

Supplementary Material to: Altruism through Beard Chromodynamics by Vincent A.A. Jansen and Minus van Baalen

Description of the simulation model

Our probabilistic cellular automaton (PCA) is constructed along the same lines as in [1], that is, modelling a simple birth-death process on a fixed lattice with the main simplification that there is no movement of individuals. Specifically the environment is represented by a (fixed) network of habitable sites (typically 10000) where every site is connected to z other sites (fixed throughout the lattice). Sites may be empty (\emptyset) or occupied by a single individual with a given genotype: if there are n beard colours, the set of genotypes G is

$$G = \{C_1, C_2, \dots, C_n, D_1, D_2, \dots, D_n\}.$$

Mortality is assumed to be a density and configuration-independent event: an individual of genotype $x_i \in G$ dying and thus creating an empty site is represented as $x_i \rightarrow \emptyset$ and it is assumed that these events occur at a fixed rate (probability per unit of time) $r_{x_i \rightarrow \emptyset} = d$.

Births are conveniently described as so-called ‘edge events,’ where the event is not so much associated with a site as well as a connection between two sites. Since in our model all events are local, birth implies that an individual of genotype x_i puts an individual of type y_j in a neighbouring empty site ($x_i, y_j \in G$), where the strategy or beard colour of the offspring (y_j) may have changed through recombination or mutation (or both). Formally, such birth events, represented by the edge event $x_i \emptyset \rightarrow x_i y_j$, have the associated rate,

$$r_{x_i \emptyset \rightarrow x_i y_j} = \frac{1}{z} \phi_{x_i}(y_j),$$

where ϕ_{x_i} is the pay-off gained by individual x_i in interaction with its neighbours and the fraction 1 over z ensures that this individual’s birth rate does not depend on connectivity itself (it has $z - 1$ other neighbouring sites that it potentially could reproduce in). An essential but complicating aspect of our model is that the rate of reproduction of individual x_i is that it depends on the state of its neighbouring sites. Denoting the proportion of y_j -neighbours

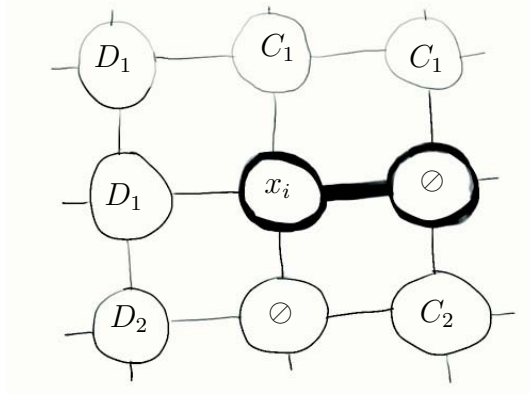


Figure 1: Example of a local configuration on the lattice. The quantity $y_i|_{x_i\emptyset}$ gives the proportion of neighbours of the x_i -individual in the $x_i\emptyset$ -pair that has genotype y_i ; in the depicted example, $C_1|_{x_i\emptyset} = 1/4$.

of the individual of genotype x_i in an $x_i\emptyset$ pair by $y_j|_{x_i\emptyset}$ (see Figure 1 for an example), the pay-offs ϕ_{x_i} are given by

$$\begin{aligned}\phi_{C_i} &= R C_i|_{C_i\emptyset} + S D_i|_{C_i\emptyset} + P (1 - C_i|_{C_i\emptyset} - D_i|_{C_i\emptyset}) \\ \phi_{D_i} &= T C_i|_{D_i\emptyset} + P (1 - C_i|_{D_i\emptyset})\end{aligned}$$

where it is assumed that interaction with an empty site, like interaction with differently coloured beards, yields P . The simplified model analysed in the main text results from the assumptions that $y_j|_{x_i\emptyset} = v + (1-v)x_i$ for $x_i = y_j$ and $y_j|_{x_i\emptyset} = (1-v)y_j$ for $x_i \neq y_j$. The simulations were carried out using the full model, explicitly calculating the $y_j|_{x_i\emptyset}$ for all reproducing individuals.

