Culture, space, and metapopulation: a simulation-based study for evaluating signals of blending and branching☆

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ABSTRACT

This paper explores the robustness of phylogenetic methods for detecting variations in branching and blending signals in the archaeological record. Both processes can generate a spatial structure whereby cultural similarity between different sites decays with increasing spatial distance. By generating a series of artificial records through the controlled and parameterised environment of an agent-based simulation, we: a) illustrate the weakness and the strength of different analytical techniques (empirical distogram, Mantel test, Retention Index, and δ-score); b) determine whether they are capable of assessing how spatial isolation determines cultural diversity; and c) establish whether they can detect variations in the nature of horizontal transmission over time. Results suggest that variables other than the spatial range of interaction (e.g. the frequency of fission events, population dynamics, and rates of cultural innovation) have different effects on the output of some phylogenetic analyses.

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1. Introduction

The spatial patterning of culture (*sensu* Childe, 1929) can be explained by three interrelated processes. Two communities might share a number of cultural traits due to: 1) a parallel and convergent adaptation to similar selective pressures; 2) common ancestry and inheritance (*branching*); and 3) horizontal transmission by means of inter-group interaction (*blending*) (Mace and Pagel, 1994; Borgerhoff Mulder et al., 2006; Collard et al., 2006; Mace and Jordan, 2011; for the earliest accounts of this problem: Boas 1896, Kroeber, 1948). These processes are all characterized by a deep relationship with space (Freckleton and Jetz, 2009; Premo and Scholnick, 2011): the positive autocorrelation of most climatic and environmental variables ensures that two communities in close distance are likely to share similar environment and selective pressures; offspring settlements emerging from fission events are often located in spatial proximity; and inter-group interaction and possible exchange of information are shaped by a distance decay. Albeit the exact scale and nature of the spatial structuring may differ between these processes, the general assumption is that, other things being equal, the cultural similarity between two communities will decay as a function of their physical inter-distance.

Consequently, samples cannot be regarded as truly independent, as different communities might share similarities due to common ancestry and interaction, affecting in turn the inference of cultural processes (Loftin, 1972; Mace and Pagel, 1994). Moreover, analysing the spatial distribution of cultural traits is often not sufficient to discern which, among the three processes listed above, determined the observed pattern.

Yet this spatial structure plays a pivotal role in many disciplines and its implications in archaeology are paramount (e.g. Lipo et al., 1997; Shennan and Bentley, 2008; Premo and Scholnick, 2011). If we ignore instances of adaptive convergent evolution and focus exclusively on neutral traits (Dunnell, 1978), the cultural similarity between two communities is the result of *branching* and *blending*.[1] Several authors have supported one or the other as the dominant force in cultural evolution, with their argument based on both empirical and theoretical grounds (see Collard et al., 2006 for a review).

Part of this discussion was also fomented by a methodological debate on whether some of the analytical techniques developed in

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[1] The convergent evolution of neutral traits is *possible* but their likelihood is heavily biased by the granularity of our classification system, and their occurrence can be regarded as negligible in most cases (O'Brien and Lyman, 2003: 154).

evolutionary biology are applicable for cultural data or not (see Borgerhoff Mulder, 2001; Collard et al., 2006; Eerkens and Lipo, 2007; Gray et al., 2007; Currie et al., 2010; Nunn et al., 2010). The reconstruction of phylogenetic trees (O'Brien et al., 2001; O'Brein and Lyman, 2003) offers a good example of this. One of its core assumptions relies on the notion that most of the shared traits are a result of common ancestry rather than the consequence of horizontal transmission between groups. If the dominant process is the latter, hypothesised trees will not be able to accurately represent the population history. Recent studies are thus increasingly coupling the reconstruction of phylogenetic trees with network-based analysis (see e.g. Coward et al., 2008, Cochrane and Lipo, 2010), an alternative set of techniques where blending is represented as a reticulated graph (see Heggarty et al., 2010 for a review). Yet, despite methodological discussions over a decade, inferring cultural interaction and blending processes from the study of material culture is still a complex task that often requires the support of external data (e.g. language trees, as in Tehrani et al., 2010) or an excellent prior knowledge of historical events (e.g. Beheim and Bell, 2011), both unavailable in most archaeological contexts.

This paper contributes to this methodological debate by investigating whether the rich body of tools borrowed from biological sciences is sufficiently robust for archaeological inferences on the evolutionary history of a human population. We approach this problem by developing a "methodological" simulation (Lake, 2010:15), whereby we first generate a series of artificial archaeological records with known and parameterised evolutionary processes and, subsequently, determine whether specific methods are capable of identifying and distinguishing these. This is an increasingly common solution for evaluating the efficiency of a variety of analytical tools in archaeology (e.g. Eerkens et al., 2005; Surovell and Brantingham, 2007; Rubio-Campillo et al., 2011).

The paper is structured as follows. Section 2 reviews some of the methods used to evaluate branching, blending, and patterns of spatial variation in culture; Section 3 introduces the simulation model and its scientific rationale, as well as the proposed experiment design; Section 4 illustrates our results; Section 5 discusses their broader implications in archaeology; and Section 6 presents our conclusions.

2. Branching and blending in space

Consider a matrix **C** with rows representing communities located at different spatial coordinates, columns representing specific cultural traits, and cell values indicating their presence/absence (or frequency). The character matrix **C** can be converted into a cultural distance matrix **H** based on the dissimilarity **h** between different communities, so that communities that share a similar distribution of traits (i.e. have the same traits) can be regarded as "closer". The actual computation of **h** can vary according to the type of data and the underlying assumptions on the nature of the traits. For example, presence/absence data are usually measured using either *Hamming* or *Jaccard* distances. The former considers the presence and absence as character states, so that shared absence is treated in the same way as shared presence. Jaccard distance considers instead only the co-presence of traits, ignoring the number of shared absences. Both measures have been extensively used for archaeological analysis; for example Cochrane and Lipo (2010) examined the cultural evolution of Lapita pottery using Hamming distance, while Shennan and Bentley (2008) studied the decorative traits of LBK pottery using Jaccard distance.

