

Determinism in a Transient Assemblage: The Roles of Dispersal and Local Competition

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ABSTRACT: Both dispersal and local competitive ability may determine the outcome of competition among species that cannot coexist locally. I develop a spatially implicit model of two-species competition at a small spatial scale. The model predicts the relative fitness of two competitors based on local reproductive rates and regional dispersal rates in the context of the number, size, and extinction probability of habitat patches in the landscape. I test the predictions of this model experimentally using two genotypes of the bacteriophagous soil nematode *Caenorhabditis elegans* in patchy microcosms. One genotype has higher fecundity while the other is a better disperser. With such a fecundity-dispersal trade-off between competitors, the model predicts that relative fitness will be affected most by local population size when patches do not go extinct and by the number of patches when there is a high probability of patch extinction. The microcosm experiments support the model predictions. Both approaches suggest that competitive dominance in a patchily distributed transient assemblage will depend upon the architecture and predictability of the environment. These mechanisms, operating at a small scale with high spatial admixture, may be embedded in a larger metacommunity process.

Keywords: dispersal, trade-off, experimental evolution, spatio-temporal heterogeneity, *Caenorhabditis elegans*, spatial scale.

In seeking explanations for the co-occurrence of competing species, it has become increasingly common to consider the use of space in patchy landscapes as an axis of differentiation (Tilman and Kareiva 1997; Chesson 2000). Competitors may coexist by trading local competitive ability for dispersal ability (Tilman 1994). Indeed, field studies

have shown a prevalence of dispersal-adapted species in disturbed or fragmented habitats (Pajunen 1982; Thomas 2000; Schnitzer and Carson 2001) and a positive correlation between dispersal propensity and habitat stability even among disparate populations of the same species (Denno et al. 1996). These examples suggest that dispersal has a real fitness benefit that may balance local competitive ability in a fluctuating environment and permit species coexistence where a nonspatial model would predict monodominance (Hanski 1999). There is both recent and historical interest, however, in the idea that natural systems, regardless of the stability of the species pool at larger spatial scales, contain local groups of species that co-occur without equilibrium (Gleason 1926; Whittaker 1956; MacArthur and Wilson 1967; Sale 1977; McPeck and Brown 2000; Hubbell 2001). In these transient assemblages, diversity declines without recurrent immigration from outside the system for want of stabilizing mechanisms (Chesson 1994, 2000). By definition, neither differential local competitive ability nor differential dispersal will stabilize a transient assemblage, but it would be valuable to estimate their separate contributions to the rate and direction of change in community composition.

The factors that drive community dynamics change dramatically at different spatial and temporal scales (Ricklefs and Schluter 1993). I focus on a spatial scale at which habitat patches exchange a large number of individuals every generation such that local and regional dynamics occur on the same temporal scale (a situation that further prevents coexistence; Hanski 1983). I envision a set of contiguous patches, such as host plants or entire agricultural fields, that can fluctuate independently but are not isolated by any great distance. Just as high migration rates reduce spatial variance in allele frequencies (Whitlock 2001), I expect the relative abundance of competing species to be similar in all patches.

The particular problem of considering a spatial scale smaller than any spatial structure in the community may afford a novel ecological model. The classic metapopulation concept with relatively instantaneous local population dynamics (Levins 1969; Levins and Culver 1971; Hanski

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1983) is not the right description of this spatial scale (Hanski 1999). Meanwhile, a coupled logistic map is a mathematically cumbersome approach to such regionally synchronous population dynamics. In this article, I present a model addressing the specific problem of competition between two species in a well-mixed, patchy community that is closed to outside immigration. The model makes four general predictions, all supported by previous theoretical investigations. First, competitive dominance will depend solely upon relative demographic rates in the absence of patch extinctions (McPeck and Holt 1992). Second, relative fitness will be positively correlated with a species' ability to redistribute itself over the landscape after disturbance (Comins et al. 1980; Kuno 1981; Johnson and Gaines 1990). Third, any advantage to dispersal will decrease with an increasing number of patches in the landscape (Kuno 1981). Fourth, the rate of competitive exclusion is lower in larger populations (Charlesworth 1994).

I test the model qualitatively with an experiment using the soil nematode *Caenorhabditis elegans* growing on a patchy resource as an analogue to a two-species community. The ease of manipulating *C. elegans*'s environment and the variety of behavioral mutants available for study make it possible to isolate the effects of patch number, population size, and a fecundity-dispersal trade-off on relative fitness in a transient two-species assemblage. The experimental results agree with the model's predictions, suggesting that the trajectory of a transient assemblage, though contextual, has a strong deterministic element stemming from the interplay of dispersal and local competition. I also discuss the linkage between this and larger-scale models of community assembly.

The Model

Change in the relative abundance of two competing species is analogous to the change in frequency of two alleles at a single haploid locus, since, in both cases, genetic variance is expected to be greater between than within the units under selection and hybridization between units cannot occur. The analogy is fortunate, since simple models for the effects of population size, allele frequency, and environmental variance on a population's response to selection have existed for some time.

In a stable environment, the rate of change in the frequency of two nonneutral haploid alleles is

$$\frac{dp}{dt} = p(1-p)(r_1 - r_2), \quad (1)$$

where p is the frequency of allele 1, and r_i is the natural log transform of the geometric growth rate of allele i (Crow and Kimura 1970). The rate of response to selection is

proportional to the strength of selection, $r_1 - r_2$, and the genetic variance at the locus, $p(1-p)$ (Fisher 1930). These familiar predictions will hold for the analogy to a two-species community, where p is the frequency of species 1 and r_i is the intrinsic growth rate of species i . The rate of change in the allele frequencies decreases as p approaches 0 or 1.

Competitive exclusion may proceed differently in a variable environment. Geometric population growth is slowed by environmental variation (sensu Jensen's paradox; Wiener and Tuljapurkar 1994; Ruel and Ayres 1999), affecting the similarity and even the hierarchy of competitive ability among species. If a species' intrinsic growth rate is normally distributed with mean r_i and variance σ_{ri}^2 , then the expected change in the frequency of the focal species in a two-species community after one generation is

$$\Delta p = \frac{p(1-p)}{n} \left[r_1 - r_2 + \frac{1}{2}(\sigma_{r_2}^2 - \sigma_{r_1}^2) \right], \quad (2)$$

provided that generations are discrete and selection diminishes with population size, n (Gillespie 1975). The population size effect satisfies the assumptions of a diffusion approximation (O. Ronce, personal communication). I believe the effect has heuristic value, as selection can diminish with increasing population size due to an effect of density or area.

