

ABSTRACT

HAMILTON, MATTHEW WILLIAMS. Local Dispersal and Coexistence in a Metacommunity Model with Trophic Structure. (Under the direction of Dr. Kevin Gross.)

One of the major goals of ecology is to understand the mechanisms which promote species coexistence. Much progress has been made in recent years in understanding how spatial processes influence diversity. Here we present a pair of models designed to investigate the role of one spatial process, localized dispersal, in promoting regional species coexistence when trophic structure is present. The model community considered is a two-predator, two-prey assemblage with cyclic endstates. Through analysis and simulation, we show that increasing the range of species dispersal can inhibit regional species coexistence. This result is at odds with the conclusions of some previous studies which considered locality within a single trophic level, and suggests that the relationship between dispersal distance and regional coexistence may be more complicated than previously realized.

**LOCAL DISPERSAL AND COEXISTENCE IN A
METACOMMUNITY MODEL WITH TROPHIC STRUCTURE**

By

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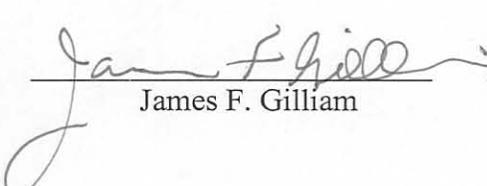
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BIOGRAPHY

Matthew was born in Johannesburg, South Africa in October 24, 1980 to Harvie and Anne Hamilton. His sister Sarah was born three years later on the same date. Matt graduated from the Leysin American School in Switzerland in 1999. He attended college at NC State, originally majoring in English before switching to physics and mathematics. Following graduation in 2004, Matt stayed on at NC State to study theoretical ecology under Dr. Kevin Gross.

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1. Introduction and Background

A fundamental goal of ecology is to understand the mechanisms that allow large numbers of species to coexist. Estimates of the number of species alive today on earth differ wildly, but most place the number somewhere between 10 and 100 million (May 1988, Erwin 1991, Bunge and Fitzpatrick 1993, Wilson 1999). Why so many? What processes act to restrict the number of species, and which act to augment it? The body of literature addressing these questions is enormous. Competition for limited resources, both within and between species, is thought to play a role in limiting the number of species. The principle of competitive exclusion, restated and developed repeatedly since the 1930s, states that the number of competing species cannot exceed the number of limiting resources (e.g., Hutchinson 1961, Tilman 1977, Armstrong and McGehee 1980). Rarely in nature is this “principle” strictly satisfied. Yet it remains theoretically useful, in that one way of approaching the problem of species coexistence has been to pose this principle as a rule and then search for the mechanisms by which ecological communities manage to circumvent it.

A very wide variety of these coexistence mechanisms has been identified in the literature. In a sense, they all work in the same way: by differentiating species sufficiently to mitigate the limiting effects of competition. Often this means increasing the importance (strength, frequency) of intraspecific competitive interactions (between individuals of the same species) relative to that of interspecific competitive interactions (between individuals of different species). Beyond this, a synthesis of coexistence mechanisms proves difficult. What makes the study of species coexistence challenging is

the vast number of possible axes of differentiation available in the ecological world. For the purposes of this work, coexistence mechanisms can be usefully divided into spatial mechanisms, which depend on aspects of the spatial environment, and non-spatial mechanisms.

Coexistence mechanisms of the non-spatial variety include niche differentiation, environmental fluctuation, non-equilibrium dynamics, competitive intransitivity, and tradeoffs between species' competitive ability and rates of colonization or fecundity. (For a good review of coexistence mechanisms, see Chesson 2000a.) Hutchinson (1957) defined the concept of a species' niche in terms of the n -dimensional space of all biotic and abiotic factors which determine the species' abundance. A species' fundamental niche is the volume of this space inside which it can persist in the absence of competition. The realized niche is the subset of this space actually inhabited by the species in the local community. In general, the greater the overlap in two species' fundamental niches, the more intense competition between them will be. The phenomenon of character displacement or niche differentiation occurs when natural selection acts to partition the region of fundamental niche overlap, in order to minimize competition and promote coexistence.

Temporal fluctuation in environmental conditions promotes coexistence by shifting the competitive playing field over time, and thereby varying species' competitive abilities. Because rates of predation tend to increase with prey abundance, predation (or more generally, the presence of trophic structure) acts to inhibit competitive exclusion at lower trophic levels. Tradeoffs between competitive ability and rates of colonization or fecundity have been shown to promote regional coexistence in theoretical and

experimental work (Levins and Culver 1971, Hastings 1980, Tilman 1994). For example, species A may competitively exclude species B wherever the two coincide, but B could persist in the landscape indefinitely by colonizing vacant habitat (new or recently disturbed) first, reproducing rapidly, and dispersing again before A arrives to drive it locally extinct. “Non-equilibrium dynamics” refers to the idea that ecological communities are in a state of constant flux. Thus, even if an equilibrium exists permitting only a small number of species to coexist, many more species manage to stay alive by virtue of the flux inherent in a highly nonlinear system. Chaos as a mechanism of coexistence falls into this category (e.g., Huisman and Weissing 1999, 2001a, 2001b).

Spatial coexistence mechanisms include environmental heterogeneity, conspecific aggregation, heteromyopia, and locality in both species interactions and dispersal (see Tilman and Kareiva 1997, Chesson 2000a, Amarasekare 2003). Environmental heterogeneity is the spatial analogue of temporal fluctuation. When conditions vary across a landscape, the outcome of competition will vary also, allowing species to coexist regionally which cannot do so locally. Aggregation or clustering of conspecifics refers to a spatial distribution of individuals in which individuals of the same species tend to occur together. Because species interactions are always local to some degree, the importance of intraspecific interactions relative to interspecific is increased. Conspecific aggregation will result from localized dispersal even in a uniform landscape, but may be augmented by environmental heterogeneity. Murrell and Law (2003) introduce the idea of heteromyopia, which is the idea that conspecifics interact over longer distances than heterospecific individuals, so that individuals effectively have a “myopic” view of their heterospecific neighbors. Their theoretical work demonstrates that this mechanism could

promote coexistence, but does not answer the question of whether it actually occurs in nature.

This project examines the intersection between two particular coexistence mechanisms: localized species dispersal and competitive intransitivity. Recent work (Kerr et al. 2002) has suggested that locality promotes coexistence in simple species assemblages characterized by intransitive competition. Here, we extend this work to ask how localized dispersal and intransitivities affect coexistence in systems with multiple trophic levels. Before proceeding, however, it will be useful to describe what has been learned so far about both competitive intransitivity and locality.

Intransitivity in species' competitive rank has been linked to coexistence in both theoretical and experimental work (May and Leonard 1975, Petraitis 1979, Durrett and Levin 1997, Kerr et al. 2002, Laird and Schamp 2006). A community of competing species is described as intransitive or non-hierarchical if no one species can out-compete all the others in pairwise competition (Petraitis 1979, Laird and Schamp 2006).¹ Thus, for example, a collection of three species denoted A, B and C is perfectly intransitive when A out-competes B in pairwise competition, B out-competes C, and C out-competes A. This simple three-species case is known as rock-paper-scissors intransitivity (May and Leonard 1975, Durrett and Levin 1997, Kerr et al. 2002).

