models of settlement hierarchy based on partial evidence. *Journal of Archaeological Science, 40*(5), 2415–2427.

Bond, G., Showers, W., Cheseby, M., Lotti, R., Almasi, P., deMenocal, P., et al. (1997). A pervasive millennial-scale cycle in North Atlantic Holocene and Glacial climates. *Science, 287*, 1257–1266.

Bonner, J. T. (2004). Perspective: The size-complexity rule. *Evolution, 58*, 1883–1890.

Boone, J. L. (1992). Competition, conflict, and the development of social hierarchies. In E. A. Smith & B. Winterhalder (Eds.), *Evolutionary ecology and human behaviour* (pp. 301–337). New York: Aldine de Gruyter.

Carballo, D. M., & Pluckhahn, T. (2007). Transportation corridors and political evolution in highland Mesoamerica: Settlement analyses incorporating GIS for northern Tlaxcala, Mexico. *Journal of Anthropological Archaeology, 26*(4), 607–629.

Cashdan, E. (1992). Spatial organization and habitat use. In E. A. Smith & B. Winterhalder (Eds.), *Evolutionary ecology and human behaviour* (pp. 237–266). New York: Aldine de Gruyter.

Clark, C. W., & Mangel, M. (1984). Foraging and flocking strategies: Information in an uncertain environment. *The American Naturalist, 123*(5), 626–641.

Clark, C. W., & Mangel, M. (1986). The evolutionary advantages of group foraging. *Theoretical Population Biology, 30*, 45–75.

Crema, E. (2013a). Modelling settlement rank-size fluctuations. In G. Wurzer, K. Kowarik, & H. Reschreiter (Eds.), *Agent-based modeling and simulation in archaeology*: Springer. In press.

Crema, E. R. (2013b). *Spatial and temporal models of Jomon settlement*. Unpublished PhD Thesis, University College London, London.

Crema, E. R. (2013c). Cycles of change in Jomon settlement: A case study from Eastern Tokyo Bay. *Antiquity*. In press.

Crema, E. R., Bevan, A., & Lake, M. (2010). A probabilistic framework for assessing spatio-temporal point patterns in the archaeological record. *Journal of Archaeological Science, 37*(5), 1118–1130.

Dean, J. S., Gumerman, G. J., Epstein, J. M., Axtell, R. L., Swedlund, A. C., Parker, M. T., et al. (2000). Understanding Anasazi culture change through agent base modeling. In T. A. Kohler & G. J. Gumerman (Eds.), *Dynamics in human and primate societies: Agent based modeling of social and spatial processes* (pp. 179–205). Oxford: Oxford University Press.

Dewar, R. E., & McBride, K. A. (1992). Remnant settlement patterns. In J. Rossignol & L. Wandsnider (Eds.), *Space, time, and archaeological landscapes* (pp. 257–282). New York: Plenum Press.

Drennan, R. D., & Peterson, C. E. (2004). Comparing archaeological settlement systems with rank-size graphs: A measure of shape and statistical confidence. *Journal of Archaeological Science, 31*, 533–549.

Dunbar, R. I. M. (1993). Coevolution of neocortical size, group size and language in humans. *Behavioral and Brain Sciences, 16*, 681–735.

Falconer, S. E., & Savage, S. H. (1995). Heartlands and hinterlands: Alternative trajectories of early urbanization in Mesopotamia and the Southern Levant. *American Antiquity, 60*, 37–58.

Fletcher, R. (1995). *The limits of settlement growth: A theorethical outline*. Cambridge: Cambridge University Press.

Fortin, M.-J., & Dale, M. (2005). *Spatial analysis: A guide for ecologists*. Cambridge: Cambridge University Press.

Fretwell, S. D., & Lucas, H. J. J. (1970). On territorial behaviour and other factors influencing habitat distribution in birds. *Acta Biotheoretica, 19*, 16–36.

Giraldeau, L.-A., & Caraco, T. (1993). Genetic relatedness and group size in an aggregation economy. *Evolutionary Ecology, 7*, 429–438.

Gould, R. A., & Yellen, J. E. (1987). Man the hunted: Determinants of household spacing in desert and tropical foraging societies. *Journal of Anthropological Archaeology, 6*, 77–103.

Greene, C. M., & Stamps, J. A. (2001). Habitat selection at low population densities. *Ecology, 82*, 2091–2100.

Griffin, A. F. (2011). Emergence of fusion/fission cycling and self-organized criticality from a simulation model of early complex polities. *Journal of Archaeological Science, 38*, 873–883.

Halstead, P., & O'Shea, J. (1989). Introduction: Cultural responses to risk and uncertainty. In P. Halstead & J. O'Shea (Eds.), *Bad year economics: Cultural responses to risk and uncertainty* (pp. 1–7). Cambrdige: Cambridge University Press.

Hamilton, M. J., Milne, B. T., Walker, R. S., & Brown, J. H. (2007). Nonlinear scaling of space use in human hunter–gatherers. *Proceedings of the National Academy of Sciences of the United States of America, 104*(11), 4765–4769.

Hardin, G. (1968). The tragedy of commons. *Science, 162*, 1243–1248.

Hawkes, K. (1992). Sharing and collective action. In E. A. Smith & B. Winterhalder (Eds.), *Evolutionary ecology and human behaviour* (pp. 269–300). New York: Aldine de Gruyter.

Henrich, J. (2001). Cultural transmission and the diffusion of innovations: Adoption dynamics indicate that biased cultural transmission is the predominate force in behavioral change. *American Anthropologist, 103*(4), 992–1013.

