

Rock–scissors–paper and the survival of the weakest

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In the children's game of rock–scissors–paper, players each choose one of three strategies. A rock beats a pair of scissors, scissors beat a sheet of paper and paper beats a rock, so the strategies form a competitive cycle. Although cycles in competitive ability appear to be reasonably rare among terrestrial plants, they are common among marine sessile organisms and have been reported in other contexts. Here we consider a system with three species in a competitive loop and show that this simple ecology exhibits two counter-intuitive phenomena. First, the species that is least competitive is expected to have the largest population and, where there are oscillations in a finite population, to be the least likely to die out. As a consequence an apparent weakening of a species leads to an increase in its population. Second, evolution favours the most competitive individuals within a species, which leads to a decline in its population. This is analogous to the tragedy of the commons, but here, rather than leading to a collapse, the 'tragedy' acts to maintain diversity.

Keywords: rock–scissors–paper; intransitive competition; Prisoner's Dilemma; voter model

1. INTRODUCTION

The principle of competitive exclusion states that, at equilibrium, the number of competing species that can coexist is no greater than the number of limiting resources (Hardin 1960). This raises the question of how biological diversity is maintained. Environmental disturbance may prevent an ecosystem from reaching equilibrium, with intermediate disturbance levels promoting high diversity (Connell 1978). If external influences are unimportant, then the intrinsic dynamics of the ecosystem may keep it away from equilibrium, thereby allowing the coexistence of more species than expected (Huisman & Weissing 1999). Here we consider competition for space. Many previous studies of this problem have focused on two species, with the result that, if they differ only in their competitive ability, one species will eventually displace the other (Durrett 1988). In most ecosystems there are many interacting species and these will have complex networks of competitive relations (Buss & Jackson 1979; Buss 1980, 1986; Kay & Keough 1981; Russ 1982; Rinkevich *et al.* 1992; Shipley 1993; Tanner *et al.* 1994; Goldberg 1997; Burrows & Hawkins 1998). The simplest non-trivial cyclic network is three species that have relationships analogous to the game of rock–scissors–paper, with the first outcompeting the second, the second outcompeting the third and the third outcompeting the first. This is the system that we explore here. Although we use the term species throughout, the same analysis applies to any replicators with a similar cyclic competitive structure. One of the best-described biological examples is the mating strategies of side-blotched lizards (Sinervo & Lively 1996). Others include overgrowths by marine sessile organisms (Buss 1980; Burrows & Hawkins 1998), competition between mutant strains of yeast (Paquin & Adams 1983) and the possible cyclic competition amongst outlaw genes (Sigmund 1993). Successional systems such

as space–grass–trees may also have similar dynamics (Durrett & Levin 1998). It has previously been shown that cyclic competition may be dynamically stable (Gilpin 1975; May & Leonard 1975; Weissing 1991; Durrett & Levin 1994; Johnson 1997). Here we consider the effect of evolution on cyclic competition for space.

2. THE MEAN-FIELD MODEL

We consider a model world that has N available sites (Silvertown *et al.* 1992). The sites are occupied by three species, namely species r (rock), s (scissors) and p (paper), which occur in the proportions n_r , n_s and n_p (with $n_r + n_s + n_p = 1$). Two sites are chosen at each time-step. The occupant of the first replicates into the second with a given probability—an individual of species r can invade a species s with probability P_r , a species s invades a species p with probability P_s , a species p invades a species r with probability P_p and all other invasion probabilities are zero. If the two competing individuals are chosen randomly at each time-step (corresponding to long-range dispersal), then encounters between the different species occur with probabilities proportional to their overall densities. In the limit of large N , the rate of change of each population density is then given by the mean-field equation (Durrett & Levin 1994). For species r this is

$$dn_r/dt = n_r(n_s P_r - n_p P_p), \quad (1)$$

with similar equations for species s and p being obtained by substitution. Here a unit of time t is N individual time-steps, which we refer to as an epoch. Note that the dynamics is invariant under a simultaneous rescaling of the invasion rates and of t . The population densities form closed orbits around the non-trivial fixed point of the mean-field equations, which is obtained by setting the rates of change to zero (figure 1a). Oscillations of exactly this type have been seen in both empirical and modelling studies of the mating strategies of side-blotched lizards

