

CHAPTER FOUR

Local Community Dynamics under Ecological Drift

In previous chapters I examined current models of relative species abundance based on niche-assembly theories, and then a small class of dynamical models whose predictions derive from birth, death, and dispersal processes. I now discuss one of the latter models in greater detail, zero-sum ecological drift, the foundation for a unified theory of biodiversity and biogeography. It is useful to divide the problem into two spatio-temporal scales for analysis: local community dynamics, which are relatively rapid, and metacommunity dynamics, which are much slower and occur on large scales. In this chapter, I study local community dynamics from the perspective of a single arbitrary species undergoing ecological drift in the community. In the next chapter, I consider metacommunity dynamics and the coupling of metacommunity and local community dynamics that results in the full multispecies ecological drift process under the unified theory.

Consider a local community saturated with individuals as, for example, trees in a closed-canopy forest. Let the community consist of J trees, regardless of species. Suppose individuals resist displacement until killed by some disturbance. Let each disturbance kill D individuals at random in the community. Let M of these individuals be replaced by immigrants from the metacommunity. Let the $D - M$ local replacement individuals be drawn at random from the species that survive, with probabilities set by their post-disturbance relative abundances.

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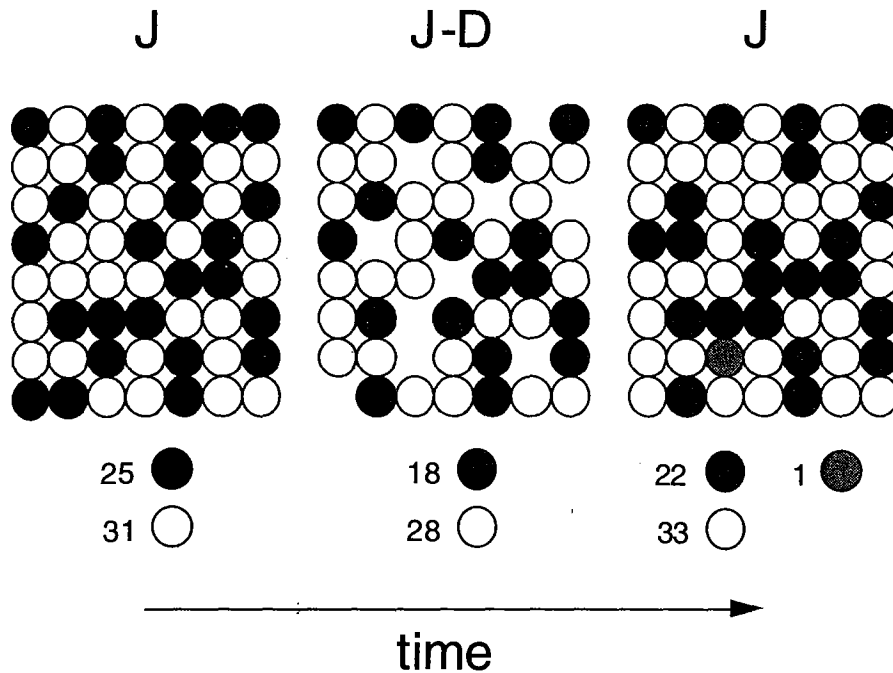


FIG. 4.1. Cartoon of one disturbance cycle in a model community undergoing zero-sum ecological drift. At the beginning of the cycle are two species whose individuals occupy all sites or resources (*left*). Immediately after the disturbance, which killed several individuals of both species, vacant sites or unutilized resources are opened up (*middle*). These are occupied by recruits from the two species in the local community, and by an immigrant individual of a third species from the metacommunity source area (*right*).

The process can be visualized by a simple cartoon (fig. 4.1). The community starts each disturbance cycle completely filled with individuals of the various species in the community (left panel). Then a disturbance occurs, killing D individuals, which creates openings or unused resource (middle panel). Then recruitment fills the openings, either with local recruits or immigrants from the metapopulation source area (right panel). A new species recruited a single individual from the source area in this example (gray circle).

The cartoon in figure 4.1 illustrates the full multispecies random walk under zero-sum ecological drift. To present the multispecies theory mathematically, however, it is useful

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first to analyze the dynamical behavior of a single arbitrary species i in the local community. In this chapter, I concentrate on the fate of the i th species against a backdrop of all other species dynamically lumped together. I then analyze full multispecies ecological drift in the local community in chapter 5. I analyze species i under two scenarios, first a community that is isolated and receives no immigrants from outside, and second a community that receives immigrants from an external metacommunity. Let the number of immigrant individuals per disturbance cycle be M where $M < D$. Thus, the community will undergo independent ecological drift if $M = 0$, and it will be influenced by the relative abundances of species in the source area if $M > 0$. I will use lower case m to denote the per capita or per birth probability that an individual is replaced by an immigrant. Case I is the so-called *absorbing* case, because once species go extinct or reach monodominance there is no further change (so these are final “absorbing” states). Case II is called the *ergodic* case because all states of abundance are reachable from one another, i.e., local extinction and monodominance are not permanent and final states.

Consider the isolated community first, the absorbing case. Let us now follow the fate of a single member species, species i . An important question to answer is: How long does it take an arbitrary species to go extinct or to achieve complete dominance under zero-sum ecological drift? Species drift to the absorbing abundance states of 0 or J . The time to “fixation” or absorption will depend on the size of the community J , the disturbance rate, D , and the initial abundance of the focal species, N_i . I first focus on the analytically more tractable case of $D = 1$. The transition

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probabilities are

$$\begin{aligned} \Pr\{N_i - 1|N_i\} &= \mu \binom{N_i}{J} \binom{J-N_i}{J-1} \\ \Pr\{N_i|N_i\} &= 1 - \mu + \mu \binom{N_i}{J} \binom{N_i-1}{J-1} \\ &\quad + \mu \binom{J-N_i}{J} \binom{J-N_i-1}{J-1} \\ \Pr\{N_i + 1|N_i\} &= \mu \binom{J-N_i}{J} \binom{N_i}{J-1}, \end{aligned}$$

where μ is the probability of one death per time step. A numerically equivalent and simpler combinatorial form for the transition probabilities is

$$\begin{aligned} \Pr\{N_i - 1|N_i\} &= \Pr\{N_i + 1|N_i\} = \frac{\binom{J-2}{N_i-1}}{\binom{J}{N_i}} \mu \\ \Pr\{N_i|N_i\} &= \frac{\binom{J}{N_i} - 2\mu \binom{J-2}{N_i-1}}{\binom{J}{N_i}}. \end{aligned}$$

For simplicity and with no loss of generality, I will hereafter rescale time by the average death rate in the community, so that one death occurs per time step (i.e., $\mu = 1$). The Markovian matrix M for the absorbing case of zero-sum ecological drift for focal species i and for the special case for $D = 1$, is

$$M = \begin{pmatrix} 1 & 0 & 0 & 0 & \dots & 0 & 0 & 0 & \dots & 0 & 0 & 0 \\ \frac{1}{J} & \frac{J-2}{J} & \frac{1}{J} & 0 & \dots & 0 & 0 & 0 & \dots & 0 & 0 & 0 \\ 0 & \frac{2(J-2)}{J(J-1)} & \frac{J(J-1)-4(J-2)}{J(J-1)} & \frac{2(J-2)}{J(J-1)} & \dots & 0 & 0 & 0 & \dots & 0 & 0 & 0 \\ \vdots & \vdots & \vdots & \vdots & \vdots & \vdots & \vdots & \vdots & \vdots & \vdots & \vdots & \vdots \\ 0 & 0 & 0 & 0 & \dots & \frac{\binom{J-2}{k-1}}{\binom{J}{k}} & \frac{\binom{J}{k}-2\binom{J-2}{k-1}}{\binom{J}{k}} & \frac{\binom{J-2}{k-1}}{\binom{J}{k}} & \dots & 0 & 0 & 0 \\ \vdots & \vdots & \vdots & \vdots & \dots & \vdots & \vdots & \vdots & \dots & \vdots & \vdots & \vdots \\ 0 & 0 & 0 & 0 & \dots & 0 & 0 & 0 & \dots & \frac{1}{J} & \frac{J-2}{J} & \frac{1}{J} \\ 0 & 0 & 0 & 0 & \dots & 0 & 0 & 0 & \dots & 0 & 0 & 1 \end{pmatrix}$$

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This transition probability matrix is square with $J + 1$ columns and rows corresponding to the k possible abundance states, 0 to J , of the i th species. The rows correspond to the abundance of the i th species at time t and the columns to its abundance at time $t + 1$. So, for example, the entry in row 2, column 1, corresponds to the probability that the i th species, starting at abundance 1 at time t will go extinct (have abundance 0) at time $t + 1$, which is $1/J$. Most of the entries in the matrix are zero because we allow only one death and one birth per time step. Thus, there are probabilities along the principal diagonal, which correspond to no change in abundance, and immediately on either side of the principal diagonal, corresponding to a decrease or an increase in abundance of one individual in one time step. Note that the probabilities across the columns in a given row sum to unity. If $N(t)$ is a row vector of probabilities that species i is at abundances 0 through J at time t , then the row vector of probabilities at time $t + 1$ can be found simply as

$$N(t + 1) = N(t) \cdot M.$$

For a very clear introduction to the matrix methods used hereafter in this chapter, and the fundamental theorems needed for analyzing the behavior of Markovian stochastic processes, I recommend the excellent book, *Finite Markov Chains*, by Kemeny and Snell (1960).

Matrix M can be put into the general canonical form of an absorbing Markov chain by arranging the two absorbing states of abundances 0 and J to be the first two states (upper left corner). Then matrix M can be partitioned into four submatrices,

$$M = \begin{pmatrix} I & 0 \\ R & Q \end{pmatrix},$$

where I is the identity matrix representing the submatrix of absorbing states. Submatrix Q represents transitions among

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transient abundances, 1 through $J - 1$. Over Q is a submatrix of zeros (because by definition the absorbing abundance states of 0 and J cannot be left), and submatrix R represents the final transitions to the absorbing states. The rearranged matrix M is the standard form of an absorbing Markov chain. Then the fundamental matrix A of the absorbing ecological drift process for focal species i is given by

$$A = (I - Q)^{-1}.$$

The elements $a_{j,k}$ of fundamental matrix A give the expected number of times that species i passes through abundance N_k having started in abundance N_j , before extinction or complete dominance. Matrix A allows us to determine the total number of births and deaths that will occur in the community before extinction or complete dominance, starting with abundance N_i . The vector $T(N)$ of fixation times is

$$T(N) = A\zeta,$$

where ζ is a column vector with all entries equal to unity. After some algebraic manipulation, one can show for the special, sparse-matrix case of $D = 1$ that

$$T(N_i) = (J - 1) \left[(J - N_i) \sum_{k=1}^{N_i} (J - k)^{-1} + N_i \sum_{k=N_i+1}^{J-1} k^{-1} \right]$$

(Hubbell and Foster 1986a). The first term in this expression is the mean time that species i is expected to spend at abundances less than or equal to N_i , and the second term is the mean time species i will spend at abundances greater than N_i before absorption. Note that these times are relative and are measured in the total number of deaths happening in all species in the community. The vector of variances $\text{Var}(T)$ in the time to absorption is also computed from the fundamental matrix A :

$$\text{Var}(T) = (2A - I)T - T_{\text{sq}},$$

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where T_{sq} is the vector $T(N)$ with every element squared. Unfortunately, $\text{Var}(T)$ is not a compact expression to write down as an explicit algebraic function of N_i and J , but it is numerically straightforward to compute its exact value.

