

Appendix A from J. Usinowicz, “Limited Dispersal Drives Clustering and Reduces Coexistence by the Storage Effect” (Am. Nat., vol. 186, no. 5, p. 000)

Derivation of Mean-Field, Local-Dispersal (LD), and Pairwise Approximations Mean-Field Approximation

The mean-field approximation uses the minimum amount of information to characterize the global state of each species. It assumes that every potential recruit can reach any open site on the lattice. Thus, the mean-field approximation ignores local interactions created by limited dispersal.

The global density of each species is represented by the variables $p_1(t)$ and $p_0(t)$, which count the proportion of sites occupied by the invader and resident species, respectively, so that $p_1(t) + p_0(t) = 1$. This means that $p_1(t)$ can be treated as the probability of finding a site that is occupied by species 1. The law of total probability then makes it possible to write $p_1(t + 1)$ as a function of two conditional probabilities: the probability that a resident site becomes an invader and the probability that an invader site becomes an invader, which I write as $p_1(t + 1) = p_0(t)P[0 \rightarrow 1] + p_1(t)P[1 \rightarrow 1]$, where the arrows indicate a conditional probability (Hiebeler 2000; Ives et al. 1998). Writing out expressions and simplifying leads to

$$p_1(t + 1) = \gamma_{\text{mf}}(t)\delta + p_1(t)(1 - \delta). \quad (\text{A1})$$

The quantity $\gamma_{\text{mf}}(t)$ represents the colonization probability for species 1 under global dispersal

$$\gamma_{\text{mf}}(t) = \frac{p_1(t)R_1(t)}{p_1(t)R_1(t) + (1 - p_1(t))R_0(t)}. \quad (\text{A2})$$

Although the notation here is slightly different, the mean-field approximation of the lottery model with limited dispersal is identical to the classic lottery model (Chesson and Warner 1981). The invasion growth rate for this approximation is given by equation (3) in the text.

LD Approximation

The simplest approximation that incorporates limited dispersal is an LD mean-field approximation (Hiebeler 1997). This approach calculates the probability that a site z_{xy} will be occupied by either species 1 or species 0 at the next time step based on the identity of z_{xy} and the average proportion of either species in the interaction neighborhood:

$$p_1(t + 1) = \gamma_{\text{ld}}(t)\delta + p_1(t)(1 - \delta), \quad (\text{A3})$$

where the colonization probability for species 1, $\gamma_{\text{ld}}(t)$, is given as

$$\gamma_{\text{ld}}(t) = \sum_{k=0}^{\Phi} \binom{\Phi}{k} p_1(t)^k p_0(t)^{(\Phi-k)} \frac{R_1(t)k}{R_1(t)k + R_0(t)(\Phi - k)}. \quad (\text{A4})$$

The LD approximation and the classic lottery model differ in their colonization probabilities, given by equations (A4) and (2), respectively. In the LD approximation, $\gamma_{\text{ld}}(t)$ is based on the average proportion of both species in N_z . It is a weighted average where possible values of $R_1(t)k/[R_1(t)k + R_0(t)(\Phi - k)]$ are each weighted by the likelihood of seeing exactly k invaders and $\Phi - k$ residents in N_z . Specifying this likelihood as $p_1(t)^k p_0(t)^{(\Phi-k)}$ assumes that the cooccurrence of invader and resident individuals is uncorrelated. This approach also implicitly assumes that $\gamma_{\text{ld}}(t)$ is the same regardless of location.

