Adaptive dynamics on a lattice: role of spatiality in competition, co-existence and evolutionary branching

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ABSTRACT

We investigated the effect of limited dispersal on co-existence and evolutionary branching on a lattice. The 'contact process', which is the minimal model of population growth on a lattice, is modified by introducing local resource competition in addition to site competition. We study phenotypic evolution in the framework of the theory of adaptive dynamics. We show that a higher birth rate cannot compensate for a lower intrinsic lifetime reproduction ratio. Speed difference alone, without resource competition or different dispersal scale, does not lead to co-existence via a competition–colonization trade-off. Co-existence and evolutionary branching become possible only when resource competition, with reduced competition between the populations, is introduced. There is a convergent stable singular point in the strategy space. The singular strategy is an evolutionarily stable strategy (ESS) below a critical strength of resource competition. Above this threshold, the singular strategy is no longer an ESS and evolutionary branching occurs. This is the first demonstration of evolutionary branching on a lattice. We compare the behaviour of the spatial simulation to its mean-field and pair approximation counterparts. This comparison demonstrates that spatiality and limited dispersal reduce the possibility of evolutionary branching, in addition to that of co-existence. We interpret this phenomenon based on the partial spatial segregation between the competing strategies.

Keywords: adaptive dynamics, contact process, evolutionary branching,
interacting particle system, limited dispersal.

INTRODUCTION

The role of spatiality is a central issue of modern theoretical ecology (Czárán, 1998; Dieckmann *et al.*, 2004). Local requirements/interactions and a limited ability to spread together determine the fate of a population. Classical evolutionary concepts, like competition and niche, were developed for spatially non-explicit models assuming no constraint on dispersal. The evolutionary implications of the ecological circumstances are relatively

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well understood in this context. On the other hand, the evolutionary consequences of spatiality have only been investigated in a relatively few cases (Axelrod, 1987; Nowak *et al.*, 1995; Boots and Sasaki, 1999; Harada, 1999; Ferriere and Le Galliard, 2001; Le Galliard *et al.*, 2003; Boots *et al.*, 2004). Most of these studies addressed evolution to an optimal phenotype; some of them relied extensively on pair approximation. We contribute to the study of spatial evolutionary problems by testing the applicability of the concepts and methods of adaptive dynamics. In particular, we investigate the possibility of evolutionary branching in the context of interacting particle systems, when dispersal limitation is important. Our basic tool is numerical simulation, through which we test also the applicability of the approximate methods, mean-field and pair approximation.

Competitive interactions often generate frequency-dependent selection regime (Christiansen, 1988). The theory of adaptive dynamics (Brown and Vincent, 1987; Dieckmann and Law, 1996; Geritz *et al.*, 1997, 1998) addresses ecology-induced frequency-dependent selection in asexually reproducing populations. It is based on the concept of invasion fitness, defined as the growth rate of a mutant population, which is rare in an already equilibrated resident population. With small mutation step-size, evolution always proceeds in the direction of the (local) gradient of invasion fitness. Frequency dependence may cause this directional evolution to converge to a minimum, instead of a maximum of the fitness function (Eshel, 1983; Taylor, 1989; Christiansen, 1991; Abrams *et al.*, 1993). Then the emerging disruptive selection splits the population and drives the evolution of the two emerging sub-populations in opposite directions (Geritz *et al.*, 1997, 1998). This process is referred to as evolutionary branching. It was suggested as the mathematical basis of competitive/adaptive speciation (Dieckmann and Doebeli, 1999).

The initial rarity of the mutant population is a central concept of adaptive dynamics. In our context, this assumption is problematic for two reasons. First, in previous spatial adaptive dynamical models (see, for example, Meszéna *et al.*, 1997; Kisdi and Geritz, 1999; Day, 2000; Metz and Gyllenberg, 2001; Mizera and Meszéna, 2003), a non-trivial assumption about the invasion process was made. It was supposed that the spatial distribution of an invader equilibrates early during the process of invasion – that is, while the invader is still rare everywhere. This assumption does not necessarily correspond to the real process of invasion. If the area of potential distribution is large and dispersal is limited, the invader population may become abundant at a given location first, and spread out from this location later. Then the assumption of initial rarity of the invaders becomes untenable. Second, in these previous studies, a large number of individuals (resident or mutant) were present in the interaction neighbourhood of a single individual. If the interaction neighbourhood of a mutant individual is restricted to a few other individuals, then local reproduction leads to over-representation of the mutants in this small neighbourhood. That is, the mutant will not be rare in the interaction neighbourhood, even if it is globally rare. Moreover, as a more specific issue, the existence of evolutionary branching is non-trivial because even the possibility of co-existence is limited in some spatial models (Neuhauser and Pacala, 1999; Bolker *et al.*, 2003).

Interacting particle systems (IPS) (Spitzer, 1974) are widely used to describe the spread of a population with limited dispersal in a conceptually infinite world. Cellular automata are a subset of IPS models with synchronized updating and deterministic transition rules. We have previously applied the basic concepts of adaptive dynamics in the IPS context for studying evolution of clonal integration in plants (Mágori *et al.*, 2003). However, this model did not allow for the co-existence of different phenotypes. Consequently, the most interesting phenomena of adaptive dynamics, such as evolutionary branching, could not

be studied using it. Here we choose a more 'strategic' (Czárán, 1998, p. xii) approach. We investigate the simplest possible IPS model permitting co-existence and evolutionary branching. Our starting point is the 'contact process' (Harris, 1974), which is the minimal model of population growth on a lattice. We modify this set-up by introducing a Lotka-Volterra type local resource competition. We will address the following questions:

1. Does higher birth rate provide a colonization advantage to compensate for the competition disadvantage of a lower intrinsic lifetime reproduction rate?
2. How does limited dispersal in the spatial model modify the pattern of co-existence induced by Lotka-Volterra type competition?
3. Is evolutionary branching possible with limited dispersal?

To examine the role of spatiality and dispersal limitation, we require a 'control experiment' model. We will compare the spatial (IPS) simulations to the mean-field approximation of the model. The latter corresponds to a non-spatial Lotka-Volterra competition model. The pair approximation, which is a frequent tool in such investigations, is also studied, as the middle ground between the IPS and mean-field approximation.

First, we introduce the model and its mean-field and pair approximations. The next section presents the results for competition between two distinct populations. Finally, we investigate competition and evolution assuming a continuous trait describing the populations.

THE MODEL AND ITS APPROXIMATIONS

Model definition

We model competing populations on a square lattice with periodic boundary conditions. Any site can be occupied by a single individual, or it can be empty. Any site can interact with its von Neumann neighbourhood (i.e. with the four adjacent cells). Time is continuous and thus possible events are characterized by their rates. For instance, the death rate d of an individual means that the site occupied by the individual becomes empty with probability $d\delta t$ during an infinitesimal time interval δt.

The precursor of our model is the contact process introduced by Harris (1974) with an epidemiological interpretation. Individuals die with rate 1. With rate λ, an individual produces an offspring at a site, randomly chosen from the four neighbouring sites, provided it is empty. In the multi-type version of the contact process considered by Neuhauser (1992), two populations with different λ values compete for empty sites. In this model, the population with the higher value of λ always outcompetes the inferior one. To examine the possibility of co-existence, evolution and evolutionary branching, we modified the multi-type contact process in two respects:

• We introduced a new type of mortality, representing resource competition between neighbours beyond the 'natural' death already present in the contact process. Therefore, there are two ways of local competition in our model: individuals compete for empty sites *and* for local resources.
• We do not normalize the natural death rate to 1 to allow the populations to differ in this respect.

First, we consider competition between two populations with different but heritable demographic rates. Resource competition between individuals of the same population will be higher than between individuals belonging to different populations. Then, we introduce a single continuous strategy variable which is inherited either faithfully or with the possibility of a mutation. The strategy of an individual determines its demographic rates. Resource competition between two individuals decreases with their increasing strategy difference.

