

Stable trimorphic coexistence in a lattice model of spatial competition with two site types

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Abstract

I examine the effect of exogenous spatial heterogeneity on the coexistence of competing species using a simple model of non-hierarchical competition for site occupancy on a lattice. The sites on the lattice are divided into two types representing two different habitats or spatial resources. The model features no temporal variability, hierarchical competition, type-dependent interactions or other features traditionally known to support more competing species than there are resources. Nonetheless, stable coexistence of two habitat specialists and a generalist is observed in this model for a range of parameter values. In the spatially implicit mean field approximation of the model, such coexistence is shown to be impossible, demonstrating that it indeed arises from the explicit spatial structure.

Keywords:

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1. Introduction

The competitive exclusion principle (Gause, 1932; Tilman, 1982; Levin, 1970) states that at most n mutually competing species may coexist on n available resources. This principle was originally given as an empirical “rule of thumb” without rigorous justification, and while, for certain simple types of population models, it can in fact be proven mathematically, many counterexamples to it have also been noted both observationally and in mathematical models.

In modern mathematical ecology, the competitive exclusion principle has been generalized and placed on a rigorous footing by the concept of the essential dimensionality of the environment (Dieckmann and Metz, 2006; Metz et al., 2008), which gives a strict upper bound for the possible number of non-neutrally coexisting types in a population. However, it is not always easy to tell, just by looking at a model, what the dimensionality of the environment in it is. Thus, the question of under what conditions the traditional version of the competitive exclusion principle holds or fails continues to be of interest.

Well known counterexamples to the competitive exclusion principle include models with internally or externally generated temporal fluctuation (Hsu et al., 1978; Armstrong and McGehee, 1980), spatially implicit models of hierarchical site competition (Adler and Mosquera, 2000; Tilman, 1994), and models with direct type-dependent competition terms or with cooperative or other nonlinear interactions between individuals. All these models illustrate different ways in which diversity can be maintained in nature.

In this paper, I present a simple spatially explicit toy model of site occupancy competition which includes none of the features mentioned above, yet which allows the stable coexistence of more types than what the competitive exclusion principle would predict. As far as I know, this particular mechanism of coexistence has not been previously noted in the literature.

2. The model

The model I examine is based on the multitype lattice contact process (Harris, 1974; Neuhauser, 1992). In this model, adult individuals (of which there may be more than one strain, hence “multitype”) are sessile and live on a regular lattice, at most one individual per site. Adults produce clonal offspring which disperse randomly to the z nearest neighboring lattice sites; for all the examples in this paper, $z = 8$. Both death and reproduction

are assumed to be Poisson processes, with individuals dying at rate μ and producing offspring at rate ϕ per unit of time per individual. Offspring which land in an occupied site die, while those which land in a vacant site become new adults, identical to their parent.

The modification I make to the basic multitype contact process is to divide the lattice sites into two distinct types A and B. These may be interpreted as representing, in an abstract sense, two distinct habitats which are mostly similar and of equal value, but which differ in some particular aspect, such that individuals must adapt to one habitat or the other to make maximal use of it.

In the version of the model I consider here, I assume that the type of each site is given *a priori* and will not change over ecological timescales. Unless stated otherwise, I will also assume that both site types are present in equal numbers on the lattice. In the simplest case, the type of each site may be chosen independently at random, but I will also consider the case where the types of adjacent sites might be correlated. To first order, these correlations may be characterized by a parameter $k \in [0, 1]$ denoting the probability of two adjacent sites (i.e. sites between which offspring might disperse) having the same site type.

The type $E = \{A, B\}$ of a site affects the probability $p_{x,E}$ that an offspring of strain x landing in that site survives to grow into an adult. In particular, I shall consider the case of two specialist strains a and b, which can only live on their respective site types, competing against a generalist strain g which can survive equally well on either site type, but is less likely to do so than a specialist on its preferred site type. Specifically, I assume that $p_{a,A} = p_{b,B} = 1$ and $p_{a,B} = p_{b,A} = 0$, while $p_{g,A} = p_{g,B} = p_g$.