The derivation of equations follows Hiebeler (2000). In the language of cellular automata, each possible arrangement of $\Phi + z_{xy}$ represents a “preimage.” A preimage determines the value of z_{xy} on the next time-step. Using the definition of $p_1(t)$ as a probability of seeing an individual of species 1, $p_1(t + 1)$ can be found by summing over all possible

preimages that lead to a site being in state 1. If g represents an individual preimage and G is the set of all possible preimages, then

$$p_1(t+1) = \sum_{g \in G} P[g] \times P[g \rightarrow 1], \quad (\text{A5})$$

where $P[g]$ refers to the probability of seeing a given preimage, and $P[g \rightarrow 1]$ is the (conditional) probability that a preimage produces a 1. In this approximation, every site is assumed to be statistically independent, which means that the actual physical arrangement of each preimage does not matter. Then preimages can be grouped together on the basis of proportions of species 1 and species 0. Independence also means that the probability of finding a particular preimage is $P[g] = p_0(t)^{\#0(g)} p_1(t)^{\#1(g)}$ where $\#0(g)$, $\#1(g)$ refers to the number of sites in state 0, state 1 in that preimage. For example, when g is all preimages with three sites occupied by species 1 and the remaining six occupied by species 0, then $P[3, 6] = p_0(t)^3 p_1(t)^6$. Grouping terms and using $p_0(t) + p_1(t) = 1$ leads to equation (A3), and $\gamma_{ld}(t)$ represents a sum over relevant preimages. The first grouping of terms, $p_1(t)^k p_0(t)^{(\Phi+1-k)}$, corresponds to the probability of finding preimage $g = [k, (\Phi + 1 - k)]$. The second grouping of terms gives the probability that species 1 can capture the open site given the particular arrangement of the two species specified by $[k, (\Phi + 1 - k)]$ based on the species-specific recruitment rates at the given time step.

The invasion criterion can be derived for the LD approximation in the same way as for the classic lottery model (Chesson and Warner 1981), yielding

$$E \left[\log \left(\frac{p_1(t+1)}{p_1(t)} \right) \right] = E \left[\log \left(1 + \delta \left(\frac{R_1(t)}{R_0(t)} \frac{\Phi}{\Phi + (R_1(t)/R_0(t) - 1)} - 1 \right) \right) \right]. \quad (\text{A6})$$

A damping coefficient can then be defined, as in the text, as the terms that multiply $R_1(t)/R_0(t)$:

$$D_{LD} = \frac{\Phi}{\Phi + (R_1(t)/R_0(t) - 1)}. \quad (\text{A7})$$

Pair-Wise Approximation

The pair-wise approximation considers ‘‘block probabilities,’’ or the likelihood of seeing pairs of sites: specifically, the pairs $p_{00}(t)$, $p_{01}(t)$, $p_{11}(t)$. Although the blocks are joint probabilities, they can be treated as population densities in an equivalent way to $p_0(t)$ and $p_1(t)$. The formalism is developed more extensively in other sources; see Gutowitz et al. (1987) and Hiebeler (2000), for example, for discussions of block probabilities in the context of cellular automata and Ives et al. (1998) for more general treatment in terms of conditional probabilities. An important property of the block probabilities is that (Gutowitz et al. 1987; Hiebeler 2000):

$$p_1(t+1) = p_{11}(t+1) + p_{01}(t+1). \quad (\text{A8})$$

The global state of the invader population can be determined from the populations of all blocks with a 1 in the right position. Because $p_0(t) + p_1(t) = 1$, it is only necessary to track $p_1(t)$ directly.

The dynamics of $p_{01}(t+1)$ and $p_{11}(t+1)$ are determined by the rates at which other blocks transition into these states:

$$\begin{aligned} p_{01}(t+1) &= p_{00}(t)P[00 \rightarrow 01] + p_{01}(t)P[01 \rightarrow 01] + p_{10}(t)P[10 \rightarrow 01] + p_{11}(t)P[11 \rightarrow 01], \\ p_{11}(t+1) &= p_{00}(t)P[00 \rightarrow 11] + 2p_{01}(t)P[01 \rightarrow 11] + p_{11}(t)P[11 \rightarrow 11]. \end{aligned} \quad (\text{A9})$$