I consider a set of patches in which environmental variation is driven by spatiotemporally random patch extinctions. If the reproductive rate of species i is high enough that $r_i \approx \ln(\text{fecundity} + 1)$, the variance of its intrinsic growth rate in a set of k patches with probability of patch extinction e is

$$\sigma_{ri}^2 = \frac{k(1-e)r_i^2 - [kr_i(1-e)]^2/k}{k-1},$$

using the machine formula for the variance of a normal distribution (Zar 1999), which simplifies to

$$\sigma_{ri}^2 = r_i^2 \frac{ke(1-e)}{k-1} = r_i^2 \sigma_E^2, \quad (3)$$

where σ_E^2 is the portion of reproductive variance due purely to environmental variation. For a given level of environmental variation, reproductive variance is greater for more fecund species. For a given risk of patch extinction, environmental variation decreases with increasing numbers of patches. For a given number of patches, environmental variation is highest at intermediate extinction risk. Equation (3) is conservative in that it treats extinction as an

arithmetic deviation from mean fitness rather than as a geometric finality.

Organisms have various life-history strategies for dealing with environmental variation (Via and Lande 1985; McPeck and Kalisz 1998). Among these strategies there is evidence, both theoretical (Comins et al. 1980; Chesson 1981; Kuno 1981; Cohen and Levin 1991; McPeck and Holt 1992; Wiener and Tuljapurkar 1994; Yoshimura and Jansen 1996; McPeck and Kalisz 1998) and experimental (Friedenberg 2003), that unconditional random dispersal increases fitness in an environment with spatiotemporally random fluctuation or extinction of habitat patches. Kuno (1981) showed that, if w_j is the proportion of a population found in patch j , a population's reproductive variance is given by $\sigma_r^2 \sum_{j=1}^k w_j^2$. By extension, the reproductive variance of species i is $\sigma_{ri}^2 \sum_{j=1}^k w_{ij}^2$. I will abbreviate the summation term as γ_i and refer to it as the sensitivity of a species' intrinsic growth rate to environmental variation.

At the individual level, w_{ij} is the probability of an individual of species i being in patch j . Consider an individual with dispersal propensity v_i in a set of k patches where each patch population goes extinct with probability e every generation. The probability that the individual is in a patch that was not previously extinct is the probability that it was either born there and did not leave or immigrated from another patch that did not go extinct,

$$w_{i, \text{extant}} = (1 - v_i) + \frac{[k(1 - e) - 1]v_i}{k - 1},$$

whereas the probability that an individual is in a patch that went extinct in the previous generation is

$$w_{i, \text{colonist}} = \frac{v_i}{k - 1}.$$

Calculating the sensitivity of a species to environmental variation is a matter of summing the squares of the above probabilities over the expected $k(1 - e)$ extant patches and ke recently extinct patches, such that

$$\gamma_i = k(1 - e) \left\{ (1 - v_i) + \frac{[k(1 - e) - 1]v_i}{k - 1} \right\}^2 + ke \left(\frac{v_i}{k - 1} \right)^2,$$

which simplifies to

$$\gamma_i = \frac{1}{k(1 - e)} \left(1 - \frac{v_i ke}{k - 1} \right)^2 + ke \left(\frac{v_i}{k - 1} \right)^2. \tag{4}$$

The sensitivity of a species to environmental variation will be highest when it does not disperse ($\gamma = 1$) and will reach its minimum, $\gamma = 1/k$, when the population is panmictic (Kuno 1981). For a given probability of patch extinction, γ will be smaller and will change less with changes in dispersal propensity as the number of patches in the landscape increases (fig. 1).

It is useful to note that $1/\gamma_i$ takes the same form as Simpson's index of evenness (Begon et al. 1996). Rather than measuring the equity of species abundance, however, $1/\gamma_i$ measures the uniformity of a species' spatial distribution one generation after patch extinction. Frequent, spatiotemporally random extinction events, differential dispersal, and local competition are likely to yield higher spatial variance than predicted by $1/\gamma_i$. However, the predicted relative uniformity, U_1 , of species 1 in a two-species system,

$$U_1 = \frac{1}{\gamma_1} - \frac{1}{\gamma_2}, \tag{5}$$

may have some utility as an estimate of relative resilience to disturbance.

Equations (2), (3), and (4) can be combined to predict the rate of change in the frequency of two species competing in a patchy landscape, such that

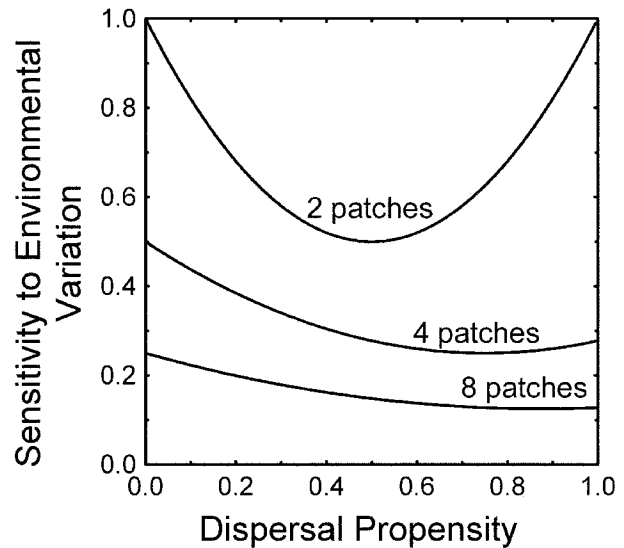


Figure 1: The sensitivity of fitness to environmental variation is a function of dispersal propensity and patch number. $v = 0.5$. A species' mean intrinsic rate of increase is depreciated by this proportion of its reproductive variance.

$$\Delta p = \frac{p(1-p)}{n} \left[r_1 - r_2 + \frac{1}{2} (\gamma_2 r_2^2 - \gamma_1 r_1^2) \sigma_E^2 \right], \quad (6)$$

where p is the frequency of species 1. Equation (6) is a continuous approximation of discrete population growth, providing an instantaneous estimate of the direction and magnitude of competitive exclusion. This model applies best to semelparous organisms with short generation times. It is suited to systems in which dispersal is common and cost free. By providing the rate and direction of community change, the model is useful for gauging the invisibility of a single-species system or the decay rate of a transient community.