The parameter $p_g \in [0, 1]$ determines the penalty which the generalist must pay for its ability to exploit both site types, and is (together with k) crucial in determining the outcome of the model. If p_g is too low, the generalist strain will not be viable, or, even if viable on its own, may lose in competition to the specialists. Conversely, if p_g is close to 1, the specialist strains gain little or no advantage over the generalist from their specialization, while paying a considerable price in being able to live on only one site type, and can thus be expected to lose to the generalist.

Classical ecological theory predicts that these should be the only possible outcomes (except for specific, degenerate parameter values where neutral coexistence occurs). I will demonstrate below that this prediction indeed holds if the populations are assumed to be well mixed. However, I shall also

show that, in the full model with explicit spatial structure, a region of stable trimorphic coexistence does exist for intermediate values of p_g .

It's worth noting at this point that the mean field results derived in the next section do not actually depend on the choice of the survival functions $p_{x,E}$, nor even on the space of possible strains, provided that these are not degenerate (e.g. survival being independent of the strain value) nor specifically chosen to make competition exactly neutral. However, for the individual-based simulations, the survival functions do need to be explicitly defined.

3. Mean field approximation

The simplest way to approximate an individual-based spatial population model analytically is the *mean field approximation*. The standard form of the mean field approximation is obtained by assuming the states of the lattice sites at a given time to be independent and identically distributed random variables, and using this assumption and the local time evolution rule of the model to write a set of ordinary differential equations describing the time evolution of this distribution.

The mean field approximation specifies, for any spatial population model, a canonical self-consistent “well mixed” model corresponding to it. In particular, it can be derived mechanistically from the original model by assuming (for models of this general type) uniform global dispersal of offspring or (more generally) some external mechanism causing rapid, global and uniform mixing of the lattice sites.

A drawback of assuming complete well mixing is that approximations derived in this way will end up completely ignoring not only the finer spatial structure of the model but also the site type correlation parameter k . For models like the one I present in this paper, a somewhat better approximation can be obtained by assuming rapid mixing of individuals only among sites of each type, but keeping the site types themselves (and, in particular, the correlation parameter k) constant.

Let $n_{x,E}$ denote the fraction of sites of type E occupied by the strain x , and let $v_E = 1 - \sum_x n_{x,E}$ be the fraction of sites of type E that are vacant. In general, the time evolution of the occupancy densities can be written as

$$\frac{d}{dt}n_{x,E} = p_{x,E}v_E\phi q_{x,E} - \mu n_{x,E} \quad \forall x, E,$$

where $q_{x,E}$ is the probability that a randomly picked neighbor of a vacant site of type E is occupied by strain x . Using the mean field approximation

$q_{x,A} = kn_{x,A} + (1 - k)n_{x,B}$, $q_{x,B} = kn_{x,B} + (1 - k)n_{x,A}$, this can be rewritten as

$$\begin{aligned}\frac{d}{dt}n_{x,A} &= p_{x,A}v_A\phi(kn_{x,A} + (1 - k)n_{x,B}) - \mu n_{x,A}, \\ \frac{d}{dt}n_{x,B} &= p_{x,B}v_B\phi(kn_{x,B} + (1 - k)n_{x,A}) - \mu n_{x,B}\end{aligned}$$

for all strains x . Equivalently, these equations may be written in matrix form as $\frac{d}{dt}\bar{n}(x) = M_x\bar{n}(x)$, where $\bar{n}(x) = [n_{x,A}, n_{x,B}]^T$ and

$$M_x = \begin{bmatrix} \phi k p_{x,A} v_A - \mu & \phi(1 - k) p_{x,A} v_A \\ \phi(1 - k) p_{x,B} v_B & \phi k p_{x,B} v_B - \mu \end{bmatrix}.$$

If the mean field version of the model has a nontrivial interior equilibrium $\tilde{n}(x)$, this necessarily implies that

$$\frac{d}{dt}\tilde{n}(x) = M_x\tilde{n}(x) = \begin{bmatrix} 0 \\ 0 \end{bmatrix} \neq \tilde{n}(x),$$

and therefore that

$$\begin{aligned}|M_x| &= \begin{vmatrix} \phi k p_{x,A} v_A - \mu & \phi(1 - k) p_{x,A} v_A \\ \phi(1 - k) p_{x,B} v_B & \phi k p_{x,B} v_B - \mu \end{vmatrix} \\ &= 0,\end{aligned}$$

for all strains x present in the population. Writing out the determinant as

$$\begin{aligned}|M_x| &= \phi^2(2k - 1)p_{x,A}v_A p_{x,B}v_B \\ &\quad - \phi\mu k(p_{x,A}v_A + p_{x,B}v_B) + \mu^2 = 0,\end{aligned}$$

we obtain, for each x , an equation containing the same two unknown variables: v_A and v_B . As the coefficients $p_{x,A}$ and $p_{x,B}$ will, in general, be different for each strain x , one can easily see that, except for degenerate choices of the parameter values, no solution will exist for more than two strains.

