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Stability and complexity on a lattice: coexistence of species in an individual-based food web model

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Abstract

Theoretical studies of the stability of food webs have generally not incorporated space as a contingency affecting coexistence of species. Here, I considered the importance of spatial heterogeneity on the stability of an individual-based food web model. Individual agents diffused on a lattice of cells and interacted according to a set of probabilistic interaction coefficients. Simulations were run on both uniform and non-uniform lattices. The model had two modes:

1. a mean-field mode with global interactions, and
2. a spatially localized mode in which species interacted within local neighborhoods.

Equilibrium number of species were compared among different simulations varying web connectance, interaction strength, and lattice heterogeneity. Local interactions resulted in more species rich webs, indicating greater stability. The addition of spatial heterogeneity to the lattice further altered relationships among species richness, web connectance, and interaction strength, and increased coexistence among species. The results did not support the stability criterion derived by May. However, an inverse relationship between web connectance and species richness was observed suggesting that the product of connectance and species richness may govern the stability of real, finite webs. © 1997 Elsevier Science B.V.

Keywords: Food web; Spatial heterogeneity; Stability; Complexity; Percolation; Fractal

1. Introduction

Since the time of Darwin's (1859) meditations on the 'entangled bank', ecologists have sought explanations for the complexity and diversity of ecosystems. Over the last 40 years, much of the debate over ecological complexity has focused on various notions of stability in trophically structured communities or 'food webs' (MacArthur, 1955; Elton, 1958; May, 1973; Pimm, 1982, 1991; Cohen et al., 1990a). Empirical studies of food web have generally considered patterns common

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among webs of varying size and complexity (Cohen, 1977; Sugihara et al., 1989; Hall and Raffaelli, 1991; Martinez, 1991, 1994; Pimm et al., 1991). Theoretical food web studies have focused on a somewhat different question: which food web patterns are dynamically stable and are thus, likely to be found in nature? (May, 1973; Pimm, 1982, 1991; Cohen and Newman, 1988). Most food web studies have been based on static webs from a single location (Closs and Lake, 1994). Only recently have food webs studies incorporated spatial and temporal variation (Winemiller, 1990; Schoenly and Cohen, 1991; Closs and Lake, 1994) and non-equilibrium dynamics (Mickalski and Arditi, 1995).

Spatial and temporal variation in species abundance have important implications for theoretical models of food webs. In particular, arguments concerning the stability and complexity of ecosystems based on non-spatial population models may be affected by considerations of spatial dynamics. Studies of species interaction in space have shown that local, non-linear interactions can lead to spatially heterogeneous population distributions and violation of the 'mean field approximation' inherent in non-spatial models (Levin, 1974; Chesson, 1981; Kareiva, 1990; Durrett and Levin, 1994a; Keitt and Johnson, 1995). Spatial, non-linear models exhibit a range of dynamic patterns including travelling waves and spatial chaos (Nicolis and Prigogine, 1977; Mimura and Murray, 1978; Gerhardt et al., 1990; Hassel et al., 1991; Vickers, 1991; Nowak and May, 1992; Holmes et al., 1994).

Dynamic spatial patterns play an important role in the coexistence of species by allowing prey species or inferior competitors to persist in ephemeral patches of low predator or dominant competitor abundance (Huffaker, 1958; Comins and Blatt, 1974; Caswell, 1978; Mimura and Kanon, 1986; Wilson et al., 1993). For example, Durrett and Levin (1994a) considered the importance of discrete individuals and spatial interactions on the outcome of a two species game model. Both for mutual competition and for predator-prey interaction, Durrett and Levin (1994a) found that individual discreteness and spatial interactions significantly altered the model outcome when compared with a corresponding non-spatial, continuous dynamical system. In simulations where an inferior competitor persisted despite the presence of a dominant competitor, local abundances were heterogeneous across the lattice, indicating that the inferior competitor survived in ephemeral patches where the dominant competitor had low abundance, i.e. as a 'fugitive species' (Huffaker, 1958; Levin and Paine, 1974; Whittaker and Levin, 1977; Tilman, 1994). Thus, species interactions which are inherently unstable when modeled without consideration of space can be stable when modeled in a spatially explicit context.

Given that spatial fluctuations in population abundance are important in determining coexistence in simple, two species systems, spatial interactions should also have important implications for species coexistence in complex, multispecies food webs. In this paper, I compared results from an individual-based, spatially-explicit food web model to the predictions of traditional, non-spatial food web theory. I consider two main hypotheses:

1. Spatial interactions allow for greater complexity in food webs than do non-spatial interactions; and
2. Increasing spatial heterogeneity of the environment leads to greater coexistence of species and hence increasingly complex food webs.

1.1. Stability and complexity

MacArthur (1955) and Elton (1958) originally suggested that complex communities, those that contain more species and more interactions, would be more stable than simple communities. Elton (1958) based his arguments on the observation that species poor communities often exhibit population cycles and sudden pest outbreaks. MacArthur (1955) argued that increased diversity of trophic links among species would result in a community more resistant to change when any one species was removed. Later, May (1972, 1973) showed that for simple community models, the opposite was true; increasing complexity, in terms of more species and greater number of interactions, resulted in decreased system stability. May's work lead to a great deal of theoretical development of food web models (reviewed in Pimm (1982)) as well as criticism (McNaughton, 1977; Paine, 1988).

Much of the debate over stability and complexity resulted from confusion over the precise meaning of stability (Pimm, 1984; Closs, 1991). Pimm (1991) identified five concepts associated with community stability that have been applied at three different levels of biological organization. For example, May's (1973) results were based on a particular mathematical definition of stability, whereas MacArthur (1955) considered resistance, i.e. the ability of the community to remain near equilibrium when one species abundance is abnormally high or low. Elton (1958) equated temporal variability in abundance with stability. Thus, it is important to define precisely what one means by stability. Since I will use stability in the mathematical sense as a null hypothesis for comparing spatial versus non-spatial models, I briefly outline the analytical method of determining stability in continuous, non-spatial population models.