I have illustrated how the time to extinction or complete dominance varies as a function of community size J and initial population size N_i in figure 4.2. Here the time to extinction or monodominance is measured in terms of the total number of deaths that occur in all species in the community prior to fixation of the i th species. The curves illustrate how this time varies in community sizes ranging from $J = 4$ to $J = 128$ individuals. The time to extinction or complete dominance is maximal when the initial abundance of the focal species that is $J/2$, and the curves are symmetrical about this abundance, with their shortest times when $N_i = 1$ and $N_i = J - 1$.

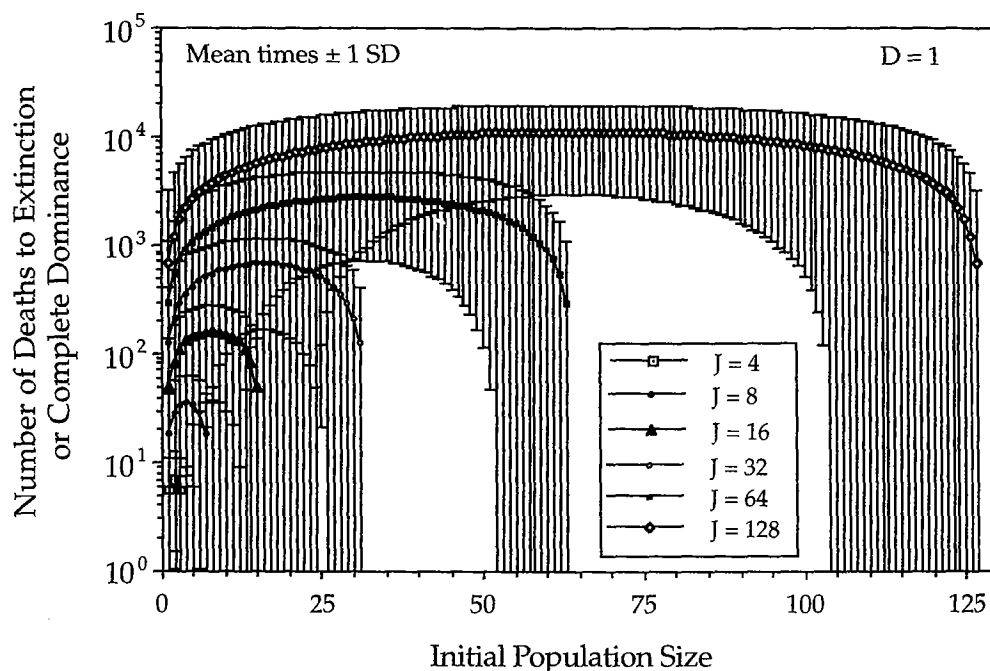


FIG. 4.2. Number of all deaths until fixation (extinction or monodominance) of arbitrary species i as a function of community size J . Note that the figure is a semilogarithmic plot. The longest times to fixation are from an initial species abundance of $J/2$.

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The most important conclusion we can draw from figure 4.2 is that the time to extinction or complete dominance rises rapidly with community size and size of the focal population (Hubbell and Foster 1986a). If the i th species represents a small fraction of the total community size, i.e., $N_i \ll J$, then $T(N_i) \cong N_i(J-1)[1 + \ln(J)]$. Thus, under the special case of $D = 1$, the time to extinction or monodominance grows as the product of the population size of the given species, times the community size, times the log of community size! This is potentially a very large number. For example, if a species comprises 10% of a community having 2000 individuals of all species, then the community will completely turn over almost seven hundred times before the species is expected to go extinct or become completely dominant. This represents nearly 1.3 million individuals that die and are replaced.

Thus, pure ecological drift to extinction can be a slow process if only a single individual is killed per disturbance. However, as we shall see later in this chapter, when $D \gg 1$, species can go locally extinct in much shorter amounts of time. The minimum time to extinction for the i th species is clearly N_i/D time steps, where N_i is the initial abundance of the species. For this reason, frequencies of times to extinction or complete dominance do not simply decline monotonically with a mode at $t = 0$, but instead are approximately gamma distributed (fig. 4.3). There is an abrupt rise to the modal value, followed by a much slower, nearly exponential decay in the frequency of fixation with increasing time. Note, however, that community dynamics under ecological drift are considerably faster if the disturbance rate is much higher ($D \gg 1$), as will be discussed later. Very short times to extinction are also likely to be prevalent when there is high demographic or environmental variance in the death rate.

I now turn to the second case, namely, a community that is open to immigration ($M > 0$). In this case the metacommunity may serve as a source of immigrants for

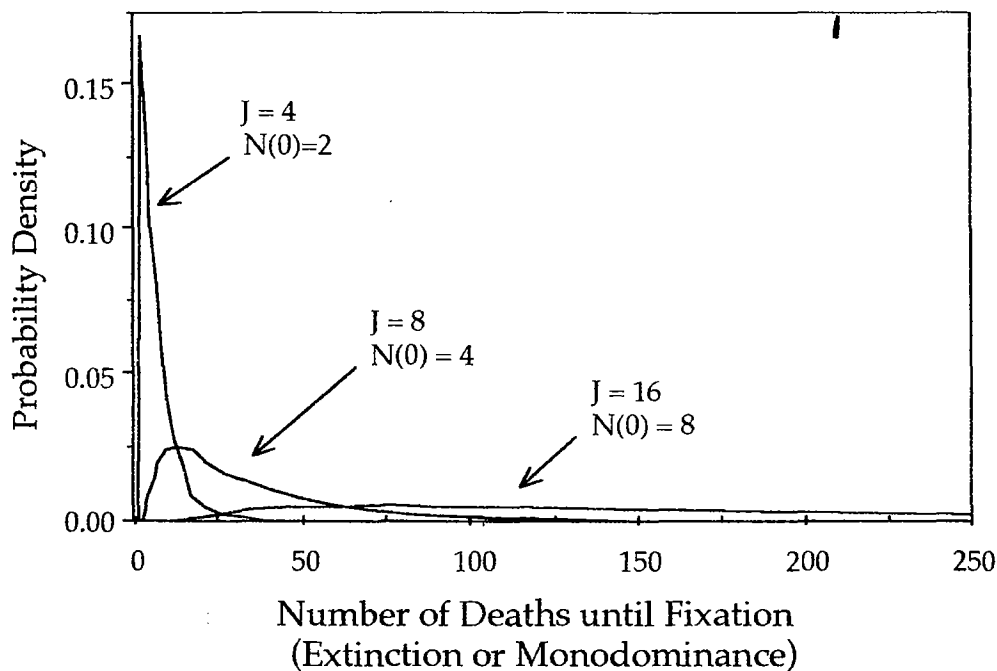


FIG. 4.3. Probability density functions for the time to fixation (extinction or complete dominance), illustrated as a function of community size J . The distributions are approximately gamma. The cases illustrated are for the longest times to fixation for the given community sizes, namely from an initial abundance of $J/2$.

any given species into the local community. The population dynamics of each species are once again Markovian, but now they are ergodic because extinction and monodominance in the local community are no longer absorbing states. Thus, under ecological drift, monodominant communities can be invaded by other species. Species are expected to go locally extinct and reimmigrate repeatedly from the source area. Unlike the absorbing case without immigration, species will have a positive expected equilibrium abundance in the ergodic community, provided that the given species also has nonzero abundance in the metacommunity.

The most fundamental question that one seeks to answer initially is: What is the expected abundance of a given species in the community at stochastic equilibrium, and what is its variance? A second related question is: What is the incidence of a given species in the ergodic community under

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zero-sum ecological drift? To answer these questions, we need to compute the abundance eigenvector of the limiting proportion of time spent at each abundance from 0 to J as $t \rightarrow \infty$. The eigenvector is very important because we can calculate directly from it the theoretically expected abundance of any species and its variance, as a function of community size, immigration rate, disturbance rate, and the relative abundance of the species in the metacommunity. The column eigenvector ψ is found by solving the equation $\psi^T B = \psi^T$ subject to the constraint that $\sum_{n=0}^J \psi(n) = 1$, where B is the transition matrix of the ergodic community. Note that we are solving for the *left* eigenvector of the transition matrix because by convention we have chosen the rows to be the current abundance state (at time t) and the columns to the next abundance state at time $t + 1$. This is not the usual convention, but it is used by Kemeny and Snell (1960), and I like it because it generates a more natural flow computationally from left to right. The expected local abundance of the i th species and its variance are simply

$$E\{N_i\} = \sum_{n=1}^J n \cdot \psi(n)$$

$$\text{Var}\{N_i\} = \sum_{n=1}^J (n - E\{N_i\})^2 \cdot \psi(n).$$

The incidence of a species is the proportion of time that the species is present in the local community. This proportion is $\sum_{n=1}^J \psi(n) = 1 - \psi(0)$, the sum of the eigenvector elements comprising all nonzero abundances. Given the important quantities that one can compute from the abundance eigenvector, it is well worth the effort to derive its algebraic expression for an ergodic community of arbitrary size J . However, I will defer further discussion of incidence functions until chapter 7. Once again assuming that exactly one death and one birth occur per time step, the transition probabilities

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for the i th species abundance N_i in the ergodic community with immigration are

$$\begin{aligned} \Pr\{N_i - 1|N_i\} &= \frac{N_i}{J} \left[m(1 - P_i) + (1 - m) \left(\frac{J - N_i}{J - 1} \right) \right] \\ \Pr\{N_i|N_i\} &= \frac{N_i}{J} \left[mP_i + (1 - m) \left(\frac{N_i - 1}{J - 1} \right) \right] + \left(\frac{J - N_i}{J} \right) \\ &\quad \times \left[m(1 - P_i) + (1 - m) \left(\frac{J - N_i - 1}{J - 1} \right) \right] \\ \Pr\{N_i + 1|N_i\} &= \left(\frac{J - N_i}{J} \right) \left[mP_i + (1 - m) \left(\frac{N_i}{J - 1} \right) \right], \end{aligned}$$

where m is the probability that a death will be replaced by an immigrant, and P_i is the fractional metacommunity relative species abundance of the i th species. It is easy to walk through these equations in words. For example, the first equation gives the transition probability for the i th species to decline in abundance by one individual. For this to happen, a death must occur in the i th species, N_i/J , and the birth must be in some other species. The first probability inside the brackets is that of an immigration event of some species other than i : $m(1 - P_i)$. The second probability is that of having no immigration event and a local birth in a species other than i : $(1 - m)(J - N_i)/(J - 1)$. Note that when the immigration rate, m , is zero, these probabilities reduce to the absorbing case.