Thus, stable coexistence of more than two strains is not generally possible in the mean field approximation of the model, as predicted by the principle of competitive exclusion. Yet, as I shall demonstrate below, this is not always the case in the full, spatially explicit model.

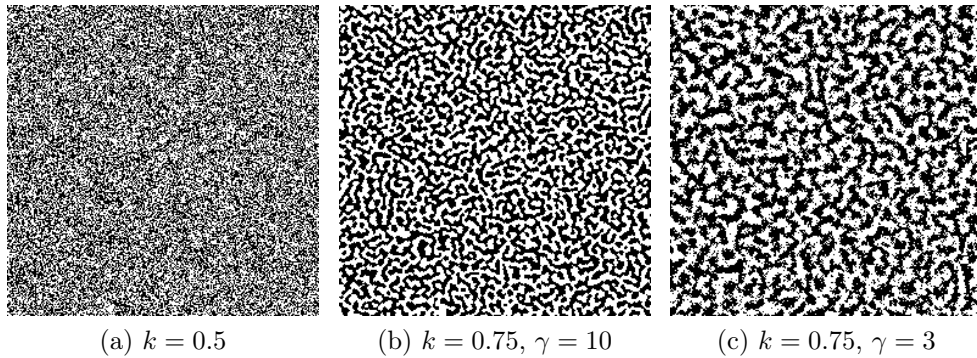


Figure 1: Examples of lattices with different site type correlation structures, used for the simulations shown in figure 3. White squares correspond to sites of type A, black squares to sites of type B. All lattices were generated from the same random initial state (which is nearly identical to lattice 1a; only a very small amount of annealing was needed to make k exactly 0.5) using the annealing method described in Appendix A. Lattices 1b and 1c have the same pairwise correlation number $k = 0.75$, but the different annealing parameters used to generate them lead to visibly different higher order correlations and to corresponding differences in population dynamics.

4. Simulation results

Studying the dynamics of the full, unapproximated model requires individual-based simulations. As such simulations tend to be computationally intensive, I have carried them out using custom, optimized programs written in the C programming language.¹ The simulation code used for this paper includes two variants of the basic contact process simulation algorithm, one using an occupancy list for low population densities, and another using a vacancy list for high densities, with the outer simulation loop periodically checking the population density and switching to the variant with the higher mean time step per iteration. For the figures shown below, I also took advantage of a coupling-based technique (Karonen, in prep.) to simulate the population dynamics for all values of $p_g \in [0, 1]$ efficiently in parallel.

All simulation runs used a square 256×256 lattice with $z = 8$ neighbors per site and with the edges wrapping around to the opposite sides. Site type distributions were generated using an annealing method as described in Appendix A. The “flea” pseudorandom number generator (Jenkins, 2007) was used to produce random numbers, although I also carried out tests using other random number generators to check that the results did not depend on such details.

Figure 2 shows the equilibrium densities of generalists and specialists observed in repeated individual-based simulations of the model. Contrary to the predictions from the mean field approximation, there is a non-degenerate region of the parameter space where the three strains can be seen to stably coexist. This region is further outlined in figure 3, which plots the observed region of coexistence against μ/ϕ and p_g . The region of stable coexistence can be seen to lie roughly along the line where the mean field approximation predicts neutral coexistence.

Although the regions of coexistence seen in figures 2 and 3 are fairly broad, it should be noted that in most parts of them the less common strain(s) are present only at very low densities. Only on a fairly narrow strip are all three strains present at roughly equal numbers. Over long timescales on a finite lattice, rare strain(s) are at risk of extinction due to stochastic fluctuations, a fact which is reflected in the rather ragged boundary of the coexistence region in the figure. Nonetheless, at least in the core of the coexistence region, where the specialist and generalist densities are of similar magnitude,

¹Source code available from author.

