



## Diet traditions and cumulative cultural processes as side-effects of grouping

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Social learning and cognitive sophistication are often assumed to be prerequisites for the origins of culture. In contrast, we studied to what extent the most simple social influences on individual learning can support cultural inheritance. We did this using a spatial individual-based model where group foragers have to learn what to eat in a diverse patchy environment, and used simple population dynamics to investigate the potential of ‘merely living in groups’ to allow for inheritance of diet traditions. Our results show that grouping by itself is a sufficient social influence on individual learning for supporting the inheritance of diet traditions. Unexpectedly, we find that grouping is also sufficient to generate cumulative group-level learning through which groups increase diet quality over the generations. Whether ‘traditions’ or ‘progressive change’ dominates depends on foraging selectivity. We show that these cultural phenomena can arise as side-effects of grouping and therefore independently of their adaptive consequences. This suggests that cultural phenomena could be quite general and shows that cumulative cultural processes already occur even for the most simple social influences on learning.

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Studies on the origins of culture focus on different social learning mechanisms and the evolution of behavioural inheritance by social learning (e.g. [Henrich & McElreath 2003](#)). In general, social learning is thought to evolve because it allows individuals to avoid the costs of individual learning. However, only sophisticated forms of social learning, such as imitation and teaching, are thought to be sufficiently accurate to allow for certain cultural phenomena, such as large traditional repertoires and cumulative cultural evolution (e.g. [Boyd & Richerson 1995](#); [Boesch & Tomasello 1998](#); [Castro & Toro 2004](#)).

Theoretical approaches to the evolution of social learning generally focus on the adaptive benefits of social learning relative to the costs of asocial learning. In such cases social learning is found to be adaptive when the environment is constant enough not to make socially learned behaviour obsolete (e.g. [Boyd & Richerson 1985](#); [Laland & Kendal 2003](#)), or social cues are more reliable than asocial cues (e.g. [Dewar 2003](#)).

In contrast, we studied cultural phenomena as side-effects of foraging behaviour. We used an opportunity-based approach drawing on the ‘ToDo’ principle ([Hogeweg & Hesper 1985](#)), which focuses on behavioural structuring by local opportunities, rather than behavioural strategies. This approach is sensitive to interactions and feedbacks that can arise, allowing for novel phenomena and self-organizing processes to occur (see [Hogeweg & Hesper 1989](#); [te Boekhorst & Hogeweg 1994](#)), and can be referred as process-oriented modelling ([Hemelrijk 2002](#)).

Using such an approach, we have previously shown that grouping will spontaneously generate social influences on diet learning in fixed groups of individuals that learn only by trial-and-error ([van der Post & Hogeweg 2006](#)). Our results show that, in patchy environments, local sharing of learning opportunities automatically leads to convergence in learning within groups, and diet differences between groups. Important is that this convergent social influence on learning arises spontaneously and is not an evolved strategy, that is, it is a side-effect of grouping in a patchy environment. Such convergent social influences therefore appear generic for group foragers and are relevant for understanding diet differences such as those found between neighbouring groups of capuchin monkeys ([Chapman & Fedigan 1990](#)).

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However, it is still an open question whether such spontaneously arising convergence in learning can lead to diet inheritance and support diet traditions. The main concern here is whether the convergent social influence on trial-and-error learning is accurate enough to allow for sufficient fidelity of transfer of food preferences. Here, we studied whether this is the case by running simulations in which we mimic transmission chain experiments (cf. Curio et al. 1978; Galef & Allen 1995). Such experimental set-ups are used to study whether a behavioural variant can be transmitted beyond the individuals that first learned and discovered the behaviour. The behavioural transmission is studied over a chain of individuals whereby, in sequence, the most experienced individual is replaced by a naïve individual (see also Laland & Williams 1997). Using such a set-up, we included group dynamics and the influx of naïve individuals in our simulations. We did not add any other feature to our model which could affect the nature of learning, and so explicitly studied the inheritance of diet preferences by trial-and-error learning, with only 'living in groups' as a social influence on learning.

## MODEL

We used an individual-based model (adapted from van der Post & Hogeweg 2006) that incorporates an explicit spatial environment in which multiple species of resources can be arranged in different distributions and densities. Individuals were modelled to move and forage in groups through the environment, and learn what to eat. A combination of local ecological and social context, and individual internal state, determines what individuals can do, making foraging dependent on the ecological and social opportunities that arise. Therefore, learning is not a fixed strategy but depends on what individuals observe. The model was built up as follows (see Appendix 1 for a complete list of parameters).

### Environment

The environment is a 2 dimensional grid where grid points represent locations where resource items can be found. As a default, we implemented 250 resource types (species) with a Gaussian quality (energy) distribution, which were distributed in patches of a single resource type with a radius of 10 grid units and about 12 items per grid location. Each patch could be visited several times by groups before they were depleted.

Resources were depleted during foraging and were renewed at the beginning of each year. This was simply done by repeating the initial resource distribution pattern and removing any resource units from the previous year. Ecological dynamics were therefore limited to single influges of all resources at the beginning of each year.

We used a grid size of 2800 square units (1 unit is scaled to 1 m) and implemented 4900 patches each consisting of about 4000 resource items. This is a larger grid than in our previous model, but this scales with the longer timescales we implemented here. Timescales are important in

learning processes, especially with respect to convergence through learning. Our timescale was set in rough correspondence to that of primates (see Fig. 1), where 1 time step = 1 min, 1 day = 12 h and 1 year = 365 days. For more details on modelling the environment see van der Post & Hogeweg (2006).

### Individuals

We modelled individual behaviour using an event-based formalism, that is, actions take time. The behaviour procedure is given in Fig. 1 and basically ensures that individuals remain in groups, find preferred food and eat, discover new resources, move forward, or do nothing while digesting after eating to satiation (maximum stomach capacity).

### Grouping

To achieve grouping, individuals were modelled to remain in close proximity to a sufficient number of other individuals (see Fig. 1). Individuals check how many neighbours are present within a distance of 10 grid units. If they have more than two neighbours, then they are 'safe' and proceed with foraging. Otherwise they move to where they observe the highest density of individuals within 150 grid units. These grouping parameters were chosen to reduce subgroup formation to focus on inter-group processes. Note that individuals do not pay any attention to any behaviour cues of other individuals, that is, whether they are eating or not does not make any difference. It is purely a case of wanting to remain in a group.