Given a (possibly) non-linear system of differential equations describing population growth

$$\frac{d\bar{\boldsymbol{N}}}{dt} = \bar{F}(\bar{\boldsymbol{N}}) \tag{1}$$

where $\bar{\boldsymbol{N}}$ is a vector whose elements contain the abundance of each populations; stability is determined by examining the behavior of a small perturbation $\bar{z}$ to an equilibrium solution $\bar{\boldsymbol{N}}^* = \bar{F}(\bar{\boldsymbol{N}}^*)$. If $\bar{\boldsymbol{N}}^* + \bar{z}$ remains bounded within a small, finite distance from $\bar{\boldsymbol{N}}$ as $t \to \infty$, then $\bar{\boldsymbol{N}}^*$ is considered a stable solution to Eq. (1). If $\bar{z}$ decays such that $\bar{\boldsymbol{N}}^* + \bar{z} \to \bar{\boldsymbol{N}}^*$ as $t \to \infty$, then the solution is asymptotically stable (Seydel, 1988).

As long as $\bar{z}$ is small, the behavior of $\bar{z}$ can be approximated by taking a Taylor series expansion about the equilibrium solution and casting out second order and higher terms, which gives:

$$\frac{d\bar{z}}{dt} = \mathbf{J}\bar{z} \tag{2}$$

where $\mathbf{J}$ is a matrix whose elements are the first partial derivatives of $\bar{F}$. The matrix $\mathbf{J}$ is often called a 'community matrix' because it describes how a change in one species abundance near an equilibrium solution with affect the abundance of any other species. If for example, the interaction between two species is negative ($j_{kl} = \delta l / \delta k < 0$), then a small increase in the first species abundance (k) will result in a decrease in the abundance of the second species (l).

Making certain assumptions (i.e. non-repeated eigenvalues) the solution to Eq. (2) is given by

$$\bar{z}_t = \sum_{i=1}^{m} \bar{\xi}_i e^{\lambda_i t} \tag{3}$$

where m is the number of species; $\bar{\xi}$ are constant vectors and; λ are eigenvalues of $\mathbf{J}$. Recalling that $\lim_{t \to \infty} \exp(\lambda t) = 0$ for $\lambda < 0$, clearly the solution will be asymptotically stable if the largest eigenvalue $\lambda_{\max}$ is less than 0 and unstable if $\lambda_{\max} > 0$. In the case of complex eigenvalues, stability is determined by the largest real part.

1.2. Stability in random Lotka-Volterra webs

The Lotka-Volterra form of Eq. (1) for a species $i \in \{1, 2, 3, \ldots, m\}$ may be written as:

$$\frac{dn_i}{dt} = n_i\left(b_i + \sum_{j}^{m} a_{ij} n_j\right) \tag{4}$$

where n_i is the abundance of species i; b_i is the intrinsic growth rate; and a_{ij} is a coefficient determining the effect of species j on species i.

May (1972) studied the statistical distribution of eigenvalues for randomly constructed community matrices. Species were assumed to be self-damping (density dependent) so the diagonal terms (i.e. j_{ii}) were set to -1. A fraction C of the remaining off-diagonal interaction terms were assigned random values with mean zero and standard deviation s. The sign of the interaction term determined the type of species interaction. A negative interaction represented predatory or parasitic interaction and a positive coefficient represented mutualism. Elements of the community matrix that were not assigned a random number were set to zero which meant that the two species corresponding to that row and column of the matrix had no effect on each other. Thus, the set of interaction coefficients, taken together, defined a particular community structure.

May (1972) proposed that random community matrices would be unstable if:

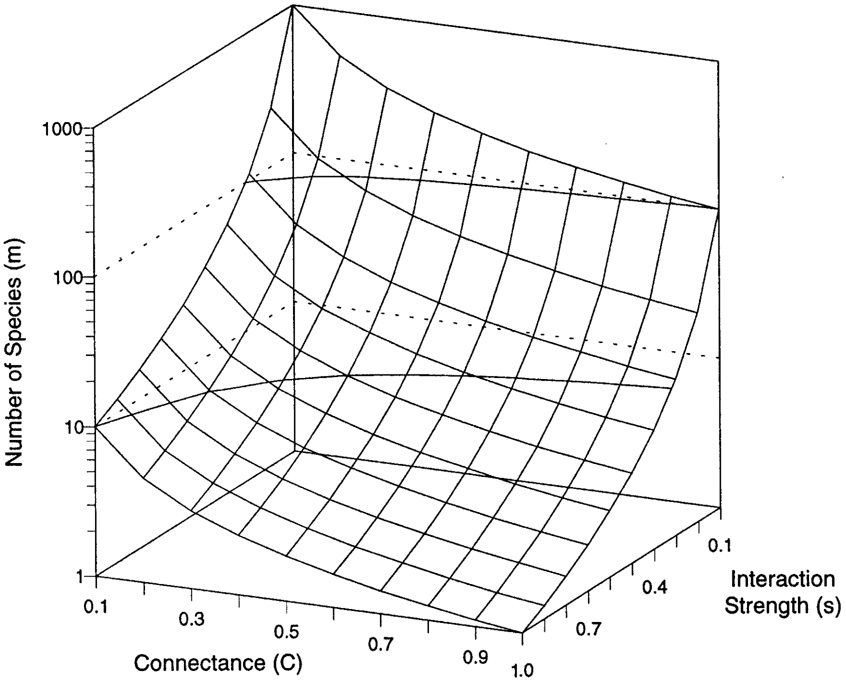

Fig. 1. Upper bound on stable species coexistence predicted by Eq. (6).

$$s(mC)^{1/2} > 1 \quad (5)$$

where m is the number of species. According to May's stability criterion, the stability of random Lotka-Volterra webs should decrease as the number of species (m), interactions (C), and interaction strengths (s) increase. Later, Cohen and Newman (1985) showed that May's criterion is not correct for random Lotka-Volterra webs in general, but only to a smaller class of food web models. However, the inverse relationship between species number and connectance implied by Eq. (5) does appear to hold (Pimm, 1982; Cohen and Newman, 1988; Cohen et al., 1990b).

