Spatially induced speciation prevents extinction: the evolution of dispersal distance in oscillatory predator–prey models

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In a discrete-generation, individual-oriented model of predator–prey interactions that exhibits oscillations, we show that the self-structuring of the populations into spiral waves induces a selection pressure for ever-increasing dispersal distances in both populations. As the dispersal distances increase, the sizes of the spatial patterns increase, until they are too large to fit into the limited space. The patterns are then lost and the predators go extinct. This scenario is, however, not the only outcome. A second selection pressure induced by the spatial boundary can cause reduction of the dispersal distances. Depending on the relative strengths of the two selection pressures, the predators and prey may speciate to give coexistence between short-dispersing boundary quasi-species and far-dispersing spiral quasi-species. Now, when pattern loss occurs, the predators switch to predating on the boundary prey quasi-species and do not go extinct. Also, if the populations reproduce sexually, local gene flow can inhibit the evolution of increasing dispersal distances, and hence the spatial patterns are not lost. Speciation and coexistence can also occur in the sexually reproducing species.

Keywords: spatial pattern formation, individual-oriented model, spiral waves, coexistence

1. INTRODUCTION

Several theoretical ecology models have shown that populations embedded and dispersing in space can be more stable than their non-spatial counterparts (Hassell *et al.* 1991; Solé *et al.* 1992; Comins *et al.* 1992; Rohani & Miramontes 1995). More stable can mean that a previously unstable equilibrium point becomes stable under a greater variety of conditions, or that an equilibrium is approached faster. In oscillatory systems where the equilibrium is a limit cycle, or more generally there exists an unstable focus, diffusion or dispersal create wave-like patterns. The two most commonly seen patterns are spiral waves and turbulence. Spirals have been shown to potentially play a very important role in ecological systems. They cause resistance to parasites in cyclical altruistic interactions (Boerlijst & Hogeweg 1991*a,b*), they allow for coexistence of mutually exclusive species (Comins & Hassell 1996; Ruxton & Rohani 1996), and they are very stable against noise (Chaté & Manneville 1996). It has recently been suggested that the oscillations seen in snowshoe hares in Canada may be due to spiral waves (Bascompte *et al.* 1997).

An assumption in these ecological models is that the life history parameters of the population are fixed or that the evolutionary time-scale is so long as to be unimportant. If the 'ecological' assumption is dropped, then mutations coupled with ecological dynamics and spatial pattern formation can lead to some very rich and counterintuitive

behaviour, e.g. in the existence of sexual species due to parasitism (Keeling & Rand 1995), interlocking ecological and evolutionary time-scales (Van der Laan & Hogeweg 1995), the evolution of a critical transmissibility in host–pathogen systems (Rand *et al.* 1995), the generation and maintenance of species diversity (Hogeweg 1994), the selection and competition pressures acting over multiple spatial and temporal scales (Savill *et al.* 1997), and evolutionary stagnation (Savill & Hogeweg 1997*a*).

In a previous paper (Savill & Hogeweg 1997*b*) we examined competition between populations with different dispersal rates or distances in a variety of formalisms that exhibit waves. We found that the population with the higher dispersal rate or distance will always out-compete the weaker dispersing population if the cost of dispersal is not too high. This result is independent of whether time, state, and space are discrete or continuous, and of the precise interactions that give rise to these waves. If, then, we allow for evolution in the dispersal rates or distances, we expect, and indeed find, that populations in a wave-exhibiting system will evolve to increasing dispersal rates or distances given a weak cost of dispersal. But as the dispersal rate or distance evolves to higher values, the size of the spatial patterns, i.e. the wavelength of the waves, increases as one would expect. When the size of the patterns is on the same scale as the size of the space, the system, for all intent and purposes, becomes well-mixed instead of diffusive. If the well-mixed system is unstable, predator or prey extinction will occur.

In this paper we use a specific discrete-generation predator–prey model that in the well-mixed case is unstable (i.e. the predator goes extinct after a few

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oscillations), to examine how speciation and sexual reproduction can prevent predator extinction. We assume that the cost of dispersal is weak so that it does not hinder the evolution of the dispersal distances. We describe some of the model's more interesting behaviour that might have some relevance to biological systems.

2. THE MODEL

The model is a two-dimensional individual-oriented model of discrete-generation predator–prey interactions. The individual-oriented formalism is used for several reasons: first, computational resources; were we to use a continuous state formalism (e.g. partial differential equations (PDEs)), we would need one equation for each dispersal distance for both predators and prey (e.g. to allow for evolution of the dispersal distance from 1 to 10 in steps of 1 would need 20 coupled PDEs!); secondly, in continuous state systems, mutation and dispersal can lead to so called nanofoxes (10^{-9} of a fox)—such numbers are unrealistic but, more importantly, they mean that all types can exist at all positions in space, even in unrealistically small amounts; thirdly, to achieve complex spatial patterns as initial conditions (which is what we require to examine the effects of spatial pattern formation) in PDEs is notoriously difficult, and usually rather unnatural circumstances must be used; and finally, individual-oriented models allow one to track individual organisms and their descendents through time and space, and moreover, we get the more realistic concepts of discreteness and stochasticity for free.

