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Competition and Species Packing in Patchy Environments

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In models of competition in which space is treated as a continuum, and population size as continuous, there are no limits to the number of species that can coexist. For a finite number of sites, *N*, the results are different. The answer will, of course, depend on the model used to ask the question. In the Tilman–May–Nowak ordinary differential equation model, the number of species is asymptotically $C \log N$ with most species packed in at the upper end of the competitive hierarchy. In contrast, for metapopulation models with discrete individuals and stochastic spatial systems with various competition neighborhoods, we find a traditional species area relationship CN^a, with no species clumping along the phenotypic gradient. The exponent *a* is larger by a factor of 2 for spatially explicit models. In words, a spatial distribution of competitors allows for greater diversity than a metapopulation model due to the effects of recruitment limitation in their competition.   © 2002 Elsevier Science (USA)

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1. INTRODUCTION

One of the central problems in ecology is how the large number of species on Earth can coexist, and what sets limits on diversity. Almost 40 years ago, Hutchinson (1961) noted that the coexistence of hundreds of species of algae in lakes is not consistent with the competitive exclusion principle, which predicts that in homogeneous and equilibrial systems, the number of coexisting species cannot exceed the number of resources. As many authors have shown, a slow approach to equilibrium, or temporal or spatial heterogeneity, can significantly increase the possibilities for biodiversity. In our studies, we will restrict our attention to systems that are physically homogeneous in their underlying properties, but are not due to endogenous heterogeneity arising from competition among species.

A problem with the competitive exclusion principle is that the simplicity of its statement can be misleading.

Species may compete for a common resource, without being limited simply by its availability, because they differ in the way they utilize the resource. Space, for example, is the direct object of competition among species in a wide variety of systems, e.g., forests, grasslands, coral reefs, and the marine benthic zones. Asynchronous gap formation, however, either due to extrinsic influences or to the natural deaths of individuals, can create opportunities for colonization and an almost infinite subdivision of successional gradients (Levin and Paine, 1974). Although space remains the ultimate limiting resource in such systems, not all space is equally available to all species. Time since disturbance provides an axis of differentiation for species; and individual species are limited not by the total amount of space, but in effect by the amount of space of a particular successional stage.

Tilman (1994), building on the metapopulation framework of Levins (1969; see also Hastings, 1980), studies a model of such systems that assumes a purely hierarchical competition scheme. It has long been known that for such systems, at least in the absence of stochastic influences (and see Turelli (1986), even for many forms of stochasticity) there is no limit to the number of competing species that can coexist (May and MacArthur, 1972). Specifically, Tilman studies coexistence among a sequence of species in which the lower-numbered species are superior competitors. Letting p_i be the fraction of patches occupied by type i and taking the limit of an infinite number of patches, he arrives at the following dynamics:

$$\frac{dp_i}{dt} = \beta_i p_i \left(1 - \sum_{j=1}^{i} p_j \right) - \delta_i p_i - p_i \sum_{j=1}^{i-1} \beta_j p_j. \quad (1)$$

where β_i and δ_i are the colonization and death rates for the ith species. The first term on the right-hand side represents births by type i onto sites that are vacant or occupied by inferior competitors. The second and third terms represent loss of sites of type i due to deaths or takeover by lower numbered species.

The first equation in (1) says $dp_1/dt = \beta_1 p_1(1 - p_1) - \delta_1 p_1$, so in equilibrium we have $p_1^* = (\beta_1 - \delta_1)/\beta_1$. In general, the equation for each p_i^* only involves $p_1^*, \ldots, p_i^*$, so the equations can be solved recursively for the equilibrium frequencies. The algebra of the exact solution is somewhat messy, but one can easily verify that an arbitrarily large number of species can coexist. If we take $\delta_i = 1$ for all i, and each β_i is in turn chosen large enough, then each $p_i^* > 0$. The differential equation (1) actually only applies in the limit of an infinite number of patches, so what Tilman's

computation shows is that in an infinite area infinitely many species can coexist. Infinite coexistence is of course impossible, and is an artifact of (i) the assumption of pure hierarchy, (ii) the myth that the parameters for a particular type are constant, and (iii) the assumption of instantaneous takeover of patches by superior competitors, implicit in the ODE framework. Elsewhere (see Durrett and Levin, 1998) we have relaxed the assumption of a strict competitive hierarchy.

In this paper, we will test the robustness of some of these assumptions by investigating the number of species that can coexist on a finite number of sites N, and by requiring that equilibrium abundances exceed a threshold level. It is also important to examine the effects of relaxing the hierarchy assumption as we have done in Durrett and Levin (1998). Nonetheless, we think that it is important to elucidate the effects of these assumptions separately, and hence we restrict our attention in this paper to the hierarchical model.

For mathematical simplicity, instead of assuming $\delta_i \equiv 1$ we will investigate the special case of Tilman's model in which all species have the same colonizing ability, $\beta_i = 1$ for all i. This case was used by May and Nowak (1994) to study the distribution of types in the discrete time system in which one repeatedly does the following:

(i) introduce a new species with death rate δ chosen at random from $(0, 1)$, and
(ii) recompute the equilibrium distribution.

The long-term behavior of this process should reflect the behavior of a system where migrations into the system are rare, and the system has a chance to relax to equilibrium between migrations. May and Nowak analyzed this system using heuristic arguments and computer simulations. Figure 1 shows a simulation of May and Nowak's process until time 100 million, and also the state at the final time. Note the slow growth in the total number of species as a function of time, and the packing of the species near the maximum value of the death rate in the final state.