In this paper, I tested whether May's stability criterion applies to a set ten of finite population interacting on a lattice. The relationship expressed in Eq. (5) implies an upper bound on the number of species that can coexist in a given food web. Rearranging terms, the maximum number of species expected to coexist in a community is

$$m = \frac{1}{s^2C} \quad (6)$$

This relationship is shown graphically in Fig. 1. The prediction made by Eq. (6) is that a 'species saturated' community starting from a point above the surface in Fig. 1 will, in the presence of any minute disturbance or noise, be subject to extinction and collapse down to a point near the maximum stable number of species. Thus, whether Eq. (5) holds for the lattice-based model can be tested by starting a series of simulations with many species initially and recording the final number of species after extinction have occurred.

2. Methods

2.1. A spatially-explicit food web model

To test the importance of spatial heterogeneity on food web stability, I constructed a spatially-explicit, individual-based model of species interaction occurring on a lattice. The implementation was similar to the 'interacting particle systems' described by Durrett and Levin (1994b), but with aspects similar to a cellular automata model (Wolfram, 1984; Hogeweg, 1988). Interactions among individual organisms were simulated on a lattice of cells. Only one individual was allowed to occupy a given cell at any one time. Interactions among individuals occurred if they tried to occupy the same cell at the same time. The outcome of these encounters were determined by a set of coefficients analogous to the interaction coefficients (a_{ij}) in the Lotka-Volterra model (Eq. (4)).

Simulations were run either in local interaction mode or in a global interaction 'mean-field' mode. When run in local mode, individuals moved to one of their four nearest neighbor cells (i.e. North, South, East or West) with equal probability. Reflecting boundary conditions were used such that no move occurred when an individual attempted to move off the lattice. In the non-local, 'mean-field' mode, individuals moved with equal probability to any cell on the lattice, thereby eliminating any spatial structure from the model.

Updates to the lattice were asynchronous, i.e. the outcome of each individual movement or interaction was immediately applied to the lattice before another individual was allowed to move. All cells in the lattice were visited in random order during each round of updates (henceforth called an iteration) to avoid biases that could occur from sweeping across the lattice in one direction. Asynchronous updating better approximates the continuous time found in nature while allowing for discrete individuals and interactions. Synchronous updating, where all interaction outcomes are determined before updating the lattice, introduces a strong temporal granularity and is responsible for many of the patterns observed in discrete-time spatial models (Huberman and Glance, 1993).

When an individual of species i attempted to move to a cell occupied by an individual of species j, the outcome of the interaction was determined by a set of interaction coefficients. The interaction coefficients ranged from $-1{:}0$ to $1{:}0$ and both the forward coefficient (a_{ij}) and the backward coefficient (a_{ji}) were used. Two probabilities were computed from the coefficients. The first was the probability p_m that an individual of species i would move to a cell occupied by species j. The probability of moving was determined by

$$p_m(i,j) = \frac{a_{ij} - a_{ji} + |a_{ij}| + |a_{ji}|}{4} \tag{7}$$

where a_{ij} is the effect (interaction term) of species j on species i, and a_{ji} is the effect of species i on species j. A successful move was determined by comparing p_m to a uniform random number $\rho \in [0, 1)$. If $\rho < p_m$ the move was successful; in which case the individual of species i would occupy the new cell and the former occupant was deleted from the lattice. Individuals always moved when encountering an available, unoccupied cell.

Secondly, I computed the probability of reproduction

$$p_r(i,j) = \begin{cases} a_{ij}(0.5 + 0.25(1 - a_{ji}) & a_{ij} > 0 \\ 0 & a_{ij} \leq 0 \end{cases} \tag{8}$$

where symbols are the same as in Eq. (7). Reproduction could only occur after a successful move to a new cell. Again, p_r was compared with a uniform random number to determine the outcome. If reproduction was successful, then the individual of species i would leave a copy of itself behind at its original location. The result of a successful move followed by reproduction was one less individual of species j and one more of species i.

The interaction coefficients in the individual-based model are analogs of the coefficients in May's community matrices. The individual-based model recasts the original Lotka-Volterra model into a stochastic framework in which the macroscopic dynamics emerge from the individual events rather than being derived under the assumption of mass action.

Qualitatively, the interaction coefficients in the individual-based model operate identically to May's model. For example, if species i has a negative interaction on species j and species j has a positive effect on species i, then the interaction is predatory. The coefficients in the individual-base model for a predatory interaction would be $a_{ij} < 0$ and $a_{ji} > 0$. Similarly, in a community matrix, a predatory interaction corresponds to $a_{ij} = \delta j/\delta i < 0$ and $a_{ji} = \delta i/\delta j > 0$. Thus, in either model, an increase in the predator population (i)

Table 1
Summary of interactions

a_{ij}	a_{ji}	Interaction type	$p_m(i,j)$	$p_r(i,j)$	$p_m \times p_r$
1.00	−1.00	Predator-prey	1.00	1.00	1.00
−1.00	1.00	Prey-predator	0.00	0.00	0.00
0.50	−0.50	Predator-prey	0.50	0.44	0.22
0.00	0.00	Null	0.00	0.00	0.00
−1.00	−1.00	Competition	0.50	0.00	0.00
1.00	1.00	Mutualism	0.50	0.50	0.25
1.00	0.00	Amensal	0.50	0.75	0.38

would result in a decrease in the prey population (j) and vice versa.

In both the Lotka-Volterra model and the individual-based model, as the absolute magnitude of the coefficients increase, the 'strength' of the interaction increases. In the individual based model, as the absolute magnitude of the coefficients (a_{ij}, a_{ji}) increase, the probabilities of movement and reproduction during an encounter of species i with species j increases; thus, the frequency of successful predation by species i on species j increases. Consequently, an increase in the population of species i will result in a decrease in species j; the magnitude of the change determined by the magnitudes of the interaction coefficients. Similarly, in the community-matrix model, large absolute magnitudes of the coefficients imply that a small change in species i will cause a large change in species j. Small absolute magnitudes in the community matrix imply a situation in which a small change in species i has a small effect on species j. This is what May (1973) referred to as interaction strength.