The model is defined as follows. Space is made up of a square lattice of $L \times L$ patches. If an individual crosses the boundary of space, it has a probability, ρ, of being lost from the system. If not, then it stays at the boundary. Therefore, we can tune the boundary conditions from fully absorbing to fully reflecting. On each generation prey and predators disperse in a random direction up to a maximum dispersal distance, d_r and d_p, respectively. After dispersal, some prey are killed if the total number of prey in a patch exceeds the predetermined carrying capacity, K. Each predator in a patch can capture and eat only one prey. If there are more predators than prey some predators will not capture a prey. Following predation, the remaining prey have a predetermined litter size, a_r, and die. The offspring have a small probability, μ_r, of a mutation in their dispersal distances. Predators that have captured a prey have a predetermined litter size, a_p, and die. The offspring have a small probability, μ_p, of a mutation in their dispersal distances. Predators that have captured no prey do not reproduce. A new generation begins. The parameters were chosen so that the predator and prey populations exhibit waves, and in the well-mixed case the system is unstable. What is seen are waves of predators 'chasing' waves of prey.

In the model we use a flat dispersal distribution, i.e. individuals can disperse with equal probability to any distance up to the maximum dispersal distance. We have done other simulations with different dispersal distributions with no qualitative change in the results. There are many ways of modelling prey–predator interactions, above is only one. Over the course of this research other methods and parameter values have been tried, including

overlapping generations. Quantitatively, results can vary, but qualitative wave-like patterns are very easy to produce and hence the evolutionary dynamics are similar.

We are assuming that dispersal distance is a strongly heritable trait. In reality the link between mutations in the genome and the resulting affect on the trait is extremely complex. Therefore, we must assume for simplicity and understanding an extremely simplified mutational scheme. We mutate the trait a fixed amount with some small probability when a new organism is born. However, we should realize that other schemes may give quantitatively different results. In the simulations that follow, we describe results for different mutation rates that do give quantitative differences but not qualitative differences. Mutations can change the offspring's dispersal distance by ± 1 relative to the parent's, i.e. $d' = d \pm 1$ where $d'(\geqslant 0)$ is the offspring's dispersal distance. When $d' = 0$, the offspring do not disperse, and if d' goes negative the mutational change is ignored. This means that the relative mutational change is large for individuals that disperse short distances, and becomes relatively smaller as individuals disperse further.

3. PREDATOR EXTINCTION DUE TO SPIRAL LOSS

A typical evolutionary simulation is shown in figure 1*a*. Initially, evolution occurs fairly rapidly but slows as the predator and prey dispersal distances evolve to higher values. The initial patterns ($t = 0$–200) are rather chaotic with short-lived spirals and turbulence. As the dispersal distances evolve, the spirals become larger and stable, and drive out the turbulence. Of course, the larger the spirals the fewer of them can fit into the limited space. Hence, spirals which exist close to the boundary are 'pushed' out.

It is clearly seen that whole spirals can be in different stages of evolution. This is due to a rather special spiral wave property: all individuals in the spiral are descended from individuals which existed in the spiral core at an earlier time (Boerlijst & Hogeweg 1991*a,b*; Savill *et al.* 1997), i.e. cores are the source of all genetic material. This means that mutants must first appear in the spiral core to become fixated, and so the populations within spirals can evolve at different rates due to stochasticity.