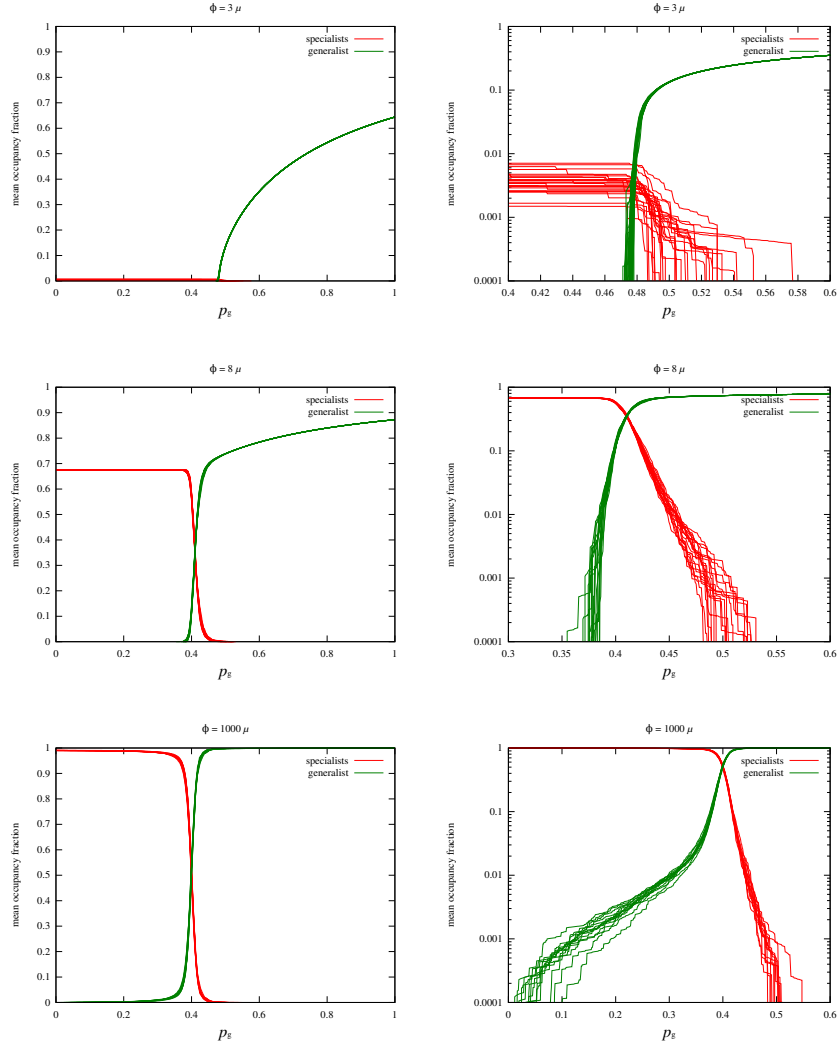


Figure 2: Plots of equilibrium specialist and generalist densities at $k = 0.5$ as functions of p_g for various values of ϕ . The graphs on the right have been plotted on a logarithmic scale and zoomed in to better show the coexistence region. Each line corresponds to one simulation run on a 256×256 lattice with reproduction to $z = 8$ nearest neighbors and wrapped edges. Each run was started with a different initial population and site type distribution. Populations were allowed to equilibrate for 1024μ time units, after which population densities were averaged over another 1024μ time units. The specialist occupancy fractions are summed over both specialist strains.