As discussed in Section 1, both branching and blending events are expected to generate a pattern where cultural similarity decays as a function of spatial distance. We can visually assess this

by plotting, for each pair of sites, their spatial inter-distance against the dissimilarity **h**. The statistical significance of the correlation between the two variables cannot be computed by standard techniques, as distance values are not independent between observations (e.g. shifting a site location in space will change the entire distance matrix), hence a permutation based statistical test known as the Mantel test (Mantel, 1967) is commonly adopted. This has been used to assess patterns of cultural discontinuities over space for a variety of purposes, from the empirical support of a "great-ape culture" (Van Schaik et al., 2003) to the assessment of the cultural geography of European folktale tradition (Ross et al., 2013). Archaeological applications include the analysis of stylistic differences in basketry (Jordan and Shennan, 2003) and pottery (Hart, 2012), as well as diversity in farming practice (Zhang et al., 2010) and variation in biological traits inferred from dental metrics (Scherer, 2007). Although the exact interpretation of the mantel test varies between these case studies, they substantially agree on interpreting the presence of positive correlation as a proxy of cultural interaction (Jordan and Shennan, 2003; Hart, 2012).

The Mantel test provides a valuable tool for testing the correlation between space and cultural dissimilarity, but does not offer direct insights on whether the primary generative process behind the observed pattern is branching or blending. One way to approach this problem is to assume a branching process, generate the best bifurcating tree model from the empirical data, and examine its goodness of fit. This will require the choice of an algorithm to search among all possible trees using some selection criterion (e.g. parsimony, maximum likelihood, etc.; see O'Brien and Lyman, 2003, Coward et al., 2008; etc.) and a measure of goodness of fit which takes into account the frequency of patterns that are not explained by branching (e.g. parallel evolution, reversion, blending, etc.). The most commonly adopted statistic for the latter is the Retention Index (RI), equivalent to the ratio $(g - s)/(g - m)$, where g is the maximum number of character changes required on a tree where all taxa are equally related, m is the total character states changes expected given by the character matrix **C**, and s is the actual number of state changes on the proposed tree (Farris, 1989-a, 1989-b). RI ranges between 1 (a perfect branching tree) and 0 (complete *homoplasy*, i.e. character states are present in unrelated branches of the proposed tree).

RI, however, does not provide a direct evaluation of the branching–blending hypothesis, as no threshold measure can be used to make a definitive statement on whether a given set of empirical data provides robust evidence of each process. Thus, archaeological interpretations of RI have often relied on Collard et al.'s (2006) meta-analysis. The study, based on the statistical comparison of 42 samples from biological and cultural data (21 for each group), showed that branching can be a dominant force in cultural evolution, with biological RIs ranging between 0.35 and 0.94, and cultural RIs between 0.42 and 0.78. Values lower than this range are rarely reported in the archaeological literature and hence few works have explored their implications. Cochrane and Lipo's (2010) obtained fairly low RI values (0.35 and 0.49) for their study of Lapita pottery, and they explain their result as evidence of a blending process with the additional support of network analysis. Coward et al.'s (2008) study on the spread of plant economy in Neolithic Europe also returned a low fit (0.46), which they explain as a possible effect of reticulation processes after initial spreading and branching events (supported by detailed analysis of individual clades in relation to the geographic distribution).

An alternative approach to RI, based on a direct assessment of the cultural distance matrix rather than the reconstruction of hypothetical trees, is offered by Holland et al.'s δ-score (2002). The

mathematical principle behind this analysis is based on the evaluation of the following score for every possible quartet q of taxa x, y, u and v:

$$\delta_q = \frac{(h_{xv} + h_{yu}) - (h_{xu} + h_{yv})}{(h_{xv} + h_{yu}) - (h_{xy} + h_{uv})} \tag{1}$$

where h is the distance between pairs of taxa defined by the subscript. Equation (1) ensures that δ_q ranges between 0 and 1, with higher values expected for matrices with a less "tree-like" structure (see Fig. 1), hence the opposite of RI. By repeating the same operation for all possible quartets in a list of taxa, we will obtain a distribution of δ_q (often plotted as a histogram known as δ-plot), from which we can derive an overall measure of tree-ness by extracting summary statistics. Despite the robustness of the δ-score, which is entirely based on the structural properties of the distance matrix and does not rely on the specification of ancestral states nor the construction of a model tree, its application outside biology has been primarily confined to linguistics (Gray et al., 2010; Heggarty et al., 2010), with rare applications in the study of material culture (but see Buckley, 2012). As for the RI, the δ-score provides a continuous measure and hence it is difficult to infer a threshold for defining whether a branching or blending hypothesis is dominant.

Table 1 compares the RI and the δ-score of ten published archaeological case studies. The expected negative correlation between the two measures is observed to some extent ($R^2 = 0.29$), though it is not supported by sufficiently high levels of statistical significance ($p = 0.11$). The meta-analysis also shows how δ-Scores appear to have a smaller range of values (0.29–0.40) compared to RI (0.46–1.0), and indicates the presence of clear outliers. For example, the Paleoindian projectile point data (Case 2) shows a comparatively high RI suggesting a fairly strong branching signal, but its δ-Score is higher than the Lapita pottery data (Case 9), which has however a smaller RI (0.49). Some degree of divergence can undoubtedly be expected by differences in the underlying assumptions and mathematical principles of the two measures, but the results depicted on Table 1 raises serious questions about the robustness of the two methods for inferring variations in the balance between branching and blending.