Laird and Schamp (2006) recently published a large simulation study of intransitive competition, generalized to communities with many more than three species. Their results indicate that species diversity under local competition increases with

¹ In mathematics, a binary relation R on a set X is called "transitive" if, for all a, b and c in X , if a relates to b , and b relates to c , then a relates to c . Examples of transitive relations include equality, greater than, less than, implication, subset and superset. In the context of competition between species, a hierarchy in competitive ability would be called transitive, and the adjective "intransitive" applied to any other arrangement.

increasing intransitivity, regardless of how many species are considered. Furthermore, species coexistence, as measured by time until first extinction, also increases with increased intransitivity. (Interestingly, the variation in both diversity and coexistence time increases as well.) These results show that, at least in principle, the absence of strict hierarchies in competitive dominance could be a contributing factor to coexistence. The authors cite multiple studies describing evidence for intransitivity or competitive rank reversals in natural communities (e.g., Buss and Jackson 1979, Buss 1980, Shipley and Keddy 1994, Cerda 1997).

Locality in species interactions and dispersal has also been shown to promote species coexistence. An ecological process or interaction is said to be local if its strength or frequency varies as a function of distance. Kerr et al. (2002) demonstrated with simulation and experiment that three competing strains of *E. Coli*, satisfying the rock-paper-scissors intransitivity, were able to coexist when the range of competition was short. In their experiment, the RPS relationship was based on a growth-rate hierarchy. The slowest-growing strain (denoted C) produced a toxin called colicin, which conferred a competitive advantage over the fastest-growing 'sensitive' strain (denoted S). The strain with intermediate growth rate (denoted R) carried a gene which made it resistant to the toxin. Thus, in pairwise competition, S excluded R, and R excluded C, through their growth rate advantage, while C excluded S by virtue of the toxin. The hierarchy in growth rate was due to the costs of producing the toxin and carrying resistance.

Kerr et al. grew these three strains together in three different environments, each imposing a different degree of locality on the range of competitive interactions. The two-dimensional nature of the 'static plate' environment (a Petri dish) effectively localized all

competitive interactions by restricting contact to adjacent neighbors. Starting from a random initial distribution in the dish, three strains spontaneously aggregated into conspecific patches. Patches of S invaded patches of R, which invaded patches of C, which in turn invaded patches of S, but all three strains persisted indefinitely. In contrast, the ‘flask’ environment (a shaken flask containing liquid media) rendered competitive interactions more global. Invariably, strain S quickly succumbed to the toxin produced by strain C, which was then out-competed by R, leaving a monoculture. The same thing happened in the third ‘mixed-plate’ environment, which conferred a degree of locality intermediate to that of the static plate and flask. (It is interesting to note that the relatively slight loss of locality in this intermediate environment resulted in a complete loss of coexistence.) The authors also conducted a simulation study based on a cellular automata model (adapted from Durrett and Levin 1997) which produced similar results.

Taken together, these experimental and simulation results suggest that locality in competitive interactions and dispersal promotes coexistence, at least within a single trophic level. This project takes the work of Kerr et al. as a starting point, and investigates the effect of locality in the presence of more than one trophic level. We consider the simplest model system with more than one trophic level and cyclic endstates: a two-predator, two-prey assemblage similar to those studied by Holt et al. (1994) and Schreiber and Rittenhouse (2004). Two models based on this model system are presented. The first is a spatially implicit model derived from the metacommunity framework presented by Law and Leibold (2005). The second is a spatially explicit lattice-based model analogous to that of Kerr et al., in which dispersal distance is characterized by a variable neighborhood size r . Using these simulations, I ask: Do

localized dispersal and intransitive interactions promote coexistence in systems with multiple trophic levels?

In the following section, we discuss in detail the assumptions underlying the metacommunity and the model system. In Section 3, we construct a spatially implicit model as a system of ordinary differential equations, and analyze its behavior. Section 4 develops a spatially explicit metacommunity model that allows the degree of localization to be varied. In Section 5, we study what happens when an assumption of equality in parameters is relaxed. Finally, in Section 6 we discuss the general conclusions of these models and their relationship to the results of other studies.

2. A Two-Predator, Two-Prey Metacommunity Model

A metacommunity is defined as a set of many individual communities that are isolated except for relatively rare dispersal and colonization events (e.g., Leibold et al. 2004). The individual community, by contrast, occurs on the spatial scale at which species encounter one another and interact (Hanski and Gilpin 1997, Law and Leibold 2005). Each community is thought of as occupying a single habitat patch within a larger regional landscape. The particular spatial organization of the individual communities in the landscape can be specified explicitly or treated implicitly by assuming a well-mixed landscape.

In this investigation, I consider a simple regional species pool consisting of two prey species, denoted N_1, N_2 , and two predator species, P_1, P_2 , subject to the following

broad conditions. First, both predator species are specialized to one prey species, so that P_1 cannot consume N_2 and P_2 cannot consume N_1 . Second, symmetric competition exists between the two prey species, so that the effect of N_1 on N_2 is identical to that of N_2 on N_1 . Within a patch, predators can persist only in the presence of their prey. Each prey species can persist indefinitely in the presence of its predator. Competition between N_1 and N_2 is sufficiently strong that, in the absence of its predator, a patch occupied by either prey species cannot be invaded by the other prey species. However, if a predator is established in a patch with its prey, the other prey species can invade, and will subsequently drive the first prey extinct. In other words, neither prey species can survive a “battle on two fronts.” Thus a patch occupied by N_1 is invulnerable to P_1 but not N_2 . Once P_1 succeeds in colonizing the patch, however, invasion by N_2 becomes possible and will inevitably lead to the extinction of N_1 and then P_1 . This arrangement generates a continual, unidirectional cycle in community composition which can be represented like this:

$$\begin{aligned}
 N_1 &\rightarrow N_1P_1 \rightarrow N_1P_1N_2 \rightarrow P_1N_2 \rightarrow N_2 \rightarrow \\
 &N_2P_2 \rightarrow N_2P_2N_1 \rightarrow P_2N_1 \rightarrow N_1 \rightarrow \dots
 \end{aligned}$$

Notice that, because we are only interested in the metacommunity as a whole, the particular nature of within-community population dynamics is left unspecified. Only the outcome, or endstate, is stipulated. This is usually justified by assuming a separation of timescales, meaning that the colonization events by which the metacommunity evolves in time are sufficiently rare that all within-community dynamics are instantaneous by comparison (Levins and Culver 1971, Hastings 1980, Leibold and Law 2005). Predation, competition, individual births and deaths, and all other ecological processes which define

community dynamics are distinguished by the timescales on which they occur from the dispersal and colonization events which comprise metacommunity dynamics. This separation of timescales allows us to neglect the particular nature of within-community dynamics, rather than having to model them explicitly (e.g., with Lotka-Volterra predator-prey equations). At the metacommunity level, we consider a community to be completely characterized by its species composition.