The possible demographic events are as follows:

1. *Birth*. For each individual present, a birth event occurs with rate b. The target site is chosen randomly from the four neighbouring sites. If the selected site is empty, an offspring appears there. If the site is already occupied, the birth event is aborted.
2. *Natural mortality*. An individual dies with rate d and the occupied site becomes empty. This event is independent of the occupancy of other sites.
3. *Competitive mortality*. This type of mortality is a consequence of competitive inter-actions between neighbouring individuals. The resource competition coefficient $A \in [0,1]$ describes the strength of competition between two individuals. For any individual, a competitive mortality event is initiated with rate k. A neighbouring site is selected randomly. If this site is occupied, then the focal individual dies with probability A. $A = 1$ for identical individuals and $A > 1$ for different ones.

The ratio b/d determines the lifetime reproductive output of an individual, when alone. We will refer to this quantity as the *intrinsic* lifetime reproductive ratio.

Simulation starts by populating every lattice site with one individual, chosen at random from the populations we consider. This initial configuration is updated step by step afterwards. In each step of simulation, a single event takes place. The type of the event and the affected individual is chosen at random such that the probability of that specific event with that specific individual is proportional to the corresponding rate.

A 'real-time' variable t is maintained for comparison purposes. As a sufficiently accurate approximation for the exponentially distributed between-event time intervals, t is increased by the inverse of the sum of the rates of all possible events for all individuals in each step of simulation.

We use a 100×100 square lattice. When competition between two populations was investigated – that is, with the exception of the evolutionary simulations – the processes were allowed to relax for 500 time units. Then we established the equilibrium densities of the two populations by averaging the densities for another 500 time units. We considered a population extinct if its averaged density was below 10% of the other population (to compare the results for different thresholds, see Fig. 1). They were considered to co-exist when none of them was extinct in this sense.

Mean-field approximation

The mean-field approximation describes populations by their densities. We define density c_i as the probability of having an individual of type i on a randomly chosen site. The approximation neglects spatial correlations – that is, it assumes that the local frequencies are
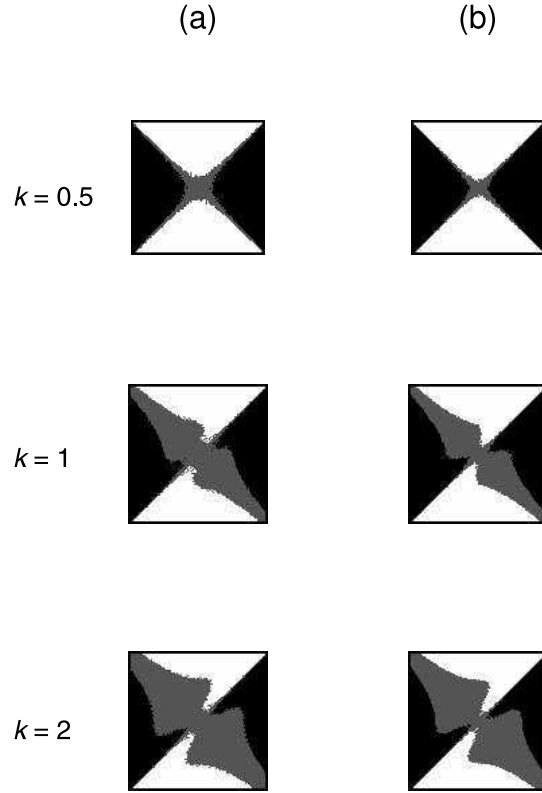
(a) (b)

$k = 0.5$

$k = 1$

$k = 2$

Fig. 1. Comparison of the results of pairwise competition in the IPS model with different rates of competitive mortality k for different extinction thresholds. Extinction thresholds are 1% (a) and 10% (b), respectively.

equal to global densities. In this approximation, the population dynamics is described by the differential equation

$$\frac{dc_i}{dt} = \left[b_i\left(1 - \sum_j c_j\right) - d - \sum_j k_i A_{ij} c_j \right] c_i \tag{1}$$

for each type i. The first term within the square brackets represents successful birth events. The second and the third terms represent natural and competitive mortality, respectively.

This dynamics can be written in the Lotka-Volterra form

$$\frac{dc_i}{dt} = \left[r_{0i} - \sum_j a_{ij} c_j \right] c_i \tag{2}$$

with the intrinsic growth rate

$$r_{0i} = b_i - d \tag{3}$$

and the overall competition coefficient

$$a_{ij} = b_i + k_i A_{ij} \tag{4}$$

The total competition a_{ij} is the sum of site competition (first term) and resource competition (second term). Obviously, the strength of site competition is independent of the character-istics of the other individual, hence it does not depend on j.

In the pairwise competition simulations, we integrated the dynamics (2) numerically until convergence. For comparability with the IPS simulations, we considered a species extinct if its density was below 10% of the other species at the end of the simulation.

Pair approximation

Pair approximation provides a natural way to bridge the gap between spatial numerical simulation and mean-field approximation. The mean-field neglects any kind of spatial information. Pair approximation takes into account pair correlations by tracking densities of pairs of sites instead of that of singlets. Higher-order correlations are still neglected.

Although the interactions are restricted to the von Neumann neighbourhood, it is useful to track the densities of pairs within the wider Moore neighbourhood. Therefore, we have both the adjacent and the diagonal pair configurations. Let the adjacent pair density p_{ij}^a be the probability that two randomly chosen adjacent sites are in states i and j. Con-figurations ij and ji are considered to be different, but $p_{ij}^a = p_{ji}^a$. We define the diagonal pair densities p_{ij}^d in a similar way for diagonal neighbour sites. The time-derivatives of pair densities are

$$\frac{dp_{ij}^a}{dt} = \sum_{i'j'} \Phi_{i'j' \to ij} - \sum_{i'j'} \Phi_{ij \to i'j'} \tag{5}$$

and

$$\frac{dp_{ij}^d}{dt} = \sum_{i'j'} \Psi_{i'j' \to ij} - \sum_{i'j'} \Psi_{ij \to i'j'} \tag{6}$$

where the values Φ and Ψ are the rates of appropriate pair transitions for the adjacent and for the diagonal pairs, respectively (see the Appendix for the calculation of these quantities). The density of a particular ij pair increases because of $i'j' \to ij$ transitions and decreases because of $ij \to i'j'$ transitions.

After testing several types of moment closures, we have decided to use the symmetric-power-2 moment closure technique to close the dynamical equations (Law *et al.*, 2003).

We solved the dynamic equations of pair approximation by numerical integration. Ini-tially ($t = 0$), all the sites were occupied, divided evenly between the two species ($c_0 = 0$, $c_1 = 0.5$, $c_2 = 0.5$) in an uncorrelated way ($p_{ij}^a = p_{ij}^d = c_i c_j$). After reaching the equilibrium ($t = 10,000$), singlet densities were calculated from pair density values:

$$c_i = \sum_j p_{ij}^a = \sum_j p_{ij}^d \tag{7}$$

We used the same criterion for extinction as for the IPS and for the mean-field. Note that the mean-field and the pair approximations are deterministic, whereas the IPS is stochastic by nature.

COMPETITION BETWEEN TWO POPULATIONS

To address Question 1 in the Introduction, first we investigate the case of $k = 0$ (i.e. the lack of competitive mortality). The outcome of competition between two populations is shown in Fig. 2. The intrinsic lifetime reproductive ratios of the competitors are shown on the two axes. The black and white areas represent the combination of the intrinsic lifetime reproductive ratios at which the first or the second process, respectively, outcompetes the other one. As seen in Fig. 2, it is always the process with the larger intrinsic lifetime reproductive ratio that wins. The grey region representing co-existence is restricted to the diagonal.