### Learning

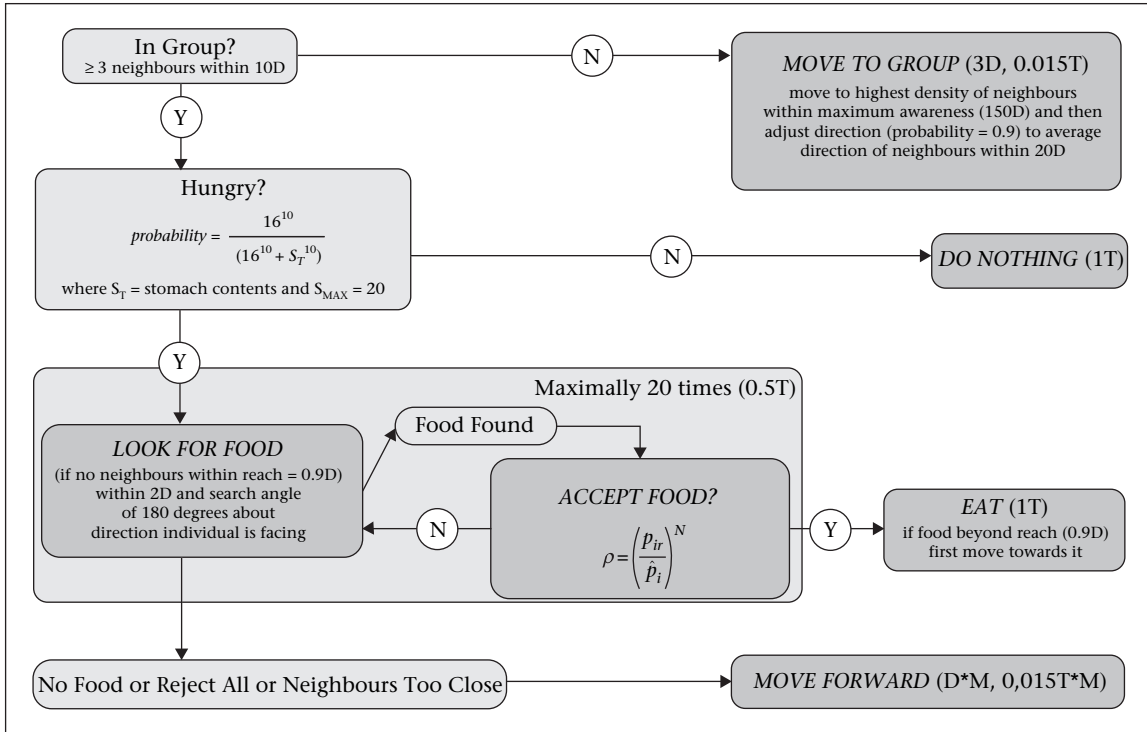
Individuals try every unknown resource (for which they do not yet have a preference) they encounter. Thus, we implemented maximum trail rates such that every individual tries everything. Once eaten, resource quality is assessed by individuals through delayed postdigestive feedbacks (every 100-time steps) and resource preferences are updated according to:

$$p_{ir} := p_{ir} + \left( U \frac{S_{ir}}{S_{it}} (\bar{E}_i - \bar{p}_i) \right) \quad (1)$$

where  $p_{ir}$  is individual  $i$ 's preference for resource  $r$ ,  $S_{ir}$  is the number of items of resource  $r$  in its stomach,  $S_{it}$  is the total number of items in its stomach,  $\bar{E}_i$  is the average energy per resource item it obtains from digestion, and  $\bar{p}_i$  is the average preference it has for the items digested. Note that equation (1) is only updated after digestion and only for the digested resources.

Preferences represent an individual's energy estimate for a given resource and  $\bar{p}_i$  therefore represents an expected energy feedback from digestion. Moreover, we draw  $\bar{E}_i$  from a normal distribution with a mean of  $\bar{E}_i$  and a standard deviation of 0.005 to add some environmental noise.

We set  $U$  to 0.01, which means that if individuals eat a resource continuously for about 7 days, their preference will be equal to half the actual quality of the resource. This at least appears to be in the order of magnitude of what is



**Figure 1.** Individual behaviour procedure.  $M$  = distance individuals move forward after not finding acceptable food,  $p_{ir}$  = resource preference,  $\hat{p}_i$  = preference expectation,  $N$  = individual selectivity during food choice,  $D$  = distance unit (length of one cell in 2D grid, scaled to 1 m),  $T$  = time unit (scaled to 1 min). For ‘moving forward’, distance and duration are scaled by  $M$ , that is,  $D^*M$  and  $T^*M$ .

found for preference development in primates (Matsuzawa & Hasegawa 1983; our estimate). Preference development is therefore a time-dependent reinforcement learning, and preference therefore depends on familiarity, that is, how well the resource is ‘known’ and has the form  $p_{ir}/q_r$ , where  $q_r$  is the quality of resource  $r$ . Both postdigestive feedbacks and familiarity are known to play a role in preference development and diet selection (Garcia et al. 1974; Provenza 1995; Galef 1996; Birch 1999).

### Foraging

Individuals search for food locally within a semicircle (radius 2 grid units) in the direction they are facing, and the preference ( $p_{ir}$ ) for each resource item found is evaluated relative to  $\hat{p}_i$ , which represents an individual’s ‘highest’ preference:

$$\rho = \left( \frac{p_{ir}}{\hat{p}_i} \right)^N \quad (2)$$

where  $N$  scales the degree to which the probability of eating less preferred resources decreases as  $p_{ir}$  drops below  $\hat{p}_i$ .  $N$  therefore affects foraging selectivity, that is, to what extent less preferred resources are consumed. We vary foraging selectivity by varying  $N$  and therewith enhance the impact of preference differences.

As individuals may not be able to find their best preferred resource, we allow  $\hat{p}_i$  to decay in each time step when individuals do not find resources, or find resources for which their preferences are lower than  $\hat{p}_i$  (if  $p_{ir} < \hat{p}_i$  then  $\hat{p}_i = 0.999\hat{p}_i$ ). However, whenever an

individual eats a resource for which its preference is greater than  $\hat{p}_i$ , its  $\hat{p}_i$  becomes equal to that preference (if  $p_{ir} > \hat{p}_i$ , then  $\hat{p}_i = p_{ir}$ ). In this way,  $\hat{p}_i$  reflects what an individual considers the best quality resource that can be found and allows an individual to adjust its food choices to prevalent conditions. We refer  $\hat{p}_i$  as an individual’s preference expectation.

### Temporary satiation aversion

In the present model version, we included temporary satiation aversion which ensures that individuals attain a temporary aversion to resources eaten to satiation (a full stomach). Individuals are therefore always forced to move to another resource after one feeding–digestion cycle. This increases the rate at which individuals encounter different patches and thus their diversity of learning, and therefore represents a harder case scenario for studying diet differences.

### Move forward

We also varied the distance with which individuals move forward ( $M$ ) when they do not find acceptable food (see Fig. 1). This has the effect of varying the time individuals spend in patches of nonpreferred resources.