Of course, in absence of mutation and recombination, $\phi_{x_i}(y_j) = 0$ for any $x_i \neq y_j$ while $\phi_{x_i}(x_i) = \phi_{x_i}$. However, because of mutation and recombination offspring may not have the same genotype as their parent. We define mutation as the replacement of an allele by an allele picked at random from the set of alleles and recombination as the replacement of an allele by its homologous counterpart of a neighbour of the reproducing individual (recombination is thus completely local). Birth events are decomposed into a number of components (listed in Table 1) that represent faithful reproduction and all permitted combinations of mutation and recombination. The

Table 1: Components of reproduction events

Component	Rate			Remark	
$x_i \circlearrowleft \rightarrow$					
$\rightarrow x_i x_i$	$(1 - \mu_s - \mu_b)$	$(1 - \rho_s)$	$(1 - \rho_b)$	ϕ_{x_i}	faithful reproduction
$\rightarrow x_i x_j$	μ_b/n	$(1 - \rho_s)$	$(1 - \rho_b)$	ϕ_{x_i}	beard colour mutation strategy ”
$\rightarrow x_i y_i$	$\mu_s/2$	$(1 - \rho_s)$	$(1 - \rho_b)$	ϕ_{x_i}	
$\rightarrow x_i x_j$	$(1 - \mu_s - \mu_b)$	$(1 - \rho_s)$	$\rho_b \bullet_j _{x_i \circlearrowleft}$	ϕ_{x_i}	beard colour recombination strategy ” double ”
$\rightarrow x_i y_i$	$(1 - \mu_s - \mu_b)$	$\rho_s y_\bullet _{x_i \circlearrowleft}$	$(1 - \rho_b)$	ϕ_{x_i}	
$\rightarrow x_i y_j$	$(1 - \mu_s - \mu_b)$	$\rho_s \rho_b y_j _{x_i \circlearrowleft}$		ϕ_{x_i}	

Here, $y_\bullet|_{x_i \circlearrowleft} = \sum_j y_j|_{x_i \circlearrowleft}$ is the probability that a given neighbour has strategy y irrespective of its beard colour and $\bullet_j|_{x_i \circlearrowleft} = C_j|_{x_i \circlearrowleft} + D_j|_{x_i \circlearrowleft}$ is the probability that a given neighbour has beard colour j . The index s refers to the strategy locus, the index b to the beard colour locus. It is assumed that mutation and recombination never occur simultaneously. For all simulations the recombination rates and mutation rates for the beard colour locus and the strategy locus were chosen equal, i.e. $\rho_s = \rho_b = \rho$ and $\mu_s = \mu_b = \mu$

overall rate of a given birth event is the sum of all components that apply. For instance, a $D_2 \circlearrowleft \rightarrow D_2 D_3$ birth event may result from mutation (the 2 mutates into a 3) or recombination (the D_2 happens to have a neighbour with beard colour allele 3), so this event occurs with overall rate

$$r_{D_2 \circlearrowleft \rightarrow D_2 D_3} =$$

$$\left(\frac{1}{n} \mu_b (1 - \rho_s) (1 - \rho_b) + (1 - \mu_s - \mu_b) (1 - \rho_s) \rho_b (C_3|_{D_2 \circlearrowleft} + D_3|_{D_2 \circlearrowleft}) \right) \phi_{D_2}.$$

In a similar fashion, a $D_2 \circlearrowleft \rightarrow D_2 D_2$ birth event may be the result of faithful reproduction of a D_2 -individual (obviously) but also of a recombination event (when the 2-allele happens to be swapped with that of a neighbour also having beard colour 2) or a mutation event (as we define mutation as replacement by a random allele, which formally includes $2 \rightarrow 2$ mutations). Note that the combination of behavioural interactions with neighbours and recombination makes that the expected rates of birth events depend in a rather complicated way on the state of the reproducing individuals' neighbourhoods. For a more formal treatment of this kind of model, see [1, 2].

