CHAPTER 21

Multispecies Lottery Competition: A Diffusion Analysis

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The lottery model is a stochastic competition model designed for space-limited communities of sedentary organisms. Examples of such communities may include coral reef fishes (Chesson & Warner 1981), aquatic sessile organisms (Fagerstrom 1988), and plant communities such as trees in a tropical forest (Leigh 1982; Hatfield et al., in press). The lottery model, and its properties and behavior, has been discussed previously (Chesson & Warner 1981; Chesson 1982, 1984, 1991, 1994; Warner & Chesson 1985; Chesson & Huntly 1988). Furthermore, explicit conditions for the coexistence of two species and the stationary distribution of the two-species model were determined (in Hatfield & Chesson 1989) using an approximation with a diffusion process (Karlin & Taylor 1981). However, a diffusion approximation for the multispecies model (for more than two species) has not been reported previously, and a stage-structured version has not been investigated. The stage-structured lottery model would be more reasonable for communities of long-lived species in which recruitment or death rates depend on the age or stage of the individuals (e.g., trees in a forest). In this chapter, we present a diffusion approximation for the multispecies lottery model and also discuss a stage-structured version of this model.

The conditions for coexistence and the stationary distribution of the lottery model are useful because they indicate whether a given community tends toward persistence in a variable environment, and if so, they provide information about the type and magnitude

of population fluctuations that the competing species experiences over time. Furthermore, if the assumptions of the lottery model apply to a given community, then the expected stationary distribution can be fit to species-abundance data collected in the field to yield information and insights about life-history parameters of the competing species (e.g., Hatfield et al., in press). The multispecies and stage-structured models are particularly important to study because these models obviously have broader application than the two-species model.

1 Multispecies Model

In the multispecies lottery model, the equation for the ith species, $i = 1, 2, \ldots, k$, is given by

$$P_i(t + 1) = [1 - \delta_i(t)] P_i(t) + \left[\sum \delta_j(t) P_j(t) \right] \frac{\beta_i(t) P_i(t)}{\sum \beta_j(t) P_j(t)}, \quad (1)$$

where $P_i(t)$ is the proportion of space occupied by species i at time t, $\beta_i(t)$ is the per capita recruitment rate of species i, and $\delta_i(t)$ is the adult death rate during the time interval $(t, t+1]$. The diffusion approximation to the multispecies lottery model is determined by its infinitesimal mean, variance, and covariance coefficients (Karlin & Taylor 1981), defined as

$$\mu_i(\mathbf{p}) = \lim_{\epsilon \to 0} \frac{1}{\epsilon} \operatorname{E} \left[P_i(t + \epsilon) - P_i(t) \right|$$
$$\mathbf{P}(t) = \mathbf{p} = p_1, p_2, \ldots, p_k], \quad (2)$$

$$\sigma_i^2(\mathbf{p}) = \lim_{\epsilon \to 0} \frac{1}{\epsilon} \operatorname{E} \left\{ \left[P_i(t + \epsilon) - P_i(t) \right]^2 | \mathbf{P}(t) = \mathbf{p} \right\}, \quad (3)$$

$$\sigma_{ij}(\mathbf{p}) = \lim_{\epsilon \to 0} \frac{1}{\epsilon} \operatorname{E} \left\{ \left[P_i(t + \epsilon) - P_i(t) \right] \right.$$
$$\left. \times \left[P_j(t + \epsilon) - P_j(t) \right] | \mathbf{P}(t) = \mathbf{p} \right\}, \quad (4)$$

where $i, j = 1, 2, \ldots, k$ and $i \neq j$.

To approximate the multispecies lottery model with a diffusion process, the model must first be rescaled for continuous time. A description is given elsewhere (Hatfield 1986; Hatfield & Chesson 1989) and involves replacing $P_i(t + 1)$ by $P_i(t + \epsilon)$ in the left-hand side of equation (1) and letting ϵ approach 0. Furthermore, the amount of change occurring per time unit must be decreased, which is accomplished by defining $X_i(t) = \ln [\beta_i(t) / \delta_i(t)]$ and assuming that $\operatorname{E} [X_i(t)] = \epsilon \mu_i$ and $\operatorname{var} [X_i(t)] = \epsilon \sigma_i^2$. In addition, let $\operatorname{cov} [X_i(t), X_j(t)] = \epsilon \theta_{ij}$, $i \neq j$, $\delta_u(t) = d_u \exp[Y_u(t)]$, $\operatorname{E} [Y_u(t)] = 0$,

and $\mathrm{cov}\left[Y_u(t), X_i(t) - X_j(t)\right] = \epsilon\theta_{uij}$. Higher-order moments are assumed to be terms of order $o(\epsilon)$.