The slow dynamics of the much larger metacommunity source area allows us temporarily to treat the distribution of P as a fixed marginal distribution. The full theory, which includes metacommunity dynamics, does not require specification of any marginal distributions (chapter 5). In the full unified theory, relative species abundances in the local community and in the metacommunity are always predictions, never givens. Eliminating the marginal distribution will obviate the need for any species-specific parameters in the unified theory.

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The simplest possible ergodic community is a community of size 1, representing the dynamics of replacement of a single individual. In this case the equations of the ergodic community reduce to the following:

$$B = \begin{pmatrix} 1 - mP_i & mP_i \\ m(1 - P_i) & 1 - m(1 - P_i) \end{pmatrix},$$

which has eigenvector $\psi_i(n) = \Pr\{0, 1\} = \{1 - P_i, P_i\}$. The entries in this simple transition matrix are easy to obtain from the transition probability equations. For example, the entry in row 1, column 1, is the probability of being at zero abundance at time t and remaining at zero abundance at time $t + 1$. From the second element of the eigenvector, the expected fraction of time that the i th species will be present at equilibrium is simply its metacommunity relative species abundance. Thus, at the scale of replacing a single individual, the presence or absence of a species must clearly be independent of the immigration rate, m . For larger communities, the abundance eigenvector is no longer independent of the probability of immigration, m . For example, for $J = 3$, the eigenvector is

$$\begin{aligned} \psi_i(n) &= \Pr \begin{Bmatrix} N_i = 0 \\ N_i = 1 \\ N_i = 2 \\ N_i = 3 \end{Bmatrix} \\ &= \left(\frac{1}{1 + m} \right) \begin{pmatrix} (1 - P_i)(1 - mP_i)(1 + m - 2mP_i) \\ 3mP_i(1 - P_i)(1 + m - 2mP_i) \\ 3mP_i(1 - P_i)(1 - m + 2mP_i) \\ P_i[1 - m(1 - P_i)](1 - m + 2mP_i) \end{pmatrix}. \end{aligned}$$

The reason for writing the eigenvector in this partially unfactored form will be clear when the eigenvector for the community of arbitrary size J is found.

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For $J = 3$, the expected abundance of the i th species is

$$\begin{aligned} E\{N_i|J = 3\} = & \left(\frac{1}{1+m}\right) \{0 \cdot (1 - P_i)(1 - mP_i)(1 + m - 2mP_i) \\ & + 1 \cdot 3mP_i(1 - P_i)(1 + m - 2mP_i) \\ & + 2 \cdot 3mP_i(1 - P_i)(1 - m + 2mP_i) \\ & + 3 \cdot P_i[1 - m(1 - P_i)](1 - m + 2mP_i)\}, \end{aligned}$$

which simplifies to $3P_i$. The variance is

$$\begin{aligned} \text{Var}\{N_i|J = 3\} = & \left(\frac{1}{1+m}\right) \{(0 - 3P_i)^2(1 - P_i)(1 - mP_i) \\ & \times (1 + m - 2mP_i) + (1 - 3P_i)^2 3mP_i(1 - P_i) \\ & \times (1 + m - 2mP_i) + (2 - 3P_i)^2 3mP_i(1 - P_i) \\ & \times (1 - m + 2mP_i) + (3 - 3P_i)^2 P_i \\ & \times [1 - m(1 - P_i)](1 - m + 2mP_i)\}, \end{aligned}$$

which simplifies to $3P_i(1 - P_i)(3 - m)/(1 + m)$.

If $P_i = 0$, the i th species is extinct in the metacommunity, and its expected abundance in the local community is zero with zero variance. Therefore, metacommunity extinction implies local community extinction. When $P_i = 1$, the species is monodominant in both the metacommunity and in the local community, with zero variance. For variation in P_i , the variance in abundance is maximal when $P_i = (9 - 3m)/6(3 - m) = 1/2$. For variation in immigration m , the variance is maximized as $m \rightarrow 0$. Thus, species abundances are more variable in local communities that are more isolated from the metacommunity.

Now consider ergodic communities of arbitrary size J . After six weeks of algebra, we find that the general solution

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eigenvector is

$$\psi_i(n) = \Pr \left\{ \begin{array}{c} 0 \\ 1 \\ \vdots \\ k \\ \vdots \\ J-1 \\ J \end{array} \right\} = \left(\begin{array}{c} \frac{\binom{J}{0}(1-P_i)(1-mP_i)\prod_{x=1}^{J-2} G(J, m, P_i, x)}{\prod_{x=1}^{J-2} [(J-1) - x(1-m)]} \\ \frac{\binom{J}{1}(1-P_i)mP_i\prod_{x=1}^{J-2} G(J, m, P_i, x)}{\prod_{x=1}^{J-2} [(J-1) - x(1-m)]} \\ \vdots \\ \frac{\binom{J}{k}(1-P_i)mP_i\prod_{x=1}^{k-1} H(J, m, P_i, x)\prod_{x=k}^{J-2} G(J, m, P_i, x)}{\prod_{x=1}^{J-2} [(J-1) - x(1-m)]} \\ \vdots \\ \frac{\binom{J}{J-1}(1-P_i)mP_i\prod_{x=1}^{J-2} H(J, m, P_i, x)}{\prod_{x=1}^{J-2} [(J-1) - x(1-m)]} \\ \frac{\binom{J}{J}P_i[1-m(1-P_i)]\prod_{x=1}^{J-2} H(J, m, P_i, x)}{\prod_{x=1}^{J-2} [(J-1) - x(1-m)]} \end{array} \right),$$

where

$$G(j, m, P_i, x) = (j-1)(1-mP_i) - x(1-m)$$

and

$$H(j, m, P_i, x) = (j-1)mP_i + x(1-m).$$

The eigenvector gives the probability density for any abundance $0 \leq N_i \leq J$, for the general ergodic community

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of size J . From the eigenvector we can calculate the equilibrium abundance of the i th species in the community and its variance. We find that the expected abundance of the i th species is

$$E\{N_i\} = \sum_{k=0}^J \psi(k) \cdot k = JP_i.$$

Thus, the expected abundance of the i th species at equilibrium in the local community is simply equal to the local community size, J , times the metacommunity relative abundance of the i th species, P_i . The mean local abundance of the i th species is thus independent of immigration rate, m . However, as we will see shortly, if m is small, then the i th species will spend a very low proportion of time at its mean abundance.

The variance depends on all three parameters, J , m , and P_i , and is given by

$$\text{Var}\{N_i\} = \sum_{k=1}^J (k - E\{N_i\})^2 \cdot \psi(k) = \frac{\sum_{k=0}^J [C(J, m, P_i, k) \cdot \prod_{x=1}^{k-1} H(J, m, P_i, k) \cdot \prod_{x=k}^{J-2} G(J, m, P_i, k)]}{\prod_{x=1}^{J-2} (J-1-x)(1-m)},$$

where

$$C(J, m, P_i, k) = \begin{cases} \binom{J}{k} (JP_i)^2 (1-P_i)(1-mP_i) & \text{for } k = 0 \\ \binom{J}{k} (k - JP_i)^2 (1-P_i)mP_i & \text{for } k = 1, 2, \dots, J-1 \\ \binom{J}{k} (k - JP_i)^2 P_i [1 - m(1-P_i)] & \text{for } k = J \end{cases}$$

and

$$\prod_{x>k-1}^{k-1} H(J, m, P_i, x) = 1 \quad \text{and} \quad \prod_{x>J-2}^{J-2} G(J, m, P_i, x) = 1.$$

We can now explore the behavior of the abundance eigenvector and the mean and variance of species i . The probability density functions for the abundance of species i in

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the local community reveal how local abundance depends on metacommunity abundance P_i , as well as on immigration rate, m , and community size, J . Figure 4.4 illustrates a family of probability density functions varying metacommunity abundance, for a community of size $J = 64$ and immigration rate of $m = 0.05$. Superficially these lines look like dominance-diversity curves, but they describe the probability that an arbitrary species i will be at a given abundance on the x -axis. For example, when P_i is large (e.g., 0.999),

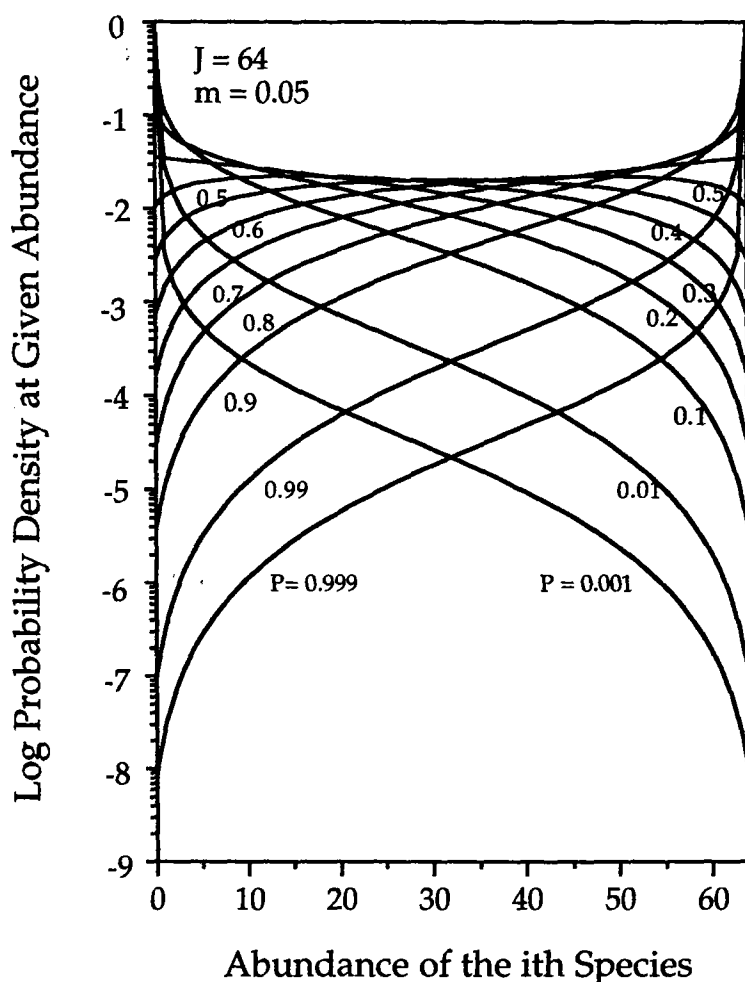


FIG. 4.4. The effect of varying the metacommunity relative abundance of the i th species on its equilibrium probability density functions in an ergodic local community undergoing zero-sum ecological drift. Numerical example of a community of $J = 64$ individuals and an immigration probability of $m = 0.05$ per replacement.