To create the graph in Fig. 2, we have examined the system every 100 time steps between times 100,000 and 100 million and averaged our observations. Here we have divided the axis of death rates into bins of width 0.01 and counted for each bin: (a) the number of species, (b) the average abundance per species, and (c) the total abundance of species in the bin. We then divided these quantities by 0.01 to compare with the predictions of May and Nowak (1994) that the density functions are given by (a) $A/(1 - \delta)$, (b) $(1 - \delta)/2A$, and (c) $1/2$. The results in Fig. 2 show good agreement between our simulations and their theory.
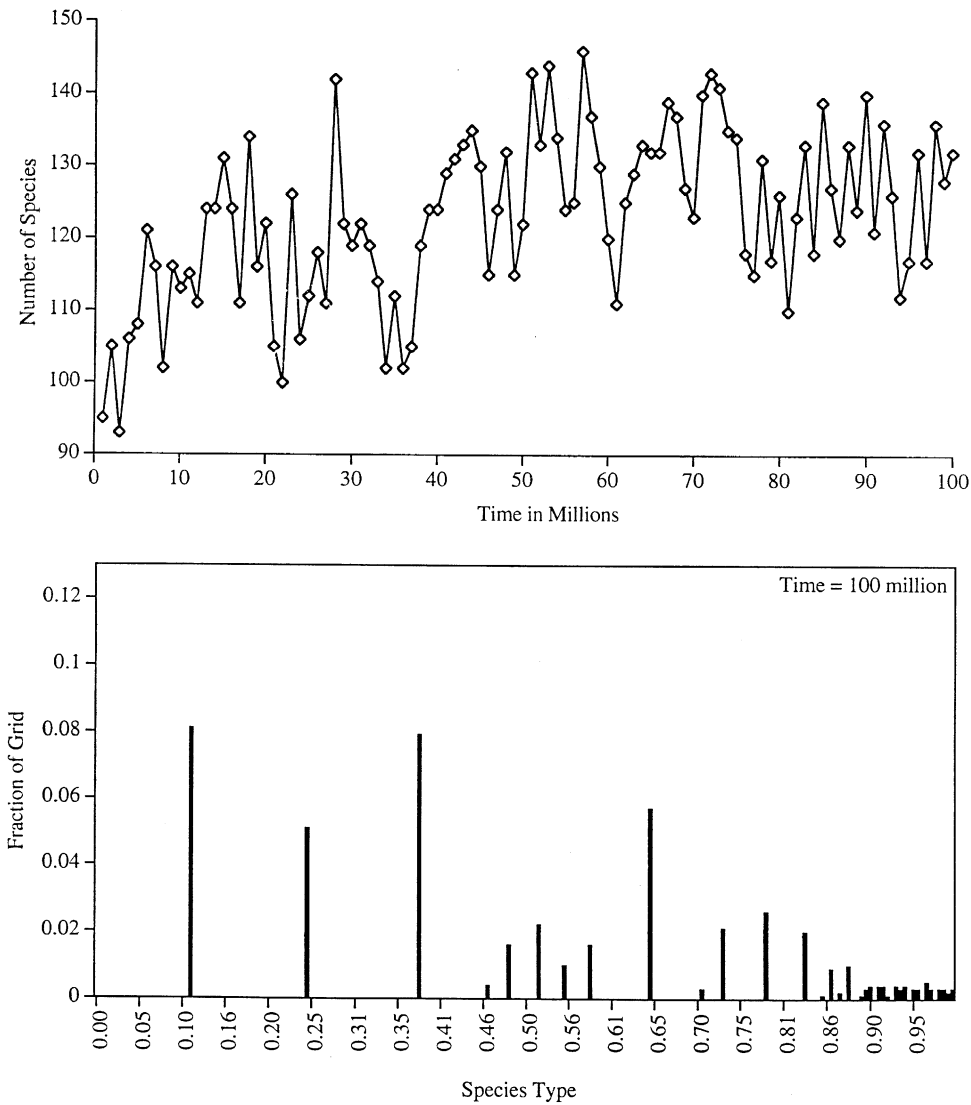
FIG. 1. Simulation of May and Nowak's process for 100 million units of time. The top panel shows the number of species versus time, and the bottom panel gives the state at the final time. Note the packing of many species of small abundances near 1.

May and Nowak have a simple heuristic argument that explains these curves. Observe that inserted species have no effect on those with higher death rates and may or may not eliminate those with a lower death rate. The exact calculation of which species are eliminated is complicated. However, if we suppose that each new species eliminates those below it independently and with a fixed probability α, then the equilibrium density will be $1/\alpha(1 - \delta)$. The value of α cannot be guessed intuitively, but extensive simulations suggest that it is about 0.114. Simple bookkeeping demands that (a) times (b) equals (c), so the shape of (b) follows from that of (c), which in

turn, as May and Nowak (1994) showed, can be derived from a simple heuristic.

Since $\int_0^1 A/(1 - \delta)\, d\delta = \infty$ the number of species in the May–Nowak model does not reach equilibrium but grows with time. If one observes that after t species have been introduced, the species with the largest death rate is at $\approx 1 - 1/t$, one can guess that the number after t insertions in their model grows like