Employing power-series expansions of $e^{\pm X_i(t)}$ and $e^{\pm Y_i(t)}$, substituting the definitions and assumptions given above into equations (2), (3), and (4), and letting ϵ approach 0 yields the diffusion coefficients for the multispecies lottery model:

$$\mu_i(\mathbf{p}) = \frac{d_i p_i}{\sum_n d_n p_n}\left\{\sum_u d_u p_u\left[(\mu_i - \mu_u)\right.\right.$$

$$+ \left(1 - \frac{d_u p_u}{\sum_n d_n p_n}\right)\theta_{uiu}$$

$$+ \left(\frac{d_u p_u}{\sum_n d_n p_n}\right)\theta_{iiu}$$

$$+ \left(\frac{d_u p_u}{\sum_n d_n p_n} - \frac{1}{2}\right)$$

$$\times \left.\left(\sigma_i^2 + \sigma_u^2 - 2\theta_{iu}\right)\right]$$

$$+ \frac{1}{\sum_n d_n p_n}\sum_u\sum_m d_u d_m p_u p_m$$

$$\times \left(\sigma_i^2 - \theta_{iu} - \theta_{im} + \theta_{um}\right.$$

$$\left.\left. + \theta_{iim} - \theta_{uim}\right)\right\}, \tag{5}$$

$$\sigma_i^2(\mathbf{p}) = \frac{d_i^2 p_i^2}{\left(\sum_n d_n p_n\right)^2}\sum_u\sum_m d_u d_m p_u p_m$$

$$\times \left(\sigma_i^2 - \theta_{iu} - \theta_{im} + \theta_{um}\right), \tag{6}$$

$$\sigma_{ij}(\mathbf{p}) = \frac{d_i d_j p_i p_j}{\left(\sum_n d_n p_n\right)^2}\sum_u\sum_m d_u d_m p_u p_m$$

$$\times \left(\theta_{ij} - \theta_{ju} - \theta_{im} + \theta_{um}\right). \tag{7}$$

The stationary distribution, $\psi(\mathbf{p})$, of the diffusion process represented by equations (5), (6), and (7) must satisfy the Kolmogorov forward equation (Keilson 1965),

$$0 = \sum_{i=1}^{k-1}\frac{\partial}{\partial p_i}\left[\sum_{j=1}^{k-1}\frac{\partial\sigma_{ij}(\mathbf{p})\psi(\mathbf{p})}{2\partial p_j} - \mu_i(\mathbf{p})\psi(\mathbf{p})\right], \tag{8}$$

where $\sigma_{ii}(\mathbf{p}) = \sigma_i^2(\mathbf{p})$. Solving equation (8) requires the following

simplifying assumptions: $\sigma_i^2 = \sigma^2$; $\theta_{ij} = \rho\sigma^2$, $i \neq j$, $0 \leq |\rho| \leq 1$; $\theta_{uiu} = \tau\sigma^2$, $\theta_{iiu} = -\tau\sigma^2$, $u \neq i$; and $\theta_{uim} = 0$, $u \neq m$, $u \neq i$, $m \neq i$. The assumption concerning the variances implies that each species experiences a similar amount of variation (i.e., environmental fluctuations) in the X_i. The assumption concerning the θ_{ij} means that the correlation between all pairs X_i and X_j is identical. The assumptions concerning θ_{uiu}, θ_{iiu}, and θ_{uim} would result from a dependence between Y_u and X_u, in addition to the independence of Y_u and X_i ($m \neq i$). Defining $\varphi = \sigma^2(1-\rho)$ and $\varphi' = \sigma^2(1-\rho-\tau)$, these assumptions yield

$$\mu_i(\mathbf{p}) = d_i p_i \left\{ \mu_i - \sum d_n \mu_n p_n \sum d_n p_n \right.$$

$$\left. + \varphi' \left[\frac{\sum d_n^2 p_n^2}{\left(\sum d_n p_n\right)^2} - \frac{d_i p_i}{\sum d_n p_n} \right] \right\}, \tag{9}$$

$$\sigma_i^2(\mathbf{p}) = d_i^2 \varphi p_i^2 \left[1 + \sum d_n^2 p_n^2 \left(\sum d_n p_n\right)^2 - \frac{2 d_i p_i}{\sum d_n p_n} \right], \tag{10}$$

$$\sigma_{ij}(\mathbf{p}) = d_i d_j \varphi p_i p_j \left[\frac{\sum d_n^2 p_n^2}{\left(\sum d_n p_n\right)^2} - \frac{d_i p_i}{\sum d_n p_n} \right.$$

$$\left. - d_j p_j \sum d_n p_n \right]. \tag{11}$$

Equation (8) is still too difficult to solve for coefficients (9), (10), and (11). Keilson (1965) proved that if the process is irrotational—that is, $(\partial/\partial p_j)\,\partial\psi/\partial p_i = (\partial/\partial p_i)\,\partial\psi/\partial p_j$—then a unique solution exists to the inner expression of equation (8):

$$0 = \sum_{j=1}^{k-1} \frac{\partial \sigma_{ij}(\mathbf{p})\psi(\mathbf{p})}{2\partial p_j} - \mu_i(\mathbf{p})\psi(\mathbf{p}), \quad i = 1, 2, \ldots, k. \tag{12}$$