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such that the species is almost monodominant in the metacommunity, it spends most of its time monodominant in the local community as well. Conversely, when P_i is small (e.g., 0.001), such that it is rare in the metacommunity, then it will almost always be absent from the local community. In all distributions, the expected abundance of the i th species in the local community is JP_i . However, when P_i is large, the probability is concentrated at high abundance, and conversely when P_i is small, the probability is concentrated at low abundance. Note the complementary shape to the probability density functions at high and low P_i . The family of curves in figure 4.4 happens to be fairly symmetrical for this particular case of $m = 0.05$, but the curves become less symmetrical as the immigration rate m is varied up or down.

The probability density function exhibits richer behavior when the immigration rate is varied (fig. 4.5). When the local community is very isolated from the metacommunity, such that immigration rate m is small, then the abundance probability density functions are U-shaped. This shape arises because ecological drift has ample time in between rare immigration events to carry the relative abundance of the i th species to 0 (locally extinct) or to 1 (monodominance) when the community is quite isolated. As the immigration rate increases, local community dynamics are more strongly coupled to the metacommunity. As the immigration rate increases, the probability density function becomes unimodal, and the limiting variance in abundance is reduced. As $m \rightarrow 1$, the mode of the density function is near JP_i , which, is equal to 6.4 ($P_i = 0.1$) in the case illustrated in figure 4.5.

The effect of increasing community size J while holding m and P_i constant is shown in figure 4.6. As J increases, the modal abundance of the probability density function increases, but the distribution also broadens considerably, and the probability of the most frequent abundance becomes lower. This is expected simply because there

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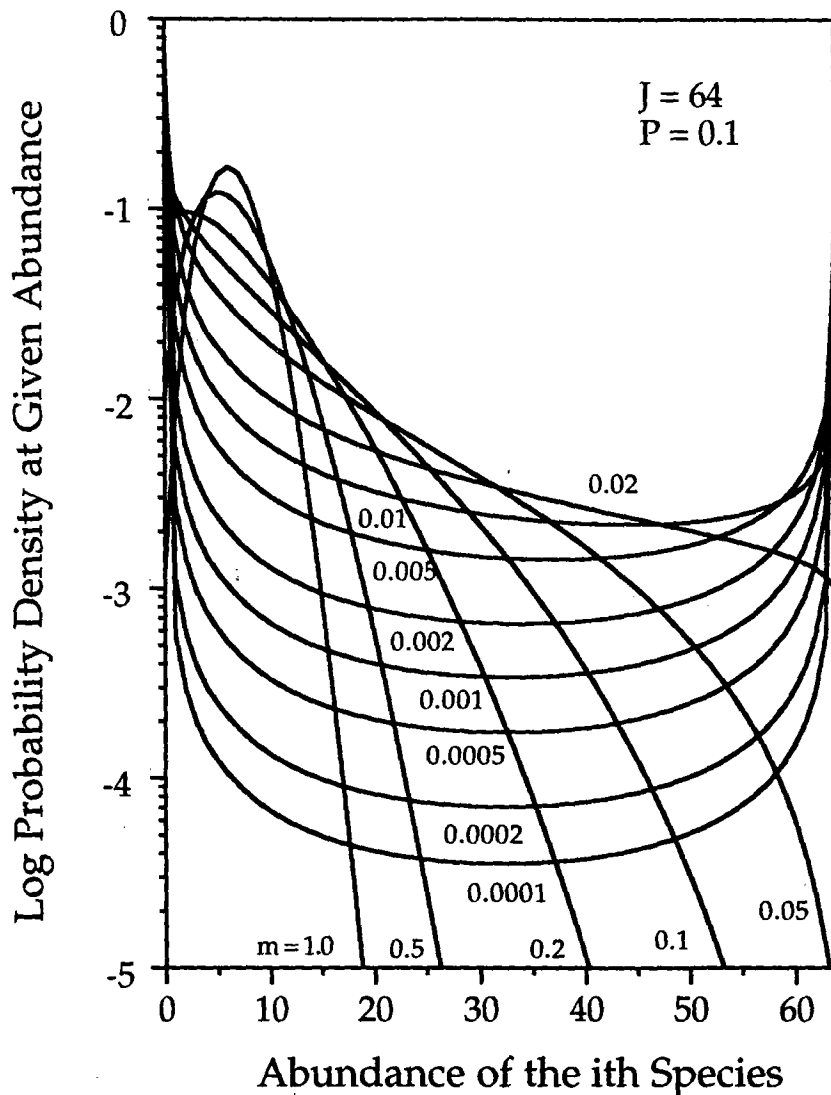


FIG. 4.5. The effect of varying the probability of immigration m on the equilibrium probability density functions for the i th species in an ergodic community undergoing zero-sum ecological drift. $J = 64$ individuals and $P_i = 0.1$.

are more abundance states that can be occupied in larger communities.

It is useful to illustrate the dynamical behavior of the i th species under ecological drift, to demonstrate the reality of the stochastic equilibria obtained analytically from the abundance eigenvector. Consider a numerical example of a very small local community consisting of just 16 individuals. Figure 4.7, top panel, shows the random walk of a species

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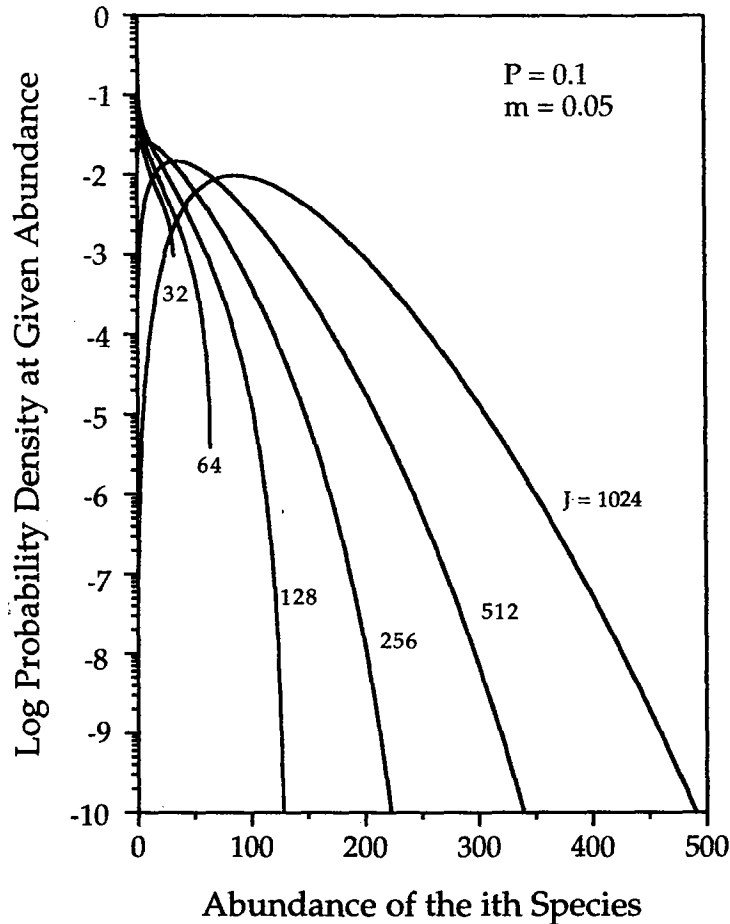


FIG. 4.6. The effect of varying community size, J , on the equilibrium probability density functions for the i th species in an ergodic community undergoing zero-sum ecological drift. P_i and m are held constant at 0.1 and 0.05, respectively. Note that the mode of the density function approximately tracks $J \cdot P_i$.

that has relative abundances P_i in the metacommunity of 0.95 or of 0.05, respectively. The bottom panel tracks the abundance of a species with a metacommunity relative abundance of 0.5. Note the greater variance for $P_i = 0.5$.

The variability of abundance of a species about the stochastic equilibrium $J P_i$ is less in larger communities that are not disturbed by high death rates. Figure 4.8 shows a species drifting in abundance in a local community of size $J = 64$, experiencing low, medium, and high disturbance, and which is increasingly isolated from the source area. In each case the metacommunity relative abundance

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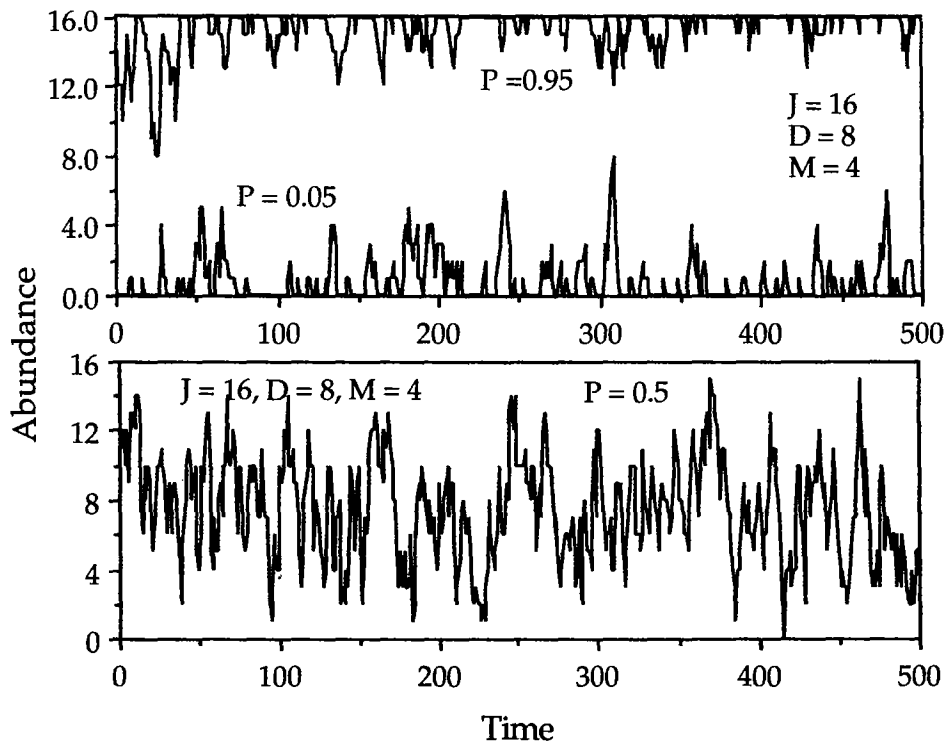