In figure 1*b*, we show the predator and prey population numbers in a patch in the centre of space for the first 10 000 generations. The change in the amplitude at around $t = 4000$ occurs when only one spiral exists and its core sits in the centre of space. This effect is well known in the theory of spatially oscillatory systems (Cross & Hohenberg 1993). In figure 2*a*, we show how the predator and prey quasi-species (Eigen & Schuster 1979; Eigen *et al.* 1989) evolve in time. The prey do not speciate initially, whereas the predators speciate multiple times. These predator quasi-species can coexist for long times in very small densities in the spiral cores (best seen in figure 1*a* at $t = 800$). The reason this occurs for the predators and not the prey is that the selection pressures are weaker in the predator core than in the prey core. The strength of the selection pressure is related to the ratio of the amplitude to the mean of the oscillations (Savill & Hogeweg 1997*a*). For the prey, the ratio is approximately 0.47 in the core, and for the predator it is 0.3. Finally, one spiral (sometimes
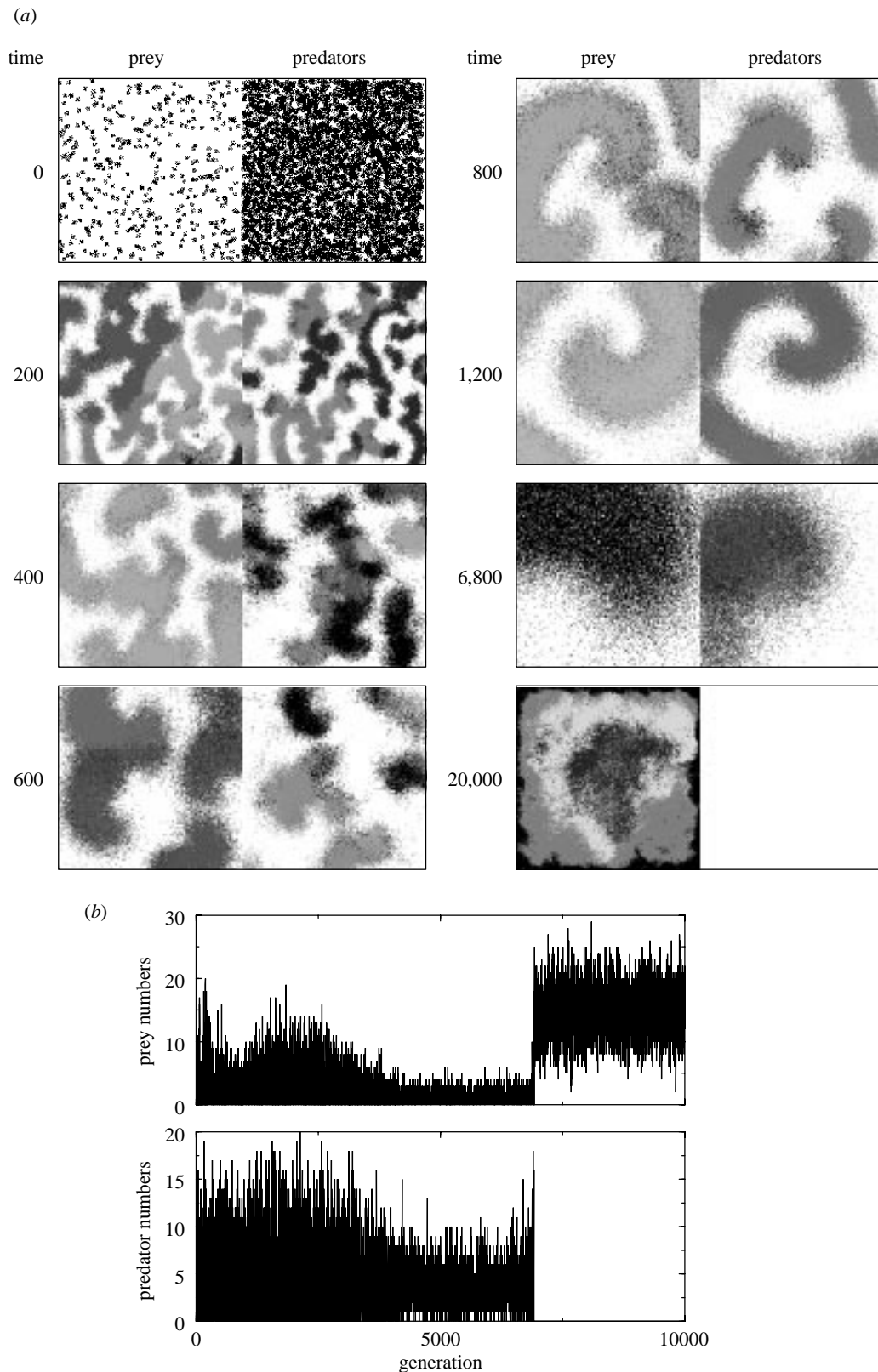
(*a*)

(*b*)

Figure 1. (*a*) A typical simulation showing eight snapshots of the evolution of dispersal distance. The predators and prey self-structure into waves that cause them to evolve to ever increasing dispersal distances. The spiral waves grow in size and become more stable until only one is left between $t = 1200$–6899. At $t = 6899$, the spiral disappears, leading to predator extinction. The prey then evolve to shorter dispersal distances because the only selection pressure acting on them is due to the boundary. The new mutants first appear on the boundary and invade inwards. The variables are $L = 200$, $\rho = 0$, $a_\mathrm{r} = a_\mathrm{p} = 3$, $\mu_\mathrm{r} = \mu_\mathrm{p} = 10^{-3}$ and $K = 5$. The grey level denotes the dispersal distance that has the most number of individuals in each patch; white patches are empty. (*b*) The time series of figure 1*a* for the first 10 000 generations in a patch in the centre of space of the predator and prey populations calculated just after the populations have reproduced and dispersed. The reduction in the amplitude between $t = 2000$–4000 is caused by the core of the single spiral moving towards the centre of space. The prey are close to their carrying capacity after the predators have gone extinct.

two) remains (t=1200–6900), and it slowly grows in size as the dispersal distances evolve. At t=6915, the core is too large to fit in the limited space, and the spiral collapses, leading to the predator's extinction.

