Emergence of cyclic competitions in spatial ecosystems

Marcus Frean

School of Mathematics, Statistics and Computer Science
Victoria University of Wellington, Wellington, New Zealand
Phone: +64 4 463-5672 Fax: +64 4 464-5054
Email: marcus@mcs.vuw.ac.nz

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ABSTRACT

This paper considers ways in which cyclic competitions between species might emerge from other systems. An approach is suggested that begins with a single species. In some regimes it leads to networks of competing species, while in others it generates evolutionary dynamics that are akin to the "red queen" effect, but within a single species. I speculate on whether these behaviours might arise from a more realistic model, and sketch the form this model might take.

Keywords and phrases: rock-paper-scissors, competition, red queen, evolution, stochastic cellular automata

1 INTRODUCTION

The outcome of competition between species is often governed by the competitive exclusion principle (Gause 1934), particularly in a homogeneous environment where fitnesses are dominated by the direct effects of interactions with other individuals. Non-transitive competitions are an exception, the simplest of these being "rock-paper-scissors" (RPS), in which species X dominates Y and Y dominates Z, but Z in turn dominates X.

RPS relationships exist in some natural systems, most notably among encrusting marine invertebrates (Buss & Jackson 1979), and have been modelled via Lotka Volterra equations (Maynard-Smith 1982) and, in a spatial context, studied via computer simulations (Frean & Abraham 2001, Johnson & Seinen 2001, Mansfield 2006, Newth 2005). If the total population is held constant, the mean field equations describing the densities of species over time describe closed cycles around a fixed point. These orbits are neutrally stable however and stochastic deviations in the densities inevitably lead to extinctions, leaving a single species. One striking property exhibited by RPS systems is "survival of the weakest": the slowest invader is the species most likely to be the one remaining.

If the competition involved is that for space in which to live, and individuals compete locally with others in their immediate neighbourhood, the system is stabilised (Kerr, Riley, Feldman & Bohannan 2002). The effect of space can be simulated by considering stochastic "invasions" among individuals occupying a spatial array. A site (say the i^{th}) is chosen at random, and its current occupant attempts to invade a randomly chosen neighbour j. The invasion is successful with some probability $P_{s(i)\to s(j)}$ that represents how well the species at i competes against the one at j. For example $P_{\mathrm{rock}\to\mathrm{paper}}$ might be zero while $P_{\mathrm{paper}\to\mathrm{rock}}$ might be 0.8. Together with spatial interactions (only neighbours are considered for interacting with) this forms a stochastic cellular automaton that is sometimes called a (spatial) voter model. Simulations show that the RPS voter model is stable, with all three species[1] coexisting at densities close to the mean field fixed point (Frean & Abraham 2001).

The counterintuitive properties and high stability of spatialised non-transitive competitions make them interesting objects for further study. Previous models have essentially assumed a RPS competitive structure that exists a priori, without addressing the question of how this might arise. The next section outlines two possibilities.

[1]Note that although the term "species" is used here, three morphs within a single species could plausibly obey the same dynamics (Sinervo & Lively 1996), or we might have 2 species, one of which has two morphs such as the system described in the next section.

2 PREVIOUS WORK ON EVOLUTION OF RPS FROM OTHER SYSTEMS

A system of competing species might plausibly arise from the disintegration or collapse of a larger system consisting of many species. (Cranefield 2001) has simulated spatially explicit models in which up to 1000 initial species are placed randomly on a spatial array. Competitive interaction strengths are pre-specified in terms of invasion probabilities, and the system is left to unfold according to the simple voter model dynamics given earlier. Most species go extinct, often leaving behind an RPS system, or several interlinked such systems. The surviving species and their interactions form a graph, but as yet a study of the typicalities of these graphs has not been carried out. While this approach is interesting, the invasion probabilites are assumed *a priori* and the model is essentially the same as the RPS system except that it involves more species. Perhaps it is not particularly surprising that the shortest non-trivial cycle is a common outcome.