The main difference between the coefficients used in the two models is that the partial derivatives in the community matrix represent the net effect of species i on j, averaged over space and averaged over all encounters. In the individual-based model, the coefficient affect the outcome of individual encounters. It is instructive to compute probabilities of movement and reproduction for different sets of interaction coefficients. This is done in Table 1. Because the individual-interaction coefficients were not, strictly speaking, equivalent to the coefficients in the community matrices, the symbol P is used instead of s to represent the interaction strength in the individual based model, defined as the mean square of the probabilistic interaction terms.

Finally, two intrinsic growth parameters were defined. The first parameter was a constant probability of mortality which was assessed on each individual before calculation of movement and reproduction probabilities. The second parameter was the probability of reproduction on encountering an available, unoccupied cell.

2.2. Simulations

Simulations were run on both homogeneous lattices, where all lattice-cells were available for occupation, and on heterogeneous lattices, where some cells were made unavailable for colonization. Simulations on homogeneous lattices examined the effect of emergent patterns, generated solely by the species interactions, on species coexistence and food web complexity. Simulations on heterogeneous lattices explored the effect of spatial heterogeneity of the lattice. Results from simulations on homogeneous and heterogeneous lattices were compared.

2.2.1. Homogeneous lattices

Three sets of simulations were run on 100 × 100 cell, homogeneous lattices. All cells in homogeneous lattices were available for occupation. In each set of simulations, a parameter space consisting of connectance (C) and interaction strength (P) was systematically explored. Connectance, or the fraction of non-zero interactions, was varied from 0.1 to 1.0 in 0.1 increments. Interaction strength, defined as the expected mean square of the non-zero interaction terms, was also varied from 0.1 to 1.0 in 0.1 increments.

Each lattice was seeded randomly with 254 species filling all cells in the lattice. Simulations were allowed to run 5000 iterations and the final number of species was recorded. In all cases, the number of species reached an equilibrium value before the end of the simulations. Ten replicate simulations with independent random seed values were run for each combination of connectance and interaction strength for a total of 1000 runs in each set.

The first set of simulations attempted to reproduce, within the constraints of the lattice-model implementation, the assumptions implicit in stability analyses of Lotka-Volterra models used in traditional food web studies (e.g. May, 1972, 1973; Pimm, 1982). Non-spatial dynamics were simulated by using a global movement rule. Species interactions were emphasized over intrinsic growth and mortality by allowing all species to reproduce when encountering empty cells and setting the background mortality rate to 0.0.

As a comparison to the non-spatial simulations and the prediction made in Eq. (6), a second set of simulations was run with all parameters identical to the first set, except that local interactions were used. Again, all species reproduced when encountering empty cells and the background mortality rate was set to 0.0.

A third set of simulations was run to examine the importance of intrinsic mortality on species coexistence. Parameters were the same as in the second set, but with a 0.05 background mortality rate. Simulations were run in local interaction mode.

2.2.2. Heterogeneous lattices

To test the effect of landscape heterogeneity on species coexistence, I ran two additional sets of simulations on heterogeneous lattices. Heterogeneous lattices had certain cells 'masked' or made unavailable for occupation. Two types of masks were used. Percolation masks (Stauffer and Aharony, 1985; Gardner et al., 1987) were constructed by making lattice cells available for colonization according to a probability $\hat{p}$ (Fig. 2). The remaining fraction of cells $(1-\hat{p})$ were unavailable.

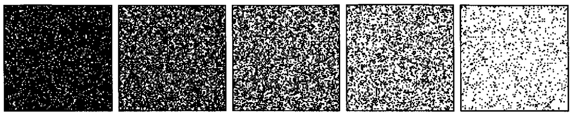

Fig. 2. Percolation masks. From left to right, fraction of available cells is 0.1, 0.3, 0.5, 0.7, 0.9.

The second type of masks used were segmented fractional-Brownian surfaces (Mandelbrot, 1982; Keitt and Johnson, 1995). Fractional-Brownian surfaces were constructed using the mid-point displacement method of generating fractals described by Saupe (1988). The surfaces were then segmented, making all locations above the mean available for colonization and all those below the mean unavailable, such that for each lattice, roughly 50% of the cells were available for colonization. The degree of contagion among cells was controlled by the Hurst exponent H ranging from 0.0 to 1.0 (Fig. 3). A Hurst exponent of 1.0 produced highly connected landscapes with most of the available habitat lumped into one or a few large patches. A Hurst exponent of 0.0 produced highly fragmented landscapes composed of many small habitat islands. Intermediate values for H produced landscapes with intermediate levels of connectivity; the available cells were distributed among a few medium-sized patches and many small patches. The effect of fragmentation (small H) was to constrain the movement of individuals which caused species interactions to be highly localized within a given patch.

To make the relationship between the Hurst exponent and landscape connectivity more intuitive, consider that, from the perspective of an individual moving on the lattices, connectivity is a function of how many neighboring cells are available for colonization. If all cells on the lattice have zero available neighbors, then the effective connectivity is zero because no individual can

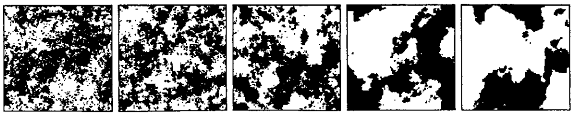

Fig. 3. Segmented fractional-Brownian masks. From left to right, Hurst exponents are 0.0, 0.25, 0.50, 0.75, 1.0.

move. When all neighbor cells are available, connectivity is at its maximum. Thus, the connectivity of the lattice is a function of the number of 'edge' cells, i.e. those with mixed available-non-available neighborhoods.

Based on fractal geometry (Mandelbrot, 1982), it is easy to show that the number of edge cells in the lattice is proportional to w^{2-H}, where w is the width of the lattice. Thus, the fraction of edge cells is given by

$$P(e) \approx w^{2-H}/w^2 = w^{-H} \tag{9}$$

where $P(e)$ is the fraction of edge cells in the lattice. Therefore, as H approaches zero, the fraction of edge cells approaches unity and connectivity is near zero. When $H = 1$, the proportion of edge cells is roughly $1/w$, and connectivity is maximized.

As was done for the homogeneous lattices, simulations were run with connectance ranging from 0.1 to 1.0. Interaction strength was held constant at 1.0. A 5% rate of mortality was included and movements were local. In addition, 5% of moves were global to allow species to colonize isolated patches. Lattices were 100 × 100 cells in size.