## SIMULATIONS AND ANALYSIS

We studied the inheritance of group-level diets by running simulations in which we conducted transmission chain experiments (cf. Curio et al. 1978; Galef & Allen 1995;

Laland & Williams 1997). Simulations were initialized with 20 naïve individuals (for which all resource preferences equal zero) and each year one of the initial individuals was replaced by a naïve individual. After 20 years, all the initial individuals had been replaced, and from then on the eldest individual was always replaced. Individuals therefore only 'died' when they were replaced, but not because of other factors such as lack of food. Simulations were run for 90 years: a 20-year start-up period in which a stable age-distribution was generated (i.e. ages 19–0 years) followed by three complete cycles of replacement. The final 10 years were included to allow three complete cycles of replacement beyond year 30, which was used as a reference to trace diet change in time (see below).

As a measure of similarity between diets, we used uncentred correlation between individual resource preference vectors, in which all preference vectors are compared relative to the origin (i.e. all preferences equal zero). This measure is conservative with respect to differences (i.e. overestimates correlation), but is useful because comparisons are based on the same reference (the origin). It is expressed as:

$$C_{a,b} = \frac{\sum_{r=1}^R a_r b_r}{\sum_{r=1}^R a_r \sum_{r=1}^R b_r} \quad (3)$$

where  $a_r$  and  $b_r$  are the preferences of individuals  $a$  and  $b$  for resource  $r$  and  $R$  is the maximum number of resources. Overlap is maximal when  $C_{a,b} = 1$ , and minimal when  $C_{a,b} = -1$ . In our simulations the minimum is effectively 0 because preferences are seldom opposite in sign.

In our analysis, we compared pairs of independent groups that developed diets in the exact same environments (i.e. different replicates). In this way, we excluded ecological reasons for differences between groups allowing us to focus on learning. To investigate diet traditions, we then used the following strict criteria: we considered traditional diet inheritance to be occurring when a group's diet remained more similar to its diet in the past than to the diet of another group.

We expressed diet overlap, within or between groups, as the average  $C_{a,b}$  of all pairwise individual comparisons, that is,  $\overline{C_{a,b}} = 1/nm \sum_a^n \sum_{b \neq a}^m C_{a,b}$ , where individuals  $a$  and  $b$  can either be from the same, or from different groups. As a measure of diet conservation in time, we calculated average diet overlap with year 30 (i.e. some point in the past, but significantly beyond the initialization period) and considered diet conservation after all individuals have been replaced (i.e. from year 50 onwards). If similarity to the past is consistently greater than diet similarity with another independent group, then this indicates traditional differences in diet preferences. We therefore used this difference (overlap with year 30 minus the overlap with another group) to represent inherited group-level diet, that is, diet traditions.

For more detailed analysis of diet traditions, we used hierarchical clustering. We clustered individuals from year 40 to year 80 (i.e. after two complete replacements of all individuals) from two independent groups and display diets in the form of a sorted data matrix. We clustered individuals using  $1 - C_{a,b}$  as distance measure and average

linkage, forming clusters of individuals that were similar in diet preferences. If individuals of a given group clustered together despite differences in time, this reflects that intergroup diet differences were maintained and inherited over time. To sort the data matrix, we clustered rows (individuals) as above and clustered columns (resources) using Manhattan distances and single linkage.

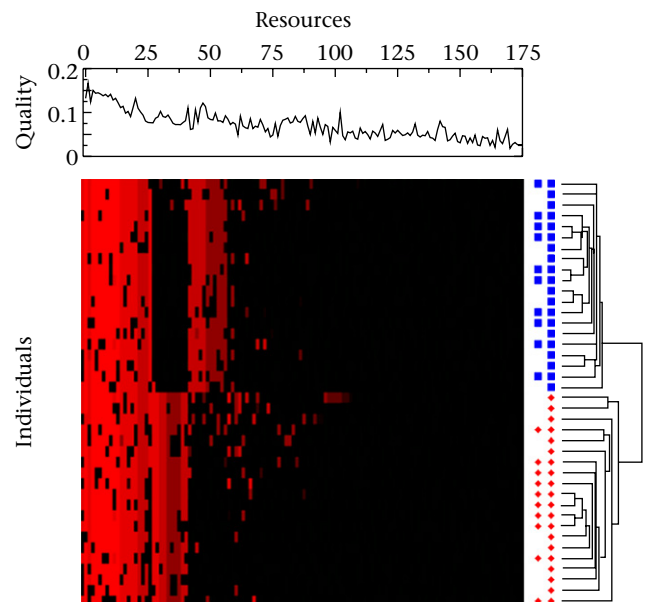
As a measure of change in diet quality, we used the slope of the linear regression of diet quality over a particular time period.

Unless stated otherwise, we only included the 10 oldest individuals during analysis. Since naïve individuals have no preferences (i.e. all are set to zero), a group's diet is only clearly expressed in more experienced individuals. Therefore, when comparing group diets and diet overlap within groups, the relatively undefined preferences of naïve individuals obscure patterns in the data.

## RESULTS

Our primary result is that trial-and-error learning in groups in patchy environments is sufficient for the emergence of diet traditions. Surprisingly, these conditions are also sufficient to generate a cumulative group-level learning process.

In our analysis of diet preferences by hierarchical clustering, we find that diet similarity of all individuals of the same group after two full replacements of individuals is greater than similarity to any individual of another group ( $N = 3$ ,  $M = 10$ ). This is shown in Fig. 2 where the



**Figure 2.** Diet traditions by trial-and-error learning ( $N = 3$ ,  $M = 10$ ). Individuals from two independent groups (square and diamond markers) at year 40 and year 80 (one and two markers, respectively) clustered according to similarity in diet preferences (average linkage, uncentred correlation distances). Dendrogram terminals and data matrix rows: individuals, data matrix columns: resources (red colour intensity indicates preference magnitude), top graph: resource qualities as ordered in the data matrix.

dendrogram represents the differences in diet between individuals (dendrogram terminals) and markers represent an individual's group (blue square or red triangle), and which year they are from (year 40 or year 80; one or two markers, respectively). The fact that distances between individuals (dendrogram terminals) are smaller within groups than between groups, despite two complete replacements of individuals between year 40 and year 80, clearly indicates that group-specific diet profiles are inherited over time. Moreover, the sorted data matrix also reveals a particular pattern of traditional differences. Above the sorted data matrix (Fig. 2), we plotted the quality of clustered resources. This indicates that the two groups are converged in preferences (high intensity red colour indicates preference strength) on the highest quality resources (columns that are red for both groups). In contrast, the groups are different in their preferences for lower quality resources (columns are red for only one group) showing that the traditional differences between groups are found on lower quality consumed resources.