An RPS system can also arise from a system of fewer than 3 species. In the usual RPS model only interspecific competition was considered. Suppose instead that intraspecific competition is also taken into account, via interactions between individuals of the same species. We assume there is some form of trade-off involved in apportioning resources or competitive effort between combatting one's own species versus another. This permits RPS cycles as a possibility without simply "wiring them in": for example, we might have all individuals of species `X` opting to specialise in interspecific competition, while those of species `Y` exist in two morphs specialised in intraspecific (`Y1`) and an interspecific (`Y2`) competition respectively. If species `Y` has greater physiological efficiency (for example) than `X`, then have a non-transitive competitive network since `X` dominates `Y1`, which dominates `Y2`, which dominates `X`. We can then simulate interactions via a stochastic cellular automaton in the same way as previously, and also follow the evolution of the trait determining intra-vs-inter specific competitiveness by allowing it to mutate slightly with each successful invasion. Mansfield (2006) has investigated this model extensively and found that a variety of RPS cycles do reliably emerge in simulations, of which the above possibility is one. The particular structure of interactions that appears in the long term depends on the relative overall competitive abilities of the two species, and on the size of mutuations.

Permitting individuals to specialise (in terms of which other individuals they are best at competing against) allows the possibility for clustering of populations into different types of specialists - in a sense, new species. If one considers a species to be any clear clustering of individuals in terms of their behaviour (meaning their interactions with other individuals), then this system exhibits a kind of speciation. It seems at least possible that the divergence of a population into inter- and intra- specialists could be a precursor to genuine speciation (meaning reproductive incompatibility).

To compare this to the same system without the effects of space, we simply choose individuals at random rather than restricting them to be neighbours. Clustering in trait space, and hence speciation, does not occur in this case.

The basic idea here has been that diversity among competitors opens the door to the spontaneous formation of networks of competing types, provided the specialists form clear clusters in their parameter space: in the preceding example this occurs if interactions are spatially structured but not otherwise. Such networks might reasonably be expected to have RPS as a natural stable state, due to its high intrinsic stability in spatial environments. The next section presents an attempt to produce these effects within a model consisting of a *single* species only.

3 A SIMPLE MODEL LEADING TO COMPETITIVE NETWORKS

Suppose we have a large number of individual agents of a single species, and that each individual can be characterised by a number between 0 and 1, taken to be the agent's "point of strength" denoted s. We might allow different agents to compete on the basis of this alone, but the competition would not be particularly interesting or novel as only transitive interactions would be possible. If each individual also has a "point of vulnerability" v in the same range, then non-transitivity becomes possible: individual `A` can dominate individual `B` if $s_A \approx v_B$, and `B` can dominate a third individual `C` if $s_B \approx v_C$, but it is also possible for `C` to dominate `A` by having $s_C \approx v_A$.

As a toy example, imagine that v and s correspond to colours: v is an animal's colour, and s is the colour it is best able to see. An animal that can see its own kind best has $s \approx v$. Slightly more generally, v could be any continuously variable trait whose value is detectable, with s being the corresponding sensory system optimized to a particular v value (at the expense of others).

We can simulate this situation in almost exactly the same way as previous RPS simulations by defining a probability $P_{X \to Y} = f(d_{XY}, d^\star, \beta)$ that `X` invades `Y`. Here d_{XY} is the distance between the strong point of `X` with the weak point of `Y`, that is $|s_X - v_Y|$. If $d_{XY} < d^\star$ then `X` is able to exploit `Y`'s vulnerability and the probability of a successful invasion is above $\frac{1}{2}$. A second parameter $\beta > 0$ controls how fast this drop occurs. I used the sigmoid function for this influence function f, so $P_{X \to Y} = [1 + e^{-\beta(d^\star - d_{XY})}]^{-1}$.

3.1 Evolution of static network structures

The important parameters of the system are the width $d^\star$ of the influence function, the size of the population (*i.e.* the width of the spatial grid) and the rate of mutation (σ). Different settings of these parameters lead to different outcomes. Rather than give an exhaustive survey I mention a few notable cases here. One "epoch" corresponds to the consideration of N possible random invasions where N is the number of sites. We start the simulation off with v and s chosen independently for each site from a uniform distribution in $[0, 1]$.