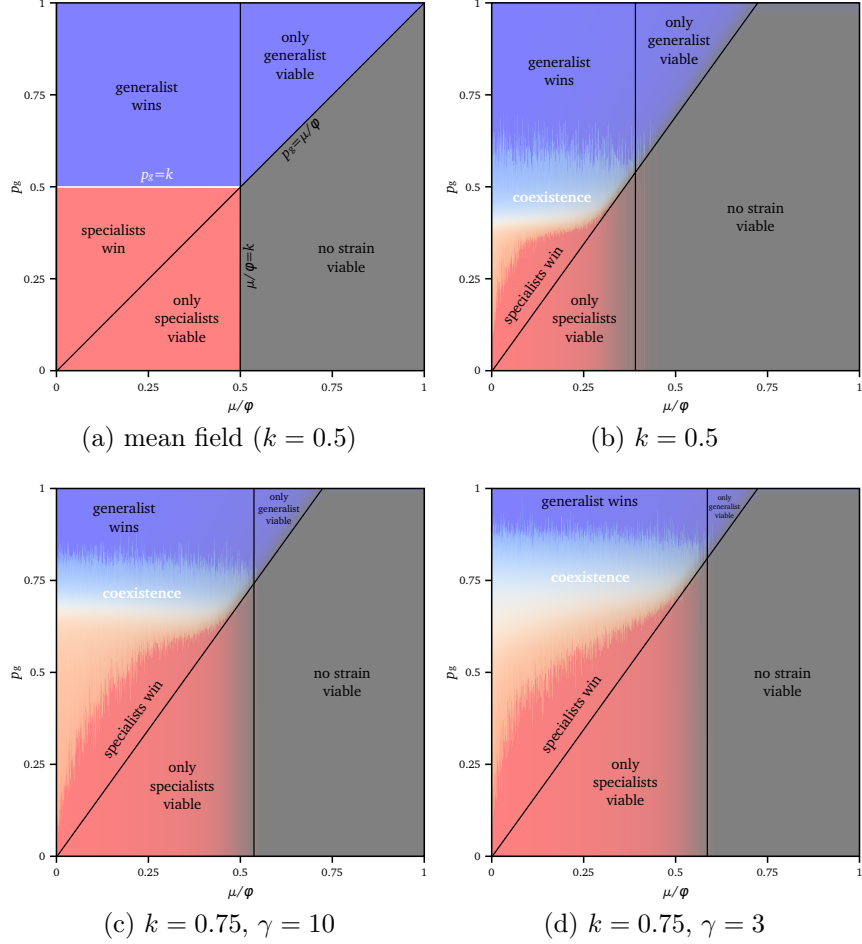


Figure 3: Outcomes of individual-based simulations as functions of μ/ϕ and p_g for various environments, with prediction from mean field approximation shown for comparison in 3a. Simulations were carried out on a 256×256 lattice with a fixed site type distribution as shown in figure 1. Populations were allowed to equilibrate for 256μ time units, after which population densities were averaged over another 256μ time units. Red and blue colors indicate generalist and specialist occupancy densities respectively, while the light area shows where all three strains survived. A non-linear mapping from occupancy density to color is used to make even small population densities visible. The lines show the approximate boundaries of the specialist and generalist viability regions.

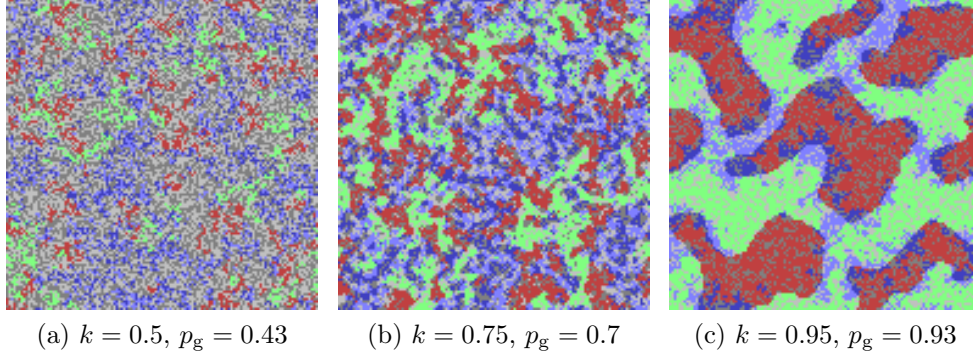


Figure 4: Snapshots of the population equilibrium after a few hundred mean lifetimes for various values of k , with p_g near the middle of the coexistence region. Snapshots were taken from simulations run on a 128×128 lattice with $z = 8$ and $\phi = 4\mu$. The red and green sites are occupied by a and b specialists respectively, the blue sites are occupied by generalists and the gray sites are vacant. For the blue and gray colors, darker shades indicate A type sites and lighter shades B type sites. These snapshots have been taken from interactive Java applets available at <http://vyznev.net/ca/coex2env/>. (The applets use an older, somewhat different landscape generation method than the one described in Appendix A, and also allow 1/1000 of all offspring to disperse globally.)

trimorphic coexistence can indeed persist over quite long timescales.