The simulations were run either on square lattices with Von Neumann neighbourhoods ($z = 4$) or on random graphs with varying neighbourhood sizes ($z = 3, \dots, 10$). The lattices were initialised with populations whose genomes were drawn randomly but heavily biased towards by D_1 -individuals with a few C_2 -s sprinkled in (to speed up the appearance of the first wave of cooperators). After the simulations were started all other beard colours could only appear through mutation. The lattice was updated asynchronously using a sufficiently small time step.

Derivation analytical model

Although it is possible to analyse dynamics of the PCA using correlation dynamics techniques [1, 2], this would result in high dimensional dynamical systems which, in order to gain interpretable results, would have to be simplified further. To avoid this step we make the following simplification. To capture the effects of viscosity we assume that an individual encounters with a probability, v an individual with an identical genotype, and with a probability $1 - v$ a random individual from the population. That is, $y|_x = v + (1 - v)y$ when $y = x$ and $y|_x = (1 - v)y$ when $y \neq x$, where v is approximately inversely proportional to the number of neighbours [1]. This results in the pay-offs ϕ_x for phenotype x :

$$\phi_{C_i} = vR + (1 - v)(RC_i + SD_i + (1 - C_i - D_i)P)$$

$$\phi_{D_i} = vP + (1 - v)(TC_i + (1 - C_i)P)$$

Incorporation of recombination, taking into account that with probability v no recombination takes place as the neighbour has an identical genotype, and ignoring mutations, leads to the following system of replicator equations

$$\begin{aligned} \dot{C}_i &= ([h + v(1 - h)]\phi_{C_i} - \Phi)C_i + (1 - v)\rho(1 - \rho)\Phi_i \sum_{j=1}^n C_j \\ &\quad + (1 - v)\rho(1 - \rho)\Phi_C(C_i + D_i) + (1 - v)\rho^2\Phi_C\Phi_i \\ \dot{D}_i &= ([h + v(1 - h)]\phi_{D_i} - \Phi)D_i + (1 - v)\rho(1 - \rho)\Phi_i \sum_{j=1}^n D_j \\ &\quad + (1 - v)\rho(1 - \rho)\Phi_D(C_i + D_i) + (1 - v)\rho^2\Phi_D\Phi_i, \end{aligned} \tag{1}$$

where $\Phi = \sum_{j=1}^n \phi_{C_j}C_j + \phi_{D_j}D_j$ represents the average fitness in the population, $\Phi_i = \phi_{C_i}C_i + \phi_{D_i}D_i$ the average fitness of individuals with beard colour i , $\Phi_C = \sum_{j=1}^n \phi_{C_j}C_j$ the average fitness of altruists and $\Phi_D = \sum_{j=1}^n \phi_{D_j}D_j$

the average fitness of defectors, and where ρ is the probability of recombination per locus, and $h = (1 - \rho)^2$ the probability that no recombination takes places.

If we ignore the small probability that an offspring inherits *both* tag and trait from the partner we can use a first order approximation in ρ . In doing so we obtain $h = 1 - 2\rho$ and after substituting the effective probabilities $h' = h + v(1 - h)$ and $\rho' = (1 - v)\rho$ we find the model equations used in the main text:

$$\begin{aligned}\dot{C}_i &= (h'\phi_{C_i} - \Phi)C_i + \rho'\Phi_i \sum_{j=1}^n C_j + \rho'\Phi_C (C_i + D_i) \\ \dot{D}_i &= (h'\phi_{D_i} - \Phi)D_i + \rho'\Phi_i \sum_{j=1}^n D_j + \rho'\Phi_D (C_i + D_i)\end{aligned}\tag{2}$$

Model Analysis if $h = 1$

The analysis of the mathematical model without recombination provides results that help to form an intuition of the general beard chromodynamics. In what follows we will give an account of the qualitative changes in the dynamics that occur if the viscosity decreases. It is assumed that $T > R > P > S$ and that $T + S > P + R$. We will discuss the qualitative changes in the dynamics that are encountered as the connectedness, $1/v$, increase