FIG. 4.7. Random walk of an arbitrary species in a small community ($J = 16$). *Top*: $P_i = 0.95$ and 0.05 . *Bottom*: $P_i = 0.5$. The dynamical behavior appears especially erratic in small communities. In these examples, the death rate per disturbance cycle was set high ($D = 8$). *Note*: The capitals D and M in these graphs are the actual number of individuals dying and immigrating per disturbance cycle, respectively. The probability of immigration m is equal to M/D .

of the focal species is 0.5. When a single individual is killed and replaced from the metacommunity (no isolation) during each disturbance cycle (top panel), the abundance of the species fluctuates around the equilibrium value of 32 by about ± 5 individuals over 500 birth-death cycles. However, when half the individuals in the local community are killed and replaced during each cycle, but only one in 32 replacement individuals is an immigrant from the source area, then the relative abundances fluctuate wildly. In this run of the ecological drift model, the species even spends some time as a monodominant and hardly shows any central tendency about its expected abundance of 32 individuals in 500 disturbance cycles.

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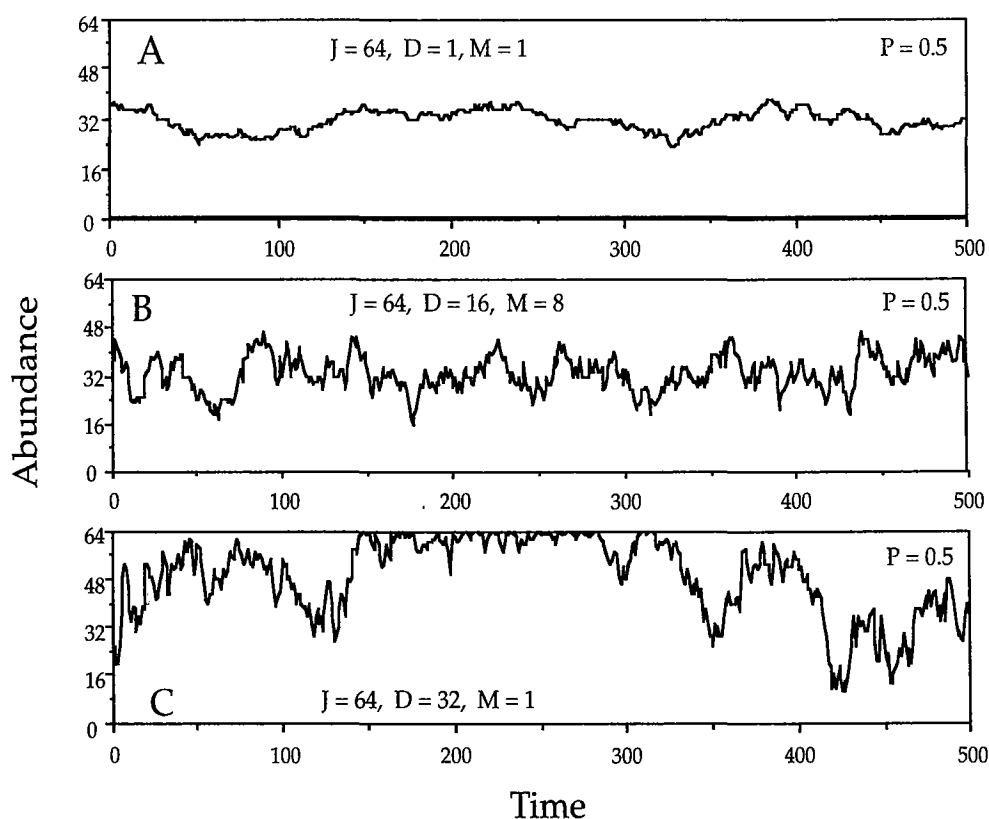


FIG. 4.8. Effect of varying the death rate, D , and the probability of immigration, $m = M/D$, where $M \leq D$. Community size, $J = 64$. *Top*, low disturbance: $D = 1, M = 1$. *Middle*, medium disturbance: $D = 16, M = 8$. *Bottom*, high disturbance: $D = 32, M = 1$. Once again, D and M in these graphs are the actual number of individuals dying and immigrating per disturbance cycle, respectively.

The theory of ecological drift predicts that the variance in local abundance of the i th species will be a parabolic function of metacommunity abundance P_i , with maximal variance when $P_i = 0.5$. The curve is parabolic when varying P_i , because a common factor in the variance is a quadratic function of P_i , namely $JP_i(1 - P_i)$. The variance as a function of P_i is shown in figure 4.9 for various values of the immigration rate m . The variance in the local abundance of the i th species increases dramatically for small m , i.e., for very isolated islands or local communities, a result that would be expected from figure 4.5. Figure 4.9 is a semilogarithmic plot of the variance and mean; these are inverted parabolas, log transformed, for various values of m .

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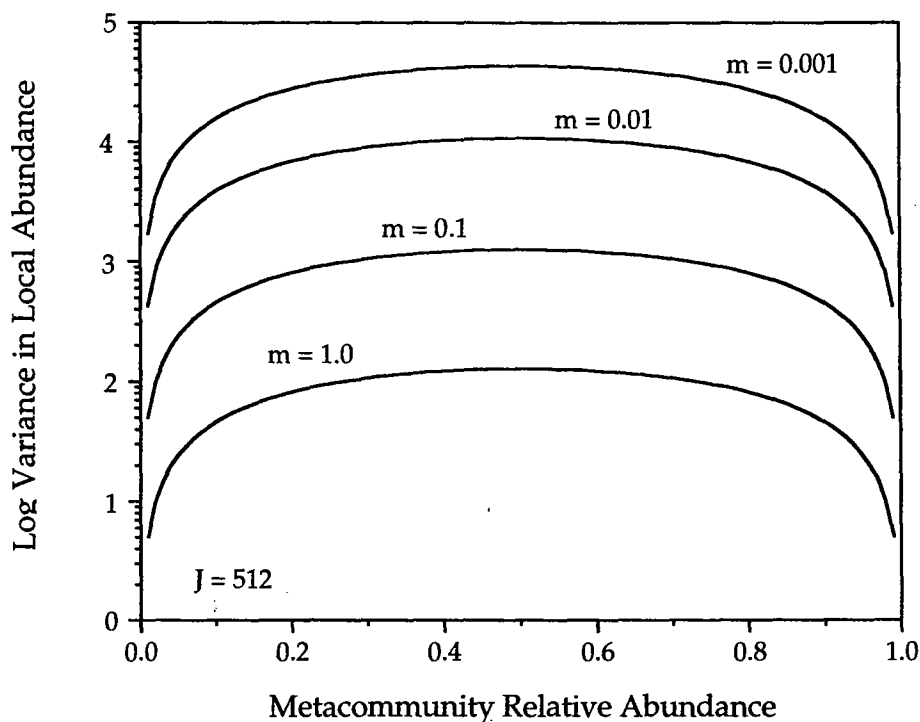


FIG. 4.9. Predicted relationship between the local variance in abundance of the i th species and its metacommunity relative abundance, for various values of the immigration rate, m . The curves are inverted parabolas that are distorted by the log transformation of the y -axis.

The quadratic curvilinearity of this relationship is not predicted by stochastic models that do not assume a zero-sum rule. Note that a quadratic relationship is also expected between the mean and variance in local abundance because the expected local abundance is proportional to P_i .

More generally, if there is a significant quadratic signature in the relationship of mean species relative abundances and their variances in a time series for a local community, this would constitute evidence in support of zero-sum dynamics. In practice, detecting this quadratic signature may be very difficult. This is because full parabolic variance curves will rarely be observed in nature. In most natural metacommunities, even the most abundant species will rarely constitute more than a few percent of the total metacommunity. If the commonest metacommunity species represents, say, less than 10% of the metacommunity, then the theory

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of ecological drift predicts that there will be nearly a perfect log-log linear relationship between mean and variance in abundance of the i th species. Figure 4.10 is a plot of log variance versus log mean for $P_i < 0.10$ and various values of m . Note that under log transformation, the slopes become essentially independent of m .

Relatively long-term data are available on the temporal dynamics of a community of more than 300 species of Macrolepidoptera in southern England. These data can be used to illustrate the relationship between variance and mean abundance predicted by the theory. Permission to use the data for these analyses was kindly given by Laurence

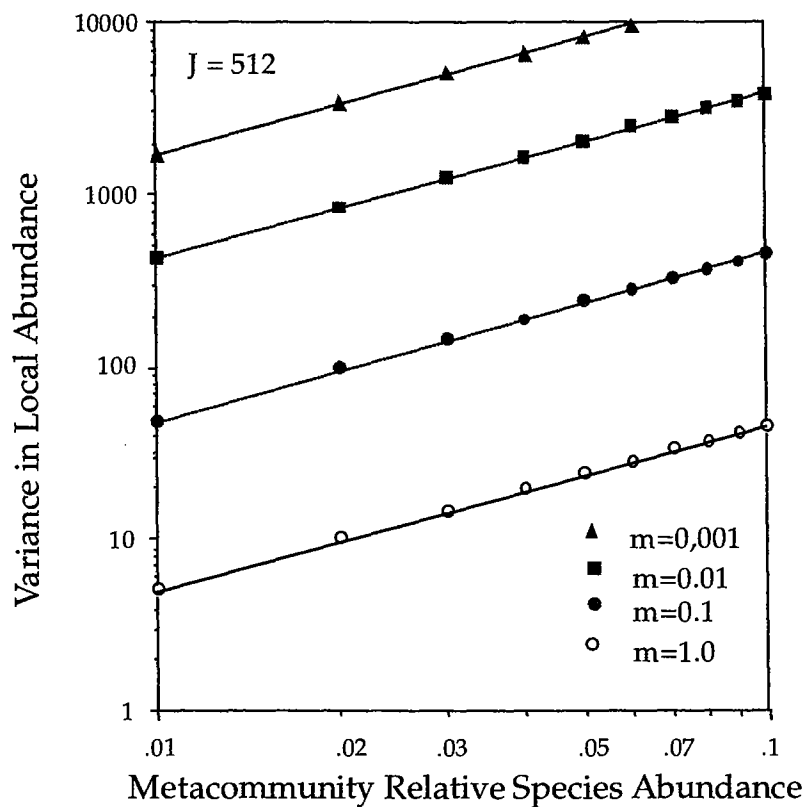


FIG. 4.10. Relationship between the log of the local variance in abundance of the i th species versus metacommunity abundance for species whose metacommunity abundances represent less than 10% of total metacommunity size, showing the log-log linearity. The intercepts but not the slopes are functions of the immigration rate m on the log-transformed plot.