The three analyses presented here provide a quantitative measure of the spatial structure of cultural diversity (Mantel Test) and the strength of tree-like signal (Retention Index and δ-Score) for any given character matrix **C**. However, their interpretation is not necessarily straightforward and multiple factors external to the process we are interested in could equally explain the observed measure. For example, a lack of statistically significant correlation

Table 1
Comparison of RI and δ-Score for 10 published archaeological case studies. RI are published values except for 1 and 3 which have been obtained from trees generated using the parsimony ratchet algorithm in the phangorn package in *R* (Schliep, 2011). δ-Scores have been manually computed using the ape package in *R* (Paradis et al., 2004) from the published character matrices, except for 8 were the results were already published. We used Jaccard distances for binary data (3, 5–7, 9–10) and Hamming distance for multi-state data (1,2, and 4).

ID	Dataset	RI	δ	References
1	Omani Monumental Tombs	1.00	0.24	Bortolini 2012
2	Paleoindian Projectile Points	0.70	0.40	O'Brien and Lyman 2003
3	Californian Basketry	0.69	0.29	Jordan and Shennan 2003
4	Maglemosian Harpoon Heads	0.64	0.32	Riede 2009
5	NW Coast Longhouses	0.64	0.29	Jordan and O'Neill 2010
6	Iranian Weaving	0.59	0.38	Tehrani and Collard 2009
7	NW Coast Subsistence Strategy	0.55	0.35	Prentiss et al., 2013
8	Southeast Asian Weaving	0.50	0.35	Buckley 2012
9	Lapita Pottery	0.49	0.29	Cochrane and Lipo 2010
10	Plant Economy in Neolithic Europe	0.46	0.36	Coward et al., 2008

between spatial and cultural distances could be equally caused by an absence of blending and branching processes as well as a situation whereby any individual can interact with any other individual regardless of their physical inter-distance. In the former case communities will yield high inter-community cultural differentiation independent of spatial distance, while in the latter case we would expect the opposite, low inter-community cultural differentiation regardless of spatial distance. In either case, a scatterplot displaying the relation between cultural dissimilarity and spatial distance will show a flat line, although in the former case this will be higher on the *y*-axis. Computing the average cultural distance from the character matrix could potentially provide some clues, but this will be hindered by the complex interplay of other variables such as the rate of cultural evolution and the initial conditions of the system of interest.

In a recent study Nunn et al. (2006, 2010) highlighted the importance of these factors. They generated artificial datasets from a simulation of a continuous trait evolution where both branching and blending processes were mimicked. Their model consisted of a spatial grid where each cell can be occupied by one "culture", defined by continuous numbers representing each trait. At each time-step of the simulation, they updated the grid by: 1) removing random cultures from the matrix (*extinction*); 2) creating a copy of existing cultures to neighbouring empty cells (*colonisation*; *branching*); 3) allowing neighbouring cultures to copy their trait through horizontal transmission (*blending*); 4) modifying the cultural traits through random mutation. Results showed how high values (>0.6) of RI were indeed generated when the probability of horizontal transmission was small, but low values were not necessarily correlated with stronger blending processes. Instead variations in the rates of cultural evolution (i.e. innovation) and extinction were stronger explanatory variables, showing that low values of RI are not necessarily the consequence of strong blending.

3. An agent-based model of cultural interaction

The simulation study by Nunn et al. (2006, 2010) raises the question of whether their conclusion can be reproduced by presence–absence character traits, which are far more common in
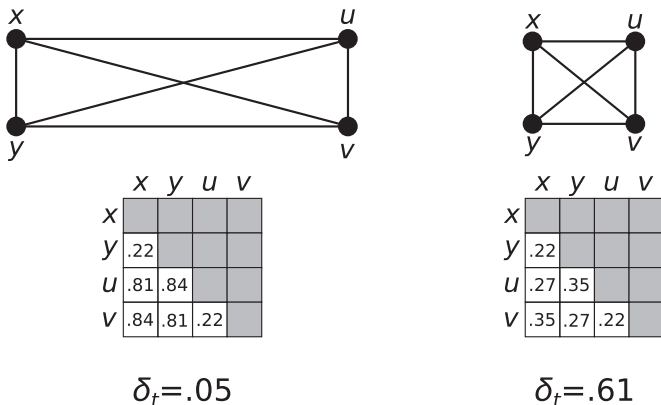

Fig. 1. Computation of δ-score for two hypothetical distance matrices.

$\delta_t = .05$ $\delta_t = .61$

archaeological data, as well as how the other analyses introduced in the previous section (correlation between spatial and cultural distances, distogram, and δ-Score) behave in the controlled environment of a simulation. We extended their work and developed a methodological simulation based on a spatially situated agent based model (ABM).

3.1. Model design[2]

Consider a square-shaped grid space[3] composed of P cells. Each cell can be occupied by a maximum of one *settlement* (thus the total number of settlements n will always satisfy the condition $n \leq P$), defined as a fixed-size group composed of g agents. Each agent is associated with a single integer c representing a cultural trait. We can thus build the same character matrix $\mathbf{C}$ discussed in Section 2, with rows representing individual settlements, columns defining unique cultural traits, and cell values filled by either the presence/absence of specific values of c within each group.