2.3. Statistical analysis

For each set of simulations, I tested whether the observed relationship between stability and complexity matched that predicted from the stability analysis of the non-spatial Lotka-Volterra webs. Assuming that a 'saturated' community will collapse to its maximum stable species richness, Eq. (5) can be rewritten as

$$s(mC)^{1/2} = 1.$$

Adding spatial interactions could have two effects. First, it could alter the relationships among number of species, connectance, and strength. This would change the steepness of the curves relating species richness to connectance and strength in Fig. 1. Second, spatial interactions could increase species richness over the entire range of connectance and strength, raising the entire surface in Fig. 1. Thus, we can generalize Eq. (6) as

$$m = \gamma s^{\alpha} C^{\beta} \tag{10}$$

where α and β determine the slope of the relationships among species richness, connectance, and strength; γ is the intercept or number of species when $s = C = 1$. Log-transformed, Eq. (10) is $\log m = \alpha \log s + \beta \log C + \log \gamma$. I tested the hypothesis that the estimated parameters, α, β, γ were equal to the expected values derived from May's stability criterion: $\alpha_0 = -2.0$, $\beta_0 = -1.0$ and $\gamma_0 = 1.0$ (SAS procedure REG). Differences between model runs were tested using ANOVA (SAS procedure GLM). Each set of simulations (global movement, local movement, local movement with mortality) was considered a treatment in a full factorial design (connectance × interaction strength × treatment).

Data from simulations on heterogeneous lattices were also fit to Eq. (10), except that P was replaced with either $\hat{p}$ or H. ANOVA was used to test for a significant effect of spatial heterogeneity on species richness.

3. Results

3.1. Emergent spatial patterns

Local species interactions resulted in a variety of spatial patterns (Fig. 4). In many cases, travelling wave patterns, involving three or more species, were observed. Persistent wave patterns occurred when there were cyclic chains of ± species interactions, i.e. the spontaneous formation of hypercycles (Eigen and Schuster, 1979). Occasionally, stable patches of a single species formed. Stable patches occurred when a patch of one species was surrounded by other, non-interacting species. However, often, these patches would eventually disappear when an interacting species (say a predator species) finally invaded the patch.

3.2. Species coexistence

For simulations using a global movement rule, power-law relationships between species richness and both interaction strength and connectance were significant ($R^2 = 0.89$, $F_{2,997} = 3862$, $P <$

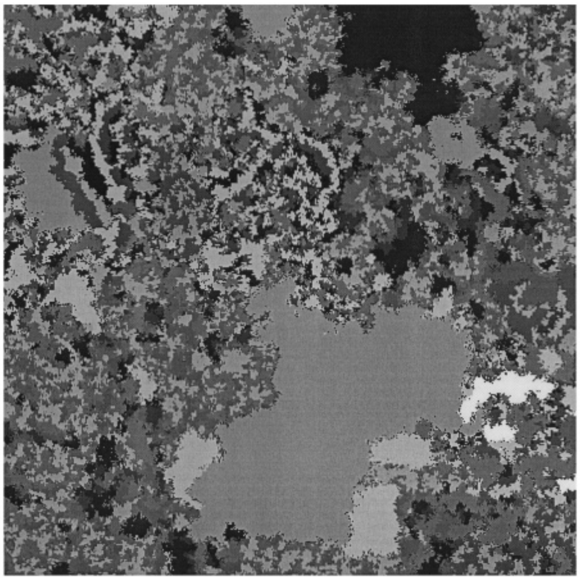

Fig. 4. Emergent spatial patterns for nine coexisting species.

0.0001) (Fig. 5). However, the regression parameters were significantly different from the expected values for May's stability criterion (Table 2). The most pronounced difference was the weak effect of interaction strength on species richness. The estimated value of $\alpha = -0.04$ was considerably higher than the expected value ($F_{1,997} = 19154$, $P < 0.0001$), resulting in fewer species coexisting than expected for low values of P. Connectance had a stronger effect on coexistence than expected ($\beta = -1.25$; $F_{1,997} = 300$, $P < 0.0001$). However, the difference between May's criterion and the lattice model in terms of stable number of species was relatively small. For $P \approx 1.0$, the difference was at most two to three species. The estimate of the intercept $\gamma = 0.91$ was significantly lower than the expected value ($F_{1,997} = 23$, $P < 0.0001$). Again, the difference was not biologically meaningful, predicting only 0.09 fewer species (0.91 versus 1.0) for $P = 1.0$ and $C = 1.0$. Thus, considering $P \approx s \approx 1.0$, the number of coexisting species was approximately the same as predicted by May's criterion. As interaction strengths decreased ($P \to 0$), fewer species coexisted than predicted by May's criterion.

The results for local interactions with no mortality (Fig. 6) were quite different than for non-spatial simulations using the same parameters (Fig. 5). Again, the regression was significant ($R^2 = 0.84$, $F_{2899} = 2414$, $P < 0.0001$) and interaction strength had a relatively small effect on coexistence ($\alpha = 0{:}26$, $F_{1897} = 4178$, $P < 0.0001$). Connectance had a strong effect on species richness. The estimated value for $\beta = 2.54$ was significantly greater than the expected value ($F_{1897} = 1378$, $P < 0.0001$). The intercept was larger than the expected value ($F_{1897} = 140$, $P < 0.0001$) and greater than that found for the non-spatial simulations (Table 2) indicating an overall increase in stability compared with the non-spatial simulations. The flattening of the response curve for low values of connectance in Fig. 6 was simply due to the limitations of the model; no more than 254 species were allowed. Simulations where no species went extinct were not included in the statistical analysis.

Adding 5% mortality to the local interaction model (Fig. 7) greatly reduced the effect of connectance on species richness. The overall regression was significant ($R^2 = 0.74$, $F_{2997} = 1405$, $P < 0.0001$). Interestingly, the estimated value of $\beta = 0.99$ was not significantly different from the analytical result, $\beta_0 = 1.0$, for non-spatial models ($F_{1997} = 0.19$, $P = 0.66$). However, the intercept was significantly higher than the expected value ($\gamma = 1.88$, $F_{1997} = 632$, $P < 0.0001$) and over twice as large as the intercept for the non-spatial simulations, indicating that spatial interactions increased model stability even in the presence of background mortality. As with the previous two results, interaction strength had a relatively small effect on coexistence ($\alpha = 0.20$, $F_{1997} = 8833$, $P < 0.0001$).