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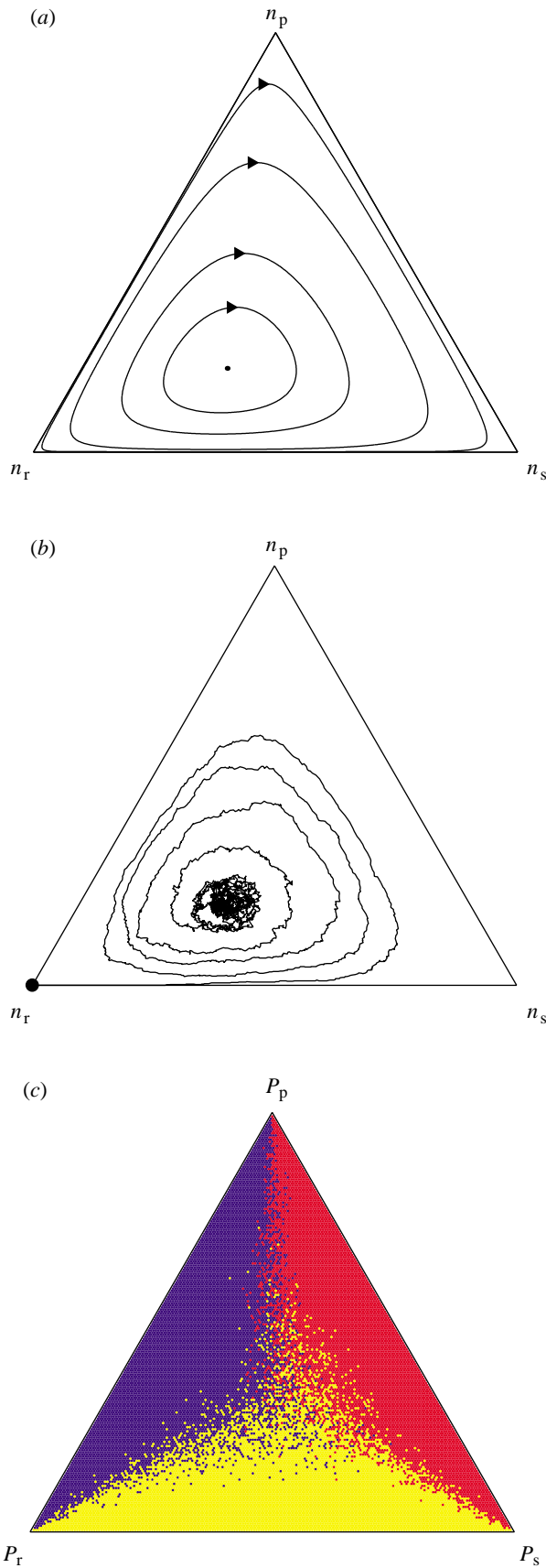


Figure 1. Dynamics of rock–scissors–paper with long-range dispersal. (a) In the limit that the total number of sites is large the populations satisfy equation (1), moving along periodic orbits around a non-trivial fixed point (equations 2–4). The figure shows several such orbits for the invasion rates $P_r = 0.2$, $P_s = 0.5$ and $P_p = 0.3$. Here n_p ranges linearly from zero along

(Sinervo & Lively 1996). If R is the population density of species r at the fixed point, it follows that

$$R = \alpha P_s, \quad (2)$$

$$S = \alpha P_p, \quad (3)$$

and

$$P = \alpha P_r, \quad (4)$$

where $\alpha = (P_r + P_s + P_p)^{-1}$. The populations are not controlled by their own invasion rates, but by the rates of the species they invade. As a consequence, the most aggressive species never has the highest fixed-point population. Moreover, if the invasion probabilities of two species are held steady, then a decrease in the competitive ability of the third leads to an increase in its fixed-point population. This result can be understood as a consequence of the cyclic nature of the system. Because there is an odd number of species in the competitive loop, a lowered invasion rate by one species leads to a decrease in the population of the species that invades it. It follows that lowering the invasion rate of a species promotes the growth of its population.