The simulation is initialised with the creation of a single founding group and proceeds with a series of discrete time-steps $t = 1,2,3.., T$ where the following four processes update the distribution and the number of settlements, as well as the cultural trait of each agent:

1) **Settlement Extinction.** A proportion γ of the groups are randomly selected and removed from the model. Complete extinction ($n = 0$) is avoided by always allowing at least one settlement to survive.
2) **Settlement Fission.** Fission enables settlements to reproduce and occupy a neighbouring[4] empty cell. This occurs with a probability ρ and consists of the following sub-steps: 1) an empty neighbouring cell is randomly selected; 2) half of the agents in the focal settlement (the "parent" settlement) are selected and moved to the destination cell, forming the "offspring" settlement; each agent of the parent and offspring settlements creates a copy of self, ensuring that both settlement have the default size g.
3) **Cultural Transmission.** At each time-step, all agents will randomly copy a cultural variant from the entire population. The probability of copying a trait m for any individual located on a group j is defined by the following equation:

$$P_j(m) = \frac{(1-\mu)\sum_{i=1}^{n} k(m_i)w_{ij}}{\sum_{i=1}^{n} g_i w_{ij}} \qquad (2)$$

where, μ is the probability of innovation (see below), n is the total number of groups, g_i is the size of a given group i, $k(m_i)$ is the number of individuals possessing the trait m in i, and w_{ij} is the following weight function:

$$w_{ij} = e^{(-\beta d_{ij})} \qquad (3)$$

where e is the base of the natural logarithm, d_{ij} is the grid distance (*Chebyshev* distance) between the focal group j and i, and β is a distance decay parameter. Equation (2) modifies the standard

model of neutral evolution by taking into consideration the spatial structure of the population. Equation (3) is in fact a stripped-down version of a spatial interaction model used in Geography (Fotheringham, 1981; see Bevan and Wilson (2013) for a recent archaeological application) which ensures that variants within the focal group have the highest impact in the transmission process ($w_{ij} = 1$), while variants located in other groups will have a smaller impact ($w_{ij} < 1$) depending on their distance to the focal group. A hypothetical example can better illustrate how the two equations work. Suppose that the variant x is only possessed by 10 individuals in the focal group and 70 individuals in another group located in the immediate neighbourhood (i.e. at *Chebyshev* distance of 1). If we ignore mutation (i.e. $\mu = 0$), assume that each group is formed by 100 individuals, and set β to 0.5, the probability of adopting x will be ca. 0.33. Increasing β to 3 will decrease the probability of adoption to 0.13, hence β will exponentially remove the role played by other groups, mimicking the effect of a decline in cultural interaction. On the other hand, if β is set to 0, the probability of adopting the trait will reach 0.4, equivalent to what we would expect if there were no population structure (i.e. the probability of adoption is the ratio between the number of individuals possessing the trait and the total population size, i.e. 80/200).

4) **Innovation.** Each agent has a probability μ of changing its cultural trait c to another random integer. This is equivalent to the infinite variants model of Kimura and Crow (1964).

The four processes described above determine temporal variation in the spatial distribution and the overall frequency of each cultural trait. Branching occurs at each fission event, while blending and horizontal transmission between different communities are calibrated by β in an exponential fashion. Fig. 2 illustrates this by plotting Equation (3) using different values of β for the same set of distances. When this is set to higher values (e.g. $\beta = 10$ on Fig. 2), we effectively mimic a complete isolation between groups, and cultural similarities are almost exclusively the result of shared ancestry. Conversely, when β is lower, the effect of blending will be more pronounced (e.g. $\beta = 2$), up to a point where space no longer exercises any constraint in cultural interaction ($\beta = 0$).

Thus, the core assumption of this model is that when unbiased cultural transmission is made spatially explicit, the likelihood that a trait will be transmitted between two individuals is positively (though not necessarily linearly) correlated with the spatial distance that separates them. This is a general assumption underlying many theoretical models that seek to describe the spatial distribution of selectively neutral cultural traits under conditions in which otherwise unbiased cultural transmission is mediated by the spatial scale of social learning (see e.g. Neiman, 1995; Holman et al., 2007; Premo and Scholnick, 2011).

3.2. Experiment design

We conducted two simulation experiments (Table 2) to evaluate how the relationship between cultural dissimilarity and spatial distance varies as a function of different parameter combinations (experiment 1), and whether RI, δ-score, and the correlation coefficient between the two variables are capable of correctly tracking variations in the balance between branching and blending processes (experiment 2). Each run of the simulation was run for 1000 time-steps with the presence/absence character matrix extracted from the final configuration. This was then used to compute the Jaccard distance between all pairs of groups as a proxy of cultural dissimilarity. This experiment design enables us to determine the expected pattern given a stationary historical process where the
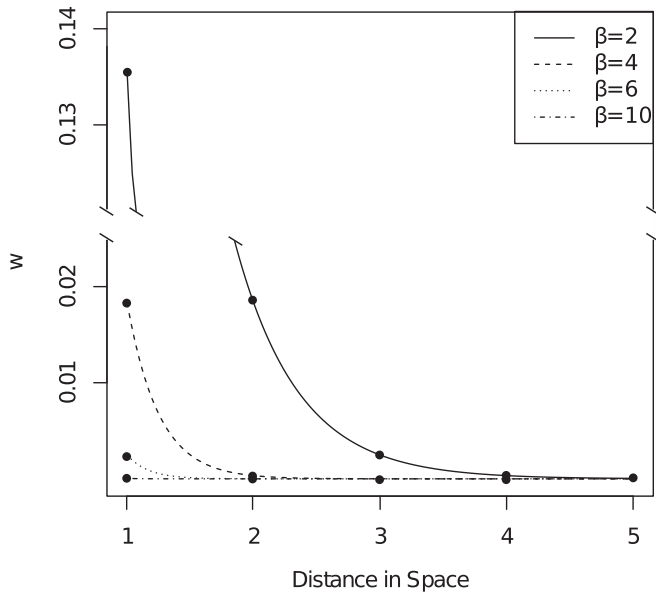
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[2] Detailed description of the model (ODD protocol, Grimm et al., 2010) and the simulation code are provided on the online supplement material.

[3] Following Nunn et al. (2010), we chose a bounded space, rather than a toroidal one. Edge effects are negligible in this case, while the systematic bias introduced by a torus might be greater, as novel variants could, in theory, be transmitted from opposite "sides" of the world.

[4] The spatial neighbourhood is defined as the 8 cells surrounding the focal cell (i.e. Moore neighbourhood).