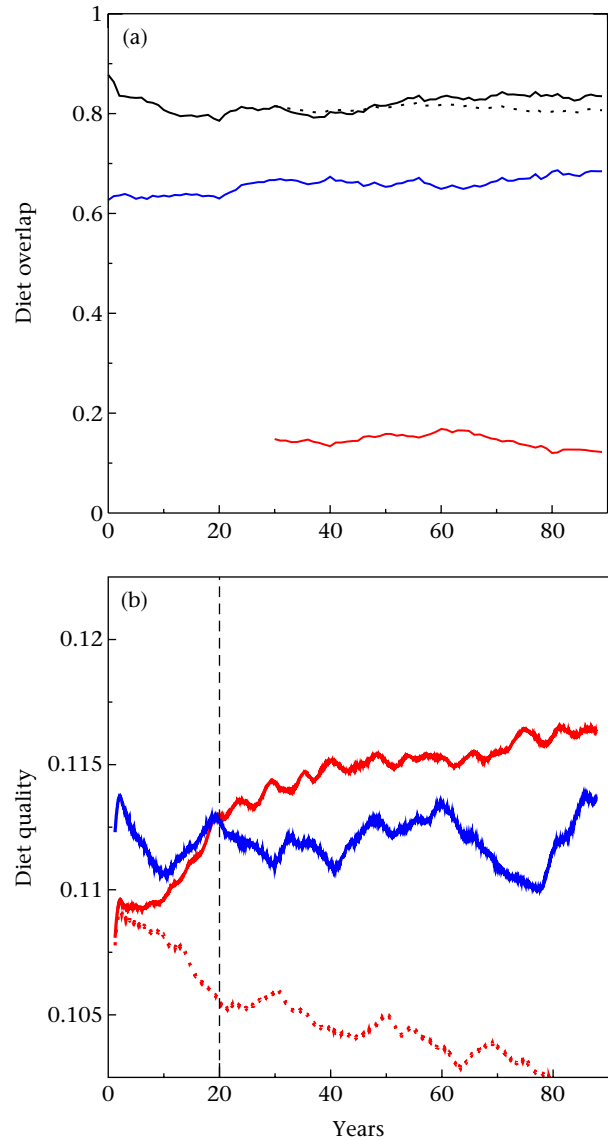
Figure 3a shows average diet overlap in time and shows that the average overlap of individuals with their group's diet at a point in the past (year 30, dashed line) remains consistency greater than overlap with another group (blue line). The difference between these two lines represents traditional differences between groups (red line). These results are in accordance with the results from the cluster analysis (Fig. 2) and shows that diet traits are transmitted and can be extrapolated to be maintained for a long time beyond the three complete replacements of individuals (i.e. between year 30 and year 90) shown here.

Figure 3b (red solid line) shows that the average diet quality in groups increases over the generations of individuals. Surprisingly, the increase continues beyond year 20, where the individual age-distribution has stabilized in the groups. This means that the increase in diet quality cannot be accounted for in terms of increased individual-level experience. Instead, it is a cumulative group-level process, through which foraging selectivity increases in groups. In contrast, in simulations without the replacement of individuals (individuals live indefinitely; Fig. 3b, red dotted-line), diet quality decreases beyond year 20 (this is due to decreasing selectivity, see below). In addition, in simulations of solitary individuals (they ignore grouping rules; Fig. 3b, blue line), with only pure individual learning, diet quality remains fairly constant in time. This shows that both grouping, which allows for social influences on learning, and population dynamics, which allows for the influx of naïve individuals and the loss of experienced individuals, is crucial for this cumulative process and allows groups to reach diet qualities that exceed those achieved by solitary individuals.

Below, we discuss the mechanisms and conditions that allow for diet traditions and such cumulative cultural processes.

## Two Contrasting Cultural Phenomena

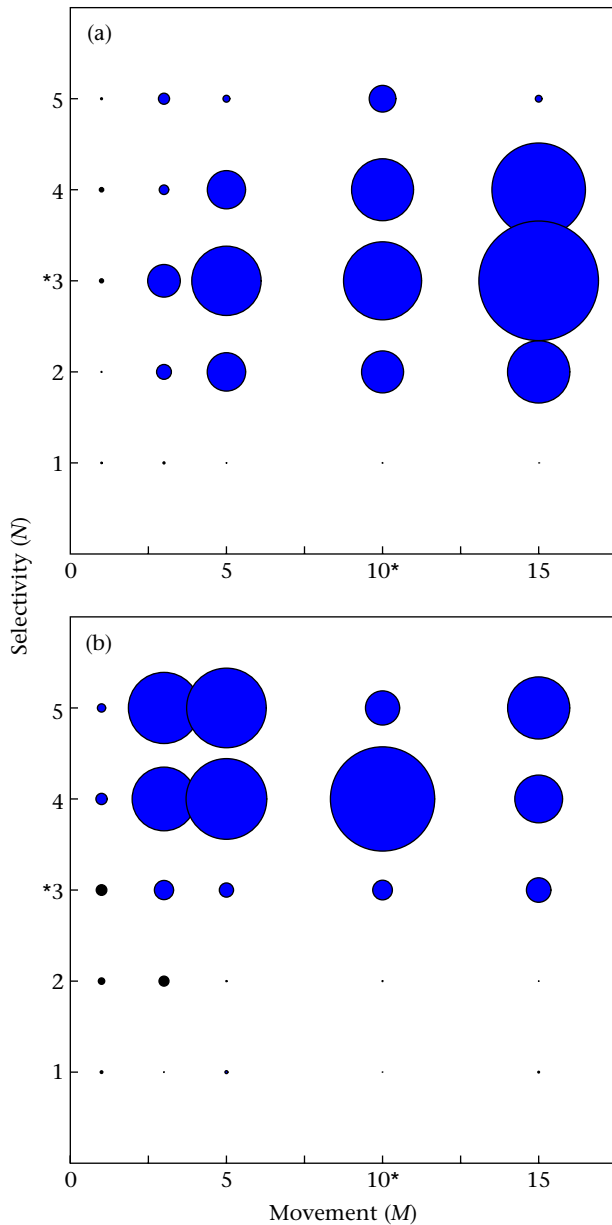
The two aspects of culture that we find, that is, diet traditions (Figs 2 and 3a) and the cumulative increase in



**Figure 3.** Diet overlap and diet quality over time. (a) Diet overlap (as defined in *Simulations and analysis*). Top to bottom: intragroup (black), overlap with year 30 (dotted), intergroup (blue), traditional differences (red = dotted – blue). (b) Average quality consumed resources. Solid red: transmission chain experiment simulations, dotted red: groups without replacement of individuals (i.e. individuals live for 90 years), solid blue: transmission chain simulations with solitary individuals. All lines are the average of five simulations.

diet quality (Fig. 3b), are contrasting in their nature; traditions are the conservation of diet, while diets change in the cumulative process. We find that foraging selectivity ( $N$ ) and distance moved after not finding food ( $M$ ) determine which cultural phenomenon dominates, although both processes can occur simultaneously.