In the left-hand panel of Fig. 2, competing populations are equivalent when their respective b/d values are equal (i.e. on the main diagonal). In line with biological common sense, as well as with the analytical results of Neuhauser (1992), the population with the higher birth rate wins, everything else being equal. In contrast, in the right-hand panel, both birth and death rates of the second population are multiplied by 10. Although events take place more frequently for the second population, this difference in speed does not affect the outcome of competition. Neither of the populations is able to outcompete the other when their intrinsic lifetime reproductive ratios are equal. The higher rate of acquisition of the sites cannot compensate for a lower intrinsic lifetime reproductive ratio. This result, which is in accordance with the conjecture of Neuhauser (1992) and the results of Bolker and Pacala (1999) in a different model, answers Question 1 in the negative.

After establishing a lack of co-existence (except along the main diagonal) without competitive mortality, we proceeded to Question 2 with local resource competition. We studied competition of two distinct processes with fixed $k > 0$. We chose $d_1 = d_2$ (i.e. no difference in speed was supposed here). We fixed b_1, varied b_2 and investigated which values of b_2 permitted co-existence. We found co-existence for a broad range of b_2 in this case (Fig. 3). Obviously, when the two populations were equivalent ($b_2 = b_1$) was always within
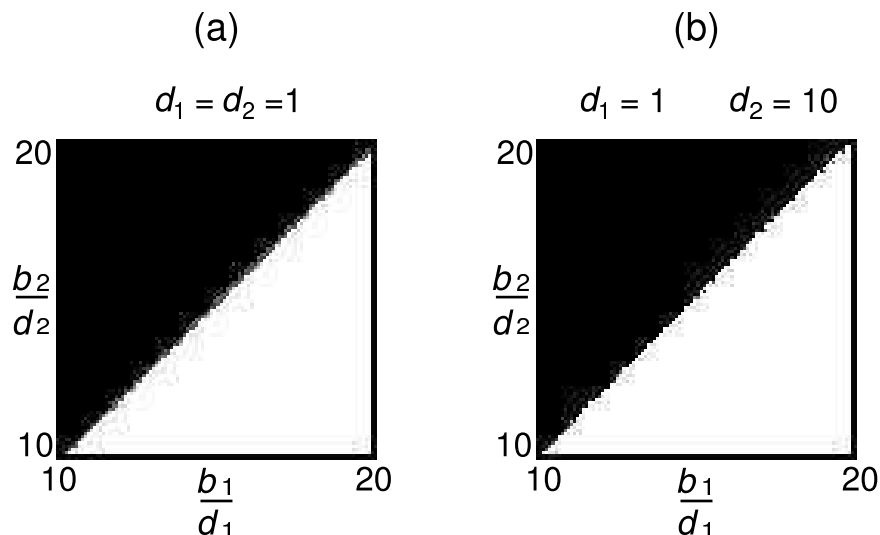

Fig. 2. Pairwise competition of populations without competitive mortality ($k = 0$). Axes correspond to intrinsic lifetime reproductive ratios of the two populations. If $b_1/d_1 \neq b_2/d_2$, either population 1 (white) or population 2 (black) wins. Along the diagonal they co-exist (grey). Plots for populations with (a) equal ($d_1 = d_2 = 1$) and (b) different ($d_1 = 1, d_2 = 10$) turnover rates.
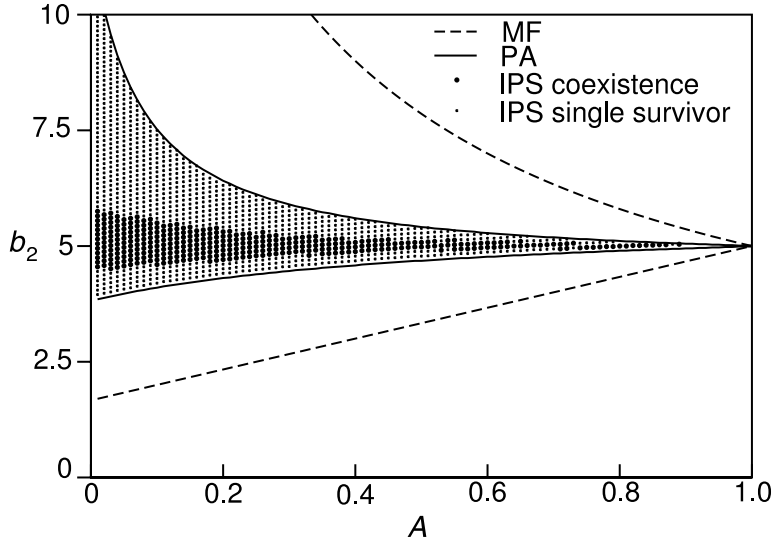
Fig. 3. Region of co-existence for two competing populations with fixed competitive mortality. Axes correspond to inter-population resource competition coefficient (A) and birth rate of population 2 (b_2). The area between the curves is the region of co-existence in mean-field approximation (dashed lines) and in pair approximation (solid lines). Dots correspond to individual IPS simulations. Populations either co-existed (large dots) or one of them excluded the other (small dots). Other parameter values: $b_1 = 5$, $d_1 = d_2 = 1$, $k = 5$.

that range. The range of co-existence narrowed with increasing inter-population resource competition coefficient $A(\leq 1)$. It shrunk to the point $b_2 = b_1$ for $A = 1$.

Recall that the intra-population resource competition parameter was set to 1. Therefore, $A = 1$ represented no distinction between the competitive effect of different populations. The simulation results were in line with the expectation of co-existence with decreased inter-specific competition.

Figure 3 illustrates that the region of co-existence is the broadest in the case of the mean-field approximation. It is significantly narrower for the pair-approximation. In the IPS version of the model, the range of parameters permitting co-existence is even narrower than in the approximations of the model. (After noting this situation, we conducted systematic investigations for the spatial model only inside the region of co-existence of the pair-approximation.)

CO-EXISTENCE AND EVOLUTION ALONG A STRATEGY CONTINUUM

Continuous strategy scale

To study phenotypic evolution of competitive contact processes, we introduced a continuous strategy variable $x \in [-1,1]$. We assume the birth rate to be a Gaussian function of the strategy as

$$b(x) = b_0 e^{-\frac{x^2}{2\omega^2}} \qquad (8)$$

where b_0 is the maximal birth rate corresponding to the optimal phenotype $x^* = 0$. The standard deviation ω characterizes the width of this optimum. Natural and competitive mortality rates (d and k, respectively) are independent of the strategy. The inter-population resource competitive coefficient $A(x, y)$ is a Gaussian function of the strategy difference

$$A(x, y) = e^{-\frac{(x-y)^2}{2\sigma^2}} \tag{9}$$

It is maximal between individuals of identical phenotypes and decreases with increasing difference in phenotype. The width of this competition function is characterized by its standard deviation σ.

Co-existence pattern

Figure 4 presents the outcome of competition between two species in the spatial model (IPS), and in its approximations (mean-field and pair) at different levels of competitive mortality k. We verified the robustness of our results by performing simulations of different initial conditions. The results were identical in the case of an equal initial distribution of the populations, and an initial density ratio of $9:1$.