Figure 1 shows the RPS system that emerges when a reasonably broad influence function is used on a fairly small spatial array (50 by 50) with $\sigma = 0.005$. For these setting RPS establishes itself reliably and quickly, and is stable once established.

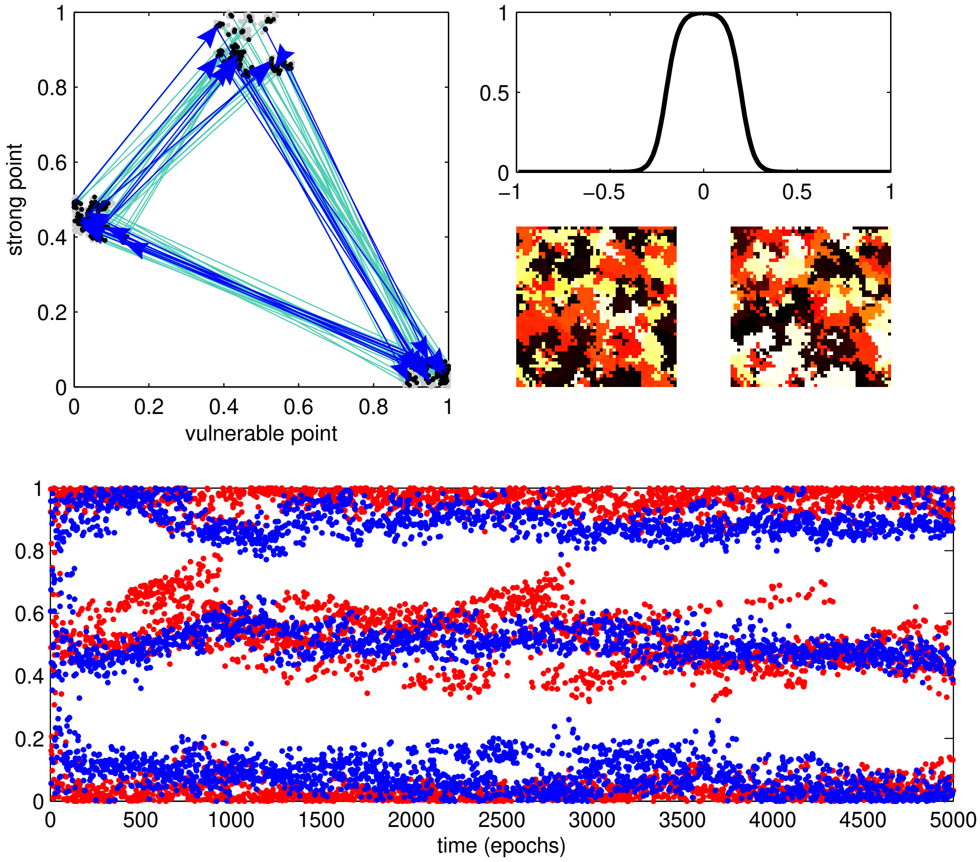

Figure 1: Simulation using a fairly broad influence function f (shown as a function of d_{XY} at top right). The plot on the left shows the individuals present (black points) after 5000 epochs with $d^\star = 0.4$. The lines indicate actual invasions and the arrows their direction. The plots on the lower right show the spatial distribution of s (left) and v (right) using a standard 'hot' colormap. In this case we arrive at 3 morphs, in a RPS structure. The lower figure shows the timecourse of v (red) and s (blue) over 5000 epochs, as a scatter plot with one sample per epoch.

The case shown in figure 2 uses the same parameters apart from having a slightly broader influence function. In this case four morphs arise, only two of which interact vigorourly. Although there is no RPS cycle the "network" appears stable. RPS systems have their own inherent stability in a spatial ecosystem, but the stability here could plausibly be due purely to the evolution of v and s: if the $(v, s) = (0, 1)$ morph's population gets low, the selection pressure holding the $(v, s) = (1, 0)$ morph in a tight cluster decreases, whereupon it spreads out, the pressure on the $(0, 1)$ population is reduced, and its numbers rise again. However this turns out not to be the case, as the equivalent *non*-spatial simulation gives a different outcome (section 3.4).