$$\int_0^{1-1/t} \frac{A}{1 - \delta}\, d\delta = A \ln t \approx 20 \log_{10} t. \qquad (2)$$
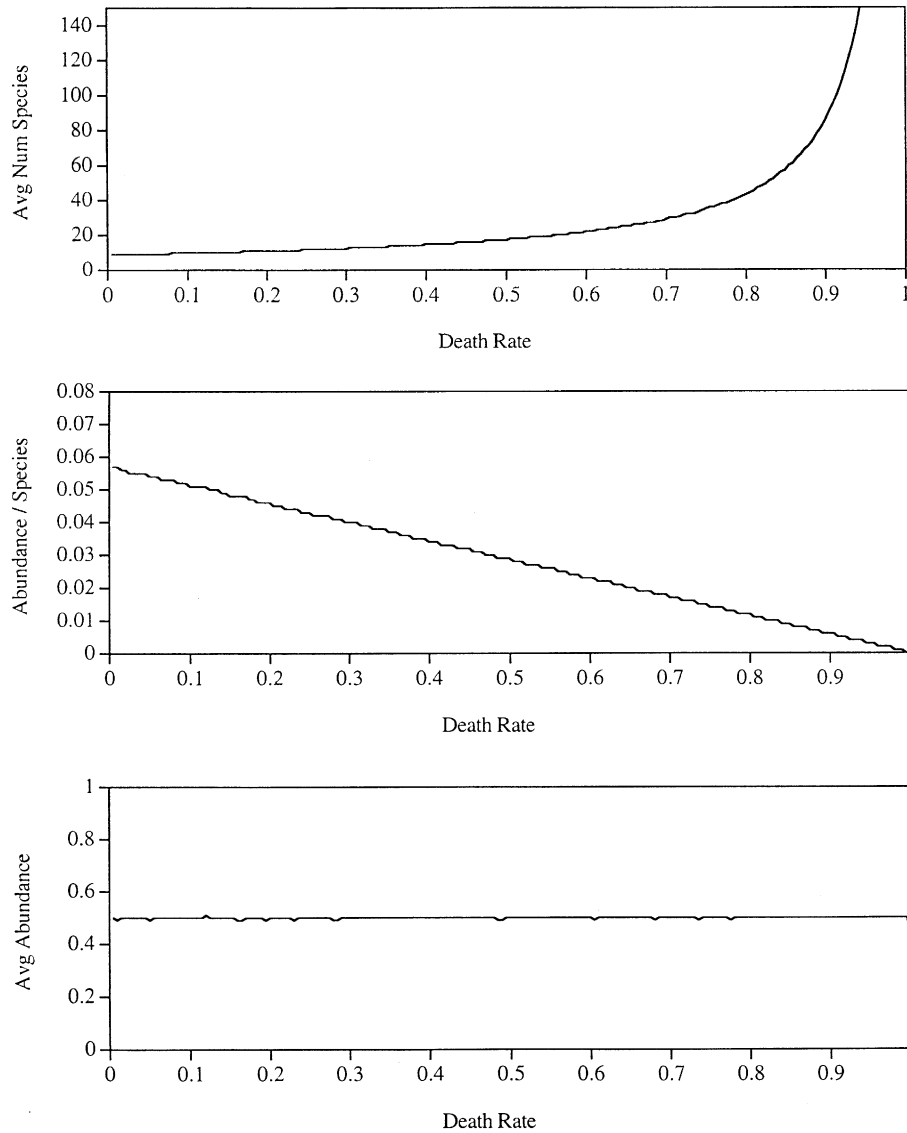
FIG. 2. Average behavior of May and Nowak's model between times 100,000 and 100 million. The axis is divided into bins of width 0.01 and in the three panels we display (a) the number of species, (b) the average abundance per species, and (c) the total abundance in the bin.

2. MODIFICATIONS OF THE MAY–NOWAK MODEL

May and Nowak's results, like Tilman's, are for a system with infinitely many patches. The first and simplest thing one could do to guess the number of species that will coexist in a discrete version of the May–Nowak model is to observe that if there are N sites, then no species can have abundance smaller than $1/N$. This implies that no species can have $\delta > 1 - 1/N$. Using the reasoning that led to (2) and realizing that other species may be eliminated by this requirement, we see that in equilibrium the number of species will be at most $20 \log_{10} N$. To gauge this numerical prediction, we note that Tilman's experiments at the Cedar Creek Natural History Area have found approximately 200 species coexisting on a 1-ha plot. If we model Tilman's study area as a grid with sites that are 1 cm on a side, then we have roughly 10^8 sites. Ignoring the fact that this is just an upper bound, the predicted value of 160 species is the right order of magnitude. While the number of species may be correct, their distribution in

parameter space is not. It follows easily from (2) that half of the species are between $1 - e^{-4} = 0.9817$ and 1.

Skeptical readers (including the three authors) can observe that by choosing our grid size carefully we can make the prediction match the Cedar Creek numbers exactly. Thus, one only gets a legitimate test of the predictions if one compares observations between at least two scales. To do this, consider, in addition, North America, which for simplicity we will consider to be a rectangle 5000×2000 km, or 10^7 km^2. This is 10^9 times as large as Tilman's 0.01 km^2 plot. However, due to the logarithmic nature of the answer, the prediction for the number of species in the larger area is only twice as large instead of the observed 100-fold increase. This multi-plicative increase suggests a power-law CN^a. Since there is a 100-fold increase when the number of sites is increased by a factor of 10^9, $a = 2/9$. Of course, Cedar Creek may not be near its species packing limit. This would decrease the power somewhat, but it would need to have almost 10,000 species (i.e., 500 times as many) in 1 ha to make the logarithmic growth correct.

To explore the generality of the prediction of logarithmic growth of species with area in models of the May–Nowak type, we will consider a variant that introduces one consequence of having a finite number of sites: existing species will be lost due to fluctuations. To see the effect of this change we have simulated a version of the May–Nowak model in which species with equilibrium abundance of <0.001 are eliminated. The simulation in Fig. 3 shows that the truncated process reaches an equilibrium in which an average of about 40 species are maintained. Though the number of species has been reduced by truncation, the patterns of their distribution are not changed. The bottom panel in Fig. 3 shows the result of averaging the behavior of the system from time 100,000 to 100 million. The result is similar to that in Fig. 2a. We have not done the analogues of the second and third curves in Fig. 2 since simulations show that the last one will be constant at $1/2$, and given this information the second one is the reciprocal of twice the first.

3. DIVERSITY IN DISCRETE AND SPATIAL MODELS

In the previous section, we considered various modifications of the May–Nowak model. All of these systems have two undesirable properties—packing of species at the top end of the competitive hierarchy and a logarithmic increase of species with area—so we will now consider two types of stochastic models with discrete individuals. In each system there is a finite set of sites S, and the state of the system at time t is described by a function $\xi_t: S \to [0, 1]$, where $\xi_t(x)$ gives the death rate of the individual at x at time t and $\xi_t(x) = 0$ indicates an empty site. Our first, *metapopula-tion*, model takes place on $S = \{1, 2, \ldots, N\}$, and evolves as follows:

 (i) The particle at x dies, i.e., becomes 0, at rate $\xi_t(x)$.
 (ii) Each site gives birth at rate 1 to an offspring of the same type.
 (iii) An offspring born at x is sent to a site y chosen at random from the grid.
 (iv) If $\xi_t(x) > \xi_t(y)$ then the value at y changes to $\xi_t(x)$.
 (v) Each site changes at rate μ to a type chosen uniformly from [0,1].