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Cook of the Manchester Museum. For 25 years, moths were collected at mercury vapor light traps in Woodchester Park Field Centre near Manchester, beginning in the late 1960s (Baker 1985, Cook and Graham 1996).

The relationship between log variance and log mean in percentage of sample abundance of 306 species is shown in figure 4.11, for all species that occurred in at least 7 years out of 25. Species with lower incidence were excluded because the variance is largely driven by presence-absence for very infrequent species. There is no significant quadratic term in the relationship. If these data do reflect zero-sum ecological drift, then the “true” metacommunity being sampled must be truly enormous with many species, each representing a small fraction of the metacommunity.

Thus far I have considered only the mildest form of disturbance to the community—the death and replacement of

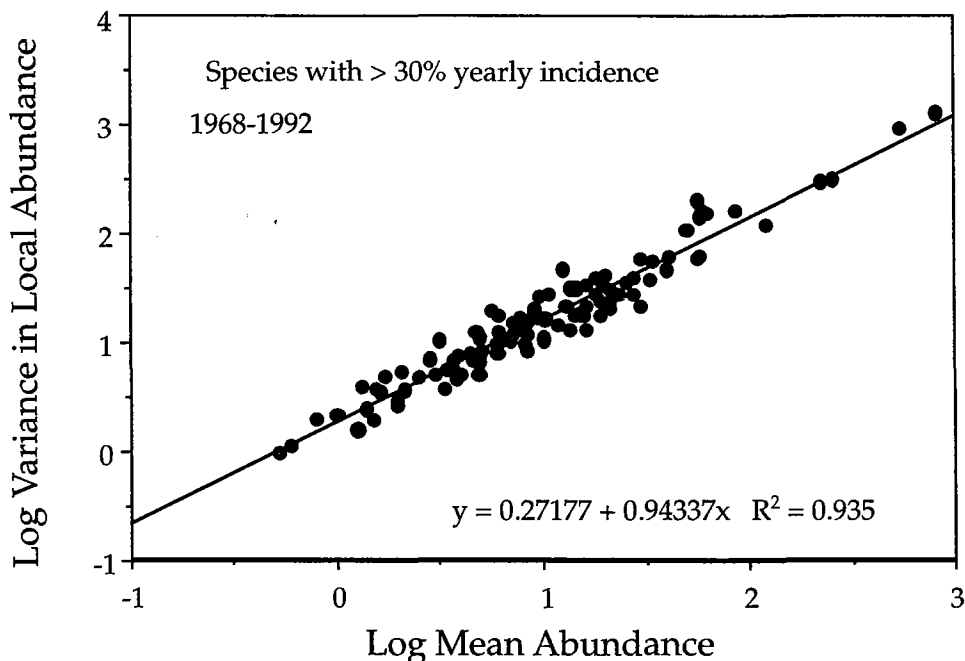


FIG. 4.11. Relationship between the log of mean annual abundance and variance in annual abundance for Macrolepidoptera collected over a 25-year period in Gloucestershire, England. Original data provided by L. C. Cook.

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a single individual at a time ($D = 1$). I now turn to the analytically more difficult cases of $D > 1$. As I will now show, persistence times—the time it takes a drifting species to go extinct in the local community—become shorter, and often much shorter, when the community is subject to more severe disturbances. The matrices for ergodic communities having $D > 1$ are also analytically solvable in the numerical sense, but their eigenvectors are much more complex and difficult to find algebraically. Nevertheless, in what follows the results presented are all exact numerical solutions to the equations. In spite of their difficulty, cases of $D > 1$ are important to study because natural communities are subject to different average rates of mortality as well as environmental stochasticity in the mortality rates themselves. Moderate to large environmental disturbances strike virtually every community at least occasionally. Communities can be suddenly and massively disturbed by events such as intense storms, landslides, fires, earthquakes, and epidemics (Lande 1993).

In this chapter I consider only demographic stochasticity because D is treated as a fixed parameter. However, as it turns out, the mean abundance of the i th species is identical under environmental variance in the death rate D , so long as zero-sum dynamics apply and the average death rate remains D . Indeed, the expected distribution of relative species abundance in the local community also remains unchanged under stochastically varying D , although the variance is affected. Thus, the analytical results for expected abundances derived under a constant death rate apply equally well to zero-sum communities subject to stochastically variable death rates having the same mean.

Consider first the case of $D = 2$. This case permits the i th species to change ± 2 individuals per disturbance cycle, provided and $N_i \geq 2$ and $\leq J - 2$. There are now five potentially

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nonzero transition probabilities:

$$\Pr\{N_i - 2|N_i\} = \frac{N_i(N_i - 1)}{J(J - 1)} \left[\begin{array}{l} m^2(1 - P_i)^2 + 2m(1 - m) \\ \times (1 - P_i) \left(\frac{J - N_i}{J - 2} \right) \\ + (1 - m)^2 \left(\frac{J - N_i}{J - 2} \right)^2 \end{array} \right]$$

$$\Pr\{N_i - 1|N_i\} = \frac{N_i(N_i - 1)}{J(J - 1)} \left[\begin{array}{l} 2m^2 P_i(1 - P_i) \\ + 2m(1 - m) P_i \left(\frac{J - N_i}{J - 2} \right) \\ + 2m(1 - m)(1 - P_i) \\ \times \left(\frac{N_i - 2}{J - 2} \right) + 2(1 - m)^2 \\ \times \left(\frac{N_i - 2}{J - 2} \right) \left(\frac{J - N_i}{J - 2} \right) \end{array} \right]$$

$$+ 2 \frac{N_i(J - N_i)}{J(J - 1)} \left[\begin{array}{l} m^2(1 - P_i)^2 \\ + 2m(1 - m) \\ \times (1 - P_i) \left(\frac{J - N_i - 1}{J - 2} \right) \\ + (1 - m)^2 \left(\frac{J - N_i - 1}{J - 2} \right)^2 \end{array} \right]$$

$$\Pr\{N_i|N_i\} = \frac{N_i(N_i - 1)}{J(J - 1)} \left[\begin{array}{l} m^2 P_i^2 + 2m(1 - m) P_i \left(\frac{N_i - 2}{J - 2} \right) \\ + (1 - m)^2 \left(\frac{N_i - 2}{J - 2} \right)^2 \end{array} \right]$$

$$+ 2 \frac{N_i(J - N_i)}{J(J - 1)} \left[\begin{array}{l} 2m^2 P_i(1 - P_i) + 2m(1 - m) \\ \times P_i \left(\frac{J - N_i - 1}{J - 2} \right) + 2m(1 - m) \\ \times (1 - P_i) \left(\frac{N_i - 1}{J - 2} \right) \\ + 2(1 - m)^2 \left(\frac{N_i - 1}{J - 2} \right) \left(\frac{J - N_i - 1}{J - 2} \right) \end{array} \right]$$

$$+ \frac{(J - N_i)(J - N_i - 1)}{J(J - 1)}$$

$$\times \left[\begin{array}{l} m^2(1 - P_i)^2 + 2m(1 - m)(1 - P_i) \\ \times \left(\frac{J - N_i - 2}{J - 2} \right) + (1 - m)^2 \left(\frac{J - N_i - 2}{J - 2} \right)^2 \end{array} \right]$$

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$$\Pr\{N_i + 1|N_i\} = \frac{(J - N_i)(J - N_i - 1)}{J(J - 1)}$$

$$\times \left[\begin{array}{l} 2m^2 P_i(1 - P_i) + 2m(1 - m)P_i \\ \times \left(\frac{J - N_i - 2}{J - 2} \right) + 2m(1 - m)(1 - P_i) \\ \times \left(\frac{N_i}{J - 2} \right) + 2(1 - m)^2 \left(\frac{N_i}{J - 2} \right) \left(\frac{J - N_i - 2}{J - 2} \right) \end{array} \right]$$

$$+ 2 \frac{N_i(J - N_i)}{J(J - 1)}$$

$$\times \left[\begin{array}{l} m^2 P_i^2 + 2m(1 - m)P_i \left(\frac{N_i - 1}{J - 2} \right) \\ + (1 - m)^2 \left(\frac{N_i - 1}{J - 2} \right)^2 \end{array} \right]$$

$$\Pr\{N_i + 2|N_i\} = \frac{(J - N_i)(J - N_i - 1)}{J(J - 1)}$$

$$\times \left[\begin{array}{l} m^2 P_i^2 + 2m(1 - m)P_i \left(\frac{N_i}{J - 2} \right) \\ + (1 - m)^2 \left(\frac{N_i}{J - 2} \right) \end{array} \right].$$

Although tedious, the verbal interpretation of these transition probabilities is straightforward. For example, the first equation is the probability that the i th species will suffer a loss of two individuals in the next disturbance cycle. For this to happen with $D = 2$, both deaths must occur in the i th species (note sampling without replacement) and the births or immigrants must be of other species. The probability of two deaths in species i is then multiplied by the sum of three probabilities, each representing a unique way for the deaths to be replaced by other species. The first expression inside the brackets is the probability of two immigrant individuals of species other than i ; the second expression is the probability of one immigrant and one local birth, neither of which is species i (times two combinations); and the third expression is the probability of two local births occurring in species other than i .

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Continuing in this manner, we can fully generalize the process to accommodate disturbances of arbitrary size, $1 \leq D \leq J$. Let us now calculate an arbitrary transition probability in which the i th species suffers a net loss of d individuals, $d \leq D$. Let us divide the problem into two parts. We will first calculate the death process and secondly the replacement process. If x deaths befall species i , then $D - x$ deaths must occur in all other species. The probability $\mu(x)$ that species i will suffer the death of x individuals is hypergeometrically distributed:

$$\mu(x) = \Pr\{x|N_i\} = \frac{\binom{N_i}{x} \binom{J-N_i}{D-x}}{\binom{J}{D}}$$

for $x \leq N_i$, and $\mu(x) = 0$ for $x > N_i$. If species i is to experience a net loss of d individuals in the current disturbance cycle, then the *minimum* number of deaths that the i th species can suffer is also d . We therefore must consider all terms of $\mu(x)$ in which $d \leq x \leq D$. If $x = d$, then all replacement individuals must be of species other than i (since species i must show a net loss of d individuals). However, if $x > d$, then precisely $x - d$ of the replacement individuals must be of species i , and the remainder $D - x + d$ must be of species other than i , in order for the i th species to show a net loss of exactly d individuals.