Comparing all three sets of simulations on homogeneous lattices, both connectance and interaction strength had a significant effect on species coexistence (Table 3). A significant interaction effect between connectance and strength was not observed. Simulations with local interactions supported greater species richness than did the mean-field simulations; local movement without mortality resulted in the greatest species richness followed by local movement with mortality, then global movement (Tukey's test; all comparisons significant at $\alpha = 0.05$). Significant interaction effects were found for connectance-by-treatment, strength-by-treatment and connectance-by-

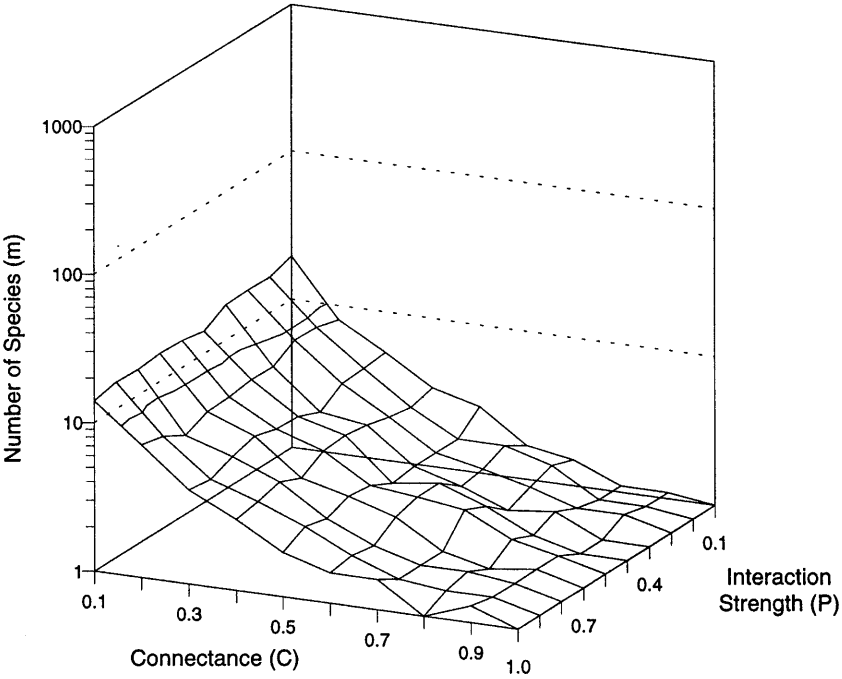

Fig. 5. Simulated species richness using global movement.

strength-by-treatment (Table 3). Thus, the relationship between community structure and stability is not as simple as suggested by studies that do not incorporate spatial heterogeneity.

Two additional sets of simulations were run on heterogeneous lattices. Simulations on percolation maps produced a strongly non-linear response in species richness to the degree of heterogeneity in the lattice (Fig. 8). The number of species initially increased as spatial heterogeneity increased, peaking at $\hat{p} = 0.3$, and then decreased for small values of $\hat{p}$. The decrease in species richness was probably due simply to the decrease in total number of available cells as $\hat{p}$ decreased. A regression through the log-transformed data was significant ($F_{2997} = 512$, $P < 0.0001$), but the R^2 dropped to 0.51 as one would expect when fitting a linear model to the non-linear pattern of species number. The effect of connectance on species coexistence was somewhat reduced, compared with other simulations with local interactions, as well as lower than for the stability analysis results ($\beta = 0.78$, $F_{1997} = 29$, $P < 0.0001$).

The effect of $\hat{p}$ on species richness was tested. Heterogeneity had a significant effect on number of species ($F_{9900} = 1127$, $P < 0.0001$). The relationship between connectance and species coexistence appeared to vary with lattice heterogeneity (Fig. 8). This resulted in a significant interaction effect between connectance and $\hat{p}(F_{81\,900} = 80$, $P < 0.0001)$.

Species richness was greater on increasingly heterogeneous fractal lattices ($F_{101\,099} = 235$, $P < 0.0001$)(Fig. 9). Unlike the simulations on percolation lattices, the increase in species richness was roughly monotonic with increasing heterogeneity, thereby supporting the assertion that the decrease for low $\hat{p}$ was due to reduced area. A significant connectance-by-Hurst-exponent interaction was found ($F_{901\,099} = 1.86$, $P < 0.0001$). The regression estimate of $\beta = 1.06$ was consistent with other simulations using local movement ($R^2 = 0.85$, $F_{21\,097} = 3049$, $P < 0.0001$). The slope of the relationship between the Hurst exponent and number of species was -0.67. Thus, more species coexisted as the heterogeneity of the lattice increased.

Table 2
Summary of regression results

Fig.	Movement	Mort.	$\alpha \pm$ S.E.	$\beta \pm$ S.E.	$\gamma \pm$ S.E.
5	Global	0.0	-0.04 ± 0.014	-1.25 ± 0.014	0.91 ± 0.019
6	Local	0.0	-0.26 ± 0.027	-2.54 ± 0.037	1.54 ± 0.036
7	Local	0.05	-0.20 ± 0.019	-0.99 ± 0.019	1.88 ± 0.025
8	Local[a]	0.05	—	-0.78 ± 0.040	—
9	Local[b]	0.05	—	-1.06 ± 0.016	—

[a] Local movement on percolation lattices.

[b] Local movement on fractal lattices.

4. Discussion

These results establish local interactions and spatial heterogeneity as contingencies affecting the coexistence of species. Adding spatial interaction not only increased species coexistence compared with non-spatial models, but also altered the relationship between interaction strength, connectance and stability. Adding spatial heterogeneity to the environment further altered stability-complexity relationships and lead to increased coexistence among species.