If the connectedness is very low (i.e. if $\frac{1}{v} < \frac{T-P}{T-R}$) cooperators with a single beard colour dominate the population and can exclude defectors. In this case the equilibrium $(C_1, D_1) = (1, 0)$ is stable and no further beard colour can invade. If the connectedness increases cooperators and defectors in the same beard colour can coexist in the equilibrium $(C_1, D_1) = (\bar{C}(1), (1 - \bar{C}(1)))$, this equilibrium is always stable if no further beard colours are present. The equilibrium density of the cooperators decreases with viscosity, and if the viscosity is too low (i.e. $\frac{1}{v} > \frac{R-S}{P-S}$) cooperation cannot be maintained with only a single beard colour and the equilibrium $(C_1, D_1) = (0, 1)$ is stable. Since a single beard colour does not allow for discrimination the dynamics with a single beard colour are identical to those generated through blind kin selection.

Without recombination a defector with a new beard colour can never increase in numbers because such a defector has no cooperators to exploit. A cooperator in a new beard colour potentially can invade because, it cannot be exploited if defectors in the new beard colour are not present, and it therefore has an advantage over the cooperators already present. When rare, a cooperator in a new beard colour has a pay off of vR . Because the average

pay off decreases with increasing connectedness, this cooperator can invade, when rare, if its payoff when exceeds the average fitness in the population. This is if

$$\frac{1}{v} > 1 + \frac{(R - P)(S - R)}{(S - P)(T - P)}.$$

This new beard colour can invade in the population, and mostly oust the cooperators and defectors present with original beard colours. For certain combinations of parameters this new colour can coexist with the existing colour at a low density if the viscosity is slightly larger than the invasion threshold, to be precise, this requires.

$$\frac{1}{v} < \frac{2(T - P)}{S - R + T - R + \sqrt{(S - R + T - R)^2 - 4(S - P)(T - P)}}.$$

However, the parameter region of such coexistence is very small, and most frequently the newly introduced beard colour will invade the population and outcompete and exclude the existing beard colour.

Once a novel beard colour can invade and dominate a population we will encounter the following sequence of events: starting from a state of coexistence of cooperators and defectors of the same beard colour, invasion of a cooperator in a new beard colour leads to this new beard colour completely taking over, resulting in a population consisting of cooperators in a single beard colour. This population can be invaded by a defector in the same beard colour and lead to coexistence of cooperators and defectors in the new beard colour. This new state can be invaded by a cooperator in the original (or a new, different beard colour) and this sequence of events can repeat indefinitely. Hence, we have established that there exists a heteroclinic connection between the equilibria (denoted as: (C_1, D_1, C_2, D_2)):

$$\begin{aligned} &(\bar{C}(1), 1 - \bar{C}(1), 0, 0) \rightarrow (0, 0, 1, 0) \\ &\rightarrow (0, 0, \bar{C}(1), 1 - \bar{C}(1)) \rightarrow (1, 0, 0, 0) \rightarrow (\bar{C}(1), 1 - \bar{C}(1), 0, 0) \end{aligned}$$

Together these connections form a heteroclinic cycle. The stability of a heteroclinic cycle, which determines whether or not the heteroclinic cycle attracts orbits, can be established by comparing the product of the positive and the negative (also called contracting and expanding) eigenvalues [3].) The heteroclinic cycle always attracts if it exists.

An alternative sequence of events develops if no coexistence between cooperators and defectors is possible in the same beard colour (i.e. if $\frac{1}{v} > \frac{R-S}{P-S}$).

In this case a heteroclinic cycle exists of the form:

$$(1, 0, 0, 0) \rightarrow (0, 1, 0, 0) \rightarrow (0, 0, 1, 0) \rightarrow (0, 0, 0, 1) \rightarrow (1, 0, 0, 0)$$

This cycle is always attracting within the 4D state space if it exists. In Figure S1 the stability boundaries are depicted as a function of the model parameters.

More complicated heteroclinic cycles, involving more beard colours, can exist, but they all share the property that the beard diversity is limited to one colour for most of the time, and these more complicated cycles can only exist if the heteroclinic connection exist, therefore they are of limited interest here.