Fig. 2. Relation between *w* and spatial distance for different settings of β.
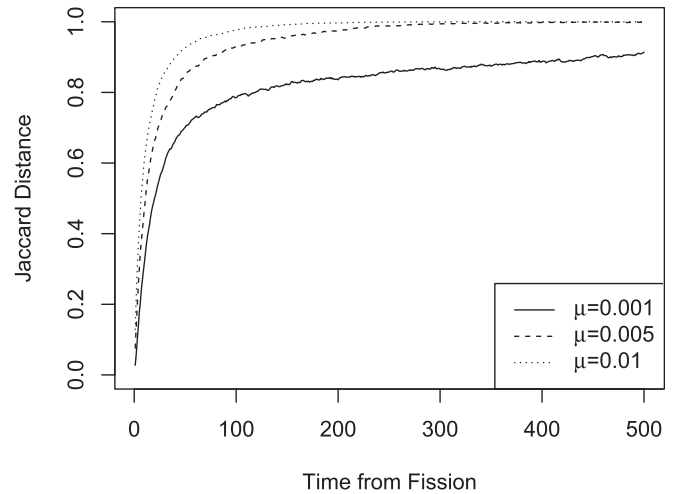

Fig. 3. Jaccard distance between parent and offspring communities after fission (average over 5000 simulations, with *g* = 50).

equilibrium between branching and blending is controlled by the simulation parameters.

For experiment 1 we choose to select a fixed set of values for each parameter, so that we could fix the number of parameter combinations and define the number of repetitions for each. For experiment 2 we randomly selected the model parameters using Latin Hypercube sampling (McKay et al., 1979; Iman et al., 1981), which ensures a uniform coverage of the multi-dimensional parameter space.

For the purpose of this paper, we chose to explore the effect of three parameters: 1) the frequency of settlement fission (branching) events; 2) the rate of cultural innovation; and 3) the shape of the distance decay function (correlated with the intensity of blending). For the first process we fixed the frequency of fission ρ to 1, and chose to sweep the extinction rate γ between 0.05 and 0.2 (using 0.05, 0.1, and 0.2 for experiment 1). Thus, in this particular case, γ can be effectively interpreted as a "replacement" rate, with high values enabling higher frequency of settlements substituted by new settlements originating from fission (branching) events. The rate of cultural innovation, was controlled by ranging the mutation rate μ from 0.001 to 0.01 (0.001, 0.005, and 0.01 for experiment 1). Fig. 3 illustrates the effects of variation in μ, resulting in different rates of diversification between settlements with initially identical distribution of traits. The third process, i.e. the spatial range of interaction, has been controlled by sweeping the distance decay parameter β from 0 to 10 (constraining the interval to 2 for experiment 1). This ensured a range of configurations, from a complete lack of spatial constraint where agents could copy from anyone in the model with the same probability ($\beta = 0$) to an

Table 2
Model parameters and values.

Symbol	Parameter name	Sweep values
P	Total number of cells	100
T	Number of timesteps	1000
g	Number of agents per group	50
γ	Extinction rate	0.05–0.2 (0.05, 0.01, and 0.02)
ρ	Fission rate	1
μ	Innovation rate	0.001–0.01 (0.001, 0.005, and 0.01)
β	Distance decay parameter	0–10 (0,2,4,6,8, and 10)

almost complete isolation ($\beta = 10$), where the probability of copying from an agent in the closest neighbour group is more than 22,000 times less likely than copying from someone in the same settlement (see also Fig. 2). The resulting parameter space was defined by three dimensions (γ, μ, and β), with fifty-four unique parameter combinations for experiment 1.

4. Results

4.1. Experiment 1

Fig. 4 shows the distribution of Jaccard dissimilarity for different Chebyshev distances obtained for each of the fifty-four parameter combinations. The boxplots show a variety of patterns, from a flat line where cultural similarity is uncorrelated with spatial distance (e.g. at $\beta = 0$, $\mu = 0.001$, $\gamma = 0.05$), to positive correlations confined to shorter (e.g. at $\beta = 8$, $\mu = 0.005$, $\gamma = 0.1$) or longer (e.g. at $\beta = 2$, $\mu = 0.001$, $\gamma = 0.1$) distance ranges.

Higher values of β determine an increasing isolation of each settlement, *de facto* reducing the effective population size to the minimum (g) and promoting random drift (Bentley et al., 2004). As a consequence of this, given a sufficient amount of time and mutation events, the dissimilarity between two isolated groups increases (i.e. a *cladogensis*), reaching in this case its theoretical maxima of a Jaccard distance of 1 (cf Fig. 3). On the other hand, when β is equal to 0, there is no population structure, and the effective population size becomes *gn*. The dissimilarity between any pair of settlements will be equivalent to what we would expect if we sample two random subsets of individuals from the same unstructured population. Difference between the two scenarios will thus be in the average dissimilarity, which is higher for the former and lower for the latter (cf. discussions on population differentiation in population genetics, Wright, 1950; Excoffier, 2001). This can be observed for all combinations of γ and μ, although the difference is more pronounced when the mutation rate is low. This is unsurprising, as higher mutation promotes more diversity, and hence differences between two random sets of individuals from the same population are more likely to be higher (cf. $\beta = 0$ for all settings of μ).