According to equation (6), an increase in r_i can decrease a species' relative fitness in a fluctuating environment (Gillespie 1975). All else being equal, a species' mean intrinsic rate of increase, $r_i - \sigma_i^2/2$ (Gillespie 1973), is a concave down function of r_i . Hence, there is a value of r_i that maximizes growth (as in fig. 2A). The optimal r_i increases with the number of patches in a landscape (fig. 2B). In the parameter space where increased r_i reduces the mean growth rate, change in dispersal propensity has a greater effect on fitness than does reproduction (fig. 2A). Thus, there is an area in fecundity-dispersal space—largest in small sets of patches—in which competition between species is likely to be driven by differential dispersal when a community neighborhood comprises very few patches.

Equation (6) makes four general predictions. First, because all environmental variation comes from patch extinctions and dispersal has no cost, competitive dominance will depend solely upon relative demographic rates in the absence of patch extinctions. Second, fitness will be positively correlated with a species' ability to redistribute itself over the landscape after disturbance, meaning that differential dispersal may alter the competitive hierarchy and the rate of exclusion. Third, any advantage to dispersal will decrease with an increasing number of patches in the landscape, as the contribution of individual patch extinctions to environmental variation decreases. Fourth, competitive exclusion will take longer in a larger population such that a dominant species will realize lower relative fitness in a given period of time; competitors will appear more equivalent in large populations.

Model Predictions and Experimental Methods

The remainder of this article deals with testing particular predictions made by equation (6) and its components. I used two genotypes of the soil nematode *Caenorhabditis elegans* in microcosms consisting of patches of food on an agar plate to simulate competition in a set of habitat patches. *Caenorhabditis elegans* is a selfing hermaphrodite;

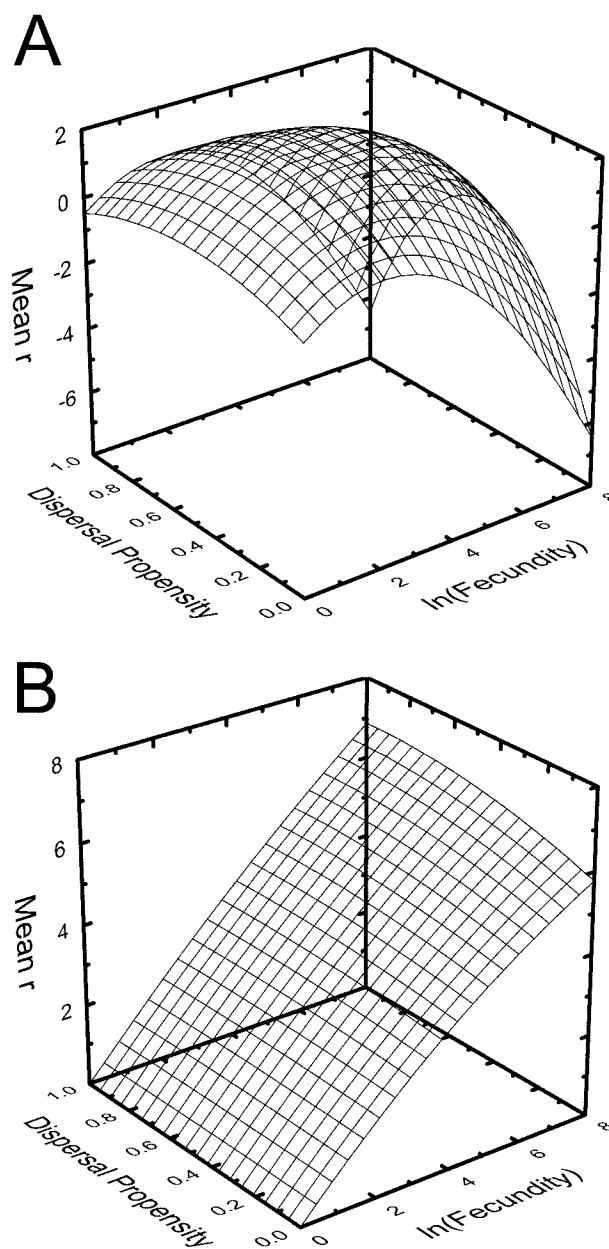


Figure 2: Mean intrinsic rate of increase of a single species as a function of dispersal propensity and fecundity in a fluctuating environment. Surfaces represent the difference $r - \gamma\sigma_i^2$. See text for an explanation of terms; $e = 0.5$. A, In a landscape of two patches and frequent patch extinction, rates of increase are sensitive to both fecundity and dispersal rates. B, In a landscape of eight patches and frequent patch extinction, dispersal has little effect on a species' rate of increase.

the production of outcrossing males is rare (Riddle et al. 1997), and the genotypes did not hybridize during the course of the experiments. I present results in terms of genotypes but interpret the results as analogous to species

competition. The worms' ability to move and the scale of the microcosms was such that a large number of migrants often moved between patches. Thus the experiment, like the model, dealt with a well-mixed system in which both species are expected to be present in all patches. I was able to control patch extinction rate, the number of patches, and the size of patches and their populations.

The two worm genotypes, each about 1.5 mm in length at sexual maturity, differ in their fecundity and propensity to disperse between food patches on an agar plate. Twenty individuals of genotype CB91, a *rol-1* mutant, produced an average of 67.7 offspring (SD = 26.0) when placed individually on lawns of *Escherichia coli* (OP50) for 3 d at 21°C. In the same period, 20 individuals of genotype PD1856, a transgenic worm that expresses green fluorescent protein in its pharynx, produced an average of 42.9 offspring (SD = 17.2). Offspring of the less fecund genotype, PD1856, were 12% more likely to disperse between two 2-cm patches of *E. coli* 3 cm apart on an agar plate in 3 d than offspring of CB91 in the same populations (SD of paired difference in dispersal = 2%, N. A. Friedenber, unpublished manuscript). The apparent fecundity-dispersal trade-off between the genotypes is a coincidence of their independent histories of mutagenesis. In fact, I have not built a trade-off into the assumptions of the model. I screened many genotypes in search of a pair that would differ in their dispersal propensity but not their fecundity. These two genotypes were desirable because their difference in dispersal propensity is large and the lesser disperser has no inherent disadvantage.