For $p_{01}(t+1)$, the first term gives the current population of $p_{00}(t)$, multiplied by the transition rate $P[00 \rightarrow 10]$. In the transition $P[00 \rightarrow 01]$, there are two things that must occur: the right site becomes occupied by the invader, species 1, and the left site stays occupied by the resident, species 0. There is only one way that a site can switch from a 0 to a 1: the resident species 0 must die, allowing the open site to be colonized by the invader. This happens with probability $\delta \gamma_{pw}(t)$, where $\gamma_{pw}(t)$ is the colonization probability in the pair-wise approximations. There are two ways that a site occupied by the

resident can stay in that state: the current resident can survive, or the current resident can die and be replaced by a new member of species 0. This probability is $(1 - \delta) + \delta[1 - \gamma_{pw}(t)]$. Putting these together gives

$$P[00 \rightarrow 01] = [(1 - \delta) + \delta(1 - \gamma_{pw}(t))][\delta\gamma_{pw}(t)]. \quad (\text{A10})$$

The remaining block transitions can be specified following the same logic to give

$$\begin{aligned} p_{01}(t+1) = & \\ & p_{00}(t)[(1 - \delta) + \delta(1 - \gamma_{pw}(t))][\delta\gamma_{pw}(t)] + \\ & p_{01}(t)[(1 - \delta) + \delta\gamma_{pw}(t)][(1 - \delta) + \delta(1 - \gamma_{pw}(t))] + \\ & p_{10}(t)[(1 - \delta)(1 - \gamma_{pw}(t))][(1 - \delta)\delta\gamma_{pw}(t)] + \\ & p_{11}(t)[(1 - \delta) + \delta(1 - \gamma_{pw}(t))]^2, \end{aligned} \quad (\text{A11})$$

$$\begin{aligned} p_{11}(t+1) = & \\ & p_{00}(t)[\delta\gamma_{pw}(t)]^2 + \\ & 2p_{01}(t)[\delta\gamma_{pw}(t)][(1 - \delta) + \delta\gamma_{pw}(t)] + \\ & p_{11}(t)[(1 - \delta) + \delta(1 - \gamma_{pw}(t))]^2. \end{aligned} \quad (\text{A12})$$

Combining these two equations and simplifying leads to

$$p_1(t+1) = p_{00}(t)[\delta\gamma_{pw}] + p_{01}(t)[(1 - \delta) + \delta\gamma_{pw}] + p_{10}(t)[\delta\gamma_{pw}] + p_{11}(t)[\delta(\gamma_{pw} - 1) + 1]. \quad (\text{A13})$$

The colonization probability, $\gamma_{pw}(t)$, incorporates the likelihood of finding a site with a given arrangement of neighbors and the likelihood that any neighborhood configuration leads to a site capture by either species. For each block, one neighbor is already known; at least one neighbor is of species 0. Because pairs of sites are assumed to be correlated, the conditional probability of finding a site among the remaining unknown neighbors that is occupied by species 1 is $P(01|0) = p_{01}(t)/p_0(t)$. The assumption that only neighbors are correlated leads to statistical independence between blocks. That is, if site z_a and z_b constitute a block, and z_c is a third site in the neighborhood of both sites, then the probability of finding $[z_a z_b]$ in a given state is independent of the probability of finding either $[z_a z_c]$ or $[z_b z_c]$ in any given state. This leads to the general form of $\gamma_{pw}(t)$,

$$\lambda_{pw} = \sum_{k=0}^{\Phi} \binom{\Phi}{k} \left(\frac{p_{01}(t)}{p_0(t)} \right)^k \left(1 - \frac{p_{01}(t)}{p_0(t)} \right)^{(\Phi-k)} \frac{R_1(t)k}{R_1(t)k + R_0(t)(\Phi + 1 - k)}. \quad (\text{A14})$$

The form of $\gamma_{pw}(t)$ is similar to $\gamma_{ld}(t)$ for the LD approximation. The primary difference is in the terms describing the likelihood of finding a particular neighborhood configuration. It is also worth noting that this form is not directly generalized to neighborhoods that include sites beyond nearest neighbors only. Larger neighborhoods require reformulating the conditional probabilities in $\gamma_{pw}(t)$ (Gutowitz et al. 1987; Hiebeler 2000).