Figure 4 contain snapshots of simulations run on lattices with different site type patterns. It can be seen that, when sites of the same type are strongly clustered, large contiguous clusters are dominated by the respective specialist strain, while the generalist strain is able to persist in areas near cluster boundaries and in isolated minor clusters too small to support a stable specialist population.

On the other hand, when site types are uncorrelated, a different pattern is observed. Such lattices contain no large contiguous clusters that could be dominated by one specialist strain; instead, the two specialist strains tend to occur together in regions where the random distribution of site types happens to favor one or both of them. Through competition with the generalist strain, the two specialist strains indirectly support one another, even though there is no direct interaction between them.

5. Discussion

In this paper I've demonstrated, using a simple toy model of competitive population dynamics on a lattice, that spatial heterogeneity is one of the mechanisms by which the competitive exclusion principle can be violated. The fact that this cannot occur in well-mixed populations shows that population viscosity and explicit spatial structure are essential to this mechanism.

Had the model included more than two habitat types, temporal variation, hierarchical competition or nonlinear interactions between individuals, the coexistence of multiple strains would not have been at all surprising. Yet it has none of these, and can still support more than two strains in stable coexistence. All that allows such coexistence to persist in this model is the combination of environmental variation, persistent spatial structure and limited dispersal; eliminating any of these reduces the model to one capable of supporting no more strains than would be predicted by the competitive exclusion principle.

Real organisms do not usually live in a completely homogeneous environment, nor do most of them disperse uniformly over their entire habitat. It is obvious and commonly acknowledged that environmental variation can increase diversity, yet the fact that, when combined with limited dispersal, this increase can be more than linear seems to have attracted little attention. Yet the ubiquity of habitat edges and fragmented landscapes in nature suggests that it should be possible to find examples of this type of coexistence in nature, and indeed that such "edge effects" may contribute, at least in part, to the generation and maintenance of ecological diversity in many, if not most, ecosystems.

I find, however, that in many ways this work has raised more questions than it has answered. For example, an obvious question would be whether the model allows the stable coexistence of more than three strains. Another natural question is whether the coexistence of three or more strains in this type of model can also be evolutionarily stable, and further, whether it might arise from a mono- or dimorphic state through evolutionary branching ([Geritz et al., 1998](#); [Mágori et al., 2005](#)).

Based on limited simulation experiments, the answer to all of these questions appears to be "yes", although the conditions still need to be explored more thoroughly.

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Appendix A. Landscape generation

To simulate realizations of the model, it is necessary to assign types to the lattice sites in such a way as to yield a desired value for the correlation parameter k . To achieve this, I use an iterative annealing process as described below.

First, I assign a type to each site independently at random. To minimize variation in the frequencies of the site types on the (finite) lattice, I count the number of sites of each type on the lattice and flip the type of randomly chosen sites of the more numerous type until the numbers are equal.

I then count the total number N_P of pairs of adjacent sites having the same type and compare this to the desired number $kNz/2$, where N is the number of sites on the lattice and z the number of neighbors per site. If $N_P < kNz/2$, I then pick a random pair of adjacent sites with different types, and exchange their types with probability $p = a/(a+b)$, where $a = d^\gamma$, $b = (1-d)^\gamma$, d is the fraction of all the adjacent site pairs including one (but not both) of the two chosen sites which have different types, and the exponent γ controls the “temperature” of the process. I repeat this process until N_P reaches the desired value. Conversely, if $N_P > kNz/2$ initially, I apply the same process, except with $p = b/(a-b)$.

When $\gamma = 1$, the probability of exchanging the types of a chosen site pair is a linear function of d . This tends to produce fairly slow convergence and rough, jagged cluster boundaries. At high values of γ , p approaches a step function, producing faster initial convergence and smoother cluster boundaries, but also increasing the risk of the process getting stuck at a local maximum (or minimum) of N_P . In my experience, best convergence is usually obtained for γ in the range from around 2 to 10.

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