In figure 2b, we show how the spiral loss leads to predator extinction. At t=6893, the spiral is on its last rotation and the core is almost on the same scale as the size of the space. The spiral is lost at t=6899, but there are enough predators and prey to initiate a new wave in the form of a target pattern from t=6902–6911. But because of the local extinction of the predator between waves, no predators survive to infect the new wave of growing prey at t=6914, and hence they go extinct.

After predator extinction something interesting happens to the prey. Because there are no predators the prey are close to their carrying capacity (figure 1b) and there are no waves (figure 1a, t=20 000). This means there is no selection pressure to higher dispersal distances (Savill & Hogeweg 1997a). However, as can be seen in figure 2a, there is speciation and selection to lower dispersal distances. In figure 1a, we see that the low dispersal mutants originate from the boundary and invade inwards.

This can be understood by realizing that individuals close to the spatial boundary lose almost half of their offspring that disperse across the boundary. The shorter the dispersal distance, the fewer offspring will be lost. This effect is seen for $\rho < 1$, i.e. if individuals are lost from the system through the boundary. If $\rho = 1$, we have fully reflecting boundary conditions and there is no selection pressure to lower dispersal distances at the boundary. In the centre of space, farther dispersing prey coexist because they do not feel the effect of the boundary, i.e. there is neutral selection in the centre of space.

So it appears we have two selection pressures acting on the predators and prey. The first is selection for higher dispersal distances induced by the self-structured patterns of spiral waves. The second is selection for shorter dispersal distances induced by the spatial boundary. In this simulation it appears that the former selection pressure is stronger over all of space. It should be noted that the same parameters for the simulation in figure 1a but with different random seeds will give quantitatively different results, e.g. time of spiral loss, number of predator speciations, etc. But the qualitative behaviour remains.

4. PREY SPECIATION PREVENTS PREDATOR EXTINCTION

In the next simulation, however, we see prey speciation and the coexistence of short-dispersing boundary prey quasi-species and a far-dispersing spiral prey quasi-speciess (figures 3a, 4a). The only difference between this simulation and the first is a change in the litter sizes from $a_r = a_p = 3$ to $a_r = a_p = 2$. This has the effect of reducing the ratio of the amplitude to the mean of the oscillations on the boundary (0.66 for the prey in figure 1a and 0.46 in figure 3a), and consequently the strength of the selection pressure to higher dispersal distances due to the waves (Savill & Hogeweg 1997a). Therefore, the boundary-induced selection pressure must be stronger than the wave-induced selection pressure. The predators also speciate at a later time into a spiral quasi-species,

and a diffuse boundary quasi-species which appears to have speciated in response to the prey speciation. The predators also show multiple speciations in the spiral core.

Now, when the spiral waves are lost, the predators do not go extinct. What is happening is that the prey boundary quasi-species is able to sustain the predators because it acts as a constant and predictable source of food (figure 3b). When a wave of predators travels through space it does not kill off all of the boundary prey (t=6893–6902). Enough prey survive to sustain small numbers of predators until the next wave begins (t=6905). The predators switch strategies from feeding in the self-structured spiral wave to the spatial boundary.

This result is robust to changes in the other parameters. As long as boundary prey quasi-species can form, the predators will not go extinct when the self-structured spiral patterns are lost due to evolution of dispersal distance. If $\rho < 1$, boundary prey quasi-species can form, but if $\rho = 1$, there is no selection to lower dispersal distances on the boundary and hence no boundary prey quasi-species can form and the predators will go extinct when spiral loss occurs. In figure 4b, we show a simulation for K=10. The prey do not show a speciation event to a second more diffuse boundary quasi-species, and after spiral loss the far-dispersing prey speciate into two quasi-species, most likely due to random drift. The predators again show multiple speciations. When spiral loss does occur, the shorter-dispersing quasi-species dies off and the farther-dispersing quasi-species evolves to take its place and shows, in the long run, similar behaviour as the predator in figure 4a. In figure 4c, we show a simulation for a lower mutation rate of $\mu_r = \mu_p = 10^{-4}$. The quasi-species' widths are much narrower and evolution occurs at a slower rate, but the qualitative behaviour is the same as that shown in figure 4a. After 20 000 generations spiral loss has still not occurred.