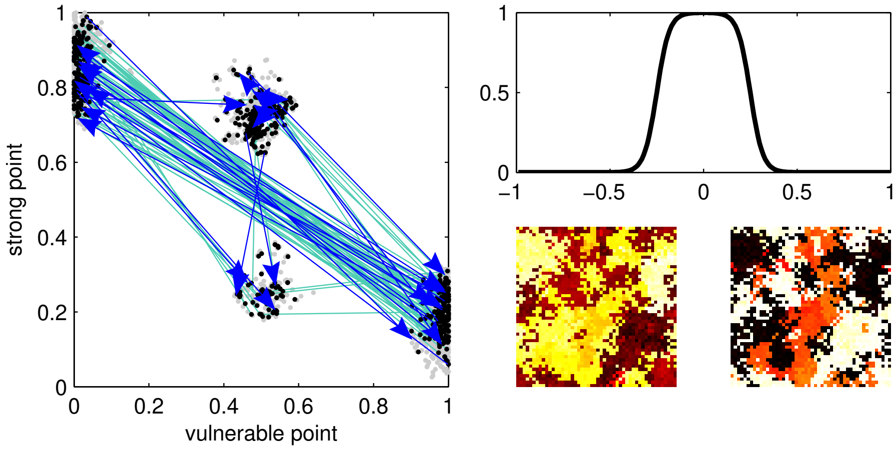

Figure 2: Here $d^\star = 0.5$. Four morphs evolve, only two of which interact vigorously (blue lines).

The situation shown in figure 3 illustrates the effect of using a slightly more *narrow* influence function instead. There appear to be two broad populations here, with rather little "internal" conflict within each.

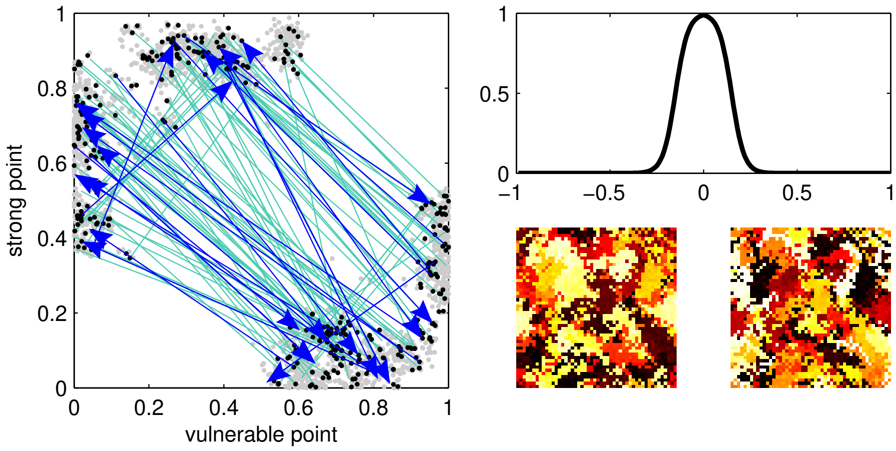

Figure 3: A slightly narrower influence function ($d^\star = 0.3$) than the one that gave the RPS system. In this case the situation was not dynamically stable: it constantly shifted during the course of the simulation.

Finally, a larger grid (150) and a smaller mutution rate ($\sigma = 0.002$) allow a richer network structure to establish itself, as illustrated in figure 4. In this case the resulting interactions are rather complicated. For example, although we might expect that the two populations at the top ($s = 1$) should be invading both the groups on the far right ($v = 1$) equally, they are tending to attack one group each. This is therefore a result of shielding due to spatial structure in the population.

3.2 An analog for intra-specific competition

When dispersal is local, natural systems tend to exhibit traits associated with intra-specific competition. I have been treating the (v, s) space as if it were the trait-space for a single species and so in that sense all competition here is intra-specific, but one can perhaps think of it in more general terms. Notice that an individual with v similar to its own s is best at competing against "itself" or, more to the point, its close relatives. This gives us a continuous analog for intra-specific ($v \approx s$) versus inter-specific ($v \neq s$) competition.