The qualitative behaviour of the system is similar for the spatial model and for its two approximations. In particular, the outcome of competition between two populations of similar strategies is very generic. It is always the population with the strategy nearer to the value $x^* = 0$ that wins in such a contest. This phenomenon implies that strategy 0 (corresponding to maximal birth rate) is an attractor in an evolutionary sense. Were the
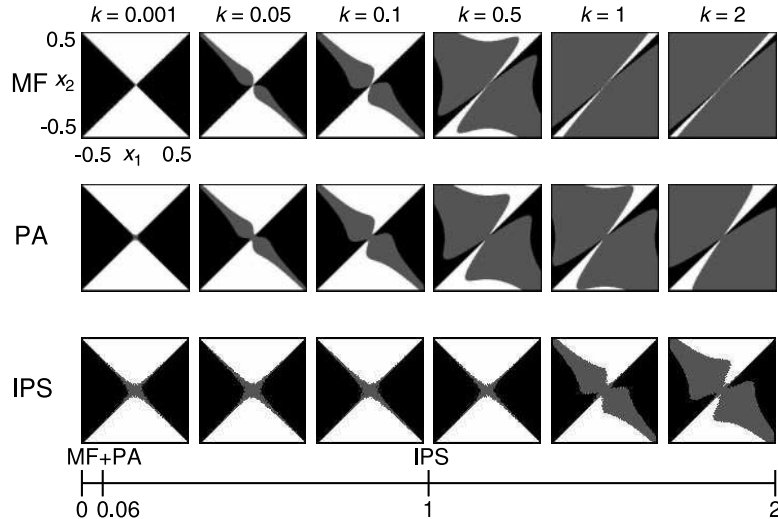

Fig. 4. Pairwise competition with increasing rates of competitive mortality k. The three rows show the results for mean-field approximation (MF), pair approximation (PA) and IPS. The three possible outcomes are: victory by population 1 (white), victory by population 2 (black) and co-existence (grey). The scale at the bottom shows the critical competitive mortality rates k_c obtained from IPS, MF and PA. Other parameter values: $b_0 = 10$, $d_1 = d_2 = 1$, $\sigma = 0.1$, $\omega = 0.5$.

strategy an evolving parameter, as we will show later, its evolution would converge to the strategy 0. Following the terminology of Geritz *et al.* (1997), we will refer to strategy 0 as a convergent stable strategy.

Another generic feature is that the region of co-existence widens considerably as the competitive mortality rate k increases. For low values of k, the singular strategy is an ESS, as no other strategy can survive against it. However, above a critical value k_c, the singular strategy loses its evolutionary stability, while it remains convergence stable. As we increase k even further, more and more strategies are able to co-exist.

While the results of the IPS model and its approximations resemble each other, there are significant differences. In line with our findings in the previous section, the area of co-existence is much wider for the mean-field approximation than for the IPS simulation. The behaviour of the pair approximation is in between the other two model versions. The critical value of the parameter k, above which the singular strategy loses its evolutionary stability, is very similar for the mean-field and for the pair approximation: $k_c \approx 0.06$. In contrast, the value for the IPS model is $k_c \approx 1.0$.

Comparison of the IPS and the mean-field approximation demonstrates that limited dispersal reduces the range of co-existence. With limited dispersal, we need a much higher rate of competitive mortality for the co-existence of two given strategies. While pair approximation captures this effect partially, it utterly fails to predict the correct value of the threshold k_c of the spatial model.

The mean-field case

The competition plots can be obtained analytically for the mean-field approximation using invasion analysis. We assume that the mutant is rare, as compared to the resident population. Then, the growth rate of the mutant strategy y against the resident strategy x is

$$r_x(y) = b(y) - d - [b(y) + A(x, y)k]\frac{b(x) - d}{b(x) + k} \tag{10}$$

Note that the selection gradient

$$D(x) = \frac{\partial r_x(y)}{\partial y}\bigg|_{y=x} \tag{11}$$

always points towards the central strategy – that is, $D(x) > 0$ for $x < 0$ and $D(x) < 0$ for $x > 0$. Therefore, $x = 0$ is always a convergent stable singular strategy, and this is the only singular strategy of the model (cf. Geritz *et al.*, 1997, 1998).

The singular point is an ESS if, and only if, the growth rate has a maximum there (i.e. if the second derivative of the growth rate is negative):

$$\frac{\partial^2 r_x(y)}{\partial y^2} = b''(y) - [b''(y) + \partial_{11}A(y, x)k]\frac{b_x - d}{b_x + k} < 0 \tag{12}$$

With the parameter values of Fig. 4, this condition leads to the critical value $k_c = 0.0465116$. Note the discrepancy with the simulation result $k_c = 0.06$. This is due to the fact that in the simulations, victory by a species was defined by the approximate condition that $c_j < 0.01c_i$.

Simulation of evolution

In this section, we simulate the process of evolution explicitly via small mutation steps. Simulations start with a population of individuals of the same strategy value x_0 filling up the whole lattice. Mutations may occur with probability μ at each birth event. The strategy of the mutant individual is chosen randomly in the ε neighbourhood of the strategy of its ancestor. We observe the process of evolution until $t = 10{,}000$. Figure 5 presents three evolutionary trajectories corresponding to different competitive mortality rates.

In line with the convergence stability of the central strategy predicted earlier, there is directional selection towards this strategy for any value of k. If the central strategy is an ESS (i.e. $k < k_c$), it is the final rest point of evolution. In contrast, if the central strategy is evolutionarily unstable (i.e. $k > k_c$), it is an evolutionary branching point. In line with the predictions of the theory of Geritz *et al.* (1997, 1998), evolutionary branching occurs at any convergent stable but non-ESS singular strategy. After converging to this strategy, disruptive selection splits the population. Then the emerging sub-populations evolve away from each other. This prediction is clearly supported by our simulation result in Fig. 5.

This is the first published documentation of evolutionary branching in the IPS context.

DISCUSSION

Now we are able to answer the questions we posed in the Introduction:

1. Higher birth rate does not compensate for a lower intrinsic lifetime reproductive ratio, and there is no co-existence based on a competition–colonization trade-off in our model.
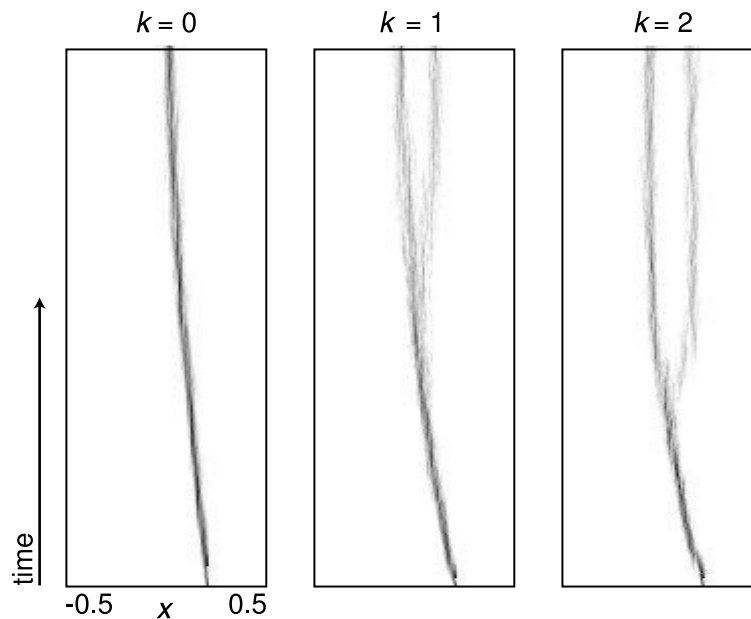

Fig. 5. Evolutionary trajectories in IPS simulations with increasing competitive mortality rates k. Density values are represented by different shades of black (dark represents high density). Parameter values: $d = 1$, $b_0 = 10$, $x_0 = 0.2$, $\sigma = 0.1$, $\omega = 0.5$, $\mu = 0.004$, $\varepsilon = 0.01$.

2. Limited dispersal significantly decreases the possibility of co-existence induced by Lotka-Volterra competition.
3. Evolutionary branching is possible with limited dispersal, although in a reduced parameter range.

For the interpretation of our results, it is necessary to distinguish between local and global competition. While the properties of local competition are set by the stochastic transition rules of the IPS, competition on the global scale is an emergent property of a spatial model. Building the connection between the local and global levels is the main goal of spatial ecological modelling.

The model of Neuhauser (1992), which employs only site competition, is the minimal model of competition on a lattice. In this case, the result of local competition translates directly to the global outcome. The locally superior population wins. As there is no possibility for reduced competition at the local level, no co-existence is possible globally, either. We investigated two different modifications of this model to determine whether they alter the trivial situation. While the original model was susceptible to analytical study, we resorted to numerical simulations. In line with the conjecture of Neuhauser (1992), we found no new phenomenon introducing differences in birth rate with an equal intrinsic lifetime reproductive ratio between the populations. On the other hand, introducing resource competition on the local level resulted in the emergence of co-existence and evolutionary branching.