Because extinction dynamics occur on the faster community-level timescale, all but four of the possible combinations of species are considered transient. At the metacommunity timescale, the cycle of community composition reduces to:

$$N_1 \rightarrow N_1P_1 \rightarrow N_2 \rightarrow N_2P_2 \rightarrow N_1 \rightarrow \dots$$

These four community types are referred to as *permanent*. To an observer living on the metacommunity scale, only permanent community types are noticed, and the only ecological processes are dispersal and colonization. Mathematically, a permanent community is one in which the density of any single species will tend to increase from low density in the presence of the other species (Law and Morton 1996).

Finally, we will add a third metacommunity-scale process: stochastic patch extinction. At a constant rate e , patches within the landscape are wiped out and rendered vacant by catastrophe or some other density-independent disturbance. These vacant patches can be colonized by either of the two prey species. Whatever biotic resources are destroyed in the cataclysm but which are needed to support prey are assumed to

regenerate in community time, or instantaneously with respect to the metacommunity timescale.

3. Spatially Implicit Model

3.1 Model Construction

It is possible to model metacommunity dynamics without explicitly incorporating space, by assuming that all patch types are well-mixed in the landscape. The state variables we will consider are the proportions $p_1, p_2, p_3,$ and p_4 of patches which are occupied by each of the four permanent community types $N_1, N_1P_1, N_2,$ and $N_2P_2,$ respectively. The total number of patches in the landscape is assumed constant, so that these four proportions together, along with the proportion p_0 of empty patches, sum to 1. We construct the model equations below, which describe how these proportions change in time (Levins and Culver 1971, Hastings 1980, Tilman 1994, Law and Leibold 2005).

$$\begin{aligned}
 \dot{p}_1 &= c_1(p_0 + p_4)(p_1 + p_2) - c_2p_1p_2 - ep_1 \\
 \dot{p}_2 &= c_2p_1p_2 - c_1p_2(p_3 + p_4) - ep_2 \\
 \dot{p}_3 &= c_1(p_0 + p_2)(p_3 + p_4) - c_2p_3p_4 - ep_3 \\
 \dot{p}_4 &= c_2p_3p_4 - c_1p_4(p_1 + p_2) - ep_4
 \end{aligned} \tag{1}$$

Because these are proportions, the rates \dot{p}_i must sum to 0, and so the equation defining \dot{p}_0 is redundant. The parameters c_1 and c_2 specify the rates at which prey and

predators, respectively, disperse from their patches to colonize new patches. The parameter e specifies the rate of density-independent patch extinction, which is assumed to affect all four non-vacant community types in proportion to their abundance. All terms except the extinction rates take the form of “mass-action” responses. Thus, for example, the “birth rate” of type 1 patches (containing only N_1) is simply the product of the proportion of patches from which N_1 is dispersing ($p_1 + p_2$) and the proportion of available target patches ($p_0 + p_4$), multiplied by the rate of prey dispersal c_1 . The second term $-c_2 p_1 p_2$ gives the rate at which patches of type 1 are colonized by predators P_1 dispersing from patches of type 2 at rate c_2 . The final term ep_1 gives the rate at which patches of type 1 are rendered vacant.

Similarly, type 2 patches are born via the positive term $c_2 p_1 p_2$, which formed part of the death rate of type 1 patches. Type 2 patches are changed into type 3 patches at the rate $-c_1 p_2 (p_3 + p_4)$, which is the product of the proportion of patches containing the colonizer N_2 , the proportion of its target patches of type $N_1 P_1$, all multiplied by c_1 . Type 2 patches are rendered vacant at rate ep_2 . The equations for p_3 and p_4 follow by analogy.

3.2 Model Analysis

We begin our analysis by investigating a series of simple cases of the model, using invasion analyses and finding equilibria. This is intended to provide insight into the structure of the model equations. Next, we derive an internal equilibrium at which all four patch types persist in the landscape, and study its stability. We also describe the existence of a limit cycle at which all four species coexist. Finally, we present and analyze a phase

diagram describing the regions of the (c_1, c_2) -plane (for fixed e) for which each of four qualitatively distinct behaviors of the model are observed.

First we examine what happens in the absence of both predators: $p_2 = p_4 = 0$. In this case, the per capita growth rates of p_1 and p_3 are identical:

$$\frac{\dot{p}_1}{p_1} = \frac{\dot{p}_3}{p_3} = c_1(1 - p_1 - p_3) - e \quad (2)$$

Setting equation (2) equal to zero and solving yields an expression for the sum of the two variables.

$$p_1 + p_3 = 1 - \frac{e}{c_1} \quad (3)$$

Note that when $c_1 < e$, neither prey species is able to persist in the landscape (Figure 1a).

If we are thinking about patches in landscape, then when $c_1 > e$, the right hand side of Equation (3) is the proportion of patches which are occupied by N_1 or N_2 . If either p_1 or $p_3 = 0$, then the surviving prey will exist at this fixed value. This simple case was analyzed as the original metapopulation model by Levins and Culver (1971). When both p_1 and p_3 are both positive, we are left with a free variable (since only the sum is constrained to be fixed) and the specific values of p_1^* and p_3^* depend on the initial conditions. Figure 1b shows a plot depicting the behavior of the model when both prey species persist in the absence of predators.

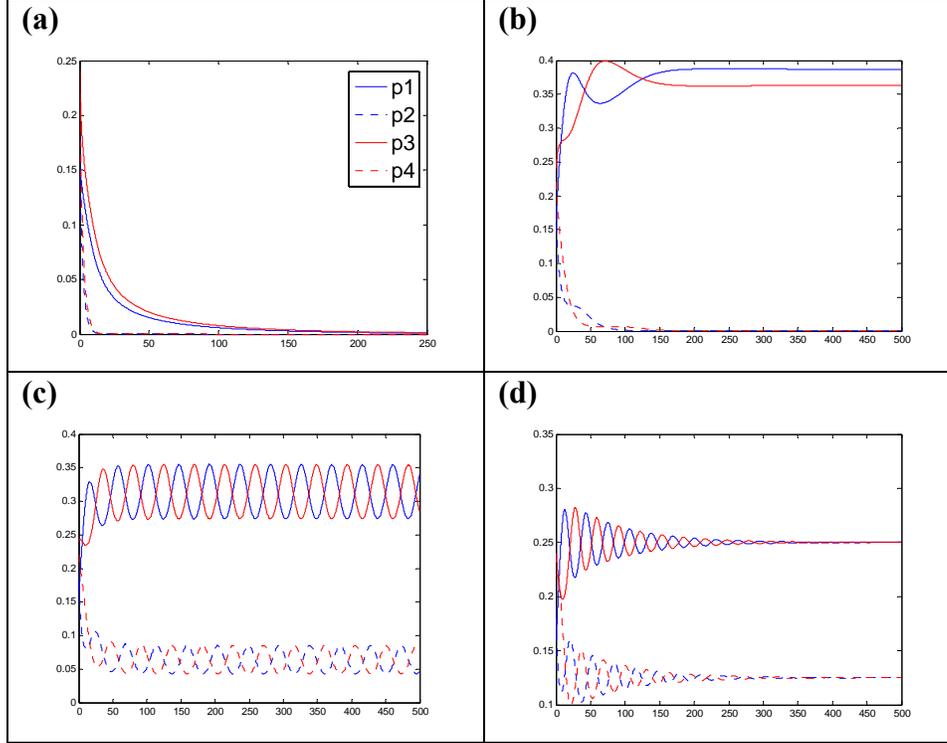


Figure 1: Examples of the four classes of model dynamics. (a) $c_1 < e$ results in all proportions approaching zero. (b) Reducing e below c_1 allows prey to persist. Long-run densities depend on initial conditions. (c) Increasing c_2 relative to c_1 allows predators to persist. The cycling behavior indicates the presence of a limit cycle for this set of parameters. (d) Increasing c_2 still further results in stable four-species point equilibrium. **Parameter values shown:** (a) $c_1 = 0.4$, $c_2 = 0.6$, $e = 0.41$ (b) $c_1 = 0.4$, $c_2 = 0.6$, $e = 0.1$ (c) $c_1 = 0.4$, $c_2 = 0.8$, $e = 0.1$ (d) $c_1 = 0.4$, $c_2 = 1.0$, $e = 0.1$.