Henrich, J. (2004). Demography and cultural evolution: How adaptive cultural processes can produce maladaptive losses: The Tasmanian case. *American Anitquity, 69*(2), 197–214.

Hill, K., & Hawkes, K. (1987). Neotropical hunting among the Aché of Eastern Paraguay. In R. B. Hames & W. T. Vickers (Eds.), *Adaptive responses of Native Amazonians* (pp. 139–188). New York: Academic Press.

Horn, H. S. (1968). The adaptive significance of colonial nesting in the Brewer's Blackbird (*Euphagus* cyanocephalus). *Ecology, 49*(4), 682–694.

Illian, J., Penttinen, A., Stoyan, H., & Stoyan, D. (2008). *Statistical analysis and modelling of spatial point patterns (statistics in practice)*. Chirchester: Wiley.

Jeanson, R., Fewell, J. H., Gorelick, R., & Bertram, S. M. (2007). Emergence of increased division of labor as a function of group size. *Behavioral Ecology and Sociobiology, 62*, 289–298.

Jochim, M. A. (1976). *Hunter–gatherer subsistence and settlement: A predictive model*. London: Academic Press.

Johnson, G. A. (1980). Rank-size convexity and system integration: A view from archaeology. *Economic Geography, 56*, 234–247.

Kennedy, J. (1998). Methods of agreement: Inference among the EleMentals. In *Intelligent control (ISIC), 1998. Held jointly with IEEE International Symposium on Computational Intelligence in Robotics and Automation (CIRA), Intelligent Systems and Semiotics (ISAS), Proceedings, Piscataway, NJ,* (pp. 883–887): IEEE Service Center

Kennett, D., Anderson, A., & Winterhalder, B. (2006). The ideal free distribution, food production, and the colonization of oceania. In: D. J. Kennett & B. Winterhalder (Eds.), *Behavioral Ecology and the Transition to Agriculture* (pp. 265–288). Berkeley: University of California Press.

Kohler, T. A., & Varien, M. D. (2010). A scale model of seven hundred years of farming settlements in Southwestern Colorado. In M. S. Bandy & K. R. Fox (Eds.), *Becoming villagers: Comparing early village societies* (pp. 37–61). Tucson: University of Arizona Press.

Lake, M., & Crema, E. R. (2012). The cultural evolution of adaptive-trait diversity when resources are uncertain and finite. *Advances in Complex Systems, 19*, 1150013

McGlade, J. (1995). Archaeology and the ecodynamics of human-modified landscapes. *Antiquity, 69*, 113–132.

McRae, B. H. (2006). Isolation by resistence. *Evolution, 60*(8), 1551–1561.

McRae, B. H., Dickson, B. G., Keitt, T. H., & Shah, V. B. (2008). Using circuit theory to model connectivity in ecology, evolution, and conservation. *Ecology, 89*, 2712–2724.

Mithen, S. (1990). *Thoughtful foragers: A study of prehistoric decision making*. New York: Cambridge University Press.

Møller, A. P. (1995). Developmental stability and ideal despotic distribution of blackbirds in a patchy environment. *Oikos, 72*, 228–234.

Odling-Smee, F. J., Laland, K. N., & Feldman, M. W. (2003). *Niche construction: The neglected process in evolution*. New Jersey: Princeton University Press.

Renfrew, C., & Poston, T. (1979). Discontinuities in the endogenous change of settlement pattern. In C. Renfrew & K. L. Cooke (Eds.), *Transformations: Mathemathical approaches to culture change* (pp. 437–461). New York: Academic Press.

Roberts, B. K. (1996). *Landscapes of settlement: Prehistory to the present*. London: Routeledge.

Savage, S. H. (1997). Assessing departures from log-normality in the rank-size rule. *Journal of Archaeological Science, 24*, 233–244.

Scheffer, M. (2009). *Critical transitions in nature and society*. New Jersey: Princeton University Press.

Shennan, S. (2001). Demography and cultural innovations: A model and its implications for the emergence of modern human culture. *Cambridge Archaeological Journal, 11*(1), 5–16.

Shennan, S. J., & Bentley, A. M. (2008). Interaction, and demography among the earliest farmers of Central Europe. In: M. J. O'Brien (Ed.), *Cultural transmission and archaeology: Issues and case studies* (pp. 164–177) Washington DC: SAA Press.

Sibly, R. M. (1983). Optimal group size is unstable. *Animal Behaviour, 31*(3), 947–948.

Smith, E. A., & Choi, J.-K. (2007). The emergence of inequality in small-scale societies: Simple scenarios and agent-based simulations. In T. Kohler & S. Leeuw (Eds.), *The model-based achaeology of socionatural systems* (pp. 105–119). Santa Fe: SAR Press.

Sutherland, W. J. (1983). Aggregation and the "ideal free" distribution. *Journal of Animal Ecology, 52*, 821–828.

Vaesen, K. (2012). Cumulative cultural evolution and demography. *PloS ONE, 7*(7), e40989.

Winterhalder, B., Kennett, D. J., Grote, M. N., & Bartruff, J. (2010). Ideal free settlement of California's Northern Channel Islands. *Journal of Anthropological Archaeology, 29*, 469–490.

Wren, C. D., Zue, J. X., Costopoulos, A., & Burke, A. (under review). The role of spatial foresight on models of hominin dispersal. *Journal of Human Evolution*.

Xue, J. Z., Costopoulos, A., & Guichard, F. (2011). Choosing fitness-enhancing innovations can be detrimental under fluctuating environments. *PloS ONE, 6*, e26770.

Zipf, G. K. (1949). *Human behavior and the principle of least effort*. Cambridge: Harvard University Press.