The first modification was motivated by the concept of ruderal strategies (Krebs, 2001, p. 201) and competition–colonization trade-offs (Bolker and Pacala, 1999; Bolker *et al.*, 2003). Bolker and Pacala (1999) studied the competition of spatial strategies differing in their dispersal distance in a community of perennial, clonal plants in a continuous, homogeneous individual-based point-process model. According to their results, a competitively inferior, globally dispersing invader can successfully compete with a competitively superior, locally dispersing resident, which matches the classical competition–colonization trade-off. As all processes disperse locally in our model, this scenario is not possible. In our model, the analogon of which is also investigated in Bolker and Pacala (1999), the population with the higher intrinsic lifetime reproductive ratio wins irrespective of its birth rate. At a fixed intrinsic lifetime reproductive ratio, the birth rate b cannot be increased without increasing the death rate d also. Thus, increased birth rate cannot counter low competitiveness.

Note that the irrelevance of birth rate increase is obvious in the mean-field approximation. In this context, the populations affect each other only through the fraction $\rho = 1 - \Sigma n_j$ of empty sites. A population grows if its b/d ratio is larger than $1/\rho$. The population with the highest intrinsic lifetime reproductive ratio has the smallest equilibrium ρ value, so it can oust any other strategy (cf. Metz *et al.*, 1996).

Note that the general relation between the lifetime reproductive ratio and the growth rate depends strongly on the way density dependence is implemented in the model. They are equivalent when they are evaluated at the equilibrium density. However, in general, neither the comparison of the intrinsic growth rates nor the comparison of the intrinsic lifetime reproductive ratios (i.e. the quantities evaluated at zero density) predict the outcome of selection between two populations (Pásztor *et al.*, 1996). It is a peculiarity of the current model that the intrinsic lifetime reproductive ratio is a good predictor.

Our second modification of the model of Neuhauser (1992) was reduced competition between different populations. We introduced a new source of local mortality, described by

a Lotka-Volterra phenomenology and interpreted as resource competition. In this case, the mean-field approximation already predicts co-existence. Therefore, it is not surprising to see co-existence in the spatial simulations as well. However, the parameter range enabling co-existence was considerably narrower for the IPS model than for the mean-field approximation.

Earlier results suggested that spatial structure reduces the possibility of co-existence instead of enhancing it. Neuhauser and Pacala (1999) considered a slightly different but similar IPS version of the classical Lotka-Volterra competition model with interspecific competition. They assumed a high-density limit, when fecundity is much greater than mortality, and there are no empty spaces in the habitat. Mortality was density dependent, and replacement after death was proportional to the respective weighted local frequencies of the two species. They proved by analytical means that local competitive interactions and the discreteness of the individuals result in an increase of the parameter region leading to the extinction of one of the competitors, thus decreasing the region of co-existence. The competing species spatially segregate in the same parameter region. They could not prove, but conjectured, that the phenomenon of founder control is completely missing in the spatial model due to the discreteness of the neighbourhood. Bolker *et al.* (2003) summarized a vast body of data obtained from IPS models, moment equations for spatial-point processes, and metapopulation or patch models. They found in the broad range of these models that if interspecific competition is nearly as strong as intraspecific competition, the combination of local competition and the discreteness of the individuals reduces co-existence.

The case of increased inter-population competition also hampers co-existence (Durrett and Levin, 1997; Iwasa *et al.*, 1998). Increased inter-population competition leads to a disadvantage of the locally rare type. In the context of mean-field approximation, this results in dependency on the inital conditions – that is, the initially rare type will disappear. In the spatial case, rare disadvantage leads to an almost complete spatial segregation of the different types into distinct spatial domains. The movement of the domain wall eventuates in the unavoidable extinction of one of the two types. That is, co-existence is not possible either in the mean-field approximation or in the IPS model with increased inter-population competition. Gandhi *et al.* (1998) provides a similar case of complete spatial segregation. However, in this model, the two populations were equivalent and if their initial densities were equal, the loss of one of the populations required domain wall diffusion. While competitive exclusion was also inevitable here, it became extremely slow in this structurally unstable case.

In contrast to these investigations, our model exhibits an advantage of the locally rare type, since it is advantageous to live in the neighbourhood of a different individual. Consequently, there is a tendency for intra-population segregation, and thus mixing of the populations. On the other hand, local reproduction and a limited capability for spreading creates continuous intra-population aggregation. As a result of these conflicting tendencies, the populations segregate partially. The partial spatial segregation of the populations, demonstrated in Fig. 6, might suggest reduced inter-population competition favouring co-existence in the spatial model in contrast with the non-spatial mean-field approximation.

Generically, reduced inter-population competition leads to co-existence, because it implements a regulating feedback that stabilizes the co-existence. If inter-population competition is weaker than intra-population competition, then an increase (decrease) in size of either population results in a decrease (increase) in the growth rate of the same population. In our model, the partial spatial segregation of the populations weakens this stabilizing effect. The partial segregation does not exclude, but reduces the possibility of,
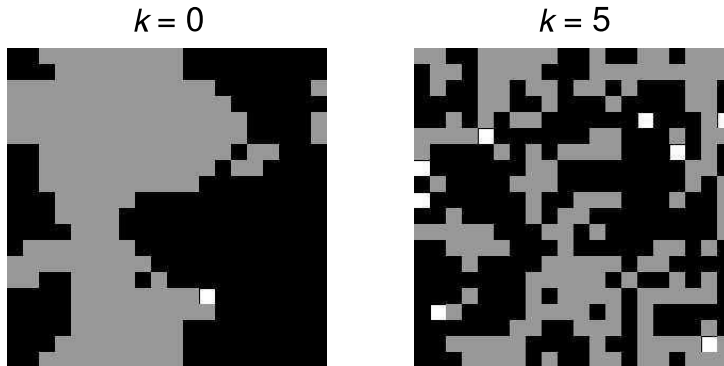
$$k = 0 \qquad\qquad k = 5$$

Fig. 6. Snapshots (20×20) of the lattice after relaxation at different competitive mortality rates k. Cells can be empty (white) or occupied by individuals of population 1 (black) or population 2 (grey). Parameter values: $b_0 = 200$, $d_1 = d_2 = 1$, $x_1 = 0.1$, $x_2 = -0.1$.

co-existence, similar to the results of Neuhauser and Pacala (1999) and Bolker *et al.* (2003). According to our results, although evolutionary branching is possible, the reduced possibility of co-existence restricts the possibility of evolutionary branching. (We are preparing papers on the relation between population regulation, generic co-existence and limiting similarity.)

Note that the reduced co-existence due to dispersal limitation contradicts the intuitive picture, that the deceleration of competitive exclusion due to limited dispersal would enhance diversity (Huston, 1979).

Generally, the pair approximation exhibits an intermediate behaviour between IPS and mean-field approximation. In the pair approximation, the non-random distribution of the populations relative to each other is measured by pair frequencies. However, pair approximation neglects the higher-order correlations involving more than two individuals. Accordingly, pair approximation provides a co-existence pattern intermediate between those of IPS and the mean-field approximation. The pair approximation provides a good qualitative prediction with respect to the decreased range of co-existence, as it already takes into account segregation. Nevertheless, we stress that the quantitative prediction of the pair approximation is very poor. In particular, it fails completely to predict the difference between the IPS and the mean-field approximation with respect to the branching threshold. This is partly because this difference is connected to segregation and clustering, which create large-scale structures pair approximation is unable to take into account.

The applicability of pair approximation is well accepted for a single population. It predicts the equilibrium density quite well away from the extinction threshold. However, the extinction itself corresponds to a 'second-order phase transition' with large fluctuations and long correlations (Marro and Dickman, 1999; Hinrichsen, 2000; B. Oborny, G. Meszéna and G. Szabó, in prep.). Emergence of the large-scale structure destroys the qualitative predictions of the pair approximation. For instance, the extinction threshold for a single contact process is $\lambda_c = 1$ for the mean-field approximation, $\lambda_c = 4/3$ for the pair approximation and $\lambda_c = 1.6488$ for the IPS with $d = 2$. A similar failure of the pair approximation to predict co-existence (= extinction) boundaries is not surprising. The even worse performance of pair approximation in an adaptive dynamical context might be related to the fact that the fitness

differences are small at a higher order in the vicinity of a singular point. This is especially so at parameter values corresponding to the transition between ESS and non-ESS.