5. SEXUALLY REPRODUCING SPECIES

The model is changed so that when two individuals mate their offspring have the average of their dispersal distances with a small chance of mutation. Mating can occur either during or after dispersal. Whichever method we use the local gene flow acts to weaken the selection to increasing dispersal distances. If we use the parameters from figure 3a, both the predators and prey do not evolve from their initial dispersal distances of 1. Hence, we do not lose the spirals and the system remains stable.

If we increase the size of the oscillations by increasing the carrying capacity, K, to 30, then the selection to higher dispersal distances is strong enough to overcome the weakening due to local gene flow. A simulation with mating after dispersal is shown in figure 4d. After a few hundred generations, the prey speciate into a spiral and a boundary quasi-species. Mating of the two prey quasi-species causes the birth of prey types between the two quasi-species. Still, the boundary selection pressure is strong enough to cause the two quasi-species to remain distinct.

At t=1700, the patterns are lost and the predators go extinct. This is because to reproduce a predator must find a mate and, as shown in figure 3b, when the predator density becomes very low, most predators are the only
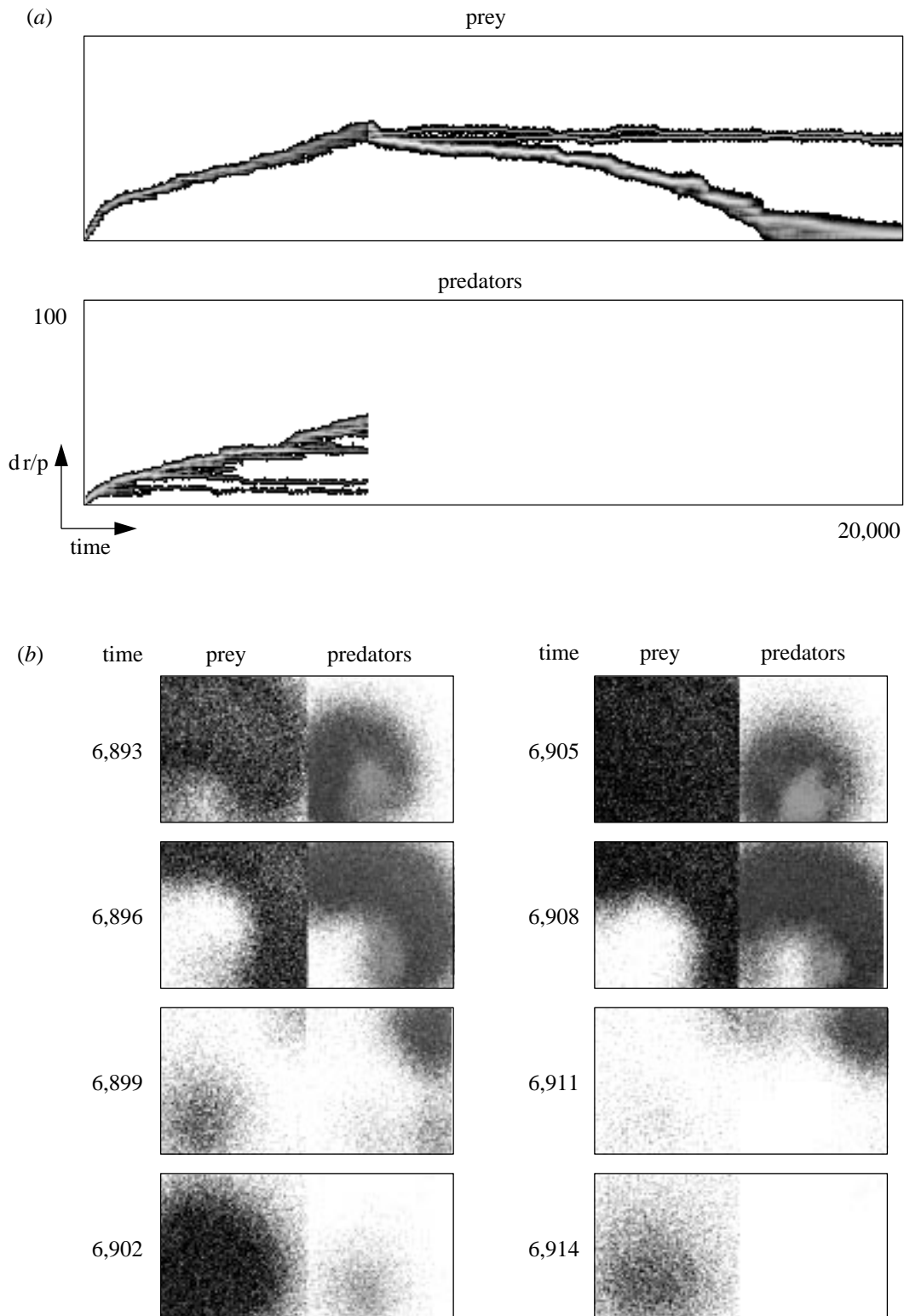
(*a*)

prey

predators

(*b*)

time	prey	predators		time	prey	predators
6,893				6,905		
6,896				6,908		
6,899				6,911		
6,902				6,914		