I parameterized equation (6) with the fecundity and dispersal propensity of the two worm genotypes and iterated it through four discrete generations to predict the outcome of competition under a variety of conditions. To test the respective roles of fecundity and dispersal in a transient community, I compared change in the frequency of the better disperser between sets of patches with and without extinction risk in combination with various landscape architectures. To test the effect of population size on the rate and direction of competitive exclusion, I compared the model's prediction in a set of two small patch populations to a set of two large patch populations. To test the interaction of patch number with the roles of fecundity and dispersal, I compared the dynamics of two small patches to eight small patches. Thus, I compared the numerical results of the model in a two-way design, crossing the presence or absence of patch extinction with three landscape architectures differing in either the size or number of patches.

It was possible to create conditions that met or approximated the model's assumptions using the *C. elegans* microcosms. I was able to manipulate the number and size of patches and their probability of extinction in an

experimental design that matched my numerical analysis of the model. I maintained 20 replicate microcosms each of two small food patches, two large patches, and eight small patches. Half the replicate microcosms of each architecture were prone to frequent patch extinctions. Previous work from this system shows that there is no cost to dispersal (Friedenberg 2003).

Microcosm Construction

A patchy landscape for *C. elegans* can be constructed by creating patches of bacteria on an agar plate. To obtain a controlled source of bacteria with which to create patches, I grew liquid cultures of *E. coli* OP50 in Luria broth to saturation at 37°C. I separated bacterial cells from their growth medium by centrifugation and froze aliquots of the resuspended slurry in a 15% glycerol solution at -80°C. All bacteria used in the experiment came from the same common slurry. I created a patch by pipetting a small volume of slurry onto the surface of an agar plate and allowing it to dry. If care was taken not to disturb plates during the drying process, patches of equal volume had similar areas. Plates were S-basal saline buffer (Lewis and Flemming 1995) and 2.5% agar. In the interest of preventing the growth of contaminants and the disruption of patch structure by bacterial growth, the plates contained no nutritive growth media. I manipulated the size of patches by controlling the volume and dilution of food slurry used to construct them (fig. 3). I arranged patches to maintain similar interpatch distances among treatments while maximizing the number of neighbors in eight-patch replicates.

Worm Culture and Experimental Manipulations

In order to maintain clean, uncrowded conditions, plate populations of worms must be serially transferred to new plates every generation (3 d at 21°C). I kept initially isogenic lines of the two genotypes on a nutritive agar medium (NGM; Lewis and Flemming 1995) seeded with a lawn of *E. coli* OP50 in 60-mm petri plates for three generations to equilibrate to lab conditions at 21°C, transferring 12 fourth-stage hermaphrodite larvae between generations. I initiated the first generation in the experimental microcosms with 10 μ L of each genotype in aqueous suspension (about 20 individuals per genotype) created by washing worms off of 3-d-old stock plates with 1 mL of 0.1% dissolved agar. The agar prevented the suspended worms from settling. Worms were placed in one patch and allowed to grow and disperse.

I transferred small haphazard samples of individuals from old to new plates each generation by scraping each subpopulation along its diameter with the pointed tip of

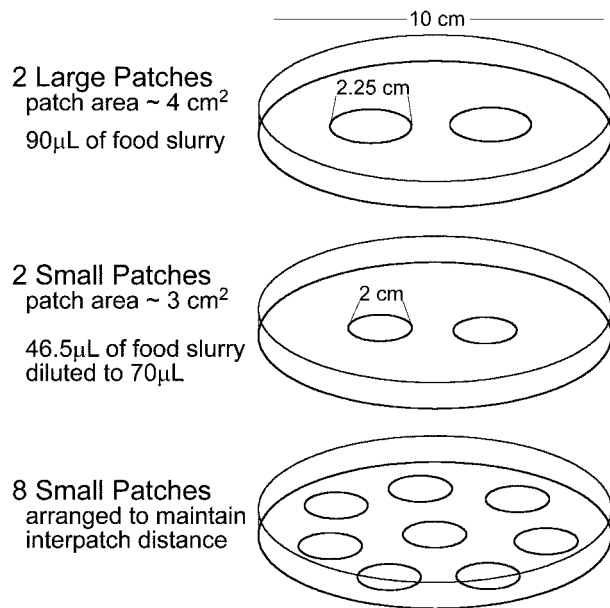


Figure 3: Construction of patchy microcosms. Petri plates with patches of bacterial slurry acted as arenas for competition between two genotypes of a soil nematode. The number and size of patches were manipulated as shown.

a sterile spatula (1 mm in thickness and 4 mm in width), then touching the tip to the agar surface of the new plate beside an empty patch (uninterrupted arrow in fig. 4). Sampling patch populations in this manner creates strong pressure within patches to increase in frequency but such change does not affect total population size in the following generation. When transferring individuals between plates of small patches, I used a single sample from each patch (about 20 individuals). When transferring individuals between plates of large patches, I sampled each patch twice (about 40 individuals).

I imposed patch extinction by failing to passage a patch population to the next generation's plate (interrupted arrow in fig. 4). In replicates with extinction, only half the patches in a metapopulation donated individuals to the succeeding generation. I chose the surviving patches independently and randomly for each replicate. Randomization was accomplished using the random matrix function of the linear algebra library in Maple 7 (Waterloo Maple 2001).

Response Variables

I photographed two 1.5×1.6 -cm subsections of each patch under a mix of GFP filter illumination and full spectrum light at $\times 10$ magnification and counted the individuals in the photographs. The GFP in the pharynx of

the better disperser allowed me to differentiate the genotypes. I recorded the total number of each genotype counted in each patch and calculated the frequency of the better disperser from the sum of all patches in each replicate metapopulation. Counts were made at the end of the first and fifth generations, before transferring individuals to new plates. All census data were density estimates, as they were based on counts of equal area, regardless of patch area. To compare patch population size between treatments with large and small patches, I multiplied the density estimates from large patches by 1.3 to standardize for patch area.

Geometric mean relative fitness could be calculated from the change in genotype frequencies between the first and fifth generation as the familiar intrinsic growth parameter

$$r = \frac{1}{4} \ln \left(\frac{p_5 q_1}{q_5 p_1} \right), \quad (7)$$

where p and q are the genotype frequencies of the better disperser and the better reproducer, respectively, and subscripts refer to generations (Crow and Kimura 1970; Gillespie 1973).