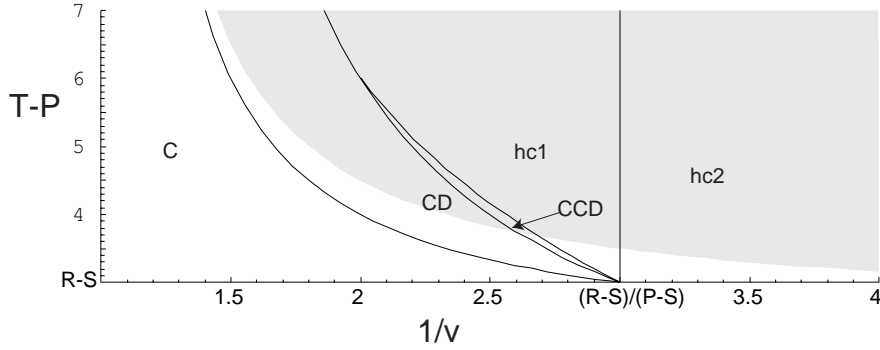


Figure 2: Stability boundaries of the dynamics with 2 beard colours without recombination, as a function of the parameters $T - P$ and $1/v$. In the region labelled C a cooperator in a single beard colour dominates the population. In the region labelled CD a cooperator and defector in a single beard colour stably coexist. In the small region labelled CCD two cooperators, in different beard colours, stably coexist with a single defector. In the region labelled $hc1$ a heteroclinic cycle exist in which coexistence equilibria are included, in the region labelled $hc2$ the heteroclinic cycle connects defector and cooperator only equilibria. In the grey shaded area an unstable symmetric equilibrium with two beard colours exists. Parameters: $R = 3$, $S = 0$, $h = 1$.

Model Analysis if $h < 1$

If $h < 1$ this heteroclinic cycle disappears, and gives rise to a family of limit cycles on which, for low recombination rates, the average beard colour diversity remains low. A full analysis of the case $h < 1$ is complex and does not lead to transparent results. We will therefore restrict ourselves to study the potential for invasion of a rare beard colour if the rest of the population is at an equilibrium. This gives some insight in the maximum beard colour diversity.

A rare beard colour, j , with densities $C_j, D_j \approx 0$ has a pay-off of $\phi_{C_j} = vR + (1-v)P$, $\phi_{D_j} = P$. The Jacobian matrix for the linearised dynamics of a rare beard colour invading a population in which n further beard colours stably coexist at equal densities is:

$$\begin{bmatrix} h'\phi_{C_j} - \bar{\Phi} + n\bar{C}\rho'(\phi_{C_j} + \bar{\Phi}) & n\bar{C}\rho'(\phi_{C_j} + \bar{\Phi}) \\ (1 - n\bar{C})\rho'(\phi_{D_j} + \bar{\Phi}) & h'\phi_{D_j} - \bar{\Phi} + (1 - n\bar{C})\rho'(\phi_{D_j} + \bar{\Phi}) \end{bmatrix}$$

where $\bar{C} = C(n)$. Using the determinant of the Jacobian matrix it can be shown that the dominant eigenvalue of the jacobian matrix is proportional to

$$(\phi_{D_j} - \bar{\Phi})(h'\phi_{C_j} - \bar{\Phi}) - (1 - h')n\bar{C}(\phi_{C_j} - \phi_{D_j})\bar{\Phi}$$

Because $\phi_{D_j} < \bar{\Phi}$ a rare beard colour requires $\phi_{C_j} > \bar{\Phi}$ in order to invade, i.e. a rare beard colour can never invade with recombination if it would not invade without recombination. A second condition for invasion is that $h'\phi_{C_j} < \bar{\Phi}$, i.e., rare beard colours cannot invade if the recombination rate of the tag-trait combination is excessively high, but note that the absolute value of this lower boundary depends on the average pay-off. Because the average pay-off, $\bar{\Phi}$, increases with the number of beard colours, with every next beard colour that can invade the invasion criteria become more stringent and, once a certain number of beard colours is present, no further beard colour can invade.

References

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