Rules (i), (ii), and (iv) are the natural generalization to this setting of the constant fecundity case, $\beta_i \equiv 1$, of Tilman's system. Rule (v) incorporates migration of new types into the system as in the May–Nowak process. Rule (iii) is the dispersal function of a metapopulation model. In our second, *spatially explicit*, model $S = [1, L]^2 = \{(m, n): 1 \leqslant m, n \leqslant L\}$. All the rules stay the same but (iii), which becomes:

(iii′) An offspring born at x is sent to a neighbor y chosen at random.

We examine the second process on a torus, for convenience. That means that y is a neighbor of x if $(y_1 - x_1, y_2 - x_2) \in \mathcal{N}$, where the differences of the components $y_i - x_i$ are computed modulo L. The use of modulo arithmetic gives us *periodic boundary condi-tions*. In words, sites on the left edge of the square are neighbors of those on the right, and those on the top are neighbors of those on the bottom. Here, we will only be concerned with two kinds of neighborhoods $\mathcal{N}$: the four nearest neighbors $\mathcal{N}_1 = \{(1, 0), (0, 1), (-1, 0), (0, -1)\}$ and the 5×5 neighborhood $\mathcal{N}_2 = \{z: \max_i |z_i| \leqslant 2\}$.

The first step in understanding the behavior of these models is to simulate the systems for one fixed set of parameter values. Let the side length of the square $L = 400$, and the number of individuals $N = 400^2 = 160,000$. That is, we are considering a 400×400 spatial grid or a metapopulation model with 160,000 sites. Figures 4–6 give the results of the simulations for the discrete metapopulation model and for the spatial model with the 5×5 neighborhood $\mathcal{N}_2$ and the four nearest neighbors $\mathcal{N}_1$ defined above. In
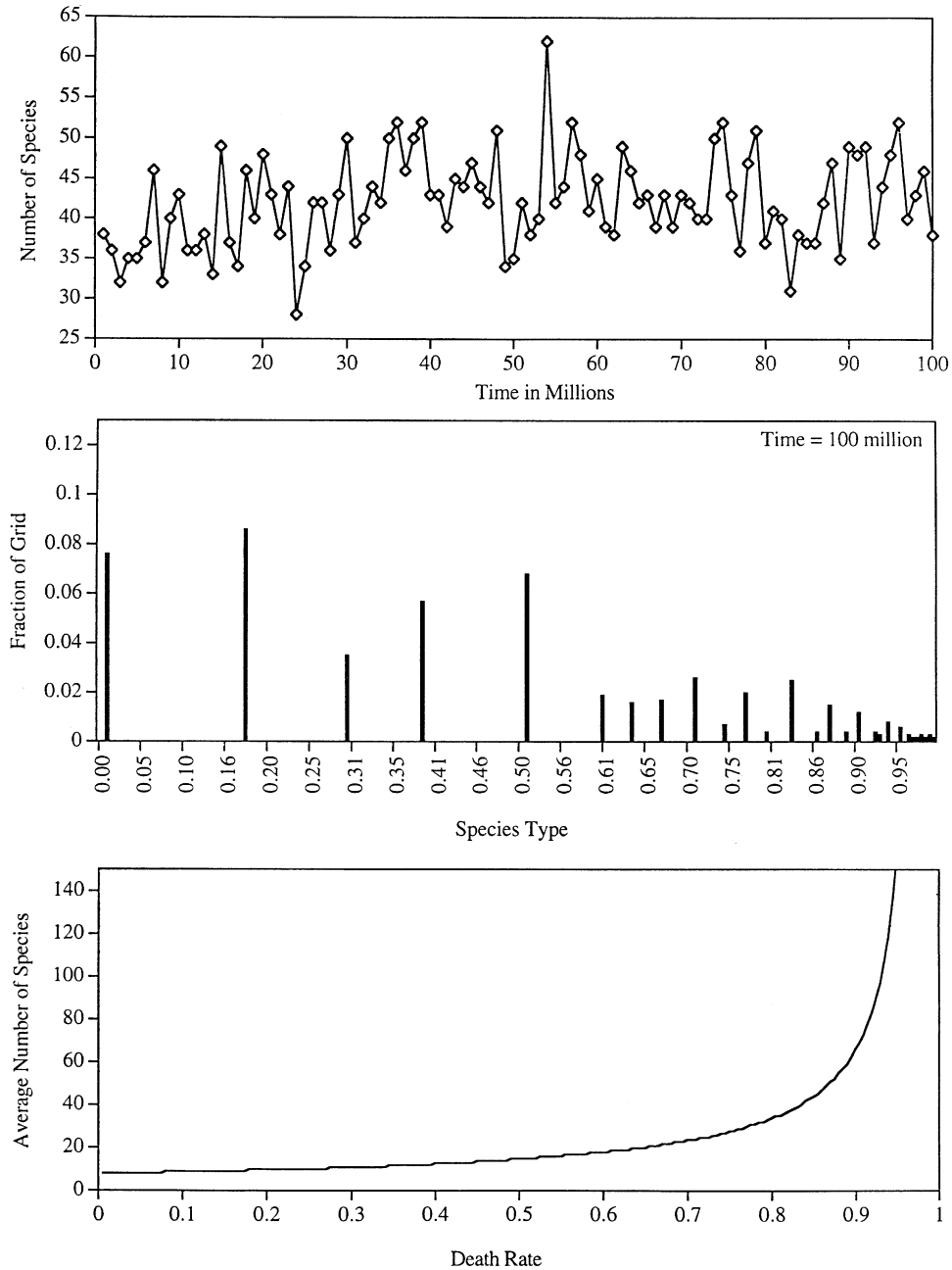
FIG. 3. Simulation for 100 million time units of a version of the May–Nowak model in which species with equilibrium abundance smaller than 0.001 are eliminated. The top panel gives the number of species versus time, the middle gives the state at the final time, while the bottom gives the average number of species observed in bins of width 0.01, just as in Fig. 2a.

each case, the number of migrants per generation $N\mu = 1$.