Figure 4a shows the average traditional differences in diet at year 90 as they vary with  $N$  and  $M$ , where circle size represents the degree of traditional differences between two independent groups (i.e. red line at year 90 in Fig. 3a, see also *Simulations and analysis*). Likewise, Fig. 4b shows the average cumulative change in diet from year 20 to year 90,



**Figure 4.** Effect of selectivity ( $N$ ) and moving forward ( $M$ ) on cultural phenomena where circle size indicates magnitude. (a) Traditional differences at year 90 (average of five intergroup comparisons; see Simulations and analysis and Fig. 3a, red line). (b) Cumulative cultural increase in diet quality: slope of linear regression of diet quality between years 20 and 90 (average of five simulations). \*Indicates default ( $N = 3$ ,  $M = 10$ ) which can be used for reference, that is, Fig. 3a, red line for traditional differences, Fig. 3b for cumulative process.

where circle size represents the degree of increase in diet quality over that time.

Figure 4a shows that traditional differences increase as  $M$  increases, indicating the role of movement in the inheritance of diet preferences. Moreover, traditional differences clearly require sufficient foraging selectivity ( $N > 1$ ), and reach a maximum at intermediate values ( $N = 3$ ). In contrast, Fig. 4b shows that  $M$  does not play a large role in the cumulative increase in diet quality, where  $M = 3$  is

already sufficient. However, the cumulative process is highly dependent on foraging selectivity ( $N$ ) and is maximal for the highest selectivities ( $N > 3$ ). This means that the cumulative process is strongest when traditional differences have been largely reduced (compare Fig. 4a and b). In this sense, the two processes appear to be mutually exclusive, although they do occur simultaneously in intermediate conditions.

### Familiarity Biases and the Role of Selectivity

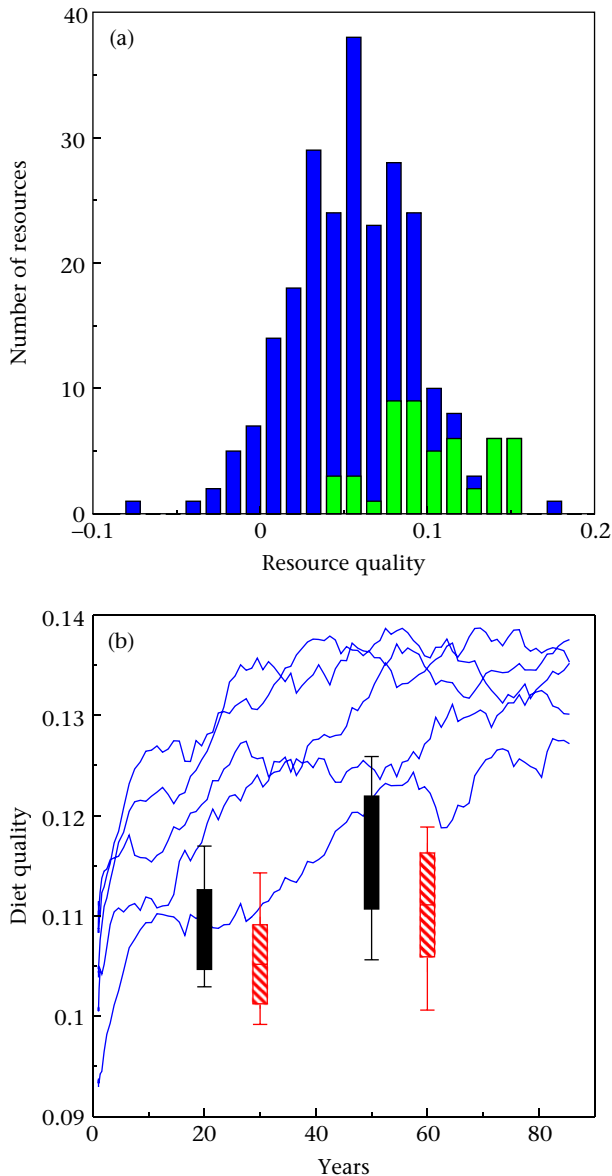
The impact of selectivity ( $N$ ) on the type of cultural phenomena observed depends on how it generates familiarity biases. Selectivity allows individuals to bias their foraging to high quality resources and so causes convergence in diet between individuals. However, learning is a stochastic process and some resources are eaten more often than others, resulting in differences in familiarity (where familiarity refers to how well individuals have evaluated resources, i.e.  $p_{ir}/q_r$ ). Although higher quality resources are generally more preferred because they give greater feedbacks during digestion, it is therefore possible for lower quality resources to be more preferred because they are more familiar.

Since foraging depends on preference, a positive feedback arises between foraging and familiarity. This reinforces familiarity biases and causes divergence in preferences between individuals, despite the fact that all individuals sample all resources. Increasing selectivity ( $N$ ) enhances these effects and causes a gradual change from totally inclusive diets (no selectivity), intermediate diets focused on higher quality resources (intermediate selectivity), to diets that are restricted to very high quality resources (high selectivity).

Although we set selectivity with  $N$ , familiarity biases can lead to an *effective* selectivity that exceeds that of individuals which have perfect preferences (i.e. preferences equal to resource quality). This is because familiarity biases tend to cause a relative over- and underestimation of familiar and unfamiliar resources, respectively, allowing for greater discrimination between them. As individuals gain experience they lose familiarity biases and therefore lose selectivity, which explains why groups without replacement of individuals have decreasing diet quality (see Fig. 3b, dotted red line).

### Intermediate selectivity, group movement and traditions

Traditional differences between groups require diet differences between groups, which means selectivity should be high enough to allow for familiarity biases. However, selectivity should not be so high as to restrict diets too much, as this reduces the opportunity for diet differences. Figure 5a shows a group's ( $N = 3$ ,  $M = 10$ ) feeding distribution (green bars) on top of the resource quality distribution (blue bars), indicating that the group's diet has converged towards a subset of higher quality resources. Clearly, the majority of the highest quality resources (these give the largest digestive feedbacks) is included in the diet, whereas only subsets of lower quality resources are included in the diet. Different groups therefore have much greater opportunity



**Figure 5.** (a) Resource quality distribution (blue) and a group's resource quality feeding distribution ( $N = 3$ ,  $M = 10$ ; green). (b) Lines: the diet quality of 1 year olds over time for five simulations ( $N = 4$ ,  $M = 10$ ). Box plots: average diet quality for 20 year olds at year 20 for transmission (black) and nontransmission (red striped) simulations: left pair:  $N = 3$ , right pair:  $N = 4$  ( $M = 10$ ).

to differ in diet on lower quality resources than high quality resources. In fact, given that high quality resources are so fully exploited, there is hardly any opportunity for groups to differ on these resources. Traditional differences in diet are therefore found on lower quality resources, and are maintained through shared familiarity biases.