Fig. 4 illustrates how branching and blending can equally generate a spatial structure, although with some key differences in how cultural dissimilarity increases as a function of geographic distance. When blending is virtually absent (i.e. $\beta = 10$), we observe
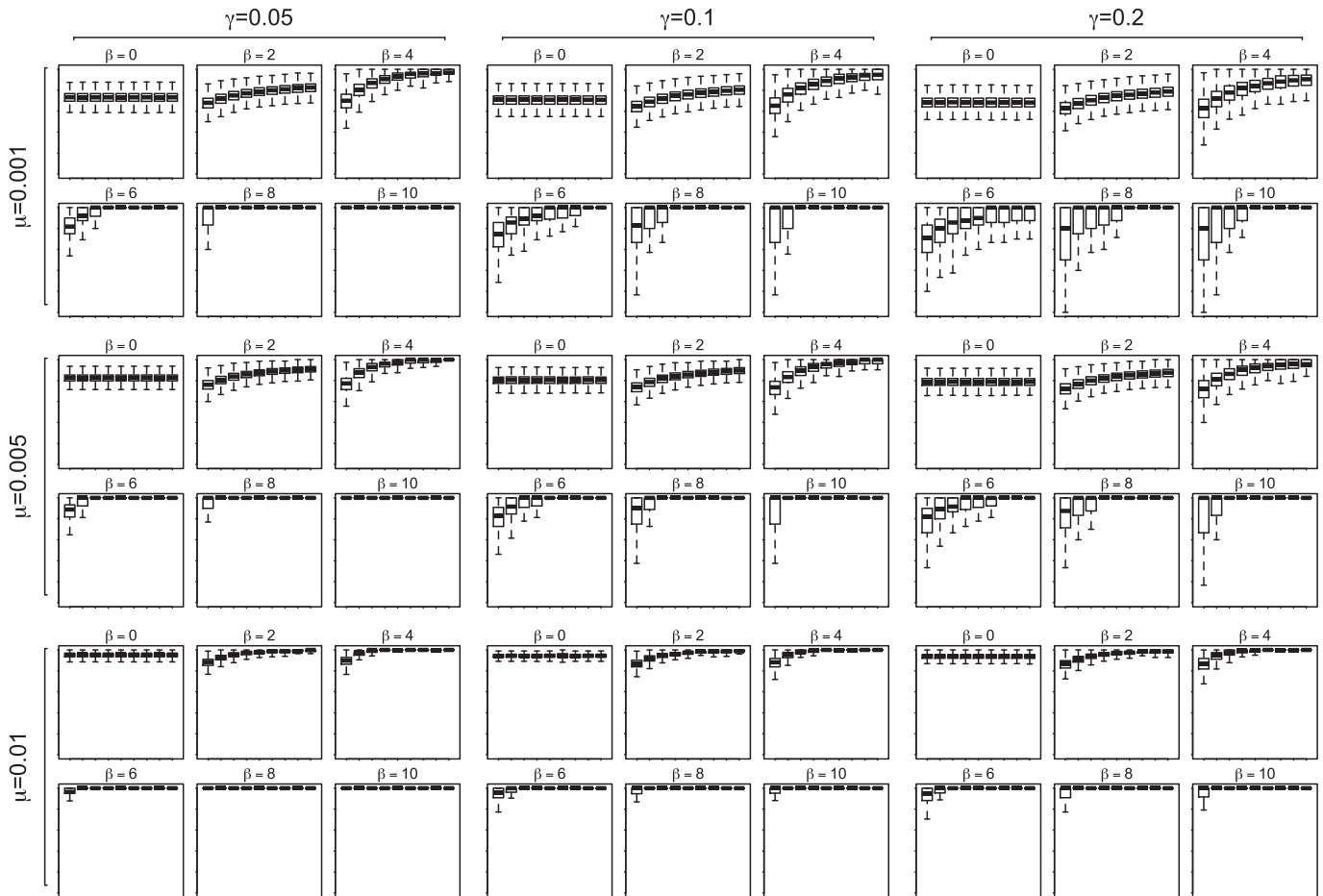
Fig. 4. Boxplot depicting the relationship between cultural dissimilarity (Jaccard distance and space (Chebyshev distance) for different parameter combination of β, μ, and γ (distribution obtained from 100 runs for each parameter combinations).

differences in the boxplots as a function of the mutation rate (μ) and the extinction/replacement rate (γ). When μ is low and γ is high, settlements exhibit some degree of cultural similarity at short distance range as a result of the high number of shared ancestral traits. This pattern, however, is characterised by a high variance reflecting a mixture of low and high cultural dissimilarities. The landscape is thus highly heterogeneous, a consequence of the stochastic nature of the fission events, which can easily determine the geographic proximity of pairs of settlements with shorter and longer phylogenetic distances. Increasing the mutation rate leads to a loss of this pattern, a consequence of the higher speed in the divergence between offspring settlements (cf. Fig. 3). Not surprisingly, a similar result is also observed when the actual number fission events is reduced (lower γ).

On the other hand, when blending is the dominant force ($\gamma = 0.05$ and $\beta = 2$), the boxplots show a gradual but constant increase in cultural dissimilarity over increasing spatial distance. This continuous gradient is also characterised by a fairly narrow range of cultural dissimilarities observed at each distance bin, a consequence of the homogenous flow of information through the landscape.

A mixture of blending and branching determines a variety of patterns. When $\beta = 2$, increase in the number of fission events (γ) does not lead to any tangible variations in the boxplot. In other words, when the degree of intergroup interaction is high, signals of branching becomes invisible. When the effect of blending becomes weaker we can detect an increase in the variance of cultural

dissimilarity and a transition to a steeper curve. Interestingly, the effect of blending can be observed even when β is above 6, showing that the smallest chance of interaction (cf. Fig. 2) is sufficient to generate a spatial structure that is distinguishable from a pure branching process (e.g. compare $\mu = 0.001$, $\gamma = 0.2$, $\beta = 6$ and $\mu = 0.001$, $\gamma = 0.2$, $\beta = 10$), especially when the mutation rate is comparatively low.