Figure 2. (*a*) The predator and prey quasi-species' evolution of figure 1*a*. Time runs from 0 to 20 000 horizontally, dispersal distance runs from 0 to 100 vertically. The grey scale indicates total number if individuals with a given $d_{r/p}$, lighter denotes greater numbers. At $t=6899$, the spiral collapses, resulting in the predator extinction. Some prey then evolve to lower dispersal distances because the only selection pressure acting on them is due to the boundary. Speciation occurs because prey in the centre of space do not feel the boundary's influence. The predator speciation events occur in the spiral core due to the low amplitude to mean ratio of the oscillations. (*b*) The last few generations of the simulation in figure 1*a* showing how the predators go extinct. At $t=6893$, the spiral is on its last rotation and the core is almost on the same scale as the size of the space. The spiral is lost at $t=6899$, but there are enough predators and prey to initiate a new wave in the form of a target pattern at $t=6902-6911$. But because of the local extinction of the predator between waves, no predators survive to infect the new wave of growing prey at $t=6914$, and hence they go extinct.
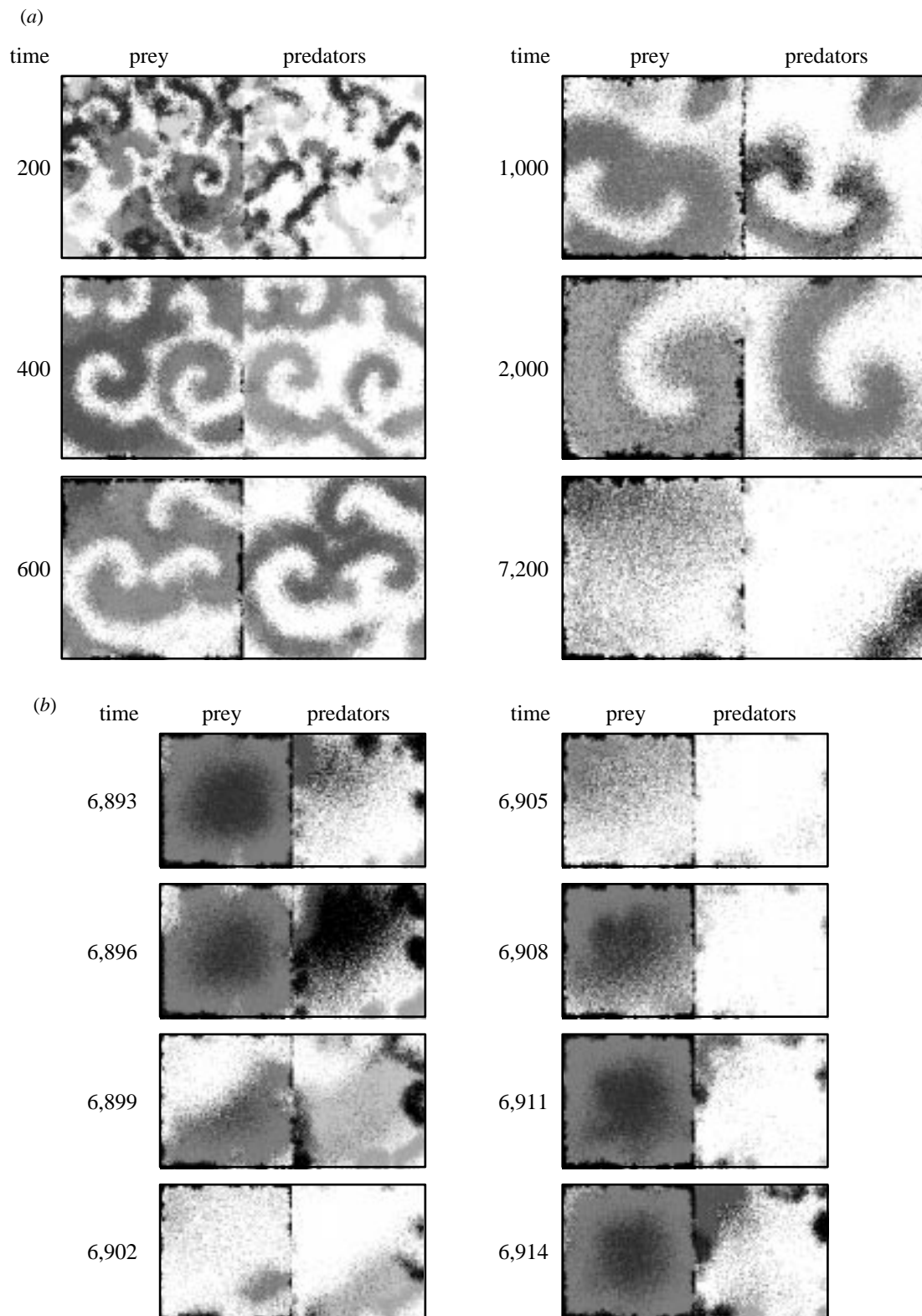
(*a*)