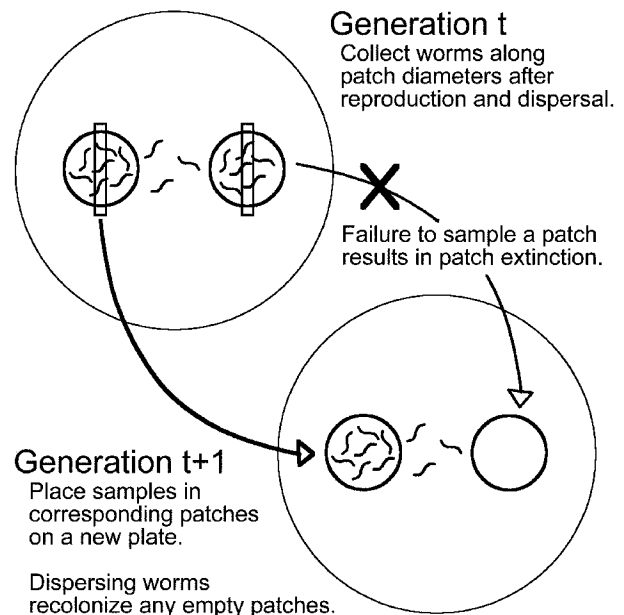


Figure 4: Serial transfer of patch populations and the imposition of patch extinction. In replicates without patch extinctions, individuals were sampled along patch diameters and transferred from all patches every generation to avoid overcrowding and contamination. In replicates with patch extinctions, half the patches were chosen at random to donate individuals to the next generation.

I also calculated the better disperser's relative spatial uniformity. I found the fraction of each genotype's total population occupying each patch, then took the difference of the inverse of sums of squared fractions. This metric is the experimental realization of equation (5). The model proposes that relative uniformity is a measure of the relative sensitivity of the genotypes to spatiotemporally random patch extinctions. As such, relative uniformity should be positively correlated with relative fitness in replicates with patch extinction and uncorrelated in stable replicates. I tested these predictions by ANCOVA with patch extinction as a categorical variable and relative uniformity as a covariate.

Results

Patch Population Estimates

Mean patch population estimates ranged from 30 to 245 individuals. Although I transferred the same number of individuals in all replicates with small patches and twice as many individuals in all replicates with large patches, patch population estimates differed not only between patch sizes but also between treatments of patch number. As intended, patch populations were smaller in replicates with two small patches than in replicates with two large patches (architecture $df = 2, 54, F = 36.85, P < .0001$). However, patch populations in replicates with eight patches were intermediate in size; population sizes in all architectures were significantly different (Tukey HSD, $P < .5$). Extinction decreased population sizes in all architectures (extinction $df = 1, 54, F = 11.92, P = .0011$); extinction and architecture did not interact (interaction $df = 2, 54, F = 0.13, P = .88$).

The population size parameter, n , in the denominator of equation (6) scales the rate (not the direction) of change in the frequency of genotypes over time. The census population numbers are too large for n , as the rate of change approaches zero with these values. Even an estimate of the number of worms transferred between generations is too large. Thus, I treated n as a scaling constant, using a value of 1.3 that made the model match the behavior of replicates with two small patches in the absence of extinction. I used this same value to simulate frequencies in small patches and doubled the value to 2.6 to simulate large patches, reflecting my effort to transfer twice as many individuals to large patches as to small ones.

Relative Fitness

In a fluctuating environment of similar habitat patches, dispersal can increase geometric mean fitness by promoting spatial uniformity (Kuno 1981). Equation (6) predicts

that relative fitness should be positively correlated with relative uniformity (U_i , eq. [5]) when there are patch extinctions (fig. 5, *solid line*). In contrast, dispersal does not affect fitness in a stable, homogeneous environment (McPeck and Holt 1992), and the model predicts no correlation between relative fitness and relative uniformity in the absence of patch extinctions (fig. 5, *dashed line*). The experimental data show a significant interaction of extinction risk with the effect of relative uniformity (ANCOVA interaction $df = 1, 56, F = 7.27, P = .0092$). As in the model, relative fitness increases with uniformity in replicates with extinction ($df = 1, 28, R^2 = 0.42, F = 20.11, P < .001$) but not in those without ($df = 1, 28, R^2 = 0.06, F = 1.82, P = .189$, data points in fig. 5).

Equation (6) predicts that the more fecund genotype will be the dominant competitor in the absence of patch extinction risk, regardless of the number of patches (fig. 6A). When patches do randomly go extinct, the better disperser should dominate in sets of two patches but not in sets of eight (fig. 6A). The difference between genotypes should be smaller in larger patches (fig. 6A). In the experiment, the realized relative r of the high dispersal ge-

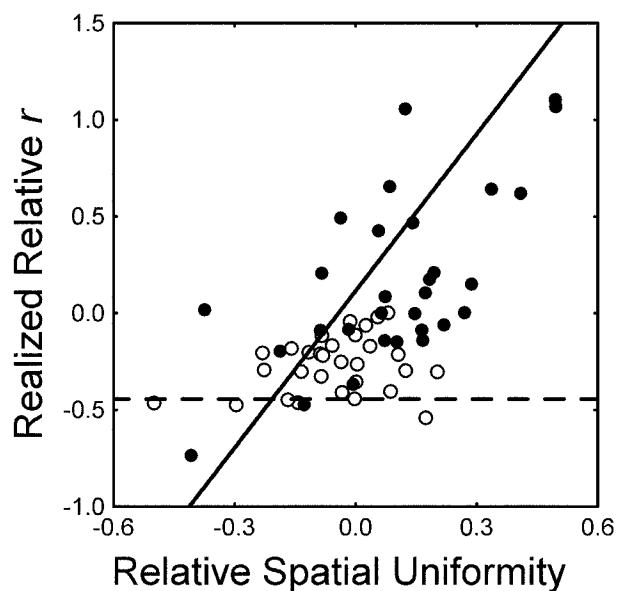


Figure 5: The better disperser's realized intrinsic growth rate after four generations as a function of its relative spatial uniformity. Solid data points are from replicates with patch extinction. Empty data points are from replicates without patch extinction. The solid line is a regression through the predicted relative r given the observed relative uniformity and number of patches in replicates with extinction ($r^2 = 0.71$), calculated from equation (6). The dashed line is the relative r predicted for any replicate without extinction. Parameter values for the two worm genotypes are given in the text.