If $d^\star$ is small an individual with strength point s is only able to assert dominance over those individuals with v values that are very close by. The local nature of invasions in the current scenario ensure that an individual's neighbours (i.e. those it finds itself in direct competition with) are frequently its own relatives. This means that

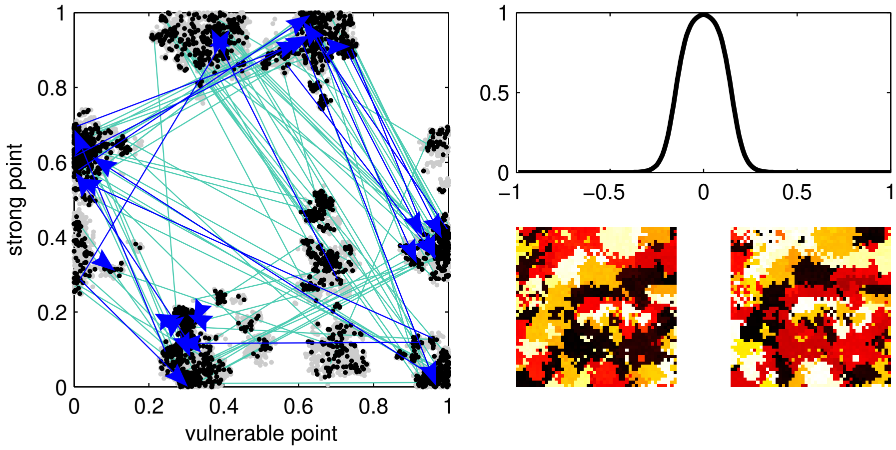

Figure 4: A larger spatial array ($n = 150$) and a smaller mutution rate ($\sigma = 0.002$) lead to a more complex interaction structure. In this case up to 10 morphs are able to co-exist. Note: only a 50-by-50 section of the final spatial array is shown here, for comparison with other figures. $d^\star = 0.3$.

the target s value is most likely to be one's own v value, leading to strong "self" interaction, directly analogous to the enhanced intraspecific competition seen in local dispersal situations in nature. Figure 5 shows the distribution of creatures present after 5000 epochs in a 100-by-100 domain, with a influence width of $d^\star = 0.1$.

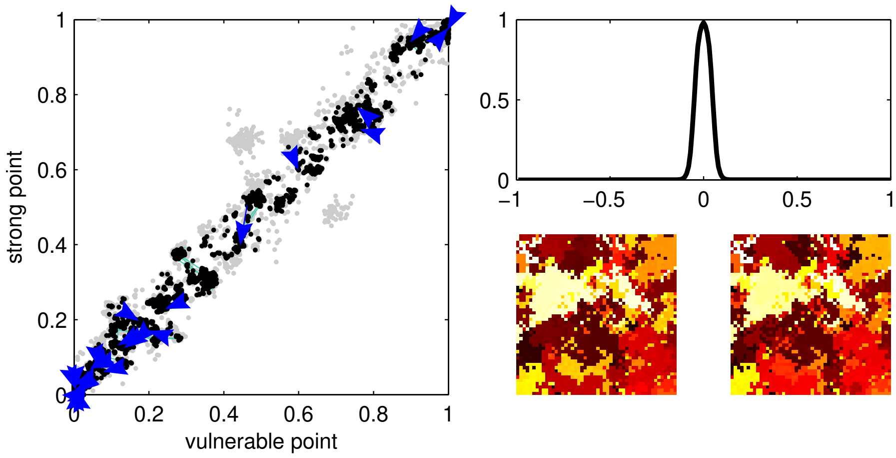

Figure 5: Beating up the relatives: points on the diagonal correspond to strong self-directed tuning of s toward v, analogous to intra-specific competition. $d^\star = 0.1$ and $n = 100$.