In a finite population the trajectory of the population densities will tend to overshoot the orbit, eventually leading to a species becoming extinct (Weissing 1991) (figure 1b). The quantity $\lambda = (n_r/R)^R (n_s/S)^S (n_p/P)^P$ is invariant along each orbit, with $\lambda = 1$ when the populations are at the fixed point and $\lambda = 0$ when one or more of the species become extinct. It can be shown that, if r_{\min} is the minimum value of n_r along an orbit, then

$$\partial r_{\min} / \partial R|_{\lambda=\text{constant}} > 0 \quad (5)$$

and so the species that has the smallest fixed-point density also has the lowest population along any orbit. If the invasion rates are unequal, then the species with the lowest fixed-point population is the one most likely to become extinct. The species that survives is then the one that has the lowest invasion rate (figure 1c). In this competitive system there is a paradoxical survival of the weakest.

3. THE LATTICE MODEL

If dispersal is local rather than being long range then the dynamics is changed. While a species may become locally extinct, distantly separated subpopulations oscillate

the base of the triangle to unity at its peak; similarly n_r and n_s increase to unity at their respective corners. (b) In a finite world the populations move from orbit to orbit, with two species eventually becoming extinct. The figure shows a simulation with $N = 1000$ and invasion rates as in (a), which was initialized with population densities close to the fixed point. After 1000 epochs species r is the sole remaining species (filled circle). (c) The weakest competitor is most likely to survive. This plot shows the surviving species from 19 701 model runs with $N = 1000$ for a range of invasion probabilities chosen to sum to unity. The simulations were initiated with population densities close to the fixed point. A red dot shows a simulation in which species r displaced the other two species; similarly a blue dot denotes the survival of species s alone and a yellow dot denotes the survival of species p alone.