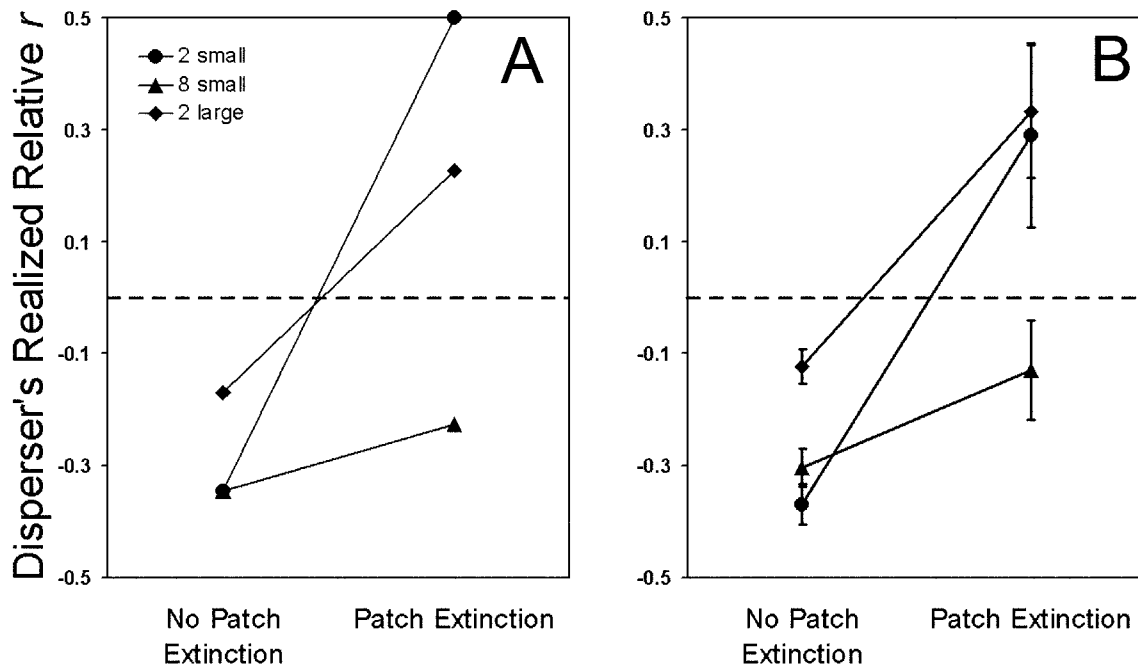


Figure 6: The better disperser's realized relative intrinsic growth rate (A) predicted by the model and (B) observed in the experiment. Model predictions are from four iterations with an initial disperser frequency of 0.6, as was observed at the end of the first generation of the experiment. $e = 0.5$ in extinction treatments. Parameter values for the two worm genotypes are given in the text.

notype (initial frequencies did not differ between treatments) was low in the absence of extinction, increased with patch extinctions ($df = 1, 54, F = 31.81, P < .0001$), and was greater in sets of two patches than in sets of eight ($df = 2, 54, F = 5.93, P = .047$). Relative r in replicates with no extinction was affected by patch size but not by patch number. As predicted, the change in relative r with extinction was greatest in sets of two small patches, smallest in sets of eight patches, and intermediate in sets of two large patches (interaction $df = 2, 54, F = 3.41, P = .0403$, fig. 6B).

Spatial Distribution

An estimate of each genotype's spatial distribution is inherent in equation (6)'s prediction of relative fitness. Equation (5) estimates the relative uniformity of the genotypes. Patch architecture should have no effect on relative uniformity in the absence of patch extinctions. With patch extinction, the better disperser should be relatively more uniform, especially in sets of two patches (fig. 7A). Extinction in the experiment increased the relative spatial uniformity of the better disperser (extinction $df = 1, 54, F = 11.66, P = .0012$) in sets of two patches but not in sets of eight (interaction $df = 2, 54, F = 3.10, P = .053$, fig. 7B).

Discussion

Results of the model and experiment suggest that the competitive hierarchy of species differing in their demographic rates and dispersal propensities can depend upon the number and stability of patch populations. The relative abundance of species changes more slowly where there are more competing individuals in larger patches. While the model assumes dispersal to be random and global, the experiment showed a departure from the model predictions for the spatial arrangement of worms in eight-patch replicates that may reflect a distance-dependent dispersal kernel. However, the experiment did produce the predicted positive relationship between relative spatial uniformity and relative fitness. This pattern indicates that the benefit of dispersal in an unstable environment stems not from dispersal itself but from the homogenization of population densities over space.

This article has dealt most strictly with a specific kind of community where only one species will remain at equilibrium, competitors are closely related in form and function, and migration is common and cost free. The decision to model a transient assemblage of competitors is neither arbitrary nor trivializing. The rate and pattern with which diversity diminishes in a heterogeneous population has been a focus of evolutionary theory, both neutral and

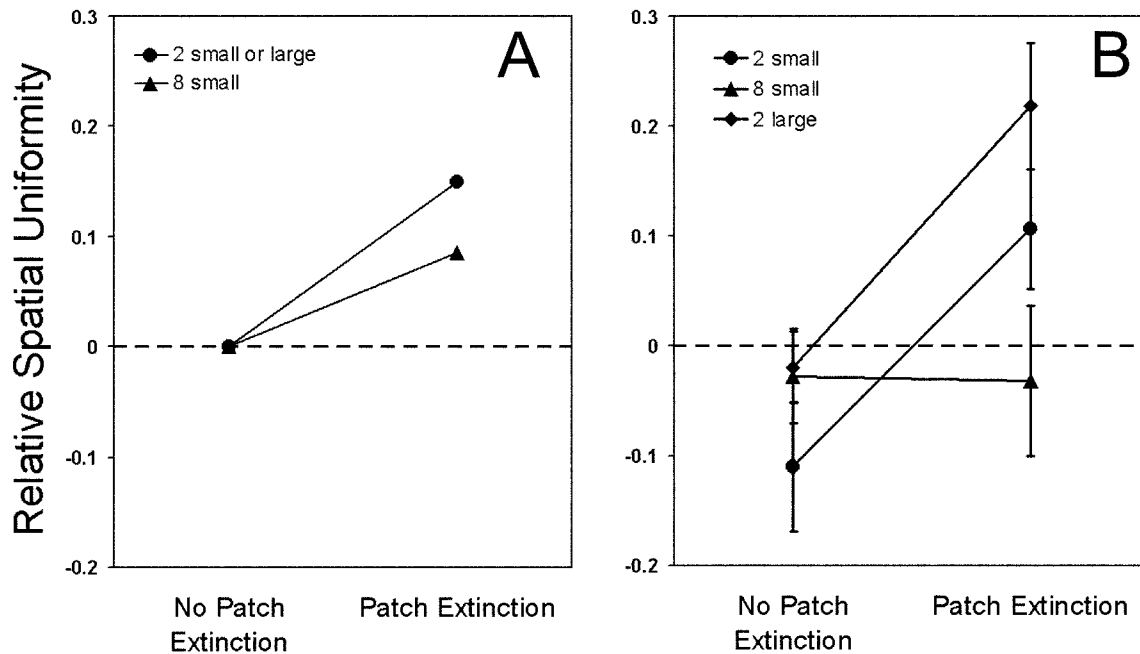


Figure 7: The relative spatial uniformity of the better disperser (A) predicted by the model and (B) observed in the fifth generation of the experiment. Relative uniformity was calculated from equation (5) using the dispersal propensities of the two worm genotypes given in the text.