The simulated results did not agree in general with May's stability criterion for random community webs. The major qualitative difference between the simulated results and May's criterion was the lack of a strong effect of interaction strength on species richness. This may have been due to the difference between the discrete probabilistic interaction terms used in the lattice model and the continuous partial differentials used in community matrices. The lack of an effect of interaction strength suggested that the magnitude of the interaction probabilities affected primarily the rate at which the communities collapsed to an equilibrium, but did not greatly alter the final number of species.

More important however were the comparisons between the model when run in non-spatial mode versus simulations with spatial interactions. Comparing the model to itself provides a robust control because all aspects of the implementation are the same. The results from those comparisons were clear; spatially structured food webs are more stable in terms of number of coexisting species than webs without spatial population structure. Comparisons among simulations run with different degrees of spatial heterogeneity in the underlying lattice also control for the model implementation, isolating only the effect of different lattices. Those comparisons also showed that coexistence and stability in food webs can be altered by spatial considerations.

The inverse power-law relationship between web connectance and number of species predicted from May's criterion was observed in all simulations. This is contrary to the result found by Cohen et al., 1990b that no simple relationship between connectance and species richness governs food web stability. Although Cohen et al. disprove the generality of May's criterion, their analysis is restricted to webs of infinite size. Food webs in nature must be limited in size due to some limiting resource. In the lattice model, space was always a limiting resource on population growth. The decrease in species richness with increasing connectance observed in the lattice model suggests a relationship similar to May's for webs in which some resource limits the maximum possible web size.

In general, the rate (β) at which species richness decreased with increasing web connectance was similar to that predicted by Eq. (6). The exception was the strong effect of connectance for simulations with local interactions and no mortality. The reason for the high degree of coexistence for low connectance and no mortality has to do with the constraint of allowing only a single individual to occupy any given cell. Thus, for any individual to move to an occupied cell, the current occupant had to be removed from the lattice. This introduced a correlation between the rate of movement

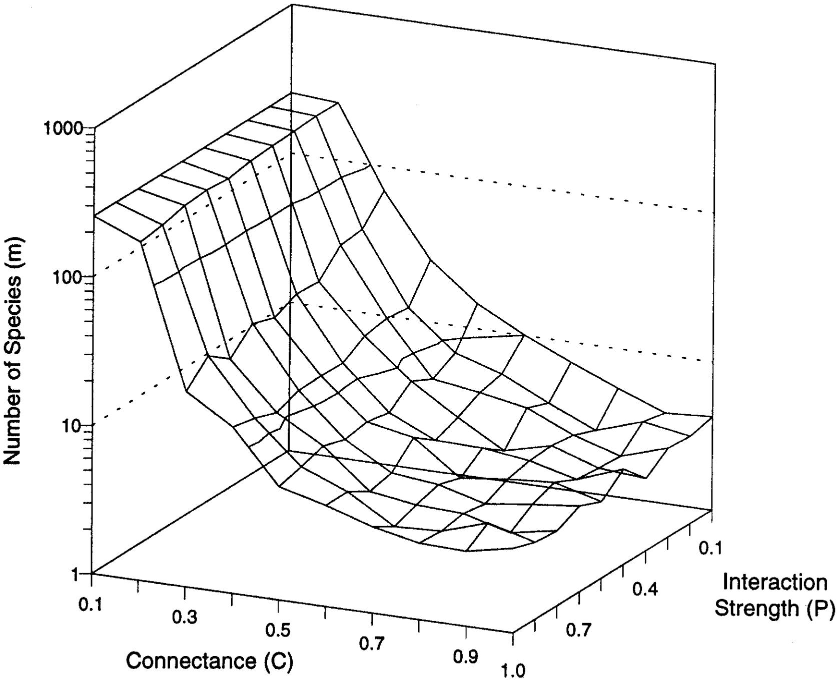

Fig. 6. Simulated species richness with local movement.

across the lattice and the interaction terms (see Table 1). For low values of connectance, the situation often arose in which an individual was surrounded by other species with which it had zero interaction terms. In the absence of mortality, the entire lattice could become essentially 'frozen' in place with no individual able to move, reproduce, or go extinct, explaining the high species richness observed (Fig. 6).

The constraint of allowing only a single individual in each cell emphasizes localization of species interactions and hence the importance of space in determining stability. Similarly, cellular automata models which have been applied to modeling ecological systems are strongly spatial, being both discrete in space and time (Hogeweg, 1988; Molofsky, 1994). Other spatial models allow for greater mixing of individuals by allowing multiple individuals within a patch or cell and decoupling interactions from dispersal. Examples include metapopulation models (Hanski and Gilpin, 1991), partial differential equation models (Holmes et al., 1994), and particle interaction models (Durrett and Levin, 1994b). At the other extreme, ordinary differential equation models such as the Lotka-Volterra system assume a completely mixed system. Thus, these models represent a spectrum of different degrees of spatial constraint on species interactions. The appropriateness of a particular model will depend on the how well it captures the spatial constraints of the system being modeled.

There are a number of ways in which the current model could be extended. For example, constraints were not placed on the topology of the randomly constructed webs. Feeding cycles were allowed and often observed in the simulated webs. Whereas the formation of stable 'feeding cycles' in spatial simulations is interesting from the standpoint of molecular evolution (Eigen and Schuster, 1979), they are not realistic in food webs (Cohen, 1977; Pimm, 1982). It would be interesting to compare results from random webs to webs generated according to the trophic cascade model (Cohen et al., 1990a) which does not allow consumer cycles. Other modifications might include intro-