The invasion growth rate for this model is approximately

$$E \left[\log \left(\frac{p_1(t+1)}{p_1(t)} \right) \right] = E \left[\log \left(1 + \delta \left(\frac{R_1(t)}{R_0(t)\Phi + [(R_1(t)/R_0(t)) - 2]} - 1 \right) \right) \right]. \quad (\text{A15})$$

This derivation is based on the observations that, during invasion, the probability of seeing anything other than a 00 pair approaches zero and that, due to the independent likelihood of invasion occurring at any site, conditional probabilities become independent.

A damping coefficient D_{PW} can be defined for equation (A15) as well:

$$D_{PW} = \frac{(\Phi - 1)}{\Phi + [(R_1(t)/R_0(t)) - 2]}. \quad (\text{A16})$$

Approximation Performance

Neither the LD nor pairwise approximations perform well against actual simulations, although both are closer to matching invasion growth rates than the mean-field model. This was true regardless of parameter values. Figures A1A and A1B demonstrate this result for the specific case when $\delta = 0.9$, $\bar{R}_1\theta = 1$, $\bar{R}_0 = 1.01$, $\sigma_0 = \sigma_1 = 1$, $\rho = 0$, $\beta = 10^{-4}$, and $L = 256$. In figure A1A, the average invasion growth rate was 0.0092 ± 0.0011 (mean \pm SD) for the limited-dispersal simulation model calculated from 3,000 runs. The invasion growth rate was 0.0676 for the lottery model. The LD and pairwise approximations give invasion rates of 0.0312 and 0.0292, respectively. The low-density growth rates for the nucleation approximations were all closer. Avrami's law slightly underpredicted at 0.0088, and the difference approximation slightly overpredicted at 0.0108. This pattern is repeated when considering the strength of the storage effect, shown as the bounds on coexistence as a function of fitness differences. Each of the spatial approximations is closer to the limited-dispersal model than the classic lottery model, but the nucleation approximations give the best predictions; Avrami's law and the difference approximation gave indistinguishable results.

Literature Cited Only in Appendix A

Gutowitz, Howard A., Jonathan D. Victor, and Bruce W. Knight. 1987. Local structure theory for cellular automata. *Physica D: Non-linear Phenomena* 28:18–48.