The first thing to notice is that the number of species is about 45 in the first case, 100 in the second, and 120 in the third. This pattern is not surprising. In the

metapopulation model all sites are adjacent to each other, so each individual interacts equally with all of the others. In the spatial models, different species can become isolated from each other, lessening interspecific competition. Comparing the results for the 5×5
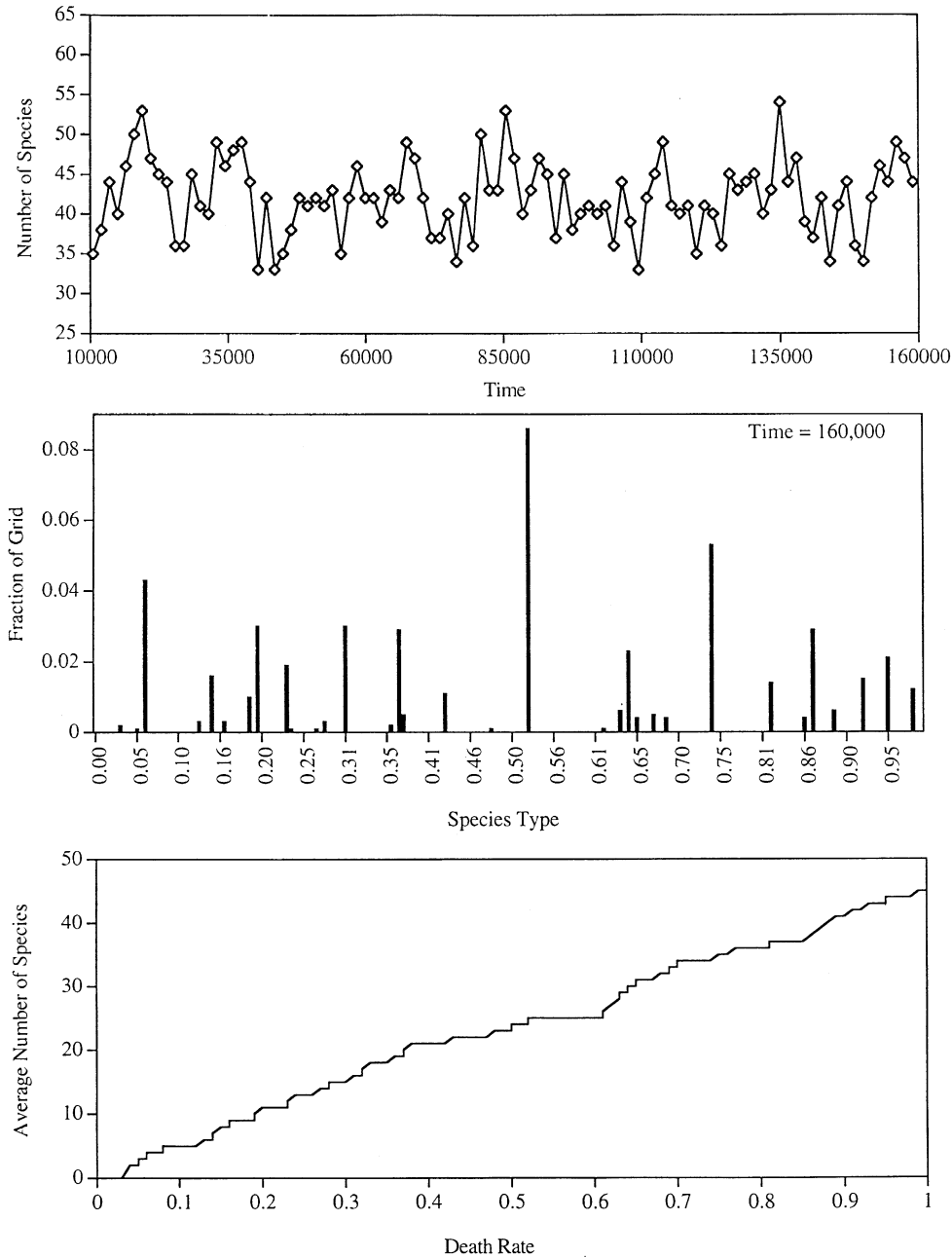
FIG. 4. Simulations of a 160,000 thousand site metapopulation model for 160,000 units of time. As the top panel shows there is a stationary distribution for the number of species. The middle panel gives a snapshot at the final time. The bottom panel gives a graph of the average number of species with death rates $\leq x$. This graph is almost linear so the underlying species are almost uniformly spread on $(0,1)$.

neighborhood and the nearest neighbors shows that reducing the dispersal distance increases isolation and further decreases interspecific competition.

The middle panels of Figs. 4–6 show snapshots of the systems at time 160,000. The first noticeable difference is that species are scattered over $(0,1)$ in the first case, over roughly $(0,2/3)$ in the second, and over roughly $(0,0.6)$