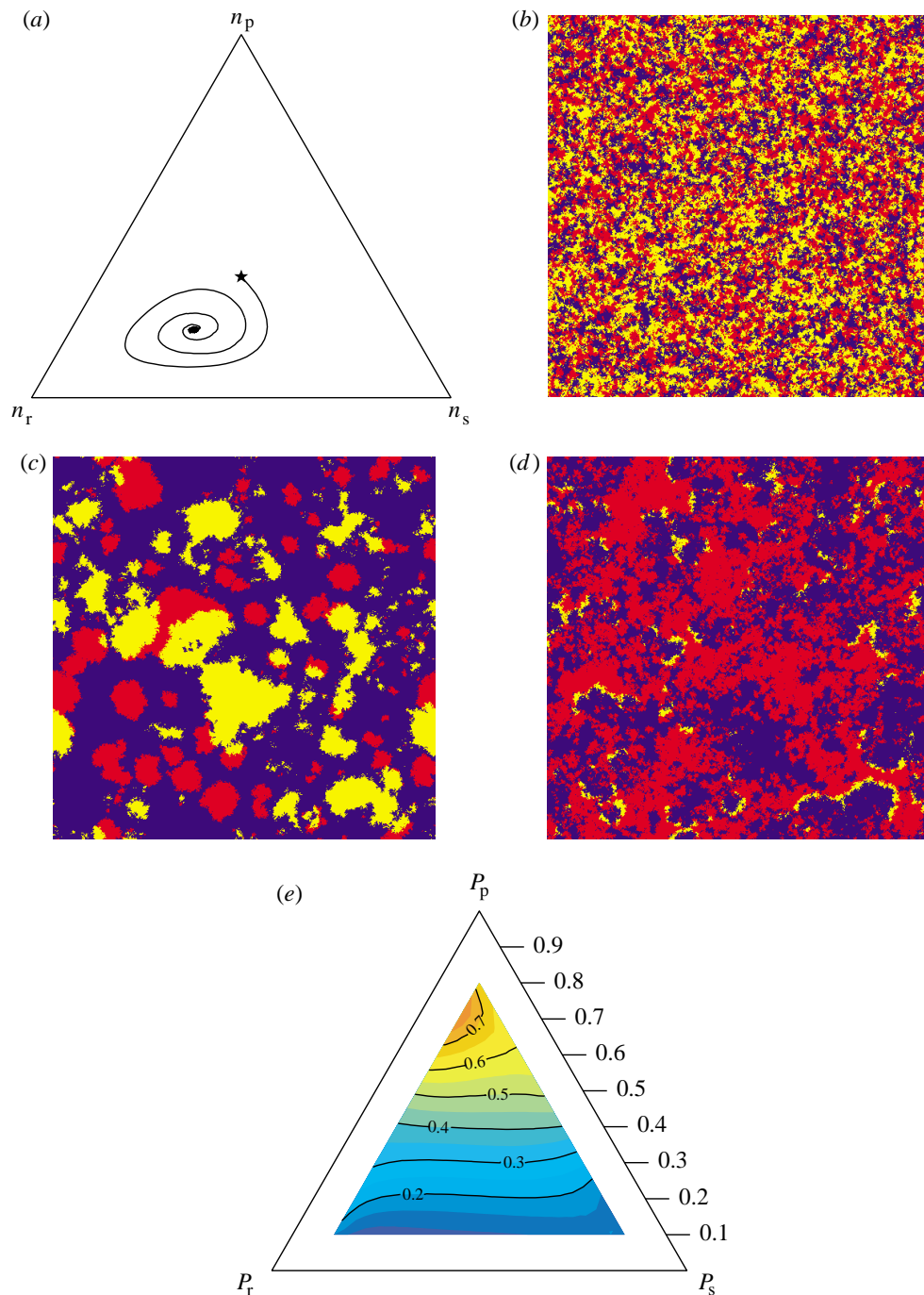


Figure 2. Dynamics of rock–scissors–paper with local dispersal. (a) An example of the dynamics with $P_r = 0.2$, $P_s = 0.5$, $P_p = 0.3$ (as in figure 1*a,b*) and $N = 500 \times 500$. The simulation was initialized with each site being randomly assigned to one of the three species (at the point shown by the star). The dynamics is stabilized and the population densities spiral in towards the fixed point. (b–d) Rock–scissors–paper on a 500×500 grid. The simulation was initialized with the sites being randomly assigned to each of the three species in fixed-point proportions. The figures show snapshots taken after 10 000 epochs (with species *r* being red, species *s* being blue and species *p* being yellow) for (b) $P_r = 0.33$, $P_s = 0.33$ and $P_p = 0.33$, (c) $P_r = 0.1$, $P_s = 0.1$ and $P_p = 0.8$ and (d) $P_r = 0.05$, $P_s = 0.475$ and $P_p = 0.475$. Note that the invasion rates do not have to sum to unity but are chosen that way in order to facilitate comparison with other figures. (e) The population densities remain close to the mean-field fixed point over much of the parameter space of invasion probabilities. The contours summarize the results of 253 simulations that are each 4000 epochs long and show the mean value of n_s over the final 1000 epochs of each model run. Data are only shown for the region that had all its invasion probabilities greater than 0.08, as outside this region the 500×500 grid was too small to stabilize fluctuations in the population densities. The value of n_s at the mean-field fixed point varies linearly from the base of the triangle to the top, which is shown by the tick marks on the right. Deviations from the mean-field approximation are seen toward the corners of the triangle, but n_s still rises with decreasing P_s .

with an unrelated phase and, on a large enough domain, global extinctions are unlikely to occur (Johnson 1997; Durrett & Levin 1998). Here the N sites of the model are taken to be sites in a periodic, square lattice and, at each time-step, the second individual is randomly chosen to be one of the eight neighbours of the first. The population fluctuations are stabilized (figure 2a), with the spatial distribution depending on the invasion rates. If the rates are equal then the populations form clumps that have a maximum size of *ca.* 100–1000 individuals (figure 2b). For unequal rates there is a variety of spatial structures. If one of the invasion rates becomes much larger than the other two, then two species form disconnected islands amongst the third (figure 2c). If one invasion rate is much smaller than the other two, then two species have similar patchy distributions, with the third persisting in fast-moving thin fronts (figure 2d). Despite the large clumps that may develop when the invasion rates are unequal, the population densities remain close to the fixed point of the mean-field equations over much of the parameter space of the invasion probabilities (figure 2e) and the paradox, that the most aggressive species does not have the largest population, still holds. On a small model grid, a decrease in the invasion rate of one species eventually leads to the other two becoming extinct and the weakest is left as the only survivor.