Shared familiarity biases are generated by the automatic convergence in trial-and-error learning that arises when groups share learning contexts (patches; van der Post & Hogeweg 2006). Such shared familiarity biases are then inherited by naïve individuals as they travel with their group. This happens because their learning is biased to patches the group prefers (i.e. where it spends time

feeding), and biased against patches the group does not prefer.  $M$  increases the efficacy of this process by causing groups to spend even less time in nonpreferred patches, giving naïve individuals less opportunity to learn from them. Group-level familiarity biases are therefore increasingly accurately transmitted, and in this way, grouping can sustain diet traditions in the face of the divergent effects of selectivity when these are not too extreme.

Traditional differences in diet therefore occur when selectivity is great enough to allow for diet specificity, but low enough that biases to such diets can remain shared within groups.

#### *High selectivity and cumulative increase in diet quality*

As selectivity increases, familiarity becomes more restricted to high quality resources causing traditional differences in diets to disappear. This not only happens because individuals are better able to select higher quality resources, but also through the cumulative process, which increases the bias to high quality resources over the generations. The reason the cumulative process only becomes large at high selectivity ( $N > 3$ ) is because only then it allows naïve individuals to be selective within the subsets of resources that have been preselected by previous generations, that is, they are able to maintain their personal (un)familiarity biases in the face of group foraging. In this way, later generations build upon experience already present in the group. This effect is clear in Fig. 5b (blue lines), which shows that naïve individuals are increasingly able to achieve greater diet quality within their first year as groups accumulate selectivity in time. With increasing individual selectivity ( $N$ ) inheritance therefore shifts from a conservative process to a selective process, and allows new generations to become effectively more selective than earlier generations.

The enhanced familiarity biases of naïve individuals towards high quality resources cause them to not prefer the lower quality resources eaten by their group, and they try to leave patches of that type. Moreover, naïve individuals can become familiar with high quality resources that are unfamiliar to the group and try to feed on them. Such behaviour affects group-level foraging by causing an increased bias for groups to leave lower quality resources, as well as increasing the time spent on high quality resources, which are not (yet) familiar to other members of the group. This is shown in Fig. 5b (box plots), where we compare the diet quality of 20-year-old individuals at year 20 in transmission experiments (black) and those without influx of naïve individuals (red). In this way, we compared the effect of naïve individuals on the diet quality of the oldest individuals, which have not yet benefited from growing up in a group which has accumulated experience. The box plots show that in simulations with naïves (black), experienced individuals achieve greater diet quality, and therefore become effectively more selective than those without naïves (red), both for  $N = 3$  and  $N = 4$  (left pair and right pair, respectively  $t$  test:  $P = 0.0086$  and  $P = 0.0041$ , respectively). Clearly, naïve individuals have an impact on group-level selectivity and although this effect may not be very large with just a single naïve

individual, it becomes stronger with the succession of naïve individuals entering groups.

It therefore appears that this cumulative process arises when individuals are selective enough to maintain their own familiarity biases in the face of the convergence influence on learning due to grouping. This allows them to become effectively more selective than their groups, and therewith increases group-level selectivity. This positive feedback generates the described cumulative cultural process.

### Ecological and Behavioural Generalizations

Our results are obtained with relatively hard-case parameter settings. We used maximum trial rates, in which every unknown resource is sampled, thus ruling out intergroup differences through differences in absolute discoveries. In fact, lower trial rates allow for even larger traditional differences, mainly because more time between discoveries leads to greater familiarity biases (results not shown). Moreover, our default Gaussian resource quality distribution is a hard-case scenario with respect to ecological pressure for convergence in diet. Alternative quality distributions with less restrictive tails of high quality resources allow for much greater scope for traditional differences (see [Appendix 2](#) for more details). More unexpectedly, greater local variation in resources, both in the sense of smaller patches, as well as patches with multiple types of resources, also increases the magnitude of traditional differences between groups by allowing selectivity to be more effective (see [Appendix 3](#) for more details). We also tested the robustness of traditional differences between groups to migration and found that diet traditions are maintained even when half the individuals of a given age (we tested up to an age of 4) are transferred between two groups, which forage simultaneously in the same environment (results not shown). This emphasizes that despite both groups continually travelling throughout the whole field, different patterns of familiarity reinforcement can lead to stable differences in diet.

In our results, familiarity biases are clearly instrumental and follow from our food choice algorithm, equation (2), which defines foraging in terms of preferences. Although the role of familiarity is reasonable to assume, a drawback is that high selectivity ( $N > 3$ ) reduces food intake because resource preferences are very restrictive and encounter rates with preferred resources are reduced. A comparison with an alternative food choice algorithm based mainly on food intake shows that familiarity biases can be significantly reduced, leading to reduced traditional differences (see [Appendix 4](#) for more details). None the less, even though familiarity does not play a direct role in this algorithm, familiarity biases are still generated and we are still able to find traditional differences in permissive environments. Moreover, we find an alternative cumulative process which increases food intake.

Therefore, although we find that diet traditions and the cumulative increase in diet quality depend on group movement ( $M$ ) and selectivity ( $N$ ), these cultural phenomena are robust properties with respect to changes in the environment and the food selection algorithm we

used. This in conjunction with our conservative measure of diet differences (see [Simulations and analysis](#)) makes us confident that our results are generic for groups foraging in patchy environments, provided preference learning is affected by familiarity.

### DISCUSSION

Our results provide a plausible parsimonious mechanism through which both traditional differences and cumulative cultural processes can arise through self-organization. These cultural phenomena are a direct consequence of population renewal, in combination with convergent social influences on learning that arise spontaneously when groups forage in patchy environments. The cultural phenomena we describe should therefore be considered as side-effects, and arise because of how spontaneous interactions between grouping and patchy environments shape the opportunities for learning. This mechanism for the origin of cultural phenomena does not need to invoke the adaptive potential of social learning, nor sophisticated forms of learning, which is required in other analyses (Boyd & Richerson 1985; Dewar 2003; Henrich & McElreath 2003; Laland & Kendal 2003; Castro & Toro 2004). Instead, we show that cultural processes arise 'for free' as soon as groups forage in patchy environments and learn what to eat by trial-and-error.

Important for these results is the positive feedback between experience and behaviour, which generates divergence in learning. This emphasizes the importance of considering learning as a time-dependent process, which allows for differences in learning histories. In particular, we show that divergence in familiarity biases, which arise through time-dependent preference learning in combination with convergence in learning due to grouping, is sufficient for supporting diet traditions. In this way, we show how selectivity allows groups to differ in diet and develop diet traditions, as long as the convergent social influence due to grouping is greater than divergence due to selectivity. As selectivity increases there is increased convergence on high quality resources and traditions disappear, while allowing individuals to be selective within the foraging context that has been preselected by their group. This allows them to achieve greater diet quality than that of their group, which subsequently feeds back on group-level selectivity. In this way, a positive feedback is generated, which drives a cumulative cultural process through which groups increase diet quality over time.