4.2. Experiment 2

We sampled 5000 parameter combinations and examined the relation between each of the three parameters and: 1) the correlation between spatial and Jaccard distances, 2) δ-score; and 3) Retention Index. Fig. 5 visualises this as a series of scatterplots, while Table 3 presents the variable importance computed for each parameter using the *random forests* algorithm (Breiman, 2001). The latter is a regression and classification tool based on the creation and combination of multiple decision trees (a statistical model that splits the data into a tree-like model, where each node is defined by a numerical condition of the independent variables). There are two reasons why we chose this particular analysis to evaluate our simulation outputs. First, decision-trees are capable of handling complex non-linear relationships between variables, and second, *random forests* outputs statistical indices of variable importance. This is computed as the mean square error increase (MSEi) that we would expect if a focal parameter were excluded from the model. In other words MSEi allows us to compute the
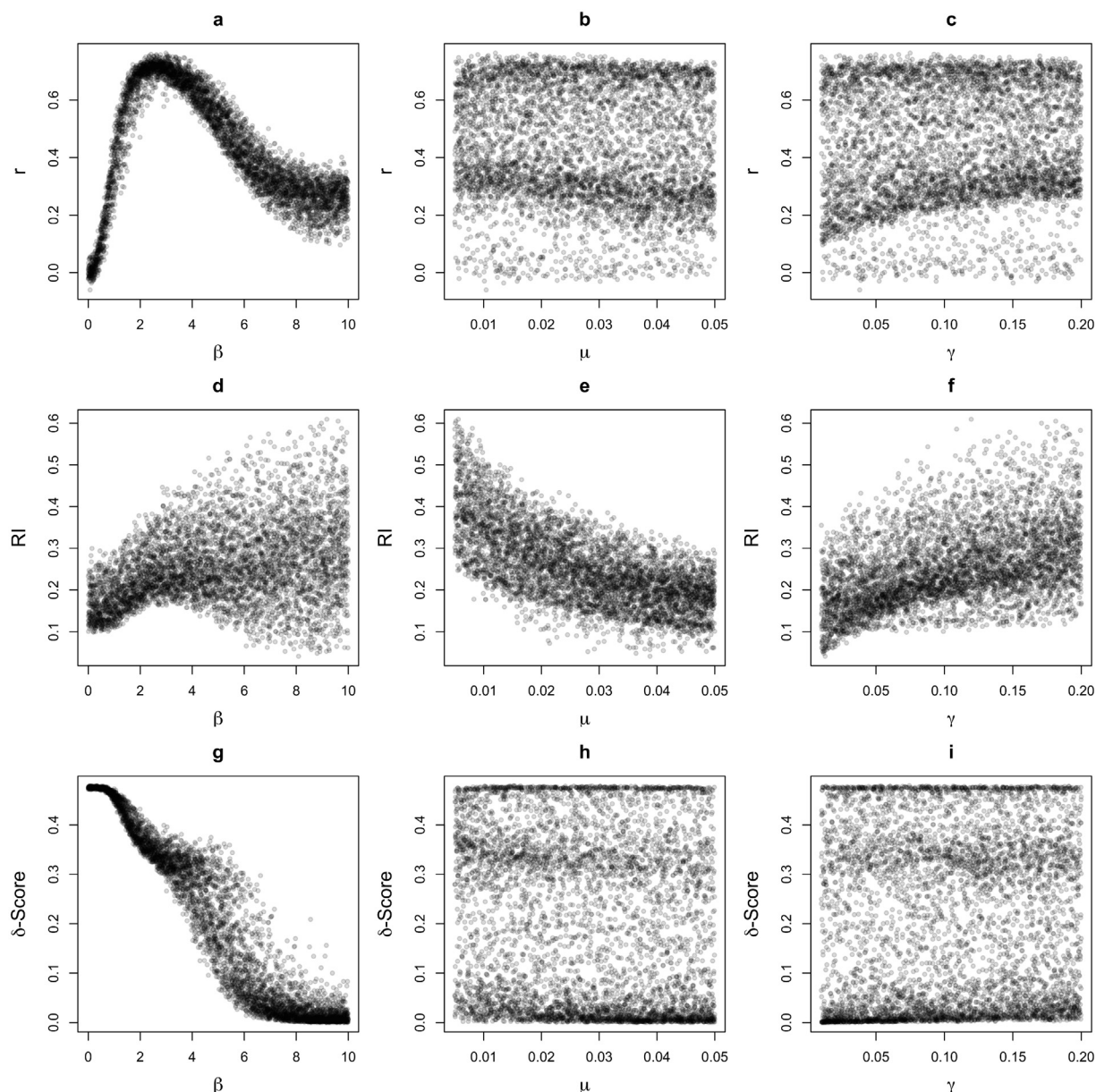
Fig. 5. Scatter plot of distance decay (β), mutation rate (μ), and extinction rate (γ) against δ-score, RI, and correlation between spatial and Jaccard distances (experiment 2).

loss of information that would occur if we did not take into account a given parameter.

The correlation between spatial and Jaccard distances (Fig. 5a–c), shows a strong but non-linear relationship with the distance decay parameter (β). Given the patterns observed on Fig. 4 this outcome is not surprising. The lowest correlation is observed when space does not exercise any constraint in the interaction between the agents ($\beta = 0$). By increasing β we build in a spatial structure, and hence we induce an increase in the correlation. However, once the isolation between groups becomes more pronounced (i.e. $\beta > 4$), the correlation between the two distances starts to gradually decline. At this point, when branching becomes the dominant evolutionary process, changes in correlation become increasingly a function of the mutation and the extinction rate (cf. Fig. 4). This can be observed in the wider range of correlation values for higher values of β (Fig. 5a), as well as in the negative correlation between r and μ (Fig. 5b) and the positive correlation

between r and γ observed when r is between 0.2 and 0.4 (Fig. 5c). An increase in the extinction rate will in fact ensure the creation of a higher number of offspring settlement at close distance, leading to an increase in the correlation between spatial and Jaccard distances that is maintained over time when the mutation rate is low. These general impressions are confirmed by the random forests analysis, with β showing by far the highest MSEi percentage (Table 3).

The scatter plots referring to RI (Fig. 5d–f) show a very different picture,[5] with all three parameters exhibiting fairly robust correlations. Increasing distance decay leads to an overall increase in RI, albeit with a strong degree of heteroscedasticity

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[5] The RIs have been calculated from 100% majority consensus trees. Phylogenetic trees have been obtained using the parsimony ratchet algorithm (Nixon, 1999) using the *Phangorn* package in *R* (Schliep, 2011).