Note that several studies of the evolutionary and ecological dynamics on a lattice have used pair approximation as a primary tool (Altmann, 1995; Keeling, 1997; Boots and Sasaki, 1999) and used numerical experiments mainly for illustrative purposes. The poor performance of the pair approximation in our simple model caution us not to take such results for granted, without verifying them first using numerical methods.

While spatiality and limited dispersal decrease the possibility of co-existence in a homogeneous space, spatial *inhomogeneity* enhances co-existence. Inhomogeneity implements a kind of niche segregation with a regulating feedback, stabilizing co-existence and enabling evolutionary branching (Czárán, 1989; Meszéna *et al.*, 1997; Day, 2000; Cheptou and Mathias, 2001; Mathias *et al.*, 2001; Mizera and Meszéna, 2003).

The present study successfully applied the adaptive dynamical methodology in an IPS model and is the first demonstration of evolutionary branching in such a context. All previous models of adaptive dynamics in a spatial context relied on the separation of time-scales of spreading and evolution. This was in accordance with the general concept of invasion fitness (Metz *et al.*, 1992). Several models have investigated adaptive evolution in the context of numerous patches with migration (Brown and Pavlovic, 1992; Meszéna *et al.*, 1997; Kisdi and Geritz, 1999; Day, 2000; Geritz and Kisdi, 2000; Mathias *et al.*, 2001; Kisdi, 2002; Mathias and Kisdi, 2002). In such cases, time-scale separation is ensured by the fast spread of the mutants in comparison with their growth rate. Then, the spatial distribution of the mutant equilibrates while it is still rare in every patch. The fate of the mutant is determined by its overall growth rate after this equilibration. The situation is similar with a limited range of a continuous environmental gradient (Mizera and Meszéna, 2003; Doebeli and Dieckmann, 2003).

In metapopulations, an infinite number of patches is considered. Since all patches can be reached on the same time-scale, spreading can still be fast enough for the above assumption to hold. While Gyllenberg and Metz (2001) and Metz and Gyllenberg (2001) introduced an effective method of calculating the mutant fitness in this context, Gyllenberg *et al.* (2002), Parvinen (2002) and Parvinen *et al.* (2003) presented applications. The dispersion models of Mathias *et al.* (2001) and Mathias and Kisdi (2002) adopt the same assumption.

For an infinite number of patches/sites with limited dispersal – that is, reproduction to neighbouring sites only – the time-scale of spreading is infinite. Then, the time-scale separation between the spread and the growth of the mutant population cannot be assumed. Ferriere and Le Galliard (2001) and Le Galliard *et al.* (2003) investigated adaptive dynamics on a random graph. In this case, the success of the pair approximation alleviates the lack of time-scale separation. As pair approximation performs extremely well on a random graph lattice, the finite time-scale of the relaxation of the pair frequencies substitutes for fast spatial relaxation.

As we have seen, pair approximation is far from exact on a square lattice. Moreover, it is known that even higher-order approximations fail to predict the behaviour of a contact process (Marro and Dickman, 1999). Consequently, we must conclude that the usual concept of invasion fitness of a rare mutant fails in the context of IPS models. Invasion is determined by the spatial spread of a locally abundant mutant. This is fundamentally different from the invasion of a rare mutant, which is spatially equilibrated already. Fortunately, the applicability of adaptive dynamical concepts and methodology depends only on the existence of *any* type of invasion criterion, which is smooth in the resident and mutant strategies.

Note that the essentially different nature of spatially infinite population models with limited dispersal manifests already in the dynamics of a single population (Marro and Dickman, 1999; Hinrichsen, 2000; Szabó *et al.*, 2002; B. Oborny *et al.*, in prep.). Metz *et al.* (2000) discuss the connection between spatial invasion and local growth rate for populations without an Allee effect.

Despite these substantial differences, our numerical study demonstrated that techniques of adaptive dynamics are applicable and useful for interacting particle systems. As a successful test, we presented the first evolutionary branching on a lattice. We created a minimal spatial model allowing for co-existence and evolutionary branching. Although, in accordance with earlier results, limited dispersal hampers co-existence and evolutionary branching, evolutionary branching is possible.

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REFERENCES

Abrams, P., Matsuda, H. and Harada, Y. 1993. Evolutionarily stable fitness maxima and unstable fitness minima in continuous trait values. *Evol. Ecol.*, **7**: 465–487.

Altmann, M. 1995. Susceptible-infected-removed epidemic models with dynamic partnerships. *J. Math. Biol.*, **33**: 661–675.

Axelrod, R. 1987. The evolution of strategies in the Iterated Prisoner's Dilemma. In *Genetic Algorithms and Simulated Annealing* (L. Davis, ed.), pp. 32–41. Los Altos, CA: Morgan Kaufmann.

Bolker, B. and Pacala, S. 1999. Spatial moment equations for plant competition: understanding spatial strategies and the advantages of short dispersal. *Am. Nat.*, **153**: 575–602.

Bolker, B., Pacala, S. and Neuhauser, C. 2003. Spatial dynamics in model plant communities: what do we really know? *Am. Nat.*, **162**: 135–148.

Boots, M. and Sasaki, A. 1999. 'Small worlds' and the evolution of virulence: infection occurs locally and at a distance. *Proc. R. Soc. Lond. B*, **266**: 1933–1938.

Boots, M., Hudson, P. and Sasaki, A. 2004. Large shifts in pathogen virulence relate to host population structure. *Science*, **303**: 842–844.

Brown, J. and Pavlovic, N. 1992. Evolution in heterogeneous environments: effects of migration on habitat specialization. *Evol. Ecol.*, **6**: 360–382.

Brown, J. and Vincent, T. 1987. Coevolution as an evolutionary game. *Evolution*, **41**: 66–79.

Cheptou, P. and Mathias, A. 2001. Can varying inbreeding depression select for intermediary selfing rates? *Am. Nat.*, **157**: 361–373.

Christiansen, F. 1988. Frequency dependence and competition. *Phil. Trans. R. Soc. Lond. B*, **319**: 587–600.

Christiansen, F. 1991. On conditions for evolutionary stability for a continuously varying character. *Am. Nat.*, **155**: 37–50.

Czárán, T. 1989. Coexistence of competing populations along an environmental gradient: a simulation study. *Coenoses*, **4**: 113–120.

Czárán, T. 1998. *Spatiotemporal Models of Population and Community Dynamics*. London: Chapman & Hall.

Day, T. 2000. Competition and the effect of spatial resource heterogeneity on evolutionary diversification. *Am. Nat.*, **155**: 790–803.

Dieckmann, U. and Doebeli, M. 1999. On the origin of species by sympatric speciation. *Nature*, **400**: 354–357.

Dieckmann, U. and Law, R. 1996. The dynamical theory of coevolution: a derivation from stochastic ecological processes. *J. Math. Biol.*, **34**: 579–612.

Dieckmann, U., Metz, J., Doebeli, M. and Tautz, D. 2004. *Adaptive Speciation*. Cambridge: Cambridge University Press.

Doebeli, M. and Dieckmann, U. 2003. Speciation along an environmental gradient. *Nature*, **421**: 259–264.

Durrett, R. and Levin, S. 1997. Allelopathy in spatially distributed populations. *J. Theor. Biol.*, **185**: 165–171.

Eshel, I. 1983. Evolutionary and continuous stability. *J. Theor. Biol.*, **103**: 99–111.

Ferriere, R. and Le Galliard, J. 2001. Invasion fitness and adaptive dynamics in spatial population models. In *Dispersal* (J. Clobert, A. Dhondt, E. Danchin and J. Nichols, eds.), pp. 57–79. Oxford: Oxford University Press.