It is important to realize, however, that the apparent mutual-exclusivity between traditional differences and the cumulative process is partly a result of the single-peaked diet quality landscape in our model, in which the cumulative process can only lead to enhanced convergence between groups. In more natural settings it is likely that ecological convergence will be less strong, especially considering balanced diets in which multiple combinations of resources could provide viable diets (multiple-peaks) and provide greater neutrality for diet differences. Thus, it is likely that there is more scope for overlap of the two phenomena. None the less our results emphasize the opposing nature of these two phenomena, that is,



conservation versus change, which is of interest when considering the nature of culture.

### Patterning of Traditions

It is interesting to note that the pattern of diet traditions we find is somewhat mirrored in wild orang-utan populations. Recent data on intergroup diet differences in two orang-utan populations show that diets are converged on high quality fruit, while divergent on lower quality fibrous resources (S. A. Wich, H. Morrog-Bernard, S. Husson, M. L. Geurts & C. P. van Schaik, unpublished data). This pattern is very similar to the results we obtain in which groups converge on high quality resources while diverging on lower quality ones. We show that this pattern emerges spontaneously because lower quality resources are more susceptible to familiarity differences because they are less intensely eaten, as well as being relatively more abundant in the environment. High intragroup convergence, in combination with low intergroup convergence, on lower quality resources could therefore be indicative of social learning and traditions. This lends support to the relevance of our results for natural foragers, where such patterns of convergence can be studied. Obviously, we cannot rule out ecological differences in the case of orang-utans (Wich et al., unpublished data) or capuchin monkeys (Chapman & Fedigan 1990), however, the relative ease with which we see traditional differences in diet arise should be taken into account. Moreover, our results suggest that traditional differences need not be due to differences in innovations between groups, as we obtain our results with maximal trial rates, but can instead arise through different behavioural reinforcement patterns.

### Cumulative Cultural Change

Generally, cumulative cultural evolution is discussed relative to the cumulative assimilation of (technical) innovations over generations of individuals, allowing progressive behavioural elaboration beyond what individuals could achieve on their own (e.g. Boyd & Richerson 1995; Boesch & Tomasello 1998; Henrich & McElreath 2003). Such a process is thought to require accurate social learning mechanisms (e.g. Tomasello et al. 1993; Boesch & Tomasello 1998; Henrich & McElreath 2003; Castro & Toro 2004), since with simple types of social influences individuals need to reinvent behavioural details thus preventing a build-up of behavioural complexity (Henrich & McElreath 2003).

Attempts to understand the evolution of such processes have focused on the conditions that allow for the evolution of social learning (Boyd & Richerson 1995; Castro & Toro 2004). In particular, the guided-variation model (Boyd & Richerson 1985, chapter 4) predicts that cultural inheritance will evolve when social information is not obsolete and the costs of individual learning are high. In the model, cultural inheritance is implemented as inheritance of the population's average phenotype, and cultural inheritance can be shown to cumulatively reduce variation due to individual learning and guides a population to converge

on the average of individual learning. Assuming that the average of individual learning is the optimum phenotype, cultural inheritance then allows cumulative convergence on the optimum. This cumulative process can, however, only proceed up to the average of individual learning.

The cumulative process we describe allows the population to exceed the average of individual learning (see Fig. 3b, compare red and blue solid lines). This is possible because group culture is inherited selectively, that is, not the average familiarities of the group, but a selected subset of familiarities for higher quality resources are inherited. As a consequence of this selection, learning can produce phenotypes that are beyond the average of the group, which then pulls the group average closer to the optimum, so redefining the limits of learning.

Nevertheless, the cumulative process we describe does not lead to increased behavioural complexity, as this is not possible in our model. However, we show that cumulative processes can arise as side-effects of trial-and-error learning in groups. Moreover, we only find a cumulative process when high selectivity leads to 'individualistic' preferences. This contrasts with the idea that cumulative cultural processes require accurate mechanisms of social learning, highlighting the paradox of expecting highly accurate transmission for a process of cultural change. Instead, at least in the cumulative process we describe here, as well as in the guided-variation model (Boyd & Richerson 1985), that it is the interplay between individualistic and group-level behaviour that drives cumulative processes.

### CONCLUSION

Obviously, we do not claim that our results explain all cultural phenomena. With respect to food processing techniques for instance, it seems unlikely that grouping itself would be sufficient to achieve shared processing techniques. Moreover, the cumulative cultural increase in diet quality generally represents a marginal effect on top of what is achieved individually, although in some cases it is really of a significant magnitude. Thus, we provide a clear example in which self-organization, as structured by opportunities and interactions, has a large role to play in generating a cumulative process, and that cumulative cultural change may be more prevalent than previously thought. We show that these cultural processes are generic, and suggest that cultural phenomena not only arise easily, but also may in fact be inescapable in group foragers. These cultural phenomena do not arise for all parameter values studied here, but depend on the selectivity and movement patterns that could evolve in foraging groups possibly for a variety of reasons. Thus, if the selection pressure happens to be towards the parameter values discussed here, cultural phenomena will arise as a side-effect thereof. We conclude that self-organized cultural phenomena should be taken into account as a baseline for considering the evolution of further cultural complexity.