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Figure 3. (*a*) A similar simulation as in figure 1*a* with the same initial conditions but with $a_r = a_p = 2$. Very early on the prey speciate into a short-dispersing boundary prey quasi-species (black) and a far-dispersing spiral prey quasi-species (grey). When the spiral waves are lost, the boundary prey quasi-species are able to sustain the predators indefinitely. The grey level is the same as that in figure 1*a*. (*b*) A typical series of events of predator–prey oscillations from the simulation of figure 3*a* after spiral loss. The dynamics are similar to (*a*), but when the predator numbers crash, they can survive by predating on the boundary prey quasi-species. The grey level is the same as that in figure 1*a*.
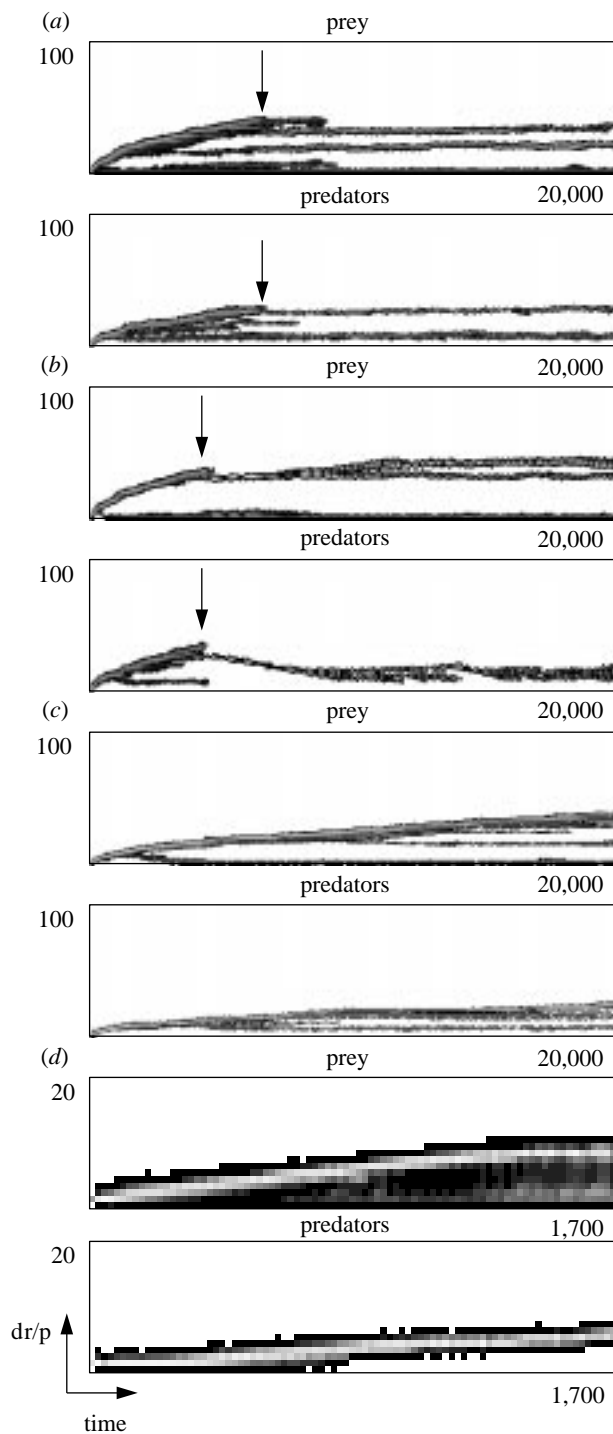
Figure 4. (*a*) The predator and prey quasi-species' evolution of the simulation in figure 3*a*. Time goes from 0 to 20 000 horizontally, dispersal distance goes from 0 to 100 vertically. The prey speciate early into a short-dispersing boundary quasi-species and a far-dispersing spiral quasi-species, and later into a second but more diffuse boundary quasi-species. The predators also show multiple speciations into spiral and boundary quasi-species. After spiral loss occurs (denoted by the arrows) some types go extinct, but the boundary quasi-species is able to sustain the predators. (*b*) Similar to (*a*) but with a larger prey carrying capacity; $K = 10$. After spiral loss (denoted by the arrows) the far-dispersing prey speciate, probably due to random drift. The short-dispersing predator quasi-species goes extinct, but the far-dispersing quasi-species evolves to take its place. (*c*) Similar to (*a*) but with mutation rates ten times smaller. The same behaviour is seen except that the quasi-species have narrower widths and the evolutionary rate is