3.3 "Red queen" dynamics

Figure 5 exhibits a very high degree of diversity, which is made possible at least partly by the large environment. If we run the same simulation but half the size of the domain, the population collapses to a single cluster, as seen in figure 6. However this cluster is not static: its mean value in (v, s)-space keeps moving, as illustrated in figure 7. Individuals on one side of the cluster in (v, s)-space are invading those on the other side. Suppose that at a certain moment the population were to consist of individuals that tend to have (say) $v \approx s + \epsilon$. Given this situation, the optimal offspring has $s = \bar{v}$, and v as far as possible from $\bar{s}$. Given the offspring are mutations about $(\bar{v}, \bar{s})$ with $\bar{v} > \bar{s}$, this v is forced to be above rather than below $\bar{s}$. These offspring outcompete all other variants, with the result that both $\bar{v}$ and $\bar{s}$ rise over evolutionary time. Once $\bar{v}$ hits the upper limit of 1, the s values that have been chasing it are able to "catch up" temporarily, before $\bar{v}$ sets off once again in the opposite direction, leading to the linear trajectories and semi-regular oscillations seen in figure 7.

This effect closely resembles the so-called “Red queen effect” (Valen 1973), an evolutionary hypothesis to explain the constant evolutionary arms race between competing species. The term is taken from the Red Queen’s race in Lewis Carroll’s *Through the Looking Glass* (”Now, here, you see, it takes all the running you can do, to keep in the same place”). The idea formed the basis of the hypothesis that sex had evolved because organisms with sex were able to continuously run away from their parasites (Hamilton, Axelrod & Tanese 1990), and is often used synonymously with this particular argument.

However in this case we have only one species, and only one morph. The effect results from one side (in terms of the toy trait space being invoked here) continually outcompeting the other, so that in a sense the population chases its own tail. The diversity present in the population is essential to this effect, and so mean field models (meaning any model that deals only with the dynamics of an average individual such as the Lotka-Volterra equations do) cannot capture this dynamic.

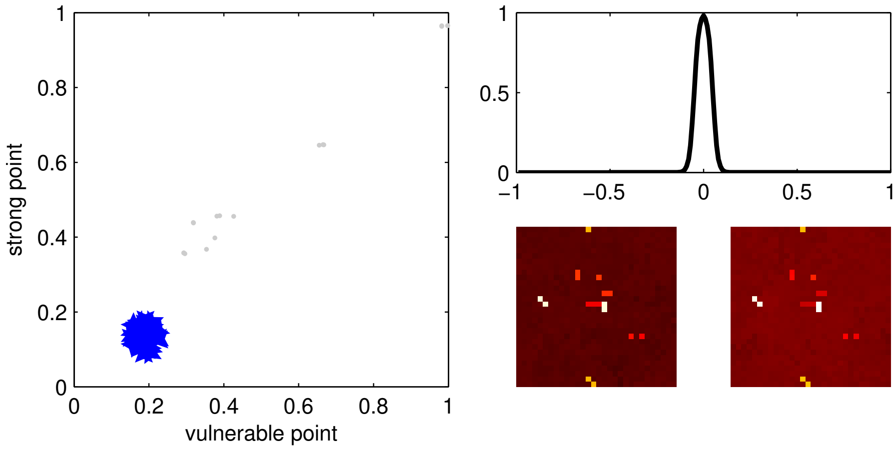

Figure 6: With a narrow influence function, and a small spatial environment, the population at any one time is tightly clustered into a small region of the (v, s) trait space. Here $d^{\star} = 0.1$ and $n = 30$.

3.4 Effect of the spatial array

The above simulations involved only local invasions in a spatial array. Without the restriction that invasions must be of neighbours however, the red queen effect is ubiquitous. Figure 8 shows two examples, for parameters that would give structured networks of interactions in the spatial case. This means that the stability seen in figure 2 is at least partly due to the spatial structure / local dispersal being imposed there.

4 DISCUSSION

There are many points on which the (v, s) model could be criticised:

- v and s are not realistic traits;
- such a precise trade-off between offensive and defensive traits seems implausible;
- in any case, there should be many interacting traits between any two combatants, not just one or two;
- the current model is all about competition: it can’t represent the possibility of mutualism (for example).