in the third. This pattern occurs since in each system species with a δ larger than the critical death rate cannot survive even in the absence of competition. The metapopulation model has $\delta_c = 1$ while the two spatial models have $\delta_c \approx 2/3$ and $\delta_c \approx 0.6$, respectively. To the naked eye the distribution of the species in the spatial models may appear to be more clumped in Figs. 5 and 6
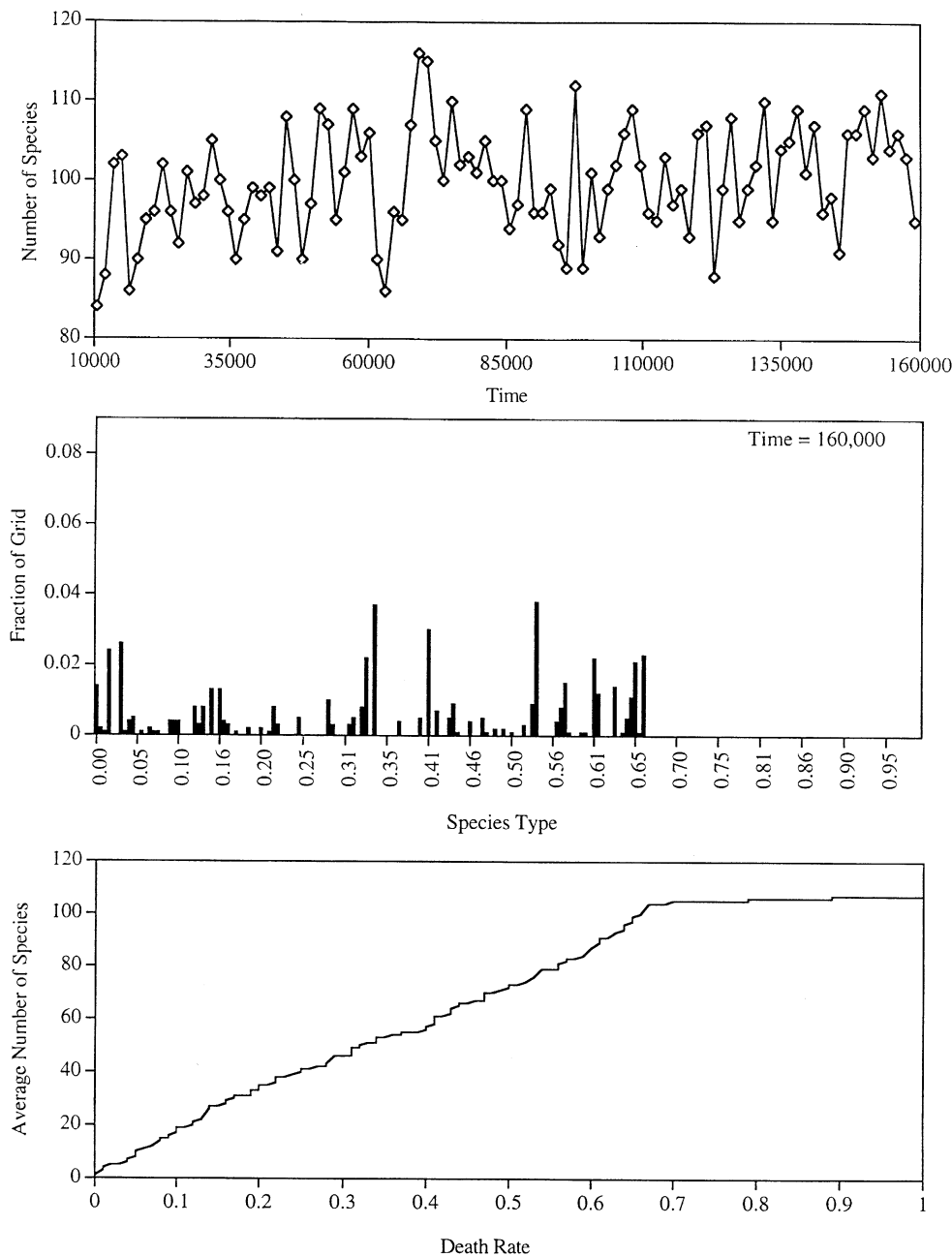
FIG. 5. Simulations of a 400 × 400 spatial model with dispersal uniform over a 5 × 5 neighborhood for 160,000 units of time. As the top panel shows there is a stationary distribution with more species on the average than in the metapopulation model in Fig. 6. The middle panel gives a snapshot at the final time. Species cannot survive above the critical value for the corresponding contact process, which in this case is ≈ 0.66. The bottom panel again gives a graph of the average number of species with death rates ≤ x. This graph is almost linear up to δ_c, so the underlying species are almost uniformly spread on $(0, \delta_c)$.

than in the metapopulation model in Fig. 4. However, comparing the bottom panels of these three figures which average the distribution of species between times 10,000 and 160,000 shows that in each case the distribution of species is approximately uniform on $(0, \delta_c)$.

To investigate the behavior of the number of species versus the size of the grid we have considered the
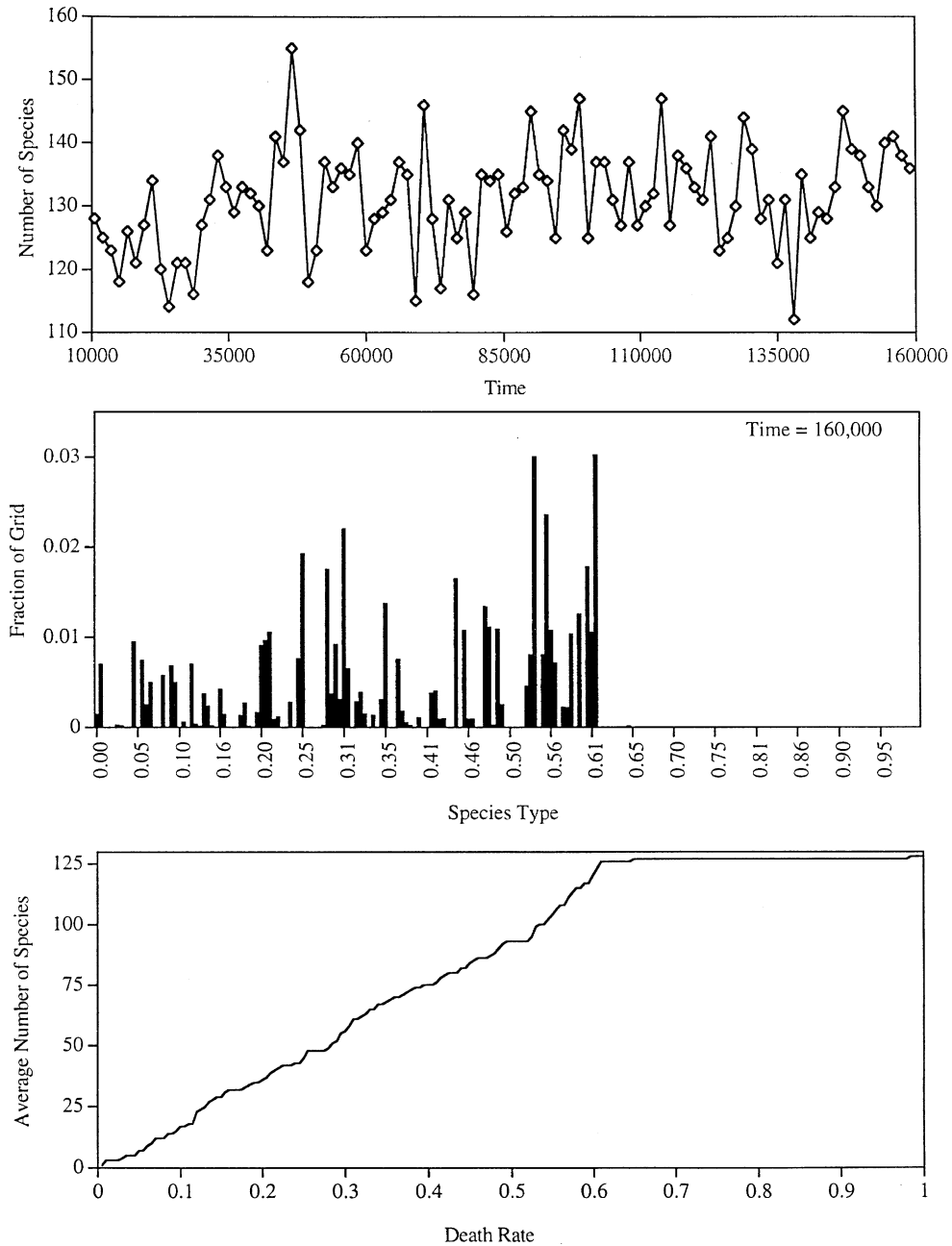
FIG. 6. Simulations of a 400×400 spatial model with nearest neighbor dispersal for $160,000$ units of time. As the top panel shows there is a stationary distribution for the number of species that has even more species than in spatial model with 5×5 dispersal neighborhood in Fig. 7. The middle panel gives a snapshot at the final time. Species cannot survive above the critical value for the corresponding contact process, which in this case is $\delta_c \approx 0.6$. However, as in the last two figures, the underlying species are almost uniformly spread on $(0, \delta_c)$.