occupants in a patch, therefore they have no one to mate with and they do not reproduce.

6. DISCUSSION AND CONCLUSION

Ecological systems display a wide variety of spatial and temporal patterns. Some of these patterns are due to external factors, for example, seasonal changes, abiotic gradients, habitat fragmentation, etc. Other patterns are due to internal factors such as density dependence, predation, etc. Identifying and measuring correlations between external factors and ecological spatiotemporal patterns is probably the easier of the two. Although, of course, just because two things appear correlated does not mean that one causes the other. For example, Sinclair *et al.* 1993 proposed that the 9–11 year oscillations in the population numbers of the snowshoe hare in Canada were correlated with sunspot activity. But Ranta *et al.* 1997 have proven this false by showing that oscillations in snowshoe hare populations in Canada and Europe are out of phase. Bascompte *et al.* 1997 have proposed that these oscillations could be due to internally generated mechanisms.

In evolutionary models, internally generated pattern formation has been shown to have interesting consequences for the evolutionary dynamics (Boerlijst & Hogeweg 1991*b*; Hogeweg 1994; Keeling & Rand 1995; Rand *et al.* 1995; van der Laan & Hogeweg 1995; Savill & Hogeweg 1997*b*; Savill *et al.* 1997). The main effect is to induce selection pressures acting over multiple temporal and spatial scales, i.e. from the level of the individuals to the level of the patterns. The interplay of these selection pressures can lead to rich transient and attractor behaviour.

In this paper we have considered how both externally and internally generated patterns of a discrete-generation predator–prey model influence the evolution of dispersal distances. First, the oscillatory predator and prey dynamics generate population waves, and these induce selection for increasing dispersal distances. However, this evolution to ever farther distances can lead the predators to their own extinction due to the spatial pattern loss. In a fitness landscape, the predator population climbs the hill only to find out that at the top is a precipice to death!

Secondly, the spatial boundary can induce a selection pressure to shorter dispersal distances so long as individuals are lost from the system across the boundary. Whether this evolution is realized or not depends on the relative strengths of the two selection pressures. If the boundary selection pressure is strong enough, the prey can speciate into a far-dispersing spiral quasi-species and a short-dispersing boundary quasi-species. This type of coexistence has been observed by Roland & Taylor (1997). They found that

slower. (*d*) A simulation of sexually reproducing species. The predator and prey mate after dispersal. A lone individual does not reproduce. The offspring receive the average dispersal of their parents with a probability of mutation. To overcome weakening of the pattern-induced selection pressure, the carrying capacity is increased to $K = 30$. The other parameter values are $L = 100$, $a_r = a_p = 2$ and $\mu_r = \mu_p = 10^{-3}$. The prey speciate but some types exist between the quasi-species due to mating of the boundary and the spiral prey quasi-species. After spiral loss the predators go extinct because of the difficulty in finding a mate.

shorter-dispersing parasitic flies of the forest tent caterpillar (*Malacosoma disstria*) have higher parasitism rates on the boundary between the forests they inhabit and deforested areas. The three farther-dispersing parasitic fly species have higher parasitism rates in more contiguously forested areas. We have shown that if speciation does occur the boundary prey quasi-species can sustain the predators after spiral loss has occurred.

Sexually reproducing species can also prevent predator extinction by the act of local gene flow weakening the selection to increasing dispersal distances, hence causing no spatial pattern loss. The strength of the selection pressure can be increased by increasing the size of the oscillations so that the populations can also speciate into boundary and spiral quasi-species. These boundary prey quasi-species are reminiscent of biological species that are observed in ecotones. Smith *et al.* (1997) have discovered that ecotone and rainforest little greenbul (*Andropadus virens*) populations are diverging both phenotypically and genetically even though there is high gene flow between the populations. They are becoming reproductively isolated due to the different habitats they encounter even though they are not geographically isolated. Our simulations show that this can indeed be true without any call for external factors.

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