The strength and directionality of the interaction between two individuals should presumably depend on their respective traits. In the original RPS work, and in any model that begins with the community matrix as its foundation, the only “trait” an individual has is its species. In the model described above, every creature has exactly one strength, and one equally compulsory vulnerability to the strengths of others. By contrast, most real traits (thick hair, rapid growth, a white coat, forward-facing eyes...) potentially have both positive *and* negative effects on their possesser. Whether a trait has a positive, neutral or negative effect depends on the individual’s environment, a significant component of which is the composition of its neighbours (*i.e.* the traits they express). A more sensible model would represent these trait-trait interactions explicitly and put them at the heart of the dynamics of competition for space.

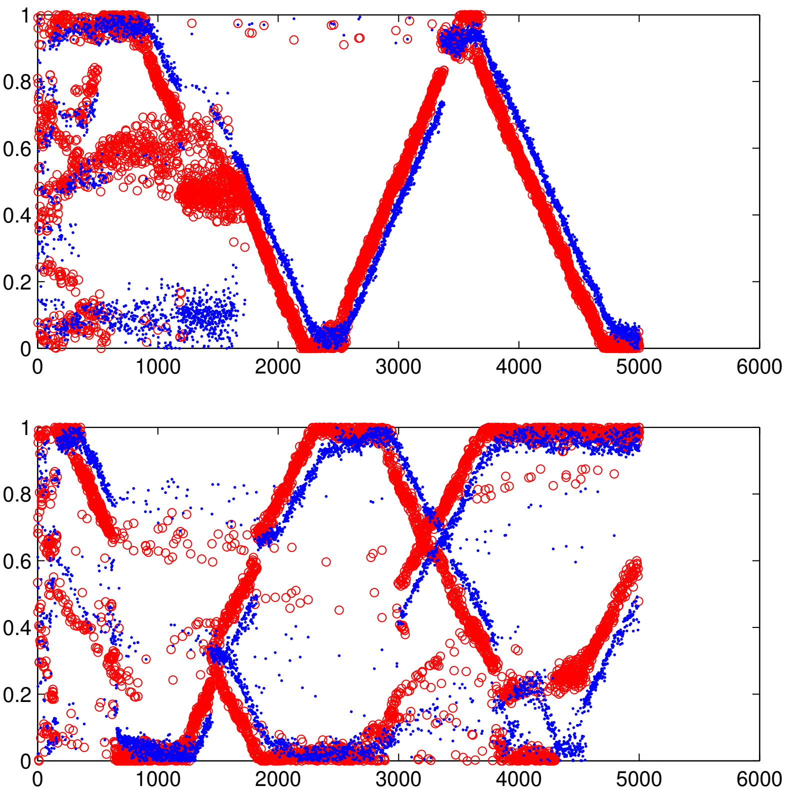

Figure 7: Red Queen dynamics. Scatter plots of the evolution of v (red circles) and s (blue dots) over 5000 epochs. In the upper plot the population settles into a single cluster which then tranverses the parameter space in alternating directions as s pursues v. The lower plot shows a population consisting of two clusters, which continue to interact over time.

The basic idea here is that traits expand the potential for an individual to compete successfully with other creatures occupying nearby space, but also expose it to risk of exploitation by those same creatures. The advantage that a given trait furnishes depends on the traits of those individuals it interacts with. It all depends who is in the neighbourhood. The same `X` trait that confers dominance against `Y` could generate a vulnerability to `Z`. This description on its own assumes a purely competitive environment however: in general the trait-trait effects on the fitnesses of the two individuals[2] come in six possibilities: competition (–), mutualism (++), predator-prey (+-), commensalism (+0), amensalism (-0) and indifference(00).