Gandhi, A., Levin, S. and Orszag, S. 1998. Critical slowing down in time-to-extinction: an example of critical phenomena in ecology. *J. Theor. Biol.*, **192**: 363–376.

Geritz, S. and Kisdi, É. 2000. Adaptive dynamics in diploid, sexual populations and the evolution of reproductive isolation. *Proc. R. Soc. Lond. B*, **267**: 1671–1678.

Geritz, S., Metz, J., Kisdi, É. and Meszéna, G. 1997. The dynamics of adaptation and evolutionary branching. *Phys. Rev. Lett.*, **78**: 2024–2027.

Geritz, S., Kisdi, É., Meszéna, G. and Metz, J. 1998. Evolutionary singular strategies and the adaptive growth and branching of evolutionary trees. *Evol. Ecol.*, **12**: 35–57.

Gyllenberg, M. and Metz, J. 2001. On fitness in structured metapopulations. *J. Math. Biol.*, **43**: 545–560.

Gyllenberg, M., Parvinen, K. and Dieckmann, U. 2002. Evolutionary suicide and evolution of dispersal in structured metapopulations. *J. Math. Biol.*, **45**: 79–105.

Harada, Y. 1999. Short- vs. long-range disperser: the evolutionarily stable allocation in a lattice-structured habitat. *J. Theor. Biol.*, **201**: 171–187.

Harris, T. 1974. Contact interactions on a lattice. *Ann. Probability*, **2**: 969–988.

Hinrichsen, H. 2000. Non-equilibrium critical phenomena and phase transition into absorbing states. *Adv. Physics*, **49**: 815–958.

Huston, M. 1979. A general hypothesis of species diversity. *Am. Nat.*, **113**: 81–101.

Iwasa, Y., Nakamaru, M. and Levin, S. 1998. Allelopathy of bacteria in a lattice population: competition between colicin-sensitive and colicin-producing strains. *Evol. Ecol.*, **12**: 785–802.

Keeling, M. 1997. Modelling the persistence of measles. *Trends Microbiol.*, **5**: 513–518.

Kisdi, É. 2002. Dispersal: risk spreading versus local adaptation. *Am. Nat.*, **159**: 579–596.

Kisdi, É. and Geritz, S. 1999. Adaptive dynamics in allele space: evolution of genetic polymorphism by small mutations in a heterogeneous environment. *Evolution*, **53**: 993–1008.

Krebs, C.J. 2001. *Ecology*, 5th edn. San Francisco, CA: Benjamin Cummings.

Law, R., Murrell, D. and Dieckmann, U. 2003. Population growth in space and time: spatial logistic equations. *Ecology*, **84**: 252–262.

Le Galliard, J., Ferriere, R. and Dieckmann, U. 2003. The adaptive dynamics of altruism in spatially heterogeneous populations. *Evolution*, **57**: 1–17.

Mágori, K., Oborny, B., Dieckmann, U. and Meszéna, G. 2003. Cooperation and competition in heterogeneous environments: the evolution of resource sharing in clonal plants. *Evol. Ecol. Res.*, **5**: 787–817.

Marro, J. and Dickman, R. 1999. *Non-equilibrium Phase Transitions in Lattice Models*. Cambridge: Cambridge University Press.

Mathias, A. and Kisdi, É. 2002. Adaptive diversification of germination strategies. *Proc. R. Soc. Lond. B*, **269**: 151–156.

Mathias, A., Kisdi, É. and Olivieri, I. 2001. Divergent evolution of dispersal in a heterogeneous landscape. *Evolution*, **55**: 246–259.

Meszéna, G., Czibula, I. and Geritz, S. 1997. Adaptive dynamics in a 2-patch environment: a toy model for allopatric and parapatric speciation. *J. Biol. Syst.*, **5**: 265–284.

Metz, J. and Gyllenberg, M. 2001. How should we define fitness in structured metapopulation models? Including an application to the calculation of evolutionarily stable dispersal strategies. *Proc. R. Soc. Lond. B*, **268**: 499–508.

Metz, J., Nisbet, R. and Geritz, S. 1992. How should we define 'fitness' for general ecological scenarios? *Trends Ecol. Evol.*, **7**: 198–202

Metz, J., Geritz, S., Meszéna, G., Jacobs, F. and van Heerwaarden, J. 1996. Adaptive dynamics, a geometrical study of the consquences of nearly faithful reproduction. In *Stochastic and Spatial Structures of Dynamical Systems* (S.J. van Strien and S.M.V. Runel, eds.), pp. 183–231. Amsterdam: North-Holland.

Metz, J., Mollison, D. and van den Bosch, F. 2000. The dynamics of invasion waves. In *The Geometry of Ecological Interactions: Simplifying Spatial Complexity* (U. Dieckmann, R. Law and J.A.J. Metz, eds.), pp. 482–513. Cambridge: Cambridge University Press.

Mizera, F. and Meszéna, G. 2003. Spatial niche packing, character displacement and adaptive speciation along an environmental gradient. *Evol. Ecol. Res.*, **5**: 363–382.

Neuhauser, C. 1992. Ergodic theorems for the multitype contact process. *Prob. Theory. Rel. Fields*, **91**: 467–506.

Neuhauser, C. and Pacala, S. 1999. An explicitly spatial version of the Lotka-Volterra model with interspecific competition. *Ann. Appl. Prob.*, **9**: 1226–1259.

Nowak, M., May, R. and Sigmund, K. 1995. The arithmetics of mutual help. *Sci. Am.*, **272**: 76–81.

Parvinen, K. 2002. Evolutionary branching of dispersal strategies in structured metapopulations. *J. Math. Biol.*, **45**: 106–124.

Parvinen, K., Dieckmann, U., Gyllenberg, M. and Metz, J. 2003. Evolution of dispersal in meta-populations with local density dependence and demographic stochasticity. *J. Evol. Biol.*, **16**: 143–153.

Pásztor, E., Meszéna, G. and Kisdi, É. 1996. R_0 or r: a matter of taste? *J. Evol. Biol.*, **9**: 511–518.

Spitzer, F.L. 1974. Recurrent random walk of an infinite particle system. *Trans. AMS*, **198**: 191–199.

Szabó, G., Gergely, H. and Oborny, B. 2002. Generalized contact process on random environments. *Phys. Rev. E*, **65**(066111): 1–6.

Taylor, P. 1989. Evolutionary stability in one-parameter models under weak selection. *Theor. Pop. Biol.*, **36**: 125–143.

APPENDIX

We need rate values Φ and Ψ for all possible $ij \to i'j'$ transitions in order to calculate pair-density derivatives. These can be derived from the rules of cellular automaton in a straightforward way.

Pair transitions may occur due to within-pair events (i.e. which do not depend on sites outside the pair) and neighbourhood-dependent events. To calculate the overall rate of a within-pair event, we multiply the appropriate rate by the pair density. To evaluate the overall rate of a neighbourhood-dependent event, we need triplet densities T_{ijk}. These are defined as the probability of a certain configuration of three adjacent sites being in states i, j and k. Four triplet configurations (see below) appear in the calculations.

$$\mathbf{T}^I \qquad \mathbf{T}^{II} \qquad \mathbf{T}^{III} \qquad \mathbf{T}^{IV}$$
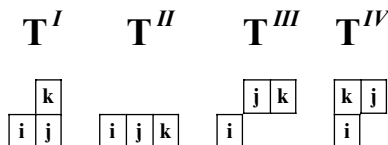
Configurations I and II are relevant for the dynamics of adjacent pair densities, while III and IV are used for the dynamics of diagonal pair densities.