The full model can be viewed as two identical predator-prey sets, coupled so as to generate a cyclic pattern in endstates. To investigate the independent behavior of one predator-prey set, take $p_1 = p_2 = 0$. We are left with

$$\begin{aligned} \dot{p}_3 &= c_1(p_3 + p_4)(1 - p_3 - p_4) - c_2 p_3 p_4 - e p_3 \\ \dot{p}_4 &= p_4(c_2 p_3 - e) \end{aligned} \quad (4)$$

The first equation gives the growth rate of patches containing only N_2 . From the second equation, we see that the remaining predator P_2 will persist in the landscape if its prey density satisfies $p_3 > e/c_2$. Setting both equations equal to zero and solving yields the equilibrium

$$p_3^* = 1 - \frac{e}{c_1} - \frac{e}{c_2}, p_4^* = \frac{e}{c_2} \quad (5)$$

Where starred values henceforth denoted equilibrium abundances. A little calculation reveals the eigenvalues of the Jacobian matrix of this two-dimensional system, evaluated at the equilibrium (5), to be

$$\begin{aligned} \lambda_1 &= e - c_1 \\ \lambda_2 &= e + \frac{c_2}{c_1}e - c_2 \end{aligned} \quad (6)$$

The equilibrium is stable when both eigenvalues are negative. The first simply requires that $c_1 > e$, shown above to be the criterion for prey persistence. The second eigenvalue can be written as a constraint on the rate of predator dispersal:

$$c_2 > \frac{c_1 e}{c_1 - e} \quad (7)$$

Equation (7) is the first indication of one of our general results: that predator dispersal must sufficiently exceed prey dispersal for predators to persist.

Having considered two simple cases (prey in the absence of predators, and the one-predator, one-prey system), we now proceed to analysis of the full model. Setting all

four equations (1) equal to zero and solving yields the following interior equilibrium point.

$$\begin{aligned} p_1^* &= p_3^* = \frac{c_1 + e}{2c_2} \\ p_2^* &= p_4^* = \frac{1}{2c_2} \left(c_2 - c_1 - \frac{c_2}{c_1} e - e \right) \end{aligned} \quad (8)$$

(The equations require that the equilibrium value of p_1 equal that of p_3 , which implies that $p_2^* = p_4^*$. This is not surprising given the symmetry of the model equations.) The value of p_1^* is positive for all parameter values. However, the value of c_2 must be sufficiently large for the value of p_2^* to exist in the positive orthant. Rearranging the inequality $p_2^* > 0$ gives the following:

$$c_2 > \frac{c_1(c_1 + e)}{c_1 - e} \quad (9)$$

Equation (9) gives the condition for persistence of predators at the equilibrium. Note that larger values of both c_1 and e force the predator to disperse more rapidly to survive. A plot of the proportions approaching this equilibrium is given in Figure 1d.

Stability analysis of the four-species equilibrium again requires us to compute the eigenvalues of the Jacobian matrix, evaluated at the equilibrium (8). The calculation is more involved for the full 4-dimensional system than for the 2D system presented in Equations (5) and (6). At this point, a computer algebra system comes in handy. Maple gives the eigenvalues to be:

$$\begin{aligned} \lambda_1 &= e - c_1 \\ \lambda_2 &= -\frac{1}{2} \left(c_2 - c_1 - \frac{c_2}{c_1} e - e \right) \\ \lambda_3 &= A + \sqrt{B} \\ \lambda_4 &= A - \sqrt{B} \end{aligned} \quad (10)$$

Where A and B are complicated polynomials involving c_1 , c_2 , and e . Notice that the second eigenvalue is proportional to the predator coordinate p_2^* of the equilibrium as $\lambda_2 = -c_2 p_2^*$. That is, $\lambda_2 < 0$ if and only if $p_2^* > 0$. Thus when the equilibrium point exists in the positive orthant of the phase space, the second eigenvalue is negative, and the equilibrium is attracting along the direction governed by λ_2 (necessary but not sufficient for stability; the real parts of the other three eigenvalues must also be negative).

In Figure 1 we saw examples of four qualitatively different classes of dynamics. The phase diagram in Figure 2a depicts the regions of the (c_1, c_2) -plane for which each of these four classes occurs. For example, when $c_1 < e$, prey species cannot colonize new patches rapidly enough to overcome patch extinction, and all proportions asymptotically approach zero (Figure 1a and red region of Fig. 2a). When $c_1 > e$, corresponding to $\lambda_1 < 0$, we have the familiar condition for prey to persist in the face of patch extinction (Figure 1b and dark blue region of Fig. 2a). Lastly, predators are able to persist when c_2 is sufficiently large relative to c_1 (Figures 1c and 1d, aqua and yellow regions of Figure 2a). In order to understand what happens at the boundaries of these regions, we can make use of the eigenvalues of Equation (10).

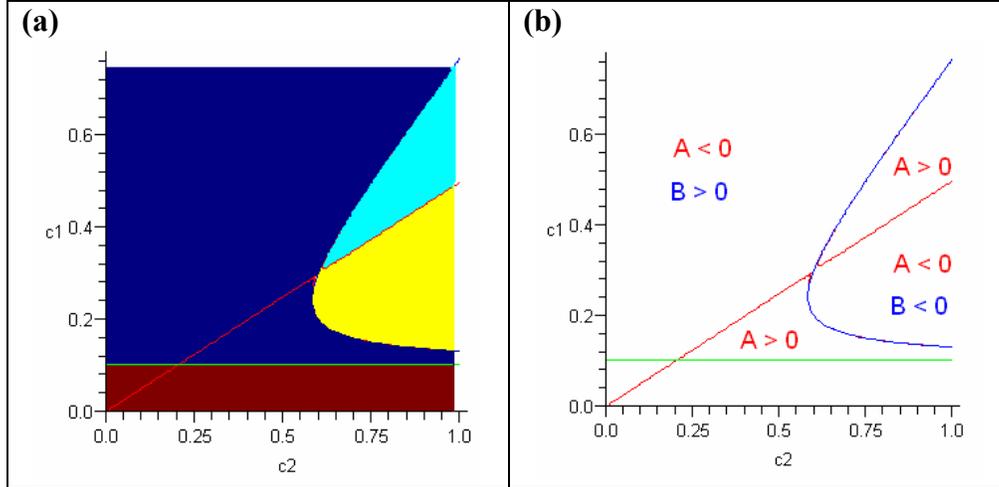


Figure 2: The (c_1, c_2) -plane. (a) Phase diagram depicting the regions of the plane associated with each of the four classes of dynamics exemplified in Figure 1 for $e = 0.1$. Red = global extinction, blue = prey persistence, yellow = stable four-species equilibrium, and aqua = limit cycle. **(b)** Plots of $A = 0$ (red), $B = 0$ (blue), and $c_1 = e$ (green) in the (c_1, c_2) -plane for $e = 0.1$. The signs of A and B (regions labeled) explain the appearance of the limit cycle observed in Figure 1c. The green line marking the boundary of prey persistence is included as a landmark for comparison with Figure 2a.