systems with $L = 100$, 200, $300, \ldots$, 800, i.e., spatial models on an $L \times L$ grid or a metapopulation model with $N = L^2$ points. In each case we have set the number of migrants per generation $N\mu = 1$. Figure 7 shows the result of a plot of the base 10 logarithm of the number of species versus $\log_{10} L$. In each case the relationship between species S and area has the form $S \sim CN^a$. However, in the metapopulation model $a \approx 0.17$ while in the two spatial models $a \approx 0.34$. Returning to the Cedar Creek versus North America comparison,
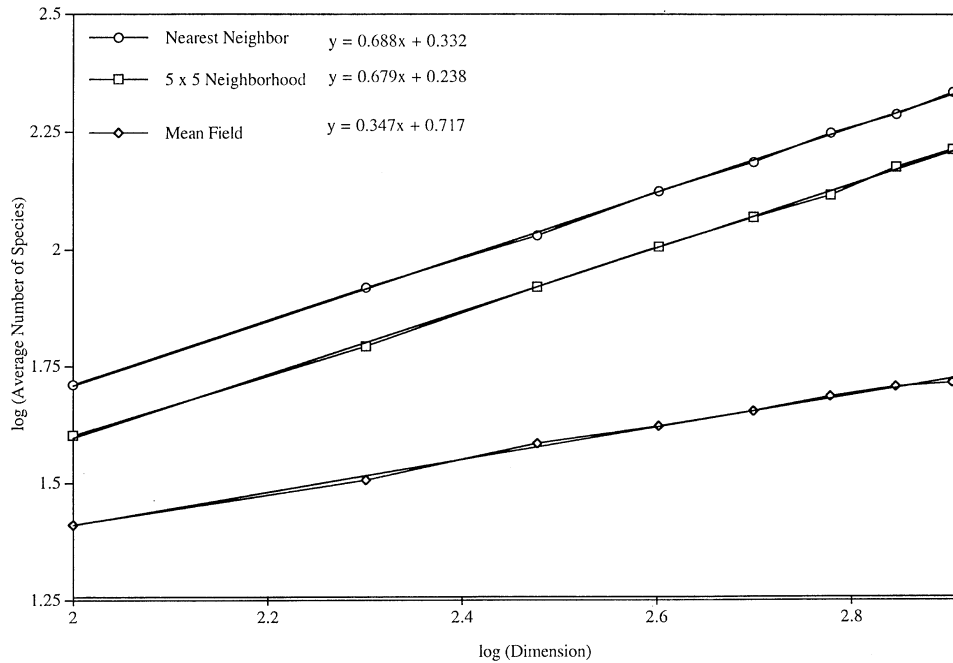
FIG. 7. For spatial models on an $L \times L$ grid or metapopulation system with L^2 sites, the logarithm of the average number of species is asymptotically linear in $\log L$. That is, there is a power law relationship between species and area. Note that the powers are larger by a factor of 2 for the spatial models compared to the metapopulation models.

we note that if $a = 1/3$ then an increase in area of 10^9 translates into a 1000-fold increase in the number of species.

In Fig. 8 we examine the average number of species in equilibrium versus migration rate $N\mu$ on a 400×400 grid. Here our estimate is the average number of species between times $100L$ and $400L$, these limits having been chosen to guarantee that the system is in equilibrium. As in the simulations with $N\mu = 1$ decreasing the dispersal distance increases the number of species in the system. In equilibrium the number of species that leave the system per unit time must be equal in the long run to the number that enter the system. Mentally rotating this graph by 90° (or mathematically looking at the inverse function) then gives the number of extinctions per unit time as a function of the average number of species in the system.

Finally, Fig. 9 plots the log of the equilibrium number of species versus the log of the number of points in the neighborhood of a site for a 400×400 two-dimensional system. Again the nearest neighbor case has the largest number of species in equilibrium; and on this log–log plot the number of species decreases linearly until a threshold is reached, after which the number is constant. Here we have used square- and diamond-

shaped neighborhoods to have more values available for the number of neighbors, but the two sets of measurements are part of one smooth curve.