Triplet densities are calculated from pair densities using the so-called symmetric power-2 moment closure suggested by Law *et al.* (2003). This closure uses the three pair configuration densities, and all three edges are weighted equally. Neighbour pair densities are denoted by p_{ij}^a or p_{ij}^d. Densities of pair configurations outside the Moore-neighbourhood are calculated by mean-field assumption:

$$T_{ijk}^{I} = \frac{1}{2}\left(\frac{p_{ij}^a p_{jk}^a}{p_j} + \frac{p_{jk}^a p_{ik}^d}{p_k} + \frac{p_{ij}^a p_{ik}^d}{p_i} - p_i p_j p_k \right)$$

$$T_{ijk}^{II} = \frac{1}{2}\left(\frac{P_{ij}^a p_{jk}^a}{p_j} + p_{jk}^a p_i + p_{ij}^a p_k - p_i p_j p_k \right)$$

$$T_{ijk}^{III} = \frac{1}{2}\left(\frac{p_{ij}^d p_{jk}^a}{p_j} + p_{jk}^a p_i + p_{ij}^d p_k - p_i p_j p_k \right)$$

$$T_{ijk}^{IV} = \frac{1}{2}\left(\frac{p_{ij}^d p_{jk}^a}{p_j} + \frac{p_{jk}^a p_{ik}^a}{p_k} + \frac{p_{ij}^d p_{ik}^a}{p_i} - p_i p_j p_k \right)$$

Having p_{ij} and T_{ijk}, one can calculate all Φ and Ψ values from event rates. Table A1 and Table A2 contain all Φ and Ψ values, respectively. As an example, consider the $11 \rightarrow 01$ transition. $\Phi_{11 \rightarrow 01}$ is a sum of four terms. The first term expresses decay probability due to natural mortality. The second term stands for competitive mortality due to intra-specific competition with site j. The third and fourth terms stand for intra-specific and inter-specific competitive mortality caused by other neighbouring sites.

Table A1. Transition rates for adjacent pairs. $i, j \in \{0,1,2\}$, denoting empty, occupied by species 1 and species 2 sites, respectively

$ij \rightarrow i'j'$	$\Phi_{ij \rightarrow i'j'}$
$00 \rightarrow 01$	$(2T^{I}_{001} + T^{II}_{001})\dfrac{b_1}{4}$
$00 \rightarrow 02$	$(2T^{I}_{002} + T^{II}_{002})\dfrac{b_2}{4}$
$00 \rightarrow 10$	$\Phi_{00 \rightarrow 01}$
$00 \rightarrow 20$	$\Phi_{00 \rightarrow 02}$
$01 \rightarrow 00$	$p^{a}_{01}d_1 + (2T^{I}_{011} + T^{II}_{011})k + (2T^{I}_{012} + T^{II}_{012})kA_{12}$
$01 \rightarrow 11$	$p^{a}_{01}\dfrac{b_1}{4} + (2T^{I}_{101} + T^{II}_{101})\dfrac{b_1}{4}$
$01 \rightarrow 21$	$(2T^{I}_{201} + T^{II}_{201})\dfrac{b_2}{4}$
$02 \rightarrow 00$	$p^{a}_{02}d_2 + (2T^{I}_{021} + T^{II}_{021})kA_{12} + (2T^{I}_{022} + T^{II}_{022})k$
$02 \rightarrow 12$	$(2T^{I}_{102} + T^{II}_{102})\dfrac{b_1}{4}$
$02 \rightarrow 22$	$p^{a}_{02}\dfrac{b_2}{4} + (2T^{I}_{202} + T^{II}_{202})\dfrac{b_2}{4}$
$10 \rightarrow 00$	$\Phi_{01 \rightarrow 00}$
$10 \rightarrow 11$	$\Phi_{01 \rightarrow 11}$
$10 \rightarrow 12$	$\Phi_{01 \rightarrow 21}$
$11 \rightarrow 01$	$p^{a}_{11}d_1 + p^{a}_{11}k + (2T^{I}_{111} + T^{II}_{111})k + (2T^{I}_{211} + T^{II}_{211})kA_{12}$
$11 \rightarrow 10$	$\Phi_{11 \rightarrow 01}$
$12 \rightarrow 10$	$p^{a}_{12}d_2 + p^{a}_{12}kA_{12} + (2T^{I}_{121} + T^{II}_{121})kA_{12} + (2T^{I}_{122} + T^{II}_{122})k$
$12 \rightarrow 02$	$p^{a}_{12}d_1 + p^{a}_{12}kA_{12} + (2T^{I}_{112} + T^{II}_{112})k + (2T^{I}_{122} + T^{II}_{122})kA_{12}$
$20 \rightarrow 00$	$\Phi_{02 \rightarrow 00}$
$20 \rightarrow 21$	$\Phi_{02 \rightarrow 12}$
$20 \rightarrow 22$	$\Phi_{02 \rightarrow 22}$
$21 \rightarrow 01$	$\Phi_{12 \rightarrow 10}$
$21 \rightarrow 02$	$\Phi_{12 \rightarrow 02}$
$22 \rightarrow 02$	$p^{a}_{22}d_2 + p^{a}_{22}k + (2T^{I}_{221} + T^{II}_{221})kA_{12} + (2T^{I}_{222} + T^{II}_{222})k$
$22 \rightarrow 20$	$\Phi_{22 \rightarrow 02}$

Table A2. Transition rates for diagonal pairs. $i, j \in \{0,1,2\}$, denoting empty, occupied by species 1 and species 2 sites, respectively

$ij \to i'j'$	$\Psi_{ij \to i'j'}$
$00 \to 01$	$(2T^{III}_{001} + T^{IV}_{001})\dfrac{b_1}{4}$
$00 \to 02$	$(2T^{III}_{002} + T^{IV}_{002})\dfrac{b_2}{4}$
$00 \to 10$	$\Psi_{00 \to 01}$
$00 \to 20$	$\Psi_{00 \to 02}$
$01 \to 00$	$p^d_{01}d_1 + (2T^{III}_{011} + 2T^{IV}_{011})k + (2T^{III}_{012} + 2T^{IV}_{012})kA_{12}$
$01 \to 11$	$(2T^{III}_{101} + 2T^{IV}_{101})\dfrac{b_1}{4}$
$01 \to 21$	$(2T^{III}_{201} + 2T^{IV}_{201})\dfrac{b_2}{4}$
$02 \to 00$	$p^d_{02}d_2 + (2T^{III}_{021} + 2T^{IV}_{021})kA_{12} + (2T^{III}_{022} + 2T^{IV}_{022})k$
$02 \to 12$	$(2T^{III}_{102} + 2T^{IV}_{102})\dfrac{b_1}{4}$
$02 \to 22$	$(2T^{III}_{202} + 2T^{IV}_{202})\dfrac{b_2}{4}$
$10 \to 00$	$\Psi_{01 \to 00}$
$10 \to 11$	$\Psi_{01 \to 11}$
$10 \to 12$	$\Psi_{01 \to 21}$
$11 \to 01$	$p^d_{11}d_1 + (2T^{III}_{111} + 2T^{IV}_{111})k + (2T^{III}_{211} + 2T^{IV}_{211})kA_{12}$
$11 \to 10$	$\Psi_{11 \to 01}$
$12 \to 10$	$p^d_{12}d_2 + (2T^{III}_{121} + 2T^{IV}_{121})kA_{12} + (2T^{III}_{122} + T^{IV}_{122})k$
$12 \to 02$	$p^d_{12}d_1 + (2T^{III}_{112} + 2T^{IV}_{112})k + (2T^{III}_{212} + 2T^{IV}_{212})kA_{12}$
$20 \to 00$	$\Psi_{02 \to 00}$
$20 \to 21$	$\Psi_{02 \to 12}$
$20 \to 22$	$\Psi_{02 \to 22}$
$21 \to 01$	$\Psi_{12 \to 10}$
$21 \to 02$	$\Psi_{12 \to 02}$
$22 \to 02$	$p^d_{22}d_2 + (2T^{III}_{122} + 2T^{IV}_{122})kA_{12} + (2T^{III}_{222} + 2T^{IV}_{222})k$
$22 \to 20$	$\Psi_{22 \to 02}$