Figure 2b indicates that the boundary separating the dark blue region from the aqua and yellow regions occurs where $B = 0$. The locus of points given by $B = 0$ is also specified by the following equivalent relations: $\lambda_2 = 0$, $p_2^* = 0$, and $c_2 = \frac{c_1(c_1 + e)}{c_1 - e}$. To the right of this curve, where $c_2 > \frac{c_1(c_1 + e)}{c_1 - e}$, predators are able to persist in the landscape. As we cross into this region, the second eigenvalue λ_2 becomes negative and p_2^* becomes positive as the equilibrium point enters the positive orthant. Simultaneously, the quantity B under the radicals of λ_3 and λ_4 becomes negative. Thus, to the right of $B = 0$, λ_3 and λ_4 are complex, yielding the oscillations observed in Figures 1c and 1d. What distinguishes the aqua and yellow regions? Inside the yellow region of Figure 2a, the equilibrium point is stable. As we cross from the yellow region into the aqua region, the real part A of λ_3

and λ_4 changes sign from negative to positive. Dynamically, the equilibrium point loses its stability, and in the same instant a stable limit cycle is born surrounding it. This is a supercritical Hopf bifurcation, which can only occur in the presence of a pair of complex-conjugate eigenvalues. As we move closer to the boundary of the aqua and dark blue regions, the limit cycle expands outward, yielding larger and larger amplitudes in the predator-prey oscillations of Figure 1c. Ultimately, at the boundary of the aqua and dark blue regions, the equilibrium point crosses out of the positive orthant, and predator coexistence is lost.

3.3 Discussion

The above analyses show that predators must disperse significantly faster than their prey to persist at the metacommunity scale. Mechanistically, the explanation for why predators must disperse more rapidly than prey lies in the fact that predators can only recruit from a single type of patch (prey-only). Prey, on the other hand, can recruit from both predator-prey patches and vacant patches. With respect to dispersal, the difficulty for predators is simply that they are restricted to patches containing their prey.

This model, like all spatially implicit models, assumes a well-mixed landscape, which implies global dispersal and the complete absence of locality. Besides the well-mixed landscape, the only fundamental assumptions are in the “mass-action” form of the equations and the assumption of intransitivity. This is a fairly general model of regional dispersal. The result that predator dispersal must exceed prey dispersal agrees with what we observe in nature. While many marine and terrestrial predators hunt via “waiting” or

“trapping” strategies, most seem to expend much of their time and energy seeking out their prey. This tendency for predators to out-disperse their prey might be thought of as an incentive for the evolution of motility in predators (and herbivores), and subsequently of animal life.

4. Spatially-Explicit Model

The spatially implicit model described in Section 3 assumes a well-mixed metacommunity, and thereby ignores the fundamentally local nature of dispersal. Everything else being equal, an organism is usually more likely to colonize near its origin than far away from it. (Possible counter-examples such as seeds that must disperse a sufficient distance from the parent tree to germinate do not apply, because we are thinking about distances at least an order of magnitude larger than the scale of individual interactions.) Therefore, with the results of the spatially-implicit model in mind, we develop an analogous, spatially-explicit model, which allows us to vary directly the range of dispersal across the metacommunity.

4.1 Model Construction

The lattice-based cellular automata model is a natural choice to address spatial considerations in a system of interacting objects (see Durrett and Levin 1994 for a good introduction). A two-dimensional lattice or grid, usually square, is seeded with an initial

distribution of objects. Some rule is defined by which the strength or range of interactions between objects scales with distance. To avoid effects of edges, wrap-around boundaries are usually employed, so that the lattice is topologically equivalent to a torus. The system is then allowed to evolve according to its governing algorithm for some length of time. A typical unit of “time” is the epoch, which is the average turnover time of the entire lattice. For a lattice with L^2 grid cells, one epoch consists of L^2 individual cell updates. (Note that in a particular epoch, not every cell will necessarily be updated, and some will likely be updated more than once.)

In our lattice model, each cell is considered to be a single patch occupied by one of the five community types: vacant, N_1 , N_1P_1 , N_2 , and N_2P_2 , and denoted by $i = 0, 1, \dots, 4$ in that order. The lattice is a square with sides of length L and wrap-around boundaries. The neighborhood of each cell is defined to include all other cells within a distance r , so that the number of cells in a neighborhood is then $(2r+1)^2 - 1$ (corners are included). What happens to a particular cell depends only on the number of other cells of each type in the neighborhood. In other words, there are really only two distances, “here” and “there”, and r controls how big “here” is.

The updating algorithm is a stochastic birth-death process with five states and ten possible transitions. Denote by “ $\#i$ ” the proportion of cells in the neighborhood of a focal cell which are of type i , where $i = 0, 1, \dots, 4$. The possible transitions are enumerated with their rates in the table below.

Table 1: Birth-death process transitions and corresponding transition rates.

Transition	Rate	Transition	Rate
$0 \rightarrow 1$	$c_1^*(\#1 + \#2)$	$0 \rightarrow 3$	$c_1^*(\#3 + \#4)$
$1 \rightarrow 2$	$c_2^*(\#2)$	$1 \rightarrow 0$	e
$2 \rightarrow 3$	$c_1^*(\#3 + \#4)$	$2 \rightarrow 0$	e
$3 \rightarrow 4$	$c_2^*(\#4)$	$3 \rightarrow 0$	e
$4 \rightarrow 1$	$c_1^*(\#1 + \#2)$	$4 \rightarrow 0$	e

Thus, for example, the rate at which an occupied cell progresses to the next stage of the occupancy cycle (e.g., $2 \rightarrow 3$) is equal to the number of cells in its neighborhood that can disperse colonizers, multiplied by the appropriate dispersal rate (c_1 or c_2). The rate at which an occupied cell becomes vacant is always e . When the neighborhood is the entire lattice, the mean behavior of the stochastic, spatially explicit model is described by the deterministic, spatially implicit model of Section 3.

4.2 Simulation Results

To investigate the behavior of the spatially explicit model, we conducted a series of simulations for a lattice of size $L = 50$. Each run lasted for 250 epochs, or until the lattice held only one type of prey-only patch, and each was repeated $N = 20$ times for each parameter combination. Increasing the lattice size to $L = 100$ and running the simulation for 500 epochs did not qualitatively alter the results. The value of e was kept constant at 0.1 throughout. The simulation was run for three values of $r = (1, 12, 23)$,

three values of $c_1 = (0.2, 0.4, 0.6)$, and nine values of c_2 ranging from 0.3 to 2.4, for a total of $20 \times 81 = 1,620$ model runs (see Table 2).