Suppose that $M_{i \leftarrow j}$ is the effect on an individual having trait i of interacting with an individual having trait j. Given n traits in all, $\mathbf{M}$ is an n by n matrix whose elements contain the trait-trait interactions. In effect this represents the fixed properties of the world. Cutting implements are always good (at least for the bearer) in terms of their interaction with soft tissue, and so on. These parameters are to be treated as immutable. We can represent an individual by a binary vector $\mathbf{X}$ having a 1 at each position where the associated trait is being expressed. The overall interaction (effectively the entry in a community matrix A) between the two individuals having trait vectors $\mathbf{X}$ and $\mathbf{Y}$ is the sum of the trait-trait interactions:

$$
\begin{aligned}
A_{X \leftarrow Y} &= \sum_{i:X_i=1} \sum_{j:Y_j=1} M_{i \leftarrow j} \\
&= \mathbf{X}^T \mathbf{M} \mathbf{Y}
\end{aligned}
$$

The usual model allows only pair-wise interactions, so that if $A_{X \leftarrow Y} = A_{Y \leftarrow X}$ the two cancel each other out, regardless of whether A is positive or negative. By contrast a mutualism (for example) intrinsically involves some third party, which the pairwise competitive dynamics of the voter model cannot represent. Instead, it is probably necessary to introduce some notion of "fitness" in the sense of an intermediate measure of an individual's fecundity, and to derive the invasion dynamics from this. Fitnesses can be given by the sum of neighbour

[2]It would be interesting and plausible to consider self-interactions of traits as well.

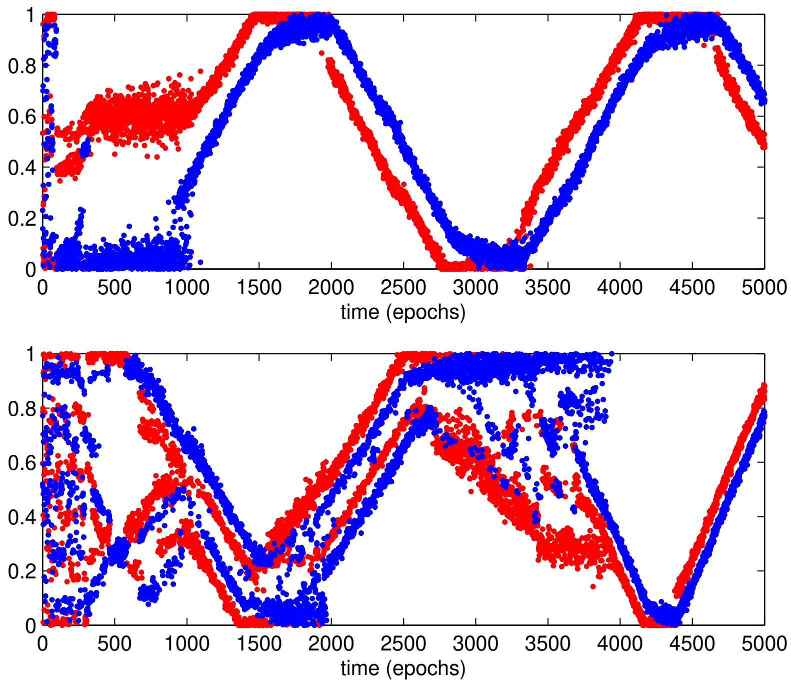

Figure 8: The upper plot shows the evolution of s and v for the same parameters as for figure 1, but with random interactions (*e.g.* due to long-range dispersal) rather than spatially localised ones. The lower shows evolution for a larger (100 by 100) array and influence width 0.2. Although this allows the two sub-populations to persist for some time, they eventually coalesce.

interactions:

$$F_X = \sum_{X'} A_{X \leftarrow X'}$$

where the sum is over neighbours of the X-containing site. One can then have a stochastic mapping from fitnesses to invasion probabilities.

The (v, s) model illustrates one way in which stable sets of interactions can crystallize out from an initially homogeneus continuous space of variability. These emergent networks include the RPS system, but a variety of other competitive networks are possible, and do occur. An unexpected aspect has been the observation of something like the red queen effect in a single species: a single cluster of individuals "chases its own tail", leading to endless oscillations as the population runs away from itself as fast as evolution will allow it. It will be interesting to see whether a directly trait-based model such as the one sketched above has analogous regimes in which it shows these same two phenomena.

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