Table 3
Variable importance (MSEi) obtained from random forest analysis (using random forest library in *R*; Liaw and Wiener, 2002).

	Distance decay (β)	Cultural innovation (μ)	Extinction (γ)
δ-score	920.37%	232.41%	61.87%
Correlation	588.25%	108.31%	43.5%
Retention Index	473.27%	595.14%	457.37%

with a range increasing from ca. 0.1–0.25 at $\beta = 0$ to 0.05–0.6 at $\beta = 10$. This implies that while an overall relation between decline in cultural interaction and increase in branching signal does exist, the level of uncertainty is extremely high with increasing isolation between groups. This is explained by the fairly strong correlation of all parameters with RI, a claim supported by high values of MSEi and by the patterns observed on the scatter plots. High values of μ, the parameter with the highest MSEi, determine a fast divergence between parent and offspring communities, leading to a loss of phylogenetic signal and a decrease in RI. This is observed even when the number of fission event is high. Fig. 5f shows in fact a general positive correlation between γ and RI, but with high levels of heteroscedasticity determined by the variations in μ.

δ-score exhibits the strongest correlation with β, with a slightly logistic shape in the scatterplot (Fig. 5g). Interestingly, the other two parameters do not exhibit any correlation (Fig. 5h–i), as shown by the fairly narrow range of δ-score for similar values of β (Fig. 5g). This is also confirmed by the analysis of the variable importance (Table 3), with β showing higher MSEi than μ and γ. It is worth noting that intermediate values of the distance decay parameter (i.e. 5–7) show a slight increase in the variance of the δ-score, though this does not seem to show any significant correlation with mutation and extinction rates. This would suggest that stochastic components of the model play a stronger role within this parameter range, leading to a consistent variation of δ-score between different simulation runs.

5. Discussion

The simulation exercise presented here has illustrated the strength and the weakness of four analytical tools used in archaeological enquires to detect signals of branching and blending. The most relevant outcome is the different sensitivity of each method to the three model parameters (mutation rate, replacement rate, and distance decay weight). Both δ-score and the correlation between spatial and Jaccard distances are strongly dependent on the degree of isolation between different communities (β), while RI is primarily a function of the mutation rate (μ), although the other two parameters also exhibit correlation.

These results are in line with the earlier simulation studies conducted by Nunn et al. (2010) on continuous trait evolution, confirming thus that some phylogenetic statistics (e.g. RI) are not always robust proxies for detecting branching vs. blending signals. The result of our study is not surprising if we consider that the two processes are defined by multiple subcomponents, each generating a different patterning in the archaeological record. Branching is affected by the post-fission rates of cultural divergence (here defined by the mutation rate), the frequency of the fission process itself, as well as where and how far the offspring settlements are located from their parents (an aspect that we have not explored in this paper). We noticed, for example, that even when cultural interaction is virtually absent ($\beta = 10$), different rates of innovation and frequency of fission events could produce a wide variety of results that might be erroneously interpreted as a stronger or weaker signal of blending. Similarly, horizontal transmission is

constrained by how spatial distance decreases the likelihood of interaction, as well as other variables that we did not address here. These include topographic constraints in spatial interaction (McRae, 2006), differences in settlement size (see the notion of "isolation by density"; Terrell, 1986), or non-spatial biases in the transmission process (Axelrod, 1997; Boyd and Richerson, 1985; Kandler and Shennan, 2013).

One key aspect that we did not examine here is the intrinsic uncertainty and the limited amount of information we can retrieve from regional archaeological data. Our simulation model showed that a stationary process recorded at an equilibrium state already exhibits a complex pattern where untangling branching and blending signals is an extremely hard exercise. When examining real-world data we also need to face differences in the quality and size of archaeological assemblages, variation in sampling strategies, and the effect of time averaging, that are likely to introduce biases in the available record. Moreover, long-term regional analyses are most likely affected by non-stationary processes. The magnitude and patterns of cultural interaction are likely to change over time, while meta-population dynamics are expected to show fluctuations between episodes of increase and decrease in fission events. If these changes occur at high frequencies the system of interest might not reach an equilibrium state and/or the temporal resolution of the archaeological record might be insufficient for discerning branching and blending signals.

6. Conclusions

This paper examined the analytical power of several techniques used to infer the spatial structure of cultural diversity and the degree to which branching and blending processes generate patterning in the observed archaeological record. We assessed these mathematical tools by creating a series of artificial datasets using a computer simulation where the spatial distribution of cultural traits was defined by branching and blending events. Our analyses have highlighted the following points:

- Correlations between spatial and cultural distances do not have a linear relationship with the degree of isolation by distance. The highest correlation is achieved when the spatial constraints in the interaction between individuals is intermediate.
- Low values of Retention Index are not good proxies of blending (Nunn et al., 2010). Other processes such as the frequency of fission and the rate of cultural innovation determine an equal, if not stronger, effect on the analytical output.
- δ-score provides a fairly robust signal of the degree to which space determines a constraint in interaction.

These results suggest caution in interpreting each of these individual statistics as pivotal cues for determining whether the observed archaeological record is primarily the result of branching or blending. The nature of the question itself also raises some concern. Conceptualising the problem as a dichotomy might in fact generate the false impression that the two processes generate distinguishable archaeological signals, while in fact the problem is endemic, and we should expect certain levels of equifinality regardless of the analytical tools in our hands. When analytical units are communities observed at a regional scale, branching is ultimately the consequence of group fission (Foley and Lahr, 2011) a process that can be characterised by different frequencies, structure, and spatial range, each determining a different archaeological signature that might enhance or contrast with patterns determined by cultural interaction.

Acknowledgements

Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.jas.2014.01.002.

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