The replacement process consists of two subprocesses: immigration from the source metacommunity, or a local birth, either of which can yield a new individual of the i th species or of some other species. We now calculate the probability of each possible combination of immigrants or local births that comprise $x - d$ replacements of species i and $D - x + d$ replacements of species other than i . Since each of these possible ways of replacing the D total deaths is mutually exclusive and unique, these probabilities are summed. The sum of replacement probabilities is then multiplied by the hypergeometric death probability $\mu(x)$ for the given x value. Finally, these products are summed from

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$x = d$ to $x = D$, yielding the total probability that species i will suffer a net loss of d individuals.

To formalize this verbal recipe for the replacement process, let us make some variable substitutions to simplify notation. There are four essential probabilities in the replacement process. Let ϕ_i be the probability of an individual of species i immigrating; let $\phi_{\bar{i}}$ (with subscript "not i ", \bar{i}) be the probability of some other species immigrating; let λ_i be the probability of a local birth in species i , and let $\lambda_{\bar{i}}$ be the probability of a local birth in some other species. The immigration probabilities are independent of the distribution of local deaths between species i and other species, and depend only on the probability of immigration and metacommunity relative species abundances: $\phi_i = mP_i$ and $\phi_{\bar{i}} = m(1 - P_i)$, respectively. However, the local birth probabilities are functions of how many deaths have just occurred in the disturbance cycle in the local population of species i and in the collective local population of all other species. If x local deaths occurred in species i , then $D - x$ local deaths occurred in other species. Therefore, the local birth probabilities are

$$\lambda_i(x) = (1 - m) \left(\frac{N_i - x}{J - D} \right)$$

$$\lambda_{\bar{i}}(D - x) = (1 - m) \left(\frac{J - N_i - D + x}{J - D} \right).$$

Recall that we are currently calculating the probability that species i will decline in abundance by d individuals in the next disturbance cycle. In this case, as noted above, precisely $x - d$ of the replacement individuals must be of species i , and the remainder $D - x + d$ must be of species other than i . These replacement individuals can be distributed in any combination of immigrants and local births. Therefore, we can now write down the probability that

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species i will suffer a loss of d individuals, $d \leq D$, in the next time step, as follows:

$$\Pr\{N_i - d|N_i\} = \sum_{x=d}^D \mu(x) \cdot \left[\sum_{y=0}^{x-d} \sum_{z=y+1}^{D-x+d} \frac{D!}{y!(x-d-y)!z!(D-x+d-z)!} \phi_i^y \cdot [\lambda(x)]_i^{x-d-y} \cdot \phi_i^z \cdot [\lambda(D-x)]_i^{D-x+d-z} \right].$$

An analogous train of logic yields the transition probability for $\Pr\{N_i + d|N_i\}$:

$$\Pr\{N_i + d|N_i\} = \sum_{x=d}^{D-d} \mu(x) \cdot \left[\sum_{y=0}^x \sum_{z=y+1}^{D-x} \frac{D!}{y!(x-y)!z!(D-x-z)!} \phi_i^y \cdot [\lambda(x)]_i^{x-y} \cdot \phi_i^z \cdot [\lambda(D-x)]_i^{D-x-z} \right].$$

Note that $\Pr\{N_i|N_i\}$ can be obtained from either equation by setting $d = 0$.

The effect of having more than one death per disturbance cycle is to reduce persistence time and hasten community turnover. This is because it takes fewer time steps to eliminate a species or make it a monodominant if larger changes per step are possible. Clearly, any species for which $N_i \leq D$ has a finite chance of going extinct in one time step. In the ergodic community, equilibrium relative abundances remain the same as in the case of $D = 1$, but they are approached faster, and the equilibrium variance about the mean is greater.

In the absorbing case ($m = 0$) with $D > 1$, the time to fixation (local extinction or complete dominance) is inversely proportional to the death rate. Figure 4.12 shows the linearity of the relationship for the case in which the initial abundance of the i th species is half the community size, $N_i(0) = J/2$. This is the case in which the mean time

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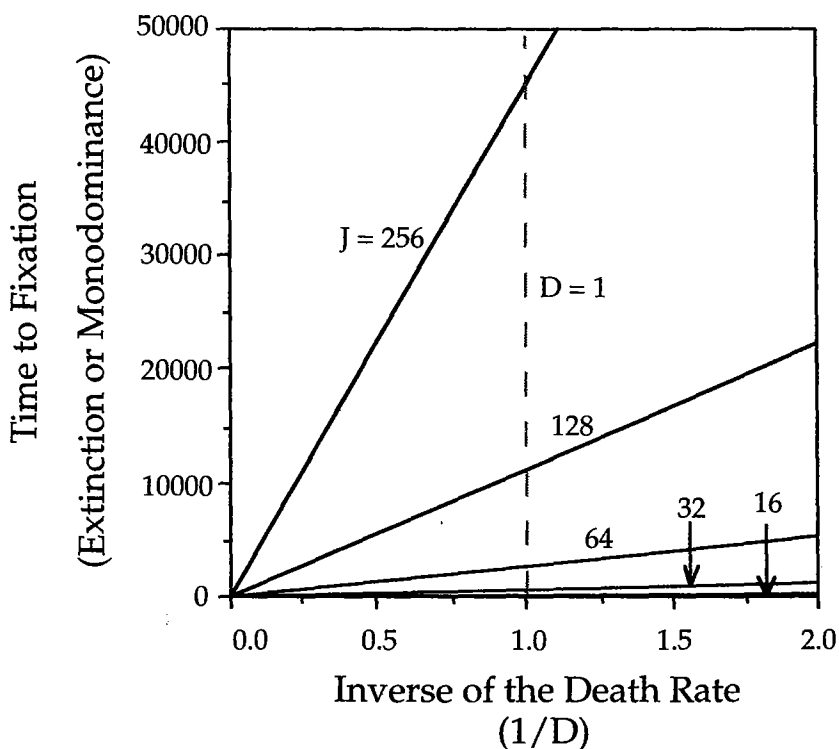


FIG. 4.12. Time to fixation (local extinction or monodominance) in the absorbing case of zero-sum ecological drift for death rates $D > 1$, for a species with an initial abundance of $J/2$. This is the abundance with the longest time to fixation. Time to fixation is inversely proportional to the death rate, D . A doubling of community size results in approximately a fourfold increase in time to fixation. Fixation times for the $D = 1$ case are indicated by the vertical dotted line.

to fixation is maximal (because the starting abundance is equidistant from the two absorbing states). A doubling of community size leads to an approximately fourfold increase in the time to fixation. Because of the rapid increase in time to fixation with increasing community size, it is useful to replot figure 4.12 on a semilogarithmic scale (fig. 4.13). This reveals the shorter times to fixation that occur as the death rate is elevated above unity. The ratio of fixation or absorption times asymptotically approaches the ratio of the death rates for large community size, J :

$$\frac{T_{D=1}}{T_{D=D'>1}} \rightarrow \frac{D'}{1} = D' \quad \text{as } J \rightarrow \infty.$$

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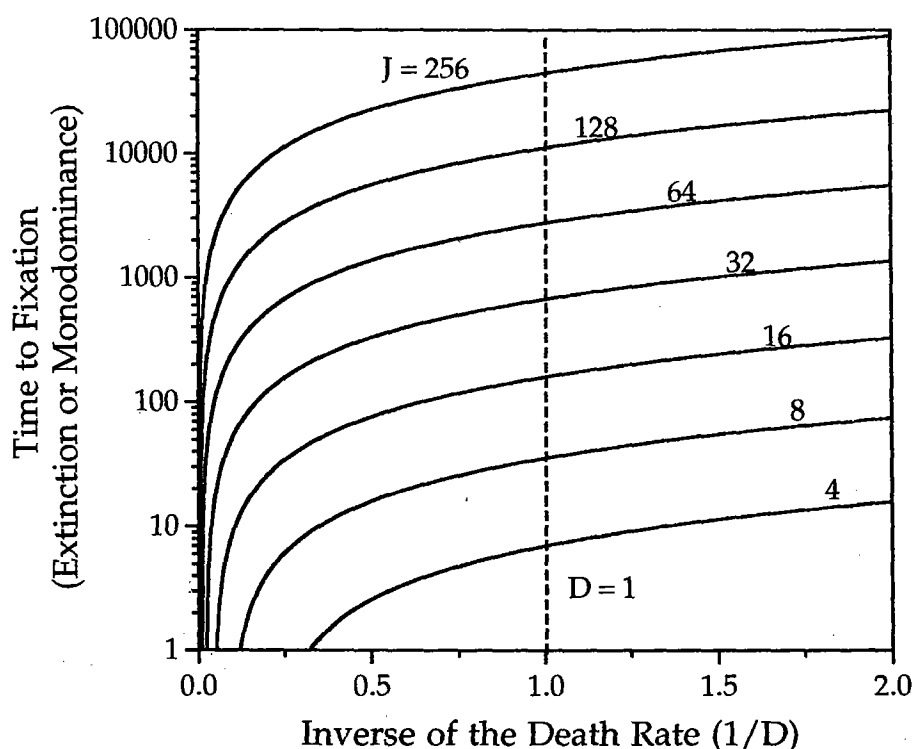


FIG. 4.13. Time to fixation (local extinction or monodominance) in the absorbing case of zero-sum ecological drift, as a function of the death rate and the size of the community. The relationship between fixation time and the inverse of death rate is linear, but the fixation time axis has been log-transformed to reveal the family of curves for different community sizes. Fixation times for the $D = 1$ case discussed earlier are indicated by the vertical cross-sectional line.