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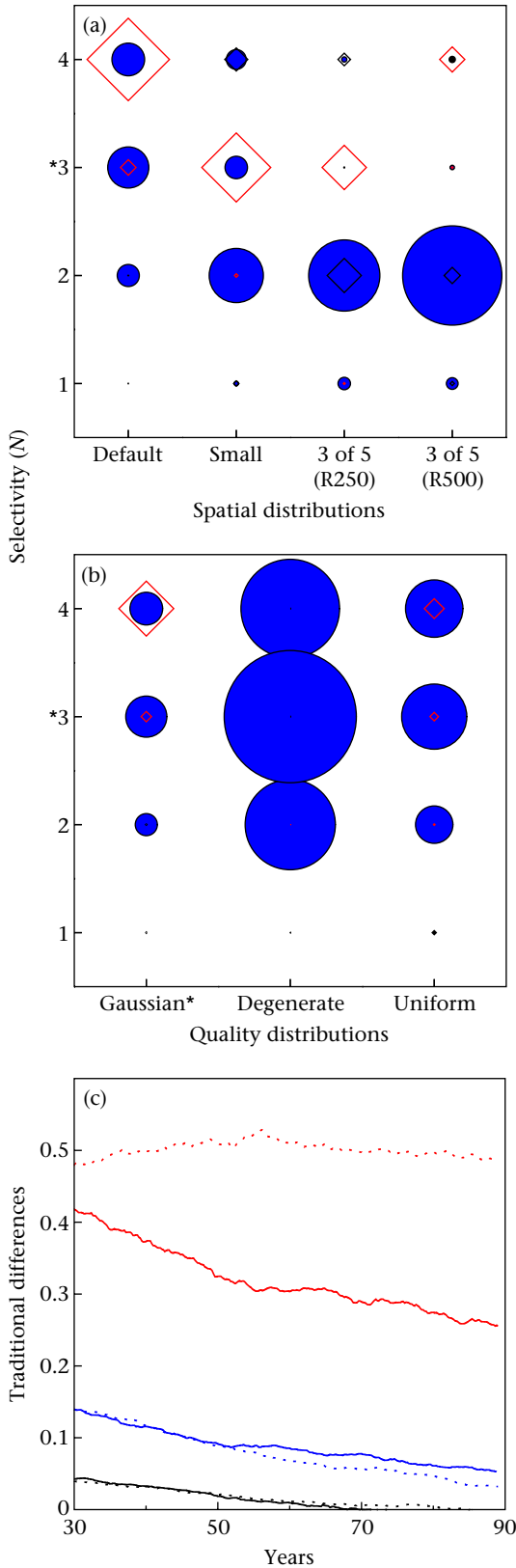
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## Appendix 1: Model Parameters

Model parameters and their values

Category	Parameter/description	Value
Timescale	$T$ (time step)	1 min
	Day	720 min
	Year	365 days
Environment	$D$ (grid unit)	1 m
	Field size	$2.8 \times 2.8$ km
	Number of resources	250
	Number of patches	4900 Patches
	Patch radius	10 m
	Number of resource items per patch	$\pm 3960$ Items
Grouping	Distance to check if safe	10 m
	Minimum number of neighbours required to be safe	3 Neighbours
	Maximum awareness for neighbours	150 m
	Probability to adjust direction after joining group	0.9
	Distance within which direction of neighbour is observed	20 m
Learning	$U$ (update constant for preference learning)	0.01
Searching and selecting food	Decay constant of preference expectation	0.999
	$N$ (selectivity during foraging)	1–5
	Maximum stomach contents	20 Items
	Private space for foraging/individual's reach	0.9 m
	Distance resources can be observed	2 m
	Field of vision	$180^\circ$
Actions	Maximum number of resource items assessed during search	20 Items
	Duration of search event	0.5 min
	Distance when moving back to group	3 m
	Duration of movement back to group	0.015 min
	$M$ (distance moving forward)	1–10 m
	Duration when moving forward	$0.015 \times M$ min
	Duration of doing nothing	1 min
	Duration of eating	1 min
	Digestion interval	100 min



**Figure 6.** Environmental conditions and food choice algorithm: effect of selectivity on traditional differences (circles) and cumulative cultural change in diet quality (diamonds; as in Fig. 4a, b). Red diamonds: increase, black diamonds: decrease. \*Indicates default ( $N = 3$ ). (a) Spatial resource distributions. Left to right: default, small

### Appendix 2: Resource Quality Distributions

We compared our Gaussian quality distribution to: (1) a uniform distribution with regular quality intervals between all resources making each quality equally available; and (2) a degenerate distribution where each resource has the same quality.

Figure 6b circles shows that both distributions allow for greater traditional differences than a normal quality distribution. Both alternative distributions lead to less ecological convergence because they are less limiting in terms of subsets of high quality resources. In contrast, cumulative increases in diet quality are of smaller magnitude in the uniform distribution as compared to the normal distribution (Fig. 6b, red diamonds). Since the quality gradient is less steep, it is more difficult for the cumulative process to detect quality differences and converge on the best quality resources.

### Appendix 3: Local Resource Variation

We compared: (1) small patches (radius 5 distance units) that are closer together; and (2) multiple resource patches (see van der Post & Hogeweg 2006 for more details). For the latter each patch type was assigned a subset of five resources. Of these five a random three were placed in patches of that type. We did this for both 250 and 500 resources.

Figure 6a (circles) shows that both for small patches and multi-resource patches the maximum traditional differences can be much larger than in our default setting and are found for lower selectivity values. Moreover, we generally find the same transition from traditional differences to the cumulative process (Fig. 6a, red diamonds), and this occurs for lower selectivity values. This happens because the effectivity of selectivity in individuals is enhanced because less time is spent between subsequent encounters with given resources. In this way,  $\hat{p}_i$  can remain at a higher level and reinforcement of preferences is more frequent than when resources are less often encountered. This enhances differentiation in familiarity biases, while at the same time the combination of resources that groups encounter can differ, leading to further differentiation, and the effects of selectivity are felt sooner.

### Appendix 4: Food Choice Algorithm

To study an alternative food choice algorithm that focuses on food intake we implemented that  $\hat{p}_i$  is updated

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patches, and patches with three of possible five resources (250 and 500 resources). (b) Resource quality distributions. Left to right: Gaussian, degenerate and uniform. Each data point is average of five simulations. Scaled to 50% of Fig. 4a ( $N = 3$ ,  $M = 10$ ). (c) Effect of alternative preference expectation algorithm on traditional differences (as in Fig. 3a, red line): different resource quality distributions. Bottom to top: Gaussian (black), uniform (blue), degenerate or all equal (red), Gaussian resources abundances (solid), equal abundances (dotted). Each line average of five simulations ( $M = 10$ ).

at digestion only dependent on the amount of food eaten. If an individual's stomach is full then  $\hat{p}_i$  increases by 10%, otherwise it decreases by 10%. In this way, individuals try to be as selective as possible, while maximizing food intake.

This algorithm is successful with respect to food intake and achieves high diet quality. However, because food choice is less specific to resource preferences, familiarity with specific resources is no longer as defining in food choice as in our default algorithm. Familiarity differences are therefore reduced and ecological convergence increases leading to a reduction in traditional differences. In Gaussian quality distributions traditional differences have disappeared by year 90, because they all converge on the same broad diet (Fig. 6c, black lines).

None the less, familiarity still plays a role and we still find traditional differences for uniform (blue) and

degenerate (red) environments (Fig. 6c). Moreover, we again find a cumulative cultural process, which is indicated by the convergence in diet in the degenerate environment despite a lack of quality differences in resources (Fig. 6c, red line). In this case the cumulative process causes convergence on the most abundant resources and 'accumulates' food intake. This is clear in comparison to simulations with equal abundances for all resources (as compared to our default Gaussian abundance distribution) where loss of traditional differences and convergence in diet does not occur (Fig. 6c, dotted red line). Interestingly this difference does not occur in normal (black) and uniform (blue) environments between equal (solid line) and nonequal (dotted-line) abundances, indicating that quality differences overrule abundance differences in those cases.