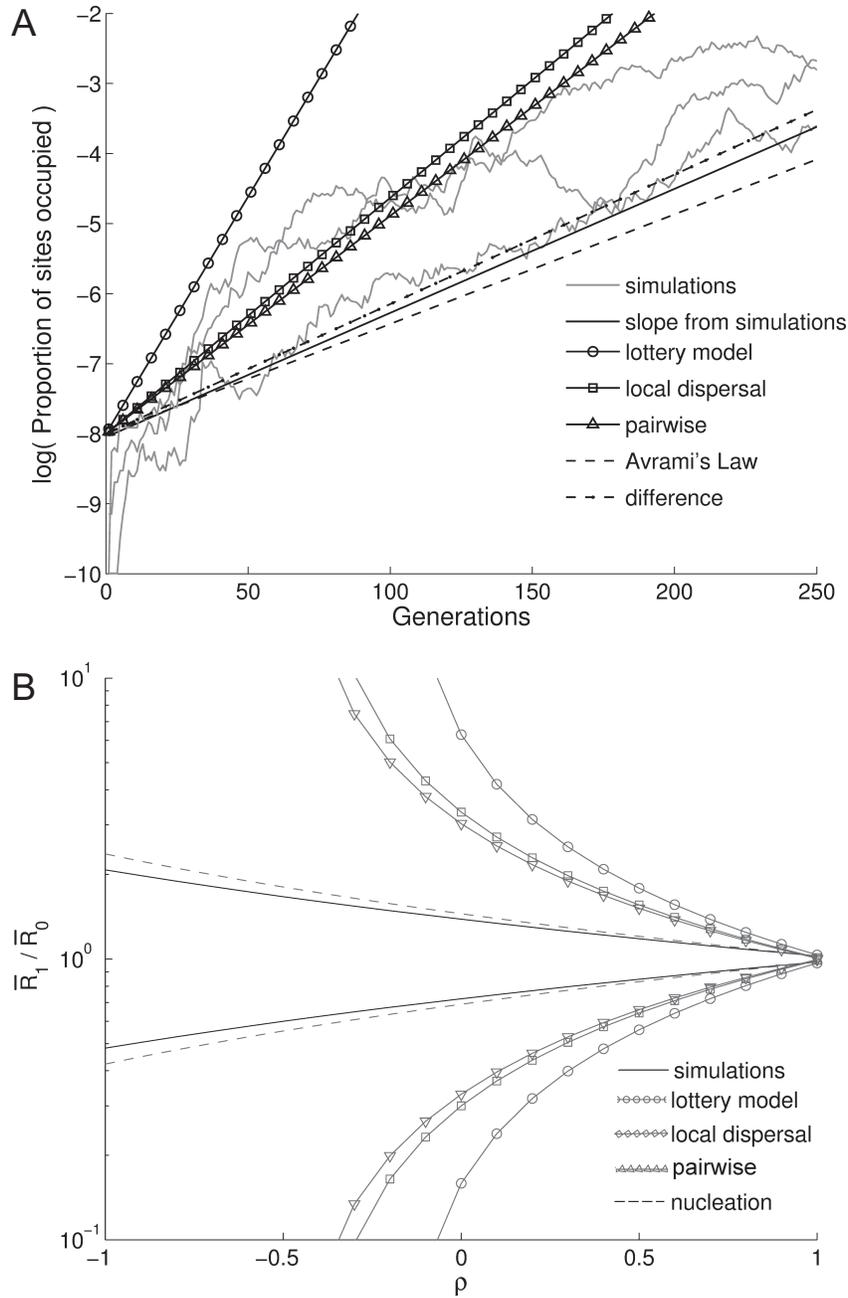


Figure A1: Invasion growth rates (A) and coexistence bounds (B) as a function of the fitness difference \bar{R}_1/\bar{R}_0 and interspecific correlation in reproduction rates ρ . A, Three example runs of the simulation are plotted against an average log-linear slope fit from 3,000 runs (\pm SD), giving $0.0092 \pm .0011$. The invasion growth rate predicted by the classic lottery model (mean-field approximation) is much larger (0.0676). The local dispersal (0.0312) and pairwise (0.0292) approximations also predict higher invasion rates. The nucleation approximations provide the best match to the actual invasion rate, with Avrami's law slightly underpredicting (0.0088) and the difference approximation slightly overpredicting (.0108). B, Each pair of curves gives the upper and lower bounds on \bar{R}_1/\bar{R}_0 that permit coexistence. The distance between upper and lower bounds measures the total strength of the storage effect as a function of ρ and other key parameters of the model (δ , σ_0^2 , σ_1^2). Coexistence is reduced in the limited-dispersal model, relative to the classic lottery model. See the text and figure 5 for additional interpretation. The local dispersal and pair-wise approximations to the limited-dispersal model incorrectly give a broader range of \bar{R}_1/\bar{R}_0 allowing coexistence. The nucleation approximations (Avrami's law) provide the most accurate prediction of species coexistence. The results of Avrami's law and the difference approximation were indistinguishable and are thus presented together. Parameter values are $\delta = 0.9$, $\bar{R}_1 = 1$, $\bar{R}_0 = 1.01$, $\sigma_0 = \sigma_1 = 1$, $\rho = 0$, $L = 256$, and $\beta = 10^{-4}$.