4. SUMMARY

The self-organization of ecological communities and the levels of biological diversity that emerge represent fundamental theoretical challenges for ecologists. Tilman (1994), expanding upon earlier models of Levins (1969) and others, introduced a competition–colonization trade-off that gave rise to characteristic patterns of abundance, but no inherent limit to diversity. Since his model was a system of ordinary differential equations, what Tilman showed was that in an infinite area infinitely many species can coexist.

Here, using several different models, we have investigated the number of species that can exist in a finite area. The first, discussed in Section 2, were several variants on the May–Nowak model. However, in each case the equilibrium distributions of these systems have two properties that are not found in nature: packing of
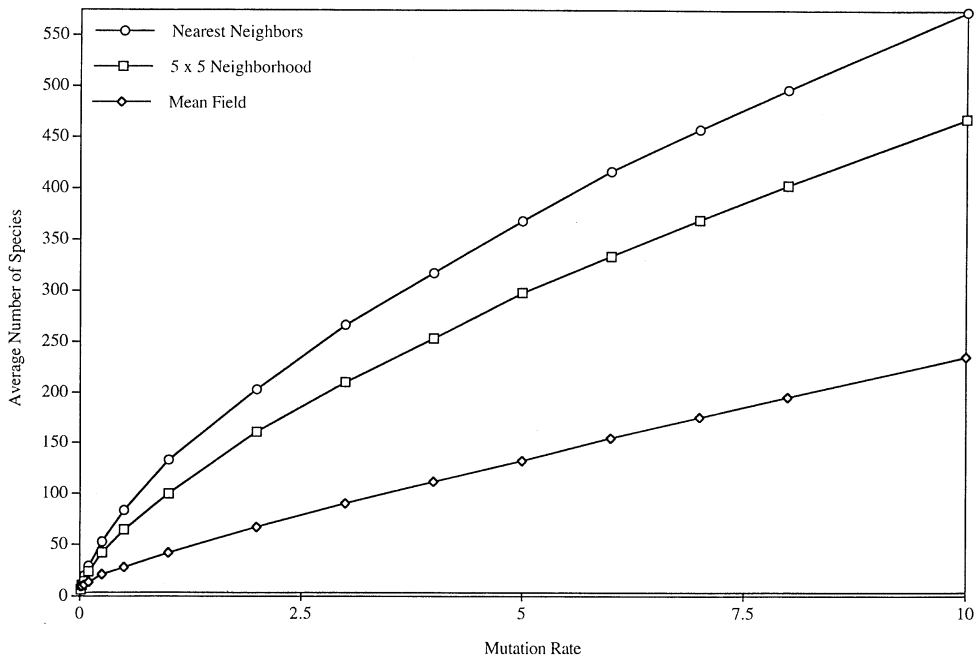
FIG. 8. The average number of species on a 400×400 grid or in a metapopulation model with 160,000 sites as the number of migrants per generation added to the grid is varied.
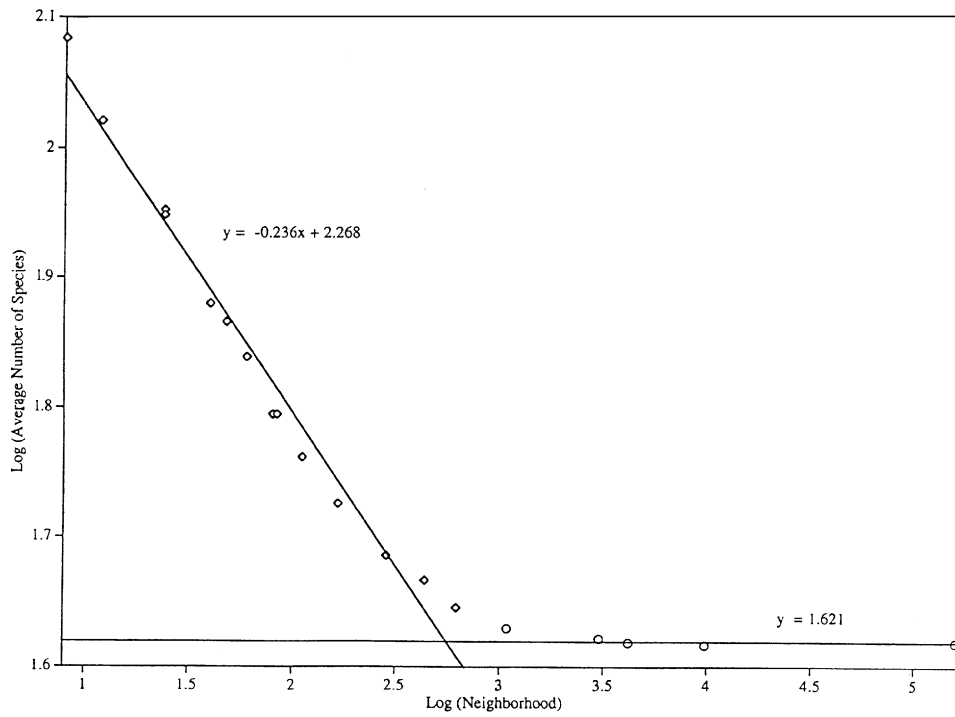

FIG. 9. Logarithm of the equilibrium number of species plotted versus the logarithm of the number of points in the neighborhood of a site for a 400×400 two-dimensional system. Square- and diamond-shaped neighborhoods were used.

species at the top end of the competitive hierarchy and a logarithmic increase of species with the size of the system.

We have also approached this question in Section 3 using a spatially explicit model, and compared the results for nearest neighbor dispersal, a 5×5 neighborhood, and the "mean field" situation in which dispersal is uniform over the system. The final "metapopulation" approach leads to a species area curve of $(2.05)N^{0.173}$ while the two spatial models have curves of $(1.39)N^{0.344}$ for nearest neighbor and $(1.26)N^{0.340}$ for the 5×5 neighborhood. In words, the spatial segregation in a metapopulation model is good for diversity, but short-range dispersal in a spatially explicit system is much better for quantifying the dependence of the equilibrium number of species on the dispersal range. It is surprising that this decrease is linear on a log–log plot until a critical threshold is reached, after which the number is constant.

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