Small communities deviate by going to fixation faster than predicted from the asymptotic expectation (i.e., $T_{D=1}/T_{D=D>1} > D'$), as shown in fig. 4.14. The asymptotic behavior for large J arises because the dynamics of the random walk of the i th species are approximately binomial in large communities. Conversely, when community size is small, the dynamics are more noticeably affected by the hypergeometric sampling without replacement in the death process, which hastens fixation. The shortening of the expected time to fixation is accompanied by a large reduction in the frequency of very long persistence times. Recall that times to fixation are approximately gamma distributed. The gamma distribution is a density function with most of

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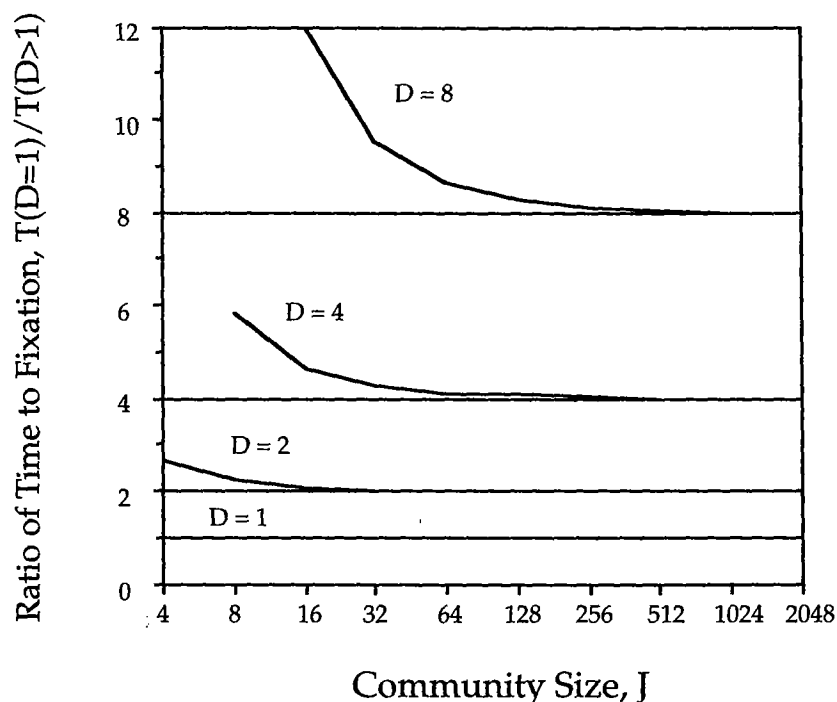


FIG. 4.14. Shortening of the time to fixation (extinction or monodominance) in the absorbing case of a community undergoing zero-sum ecological drift under a disturbance regime of $D > 1$. The y-axis is the ratio of the time to fixation for $D = 1$, to the time to fixation, for $D = D'$, where $D' = 2, 4$, and 8 are illustrated. The ratio of fixation times asymptotically approaches D' for large community size, J . Ratios deviate from D' at small community sizes due to the influence of hypergeometric death process. Curves are the ratios of fixation times for an initial abundance of $J/2$.

its probability density concentrated at low fixation times, relative to the range of possible fixation times. Therefore, for example, a twofold reduction in mean fixation time implies a major change in the shape of the distribution. Figure 4.15 illustrates the qualitatively large change in the distribution even for a very small community ($J = 8$) when the mortality is increased from $D = 1$ to $D = 4$ individuals per disturbance. The change in the distribution of extinction times is important and is often overlooked when the focus is strictly on the mean time to fixation. One of the important conclusions is that increasing the magnitude of the disturbance not only shortens the mean time to extinction, but also greatly

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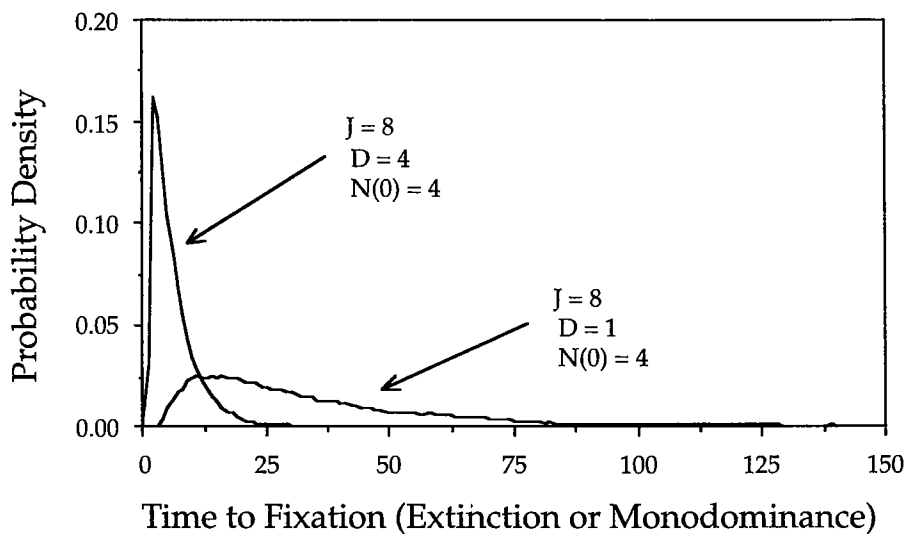


FIG. 4.15. Gamma-like distributions of the time to fixation (local extinction or monodominance) in the absorbing case of a small community ($J = 8$) undergoing zero-sum ecological drift, showing that the dramatic contraction of the tail of long fixation times with an increase in the mortality rate is increased from $D = 1$ to $D = 4$ per disturbance cycle.

curtails the chances for long-term survival through drifting relative abundance.

In discussing the effects of disturbance rates greater than $D = 1$, I have so far concentrated on the time to fixation in the absorbing case. This is because the main effect of $D > 1$ is to hasten fixation in the absorbing case, and to hasten attainment of equilibrium in the ergodic case. The expected relative abundance of the i th species in the ergodic community is unaffected by $D > 1$: the expected abundance remains JP_i . However, the variance in relative abundance increases modestly for larger D . Figure 4.16 gives a numerical example for a community of size $J = 64$, and for an immigration rate half the mortality per disturbance cycle. Even given a 32-fold difference in death rates ($D = 1$ to $D = 32$), there is a maximal increase of only about 20% in the standard deviation of relative abundance, which occurs at $P_i = 0.5$.

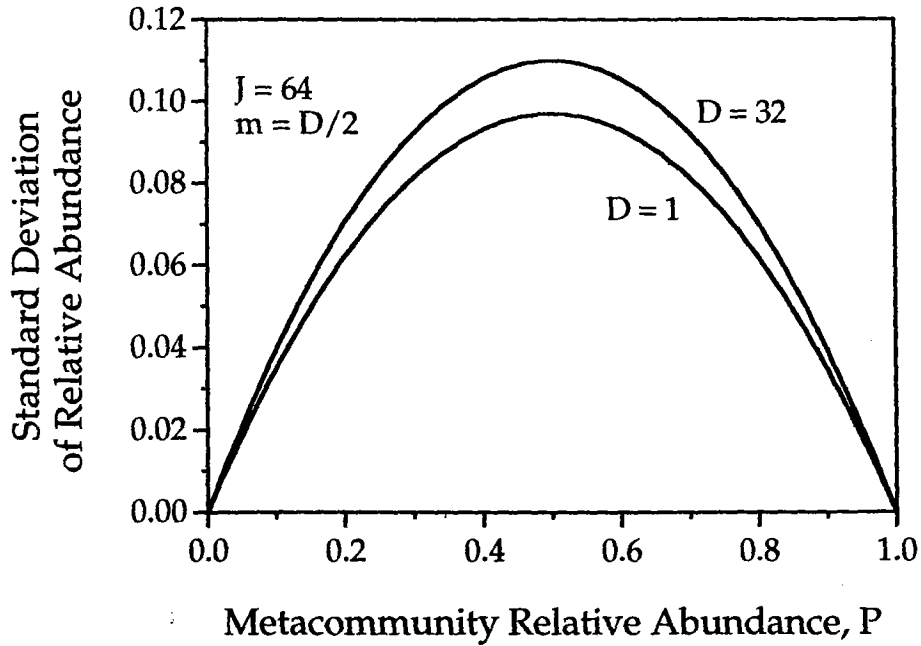


FIG. 4.16. Effect of increasing the death rate on the standard deviation of the relative species abundance of the i th species in an ergodic local community undergoing zero-sum ecological drift. The case of $J = 64$ is illustrated. The two curves compare $D = 1$ (lower curve) with $D = 32$ (upper curve), representing a wide range of disturbance regimes.

The deterministic analog to the stochastic dynamical equations of ecological drift can also be written down. The deterministic rate of change of the abundance of the i th species is given by

$$\frac{dN_i}{dt} = \frac{(J - N_i)}{J} \left[mP_i + (1 - m) \left(\frac{N_i}{J - 1} \right) \right] - \frac{N_i}{J} \left[m(1 - P_i) + (1 - m) \left(\frac{J - N_i}{J - 1} \right) \right].$$

Setting the derivative equal to zero, we find that the equilibrium abundance N^* of the i th species is: $N_i^* = JP_i$. This is identical to the expectation under ecological drift, where N_i^* is the equilibrium numerical abundance of the i th species in a community of J total individuals. Note, however, that there

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is no variance about this abundance in the deterministic case. Evaluating the stability of the equilibrium, we find that the eigenvalue of the linearized equation about N_i^* is

$$\left(\frac{\partial(dN_i/dt)}{\partial N_i} \right)_{N^*} = m(1 - J),$$

which is always negative for community size $J > 1$; hence, the equilibrium is always stable.

I now turn to consideration of the second half of the theory, namely, the theory for metacommunity dynamics. When the two halves of the theory are put together, we will unify the theories of island biogeography and relative species abundance into a single quantitative theory, and in so doing, obtain a complete analytical solution to the classical island-mainland problem posed by MacArthur and Wilson more than 30 years ago.

SUMMARY

1. This chapter develops the first half of the unified neutral theory and describes the dynamics of an arbitrary species undergoing zero-sum ecological drift in a local community as a function of local community size, the immigration rate, and the abundance of the species in the metacommunity.
2. The time to extinction or monodominance of the species in the local community can be very long if the community is large and the focal species is reasonably abundant initially. However, these times are also a function of the disturbance rate, and they are generally much shorter if the disturbance rate of the community is high.
3. The expected abundance of an arbitrary species in the local community is independent of the immigration rate and depends only on local community size and the

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abundance of the species in the metacommunity. However, the variance in abundance is also a function of the immigration rate.

4. When local communities are very isolated from the metacommunity (low rate of immigration), the probability density functions of abundance are U-shaped, and the species spends most of its time either absent from the local community (the usual case) or occasionally monodominant.
5. When local communities are strongly coupled dynamically to the metacommunity by high immigration, relative abundances in the local community are more similar to those in the metacommunity.
6. Variances in local abundance are predicted to be a parabolic function of metacommunity relative abundance. However, detecting this curvilinearity may be difficult in samples when the commonest species is still a small fraction of the metacommunity, in which case the theory predicts a log-log linear relationship between variance and mean abundance.