adaptive (Fisher 1930; Wright 1931; Crow and Kimura 1970; Gillespie 1975; Barton and Whitlock 1997), and though community ecology has long sought the mechanisms that maintain species diversity, its central dogma is the inevitable loss of similar competitors (Hutchinson 1957; Tilman 1982; Chesson 2000). Among the most successful theories of species diversity, island biogeography asserts that recurrent immigration is the only force maintaining diversity (MacArthur and Wilson 1967; Rosenzweig 1995; Hubbell 2001). Likewise, patch occupancy models generally assume that only a single species will persist at the scale of a single patch (Nee and May 1992; Tilman 1994; Tilman et al. 1997; Neuhauser 1998; but see Slatkin 1974 and Hanski 1983).

The model I have tested agrees with evolutionary and biogeographic theory that extinction rates depend on population or community size. In contrast to island biogeography and other neutral community models (Bell 2001; Hubbell 2001), competitive exclusion results from deterministic interactions (albeit in a stochastic environment) rather than from community drift. Finding the correct empirical measure of community size to predict the rate of deterministic change, rather than retrofitting the size constant to empirical data as I have done in this study, may prove difficult. Effective population size in similar population genetic models is still a contentious subject, particularly in metapopulations with local extinction and

recolonization (Wright 1931; Haldane 1939; Kimura and Crow 1963; Kimura and Ohta 1971; McCauley 1991; Barton and Whitlock 1997; Whitlock 2001). Indeed, the community size parameter may be better described as a function relating community density or area to fitness equalization.

While determinism may in some cases provide ordered rules of community assembly (*sensu* Cody and Diamond 1975; Holt et al. 1994; Brown et al. 2002), there is increasing evidence that variation in community context over a landscape, such as shifts in abiotic conditions or the presence and absence of predators, may obscure the effects of local deterministic interactions (Thompson 1994; Gomulkiewicz and Thompson 2000). The model presented in this article provides an example of how dependent deterministic interactions are on their context. The outcome of competition between two species may change according to the number of patches in the neighborhood and the predictability of fitness within patches, as might be driven by abiotic disturbance cycles or fluctuations in predator abundance. If the context of competition changes over time, so too will the relative fitness of competitors. Especially in large populations, temporal fluctuations in the number or stability of patches could maintain species co-occurrence by switching competitive hierarchies more quickly than competitive exclusion can take place.

The scenario of deterministic transience and high dis-

persal rates is meant to depict a small spatial scale. One might imagine the process described in this article as embedded within one patch of a larger-scale metacommunity (Holt 1992) drawing species from a regional pool. The mechanisms organizing communities at these various spatial scales also occur on various temporal scales, so migration rates will be lower at the metacommunity scale than within its patches. At the same time, disparate transient assemblages in the metacommunity are likely to experience different competitive contexts. As with temporal variation in the number or stability of patches, metacommunity-level spatial heterogeneity coupled with low to intermediate levels of dispersal could prolong local co-occurrence. This view of nested scales may reconcile disparate views on the organization of nature.

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Literature Cited

- Barton, N. H., and M. C. Whitlock. 1997. Evolution in metapopulations. Pages 183–214 in I. A. Hanski and M. E. Gilpin, eds. *Metapopulation biology*. Academic Press, New York.
- Begon, M., J. L. Harper, and C. R. Townsend. 1996. *Ecology*. 3d ed. Blackwell Science, Cambridge.
- Bell, G. 2001. Neutral macroecology. *Science* 293:2413–2418.
- Brown, J. H., G. A. Fox, and B. J. Kelt. 2002. Assembly rules and competition in desert rodents. *American Naturalist* 160:815–818.
- Charlesworth, B. 1994. *Evolution in age-structured population*. 2d ed. Cambridge University Press, New York.
- Chesson, P. 1981. Models for spatially distributed populations: the effect of within-patch variability. *Theoretical Population Biology* 19:288–325.
- . 1994. Multispecies competition in variable environments. *Theoretical Population Biology* 45:227–276.
- . 2000. General theory of competitive coexistence in spatially-varying environments. *Theoretical Population Biology* 58:211–237.
- Cody, M. L., and J. Diamond. 1975. *Ecology and evolution of communities*. Belknap, Cambridge, Mass.
- Cohen, D., and S. A. Levin. 1991. Dispersal in patchy environments: the effects of temporal and spatial structure. *Theoretical Population Biology* 39:63–99.
- Comins, H. N., W. D. Hamilton, and R. M. May. 1980. Evolutionarily stable dispersal strategies. *Journal of Theoretical Biology* 82:205–230.
- Crow, J. F., and M. Kimura. 1970. *An introduction to population genetics theory*. Harper & Row, New York.
- Denno, R. F., G. K. Roderick, M. A. Peterson, A. F. Huberty, H. G. Dobel, M. D. Eubanks, J. E. Losey, et al. 1996. Habitat persistence underlies intraspecific variation in the dispersal strategies of planthoppers. *Ecological Monographs* 66:389–408.
- Fisher, R. A. 1930. *The genetical theory of natural selection*. Clarendon, Oxford.
- Friedenberg, N. A. 2003. Experimental evolution of dispersal in spatiotemporally variable microcosms. *Ecology Letters* 6:953.
- Gillespie, J. H. 1973. Natural selection with varying selection coefficients: a haploid model. *Genetical Research* 21:115–120.
- . 1975. Natural selection for within-generation variance in offspring number. II. Discrete haploid models. *Genetics* 81:403–413.
- Gleason, H. A. 1926. The individualistic concept of plant association. *Bulletin of the Torrey Botanical Club* 53:7–26.
- Gomulkiewicz, R., and J. N. Thompson. 2000. Hot spots, cold spots, and the geographic mosaic theory of coevolution. *American Naturalist* 156:156–174.
- Haldane, J. B. S. 1939. The equilibrium between mutation and random extinction. *Annals of Eugenics* 9:400–405.
- Hanski, I. 1983. Coexistence of competitors in patchy environment. *Ecology* 64:493–500.
- . 1999. *Metapopulation ecology*. Oxford University Press, New York.
- Holt, R. D. 1992. A neglected facet of island biogeography: the role of internal spatial dynamics in area effects. *Theoretical Population Biology* 41:354.
- Holt, R. D., J. Grover, and D. Tilman. 1994. Simple rules for interspecific dominance in systems with exploitative and apparent competition. *American Naturalist* 144:741–771.
- Hubbell, S. P. 2001. The unified theory of biodiversity and biogeography. *Monographs in Population Biology*. Princeton University Press, Princeton, N.J.
- Hutchinson, G. E. 1957. Concluding remarks. *Cold Spring Harbor Symposia on Quantitative Biology* 22:415–427.
- Johnson, M. L., and M. S. Gaines. 1990. Evolution of dispersal: theoretical-models and empirical tests using birds and mammals. *Annual Review of Ecology and Systematics* 21:449–480.