It would appear that it is beneficial for a species to have a lower invasion rate. The evolutionary dynamics of the system may be explored by letting the invasion rates of replicating individuals be subject to mutation (figure 3). Individuals with higher invasion rates colonize the available territory more rapidly. If the invasion rates of two species are held constant while the third is allowed to evolve, the fastest individuals of the evolving species win a higher share of territory than the slower individuals. Because the population becomes more aggressive on average, the total population of the evolving species decreases. In our case the invasion rates are held to be unity or below, so the system keeps evolving until all individuals of the mutating species have an invasion rate close to unity.

4. DISCUSSION

A scenario can be envisaged in which a disease infects one species, thereby weakening its competitive ability. Bizarrely, in the system studied here, this would lead to an increase in its population. A similar paradox has been seen in a related model in which members of species *r* spontaneously change into species *s*, with the odd result that the proportion of species *r* increases (Tainaka 1993, 1995). In these systems, a naive attempt to control one species may have exactly the opposite effect to that intended.

The rock–scissors–paper model is an example of a many-player Prisoner's Dilemma, with the more aggressive strategy winning a greater share of a smaller total population. A recent ecological example of a Prisoner's Dilemma effect is the case of Argentine ants (Queller 2000; Tsutsui *et al.* 2000), the population of which is smaller when there is intraspecific competition. If all three species in the rock–scissors–paper system evolve, then the invasion rates all rise to unity, with the species

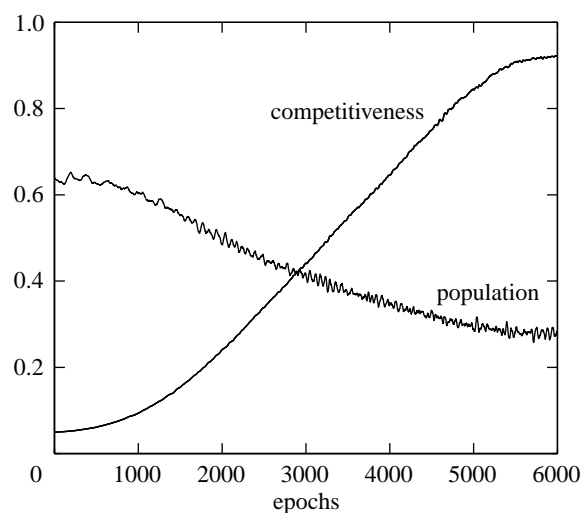


Figure 3. Evolution of species *r*. The model was run on a 500×500 grid and initially the populations had the invasion rates $P_r = 0.05$, $P_s = 0.5$ and $P_p = 0.3$. After an initial 1000 epochs (not shown), the invasion rate P_r was evolved by adding a random number to the invasion rate of a species *r* individual whenever it replicated onto a new site (the random number was uniformly distributed between $\pm 1 \times 10^{-2}$ and the new invasion rate was accepted if it was in the range $0 < P_r < 1$). The figure shows the increase in the average invasion rate and the corresponding decrease in the population density of species *r*. Ongoing mutation prevents the average P_r from reaching unity.

achieving an equal share of the resources through maximal aggression. The Prisoner's Dilemma is usually associated with the tragedy of the commons (Hardin 1968) where intraspecific competition leads to an ecological collapse. Instead, the Prisoner's Dilemma here results in a balance being maintained between the three populations.

Darwin (1873) used the metaphor of the tangled bank in order to illustrate the complexity of the relationships amongst living organisms. The bank studied here has only three species, but is stable in both a dynamic and an evolutionary sense, with no species able to displace the other two. The evolutionary stability is created by the paradox that a dominance of the system is achieved by weakening the invasion rate, an option that is not explored by evolution. This paradox is due to the self-referential nature of the competitive loop. In a real ecosystem, with its tangled web of interrelationships, self-referential effects will be common. Perturbations of the system may then have counter-intuitive results.

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