For the process determined by (9), (10), and (11), extensive algebra shows that the process is irrotational if $d_1 = d_2 = \ldots = d_k = d$. Adding this assumption to (9), (10), and (11) yields the coefficients

$$\mu_i(\mathbf{p}) = d p_i \left[\mu_i - \sum \mu_n p_n + \varphi' \left(\sum p_n^2 - p_i \right) \right], \tag{13}$$

$$\sigma_i^2(\mathbf{p}) = d^2 \varphi p_i^2 \left(1 + \sum p_n^2 - 2 p_i \right), \tag{14}$$

$$\sigma_{ij}(\mathbf{p}) = d^2 \varphi p_i p_j \left(\sum p_n^2 - p_i - p_j \right). \tag{15}$$

In this case, these equations are identical to those for a diffusion

process from the SAS-CFF model in population genetics (Gillespie 1980, 1991) and thus the solution, $\psi(\mathbf{p})$, to (12) is a Dirichlet distribution:

$$\psi(\mathbf{p}) = c \prod_{i=1}^{k} p_i^{v_i - 1}, \tag{16}$$

where $v_i = 2\left[k\left(\mu_i - \bar{\mu}\right) + \varphi' - d\varphi\right]/d\varphi k$, $\bar{\mu} = \sum \mu_n/k$, and c is the constant of integration, which allows $\psi(\mathbf{p})$ to be a probability density.

The condition for the existence of (16) as a probability density is that $v_i > 0$, which implies that

$$d < \left[\varphi' - k \max\left(\bar{\mu} - \mu_i\right)\right]/\varphi \tag{17}$$

and

$$\sigma^2 > k \max\left(\bar{\mu} - \mu_i\right)/\left[(1 - d)(1 - \rho) - \tau\right]. \tag{18}$$

Thus, equations (17) and (18) are the conditions for the coexistence of k species in this community. This does not prove that (17) and (18) are the conditions for the existence of a stationary distribution; it proves only that (17) and (18) guarantee that (16) is a probability distribution. However, Seno and Shiga (1984) showed that $v_i > 0$ is in fact the condition for the existence of the stationary distribution and thus the condition for the coexistence of the k species in this model.

Given that the k competing species are able to coexist, the stationary distribution provides information about the year-to-year population fluctuations that these species experience over time. This statistical distribution can also be used to generate expected means and variances and to evaluate the stability of the coexistence by looking at the shape of the distribution. (For a discussion of stability in population fluctuations for a community of two species, see Hatfield & Chesson 1989.)

2 Stage-Structured Model

For a stage-structured version of the lottery model, let species i have A_i stages (or ages), and let $\gamma_{ij}(t)$ be the probability that stage j of species i proceeds to stage $j+1$ during the time interval $(t, t+1]$, $i = 1, 2, \ldots, k$, $j = 1, 2, \ldots, A_i$. (Note that $\gamma_{ij} = 1$ for all i and j yields the age-structured model.) Let $\beta_{ij}(t)$ be the per

capita recruitment rate, and let $\delta_{ij}(t)$ be the death rate for stage j of species i during the time interval $(t, t+1]$. Then, the equations for the stage-structured lottery model are

$$P_{i1}(t+1) = [1 - \gamma_{i1}(t)][1 - \delta_{i1}(t)]P_{i1}(t)$$
$$+ \sum_i \sum_j \delta_{ij}(t) P_{ij}(t)$$
$$\times \frac{\sum_j \beta_{ij}(t) P_{ij}(t)}{\sum_i \sum_j \beta_{ij}(t) P_{ij}(t)} \qquad (19)$$
$$P_{i2}(t+1) = [1 - \gamma_{i2}(t)][1 - \delta_{i2}(t)]P_{i2}(t)$$
$$+ \gamma_{i1}(t)[1 - \delta_{i1}(t)]P_{i1}(t), \qquad (20)$$

$$\vdots$$

$$P_{iA_i}(t+1) = [1 - \gamma_{iA_i}(t)][1 - \delta_{iA_i}(t)]P_{iA_i}(t)$$
$$+ \gamma_{iA_{i-1}}(t)[1 - \delta_{iA_{i-1}}(t)]P_{iA_{i-1}}(t),$$

$i = 1, 2, \ldots, k$. Unfortunately, the stage-structured version of the lottery model cannot be investigated with a diffusion approximation because the rescaled continuous-time model does not appear to converge to a diffusion process. In this case, computer simulations could be used to provide insight into the behavior of this model.

The lottery model provides a simple example of species coexistence by a mechanism known as the storage effect (Chesson 1984; Warner & Chesson 1985). It is one of two general coexistence mechanisms that depend on temporal environmental fluctuations (Chesson 1994). The storage effect is most likely to occur when the various individuals in a population differ in their sensitivities to environmental factors and competition. Such differences in sensitivity occur, for example, as a consequence of the distinction between juveniles and adults in the lottery model and in general scenarios involving iteroparous organisms (Chesson 1984; Chesson & Huntly 1988). Study of the lottery model has provided important general information about the operation of the storage effect. Its stage-structured version may well provide important new understanding of this general coexistence mechanism.

Acknowledgments

learned from Shripad Tuljapurkar, Hal Caswell, the many other fine instructors, and fellow students during the summer course at Cornell University.

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