Table 2: Parameter combinations and the threshold of predator persistence.

Threshold in c_2 for predator persistence decreases with increasing r , for three values of c_1 . Dark blue squares denote parameter combinations for which no predators were found in the lattice after 250 epochs, in any of the $N = 20$ replications. Similarly, green squares denote parameter combinations for which predators persisted. Aqua squares mark the first parameter combination for which predators were seen to persist through 250 epochs, for each neighborhood size.

C_1	r	c_2								
		0.3	0.5	0.7	0.8	0.95	1.1	1.2	1.8	2.4
0.2	1	Dark Blue	Dark Blue	Dark Blue	Dark Blue	Aqua	Green	Green	Green	Green
	12	Dark Blue	Dark Blue	Aqua	Green	Green	Green	Green	Green	Green
	23	Dark Blue	Dark Blue	Aqua	Green	Green	Green	Green	Green	Green
0.4	1	Dark Blue	Dark Blue	Dark Blue	Dark Blue	Aqua	Green	Green	Green	Green
	12	Dark Blue	Dark Blue	Dark Blue	Aqua	Green	Green	Green	Green	Green
	23	Dark Blue	Dark Blue	Dark Blue	Aqua	Green	Green	Green	Green	Green
0.6	1	Dark Blue	Aqua	Green	Green					
	12	Dark Blue	Aqua	Green	Green	Green				
	23	Dark Blue	Aqua	Green	Green	Green				

As in the spatially implicit model, for given values of e and c_1 , the value of c_2 had to be larger than some threshold for predators to persist in the landscape. The essential result is visible in Table 2 as r increases from 1 to 23 (going from short- to long-range dispersal): the threshold value of c_2 for which predators are able to persist in the lattice *decreases*. To put it another way, increased locality in dispersal reduces the range of parameter values for which predators are able to persist. Based on this observation, we conclude that locality in dispersal (smaller r) tends to inhibit regional coexistence in this model.

Figure 3 shows sample snapshots of the lattice after 250 epochs, for $c_1 = 0.2$, $c_2 = (0.7, 0.8, 0.95, 1.1)$ and all three values of r (the subset of simulations for which the threshold in c_2 was most clearly observed). Note the aggregation of cell types which is visible for $r = 1$.

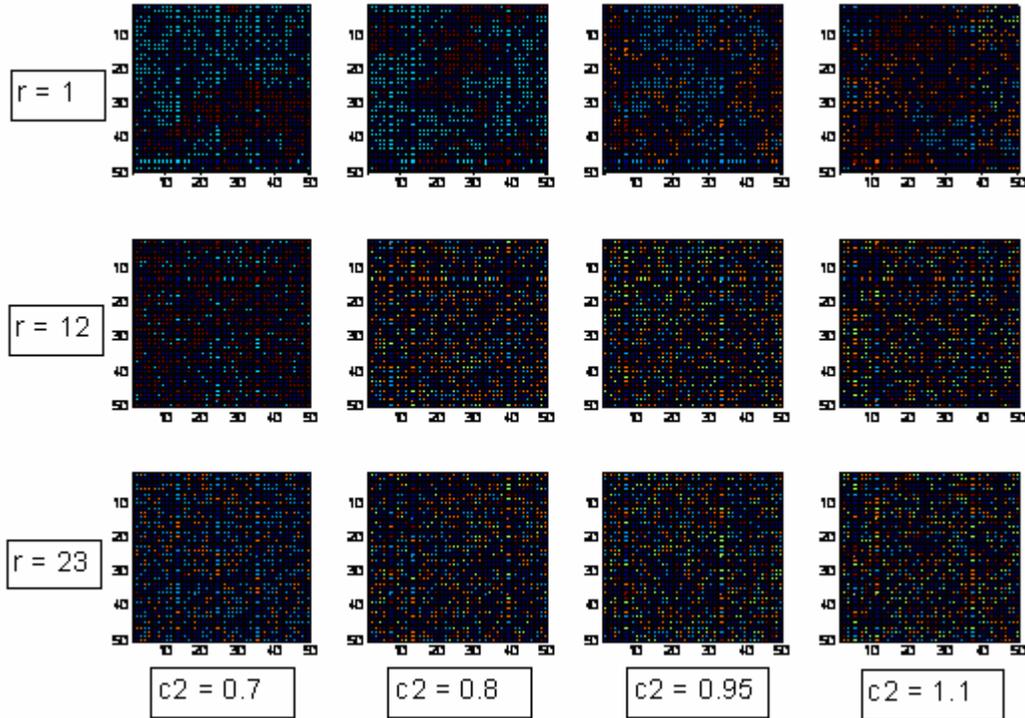


Figure 3: Sample snapshots of the lattice after 250 epochs, showing reduced threshold for predator persistence. In all snapshots, dark blue cells are vacant. Lattices at the top right with only two other colors (aqua and dark red) contain only N_1 and N_3 . Lattices with orange or green cells contain predators. (As indicated in Table 2, predators were observed for other replicates of $r = 12$ and $c_2 = 0.7$, but merely not for this one.)

4.3 Discussion

The explanation for why increased locality in species dispersal inhibits coexistence relies on a basic property of these models which was noted in Section 3.3.

While prey can colonize both vacant patches and predator-prey patches, predators can only colonize prey-only patches. That is, predators are effectively constrained to live on a smaller subset of the lattice than are prey. Larger values of e result in more vacant patches on average, and thereby enhance this effect. Because this constraint is a natural property of trophic relationships, the effect of localized dispersal observed here may be regarded as fairly general. It should be expected to apply whenever an additional trophic level is added to the regional food web. It is also interesting to note how the increase in r from 1 to 12 did more to lower the threshold in c_2 than the increase from 12 to 23. This indicates that decreased locality in dispersal takes effect rapidly. It would be interesting to simulate for smaller values of r , e.g., between 2 and 6.

Another way of describing the mechanism underlying this result involves aggregation of like patch types, introduced in Section 1. In competitive communities, aggregation of conspecifics has been described as a mechanism for increasing the importance of intraspecific interactions relative to interspecific interactions, and thereby promoting coexistence (Murrell et al. 2001). Random fluctuation eventually creates a cluster in which there are many patches of the same type. When the dispersal range is smaller than the radius of a cluster, colonizers cannot penetrate to the interior. Hence, aggregation is expected for smaller values of r , but not for larger values. It is also evident from Figure 3 that a relatively slight decrease in locality (from $r = 1$ to $r = 12$) tends to go a long way toward preventing aggregation.