- Kimura, M., and J. F. Crow. 1963. The measurement of effective population number. *Evolution* 17:279–288.
- Kimura, M., and T. Ohta. 1971. Theoretical aspects of population genetics. Princeton University Press, Princeton, N.J.
- Kuno, E. 1981. Dispersal and the persistence of populations in unstable habitats: a theoretical model. *Oecologia (Berlin)* 49:123–126.
- Levins, R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bulletin of the Entomological Society of America* 15:237–240.
- Levins, R., and D. Culver. 1971. Regional coexistence of species and competition between rare species. *Proceedings of the National Academy of Sciences of the USA* 68:1246–1248.
- Lewis, J. A., and J. T. Flemming. 1995. Basic culture methods. *Methods in Cell Biology* 48:3–29.
- MacArthur, R. H., and E. O. Wilson. 1967. The theory of island biogeography. Princeton University Press, Princeton, N.J.
- McCauley, D. E. 1991. Genetic consequences of local population extinction and recolonization. *Trends in Ecology & Evolution* 6:5–8.
- McPeck, M. A., and J. M. Brown. 2000. Building a regional species pool: diversification of the *Enallagma* damselflies in eastern North America. *Ecology* 81:904–920.
- McPeck, M. A., and R. D. Holt. 1992. The evolution of dispersal in spatially and temporally varying environments. *American Naturalist* 140:1010–1027.
- McPeck, M. A., and S. Kalisz. 1998. On the joint evolution of dispersal and dormancy in metapopulations. *Archea Hydrobiologia Special Issues in Advanced Limnology* 52:33–51.
- Nee, S., and R. M. May. 1992. Dynamics of metapopulations: habitat destruction and competitive coexistence. *Journal of Animal Ecology* 61:37–40.
- Neuhauser, C. 1998. Habitat destruction and competitive coexistence in spatially explicit models with local interactions. *Journal of Theoretical Biology* 193:445–463.
- Pajunen, V. I. 1982. Replacement analysis of non-equilibrium competition between rock pool Corixids (Hemiptera; Corixidae). *Oecologia (Berlin)* 52:153–155.
- Ricklefs, R. E., and D. Schluter. 1993. Species diversity in ecological communities. University of Chicago Press, Chicago.
- Riddle, D. L., T. Blumenthal, B. J. Meyer, and J. R. Priess. 1997. *C. elegans*. II. Cold Spring Harbor Laboratory, Plainview, N.Y.
- Rosenzweig, M. L. 1995. Species diversity in space and time. Cambridge University Press, New York.
- Ruel, J. J., and M. P. Ayres. 1999. Jensen's inequality predicts effects of environmental variation. *Trends in Ecology & Evolution* 14:361–366.
- Sale, P. F. 1977. Maintenance of high diversity in coral-reef fish communities. *American Naturalist* 111:337–359.
- Schnitzer, S. A., and W. P. Carson. 2001. Treefall gaps and the maintenance of species diversity in a tropical forest. *Ecology* 82:913–919.
- Slatkin, M. 1974. Hedging one's evolutionary bets. *Nature* 250:704–705.
- Thomas, C. D. 2000. Dispersal and extinction in fragmented landscapes. *Proceedings of the Royal Society of London Series B, Biological Sciences* 267:139–145.
- Thompson, J. N. 1994. The coevolutionary process. University of Chicago Press, Chicago.
- Tilman, D. 1982. Resource competition and community structure. *Monographs in Population Biology*. Vol. 17. Princeton University Press, Princeton, N.J.
- . 1994. Competition and biodiversity in spatially structured habitats. *Ecology* 75:2–16.
- Tilman, D., and P. Kareiva. 1997. Spatial ecology: the role of space in population dynamics and interspecific interactions. Princeton University Press, Princeton, N.J.
- Tilman, D., C. L. Lehman, and C. Yin. 1997. Habitat destruction, dispersal, and deterministic extinction in competitive communities. *American Naturalist* 149:407–435.
- Via, S., and R. Lande. 1985. Genotype-environment interaction and the evolution of phenotypic plasticity. *Evolution* 39:505–522.
- Waterloo Maple. 2001. Maple. Version 7. Waterloo Maple Inc., Waterloo, Ontario.
- Whitlock, M. C. 2001. Dispersal and the genetic properties of metapopulations. *In* J. Clobert, E. Danchin, A. A. Dhont, and J. D. Nichols, eds. *Dispersal*. Oxford University Press, Oxford.
- Whittaker, R. H. 1956. Vegetation of the Great Smoky Mountains. *Ecological Monographs* 23:41–78.
- Wiener, P., and S. Tuljapurkar. 1994. Migration in variable environments: exploring life-history evolution using structured population models. *Journal of Theoretical Biology* 166:75–90.
- Wright, S. 1931. Evolution in Mendelian populations. *Genetics* 16:97–159.
- Yoshimura, J., and V. A. A. Jansen. 1996. Evolution and population dynamics in stochastic environments. *Researches on Population Ecology* 38:165–182.
- Zar, J. H. 1999. Biostatistical analysis. 4th ed. Prentice-Hall, Upper Saddle River, N.J.