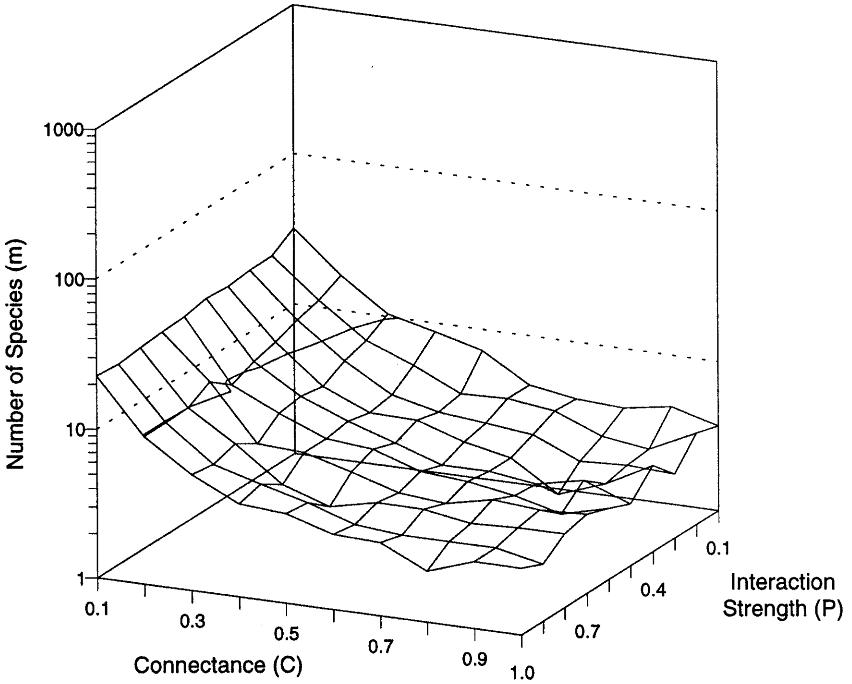

Fig. 7. Simulated species richness with 5% mortality added.

ducing differences in the movement rule depending on the trophic level of a species. For example, predator species which typically have greater body size than prey species (Peters, 1983) could be allowed to move further or cover a greater number cells in each iteration (Milne et al., 1992). It would also be interesting to explicitly model energetic constraints on movement, reproduction, prey-handling, and basal metabolism based on allometric scaling relations.

Table 3
ANOVA table comparing model treatments

Source	d*f*	MS	*F*	*P*
Connectance (*C*)	9	271.85	1950.83	<0.0001
Strength (*P*)	9	4.66	33.43	<0.0001
Connectance × strength	81	0.17	1.23	0.0851
Treatment	2	513.62	3685.75	<0.0001
Connectance × treatment	17	24.05	172.57	<0.0001
Strength × treatment	18	0.86	6.19	<0.0001
Conn. × strength × tmnt.	153	0.17	1.22	0.0351
Error	2610	0.14	–	–

In conclusion, this study has shown that for numerical simulations of species interactions on lattices, the relationships among food web connectance, interaction probabilities, and species richness vary depending on whether interactions are local in space, or global. Furthermore, the introduction of spatial heterogeneity into the lattice structure can also alter these relationships. Thus, there is a need to include spatial considerations in a theory of the stability and complexity of ecological systems.

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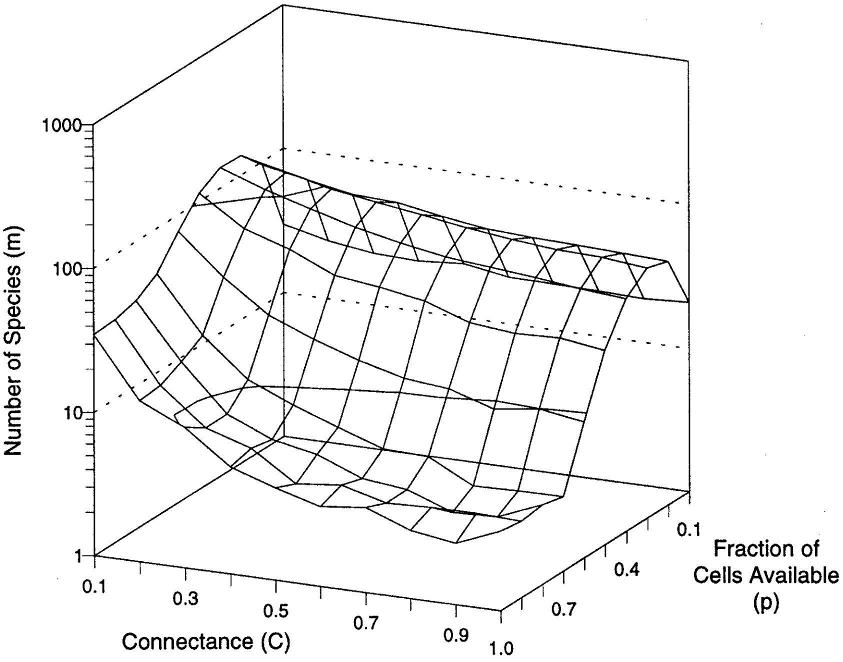

Fig. 8. Species richness on percolation lattices.

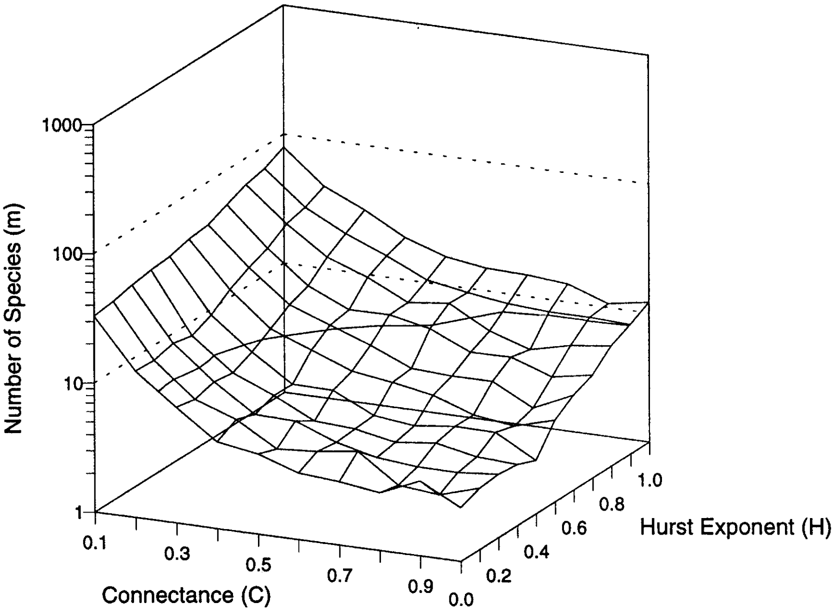

Fig. 9. Species diversity on fractal lattices.

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