5. Breaking the Symmetry in Dispersal Rates

The assumption that both prey and both predator species disperse at the same rate is most tenable if we are imagining ecologically similar species. But even then, the rates will not be identical. It is natural to wonder how sensitive the results of this work are to deviations from this symmetric case. To address this question, we first revisit the prey-only system ($p_2 = p_4 = 0$) discussed in Section 3.2, and distinguish two rates of prey dispersal: $c_{N1} = c_1 \neq c_3 = c_{N2}$. The per capita prey growth rates are then

$$\begin{aligned}\frac{\dot{p}_1}{p_1} &= c_1(1 - p_1 - p_3) - e \\ \frac{\dot{p}_3}{p_3} &= c_3(1 - p_1 - p_3) - e\end{aligned}\tag{11}$$

Regardless of the values of p_1 and p_3 , the species with the larger dispersal rate will have the larger growth rate and force the other prey extinction (analysis not shown). Thus, when the prey dispersal rates are distinct, prey cannot coexist in the absence of their predators. In order to persist, the prey with the lower rate of dispersal would have to compensate in some other way, such as with a higher per-capita rate of fecundity or superior local competitive ability, neither of which are readily added to this framework.

When predators are included, the situation is somewhat more complicated. For the moment, we will allow the two rates of predator dispersal to remain equal: $c_{P1} = c_{P2} = c_2$. In this case, even for large values of c_2 , only the predator associated with the more-

rapidly dispersing prey species is able to persist. Figure 4 shows the different regions of coexistence for $c_2 = 0.7$.

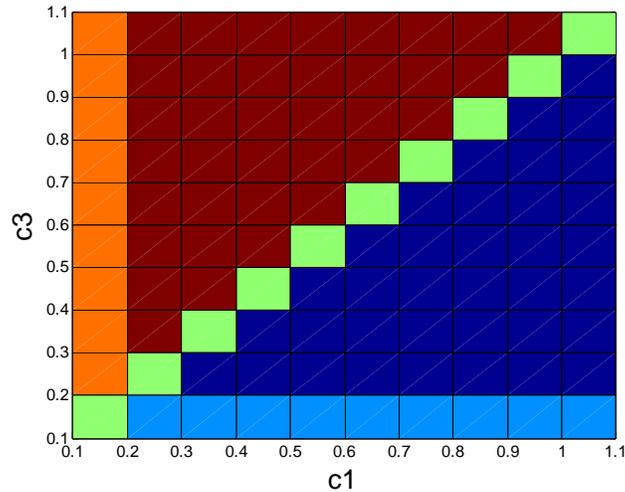


Figure 4: Regions of coexistence in (c_1, c_3) -plane with $c_2 = 0.7$ and $e = 0.1$. Predator enables slow-dispersing prey species to persist. Regions are color-coded as follows: Light blue = N_1 and P_1 are only species present; dark blue = N_1, P_1 and N_2 ; red = N_2, P_2 and N_1 , orange = N_2 and P_2 only. Along the diagonal where $c_1 = c_3$ (green) the dynamics are as discussed in Section 3.

Figure 4 reveals two interesting points. First, notice that in the dark blue and red regions, the prey species that would have been driven extinct in a system without predators is able to persist. That is, the surviving predator permits the subordinate competitor to coexist with the dominant competitor in a kind of predator-mediated coexistence. Second, the predator associated with the dominant prey species may persist when one or even both of c_1 and c_3 exceeds c_2 . When $c_1 \neq c_3$, predators must no longer disperse more rapidly than their prey to survive. Figure 5 below shows sample plots for each of the four off-diagonal regions in Figure 4.

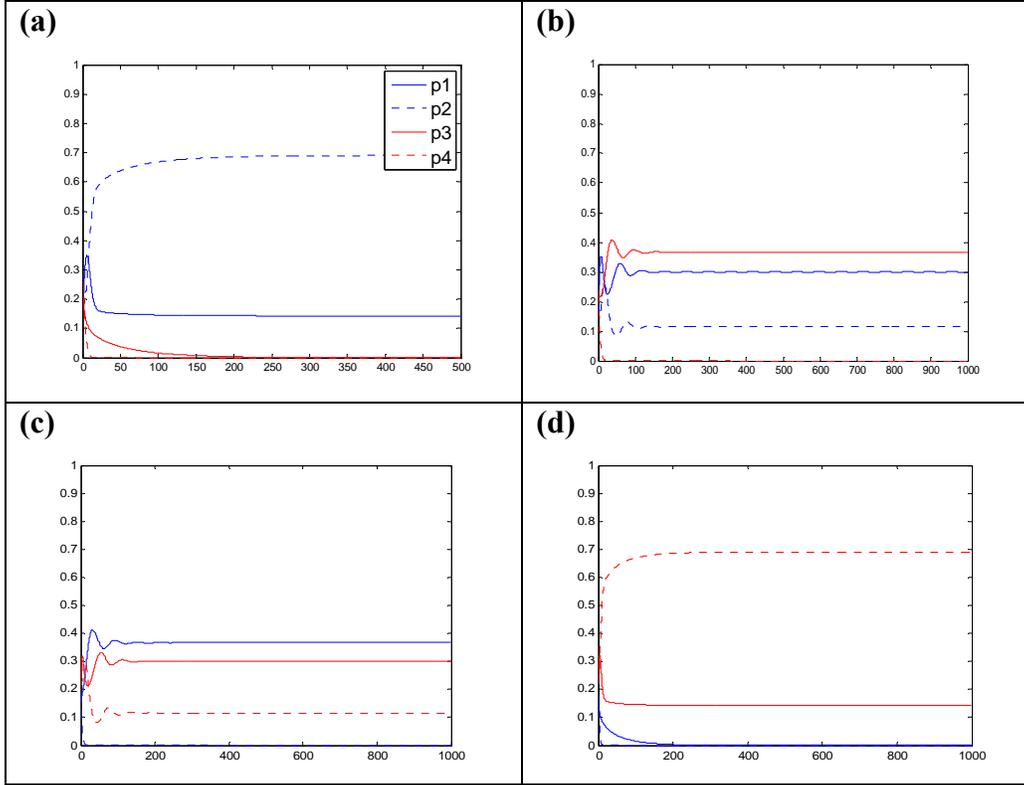


Figure 5: Four different classes of behavior when $c_1 \neq c_3$. The presence of a predator associated with the dominant prey allows the subordinate prey to persist. Predator dispersal $c_2 = 0.7$ and $e = 0.1$ throughout. **(a)** Light blue region of Fig. 4 with $c_1 = 0.6$ and $c_3 = 0.1$ **(b)** Dark blue region of Fig. 4 with $c_1 = 0.6$ and $c_3 = 0.3$ **(c)** Red region of Fig. 4 with $c_1 = 0.3$ and $c_3 = 0.6$ **(d)** Orange region of Fig. 4 with $c_1 = 0.1$ and $c_3 = 0.6$.

In the case of a single rate of predator dispersal, at most one predator is able to persist in the landscape when $c_1 \neq c_3$. Now we allow the predators to differ in their rates of dispersal also: $c_{P1} = c_2 \neq c_4 = c_{P2}$. Full exploration of this four-dimensional parameter space is challenging, but simulations shown that both predators manage to persist for many parameter combinations. Some examples are shown in Figure 6. In all cases, prey dispersal rates exceed those of predators.

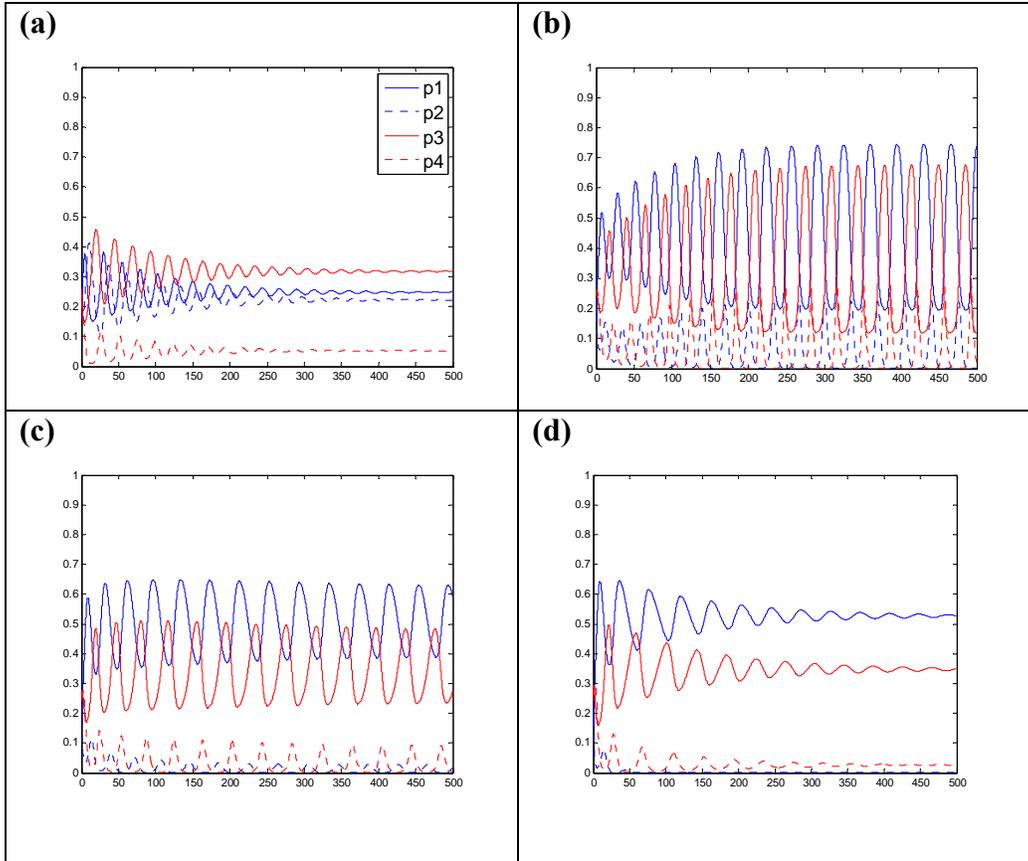


Figure 6: Four sample plots for the case $c_2 \neq c_4$ and $c_1 \neq c_3$, showing coexistence of all four species. Prey dispersal rates exceed those of predators. **(a)** Coexistence at stable four-species equilibrium. **(b)** Stable limit cycle. **(c)** Another limit cycle, showing asymmetric oscillation. **(d)** Three-species equilibrium. **Parameter values shown:** Throughout, $c_1 = 0.8$, $c_2 = 1.0$, $c_3 = 1.5$ and $e = 0.1$. **(a)** $c_3 = 0.4$ **(b)** $c_3 = 0.9$ **(c)** $c_3 = 1.1$ **(d)** $c_3 = 1.3$.

The results presented in this section demonstrate that: (1) prey cannot coexist in the absence of predators unless their dispersal rates are equal, and (2) the spatially implicit model does not, in general, require that predator dispersal rates exceed those of their prey in order to persist in the landscape. This latter result is somewhat surprising. Next steps include a search for analytical results to explain the behavior of the spatially implicit model when $c_1 \neq c_3$, as well as examining the results of the spatially explicit lattice-based

simulations under the same condition. We do not anticipate that the inhibitive effect of localized dispersal on coexistence will be altered, but the possibility warrants further investigation.

6. Discussion and Future Work

The spatially-explicit model allows us to study the role of locality of interactions in maintaining regional diversity. By varying the neighborhood size r , we can compare localized dispersal with dispersal over longer distances. Several studies have shown that localization of species interactions is strongly associated with coexistence when interactions are primarily competitive (e.g., Kerr et al. 2002, Murrell and Law 2003). In particular, aggregation of conspecifics has been shown to promote diversity (although the mechanism is disputed, see Chesson and Neuhauser 2002). The results of our spatially explicit model demonstrate that localized dispersal tends to have the opposite effect when trophic structure is present.

This result comes about because while prey can colonize two community types (vacant and predator/prey patches), predators are restricted to colonizing only one community type (prey-only patches). That is, prey can live on a larger proportion of the landscape than can predators. In order to compensate, predators must disperse at a faster rate. This result is directly analogous to the result of the spatially-implicit model, which arrived at the same conclusion for similar reasons, based on the nature of predator recruitment (versus that of prey) specified in the model equations.

Many mechanisms of species coexistence have been considered in the literature, including conspecific aggregation, environmental fluctuation and storage effects, environmental heterogeneity, intransitivity in competitive rank, heteromyopia, and others (e.g. Chesson 2000a, Amarasekare 2003). Based on the results obtained by Kerr et al., locality in competitive interactions can be added to this list. However, Kerr et al. claim that local *dispersal* accounts for the observed increased coexistence. We suspect that it was rather the local nature of the toxin-mediated competition which was promoted coexistence. Preliminary simulations to test this suspicion confirmed that local dispersal alone (in the absence of other species interactions) inhibited coexistence within a single trophic level (K. Gross, pers. comm.), but further investigation would help to confirm this. It may be that local competition and local dispersal have separate or even opposite effects of regional coexistence, even before trophic structure is considered. Regardless of this concern, however, the results of our spatially explicit simulation suggest that trophic structure in general depends on some degree of long-distance dispersal in order to persist.

An interesting extension of this work would try to unite these two results to give a single picture of the role of locality in promoting coexistence. Given that locality in competitive interactions promotes coexistence within trophic levels, and that locality in dispersal inhibits coexistence across trophic levels, it is natural to wonder if optimal species diversity is obtained for some intermediate degree of locality. To do this, our spatially explicit model could be extended to incorporate competition between prey species, with the same locality parameter r used to characterize dispersal distance. One would perhaps want to introduce a third prey species to test the role of intransitivity, or to

include a single top predator as a third trophic level. Generally, there may be much insight still to be gained from spatial simulation of simple food webs.

Locality as a mechanism of coexistence is most interesting for the simple reason that all ecological processes are necessarily local to some degree. In light of this, a full understanding of the relationship between locality, in dispersal and species interactions, and both within and between trophic levels, is needed to understand coexistence at regional scales. The combination of just three coexistence mechanisms – localized species interactions, local dispersal, and spatial heterogeneity – gives perhaps a reasonable first approximation to the real ecological world. To these we can add insights gained from the study of non-equilibrium dynamics and chaos, life-history tradeoffs, and other demonstrated coexistence mechanisms. While a general, complete and synthetic understanding of species coexistence remains elusive, a plausible picture of species coexistence in the real world begins to emerge.

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